Influence of Intrinsic and Extrinsic Factors on Anti-predatory Behaviour of Penisular Rock Agama *Psammophilus dorsalis*

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By

DEEPAK CHAVAN

Enrolment No. 003053181

Supervisor

Dr. S. Babu

Co-supervisor

Dr. Kavita Isvaran

Saurashtra University

Rajkot

Sálim Ali Centre for Ornithology and Natural History

(A Centre of Excellence under the Ministry of Environment, Forest and Climate Change, Govt. of India)

Anaikatty Post, Coimbatore – 641 108, Tamil Nadu

सालिम अली पक्षिविज्ञान एवं प्रकृति विज्ञान केन्द्र
SÁLIM ALI CENTRE FOR ORNITHOLOGY AND NATURAL HISTORY
पर्यावरण, वन एवं जलवायु परिवर्तन मत्रालय के अधीन उत्कृ ष्टता का एक केंदर, भारत सरकार
(A Centre of Excellence under the Ministry of Environment, Forests & Climate Change, Government of India)

CERTIFICATE

This is to certify that **Mr. DEEPAK CHAVAN** of Sálim Ali Centre for Ornithology and Natural History (SACON) has carried out an original research work titled, '***Influence of Intrinsic and Extrinsic Factors on Anti-predatory Behaviour of Penisular Rock Agama Psammophilus dorsalis***' in partial fulfilment of the M.Sc. (Ornithology & Conservation Biology) degree of Saurashtra University, Rajkot. This investigation was carried out under my supervision from December 2019 to August 2020. I also certify that this research work has not been submitted for any other degree to any university.

Date: 21 August, 2020
Place: Coimbatore

(Dr. S. Babu)
Senior Scientist

डॉ. एस. वावु / Dr. S Babu
वरिष्ठ वैज्ञानिक & सहायक पाठ्यक्रम निदेशक (पीजी)
Senior Scientist & Asst. Course Director (PG)
सालिम अली पक्षिविज्ञान एवं प्रकृति विज्ञान केन्द्र
Sálim Ali Centre for Ornithology and Natural History
आनैकट्टी, कोयम्बटूर – 641 108
Anaikatty (Post), Coimbatore – 641 108

आनैकट्टी, कोयम्बत्तूर – 641 108 (इंडिया)
Anaikatty (Post), Coimbatore – 641 108 (INDIA)
Tele : **+91-422-2203100, 2203103, 2203109** Telefax : **+91-422-2657088**
E-mail : **salimali@sacon.in, salimalicentre@gmail.com** Website : **www.sacon.in**

Centre for Ecological Sciences
Indian Institute of Science
Bangalore - 560 012, India

Dr. KAVITA ISVARAN
Associate Professor

Tel: 080-23600985 (Office)
Fax: 080-23601428 (Office)
kavita@iisc.ac.in

22 August 2020

CERTIFICATE

This is to certify that **Mr. Deepak Chavan** of Sálim Ali Centre for Ornithology and Natural History (SACON) has carried out an original research work titled, '***Influence of Intrinsic and Extrinsic Factors on Anti-predatory Behaviour of Juvenile Rock Agamas (Gray, 1831)***' in partial fulfilment of the M.Sc. (Ornithology & Conservation Biology) degree of Saurashtra University, Rajkot. This investigation was carried out under my co-supervision from December 2019 to August 2020. I also certify that this research work has not been submitted for any other degree to any university.

Kavita Isvaran
Place: Bangalore

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SUMMARY

In response to human disturbance in the form of habitat alteration, lizards inhabiting distinct habitats should modify their anti-predatory behaviour to match the level of risk imposed by the habitat parameters. Apart from habitat, escape decisions are expected to be influenced by multiple factors, however, most studies examine one or a few factors acting individually which hinders our understanding of their relative importance. In this study, I looked at the influence of habitat alteration on escape decisions of juvenile Peninsular Rock agama *Psammophilus dorsalis* by comparing two populations, one inhabiting a restored scrub and thorny habitat, which is naturally found and the other inhabiting an open habitat degraded because of heavy grazing. The study was conducted in thorny scrub forests around Rishy Valley School, Andhra Pradesh during January to August 2020.

I found that Escape distance (ED) but not Flight Initiation Distance (FID) was statistically different between the two populations of lizards. Lizards from the restored habitat escaped longer distances as compared to lizards from the degraded habitat probably because lizards from the degraded habitat are able to monitor an approaching predator better because of increased vigilance due to habitat openness and thus perceive lesser risk and therefore escape shorter distances. To understand the relative importance of multiple factors, I examined the effect of both, intrinsic and extrinsic factors, on escape behaviour of juvenile *Psammophilus dorsalis.* I found that escape behaviour (FID and ED) is influenced by a combination of both intrinsic and extrinsic factors. Among all the factors, both FID and ED were positively influenced by body size and Spotting Distance. Body size was a major factor influencing FID.

Predator's behaviour such as the direction of approach, gaze and persistence in approach can also influence escape decisions. Persistence in approach by a predator to capture a prey may indicate an increase in the risk of predation and therefore when experiencing persistent predatory attacks, lizards should progressively increase the magnitude of their escape responses. Contrary to this expectation, I found that the FID and ED were longer in the first approach as compared to the second approach. This could be because lizards from open habitats rely more on sprint speed, hence in response to an approaching predator, it is a safer option to flee at a longer distance in the first approach itself and remain vigilant to monitor the approaching predator followed by shorter bursts of locomotion.

This study helps in reclaiming the dynamic nature of anti-predatory behaviour of juvenile Rock agama and shows how escape behaviour is influenced by a combination of different factors.

1. INTRODUCTION

1.1. BACKGROUND

Predation is a major selection pressure for many species (Lind & Cresswell 2005). It is speculated that natural selection acts more strongly on anti-predatory behaviour than on any other behavioural trait in an organism's repertoire (Nonacs & Blumstein 2010). Anti-predatory behaviour plays an important role in influencing the population dynamics of prey-predator interactions (Ives & Dobson 1987), making it an important domain of study. Traits which favour survival are more strongly selected earlier in life than later in life (Lind & Cresswell 2005; Nonacs & Blumstein 2010). Hence, studies which examine early life stages of organisms, such as juveniles, where survival benefits through anti-predatory traits helps in attaining fitness benefits at the adult stage through reproduction are important (Cooper & Frederick 2007). Therefore, studying the anti-predatory behaviours of juveniles is crucial.

Fleeing from a predator is crucial for survival but is extremely costly because it negatively affects fitness-enhancing activities such as social interactions, mating and foraging for food (Ydenberg & Dill 1986; Samia *et al.* 2016). Therefore, the costs and benefits of fleeing or staying are the decisive factors determining the nature of anti-predatory responses shown by prey (Savvides *et al.* 2018). Escape is among one of the strategies used by prey in response to its predator. Escape behaviour can be quantified by measuring Flight Initiation Distance (FID) and Escape Distance (ED) (Blumstein 2003). FID is a potential indicator of perceived predation risk by an animal (Gotanda *et al.* 2009). It measures the distance at which the prey decides to flee from an approaching predator (Ydenberg & Dill 1986). ED is another potential indicator of perceived predation risk which measures the distance fled by a prey in response to an approaching predator (Ydenberg & Dill 1986).

