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When Fleeing Matters: Differences in Escape Behaviours of Three Northeast Asian Anurans

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Abstract Prey species may have their own optimal escape strategy to balance predation risks and the energetic cost of fleeing. Some species have an advantage when maintaining a short fleeing distance, while others may favour an earlier escape based on microhabitat, size, or body condition. Here, we examined the escape behaviour of the three syntopic Northeast Asian anuran species: Mongolian toads (*Strauchbufo raddei*), Amur brown frogs (*Rana amurensis*), and Japanese treefrogs (*Dryophytes japonicus*) in Mongolia, Russia, China and DPR Korea. We examined flight initiation distance (FID; the distance from a potential predator to the point when the individual starts to flee) and distance fled (DF; distance between flight initiation and flight termination points) of each species and the effects of microhabitat, sex, and body size. *Strauchbufo raddei* and *R. amurensis* had a longer FID than *D. japonicus*, and *S. raddei* also had a longer DF than *D. japonicus*. These trends remained similar when dividing FID and DF by a size proxy (snout-vent length) for all individuals. This suggests that the treefrog *D. japonicus* used a strategy to stay immobile even when they were detected, and the toad *S. raddei* reacted quicker and more sensitively to predators despite the presence of toxin. Female *S. raddei* had a significantly longer FID than males suggesting that females are more sensitive to predation risk in this species, but body size was not significant for any of the three species. Our results indicate that the three sympatric species have different escaping strategies, likely related to differences in physiology and crypticity.

Keywords amphibian, distance fled, escape behaviour, flight initiation distance, predation

1. Introduction

"Different animals have different flight distances, and they gauge them in different ways. Cats look, deer listen, bears smell. Giraffes will allow you to come to within thirty yards of them if you are in a motor car but will run if you are 150 yards away on foot. Fiddler crabs scurry when you're ten yards away; howler monkeys stir in their branches when you're at twenty; African buffaloes react at seventy-five…"——Yann Martel, 'Life of pi'

Prey species may have their own optimal escape strategy to balance predation risks and the energetic cost of fleeing. While the benefit of escaping is clear, not to be predated, the costs of fleeing might include loss of opportunity for feeding, mating or thermoregulating, and an increase of oxidative stress

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associated to escape behaviours (Zamora-Camacho *et al*., 2015). The optimal escape theory explains the trade-off between risks and costs (Ydenberg and Dill, 1986) and relies principally on the flight initiation distance (FID; distance from a potential predator to the point where the individual starts to flee) and the distance fled (DF; distance between flight initiation and flight termination points). Thus, the optimal escape theory demonstrates how individuals perceive and react to potential predators, resulting in a semi-random (Domenici *et al*., 2008) and context dependent (Ydenberg and Dill, 1986; Samia *et al*., 2016) set of escape behaviours. Besides, FID and DF are optimised by fleeing individuals based on variables such as predators (Relyea, 2001), sex (Domínguez-López *et al*., 2016), age, body condition (Seltmann *et al*., 2012), body size (Stankowich and Blumstein, 2005; Moreno-Rueda *et al*., 2020), and habitat use (Cooper, 2008).

Amphibians have many predators, including birds, fish, reptiles, and bats (Wells, 2010), and thus some species have developed toxins to defend themselves. For instance, toads from the Bufonidae family produce bufotoxin, which will deter or reduce predation and potentially kill non-resistant predators (Letnic *et al*., 2008; Shine, 2010; but see Antczak *et al*., 2005). Other species avoid detection through the use of disruptive colours or patterns, while others are able to change colour to match their surroundings (Kang *et al*., 2016). Finally, some amphibians have specific antipredator behaviours, such as crouching or remaining motionless, and thus decreasing the risk of being detected and caught (Heinen and Hammond, 1997; Marchisin and Anderson, 1978). For instance, when facing predation, Ranidae predominantly remains motionless while Hylidae generally flees more often when compared to Bufonidae, although all remain motionless more than actively fleeing (Marchisin and Anderson, 1978).

