



ORIGINAL RESEARCH

Tongue flicking heralds flight behaviour following passive antipredator displays in dice snakes

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antipredator behaviour; death feigning; Golem Grad; immobility; *Natrix tessellata*; predation risk assessment; escape behaviour.

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Abstract

When captured, many prey respond by biting the predator or struggling to get free. However, one indirect escape option is death feigning (DF), in which complete immobility supposedly “tricks” the predator into abandoning its meal. But lying motionless and exposed to a predator is dangerous; therefore, individuals should optimize DF occurrence and duration. We captured colour polymorphic dice snakes (*Natrix tessellata*, Natricidae) ($N = 271$) in the field and measured two behavioural responses: (1) the occurrence and duration of immobility/DF; (2) the number of tongue-flicking sequences (TF). Tongue flicking is an essential component of a key sensory mechanism to check the safety of the environment before attempting escape. We experimentally assessed the relationship between these two behaviours and the effects of phenotypic characteristic of snakes on the occurrence and duration of immobility and of TF. Snake phenotype had multiple effects. Gravid females avoided DF and displayed more TF sequences during the tests compared to non-gravid females and males. Blotched snakes stayed immobile longer than green and melanistic snakes. Larger individuals remained in DF for longer and showed fewer TF sequences than smaller individuals. Snakes burdened with a recent meal postponed fleeing and displayed more TF sequences than snakes without food. Finally, snakes showing more TF sequences postponed fleeing, which suggests that dice snakes assessed predatory risks and adapted escape behaviour to their risk status. Future studies should examine how individuals estimate the appropriate timing to shift from immobility to escape.

Introduction

Predators impose strong selective forces on their prey, promoting adaptations such as aposematic and cryptic colouration (Gittleman et al., 1980; Ruxton et al., 2019), chemical defence (Greene, 1988), and various defensive behaviours (Sih et al., 2004). Antipredator attributes and behavioural responses can function in isolation or in conjunction, sometimes generating extensive defensive repertoires (Kikuchi et al., 2023; Moore & Williams, 1990). Complex and multi-stage antipredator behaviours allow individuals to assess predatory threat and to adjust their antipredator response during an interaction (Barshaw et al., 2003; Hemmi & Pfeil, 2010). During a given antipredator sequence, each behavioural shift presumably corresponds to the most appropriate response available, given the particular circumstances (Bowers et al., 1993). In many species, an elevated predatory risk triggers fleeing, deterring, or bluffing behaviours (Cloudsley-Thompson, 1995; Kazandjian

et al., 2021). However, deterrence and bluffing may not always halt a predator’s attack, and various post-capture defences, such as struggling and biting, can be brought into play if the prey winds up in the grip of the predator (Cooper & Blumstein, 2015; Gregory, 2016; Horváth et al., 2020). In strong contrast to active defensive behaviours, some animals display strikingly passive behaviours when caught. One good example is death feigning (DF, i.e. thanatosis), in which the prey remains immobile, often exposing its vulnerable body parts to the predator (Humphreys & Ruxton, 2018). Feigning death is an intricate display, varying among taxa, but not always easy to distinguish from other types of immobility induced by predators (e.g., specific freezing posture of insects that mechanically hampers swallowing via folded-up legs; Honma et al., 2006). Perhaps the most elaborate death-feigning displays are seen in snakes, which may flip onto their backs, gape their mouths, and discharge foul smelling fluids (reviewed by Fuentes Magallón et al., 2021). In any case, immobility is

crucial. The absence of movement supposedly “tricks” the predator into “thinking” it has successfully killed its prey, after which the predator stops attacking the prey or even mistakenly caches it for later consumption (Sargeant & Eberhardt, 1975; Thompson *et al.*, 1981). Similarly, resembling a corpse prey might exploit the predator’s aversion towards dead prey (Skelhorn, 2018), all of which grants the prey potential chances to escape. Such passive tactics seem extremely risky; however, the fact that they have evolved repeatedly in animals suggests that they are effective (Humphreys & Ruxton, 2018), but how selective forces may favour immobility and DF is not yet fully understood (Gregory *et al.*, 2007; Humphreys & Ruxton, 2018; Miyatake *et al.*, 2004).

