Intrasexual Signalling and Aggression in male rock agama, *Psammophilus dorsalis*

Thesis submitted in partial fulfilment of the requirements of the

BS-MS Dual Degree Program at IISER, Pune
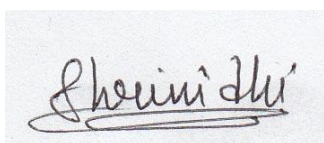
IISER PUNE

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M.S. Thesis

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CERTIFICATE

This is to certify that this dissertation entitled "Intrasexual Signalling and Aggression in male rock agama, *Psammophilus dorsalis*" towards the partial fulfilment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research, Pune represents research carried out by Shrinidhi Mahishi at the Indian Institute of Science, Bengaluru under the supervision of Dr. Kavita Isvaran, Assistant Professor, Centre for Ecological Sciences during the academic year 2016-2017.
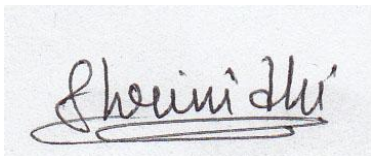
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DECLARATION

I hereby declare that the matter embodied in the report entitled "Intrasexual Signalling and Aggression in male rock agama, *Psammophilus dorsalis*" are the results of the investigations carried out by me at the Centre for Ecological Sciences, Indian Institute of Science, under the supervision of Dr. Kavita Isvaran and the same has not been submitted elsewhere for any other degree.

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Abstract:

Contests between males are costly, and hence animals have evolved signalling tactics which are modulated based on the level of threat that they encounter. I studied intrasexual competition in male *Psammophilus dorsalis*, or the Indian Rock Agama, in the field, by presenting model lizards representing different levels of threat in the home range of residents. There were two types of model presentations: 1) On a rock perch, where the lizards are usually found, and 2) On the ground, next to rock perch occupied by the males. Intruder at these two locations were expected to represent different threat levels. In addition, a PVC pipe was presented on the perch in order to verify that the models are indeed treated as intruders, and not as any novel object. Focal observations of these individuals were done prior to and after model presentation. I found that individuals do show a higher level of a few aggressive behaviours, namely lateral compression and gular extension to the intruder on the perch as compared to the novel object and to focal observations without intruders. However, there were no clear differences in behavioural responses to the models presented on the perch and on the ground, except that individuals came close to the model consistently more often when model was presented on perch. This study provides evidence that male *Psammophilus dorsalis* indeed defend their home ranges against intruders. But, the position of the intruder within the home range with respect to the rock perches does not seem to matter. To the best of our knowledge, this study provides the first instance of documentation of response of a tropical lizard to a simulated intruder in the field.

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Last, but definitely not the least, I thank my family for supporting my decision to pursue science, and giving me the freedom to chase my dreams.

Introduction:

Male-male competition is ubiquitous in nature. Since its description by Darwin (Darwin, 1871), it has been extensively studied in numerous species. Males compete for a plethora of reasons. Access to females is one of the major causes of competition (Cox and Le Boeuf, 1977). In many species, especially those that seem to lack active female choice, competition between males determines the winner, which has a higher chance of mating with the females. In order for a male to achieve copulations, he has to ward off intruders and hence, it is expected that an individual's success will be influenced by the number of competing males and receptive females in the region (Boesch et al., 2006). Hence, competition can have immense fitness consequences for males. In addition to competing for females, males can also compete for territories. Since quality of male territory is used by females to assess males in some species, there is ample motivation for males to compete for it. Contests will determine winners, and females typically choose males based on difference in territory quality (Alatalo et al., 1986).

Although the gains from competing are often high, competition in the form of aggressive contests is immensely costly for both individuals (Vehrencamp et al., 1989). It can result in loss of energy and hence, only those with sufficient energy reserves can engage in fights. Accumulation of lactic acid can take place during a physical fight along with depletion of oxygen reserves, which can be detrimental to the organism (Briffa and Elwood, 2005). Combats can often result in serious injuries, with some animals suffering from mortality as a result of the fight (Alvarez, 1993). Even those suffering from minor injuries may have reduced chances of future mating, as females generally do not prefer to mate with injured males. Competing individuals also expose themselves to predators, hence, making them vulnerable to predation (Hernandez-Jimenez and Rios-Cardenas, 2012). Valuable time, which can be spent in foraging, is lost due to competition (Alberts et al., 1996). Given these costs, assessing the opponent and deciding whether to fight or flee or ignore the opponent can be immensely useful for animals as opposed to indiscriminate fighting (Parker, 1974).

