Death-feigning propensity varies within dice snake populations but not with sex or colour morph

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Abstract

Once cornered by a predator, prey can try to intimidate the assailant or repel it, with irritating sprays for example. If seized, they may scratch, bite or struggle to cause the predator to release its grip. At the other extreme, they can adopt passive behaviours such as death feigning (DF, i.e. thanatosis). DF is observed widely across the animal kingdom; it usually involves a combination of displays such as immobility, supination, leg-folding, mouth opening and release of nauseating secretions. When displaying DF, individuals are highly vulnerable and effectively bet on the attitude of the predator; this risky choice is presumably under positive selection. We explored how propensity for DF varies among and within populations of dice snakes (*Natrix tessellata*). We also considered the influence of sex, body size, reproductive status, colour morph and presence of injuries ($N = 2760$ snakes; five populations). DF propensity differed among populations, possibly due to variation in local predation pressures. Larger snakes displayed DF more frequently and carried more signs of probable past predation attempts (scars and recent injuries). We found no sex effect on antipredator behaviour. Gravid females used DF less frequently compared with non-gravid females. Differential expression of DF across populations, body sizes and reproductive status suggests that this complex behaviour was selected to respond to environmental and intrinsic factors. Future studies should explore which elements affect duration, intensity and success of DF in defence against various predators.

Introduction

Behaviours, driven by complex interactions between intrinsic and extrinsic factors, enable individuals to rapidly respond to environmental conditions (Roth & Johnson, 2004). They vary among individuals, during an individual's lifespan and over short time scales. For example, phenotype, ontogenetic shifts, sexual maturity, experience, resource availability and daily or seasonal environmental variations can deeply influence behaviours (Alcock, 2009; Davies, Krebs & West, 2012). Presumably, natural selection shaped the diversity of behavioural repertoires (Alcock, 2009). In this context, antipredator behaviours occupy a central position in evolutionary ecology as they directly influence survival and influence the expression of other behaviours in complex ways (Lind & Cresswell, 2005). The most frequently observed antipredator behaviours range from secretive habits to avoidance tactics; circumventing costly and perilous flight or risky combat is an efficient tactic (Brodie, Formanowicz & Brodie, 1991; Miller et al., 2015).

Yet, direct physical contacts with predators are sometimes inevitable. Predators are well equipped and skilled; however, many kinds of prey are capable of retaliation and take extreme reactions to escape death. Once cornered or seized by a predator, prey can struggle, bite or scratch to release the predator's grip (e.g. Iwamoto et al., 1996; Segovia, Murayama & Willemart, 2019). Besides physical combat, they can also try to daunt and repel the assailant, by intimidating predators with visual and sound displays, or expelling irritating/deterring sprays (e.g. skunks – Fisher & Stankowich, 2018, bombardier beetles – Sugiura, 2018). At the other extreme of the spectrum of antipredator defences, potential prey can adopt passive behaviours such as death feigning (DF, i.e. thanatosis). DF is a complex behaviour that often involves a set of features, such as immobility and leg-folding, supination, display of colour pattern, mouth opening or expulsion of nauseating/noxious

secretions (e.g. Miyatake *et al.*, 2004; Honma, Oku & Nishida, 2006; Humphreys & Ruxton, 2018; Mesquita *et al.*, 2018; Li *et al.*, 2019; Ramalho *et al.*, 2019; Segovia *et al.*, 2019). DF is observed widely across the animal kingdom and thus is assumed to confer substantial fitness benefits in many circumstances; yet, it is also a risky strategy because individuals become very easy prey (Humphreys & Ruxton, 2018, 2019).

Snakes are ectothermic and, at least with respect to predatory birds and mammals, slow-moving. Perhaps as a consequence of this performance disadvantage, they display a wide repertoire of antipredator responses when cornered, including impressive warning displays, bluff, retaliation bites, fleeing attempts and DF (Shine *et al.*, 2000; Placyk, 2012; Gregory, 2016). In addition, snakes show great phenotypic plasticity and thus exhibit considerable intra-specific and intra-population morphological variability, notably of body size (Madsen & Shine, 1993). The dice snake (*Natrix tessellata*) is a widespread highly polymorphic species (e.g. wide range of colour morphs), which exhibits pronounced sexual size dimorphism (females are larger than males), and which is preyed upon by a wide range of predators (e.g. Ajtić *et al.*, 2013; Šukalo *et al.*, 2019). Because individual females typically reproduce less often than annually, both gravid and non-gravid adult females occur simultaneously in the population in any given reproductive season, facilitating comparisons between them under the same general conditions, as well as comparisons with other groups such as juveniles and adult males (e.g. Ajtić *et al.*, 2013). Therefore, dice snakes represent a suitable model system to explore the relationships between individual status, phenotype and antipredator behaviours.