During a DF display, the prey should remain alert until escape is possible (Arduino & Gould, 1984; Hugie, 2003; Lima & Dill, 1990). The decision to flee or remain immobile should maximize the probability of survival; thus, it is crucial for the prey to select the right moment to escape as trying to escape too early may re-attract the unwanted attention of the predator (Sih, 1997; Ydenberg & Dill, 1986). Such a fine-tuned decision is presumably based on information gained through various sensory channels. Visual clues should be important but might be limited in a motionless individual lying supine on the ground. In such cases, other sensory information, such as chemosensory information, might play an essential role in estimating risks involved with escape (Elvidge & Brown, 2014; Kats & Dill, 1998; Punzo, 2007). The vomeronasal organs comprise the key chemosensory organ in squamate reptiles; these organs process information from volatile and non-volatile molecules from the air or substrate relayed to them through tongue flicking (TF; Daghfous *et al.*, 2012; Filoramo & Schwenk, 2009; Shine & Mason, 2012). As a sensory behaviour that is directly involved in information gathering and transfer, TF can play a crucial role in risk assessment.

In this study, we focused on the occurrence and duration of immobility and DF as metrics of a snake’s decision to shift from active to passive antipredator behaviour before shifting again to active escape. We performed our experiments immediately after capturing snakes in the field while simulating handling by a “predator”, thus imitating a real encounter as much as possible. We studied a dense population of colour-polymorphic dice snakes, which enabled us to obtain a large sample and explore the effects of colour morph, sex, body size, reproductive status, feeding status, cloacal temperature, scars, and injuries (a proxy of past predation experience) on the incidence and duration of death-feigning behaviour. Specifically, the variation in the dorsal pattern could play a noteworthy role in antipredator displays. For instance, snakes with blotched patterns exhibit a greater propensity for pre-capture immobility, whereas uniformly coloured snakes tend to rely on flight when confronted by predators (Allen *et al.*, 2013; Jackson *et al.*, 1976). The assumption is that the blotched pattern offers reference points that aid the predator in the visual tracking of the snake’s movements. In the Golem Grad population, it is anticipated that all colour morphs will exhibit comparable defensive behaviours, as indicated by Golubović *et al.* (2021), although this study only considered capture behaviours. According to the results of Golubović *et al.* (2021), larger dice

snakes are expected to display DF more often, and gravid females should decrease DF propensity, although the duration of immobility and DF was not previously measured or analysed. To our knowledge, this study is one among very few studies that consider the sequences and durations of antipredator behaviour in snakes (along with Burghardt & Greene, 1988; Durso & Mullin, 2014; Gerald, 2008).

Finally, we considered how the number of tongue flicking sequences, a unique sensory behaviour in squamates, might influence the decision of individuals to attempt escape. We expected tongue flicks to signal a snake’s willingness to explore options to flee and thus the possible imminence of the decision to flee or not. Alternatively, TF could indicate a pre-cautious exploration of the environment and be associated with a delay in the decision to flee. Either way, by increasing the amount of the information gathered, individuals should be better able to assess the risk they run by choosing to flee (Daghfous *et al.*, 2012; Kats & Dill, 1998; Lima & Dill, 1990).

Materials and methods

Study species

The dice snake (*Natrix tessellata*) is a non-venomous oviparous colubrid snake with an extensive geographic range (Mebert, 2011; Mebert *et al.*, 2013). This semi-aquatic piscivorous species frequently occurs in large and dense populations (Ajtić *et al.*, 2013; Carlsson *et al.*, 2011; Gruschwitz *et al.*, 1999). Additionally, dice snakes are prey to a great diversity of predators (*Hierophis gemonensis*, Jelić & Lauš, 2011a; *Larus cachinnans*, Jelić & Lauš, 2011b; Accipitridae, Ardeidae, Corvidae, *Lutra lutra*, Ajtić *et al.*, 2013). Dice snakes are sexually dimorphic, with males being smaller and reaching maturity at a smaller size than females. When seized by a human, dice snakes display a variety of antipredator behaviours. Like other natricine snakes, they usually start with a vigorous struggle to get free. If unsuccessful, they may rapidly discharge foul-smelling cloacal secretions mixed with faeces and urine, regurgitate recently ingested prey, or bluff an aggressive display by flattening their head while hissing and making sham strikes (Golubović *et al.*, 2021). DF is usually considered to be a last resort behaviour; individuals that display DF exhibit a decreased stress response (lower levels of corticosterone) compared to non-displaying individuals (Lakušić *et al.*, 2020). Such physiological bases of DF suggest that it is not randomly expressed.