Habitat has an important role in determining escape behaviour (Salas 2016) and escape behaviour is expected to vary with the type of habitat (Cooper & Whiting 2007). Human disturbance in the form of habitat alteration can induce a shift in escape behaviour (Lacy & Emília 2003), affecting prey-predator interactions and ultimately having an effect on the long-term persistence of populations (Hecnar & M'Closkey 1998; Lacy & Emília 2003; French *et al.* 2010; Marnocha *et al.* 2011). Lizards being particularly sensitive to habitat modification (Pianka 1989; D'Cruze & Kumar 2011), provide an opportunity to document the influence of habitat alteration on organisms (Zeng *et al.* 2014; Beauchamp *et al.* 1998). Vegetation structure is a definitive feature of lizard habitat preference (Singh *et al.* 2002) and is known to affect how they avoid predators (Martín & López 1998). Therefore, populations inhabiting habitat with distinct vegetation structure should modify their behavioural responses to predation with respect to the level of risk imposed by the habitat parameters (Pellitteri-Rosa *et al.* 2017). Populations of lizards from sparsely vegetated areas are reported to show longer approach and flight distance, indicating higher perceived risk as compared to heavily vegetated areas, owing to the differences in the availability of hiding sites (Snell *et al.* 1988; Bulova 1994; Martín & López 1995). In another study, lizards modified their escape behaviour in response to seasonal changes in vegetation structure by increasing their approach and flight distance in early spring than in summer, independent of environmental temperatures (Martín & López 1998).

Along with habitat, escape behaviour is also influenced by many other factors. To capture this dynamic nature of escape decisions, considering multiple factors, both intrinsic and extrinsic, is important but most studies investigate a set of few factors acting individually (Bhave *et al.* 2017). Therefore, considering multiple factors provides an insight into the relative importance of factors, which can considerably differ from theoretical predictions. Intrinsic factors such as body size and body weight are known to influence escape behaviour. The conspicuousness of a prey towards its predator is partly determined by the body size of the prey, hence it determines the amount of risk perceived by the prey and thereby influences its anti-predatory behaviour (Qi *et al.* 2014). Lizards being ectotherms, temperature plays a major role in determining their mobility and thus influencing their escape ability (Cooper 2011b). Body mass influences rates of heating and cooling in lizards and therefore affects their thermoregulation (Martín & López 2003b), thus influence their escape behaviour.

Extrinsic factors such as parasite load can have a detrimental effect on the health of individuals and therefore affect the locomotor capabilities of lizards, ultimately influencing their anti-predatory behaviours. Characteristics of predator's approach can also influence anti-predatory behaviour of lizards. Predators having a direct approach and gaze, and approaching with a faster speed are perceived as higher risk by lizards and therefore affects how they escape (Cooper & Whiting 2007; Cooper *et al.* 2009; Sreekar & Quader 2013). If a predator shows persistence in approaching a prey after its initial escape, it may indicate an increase in the risk of predation (Cooper 1997b; Martín & López 2003a & 2001). Therefore, through persistent predatory attacks, lizards should progressively increase the magnitude of their escape responses (Cooper 1997b; Martin & Lopez 2003a). Lizards responded to persistent predatory attacks by increasing the distance fled (Martin & Lopez 2003a), fleeing to secure (Cooper 1997b) and structurally complex (Martin & Lopez 2003a) refuges. This confirms that lizards interpret persistent predatory attacks as an increase in the risk of predation and modify the magnitude of their escape responses accordingly (Martin & Lopez 2003a).

In this study, I tried to understand the effect of habitat alteration due to heavy grazing on anti-predatory behaviour of juvenile Rock agama *Psammophilus dorsalis* by comparing between two populations, one inhabiting its natural restored habitat, which is comprised of scrub and thorny vegetation and the other inhabiting an open habitat which is degraded due to heavy grazing. I predicted that lizards from the degraded habitat with lesser vegetation cover should have longer FID and should show longer ED as compared to lizards from restored habitat. Along with habitat, to understand the relative importance of multiple factors, I investigated intrinsic factors such as morphometrics and weight; and extrinsic factors such as ectoparasite load and persistent approach. To test the effect of persistent approach, lizards were approached for the second time after its initial escape, and escape responses between the first and second predatory attacks were compared. I predicted that in response to persistent approach, lizards should increase the magnitude of their escape responses by increasing FID and ED. A previous study on *Psammophilus dorsalis* adults found that intrinsic factors such as sex and body size influenced escape responses more than extrinsic factors such as distance to the refuge and perch height (Bhave *et al.* 2017). Another study on juveniles of *Psammophilus dorsalis* found that parasite load was correlated with personality type in individuals while perch height and territory size did not show any significant relation with personalities (Kannan 2018). Therefore, I predicted that some intrinsic factors such as body size and some extrinsic factors such as ectoparasite load should influence the escape behaviour of juvenile lizards more than other factors.

1.2. OBJECTIVES

The objective of this study is to understand the influence of human disturbance in the form of habitat alteration on anti-predatory behaviour of Rock Agama *Psammophilus dorsalis*. It also tries to understand the relative importance of multiple factors by examining both, intrinsic (body size and body weight) and extrinsic factors (ectoparasite load, persistent approach).

1.3. LITERATURE REVIEW

The first graphical model to illustrate the distance at which a prey decides to flee from an approaching predator was presented by Ydenberg and Dill, in which the costs and benefits of fleeing from a predator were presented in an economic fashion (Ydenberg & Dill 1986). In this model, the prey decides to flee from an approaching predator, when the cost of remaining and the cost of fleeing are equal. Later, an optimality model was presented by Broom and Buxton to present the optimal strategies of a cryptic prey to flee or remain motionless by maintaining crypsis from an approaching predator (Broom & Ruxton 2005). In 2007, Cooper and Frederick presented another optimality model in which they modelled the optimal escape distance of prey with respect to initial expected fitness, benefits gained during encounters, cost of escaping and the probability of being killed (Cooper & Frederick 2007).

The cost and benefit of fleeing or staying from an approaching predator is determined by multiple factors (Bhave *et al.* 2017). Therefore, to capture this dynamic nature of escape decisions, I studied multiple factors, both intrinsic and extrinsic and tried to understand their relative importance (Bhave *et al.* 2017). Among intrinsic factors, I investigated morphometrics and body weight, which have a strong influence on the anti-predatory behaviour of lizards. Previous work has shown that flight initiation distance was positively correlated with body size, with larger individuals fleeing earlier than smaller individuals probably because larger individuals are more conspicuous to the predators than smaller individuals (Gotanda *et al.* 2009; Qi *et al.* 2014). Similarly, a study which examined 66 species of lizards, found that FID increased with Snout to Vent Length (SVL) (Cooper *et al.* 2014). Escape distance was inversely related to body size in sand diving lizards (Evans *et al.* 2017).

In ectotherms, temperature influences anti-predatory behaviour by influencing escape ability (Cooper 2011b). Lizard being ectotherms, the temperature can strongly influence the associated costs and benefits of fleeing from an approaching predator (Lattanzio 2014). In *Tropidurus oreadicus* (Rocha & Bergallo 1990), *Scincella lateralis* (Smith 1997), *Sceloporus virgatus* (Cooper 2011a) and *Tropidurus hispidus* (Maia-Carneiro & Rocha 2015), lizards with low body temperature exhibited longer FID than lizards with high body temperature, probably because running speed decreases at a lower temperature (Cooper 2011a) and lizards perceive higher risk because of impaired escape ability (Cooper 2011b). Rand suggested that lizards are more susceptible to predation at lower temperatures because of depressed metabolism and escape potential (Rand 1964).

On the contrary, two species of Agamas (*A. savigyni* and *A. pallida*) flee rapidly from predators at high body temperatures and at low body temperatures, which reduces sprint speed, the lizards rarely ran but instead hold their ground and attack aggressively (Hertz *et al.* 1982). This temperature-dependent switch in their defensive behaviour is probably because cold lizards that live in open habitats would have little chance of outrunning predators, which points out the inverse relationship between the degree of aggressiveness and sprint speed (Hertz *et al.* 1982). Although body temperature is an important parameter, it is difficult to measure in the field conditions. Therefore, substrate temperature which is highly correlated with body temperatures in the field was used as a proxy for body temperature (Smith 1997). Body mass also influences thermoregulation of lizards by influencing rates of heating and cooling, ultimately affecting their anti-predatory behaviour (Martín & López 2003b). Juveniles (low body mass) exhibited a shorter time of emergence from refuges because the cost of hiding for juveniles is higher as they cool faster than adults (Martín & López 2003b).

