Should I stay or should I go: escape behaviour of Russell's vipers, *Daboia russelii* (Shaw & Nodder, 1797) in India's agricultural landscapes

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Abstract

Predation exerts a strong selective force on prey, and hence prey species have evolved a multitude of ways to escape predation. One strategy by which many mobile species escape predation is by fleeing when approached by predators. However, fleeing too early can have fitness costs. Thus, optimal escape theory suggests that escape behaviour in prey depends on the risk of being eaten and the fleeing costs. Several studies on mammals, birds and lizards lend support to this hypothesis. However, few studies have explored escape behaviour in snakes. Here, using radio telemetry to track snakes in the field, we study the escape behaviour in Russell's vipers, a highly venomous and cryptic snake, responsible for the highest number of snakebite deaths in India. We show that escape response, i.e., the decision to stay or flee, was influenced by intrinsic factors such as the snake's behaviour and body temperature. We also show that the flight initiation distance, the distance at which the snake flees, was mostly determined by habitat selection, i.e., the visibility of the snake and the distance to the nearest cover. Overall, we show that different factors could determine the decision to flee and when to flee. We also highlight how understanding escape response in such highly venomous, medically important yet secretive snakes could potentially help reduce human-snake encounters and mitigate the snakebite crisis.

Introduction

Predation exerts a strong selective force on prey (Gurevitch et al., 2000), resulting in the evolution of several strategies in prey to avoid being eaten (Poulton, 1890; Ruxton et al., 2004). Many animals have evolved cryptic colourations to avoid detection by predators (Stevens & Merilaita, 2009a), while others have defences such as spines or toxins and advertise these defences through warning colourations or mimic the warning signals of others (Pfennig et al., 2001; Mappes et al., 2005; Cuthill et al., 2017). Animals may also choose to flee when approached by predators. Fleeing represents a common escape response in many animals (Stankowich & Blumstein, 2005). Although fleeing from predators clearly has its advantages, fleeing too early can have other fitness costs associated with being detected by predators or losing feeding and mating opportunities (Ydenberg & Dill, 1986; Cooper Jr & Frederick, 2007, 2010). This trade-off between staying and fleeing has sparked several studies to see how prey optimise the cost and benefits of fleeing (optimal escape theory) (see Samia et al., 2016 and references therein).

Most studies testing predictions of optimal escape theory use the flight initiation distance, the distance at which an animal flees when approached by a predator, as a measure of the risk an animal is willing to take. Several studies have indicated that predator's body size (Burger et al., 1991; Cooper Jr & Stankowich, 2010), direction and speed of approach (Burger et al., 1992; Cooper Jr, 1997a; Kramer & Bonenfant, 1997), distance to refuges (Dill, 1990; Bonenfant & Kramer, 1996; Cooper Jr, 1997b), perch height (Blamires, 1999; Amo et al., 2005; Cooper Jr, 2010), crypticity of prey (Broom & Ruxton, 2005; Møller et al., 2019), ambient temperature (Blamires, 1999; Martín & López, 1999), etc., can affect flight initiation distances (FIDs). Intrinsic factors such as reproductive state (Brown & Shine, 2004), body temperature (Rand, 1964; Shine et al., 2000; Smith & Lemos-Espinal, 2005) and previous experience of the prey (Marcellini & Jenssen, 1991; Cooper Jr, 2007; Gregory, 2013) can also affect FIDs. However, studies indicate that antipredator response can be highly context-dependent (Brodie III, 1992; Llewelyn et al., 2010), and several contrasting factors can determine the decision to flee or remain still. For instance, although temperature is considered a critical physiological variable affecting ectotherms' general ecology and behaviour (Angilletta Jr et al., 2002), the relationship between body temperature and FID is not consistent among studies (e.g., Rand, 1964; Layne & Ford, 1984; Cooper Jr & Sherbrooke, 2010). Studies have also shown geographic differences in escape response (Shine et al., 2003; Cooper Jr et al., 2014).