Escape movements can be related to numerous variables. For instance, body size also results in variations in escaping tactics as large individuals are more easily detected than smaller individuals (Stankowich and Blumstein, 2005). Moreover, the jumping capacity increases with the body size, so large anurans can have larger thresholds for their FID (Moreno-Rueda *et al*., 2020). For instance, large Southern Leopard Frogs, *Lithobates sphenocephalus*, have longer FID and DF than that of small individuals (Bateman and Fleming, 2014b); and small Iberian Green Frogs, *Pelophylax perezi*, remain immobile for longer periods and have shorter FID than large individuals (Martín *et al*., 2005). However, contrasting results on Basking Black Iguanas (*Ctenosaura similis*; Burger and Gochfeld, 1990) and on marine fish predators (Scharf *et al*., 2000) highlight the need for further studies in natural habitats.

In addition, the abundance of refuges and their ease of access make specific microhabitats favourable through the reduction of fleeing costs (Cooper and Sherbrooke, 2013; Guay *et al*., 2013; Samia *et al*., 2016). Accordingly, the lizard *Sceloporus virgatus* adjusts its FID in relation to the distance to the closest refuge (Cooper and Wilson, 2007; Zamora-Camacho, 2020). Prey immobility also increases in microhabitats optimal for camouflage as it decreases the risk of attracting predators, in comparison to fleeing (Cooper, 2008).

Among anurans occurring in continental Northeast Asia, here defined as north of 40° N, some of the most widespread species are Mongolian toads (*Strauchbufo raddei*), Amur brown frogs (*Rana amurensis*) and Japanese treefrogs (*Dryophytes japonicus*). The three species are found in sympatry in part of their range, commonly breeding in the same water bodies, and thus likely constrained by comparable predation pressures. The primary goal of our study was to examine the difference in antipredator strategy for these three species. Based on field experience, we predict that being the least cryptic, brown frogs will have the largest FID and DF (i.e., better fleeing quickly and far as the species is more likely to be visible from far away compared to other species), followed by cryptic treefrogs, and then toads due to their toxins. We also predicted that the body size, sex, and microhabitat will affect the FID and DF in these three species.

2. Materials and Methods

2.1. Study sites and species Our study focuses on three species widespread in northeast Asia. The Mongolian toad, ranging across northern China, Mongolia and southeastern Russia (Litvinchuk *et al*., 2020) and showing green and brown patterns across its body. The Amur brown frog, ranging from northern China to Artic regions, typically brown and cryptic, living in forested habitats (Fei *et al*., 2012). Finally, the Japanese treefrog, ranging across northeast Asia (Kuzmin *et al*., 2017b), and generally green with black patterns (Kang *et al*., 2016). Among these three species, only *Strauchbufo raddei* produces toxins (Daly *et al*., 2005), generally used against predation in the Bufonidae family (Hayes *et al*., 2009).

We collected data at 14 sites, all independent as more than 20 km away from each other (supplementary Figure S1; supplementary Table S1). Sampling was conducted during the peak breeding season of the focal species in June 2017 in Mongolia and in June 2018 in the other countries. The sites were all wetlands: ponds, reservoirs, streams, oxbow lakes, and rice paddies, following the limnologic definition of these habitats (for details on water quality and habitat see Borzée *et al*., 2019 and Borzée *et al*., 2021). We first searched for our

three focal species through the detection of advertisementcalls. All three focal species breed in waterbody (Kuzmin *et al.*, 2017a) and individuals were generally situated at the edge of the water bodies. All three species are cryptic due to their brown and green colours and patterns, matching with the natural habitat. As our study was conducted during the breeding season, at the breeding microhabitat where vegetation is less abundant, the general colours are related to the soil, and even treefrogs that are generally expected to be green are much darker, sometimes totally grey or brown. In addition, and there is no remarkable sexual dimorphism in colour or body size in any of the species. The temperature, predations pressure and other biotic factors are expected to be continuous through the study area as the time of day and season were constant for the behavioural trials.