Complex behaviour tends to be flexible (Qi *et al.*, 2018). This allows individuals to adjust their antipredator tactics as a function of their status (e.g. size, sex) and of environmental constraints (e.g. garter snakes, Shine *et al.*, 2003a,b; tiger snakes, Bonnet *et al.*, 2005). Contrasted phenotypes affect predation risk that in turn influence antipredator behaviours; for example, larger vs smaller, reproductive vs non-reproductive, dark vs striped individuals respond differently to predation (Radloff & Du Toit, 2004; Venesky & Anthony, 2007; Lima, 2009). Considering the wide range of phenotypes we studied, we predicted that antipredator responses should vary with body size, sex, reproductive status, colour morph and local ecological context (i.e. type and density of predators) and thus among snake populations. For example, we expected that gravid females will display DF more often than non-reproductive ones to protect their asset, and also because clutch mass impedes movement (Seigel, Huggins & Ford, 1987). In this study, we explored how DF varies with location, sex, reproductive status, colour morph, occurrence of injury and body size in dice snakes (*Natrix tessellata*).

Materials and methods

Study species

The dice snake (*Natrix tessellata*) is a semiaquatic, medium-sized, predominantly piscivorous, non-venomous species (Luiselli *et al.*, 2007). Colour polymorphism occurs regularly both within and among populations; besides the classical diced form (hence the name of the species), some individuals are uniformly grey or black (e.g. Ajtić *et al.*, 2013). Their main predators are birds (e.g. *Ardea* sp., *Corvus* sp., *Bubo bubo*, *Accipiter* sp., *Buteo* sp., *Larus* sp., *Halcyon smyrnensis*), carnivorous mammals (e.g. *Lutra lutra*, *Mustela* sp., feral cats and dogs) and other snake species (*Dolichophis jugularis*, *Hierophis gemonensis*, *Vipera ammodytes*) (Ilani & Shalmon, 1984; Jelić & Lauš, 2011a,b; Velenský, Velenský & Mebert, 2011; Ajtić *et al.*, 2013). Humans often persecute snakes (Pandey *et al.*, 2016; Landová *et al.*, 2018), including dice snakes; therefore, they should be counted as major predators.

When cornered, dice snakes perform various antipredator behaviours; primarily they try to escape while hissing. If unsuccessful (i.e. cannot escape), they can bluff while flattening their head and neck and adopting an intimidating 'S' posture. Dice snakes never bite the attacker, although they sometimes strike during bluff. If seized, they can regurgitate stomach contents, and twist their body to spray the attacker and themselves with a repelling mixture of cloacal gland secretions, uric acid and faeces. Finally, they can display DF as an ultimate option. In vertebrates, DF is expressed in animals that are actually seized by predators (Francq, 1969; Gregory & Gregory, 2006). DF involves immobility with an open mouth (Fig. 1), while the tongue protrudes; sometimes DF is accompanied by the production of small bloody bubbles forming red foam in the open mouth (blood spitting, BS; Fig. 1).

Study sites and sampled populations

This study compiled data from five isolated populations in the central part of the Balkan Peninsula (details in Table 1). Our sample includes 2760 snakes processed in 2011 and 2012. Most snakes were collected on Golem Grad Island ($N = 1909$). In each population, both sexes and a wide spectrum of body sizes were available. Colour polymorphism (dotted, black, grey morphs) was well expressed on Golem Grad only (eight grey individuals and zero black snake in the other sites). Additionally, gravid females were encountered only in Golem Grad population. Overall, this dataset allowed us to examine the influence of body size and sex across five populations, and to consider additionally colour morphs and reproductive status in Golem Grad.

Field procedures

In the course of this long-term study (2008–ongoing), we searched for snakes in the field. Snakes were detected in various situations, some were caught basking in the sunlight, others were under stones, perched in trees, on land or in the water, alone or during mating, etc. In practice, it was thus impossible to capture them in a standard way. Therefore, we introduced a step to standardize the expression of antipredator behaviours. Snakes were caught by hand and kept in cotton bags during time periods ranging from one up to five hours. When placed in a bag, individuals calmed down rapidly.