Study population

We explored antipredator behaviour in an extremely dense dice snake population (~10 000 individuals; Ajtić *et al.*, 2013). The population inhabits Golem Grad Island (N 40°52′08″, E 20°59′23″; ~18 ha; 850 m asl), located in the North Macedonian part of Lake Prespa and is a strictly protected area within the National Park “Galičica.” In this locality, dice snakes occur in three different colour morphs. Olive green snakes with black dots that make a blotched dorsal pattern characterize the most common morph (blotched morph). The two other morphs, the

uniformly olive green snakes and the melanistic morph, are also represented by a large number of individuals (Ajtić *et al.*, 2013). Because neonates, juveniles, and adults are probably exposed to different predators (due to the massive differences in body size and body mass among age classes; Ajtić *et al.*, 2013), we limited investigations of antipredator behaviour to adult snakes. To determine size thresholds of sexually mature individuals, we used a dataset containing over 6000 measured and marked Golem Grad dice snakes. Snout-to-vent length (SVL) of the smallest male found in copulation was ≥ 55 cm, whereas the SVL of the smallest gravid female in this population was ≥ 63 cm (Ajtić *et al.*, 2013). Several species of predators that prey on dice snakes (*Vipera ammodytes*, *Bubo bubo*, *Ardea cinerea*, *Corvus monedula*, *Larus* sp., *Lutra lutra*; Ajtić *et al.*, 2013) inhabit the island. Intense avian predation on the island is presumed to be responsible for the rather high occurrence of immobility and DF in this population (Bjelica *et al.*, 2023; Golubović *et al.*, 2021).

Field procedures

We searched for dice snakes in the open or sheltered under natural cover and quickly captured them by hand, mimicking successful predations, which was followed by a series of generalized predator-like actions to test for post-capture antipredator responses in the field. We assume that, although humans were proxies for natural predators (an issue previously addressed by Gregory, 2016), the same general principles apply to natural encounters between snakes and their predators. The predator-like handling procedure involved a 30-s handling sequence. Each snake was first held for 10 s with both hands, and two fingers were used to pinch the body at two fixed points, behind the head and above the cloacal region, to standardize the handling as much as possible. Then, the snake was passed from one hand to the other for 10 s and finally slightly stretched for 10 s to imitate a generalist predator handling its prey. The snake was then placed on its back, and the person handling the snake (VB) stepped out of view of the snake, mimicking predator hesitation or latency to eat the prey. Another observer (MM) remained motionless at 1 m (crouching) to record the snake's behaviours. From the moment when the snake was put on its back (i.e., start of the post-capture test), we recorded measurements of the following sequence of variables:

Occurrence of immobility: If the snake remained entirely immobile for a measurable period (≥ 1 s), we considered this a display of immobility.

Duration of immobility: This measurement includes DF and is defined as the time elapsed from the start of immobility until the snake makes its first visible head movement (Fig. 1). We assumed that this timing corresponds to the moment the snake starts actively surveying its surroundings, likely visually assessing the opportunity to escape. Following their first visible movement, all snakes fled rapidly, but with a variable delay.

Occurrence of death feigning (DF): If the snake had an open mouth and a protruding tongue during immobility, we

considered it as DF, a more intensive display than immobility alone (Gregory, 2008).

Duration of death feigning: Defined as the time elapsed from the onset of DF until the snake closed its mouth (i.e., end of DF). TF never occurred during DF.

Decision to escape: Time elapsed from the end of immobility until a clear escape attempt was recorded, with the snake either starting to move slowly or rapidly darting away.

Tongue flicking: Tongue flicking rate is an important variable commonly used in behavioural tests (Baeckens *et al.*, 2017; Punzo, 2007). However, since accurately counting the exact number of tongue flicks was impossible from a distance of 1 m, we recorded the number of tongue flicking events during the tests. TF during post-capture immobility usually starts after several seconds of complete immobility or after DF. Individuals rapidly flick their tongue for less than a second, stop and retract their tongue, and such tongue flicking sequences were easily counted (TF_{seq}). An overview of the different phases and parameters we measured is given in Fig. 1.