Environmental (extrinsic) factors can influence prey-predator interactions (Diego-Rasilla 2003) and thereby influence the anti-predatory behaviour of prey species (Evans *et al.* 2017). A meta-analysis compiling fifty years of work done on anti-predatory behaviour of lizards found that habitat has moderate to large effect sizes on FID (Samia *et al.* 2016), and therefore, is an important component of a lizard's anti-predatory behaviour. Human disturbance to critical habitat components can result in loss of microhabitats needed for predator avoidance (Hecnar & M'Closkey 1998). This can have long term effects on persistence of natural populations (French *et al.* 2010; Marnocha *et al.* 2011) by influencing prey-predator abundance and their interactions (Lacy & Emília 2003; Zeng *et al.* 2014). Documenting how organisms respond to habitat alteration can provide insight into the effect of anthropogenic disturbances on species (Beauchamp *et al.* 1998; Zeng et al 2014).

Lizards are particularly sensitive to habitat alteration (D'Cruze & Kumar 2011), and are therefore excellent models to study the effect of anthropogenic disturbances (Valentine

2007). Habitat alteration can have a strong negative influence on lizard communities (D'Cruze & Kumar 2011) because they are strongly dependent on habitat structure for their survival (Valentine 2007). Vegetation structure is a definitive feature of lizard habitat preference (Singh *et al.* 2002); it affects their ability to avoid predators (Martín & López 1998). Therefore, populations inhabiting different habitats with distinct vegetation structures should modify their behavioural responses with respect to the risk imposed by habitat characteristics, which is critical for their survival (Lacy & Emília 2003; Pellitteri-Rosa *et al.* 2017).

Tropidurus albemarlensis showed significant variation in wariness with respect to vegetation cover; both male and female from sparsely vegetated areas exhibited longer FID and escape distance than those from heavily vegetated areas (Snell *et al.* 1988). Similarly, the population of *Callisaurus draconoides* showed longer FID and escape distance from the site with the least plant cover (Bulova 1994). This variation in wariness with respect to the amount of vegetation cover could be a result of noticeable differences in availability of hiding sites (Snell *et al.* 1988) and presence of nearby cover (Bulova 1994). Vegetation structure is subject to seasonal changes; therefore, lizards should modify their escape behaviour accordingly. Independent of environmental temperatures, FID and escape distance of *Psammodromus algirus* was greater in early spring than in summer and are greater in microhabitats with less vegetation cover (Martín & López 1998). In the sandhills of Nebraska, two wide-ranging lizard species (*Sceloporus undulatus* and *Holbrookia maculata*), showed a drastic decline in their population with respect to increase in vegetation cover (Ballinger & Watts 1995), which demonstrates the effect of habitat alteration on the long-term persistence of lizards.

Apart from vegetation structure, other extrinsic factors such as characteristics of perch can also influence escape decisions since perch is used by lizards for various activities such as basking, foraging, and social interactions. Perch height is an important risk factor and its influence on FID varies with the type of lizard's ecomorph. In Puerto Rican anoles, FID decreased as perch height increased for four arboreal species that escape by climbing out of reach, whereas for two species of grass-bush anoles that escape by fleeing to the ground, FID increased with perch height (Cooper 2006). In arboreal lizard species that flee upwards, FID is predicted to decrease as perch height increases because lizards above some height are out of reach from terrestrial predators. This pattern was observed in two species of Jamaican anoles (Cooper 2010) and *Plestiodon laticeps* (Cooper 1997a). Perch diameter, another perch parameter can also influence the escape behaviour of lizards. In four species of anoles lizards, sprint speed declined with decreasing perch diameter and as the diameter decreased, lizards in all but one species shifted to alternative escape strategy (Losos & Irschick 1996).

Parasitism, an another extrinsic factor can have multiple effects on the anti-predatory behaviour of lizards (Cooper & Frederick 2010). Ectoparasites can alter the health of individuals, thereby influencing their escape abilities. In Balearic lizards, individuals with higher parasite loads had longer FID and escaped shorter distances (Garrido 2014). In response to an approaching predator, animals generally flee to a refuge, therefore, refuge characteristics strongly determine escape responses of lizards. Distance to a refuge can influence the amount of risk perceived by lizards because the risk is greater farther from the refuge (Cooper 2011b). A study conducted on two sympatric species of lizards differing in microhabitat use found that FID increases with the distance to the refuge (Cooper & Whiting 2007). A study on lacertid lizards found that lizards which used refuges, fled shorter distances than lizards which did not hide (Biaggini *et al.* 2010).

Characteristics of a predator's approach are also known to influence escape decisions of prey. Starting distance of a predator can influence FID of lizards. Starting distance was positively correlated with FID in lizards (Cooper 2005; Qi *et al.* 2014; Evans *et al.* 2017), probably because it accrues monitoring cost of approaching predator (Blumstein 2003). FID of lizards was longer during direct approaches with direct gaze as compared to tangential approaches with averted gaze (Sreekar & Quader 2013). Faster approach speed and more direct approach of predator was perceived as higher risk and therefore lizards responded by having a longer FID (Cooper & Whiting 2007; Cooper *et al.* 2009).

After a prey escapes from an approaching predator, the predator may search elsewhere or launch a new attack, which shows persistence in attempting to capture that particular prey, thereby indicating an increase in the risk of predation (Cooper 1997b; Martín & López 2001 and 2003). Therefore, through persistent predatory attacks, lizards should increase the magnitude of their escape responses (Cooper 1997b; Martín & López 2003a). Cooper simulated a persistent predatory attack on *Eumeces laticeps* by approaching the lizard twice and observed that upon the second approach, the lizards are more likely to flee to more secure refuges of trees than elsewhere (Cooper 1997b). Martín and López approached *Acanthodactylus erythrurus* thrice to simulate a persistent attack and found that lizards responded from first to successive predatory attacks by fleeing longer, using more structurally complex refuges and escaping into microhabitats with an increased cover (Martín & López 2003a). Lizards also changed their escape strategy from remaining vigilant after running in the first attack to hiding in the subsequent attacks (Martín & López 2003a). This suggests that lizards interpret persistent approach as an increase in the risk of predation and modify their escape responses with respect to the level of predation risk (Cooper 1997b; Martín & López 2001 and 2003a).

2. METHODS

2.1 STUDY SITE AND STUDY SPECIES

The study was conducted from December 2019 to June 2020 in the mid-elevated hills of Rishi Valley (13°32’N, 78°28’E; ca. 750 m elevation), Chittoor district, Andhra Pradesh, India. This area receives rainfall from May to November and the local temperatures are particularly high from March to May, having a stark seasonality in temperature and precipitation (Deodhar & Isvaran 2017). The hilly slopes primarily consist of thorny scrub vegetation interspersed with granite boulders and sheet rocks. I conducted behavioural sampling at four sheet rocks, namely Bodi bunda (BB), Gyada doda bunda (GDB), Tent rock (TR) and Horseshoe rock (HR). BB and GDB are present inside Rishi Valley School, where the natural habitat has been restored into thorny scrub vegetation, whereas TR and HR are present outside school which has an open degraded habitat due to heavy grazing. Inside school, sheet rocks are surrounded by dense vegetation comprising of trees, shrubs and grasses, whereas sheet rocks outside the school are surrounded by short grasses and sparsely distributed shrubs, representing an open habitat.