FIDs have been well studied in several taxa but more extensively in lizards (Samia et al., 2016). Although snakes exhibit diverse antipredator behaviours (Greene, 1988), comparatively fewer studies have explored escape behaviour and the factors affecting FIDs in snakes, most of these studies being focused on natricine snakes (Layne & Ford, 1984; Weatherhead & Robertson, 1992; Shine et al., 2000, 2003; Brown & Shine, 2004; Cooper Jr et al., 2008; Gregory, 2013). While studies have examined antipredator responses in venomous elapid and viperid snakes, these

studies mostly address questions on defensive strike responses towards humans (Goode & Duvall, 1989; Gibbons & Dorcas, 2002; Shine et al., 2002; Glaudas et al., 2005), with only few studies explicitly examining escape responses (e.g., Maritz, 2012). This paucity of studies on snakes could be because snakes are generally less exposed and more cryptic than lizards, making them hard to spot from a distance. The lack of studies on snakes adds a considerable gap to the understanding of escape behaviours in snakes. Understanding the factors influencing FIDs in snakes can also directly impact our understanding of venomous snakebites in humans. Snakebite is now considered a neglected tropical disease (Chippaux, 2017) and is estimated to kill as many as 94 000 people yearly (Kasturiratne et al., 2008). A large portion of these snakebites occur in agricultural fields when these snakes are accidentally trampled upon by humans (Suraweera et al., 2020). Thus, understanding what factors determine when a snake flees can have important outcomes to mitigating the snakebite problem.

Russell's vipers are a dangerously venomous snake found commonly across the Indian subcontinent from Pakistan, across Nepal, India and Sri Lanka, to Myanmar (Whitaker & Captain, 2004). In India, they are found in forested habitats, but are also commonly seen in urban and semi-urban landscapes, particularly in agricultural fields, where people regularly encounter these snakes while working in the fields. Russell's vipers are one of the four most medically important snakes in India and account for ca. 48% of the country's snakebite-related deaths (Suraweera et al., 2020), and are hence generally killed when encountered by people in agricultural fields. Most of these snakebites occur in rural India when these snakes are accidentally stepped on by people working in the fields (Suraweera et al., 2020). These snakes, being ambush predators, have a notorious reputation for remaining motionless even when approached by people (Whitaker & Martin, 2015). Here, we study the escape behaviour in these venomous vipers by using radio telemetry to track and locate these snakes. Russell's vipers are highly cryptic and rarely seen while searching for them in the field. However, radio telemetry allowed us to locate these cryptic snakes and record behaviours regularly. Using field observations on 16 tracked snakes, we show that extrinsic factors such as distance to cover and visibility of the snakes and intrinsic factors such as body temperature influence escape behaviour in these snakes.

Materials and methods

Radio telemetry

We studied the escape behaviour of Russell's vipers in agricultural fields in villages around Ratnapuri taluk of Hunsur district in Karnataka, India. Russell's vipers were being tracked since January 2019 as part of a larger radio telemetry study to understand movement patterns and the risk of snakebite. Russell's vipers were caught opportunistically between January 2019 and December 2020 and implanted with epoxy-coated transmitters. Adult snakes caught between 2019 and September 2020

were implanted with standard transmitters of frequency 143-148 MHz, while snakes found between September and December 2020 were implanted with thermosensitive SI-T2 Transmitters (Holohil Systems Ltd., Carp, ON, Canada) of frequency 151.3-151.9 MHz. Two of the snakes that previously had standard transmitters implanted in 2019 had these replaced with thermosensitive transmitters when we recaptured them in 2020. Thus, 13 of the 16 snakes were implanted with thermosensitive transmitters during our study period. Snakes caught were anesthetised using isoflurane, following which the sex was determined by cloacal probing, and snout-vent length, tail length and weight were recorded. Transmitters were surgically implanted into the snakes' coelomic cavity while the transmitter's antenna was inserted subcutaneously following Reinert & Cundall (1982). Transmitters weighed less than 5% of the body mass of each snake. Snakes were monitored for 24 hours after the surgery and then released back to the same spot they were captured. Snakes were then tracked using an RX-1000 telemetry receiver (Communications Specialists Inc., Orange, CA, USA). All applicable international and national guidelines for the care and use of animals were followed. The radio telemetry and behavioural study on Russell's vipers was approved by the Karnataka State Forest Department under permit no. FEE-178-FWL-2017 dated 18 August 2017.