All tests were timed using a digital stopwatch (± 0.1 s). We limited the tests to 5 min per snake since only six of the 271 snakes tested ($\sim 2\%$) remained immobile for longer than 5 min. These six individuals were included when examining the occurrence of DF and immobility but were excluded from the analysis of the duration of these behaviours. After the completion of behavioural tests, we recorded colour morph, sex, body size (SVL, snout-to-vent length), the presence of scars, and injuries and measured the cloacal temperature using a probe thermometer. Visible bite and claw marks were considered indicative of past confrontations with predators (Bonnet *et al.*, 2010; Gregory & Isaac, 2005), while their size and number were not further coded. Furthermore, we only tested snakes that appeared to be in good condition, i.e., snakes that did not have debilitating injuries. We also palpated the abdomen of each snake to determine its feeding status (presence/absence of prey in the gut) and, if female, its reproductive status (gravid or not). By using ventral scale notching with scissors, each snake was given a long-term and unique mark for later identification and released at the capture site. Each individual was represented only once in the analyses, and recaptures from the ongoing capture-mark-recapture studies were not included.

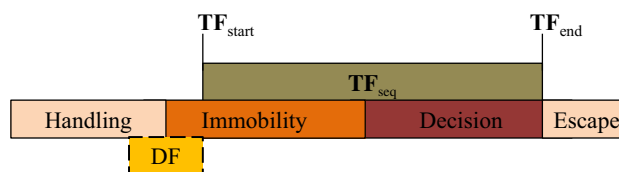


Figure 1 Different phases that we timed and measured during the course of the DF test. Dice snakes sometimes displayed DF during predator-like handling, but was not measured in this phase. TF sequences were counted during immobility and after DF, until a clear escape attempt was made.

Statistical analyses

To model the factors that influenced the occurrence and duration of post-capture immobility and DF, as well as the number of TF sequences, we used generalized linear models (GLM). For our set of predictors, we considered the additive effects of colour morph (blotched, green and melanistic snakes), sex and reproductive status (male, nongravid female, and gravid female), presence of food (yes/no), presence of injuries (yes/no), snout-to-vent length (SVL; continuous variable), cloacal temperature (continuous variable), and TF_{seq} (discrete variable). We used binomial GLMs to model the occurrence of each specific phase of the tests (DF, Immobility; no – 0 s/yes ≥ 1 s), Gaussian and gamma GLMs to model the duration of DF, immobility, and the decision phase and Poisson GLM to model the number of TF sequences.

We used a stepwise regression with the backward model selection procedure, starting with a model that included all explanatory variables and dropping the terms that caused an increase in Akaike Information Criterion (AIC) values (Crawley, 2013; Zuur *et al.*, 2009). With similar competing models ($\Delta\text{AIC} \leq 2$), we chose the model with the fewest parameters. With multilevel categorical variables, we performed Wald Chi-Squared tests to determine if the association of the predictor and response variable was significant. We then plotted the effects of significant variables from the best-fit models using the sjPlot package (Lüdtke, 2022). Statistical analyses were done using R (R Core Team, 2023) and the MASS (Venables & Ripley, 2002) package. Summaries of the best-fit models (odds ratios, coefficients, standard errors, and *P* values) are available in the Tables S1 and S2.

Results

A breakdown of the dice snakes that displayed immobility (I) and death feigning (DF) is presented in Table 1.

Immobility

The occurrence of immobility was high (~65%, 175 out of 271 tested snakes). It was non-significantly associated with the presence of injuries. The duration of immobility was influenced by morph (*P* = 0.008). Blotched snakes remained immobile longer compared to uniformly green and melanistic snakes,

Table 1 Breakdown of dice snake data set by sex and colour morph

Colour morph	Males			Non-gravid females			Gravid females		
	<i>N</i>	I (%)	DF (%)	<i>N</i>	I (%)	DF (%)	<i>N</i>	I (%)	DF (%)
Blotched	34	67.6	23.5	27	59.2	40.7	36	63.9	30.5
Green	28	57.1	21.4	30	66.7	40	26	65.4	23.1
Melanistic	32	71.9	40.6	30	50	40	29	75.9	44.8

Sample size (*N*) of tested individuals and percentages of snakes that exhibited immobility (I) or death feigning (DF) are provided.

while these two morphs showed a similar duration of immobility.

Death feigning

One-third of the snakes displayed DF (~34%, 92 out of 271 individuals). We found significant effects of sex and reproductive status on the occurrence of DF (*P* = 0.030). Nongravid females displayed DF more often than gravid females, while gravid females displayed DF more often than males. The duration of DF was positively associated with SVL (*P* = 0.043). Larger snakes remained in DF for longer amounts of time.

Decision to escape

The decision to escape was influenced by the presence of food in the gut (*P* < 0.001) and by the number of TF_{seq} (*P* < 0.001). Individuals with empty stomachs fled sooner than the snakes that had ingested prey. Higher values of TF_{seq} were associated with delayed flight (Fig. 2).