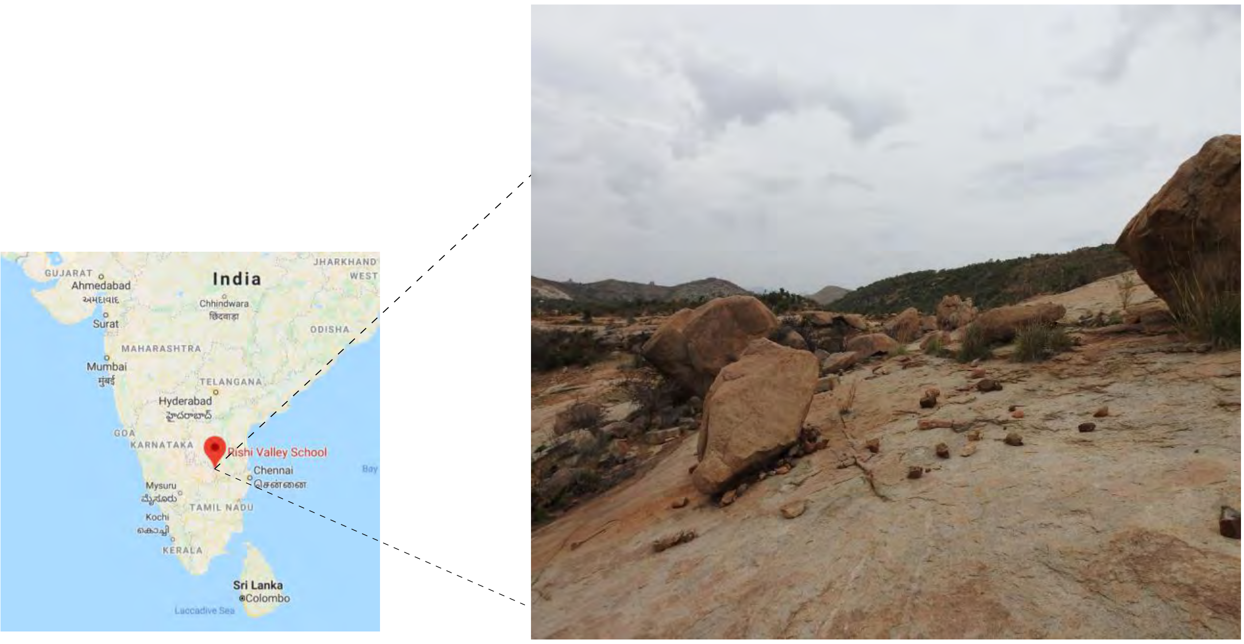

Figure 1: The study site Rishi valley, Andhra Pradesh and an image (right side) representing one of the sheath rocks.

Peninsular Rock Agama (*Psammophilus dorsalis*) predominantly occurs on these sheet rocks (Radder *et al*. 2006). *P. dorsalis* is a diurnal, rock-dwelling lizard, which has an annual life-cycle, in which most of the adults die after the breeding season (Deodhar & Isvaran 2017). It is a territorial and sexually dimorphic species, in which the males are larger than the females and display bright colouration during the breeding season, May to September (Deodhar & Isvaran 2017). This study exclusively focused on juveniles, since the study period coincides with the non-breeding season, which is when juveniles are predominantly found (Deodhar & Isvaran 2017).

Figure 2: The difference in vegetation structure between inside (left side) and outside school (right side). Inside school is densely vegetated due to restoration efforts and outside school is a degraded habitat due to heavy grazing.

Figure 3: A tagged juvenile Psammophilus dorsalis.

2.2 TAGGING INDIVIDUALS

Lizards were captured and tagged for individual identification. They were captured using a noose made of fishing line. After capturing, the lizard was placed in a cloth bag and to anaesthetize the lizard, this bag was placed in a box of crushed ice. The duration of this cold treatment depended on the size of the lizard. Tagging was done using a unique combination of colourful ceramic beads (Fisher & Muth 1989). Beads were stitched onto the base of the tail using a sterilized needle and a nylon thread. The number of beads stitched depended on the Snout-Vent Length (SVL) of the individual captured. If the SVL was lesser than 5 cm, either 1, 2 or 3 beads were used, but if the SVL was greater than 5 cm then 4 beads were used. Each lizard had a unique bead code and a unique ID which was based on the sheetrock from which it was captured. The handling time was restricted to twenty minutes, to reduce the stress caused to the lizards. After tagging, lizards were released at the exact location from which they were captured.

2.3 MORPHOMETRIC MEASUREMENTS

A dial Vernier calliper (SPI 2000) was used to measure Snout-Vent Length (SVL), inter-limb, head-height, head-width, head-length and tail-base (least count 0.1 mm). Tail length was measured using a measuring scale (least count 1 mm). To measure body weight a spring balance (PESOLA, 100g) was used (least count 0.1 g). Parasite load was measured by manually counting the number of ectoparasites from different parts of the lizard, such as the head, neck, left and right forelimb, back, belly, left and right hind limb, and tail. A total of 59 individuals were tagged during the study period and used for conducting behavioural trials.

2.4 FLIGHT INITIATION DISTANCE

Flight Initiation Distance (FID) trials were conducted in the mornings (0700 to 1200 hrs) and only tagged basking individuals were included, as vigilance levels in basking (stationary) and foraging lizards may vary (Devereux *et al.* 2006). Direct approach and gaze were used by a human simulated predator to approach the lizards (Sreekar & Quader 2013). All the lizards were approached by the same person (DC), using the same set of clothes to control for observer clothing (Putman *et al.*2017). After spotting the lizard, a photo was taken to identify the unique bead code combination using Nikon COOLPIX P900 Digital Camera (24-2000mm). Markers were used to mark different points during the approach.

The distance between the point at which the observer started walking towards the lizard and the initial position of the lizard is the starting distance (1). The distance between the observer and the lizard at which the lizard decided to flee from its initial position is Flight Initiation Distance (1). The distance ran by the lizard until it stopped, is escape distance (1). To simulate a persistent approach, the lizard was approached for the second time. The distance between the point at which the lizard stopped after escaping the first time and the observer is starting distance (2). The distance at which the lizard decided to flee the second time is Flight Initiation Distance (2) and distance ran by the lizard until it stopped is escape distance (2).

2.5 HABITAT PARAMETERS

Perch parameters such as perch height, perch temperature, top surface area and percent canopy cover were measured for the perches on which an experimental trial was conducted. Perch height is the height of perch on which the lizard was perched, whereas lizard perch height was the point on the perch where the lizard was perched from the ground. Perch temperature was measured using a Fluke 62 Max Infrared Thermometer. The top surface area of a perch was calculated by looking at the perch from a bird's point of view, and recognizing the geometric shapes of the perch and using an appropriate geometric formula to calculate the top surface area. Percent canopy cover was calculated by using a spherical crown densiometer.

Habitat parameters were measured in a circular plot of 5 m radius centred on each focal perch/point on which the lizard was perched when FID trial was conducted. This circle was divided into 4 quadrants and habitat parameters, specifically, number of boulders, the average height of boulders, % occupancy of boulders, number of vegetation patches, average the height of vegetation patches, % occupancy of vegetation patches, number of trees, the average height of trees, number of shrubs, and number of *P.dorsalis* individuals, were measured within each quadrant. For each circular plot average % occupancy of the boulder and average % occupancy of vegetation was calculated by taking an average of percent occupancy of 4 quadrants.

Boulders greater than 10 cm in height and 20 cm in width were counted, because boulders lesser than those were not seen to be used by lizards for perching (anecdotal observation). For each quadrant, percent occupancy of boulders and vegetation was calculated by ocular estimation. The average height of vegetation patches and boulders was also calculated by ocular estimation. Trees inside the circular plot with a GBH greater than 21 cm were counted as trees, otherwise included as shrubs. The average height of trees was also measured through ocular estimation. The number of conspecific individuals surrounding the focal lizard, occurring inside the circular plot were counted before conducting the behavioural trial. Distance to edge vegetation was measured using a 30 m tape. If two focal perches on which trials were conducted, were less than 1 m apart, then the habitat parameters measured for the first perch were also used for the second one.