A total of 16 adult Russell's vipers (eight females and eight males) were tracked from 10 November 2020 to 20 January 2021 to study escape response. A two-member team tracked all the snakes every day except for a few days with unfavourable weather conditions, during which we tracked as many snakes as possible or skipped tracking altogether. We started tracking each snake from a point 20-30 m from the snake's previous location and walked directly towards the snake upon catching a signal on the receiver. We reduced the walking speed as we reached a distance of ca. 15-20 m from the snake (estimated by adjusting the receiver's signal strength) to locate the snake.

Escape behaviour and flight initiation distance

To study escape response in these snakes, one of the investigators (VPC) simulated a predation threat by approaching the snakes at a very slow (ca. 5-10 m/minute) but approximately constant speed until the snake was spotted. We used such a slow speed of approach because of the potential risk involved with accidentally stepping on the snake, and because such slow speeds are typical of farm workers planting or harvesting crop. This method has been used extensively to study escape behaviour in reptiles (e.g., López et al., 2005; Cooper Jr et al., 2008). Humans have been regularly killing these snakes when encountered in agricultural fields and thus, it is likely that these snakes respond to approaching humans as if they were predators. Upon spotting a snake, we stopped approaching the snake, and recorded its escape response (i.e., whether the snake moved away or not), its behaviour, microhabitat features and the tracker's distance. The tracker's distance was recorded as the distance from the snake to the point where the observer first detected the snake. If the snake moved away upon detection, the tracker's distance was considered as the

FID. In many cases, the snakes were only partially visible; thus, we estimated the tracker's distance and the FID to the nearest 0.5 m. Our approach differs considerably from most other studies on escape behaviour and FID in that we did not have a fixed starting point after which we approached the subject until it moves away to record FID. We did not have such an experimental approach for two main reasons: (1) Russell's vipers are highly cryptic, and spotting them from a distance greater than 5 m, especially when in thick undergrowth, was generally not possible; (2) as these snakes were part of a more extensive radio telemetry study, we wanted to keep our disturbance to a minimum so that our presence did not affect their movement pattern. When initially observed, the behaviour of the snake was recorded as 'basking', 'resting', 'ambush', 'courtship' or 'unknown' (see supplementary table S1 for definitions). We noted the visible part of the snake's body from the observer's point as 'not visible', 'small coils visible', 'under half visible', 'more than half visible' and 'completely visible'. In a few cases (16 observations), even if we were unable to see the snake due to thick undergrowth, we could still estimate the snake's initial location based on the sound produced when the snake slithered away when the observer was at close distances (usually less than 2 m). Environmental variables recorded included the microhabitat (see supplementary table S1 for definitions), the ambient temperature and humidity (measured at the observer's point), and the distance to the nearest cover (to the closest 0.25 m). In cases where we observed the snake from a distance of more than 3 m, we slowly moved closer without disturbing the snake as much as possible after recording other data to estimate the distance to the cover. We also recorded the signal pulse per minute on the receiver for the 13 snakes implanted with thermosensitive transmitters to estimate body temperature. Body temperatures were calculated using quadratic equations obtained from the calibration graph provided by Holohil Systems Ltd.