Tongue flicking

The number of TF_{seq} was significantly associated with sex and reproductive status (*P* < 0.001), SVL (*P* < 0.001), presence of food in the gut (*P* = 0.005), and the occurrence of DF (*P* < 0.001). Gravid females had the most TF sequences during our experiments followed by nongravid females and males, respectively (Fig. 2). Smaller snakes (lower SVL) had more TF_{seq}, while the presence of food and the occurrence of DF had a positive association with TF_{seq} (Fig. 3).

Discussion

When squamates are presented with chemical stimuli related to a predator, they usually respond by increasing the rate of TF (Cooper, 1994, 2005; Pianka & Vitt, 2003; Punzo, 2007). This behaviour allows them to detect the presence of a predator, subsequently influencing their escape response after capture, which has been identified as a crucial component in antipredator behaviour (Brown *et al.*, 2006; Clermont *et al.*, 2017; Curio, 1975; Lohrey *et al.*, 2009; Sih, 1986; Sih *et al.*, 1998). By increasing the number of TF sequences, dice snakes effectively gather more information from their surroundings and presumably more accurately assess the risks involved when trying to escape. Our results indicate that the more vulnerable categories of snakes, such as smaller individuals and those burdened by growing follicles (or eggs) or a recent meal, explored their surroundings more intensively, showing a greater number of TF sequences prior to breaking immobility and trying to escape (Figs 2 and 3). Accordingly, snakes that showed more TF sequences postponed fleeing. Our results indicate a complex relationship between passive antipredator behaviours (DF and immobility) and the risk assessment mediated by TF.

An animal's decision of when to start moving is presumably based on the information gained through a wide array of sensory systems (Kats & Dill, 1998; Punzo, 2007) until,

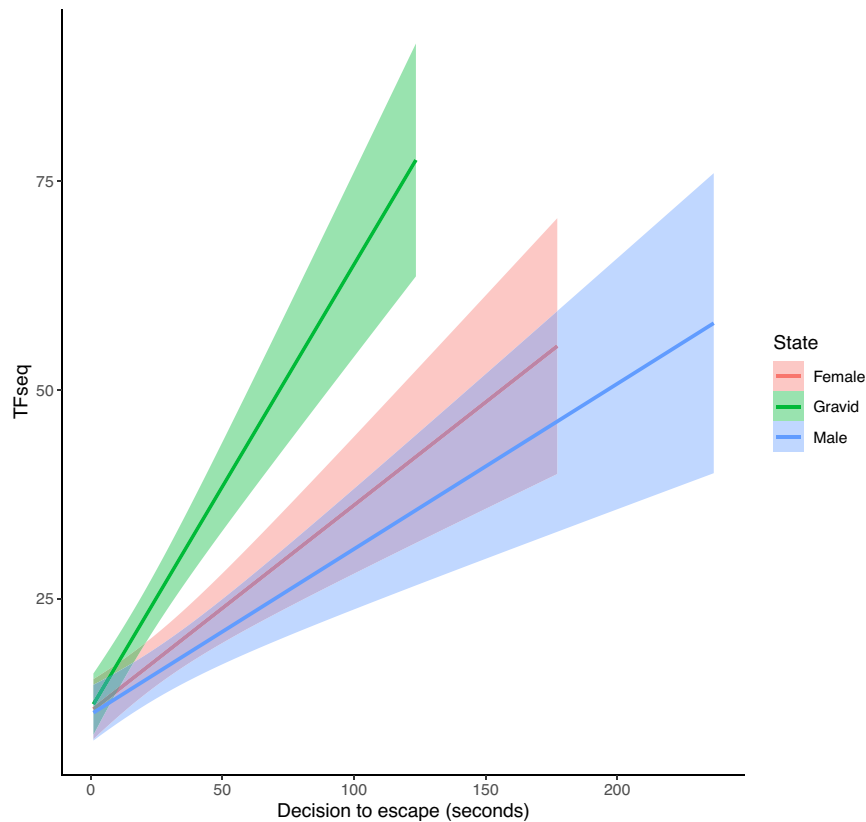


Figure 2 The number of TF sequences versus time from decision to attempt escape to actual escape (in seconds) during the post-capture immobility phase. Linear regression lines, with shaded areas representing 95% confidence intervals on the predicted value of the number of TF sequences are presented for males (blue, $N = 94$), non-gravid females (red, $N = 87$), and gravid females (green, $N = 91$).