2.6 DATA ANALYSIS

2.6.1 The relative importance of factors potentially influencing escape behaviour

All analyses were conducted in R (version 3.6.2) (R Core Team 2019). Using multiple regression, I built maximum models for FID 1 (Table 2) and ED 1 (Table 4), which included all explanatory variables based on a priori hypotheses, to assess the relative effects of these variables. Explanatory variables considered in the maximum models for FID 1 and ED 1 were

Spot Distance 1, perch temperature, average percent boulders, average percent vegetation, percent canopy cover, distance to edge vegetation, SVL, number of shrubs, average height of boulders, average height of vegetation patches, average height of trees, the total number of vegetation patches, nearby individuals, the total surface area of perch, total ectoparasites, perch height and location (categorical variable with two levels, inside (natural habitat) and outside (degraded habitat)). To control for variation in FID due to varying observer starting distances, Spot Distance 1 was included in the model as a fixed effect. FID 1, ED 1 and Spot Distance 1 were logarithmically transformed to linearize relationships.

To satisfy the model assumption of no multicollinearity among explanatory variables, an R package called 'corrplot' was used to draw a correlation matrix between explanatory variables. Highly correlated explanatory variables ($r > 0.6$) were identified and the variable which best explains the response variable was included in the maximum model and the other one was excluded. Predictor variables which were highly correlated with each other were, perch height and lizard perch height ($r_{(160)} = 0.96$, p-value < 0.001); total number of boulders and average percent of boulders ($r_{(160)} = 0.76$, p-value < 0.001); number of trees and average height of trees ($r_{(160)} = 0.78$, p-value < 0.001) and SVL and body weight ($r_{(160)} = 0.94$, p-value < 0.001). Perch height, average percent boulders, the average height of trees and SVL were retained in the analysis since they are a better representative of our hypothesis. Therefore, the dropped predictor variables could equally contribute and explain the variation in escape decisions. Other model assumptions such as normality of residuals and homoscedasticity assumptions were also met.

I used drop1 function in R which compares all possible models that can be constructed by dropping a single model term through backward deletion criteria. I used p-value, derived from F-test for dropping the non-statistically significant explanatory variables to arrive at a minimal adequate model for FID 1 and ED 1 which contained all statistically significant explanatory variables. I calculated both multiple R^2 and adjusted R^2. In order to compare the relative effects of each explanatory variable, I calculated the percentage change in multiple R^2 after adding the statistically non-significant explanatory variable, one at a time to the minimal adequate model. To understand the contribution of statistically significant explanatory variables within the minimal models, each explanatory variable was dropped one at a time from the minimal model and the percentage change in multiple R^2 was reported. For assessing the statistical significance of explanatory variables, marginal F tests were used.

2.6.2 Persistent Approach

To test whether escape response differed between the first and second approaches, FID and ED were log-transformed and a paired t-test was used to check whether FID 1 was detectably different from FID 2; and whether ED 1 was detectably different from ED2.

3. RESULTS

3.1 RELATIVE IMPORTANCE OF FACTORS POTENTIALLY INFLUENCING ESCAPE BEHAVIOUR

I tagged a total of 99 juvenile lizards and conducted 169 behavioural trials on a total of 59 juvenile *Psammophilus dorsalis* during the study period, with an average of 3 trials per individual. All the trials were conducted within a period of 15 days. The minimal adequate model for FID1 (Table 1) consisted of explanatory variables which were statistically significant in explaining variation in FID1 and statistically non-significant explanatory variables were dropped. The variables included in the minimal adequate model of FID 1 are perch temperature (mean = 32.22°C, 95% CI = 31.6 – 32.84), Spot Distance 1 (mean = 16.34m, 95% CI = 15.72 – 16.96), average percent boulders (mean = 17.66 %, 95% CI = 15.58 – 19.74), average percent vegetation (mean = 19.87%, 95% CI = 17.94 – 21.8), percentage canopy cover(mean = 7.9%, 95% CI = 4.44 – 11.36), distance to edge vegetation(mean = 5.35m, 95% CI = 4.79 – 5.91) and SVL (mean = 5.79cm, 95% CI = 5.61 – 5.97). This model accounted for 23.61% (multiple $R^2 = 0.236$, adjusted $R^2 = 0.201$) of variation in FID 1 (F-value = 6.8, df = 154, p-value <0.001). Among all the explanatory variables, SVL (F-value = 18.884; p value <0.001) explained most of the variation in FID 1 (Table 2). Within this minimal adequate model, FID 1 was positively influenced with perch temperature, Spot Distance [log], average percent boulders and SVL (Figure 4), whereas FID 1 was negatively influenced with average percent vegetation, % canopy cover and distance to edge vegetation (Table 1).

Table 1: Parameter estimates and uncertainty measures of minimal adequate model with In[Flight Initiation Distance 1] as a response variable and the different intrinsic and extrinsic variables as predictors in a linear regression model.

	Flight Initiation Distance 1 [log]	
Variables	*Beta Coefficient Estimates*	*CI (95%)*
Intercept	-1.89	-3.29 – -0.49
Perch Temperature	0.03	0.01 – 0.06
Spot Distance 1 [log]	0.47	0.11 – 0.83
Average Percent Boulders	0.01	0.00 – 0.01
Average Percent of Vegetation	-0.01	-0.02 – -0.00

Percent Canopy Cover	-0.01	-0.01 – -0.00
Distance to Edge Vegetation	-0.03	-0.06 – -0.00
Snout to Vent Length	0.18	0.10 – 0.26
Observations	162	
R^2 / R^2 adjusted	0.236 / 0.201	

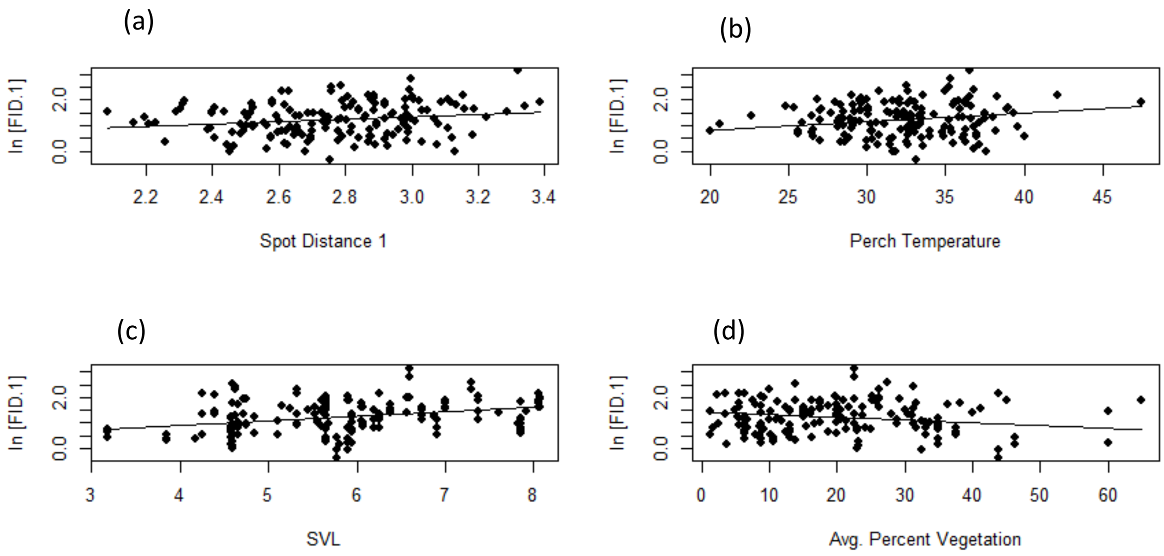

Figure 4: Scatter plots displaying the relationship between Flight Initiation Distance FID1 [log] and (a) Spot Distance 1 [log], (b) Perch temperature, (c) SVL, and (d) Average percent Vegetation. Solid lines are model predictions drawn using coefficients from the minimal adequate model. Flight Initiation Distance FID1[log] is positively influenced by Perch temperature, Spot Distance 1 [log] and SVL; whereas negatively influenced by average percent vegetation.