Statistical analyses

All analyses were carried out in R version 3.3.2 (R Core Team, 2016). We made 229 observations on 16 snakes during the study period, from which we excluded observations where the snake was found moving or the behaviour was unknown, giving a dataset with 178 observations. Since our dataset consisted of repeated observations of the same individual, we used generalised linear mixed-effect models (GLMMs) to account for individual differences in escape response and FID. To test the effect of different predictors on escape response, i.e., whether or not a snake moved away when approached, we used GLMMs with escape response as a dependant variable with a binomial logit link function using the package *lme4* v. 1.1-12 (Bates et al., 2015). We included sex, behaviour, microhabitat, the snake's visibility, distance to cover, tracker distance, ambient temperature and relative humidity as fixed factors and the snake ID and sampling day as random factors. We compared this model's fit with less inclusive models from a stepwise backward elimination process by examining the Δ Akaike Information Criterion value corrected for small sample sizes (ΔAICc). We then carried out a Tukey *post-hoc* test to test for homogeneity across

groups on the best-fit model with the *multcomp* v. 1.4-8 package (Hothorn et al., 2008). Since not all snakes had temperature-sensitive transmitters, we could only estimate body temperature for a subset of the observations ($N = 138$). Thus, we performed a separate analysis to test whether body temperature predicted escape response using a GLMM with individual ID and sampling day as random factors using a binomial logit link function. We compared this model's fit to a null model, which only included the random factors, by examining the ΔAICc values. To test for predictors of FID, we used the reduced dataset, which included the body temperature of the snakes and carried out a GLMM analysis with FID as the dependent variable using a gamma log link function in *lme4*. We fit a model with sex, behaviour, microhabitat, snake's visibility, distance to cover, and body temperature as fixed factors and individual ID and sampling day as random factors. We did not include ambient temperature and relative humidity as fixed factors because they were significantly correlated to body temperature. We then fit multiple GLMMs by stepwise backward elimination of variables and compared these models by evaluating the ΔAICc values. We followed this with a Tukey *post-hoc* test. Following Burnham & Anderson (2002), we considered ΔAICc values of 2-10 as moderate support and ΔAICc above 10 as strong support against a model. AICc values and Akaike weights were calculated using the package *qpcR* v. 1.4-1 (Spiess, 2018).

Results

Escape response

The GLMM on Russell's vipers' escape response indicated that the snake's behaviour best explained the probability of the snake moving away when approached. This model had moderate to strong support compared to all the other models (GLMM with binomial logit link function: ΔAICc > 2) (supplementary table S2). We found that basking snakes had a higher probability of moving away when approached than resting snakes (Tukey *post-hoc* test, Estimate $= 1.796$, $Z = 3.035$, $P = 0.01$; fig. 1) (supplementary table S3). Body temperature significantly affected the probability of moving away and this model was moderately supported against the null model (GLMM with binomial logit link function: ΔAICc $= 2.935$). The analysis indicated that the probability of moving away when approached was significantly greater in snakes with higher body temperature (GLMM with binomial logit link function: Estimate $= 0.088$, $Z = 2.163$, $P = 0.03$; fig. 2).

Flight initiation distance

GLMM indicated that the snake's visibility and the distance to nearest cover best explained FIDs in Russell's vipers, and this model was moderately supported against most other models (GLMM with gamma distribution: ΔAICc > 2) (supplementary table S2). However, this model was not supported against a model with the snake's visibility, distance to cover and sex as fixed factors (GLMM with gamma
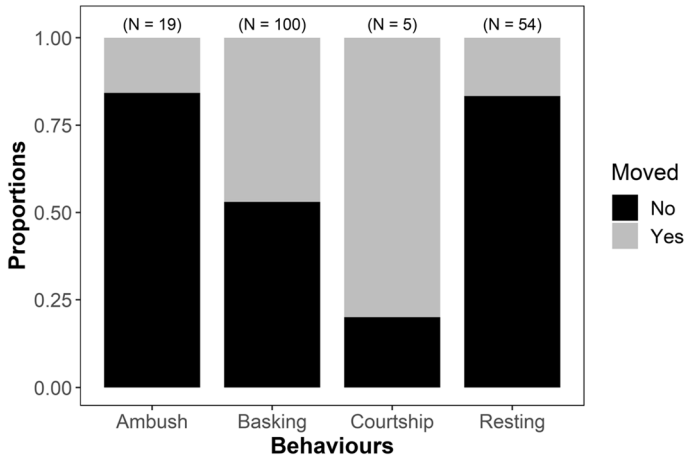
Figure 1. Comparison of the proportion of Russell's vipers (*Daboia russelii*) that moved away when approached (escape response) under different behaviours. The behaviours included snakes in ambush, basking, courtship and resting.