2.2. Data collection We searched for anurans following the spotlight-search method such as described by Corben and Fellers (2001), but adapted to our field conditions. Once we detected an individual *c.a.* five meters away, we approached slowly (*c.a.* 1 m/s) following the protocol set by Bateman and Fleming (2014b). We used head lanterns to detect the anurans at night and whenever we detected an individual, we turned the light off before approaching the individual. We approached the focal subjects from the direction the individual was originally facing to control for a potential difference between data collected during daytime and night-time by ensuring the visual detection of researchers by the focal individual. When an individual started fleeing, we waited until the frog terminated fleeing (immobile for at least 3 sec). We then marked the position of the researcher and the position from which the frog had started fleeing and measured the flight initiation distance (FID), such as the distance between these two points. We also measured the distance fled (DF), such as the distance between the original and final positions from and to which the frog had fled (Figure 1). In addition, we recorded the microhabitat (water body or ground) where the individual was detected when fleeing. When we could gently touch the focal individual with our boots without having it fleeing, we recorded FID as 0 cm. If an individual did not flee even after being touched, we recorded DF as 0 cm. After fleeing, individuals were caught and measured for snout-vent length (SVL; cm), and weight (g). We also identified the sex of each individual, through the production of advertisement calls when captured, or the occurrence of nuptial pads for males.

2.3. Data analysis First, to check the absence of differences between sexes in SVL, we ran three ANOVAs for each species and found no significant differences (all P value > 0.05). Then, to understand the variables regulating the escape behaviour of these species, we analysed the dataset with FID and DF as dependent variables for all species pooled together. First, to understand whether there is a difference in FID and DF between the three species, we analysed the data through a pair of Generalized Linear Mixed Models (GLMM), one with FID and the other with DF as response variables, and with species as independent variable, sex, temperature and microhabitat as control variable and site ID as random factor for both GLMM. Then, to examine whether the differences between species were maintained when controlling for inter-species size difference, we ran two additional GLMMs with FID divided by SVL and DF divided by SVL as response variables, and with the same independent, control and random factors. Lastly, to examine the species-specific escape behaviour related to body size (i.e., SVL) and sex, we segregated the dataset by species and then ran a GLMM for each species. We included FID and DF as response variables for each model separately, and the interaction between body size and sex as independent variable, microhabitat and temperature as control, and site ID as random factor for both of the models.

We z-transformed the body size to facilitate model convergence. We visually checked homoscedasticity, homogeneity of variances and multicollinearity, and

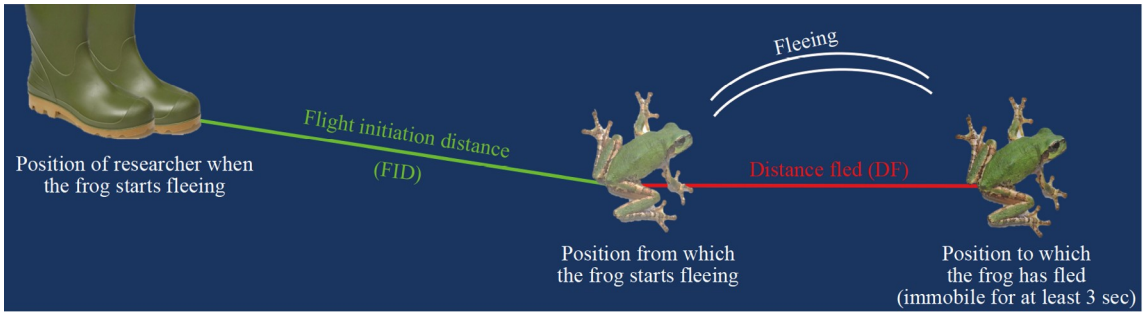


Figure 1 Data collection methods for flight initiation distance (cm; FID, length of the green line) and distance fled (cm; DF, length of the red line) of *Dryophytes japonicus*, *Rana amurensis* and *Strauchbufo raddei* in Mongolia, Russia, China and DPR Korea between 2017 and 2018.

confirmed there were no critical problems (VIF values all lower than 2) and the assumptions were not violated. All biostatistical analyses were computed using R (version 4.1.1; R Core Team, 2021).

2.4. Ethical notes Our research adheres to the ethical guidelines of Nanjing Forestry University and was approved under the Research Ethic Permit 202-20-14. As the main aim of our study is to observe the behavioural responses of amphibians, we only handled the individuals briefly to measure SVL and body weight, and all individuals were placed right afterwards where we found them, without causing any kinds of injury to them.