Table 2: Statistical hypothesis tests of different intrinsic and extrinsic predictors evaluated through marginal F tests. Each predictor variable was added one at a time to the minimal adequate model and the change in F-value, p-value and the percentage change in multiple R^2 was calculated. Within the minimal model, each predictor variable was dropped one at a time and the percentage change in multiple R^2 was reported. In[Flight Initiation Distance] is the response variable.

Flight Initiation Distance 1 [log]				
Predictors	**df**	**F-value**	**p-value**	**R^2**
Perch Temperature	1	7.816	**0.006**	**3.88 %**
Spot Distance 1 [log]	1	6.619	**0.011**	**3.28 %**

Average Percent Boulders	1	4.392	**0.038**	**2.18 %**
Average Percent of Vegetation	1	6.776	**0.010**	**3.36 %**
Percent Canopy Cover	1	7.261	**0.008**	**3.6 %**
Distance to Edge Vegetation	1	4.598	**0.034**	**2.28 %**
Snout to Vent Length	1	18.884	**<0.001**	**9.37 %**
w/ Total Number of Shrubs	1	2.141	0.145	1.05 %
w/ Average height of boulders	1	1.473	0.227	0.73 %
w/ Location	1	0.172	0.679	0.1 %
w/ Average height of trees	1	0.938	0.334	0.47 %
w/ Total number of Vegetation Patches	1	1.984	0.161	0. 98 %
w/ Nearby Individuals	1	0.525	0.470	0. 26 %
w/ Total Surface Area	1	0.065	0.799	0.03 %
w/ Total Ectoparasites	1	0.090	0.764	0.05 %
w/ Perch Height	1	0.177	0. 675	0.1 %
w/ Average Height of Vegetation Patches	1	0.373	0.542	0.19 %

The minimal adequate model for ED 1 (Table 3) consisted of explanatory variables which were statistically significant in explaining variation in ED1 and statistically non-significant explanatory variables were dropped. This model explained a variation of 10.38% (R^2 = 0.104, R^2 adjusted = 0.075) in ED1 (F-value = 3.612, df = 156, p-value = 0.004). This model consisted of the following explanatory variables: location (restored and degraded habitat) (Figure 6), Spot Distance 1 (mean = 16.34m, 95% CI = 15.72 – 16.96), average height of boulders (mean = 3.56m, 95% CI = 3.55 – 3.57), percent canopy cover (mean = 7.9%, 95% CI = 4.44 – 11.36) and SVL (mean = 5.79cm, 95% CI = 5.61 – 5.97). All the explanatory variables in the minimal model explained variation in ED1 more or less equally. Among explanatory variables, ED 1 was positively influenced with Spot Distance 1 [log] and SVL (Figure 5), whereas ED 1 was negatively influenced with average height of boulders and percent canopy cover (Table 4).

Table 3: Parameter estimates and uncertainty measures of minimal adequate model with ln [Escape Distance 1] as a response variable and the different intrinsic and extrinsic variables as predictors in a linear regression model.

	Escape Distance 1 [log]	
Variables	*Beta Coefficient Estimates*	*CI (95%)*
Intercept	-1.48	-2.88 – -0.09
Location	-0.31	-0.56 – -0.06
Spot Distance 1 [log]	0.47	0.02 – 0.92
Average height of Boulders	-1.31	-2.35 – -0.26
Percent Canopy Cover	-0.00	-0.01 – 0.00
Snout to Vent Length	0.13	0.03 – 0.23
Observations	162	
R^2 / R^2 adjusted	0.104 / 0.075	

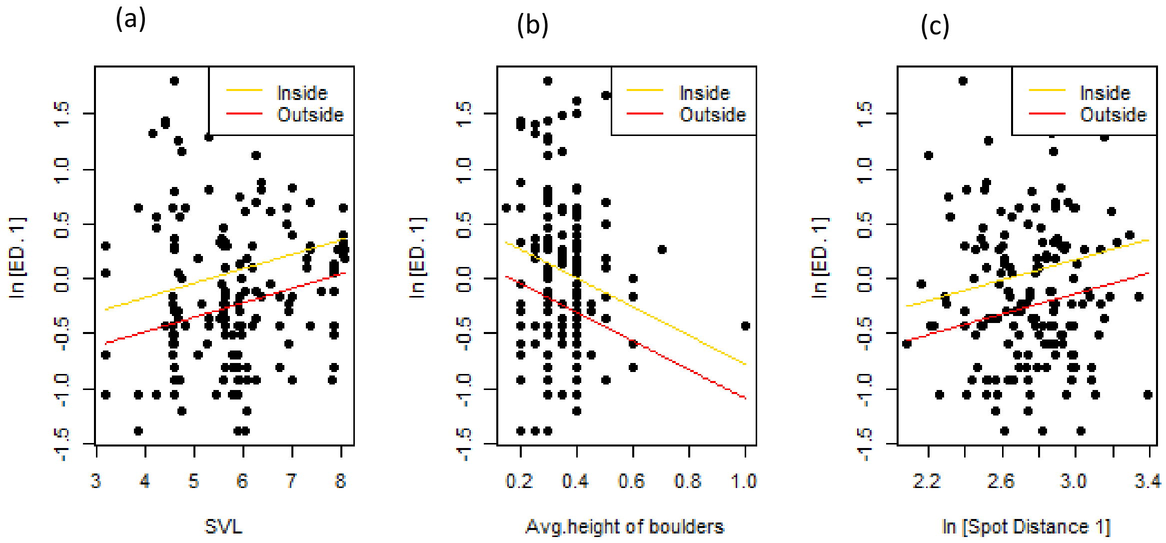

Figure 5: The relationship between Escape Distance ED1 [log] and (a) SVL, (b) Avg. height of boulders, (c) Spot Distance 1 [log]. Solid lines are model predictions drawn using coefficients from the minimal adequate model with respect to location (inside = yellow; outside = red). Escape Distance 1 (ED1) [log] is positively influenced by SVL and ln[Spot Distance 1], whereas negatively influenced by Average height of boulders.

Table 4: Statistical hypothesis tests of different intrinsic and extrinsic predictors evaluated through marginal F tests. Each predictor variable was added one at a time to the minimal adequate model and the change in F-value, p-value and the percentage change in multiple R^2 was calculated. Within the minimal model, each predictor variable was dropped one at a time and the percentage change in multiple R^2 was reported. In[Escape Distance] is the response variable.