distribution: ΔAICc $= 1.001$). Nonetheless, sex did not have a significant effect on FID (GLMM with gamma distribution: Estimate $= 0.357$, $T = 0.891$, $P = 0.373$). FID significantly increased when the distance to the nearest cover was farther away (GLMM with gamma distribution: Estimate $= 0.170$, $Z = 2.429$, $P = 0.01$; fig. 3). The snake's visibility also significantly affected FID wherein snakes that were not visible or detectable had significantly lower FIDs compared to snakes with under half (Tukey *post-hoc* test: Estimate $= -0.6594$, $Z = -3.057$, $P = 0.018$) or more than half the body exposed (Tukey *post-hoc* test: Estimate $= -0.844$, $Z = -3.236$, $P = 0.01$; fig. 4) (supplementary table S3).
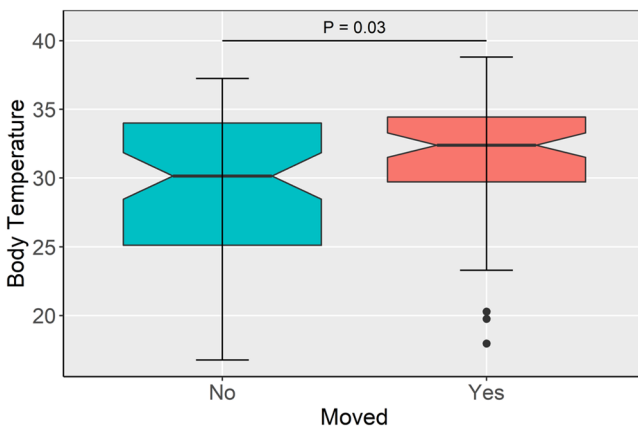

Figure 2. Box-plots showing comparison of body temperature of Russell's vipers (*Daboia russelii*) estimated from the temperature-sensitive transmitters between snakes that remained still and those that moved away when approached.
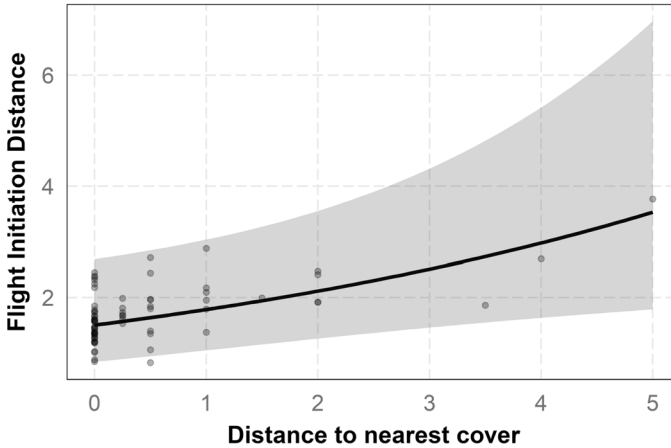
Figure 3. Partial residual plot of the flight initiation distance (FID) in Russell's vipers (*Daboia russelii*) as a function of distance to nearest cover based on the best-fit model recovered from the generalised linear mixed-effect model (GLMM) analysis. The grey areas represents the 95% confidence intervals of the fitted values. All distances are in meters.