3. Results

We collected data for 30 *Strauchbufo raddei*: six females and 24 males; 17 *Rana amurensis* (seven females and ten males), and 31 *Dryophytes japonicus* (seven females and 24 males). The FID was 16.61 ± 19.30 cm in *D. japonicus*, 53.53 ± 33.40 cm in *R. amurensis*, and 56.47 ± 58.56 cm in *S. raddei* (mean ± SD). Individuals that did not move until the researchers could touch them (i.e., FID = 0 cm) included 39% of *D. japonicus*, 23% of *S. raddei*, and 5% of *R. amurensis*. The first GLMM investigating the FID revealed that *D. japonicus* had a significantly shorter FID compared to *R. amurensis* and *S. raddei* (full-null model comparison: $\chi2 = 10.753$, $df = 2$, $P < 0.001$; Figure 2A; Table 1). The DF was 20.65 ± 24.49 cm in *D. japonicus*, 25.35 ± 21.08 cm in *R. amurensis*, and 50.47 ± 66.62 cm in *S. raddei*. Individuals that did not flee (i.e., DF = 0 cm) included 22% of *D. japonicus*, 20% of *S. raddei*, and 5% of *R. amurensis*. The second GLMM investigating the DF was marginally significant when compared to the null models and it showed that *S. raddei* had a significantly longer DF compared to *D. japonicus*. However, we did not find a significant difference between DF in *D. japonicus* and *R. amurensis* or *R. amurensis* and *S. raddei* (full-null model comparison: $\chi2 = 4.986$, $df = 2$, $P = 0.083$; Figure 2B; Table 2).

When measured for SVL and weight (mean ± SD), *S. raddei* was 62.91 ± 9.24 cm and 23.52 ± 6.44 g, *R. amurensis* was 44.88 ± 3.03 cm and 6.10 ± 0.89 g and *D. japonicus* was

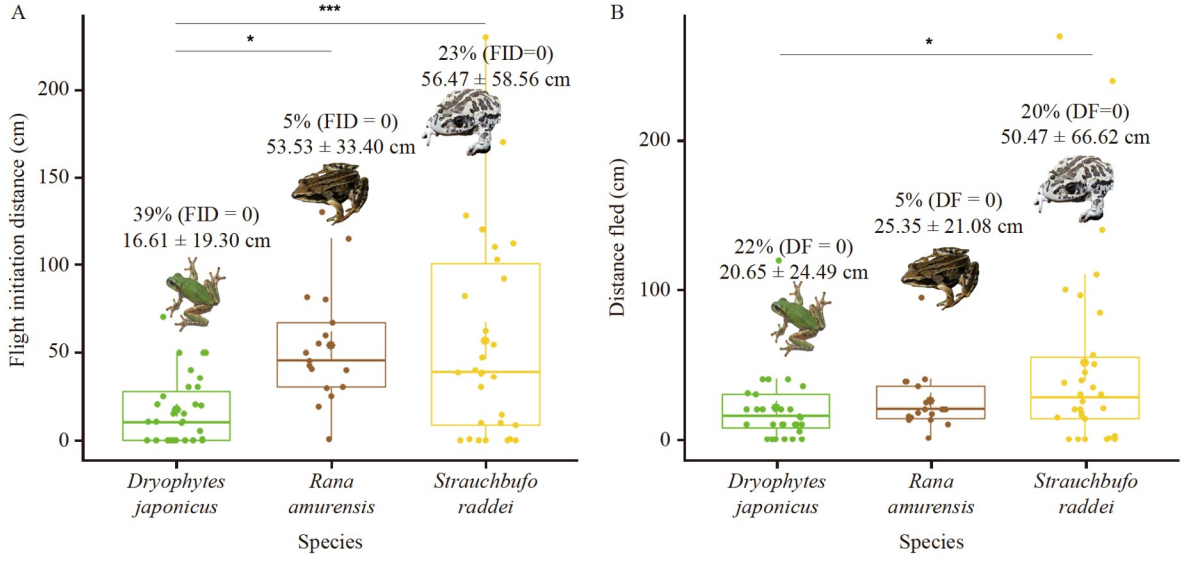


Figure 2 A: Flight initiation distance (FID; cm); B: distance fled (DF; cm) for *Dryophytes japonicus*, *Rana amurensis* and *Strauchbufo raddei* in Mongolia, Russia, China and DPR Korea between 2017 and 2018.