Escape Distance 1 [log]				
Predictors	**df**	**F-value**	**p-value**	**R^2**
Location	1	5.918	**0.016**	**3.40 %**
Spot Distance 1 [log]	1	4.217	**0.042**	**2.43 %**
Average height of boulders	1	6.117	**0.014**	**3.52 %**
Percent Canopy Cover	1	3.860	**0.051**	**2.22 %**
Snout to Vent Length	1	6.833	**0.010**	**3.93 %**
w/ Average Percent Vegetation	1	2.264	0.134	1.29 %
w/ Total Number of Shrubs	1	1.670	0.198	0.95 %
w/ Perch Height	1	0.922	0.338	0.53 %
w/ Average Percent Boulders	1	0.609	0.436	0.35 %
w/ Perch Temperature	1	0.737	0.392	0.42 %
w/ Average Height of Vegetation Patches	1	1.566	0.213	0.89 %
w/ Total number of Vegetation Patches	1	0.050	0.823	0.03 %
w/ Nearby Individuals	1	0.316	0.575	0.18 %
w/ Distance to Edge Vegetation	1	0.124	0.726	0.7 %
w/ Average height of trees	1	0.278	0.599	0.16 %
w/ Total Ectoparasites	1	0.205	0.651	0.12 %
w/ Total Surface Area	1	1.000	0.319	0.57 %

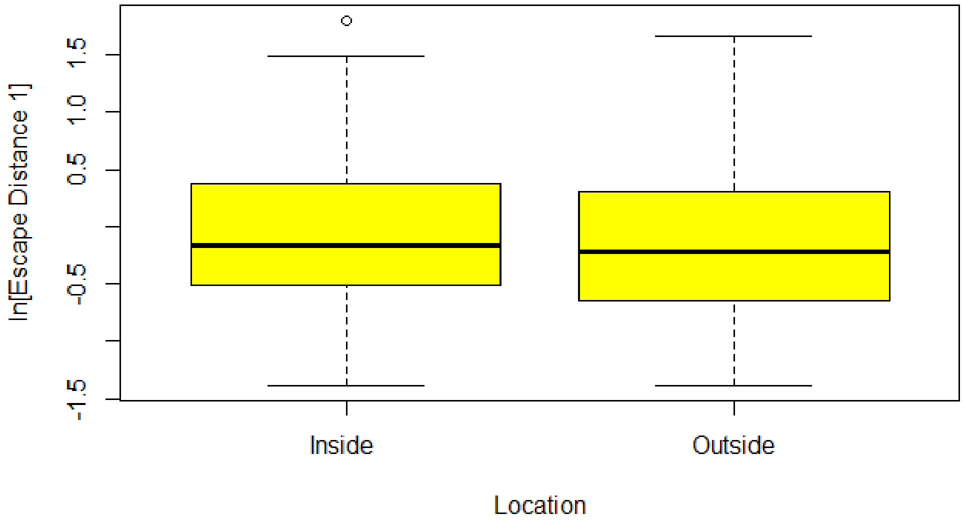

Figure 6: Log transformed Escape Distance 1 (ED1) with respect to Location (categorical variable with levels inside (restored habitat) and outside (degraded habitat)). The central dark line shows the median, the edges of the boxes are 25th and 75th percentiles and the ends of the lines are the minima and maxima within 1.5 times the interquartile range. Values outside the range are represented by individual points.

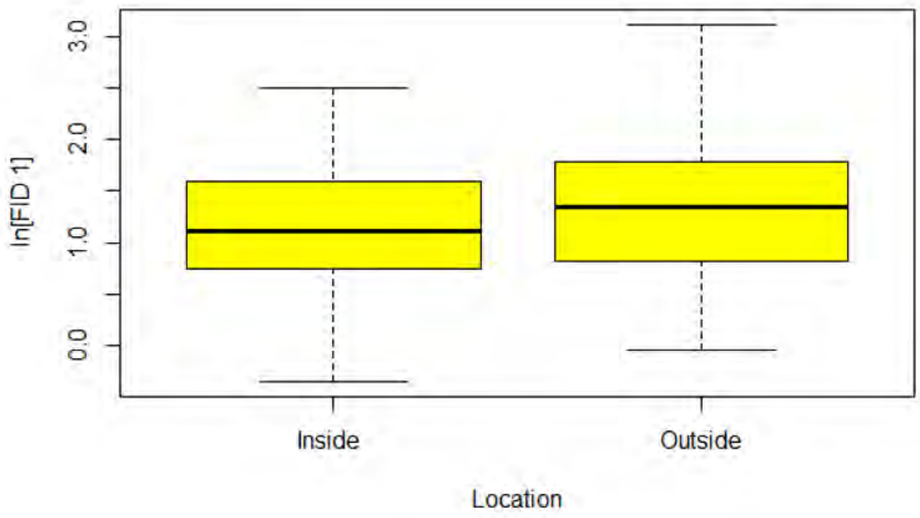

Figure 7: Log transformed Flight Initiation Distance 1 (ED1) with respect to Location (categorical variable with levels inside (restored habitat) and outside (degraded habitat)). The central dark line shows the median, the edges of the boxes are 25th and 75th percentiles and the ends of the lines are the minima and maxima within 1.5 times the interquartile range. Values outside the range are represented by individual points.

3.2 PERSISTENT APPROACH

Flight Initiation Distance 1 (mean = 3.41m, 95% CI = ± 2.06) was 35.28% larger on average than Flight Initiation Distance 2 (mean = 2.20m, 95% CI = ± 2.07); t_{161} = 12.946, p-value < 0.001 (Figure 7). Likewise, Escape Distance 1 (mean = 0.94m, 95% CI = ± 2.07) was 24.47% larger on average than Escape Distance 2 (mean = 0.71, 95% CI = 2.08); t_{161} = 3.829, p-value < 0.001 (Figure 8).

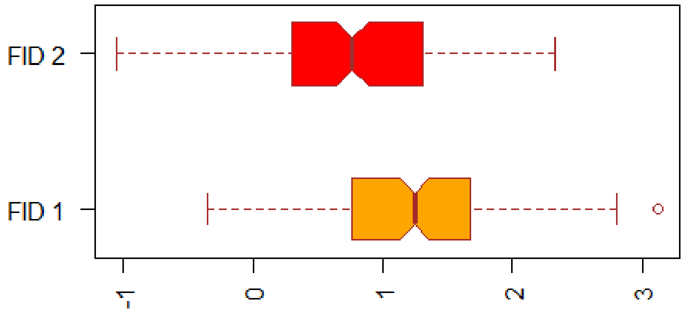

Figure 8: Log transformed Flight Initiation Distance 1 (FID1) and Flight Initiation Distance 2 (FID2). The central dark line shows the median, the edges of the boxes are 25th and 75th percentiles and the ends of the lines are the minima and maxima within 1.5 times the interquartile range. Values outside the range are represented by individual points.

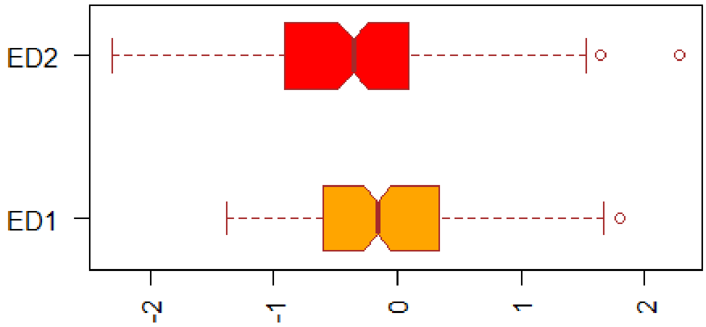

Figure 9: Log transformed Escape Distance 1 (ED1) and Escape Distance 2 (ED2). The central dark line shows the median, the edges of the boxes are 25th and 75th percentiles and the ends of the lines are the minima and maxima within 1.5 times the interquartile range. Values outside the range are represented by individual points.

4. DISCUSSION

My findings indicate that escape decisions in the wild are dynamic and sensitive to a combination of both intrinsic and extrinsic factors.