Discussion

Our analysis on the 16 Russell's vipers indicated that the snake's behaviour is a significant predictor of escape response (i.e., whether or not the snake will flee). Basking snakes had a higher probability of moving away when approached compared to resting snakes (fig. 1). We also found that snakes that moved away had a significantly higher body temperature than snakes that stayed (fig. 2). Interestingly, all the models indicated that environmental variables such as ambient temperature
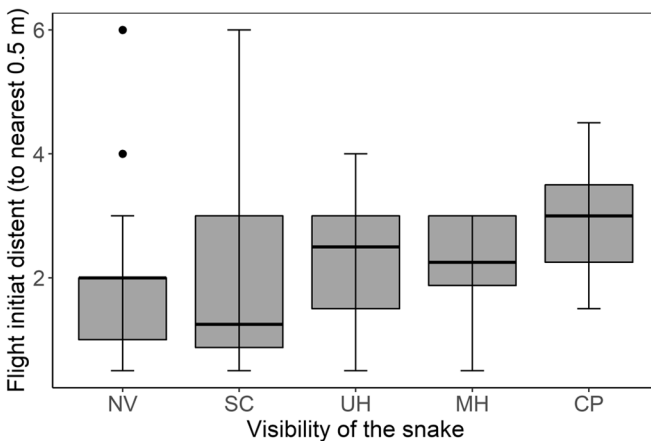
Figure 4. Box-plots showing the flight initiation distance (FIDs) of Russell's vipers (*Daboia russelii*), the distance at which the snake flees, with respect to the visibility of the snake. NV: not visible/detectable, SC: small coils visible, UH: under half of the snake's body visible, MH: more than half of the snake's body visible, CP: completely visible.

and relative humidity did not have any significant effect on the escape response. Our results also find that while body temperature significantly affected a snake's decision to move when approached, it did not have a significant impact on the flight initiation distance.

Previous studies on the effect of body and air temperature on the escape behaviour of snakes have shown no consistent patterns. Some studies show that escape response and FID are positively associated with body or environmental temperature (Shine et al., 2000; Burger, 2001; Maritz, 2012), while others indicate no effect (Weatherhead & Robertson, 1992; Burger, 2001; Brown & Shine, 2004; Cooper Jr et al., 2008) or a negative correlation (Layne & Ford, 1984). To complicate matters further, studies on the same snake species have also shown contrasting results. For example, some studies have found that the response time to approaching humans in the common water snake (*Nerodia sipedon*) increased significantly with air temperature (Burger, 2001), while others have found no effect of air or water temperature on FID (Weatherhead & Robertson, 1992; Cooper Jr et al., 2008). However, most studies on terrestrial elapid and viperid snakes have found that warmer snakes have a higher tendency to flee from approaching humans (Prior & Weatherhead, 1994; Whitaker & Shine, 1999; Gibbons & Dorcas, 2002; Shine et al., 2002; Glaudas et al., 2005). Interestingly, our results show that body temperature predicted escape response but not FIDs, suggesting that different factors could influence the decision to move away and when to move away.

Habitat selection is known to have a considerable effect on FIDs. Our analyses indicated that habitat selection by Russell's vipers significantly explained differences in FIDs. Several studies have found that FID is significantly associated with habitat features such as distance to the cover or refuge, perch height, the openness of the habitat, etc. (Stankowich & Blumstein, 2005; Domínguez-López et al., 2016). Samia et al. (2016) analysed data from 28 species of lizards and found that distance to cover had an overall large effect on FIDs. Like many of these studies, we found that FID increased when the nearest cover was further away. We also found that the snake's visibility predicted FIDs (fig. 4), with less exposed snakes having lower FID. Cryptically coloured species are hypothesised to have shorter FIDs as crypsis is usually not effective when the animal is in motion, and fleeing away can alert predators of the prey's presence (Broom & Ruxton, 2005). Several studies have shown that cryptically coloured species have lower FIDs. For instance, Møller et al. (2019) showed that birds with cryptically coloured plumages had lower FIDs. Studies on lizards have also indicated that cryptically coloured or partially concealed individuals permit closer approach than conspicuous or exposed lizards (Cooper Jr, 1998, 2006; Martín & López, 1999; Plasman et al., 2007; Cooper Jr & Sherbrooke, 2010).