Table 1 The effect of species (*Dryophytes japonicus*, *Rana amurensis* and *Strauchbufo raddei*), sex, and microhabitat on the flight initiation distance (cm). Reference level: species = *D. japonicus*, sex = female, and microhabitat = ground. Temperature was z-transformed and the original mean ± SD = 18.23 ± 1.92.

	Estimate	Std. Error	*T* value	*P*
Species (*R. amurensis*)	30.48	12.79	2.38	0.020
Species (*S. raddei*)	44.96	12.38	3.63	< 0.001
Sex (male)	−21.88	11.11	−1.97	0.053
Microhabitat (water)	−11.61	10.37	−1.12	0.267
Temperature (°C)	3.43	5.68	0.60	0.547

Table 2 The effect of species (*Dryophytes japonicus*, *Strauchbufo raddei*, and *Rana amurensis*), sex, and microhabitat on the distance fled (cm). Reference level: species = *D. japonicus*, sex = female, and microhabitat = ground. Temperature was z-transformed and the original mean ± SD = 18.23 ± 1.92.

	Estimate	Std. Error	T value	*P*
Species (*R. amurensis*)	2.98	14.50	0.21	0.838
Species (*S. raddei*)	30.56	14.10	2.17	0.046
Sex (male)	−1.99	12.50	−0.16	0.874
Microhabitat (water)	−7.85	11.67	−0.67	0.503
Temperature (°C)	0.48	6.53	0.07	0.943

37.59 ± 4.33 cm and 4.78 ± 0.54 g. The GLMMs investigating variations in FID and DF divided by SVL revealed that *D. japonicus* had a lower FID than *R. amurensis* and *P. raddei* when controlling for SVL (full-null model comparison: χ^2 = 11.740, *df* = 2, *P* = 0.003; Figure 3A). The full-null model comparison was not significant for the model investigating DF divided by SVL (χ^2 = 1.994, *df* = 2, *P* = 0.369; Figure 3B).

The GLMMs investigating variations in FID in each species revealed that *S. raddei* females (103.50 ± 70.69 cm) had a significantly longer FID than males (44.71 ± 50.15 cm), while there was no effect of the body size (full-null model comparison: χ^2 = 11.016, *df* = 4, *P* = 0.026; Figure 4; Table 3). However, the full models were not significant when compared to the null models in *D. japonicus* and *R. amurensis* (*D. japonicus*: χ^2 = 1.100, *df* = 4, *P* = 0.894; *R. amurensis*: χ^2 = 1.331, *df* = 4, *P* = 0.856). Finally, the full models of the GLMMs investigating variations in DF in each species were not significant when compared to the null models in all three species (*D. japonicus*; χ^2 = 1.458, *df* = 4, *P* = 0.834, *R. amurensis*; χ^2 = 7.180, *df* = 4, *P* = 0.127, *S. raddei*; χ^2 = 3.556, *df* = 4, *P* = 0.469), highlighting the absence of significant relation between body size and DF.

4. Discussion

In this study, we investigated the escape behaviours of three Northeast Asian anuran species. Our results did not match with our predictions expecting brown frogs to flee first, followed by treefrogs and then toads. Instead, we found that the treefrog, *Dryophytes japonicus*, had the lowest flight initiation distance (FID) and distance fled (DF), and the highest number of individuals remaining immobile even when gently touched by a putative predator (i.e., human; FID = 0: 39%, DF = 0: 22% of individuals). On the other hand, the toad *Strauchbufo raddei* had the highest FID and higher DF than *D. japonicus*, suggesting they react quicker and more sensitively to predators, despite the presence of toxins that would result in a decrease of predation events. These trends remained the same when dividing FID and DF by body size. Therefore, the result might not be related to their body size, as suggested in a