eventually, the animal chooses, based on updated sensory inputs, to try an escape. The basic dilemma is that a rapid shift from immobility to movement can once again attract the predator's attention, while prolonged immobility or a slow shift leaves the individual vulnerable for a long time. According to our results, individuals that tongue flicked more frequently hesitated to attempt escape, which supports one of our starting hypotheses (i.e., precautious intensive TF is associated with a delay in fleeing) but refutes the other (i.e., individuals showing more TF sequences should escape sooner). The indecisiveness of some individuals about moving (i.e., accompanied by more TF sequences) may indicate strong interindividual variations of risk assessment (Boissy & Bouissou, 1995), possibly revealing personality traits. Personality traits have been described in other animal species, including snakes (Bell & Sih, 2007; Briffa & Greenaway, 2011; Cote *et al.*, 2010; Mirkó *et al.*, 2013; Šimková *et al.*, 2017; Stahlschmidt *et al.*, 2016), and should be investigated in dice snakes. Other factors may also affect the decision to flee, such as the individual's health status and the relative fitness costs of fleeing or remaining still (Hemmi & Pfeil, 2010; Sih, 1997; Ydenberg & Dill, 1986).

Our study indicates a significant relationship between the occurrence of DF and the number of TF sequences, where individuals that displayed DF had more TF sequences after

exiting DF (Fig. 3). When in the state of DF, dice snakes are usually without muscle tone or visible breathing movement and may even exhibit bradycardia similar to DF displays in other snakes (e.g., *Heterodon platyrhinos*, McDonald, 1974). Such decrease in heart rhythm, respiratory rate, and sometimes even body temperature in animals (reviewed by Rogers & Simpson, 2014) has been attributed to the cortical depression hypothesis (i.e., cortical activity is assumed to be inhibited by heightened brain stem activity, Wendt, 1936). It seems that during DF, some animals, presumably even dice snakes, experience minimal activity of the sensory systems. Upon exiting DF, dice snakes could increase the number of TF sequences in order to gain the crucial information in their immediate surroundings and re-evaluate predation risk. The pattern we observed is consistent with the idea that prey animals ought to adapt their antipredator responses in accordance with the severity of the predatory threat ('threat sensitivity hypothesis', Helfman, 1989).

Different morphs in many colour-polymorphic species exhibit apparent differences in defensive behaviour (Abdel-Rehim *et al.*, 1985; Allen *et al.*, 2013; Brock *et al.*, 2022; Brock & Madden, 2022; Brodie, 1992; Jackson *et al.*, 1976; King & Lawson, 1997; Sowersby *et al.*, 2015; Sreelatha *et al.*, 2021; Tate *et al.*, 2016; Venesky & Anthony, 2007;