Figure 1 Photographs of dice snake from Golem Grad population performing death feigning (a) and blood spitting (b) (photographed by A. G. and X. B.). [Colour figure can be viewed at zslpublications. onlinelibrary.wiley.com.]

Snakes were subsequently removed from the bag and processed in a standard way for behavioural observations. Morphological measurements were performed afterwards (see below). Individuals were seized at mid-body and taken out of the bag, mimicking a successful attack from a predator. Antipredator responses were immediately recorded. It was not possible to standardize factors such as body temperature, weather conditions, lighting, time of measuring or proximity to refuges. Although these factors might affect antipredator behaviours, they were partly randomized through the distribution of field sessions across seasons and years in different sites.

Because almost all snakes struggled vigorously and hissed when seized, these behaviours were not useful for discriminating among broad behavioural phenotypes. Similarly, almost all dice snakes attempted to flee when they detected us before capture. By contrast, death feigning (DF) and blood spitting (BS) were not always exhibited; some snakes performed DF immediately while others responded only after several seconds of handling. DF was assigned to snakes that suddenly shifted from struggling to immobility (i.e. individuals seem to be dead) and that opened their mouths, without measuring the duration or intensity of DF. Those snakes that did not perform DF at all constantly tried to escape (hereinafter, actively

Table 1 List of potential predators of dice snakes within each of the localities. Initials of the author who measured snakes and the sample structure for each of the populations

Locality with coordinates, country	Avian predators	Mammalian predators and human presence	Sample structure	Researcher
Golem Grad Island, 40°52′N, 20°59′E, North Macedonia	*Bubo bubo*; *Accipiter* sp., *Buteo* sp., *Larus* sp., *Ardea* sp., *Corvus* sp.	*Lutra lutra*; Occasional tourists	1187 females, 721 males, 1 unsexed juv.	All of the authors
Skadarsko jezero lake, 40°10′ N, 19°15′ E, Montenegro	*Accipiter* sp., *Buteo* sp., *Larus* sp., *Ardea* sp., *Ciconia* sp., *Corvus* sp.	*Lutra lutra*, feral cats and dogs; Small inhabited villages	71 females, 131 males, 21 unsexed juv.	S. G.
Vrbanja River, 44°47′ N, 17°14′ E, Bosnia and Herzegovina	*Ardea* sp., *Egretta* sp., *Corvus* sp.	Feral cats and dogs; Small inhabited villages	199 females, 115 males	G. Š.
Pančevački rit, 44°50′ N, 20°29′ E, Serbia	*Accipiter* sp., *Buteo* sp., *Larus* sp., *Ardea* sp., *Ciconia* sp., *Corvus* sp.	*Lutra lutra*, *Mustela* sp., feral cats and dogs; Small inhabited villages	64 females, 95 males	M. A.
Obedska bara bog, 44°43′ N, 19°52′ E, Serbia	*Accipiter* sp., *Buteo* sp., *Larus* sp., *Ardea* sp., *Ciconia* sp., *Corvus* sp.	*Lutra lutra*, *Mustela* sp., feral cats and dogs; Small inhabited villages	70 females, 85 males	M. A.

escaping). Overall, DF *vs.* escaping provided a straightforward antipredator variable. In snakes, human-induced antipredator behaviours are not regarded as predator-specific, but rather as typical broad antipredator behaviours (Shine *et al.*, 2000; Roth & Johnson, 2004; Gregory & Gregory, 2006). On Golem Grad Island, all the authors captured and handled snakes, and scored antipredator behaviours to ensure that a common protocol would be used. Once trained on Golem Grad, three of us (S.G., G.Š, M.A.) studied four additional populations using the same protocol (details provided in Table 1).

After recording antipredator response, we measured snake body length (i.e. snout-vent length, SVL, with a measuring tape, ±0.5 cm), recorded its sex, colour morph, reproductive status (large follicles are easily detected by palpation of the abdomen), and presence/absence of injury (visible wound and/ or scar). After measuring, all snakes were permanently marked using a modified technique of scale-clipping (Bonnet *et al.*, 2002). We restricted our analyses to original captures only to avoid pseudoreplication from recapture of individuals. Snakes were afterwards released at the place of capture.