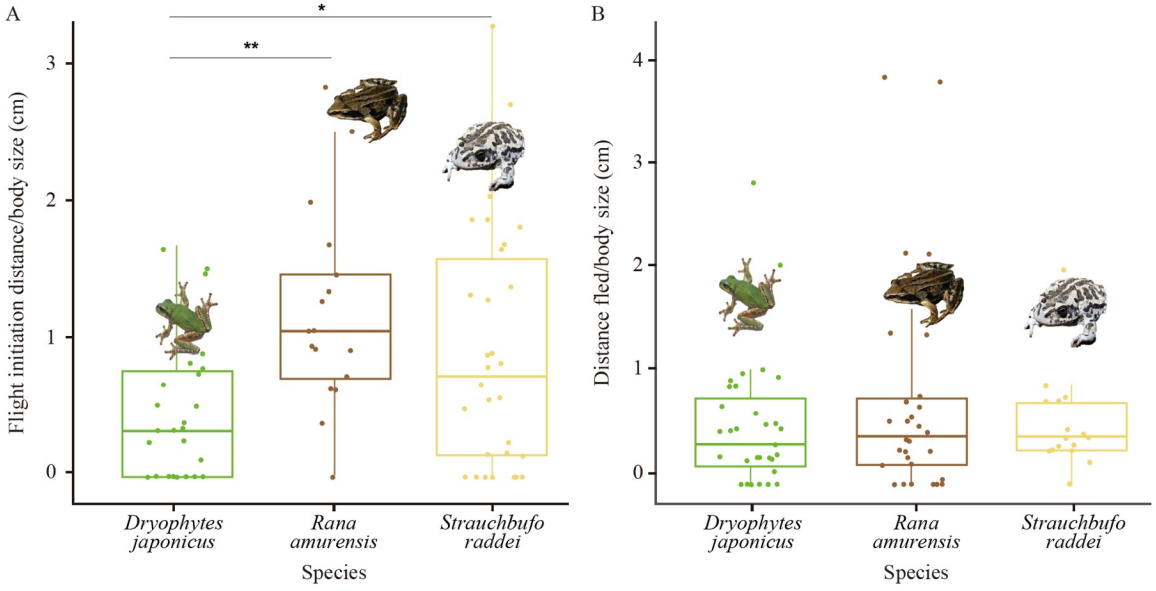


Figure 3 A: Flight initiation distance (FID) divided by body size (SVL; snout-to-vent length); B: Distance fled (DF) divided by body size (SVL) of *Dryophytes japonicus*, *Rana amurensis* and *Strauchbufo raddei* in Mongolia, Russia, China and DPR Korea between 2017 and 2018.

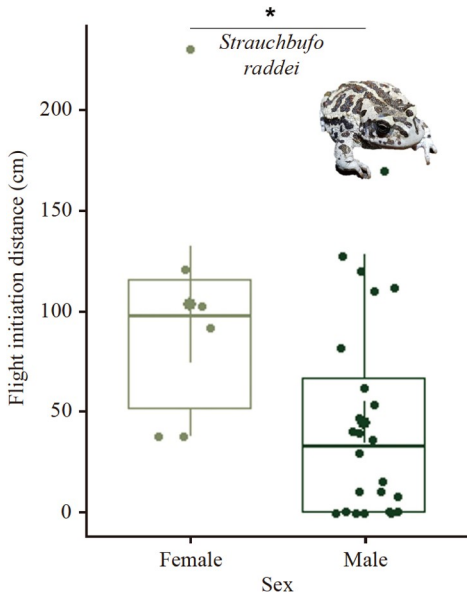


Figure 4 Difference in flight initiation distance (FID; cm) for both sexes in *Strauchbufo raddei*, regardless of the body size in Mongolia, Russia, China and DPR Korea between 2017 and 2018.

different study (Stankowich and Blumstein 2005). On the other hand, toads can be picked up and later released by birds of prey despite being toxic, resulting in sub-lethal but damaging effects (Koo *et al*., 2020). In addition, the increase in cattle as a result of the increase in human activities at the breeding sites is likely to have also facilitated an adaption to avoid trampling (Bateman and Fleming, 2014a), resulting in an earlier escape. In contrast, *D. japonicus* had a low DF, possibly linked to the crypticity of the species (Kang *et al*., 2016) and its immobility to avoid detection by predators as snakes are among the species' primary predators, and they rely on movement for prey detection (Mullin and Cooper, 1998). Finally, treefrog's preference for bushy over grassy landscape in the breeding area (Borzée *et al*., 2019) may also result in a lower risk of being trampled by cattle than for the terrestrial *S. raddei* or *Rana amurensis*.