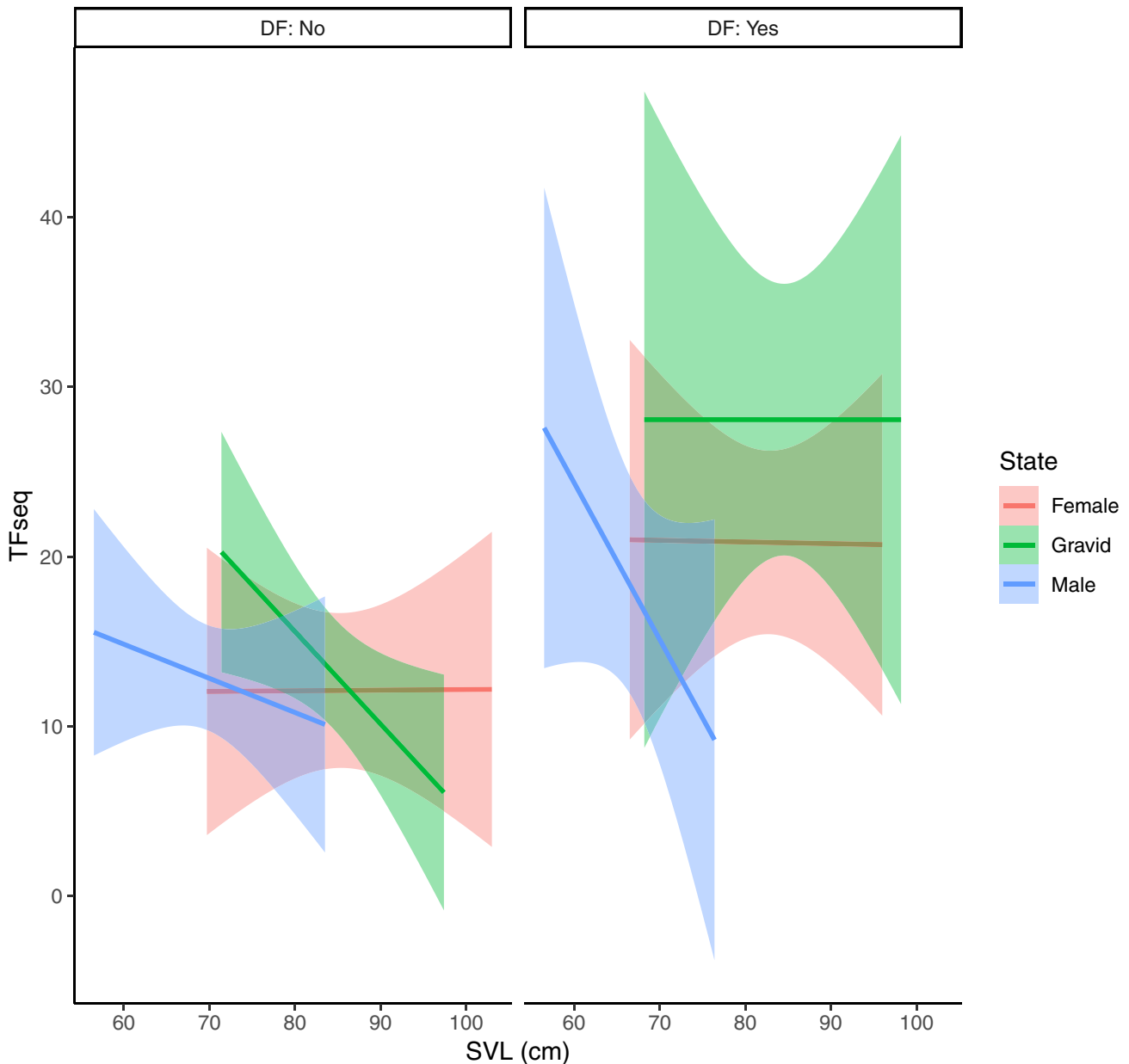


Figure 3 The number of TF sequences versus snout-vent length (SVL, in cm) of snakes for those that feigned death and those that did not during post-capture immobility. Linear regression lines, with shaded areas representing 95% confidence intervals on the predicted value of the number of TF sequences are presented on left for non-DF males (blue, $N = 67$), non-DF non-gravid females (red, $N = 51$), non-DF gravid females (green, $N = 61$), and on right for DF males (blue, $N = 27$), DF non-gravid females (red, $N = 35$), and DF gravid females (green, $N = 30$).

Williams *et al.*, 2012). For example, snakes with blotched patterns use immobility more readily, while uniformly coloured snakes rely on flight when facing a predator (Allen *et al.*, 2013; Jackson *et al.*, 1976). Although our results did not point to colour morph as a significant factor affecting the occurrence of immobility, we did find significant differences in the duration of immobility among the different morphs. Blotched snakes had the longest duration of immobility (~45 s), followed by melanistic snakes (~31 s) and uniformly green snakes (~30 s). This supports the ideas outlined by

Jackson *et al.* (1976), Allen *et al.* (2013), and Brock and Madden (2022) – blotched dice snakes rely on longer bouts of immobility than uniformly coloured dice snakes, and this distinct combination of morph and behaviour could be under natural selection (Brodie, 1992). The peculiarities of different colour morphs of dice snakes are yet to be unravelled, including their thermal, antipredator, and locomotor distinctiveness.

Differences between the sexes in antipredator behaviours are common in animals (Blanchard *et al.*, 1992; Han *et al.*, 2015; Johnsson *et al.*, 2001; Williams *et al.*, 2001), although many

snake studies did not find such a sex effect (Cooper *et al.*, 2008; Golubović *et al.*, 2021; Roth & Johnson, 2004; Shine *et al.*, 2003). Instead, our results revealed a complex pattern with significant differences between the sexes in the occurrence of DF, but no effect on the duration of DF or immobility. In snakes, males are usually the smaller and more agile sex (Bonnet, Ineich, & Shine, 2005; Lourdaïs *et al.*, 2006); if male dice snakes, which are smaller than females, are also more agile, they might be more reliant on flight in avoiding predation and, in turn, less reliant than females on a risky tactic like DF.