Analyses

To model the probability of displaying DF or BS as a function of the covariates of interest, we used binomial GLMs. Fixed covariates were locality (categorical with five levels), sex (categorical), snake morph (categorical with three levels), presence of injury (categorical with two levels) and SVL (continuous). Another set of GLMs were run only for the Golem Grad locality, additionally modelling DF and BS probability as a function of gravidity (categorical covariate with two levels, gravid and non-gravid adult females), but excluding 'locality'; finally, four sets of models were built: two for DF and two for BS. In each set, initially six biologically plausibly justified models were run, with each of the five covariates separately, and one with the additive effects of all covariates. The best-fit model (ΔAIC > 2; models with ΔAIC ≤ 2 were considered to have equally strong support and priority was given to the one with fewest parameters) was then further explored. Namely, additional interactive and additive effects were tested for a scenario that could have a notable effect on ΔAIC (e.g. if the effect of 'locality' provides the best-fit model, then all other covariates were tested separately for their additive effects or interactions with 'locality').

Ethical note

The snakes were caught in the field, kept in cotton bags during time periods ranging from one up to five hours until processed. Snakes were returned to the place of capture the same day, after processing, or in some cases one day after capture. Permits were issued by the official authorities (North Macedonia 03-246, 11-4093/5; Montenegro UPI-1003/4, UPI-389/4; Serbia 353-01-252/2011-03; 353-01-46/2012-03). When the research was conducted, a list of protected reptile species did not exist in Bosnia and Herzegovina; therefore, a permit for work on the Vrbanja population was not required. No snake was injured or presented any sign of distress when released.

Results

Model selection suggested four best-fit models to adequately describe variations of the probability of dice snakes to display antipredator behaviour (DF or BS) in function of sex, locality, colour morph, injury presence, gravidity (only in Golem Grad) and SVL (Table 2). Sex and colour morphs were not retained as significant factors for DF or BS propensity. SVL was a consistent significant predictor of antipredator behaviour (*P*-value< 0.05), DF and BS display propensity increased with body size (slope[m] = 0.3 ± 0.2 (SE) for DF and 1.1 ± 0.4 for BS). On Golem Grad, gravid females were less likely to display DF (m = −1.1 ± 0.2) and BS (m = −1.2 ± 0.5) than non-reproductive females. Pooling all sites (thus disregarding gravidity), DF propensity was higher on Golem Grad Island (m = −1.8 ± 0.5), while the presence of injuries significantly increased the probability of BS display (m = 0.6 ± 0.3).

Discussion

The adaptive value of DF has not been comprehensively evaluated in snakes, nor in most animals, and thus remains unclear, but it is widely accepted that the maintenance of complex traits in natural populations depends on positive selection (Qi *et al.*, 2018 and references therein). Although snakes primarily struggled to escape handling, many exhibited DF (~25%). We also observed marked inter- and intra-population variations that form the raw material for selection. This study was not designed to test evolutionary tenets; yet, our large sample size clearly shows that DF was frequently albeit differently expressed across five populations examined, across body sizes and reproductive statuses. These strong variations suggest that DF might well be an important adaptive antipredator behaviour in dice snakes.

Within-populations differences

Previous studies suggested that antipredator responses may vary within populations (Herzog & Schwartz, 1990; Shine *et al.*, 2003a,b; Bonnet *et al.*, 2005; Aubret, Michniewicz & Shine, 2011; Placyk, 2012). Our results provide additional evidence for intra-population variability in DF due to effect of body size and reproductive status.

While growing in size, dice snakes altered their antipredator behaviour. When handled, most of the neonates actively tried to escape whereas in larger individuals DF frequency gradually increased. This finding is in accordance with other studies about DF frequency in *Natrix helvetica* (Gregory, Isaac & Griffiths, 2007; Gregory, 2008). Neonates are more vulnerable to predation compared with adults (Gerald, 2008; Gregory, 2008), and they face different predators (e.g. small corvid birds hunt small snakes but cannot kill large ones). They also face relatively larger predators (e.g. herons) compared with large snakes; thus, they can be swallowed very rapidly before having

Table 2 Model selection procedure of GLMs modelling the probability to display death feigning (DF) or blood spitting (BS) as a function of the additive (+) and interactive (*) effects of locality (L), sex (S), colour morph (M), presence of injuries (I), SVL and gravidity (G, only on Golem Grad Island) in dice snakes