We found all three focal species to flee to avoid predation more than they remain immobile, similarly to the finding of other studies (Eilam, 2005; Kowalski *et al*., 2018). While being agile and having the best locomotor performance (Rand, 1952), *R. amurensis* (95%) indeed fled most frequently compared to the other two species (*D. japonicus*: 80%, *S. raddei*: 75%). However, this earlier escape (i.e., longer FID) may not only be related to physiological abilities or crypticity, but microhabitat adaptation, as similar *Rana* species, adapted to different microhabitats, display different escape behaviours (Licht, 1986). More individuals *D. japonicus* (39%; N = 12) stayed immobile compared to *S. raddei* (23%; N = 7) until being touched (i.e., FID = 0). However, once they were touched, 58% of *D. japonicus* (N = 7) started to flee when only 14% of *S. raddei* (N = 1) fled, indicating that treefrogs hide until they are found and then escape, while toads keep immobile even when they are detected. This contradicts our result in that *S. raddei* has the highest FID and DF, but aligns with some of the literature (Marchisin and Anderson, 1978) and it might indicate two different anti-predatory strategies in the species, either fleeing from far away and over a long distance, or remaining immobile, a behavioural dichotomy potentially linked to the abundance of toxin in the parotoid glands and the assessment of the type of predation.

When separating the species to investigate the effect of the sex and body size, we only found that *S. raddei* females had a significantly longer FID compared to males, indicating that females start fleeing earlier than males regardless of their body size. Specifically, all cases of FID being zero in *S. raddei* (N = 7) were males. Unlike *D. japonicus* and *R. amurensis*, male *S. raddei* stay near ponds and lakes after breeding, and occasionally rely on water bodies as shelters in case of danger despite being generally terrestrial (Bannikov, 1958; Borkin and Kuzmin, 1988). In addition, females of the phylogenetically related Western toads (*Anaxyrus boreas*) travel significantly longer distances from the breeding site compared to males, suggesting that females are more sensitive to predation risk (Bull, 2006; Bartelt *et al*., 2004). On the contrary, we did not find a significant effect of the body size on either FID or DF in any of the three species, while we predicted that individuals with smaller body size would have either longer FID to compensate for their vulnerability and lower DF due to their limited ability to escape. Our results are surprising since the body size, as an index of morphological and physiological trait,

Table 3 The effect of body size, sex, their interaction, and microhabitat on the flight initiation distance (cm) in *Strauchbufo raddei*. Reference level: sex = female, microhabitat = ground. Body size and temperature are z-transformed and their original mean ± SD = 56.47 ± 58.56 cm.

	Estimate	Std. Error	*T* value	*P*
Body size	20.19	19.97	1.01	0.323
Sex (male)	−68.10	25.95	−2.66	0.014
Microhabitat (water)	−47.50	23.54	−2.02	0.055
Temperature (°C)	5.26	11.57	0.46	0.678
Body size * Sex (male)	−16.23	22.39	−0.72	0.476

is known to affect individual behaviours, especially on their FID (Cooper *et al*., 2009). Nevertheless, this may explain that species-specific evolutionary traits have a stronger effect on escape behaviours than individual-specific traits.

While our study still highlights the difference in escape behaviours between syntopic anuran species, it has several limitations. First, even though we collected data from various locations to better cover a general anti-predatory strategy of species population, the result interpretation may be restricted considering the low sample size. Also, we could not estimate the predation pressure for these species, and only speculated and used human as a proxy for the natural predators. We recommend further studies to investigate the strategy for different types of predators with larger sample sizes. Furthermore, it would be interesting to investigate other factors that could influence antipredator behaviours such as prey personality types (Jones and Godin, 2010; Allan *et al*., 2020) or age/experiences (Turner *et al*., 2006; Choh *et al*., 2012).

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