Larger dice snakes performed DF for longer periods and explored their surroundings with fewer TF sequences compared to smaller individuals (Fig. 3). Body size is an important determinant of antipredator behaviour, possibly because larger animals are usually less vulnerable (Bonnet, Aubret, *et al.*, 2005; Honma *et al.*, 2006). In the context of DF, especially in a locality with strong avian predation such as Golem Grad, larger snakes can afford to remain in DF for longer; further, certain birds such as herons are gape-limited predators that cannot easily swallow large snakes (Golubović *et al.*, 2021).

Snakes with food in their stomachs showed significantly more TF sequences when assessing potential risks before escaping and took more time to start fleeing. The presence of food impairs snake movement (Garland & Arnold, 1983; Herzog & Bailey, 1987) and may limit escape ability, which in turn requires different risk assessment before an escape attempt and is reflected in the higher number of TF sequences.

Our results show that gravid dice snakes are less prone to DF displays, supporting the results of our previous study (Golubović *et al.*, 2021). Numerous studies have shown that female snakes alter their antipredator behaviour during gravidity (Brodie, 1989; Brown & Shine, 2004; Gregory, 2008, 2016; Maillet *et al.*, 2015). These changes in behaviour have been attributed to physical burden of developing eggs or embryos, which have a negative effect on locomotion. Our models also show that gravid snakes generally displayed more TF sequences during the tests (Fig. 2). This might indicate that gravid snakes are less prone to taking risks, likely because developing eggs represent a valuable asset (“asset protection principle”, Clark, 1994). By tongue flicking more often, gravid females can make an “informed” decision on when exactly to escape. This does not exclude the possibility that the effect of gravidity may vary, depending on the stage of gravidity and clutch size, which remains a direction for future study.

Unexpectedly, cloacal temperature did not significantly affect immobility displays of dice snakes. However, immobility has been shown to be associated with body temperature in other snake species (*Storeria dekay*, Gerald, 2008) and in other animal species (e.g., woodlice, Saxena, 1957; seedbeetles, Miyatake *et al.*, 2008; mealworm, Krams *et al.*, 2014). Due to the lack of a significant association between cloacal temperature and immobility displays, we can safely assume that all the snakes tested (including 89% of snakes caught in the open and 11% caught from under cover) were probably within their normal thermal range for activity. It is possible that testing snakes

further from their temperature optima might lead to significant effects of temperature on immobility/DF.

Notably, the presence of injuries was retained in several best-fit models and, although not statistically significant, had a negative effect on the occurrence and duration of post-capture behaviour (Tables S1 and S2). Previous experience with a predator is expected to shape the prey’s response in a subsequent encounter (Bonnet, Aubret, *et al.*, 2005; Gregory, 2013; Shier & Owings, 2006), and this remains another future direction to be studied in greater depth.

Conclusion

Our study clearly demonstrates the effects of multiple phenotypic traits on different sequential phases of post-capture antipredator behaviour. Tongue flicking is an important factor that indicates a delayed flight following post-capture immobility, and in turn it is significantly associated with a set of phenotypic traits. These results emphasize complex relationships between post-capture antipredator behaviour, sensory information relayed through tongue flicking, morphological traits, and physiological status. Future studies may explore how animals gauge their surroundings and perceive risk, especially in high-risk–high-reward situations such as those conducive to post-capture immobility and death feigning. Finally, the potential influence of personality, ontogenetic shifts, and locomotor performances may also have a considerable but rarely tested effect on passive antipredator displays.

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Author contributions

VB, AG, and MA conceived the ideas and designed the methodology; all authors contributed to the collection of data; VB analysed the data; VB, AG, and XB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

All data used in this study are freely available in the [Supporting Information](#).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Model selection procedure of the competitive generalized linear models built to explain variation of post-capture immobility in dice snakes, using additive (+) effects of colour morph (M), sex and reproductive state (S), presence of injuries (I), presence of food (F), cloacal temperature (T), SVL, and number of tongue flicking sequences (TF_{seq}).

Table S2. Model selection procedure of the competitive generalized linear models built to explain variation in tongue flicking during post-capture immobility, using additive (+) effects of colour morph (M), sex and reproductive state (S), presence of injuries (I), presence of food (F), cloacal temperature temperature (T), SVL and occurrence of DF (DF).

Table S3. Factors from best-fit models with associated odds ratios (OR), coefficients, standard errors and *P* values.