4.1 FLIGHT INITIATION DISTANCE 1 (FID 1)

Most studies have reported an inverse relationship between body temperature and FID, where lizards exhibited a longer FID at low body temperatures, because of depressed metabolism and impaired escape ability (Rand 1964; Cooper 2011a and 2011b). Smith (1997) showed that substrate temperatures were highly correlated with body temperatures in the field, therefore, I assumed that I could use perch temperature as a proxy for body temperature, since it was not feasible to measure body temperature in field conditions. Contrary to most studies, I found a positive relationship between FID and substrate temperature. This is similar to a study conducted on two Agama species (*A. savigyni* and *A. pallida*) which showed at high body temperatures, lizards flee rapidly from predators and at low body temperatures which reduces sprint speed, the lizards rarely ran but instead hold their ground and attack aggressively. They speculated that this could be because cold-blooded lizards that live in open habitats would have little chance of outrunning predators, which pertains to the present study species as well since it is found in open habitats. The other plausible explanation is that the assumption that body temperatures are highly correlated with perch temperatures might or might not be true for this study.

I found a positive relationship between FID 1 and SVL, which means that larger individuals fled early than smaller individuals from an approaching predator. This finding is similar to other studies who report a positive relationship between FID and body size because larger individuals are more conspicuous to the predators than smaller individuals and thus perceive a greater risk. FID 1 had a positive relationship with Spot Distance 1 which is also similar to what previous studies have found, probably because observing an approaching predator from a distance accrues monitoring cost (Blumstein 2003) and assessment by prey of greater risk during prolonged approaches (Cooper 2005).

Vegetation patches act as refuges for lizards to escape from an approaching predator. I calculated the percentage cover of vegetation patches to see how it influences escape decisions. It was observed that if the percentage cover of vegetation was high then lizards exhibit a smaller FID, allowing the predator to approach closer as opposed to when the percentage cover of vegetation was low. This is similar to other studies which report that lizards from sparse vegetation cover exhibit a longer FID and escape distance as compared to lizards from heavily vegetated areas because of a noticeable difference in the availability of hiding sites (Snell *et al.* 1988; Bulova 1994).

I expected a positive relationship between FID 1 and percentage canopy cover because an area with high canopy cover will have lower temperature because of shade and thus, lizards will exhibit longer FID due to impaired escape ability. But I observed a negative relationship between FID 1 and percentage canopy cover which implies that lizard from higher canopy cover lets the predator approach closer as compared to lizards from lower canopy cover. The plausible explanation is that even though vegetation cover (because the presence of canopy cover implies the presence of vegetation) provides refuge for escape, the cost is obstructed vigilance which makes it difficult to monitor an approaching predator. Therefore, lizards from higher canopy cover may not have been able to detect an approaching predator soon enough to flee. The other plausible explanation is that proximity to vegetation cover (indicated by higher canopy cover) decreases the risk perceived by lizards and therefore allows a closer approach of a predator.

Edge vegetation around the sheetrock can act as a refuge for lizards to escape from an approaching predator. Therefore, I expected a positive relationship between FID and distance to edge vegetation since the risk would be higher for lizards further away from the edge vegetation but I found a negative relationship. Lizards showed a longer FID when they were closer to the edge vegetation as opposed to when they were far from the edge vegetation. This could be explained by measuring other refuges available to lizards such as boulders and other vegetation patches apart from edge vegetation, which was not measured in this study and should possibly be considered in further studies.

4.2 ESCAPE DISTANCE 1 (ED 1)

I found an effect of location on Escape Distance 1. I expected, lizards from outside school, which has lesser vegetation cover to flee longer than lizards from inside the school, which has more vegetation cover but contrarily, I found that lizards from inside the school fled 9% longer on average than lizards from outside school. This could be because of differences in vigilance levels due to vegetation cover with respect to location and the associated costs of vigilance. Outside school which is relatively open, lizards can monitor an approaching predator much better than lizards from inside school, thus they may perceive lesser risk and escape at shorter distances than lizards from inside school.

I observed a negative relationship between ED1 and the average height of boulders. This means that lizards from a microhabitat with a shorter average height of boulders ran longer as compared to lizards from a microhabitat with a taller average height of boulders. The plausible explanation for this pattern is that lizards from a microhabitat with a taller average height of boulders can monitor an approaching predator better because they are perched higher as compared to lizards from a microhabitat with a shorter average height of boulders. Therefore, the risk perceived when perched on taller perches could be smaller as compared to smaller perches, enabling them to run shorter distances when perched on a taller perch.

ED 1 was positively influenced by SVL, most likely owing to the same explanation that larger individuals are more conspicuous to predators than smaller individuals and therefore perceive a higher risk and thus flee longer than smaller individuals.

Lizards from high canopy cover escaped shorter distances as compared to lizards from low canopy cover. Higher canopy cover also implies the presence of vegetation. Therefore, lizards from higher canopy cover were also in closer proximity to vegetation cover which resulted in lesser perceived risk and hence escape shorter distances.

ED 1 was positively influenced by Spot Distance 1, which means the longer the spot distance, the longer is the distance fled by the lizards fled. This is similar to what a study on sand diving lizards found, where the total flight distance covered by the lizards before burying was positively related to initial distance (Evans *et al.* 2017). But no theory has been proposed for predicting effects of starting distances on distance fled (Cooper 2005). Distance fled could be influenced by distance from the refuge (Cooper 1997a) which was not measured in this study.

4.3 PERSISTENT APPROACH

In response to persistent approach, I expected lizards to increase the magnitude of their escape responses by increasing the FID and ED in a subsequent approach. Contrarily, I found the FID and ED were larger in the first approach as compared to the second approach. This could be because lizards from open habitat, rely on their sprint speed for escaping from predators. Therefore, in the first approach itself, lizards ran a larger distance and then remained more vigilant by taking short bursts of locomotion to monitor the approaching predator. Various other factors such as characteristics of the microhabitat which the lizards escaped into after escaping from an approaching predator were not measured, which could influence the risk perceived by the lizard. Other considerations such as whether the lizard entered a refuge or went closer to a refuge or just ran away from an approaching predator were not measured which can be an explanation for the pattern found in this data. Therefore, the data collected is not sufficient enough to explain the observed pattern.

4.4 DRAWBACK OF ANALYSIS

I used multiple linear regression to look at the relative importance of multiple factors. Since I used a repeated-measures approach, multiple measurements cannot be treated as independent data points because they are pseudo-replicates. Therefore, ideally, I should use a mixed-effects model for analysis. Since mixed model effects is an advance statistical tool along with lack of time, I used multiple linear regression.

Many of the predictor variables were correlated with each other, therefore I detected the highly correlated predictor variables and dropped one of the highly correlated variables. Ideally, a Principal Component Analysis (PCA) should be used to control for the correlation between predictor variables and reduce the number of predictor variables by using composite values.

4.5 CONCLUSION

Habitat alteration in form of grazing had an effect on ED but not on FID of lizards (Figure 6 and 7). Specifically, lizards from the restored habitat escape longer distances as compared to lizards from the degraded habitat, probably because lizards from the degraded habitat which is relatively open are able to monitor an approaching predator better, following lesser perceived risk and hence escaped shorter distances. I also looked at the effect of multiple factors on escape responses of lizards and found that variation in escape responses was explained by a combination of both intrinsic and extrinsic factors. Different factors influenced escape responses differently and some factors contributed more in explaining the variation in escape responses than the others. Body size was a major factor determining FID 1 of lizards.

Contrary to our prediction of persistent approach that lizards should increase FID and ED with subsequent approaches, I found that FID and ED were larger in the first approach as compared to the second approach. This could be because lizards from open habitats rely more on sprint speed, hence in response to an approaching predator, it is a safer option to flee at a longer distance in the first approach itself and remain vigilant to monitor the approaching predator followed by shorter bursts of locomotion.

These results help in establishing the dynamic nature of escape responses. It shows how similar predictor variable can have differential effects on different escape responses. It also reclaims how already established patterns for some species might not be applicable to other species.

Further studies should examine how different types of human disturbances influences escape behaviour. Long-term studies should be conducted to investigate how these changes influence species interaction and how these changes ultimately affect species at a population and community level.

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