Russell's vipers have a distinct colour pattern with three longitudinal series of regularly arranged '8'-shaped blotches all along the body. Such contrasting

blotched patterns in snakes are generally considered to function as disruptive marking (Jackson et al., 1976; Pough, 1976; Allen et al., 2013), which help in breaking the background of the snake and reduce predator detection (Schaefer & Stobbe, 2006; Stevens et al., 2006; Stevens & Merilaita, 2009b). However, disruptive colourations fail to provide protection when the animal is in motion (Stevens et al., 2011). Thus, animals with such colour patterns would be expected to rely more on concealment than fleeing to avoid predation. It has been shown that, in a polymorphic snake species, individuals with blotched or spotted patterns rather than snakes with striped patterns exhibit antipredatory behaviours associated with crypsis (Brodie III, 1989, 1992). Further, in snakes that show ontogenetic colour shifts, juveniles with blotched patterns are more likely to show defensive behaviours, while adults with uniform patterns are more likely to flee from predators (Creer, 2005). Given that the effectiveness of disruptive colourations also depends on the background (Stevens & Merilaita, 2009b), prey may perceive the risk of predation depending on their concealment in different microhabitats. Although we do not specifically test how crypsis affects escape behaviours in Russell's vipers, our results indicate that snakes that were not detectable (likely due to their camouflage) had lower FID compared to snakes that were more exposed and visible.

Overall, we find that intrinsic factors such as body temperature influence Russell's vipers' decision to stay or flee when approached by humans. On the other hand, when they flee is determined mostly by habitat features such as the distance to the nearest cover and the snake's visibility. However, we acknowledge that although we provide insights into the factors affecting FIDs in Russell's vipers, the resolution and error of our FID data (estimated to the nearest 0.5 m) may not be robust enough to detect finer patterns in flight responses. Studies have shown that FID in animals is associated with the predator's starting distance (Cooper Jr, 2005; but see Dumont et al., 2012). However, unlike many other studies on escape behaviour, we could not have a fixed starting distance from where the observer moves towards the animal. Russell's vipers are highly cryptic and usually concealed under thick vegetation; thus, spotting these snakes from a fixed starting point was impossible. Approach speed and directness of the approach can also affect escape behaviours (Burger & Gochfeld, 1981; Cooper Jr, 1997a; Kramer & Bonenfant, 1997; Cooper Jr et al., 2007, 2009). Although we approached the snakes at a very slow pace, we were unable to predict the directness of the approach since we used radio telemetry to track these snakes. Moreover, Russell's vipers are highly venomous, and hence, approaching these snakes had to be done with extreme caution.

Our study shows that radio telemetry can not only provide valuable information about movement patterns but can also be used to study other aspects of animal behaviour, especially in cryptic and secretive animals. Here, we show that the decision to move or stay in Russell's vipers when approached by humans is determined by body temperature. However, the distance at which they move away from approaching humans is mostly determined by habitat selection. Russell's vipers are responsible for the highest number of snakebite-related deaths in India (Suraweera

et al., 2020). However, most studies on snakebite mitigation and management have been focused on the clinical aspects of snakebite with minimal emphasis on understanding snake ecology and devising strategies that can reduce human-snake interactions (Murray et al., 2020; Glaudas, 2021). Our study highlights the importance of habitat features such as refuges that reduce visibility in determining escape behaviours in Russell's vipers. Since most snakebites occur in agricultural landscapes, keeping walking paths and agricultural fields clean can enhance visibility, thus increasing the chances of snakes moving away when approached. Keeping potential refuge sites away from working areas in the field could help reduce human-snake encounters and, in turn, minimise snakebite rates. Although our study provides some preliminary insights into Russell's vipers' escape behaviour, further controlled experiments will be necessary to explore how other factors such as approach speed and direction can influence these snakes' escape responses.

Acknowledgements

Author contributions

VPC conceived the study, collected the data, analysed the data, prepared figures and drafted the manuscript; KB and LK assisted in data collection; GM provided inputs on the study, acquired funding, provided material and resources to the study and managed the project; VPC and GM critically revised the manuscript. All authors gave final approval.

Supplementary material

Supplementary material is available online at:
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