Model number	Model definition	AIC	ΔAIC
Death feigning			
1	L+SVL+L*SVL	2936.6	0
2	L+SVL	2936.7	0.1
3	L + S	2941.0	4.4
4	S + L+M + I+SVL	2942.2	5.6
5	L	2943.1	6.5
6	L + I	2944.6	8
7	L + S+L*S	2946.2	9.6
8	L + M	2947.3	10.7
9	L + M+L*M	2949.2	12.6
10	L + I+L*I	2951.2	14.6
11	SVL	3040.7	104.1
12	M	3072.9	136.3
13	S	3089.9	153.3
14	I	3097.9	161.3
DF only on Golem Grad Island			
15	G+SVL	2322.6	0
16	G + I+G*I	2323.6	1
17	G	2325.3	2.7
18	G+SVL+G*SVL	2325.7	3.1
19	G + I	2326.3	3.7
20	G + M	2327.4	4.8
21	S + G+M + I+SVL	2327.9	5.3
22	G + M+G*M	2333.5	10.9
23	SVL	2370.1	47.5
24	S	2379.1	56.5
25	M	2380.3	57.7
26	I	2381	58.4
Blood spitting			
27	SVL+I +SVL*I	874.9	0
28	SVL+I	876.3	1.4
29	SVL+L	878.2	3.3
30	SVL	878.4	3.5
31	SVL+L+SVL*L	878.8	3.9
32	SVL+M	879.6	4.7
33	SVL+S	880.2	5.3
34	S + L+M + I+SVL	881.0	6.14
35	SVL+M+SVL*M	881.5	6.6
36	SVL+S+SVL*S	882.1	7.2
37	L	885.9	11
38	M	892.6	17.7
39	I	892.8	17.9
40	S	898.7	23.8
BS only on Golem Grad Island			
41	SVL+G	715.9	0
42	S + G+M + I+SVL	717.0	1.1
43	SVL+I	717.6	1.7
44	SVL+I+SVL*I	717.8	1.9
45	SVL	718.8	2.9
46	SVL+M	718.9	3
47	SVL+G+SVL*G	719.4	3.5
48	SVL+S	720.3	4.4
49	SVL+M+SVL*M	721.1	5.2

Table 2 Continued.

Model number	Model definition	AIC	ΔAIC
50	SVL+S+SVL*S	722.2	6.3
51	G	722.4	6.5
52	I	724.3	8.4
53	M	726	10.1
54	S	729	13.1

Model order follows ascending AIC values. In each row, model definition is followed by the Akaike information criterion (AIC) and ΔAIC; chosen best models highlighted with grey.

the opportunity to display DF. Large snakes cannot be engulfed promptly; thus, they have a certain amount of time during which they may convince a predator of their unpalatability. Namely, death-feigning animals seem unpalatable to some animals (Skelhorn, 2018), and additionally, large snakes can expel larger amounts of repellent mixture, which makes their DF display even more spectacular. Thus, DF may become a safer antipredator strategy with increasing body size (Honma *et al.*, 2006). Alternatively, the change in propensity of DF with increasing body size could be due to differential survival of individuals that display this behaviour.

A higher proportion of large snakes had injuries than small ones, as expected (Gregory & Gregory, 2006; Gregory, 2008). Large individuals are probably older and thus experienced more predator attacks compared with smaller ones (Pleguezuelos *et al.*, 2010). Injuries also indicate that a snake survived. In our sample, snakes with or without injuries performed DF equally frequently. Similar findings were reported in *Natrix helvetica* and *Thamnophis elegans* (Gregory & Gregory, 2006; Gregory, 2008), suggesting that differences in experience with predators do not dictate variation in frequency of DF. Nonetheless, injured snakes (Golem Grad only) performed BS more frequently compared with non-injured individuals. Blood spitting might be a more extreme and perhaps a more effective behaviour than DF alone (Sherbrooke & Middendorf, 2004). The large dataset from Golem Grad and the good fit of the model examining the interactive effects of injury and SVL (Models 43 & 44, Table 2) exclude the possibility that this is simply the residual effect of the association of size and injury. Future studies should explore the effectiveness of such behaviours, notably DF and BS, in deterring predators as demonstrated in the Texas horned lizard (*Phrynosoma cornutum*) (Sherbrooke & Middendorf, 2004).

Sex did not influence propensities for DF or BS. Females are larger, however, and therefore, they likely represent better prey for large predators (see Ajtić *et al.*, 2013). On the other hand, high snake population density in all the surveyed sites means that predators may not benefit from spending time to make an informed choice; feasting on bounty does not require tweaked prey selection. This result is also in accordance with previous studies reporting a lack of sex effect in antipredator behaviour in snakes prior to and during physical contact with a 'predator' (Shine *et al.*, 2003a; Roth & Johnson, 2004; Cooper, Attum & Kingsbury, 2008; Maillet, Halliday & Blouin-Demers, 2015). Other studies reported a clear effect of

sex, although DF was not considered (Shine *et al.*, 2000 and references therein).

In colour-polymorphic snake species, dorsal coloration pattern can affect antipredator response prior to physical contact with predators (garter snake– Brodie, 1992; grass snake - Hagman, Löwenborg & Shine, 2015). Some colour morphs are less conspicuous than others, and this may alter their antipredator strategy (Isaac & Gregory, 2013). Within our sample, all colour morphs (black, grey and dots) showed similar frequencies of DF and BS, but this lack of effect was recorded during handling and thus did not involve possible differential detection. Although dorsal colour pattern may play a role before capture (Venesky & Anthony, 2007), there is no strong reason for this trait to influence the antipredator tactic of snakes once seized. Our data conform well to this expectation.

In contrast to our initial prediction, gravid snakes attempted to escape more actively and thus performed DF and BS less frequently, compared with non-gravid females. Our results indicate that the antipredator response of gravid females might be more complex than previous studies suggested. Previous studies found a significant negative effect of gravidity on locomotion and on the antipredator response displayed due to physical burden of developing follicles or embryos (Brodie, 1989; Olsson, Shine & Bak-Olsson, 2000; Brown & Shine, 2004; Gregory & Gregory, 2006; Maillet *et al.*, 2015). On the other hand, gravid females have an obviously enlarged abdomen and they are coveted by predatory birds (unpublished observations). DF might be inefficient for these highly palatable prey items, struggling being then the only option left.

Inter-population patterns

Variations among populations in antipredator tactics are driven by genetic traits and experience with predators (Aubret *et al.*, 2011; Placyk, 2012). Snakes from Golem Grad displayed DF more frequently compared with the other populations (Table 3). This might be the result of different predation pressures among populations (Table 1). In nature reserves (i.e. Golem Grad), raptors and carnivorous mammals are more abundant than in unprotected areas. High density of predators combined with high prey density may intensify predator-prey interactions. Frequent encounters with predators may stimulate increased diversity and intensity of antipredator behaviours while a lack of predation induces relaxed responses (Bonnet *et al.*, 2005). Golem Grad hosts many raptors and herons that often consume snakes (unpublished observations), high frequency of DF on Golem Grad might be an adaptation to strong diurnal avian

predation (accurate comparative data among sites are lacking, however).

Different predators might respond differently to the sequence of antipredator behaviour displayed by their prey (Gregory *et al.*, 2007). Captured dice snakes immediately try to escape the grip of the predator, while spraying a mixture of faeces and cloacal secretion over the predator. Plausibly, the malodorous secretion repels predators with a fine sense of smell, that is mammals. Conversely, predators with a more limited sense of smell (e.g. many birds) might be less sensitive. DF and BS might be the next option. DF might interrupt predation by sending different tactile and visual stimuli to the predator, so that it relaxes its grip and/or puts down the immobile prey before ingestion (Gregory *et al.*, 2007; Gregory, 2016), giving the snake an opportunity to flee. Future studies, including whole behavioural sequences before, during and after physical contact with different predators, are needed to assess these hypotheses.

Limits and future directions

Dice snakes perform a wide array of antipredator behaviours before capture (not assessed here), during physical contact with a predator and after release (e.g. some snakes wait before fleeing). We must point out that our study explores the specific antipredator behaviour, only during handling by the 'predator', other sections, that is prior and after physical contact were not examined. Our results reveal significant differences among and within populations. They open ample possibilities to set up experiments in the field and captivity. Future studies should explore which factors affect duration of DF, both during physical contact with a predator and after. Whether and how dice snakes select particular antipredator behaviours from their wide repertoire towards different predators should be tested. Response of various predators to DF and moving snakes should also be measured.

Acknowledgements

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Table 3 Numbers and percentages (in parentheses) of dice snakes that performed death feigning (DF), blood spitting (BS), with visible injury (I) and total sample (N)

Population	DF	BS	*I*	*N*
Golem Grad	602 (31.5)	90 (4.7)	195 (10.2)	1909
Skadarsko jezero	42 (18.8)	8 (3.6)	37 (16.6)	223
Vrbanja	20 (6.4)	4 (1.3)	40 (12.7)	314
Pančevački rit	12 (7.5)	1 (0.6)	5 (3.1)	159
Obedska bara	23 (14.8)	3 (1.9)	10 (6.5)	155

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