Signalling is that mechanism which allows assessment of the opponent. It involves a sender and a receiver, and a signal. Signalling is of great importance as it allows animals to avoid the cost of aggression, which is expensive in time and energy (Smith and Parker, 1976). Two individuals signalling to each other assess the resource-holding-potential of their opponent relative to themselves and use this information to determine whether to escalate to aggression, or to retreat (Briffa, 2008). Usually, it is the individual with better fighting ability which signals more or produces a higher quality signal, resulting in the opponent to flee (Parker, 1974). Animals use a variety of modes of communication to signal to their opponents. Frogs use vocalization to settle contests. Bigger individuals vocalize in lower frequency and they tend to win more often (Davies and Halliday, 1978). In this case, the frequency of vocalisation is an honest signal of body size. Badges of status are used by multiple species, such as, passerines and paper wasps to communicate their social rank to their contestants. Those which have higher intensity of signal have a higher rank, and generally win the contest (Tibbetts and Lindsay, 2008). Many lizard species use push up displays during encounters to resolve disputes (Decourcy and Jenssen, 1994; Martins, 1993).

But even signals are not used indiscriminately by animals. Signalling is also associated with various costs. Auditory, chemical and visual signals can be picked up by predators and parasites in addition to opponents. Male tungara frogs use repeated calls to attract females. Females of this species prefer calls with chucks, as it provides information about the male's body size. But a species of bat, which feeds on these frogs, also uses the chucks to locate their prey (Ryan et al., 1982). Hence, animals are expected to modulate the signal based on various factors like rival quality and quality of females in the vicinity (Swierk and Langkilde, 2013).

Signalling in lizards:

Lizard species use visual, auditory as well as chemical modes of signalling. In lacertids, such as *Podarcis hispanica*, males identify rivals using scent marks and decide whether to show aggression based on the cue provided by them (Carazo et al., 2008). Sagebrush lizards, *Sceloporus graciosus,* are able to signal their physiological status based on femoral pore secretion and fecal deposits. Receivers

of the signal can make decisions with regard to territory defence using the information provided by the signal (Martins et al., 2006). Male barking geckos, *Ptenopus garrulus garrulus*, display acoustic signals to the rivals. The calling frequency of these individuals is related to their body size, with bigger males having a lower dominant calling frequency (Hibbitts et al., 2007).

But acoustic and chemical communications form a small share of the vast repertoire of signalling modes displayed by lizards. Visual signalling is the dominant mode of communication in many species. It involves a wide range of body postures, movements and colour patterns, such as head bobs, push ups, leg extensions, tail raises, colour change, tongue flicks, gular extension and dewlap extension. *Anolis sagrei* lizards use head bob displays to signal to male conspecifics and they are reported to increase in frequency prior to physical aggression (Paterson and McMann, 2004). During agonistic encounters, male *Sceloporus graciosus* perform push ups and assume a body posture which exposes their blue belly, and during courtship, the males head bob, although at a much lower frequency as compared to agonistic encounters (Martins, 1993). Dewlap extension is thought to help in courtship in *Anolis sagrei* as males increase the frequency of this behaviour during heterosexual interactions (Driessens et al., 2014). Both sexes of *Calotes versicolor*, the Indian Garden Lizard, show colour change during courtship, with males showing gular extension as well (Pandav et al., 2007).

Many of the above mentioned behaviours also play a role in home range/territory defence. During a model presentation experiment to pygmy bluetongue lizard, *Tiliqua adelaidensis*, both males and females use tongue flicks and bites to attack the intruder when it was very close to the burrow entrance. However, when the model was placed farther from the burrow entrance, the response was significantly lower, indicating that individuals modulate their aggression based on the level of threat posed by the intruder (Fenner and Bull, 2011). In *Anolis sagrei*, residents showed higher level of display to intruders present on the ground as compared to intruders on the elevated perch. More number of push ups and dewlap extensions are directed towards the intruders on the ground, suggesting that residents adjust their signalling levels here as well (Calsbeek and Marnocha, 2006).

The primary aim of this study was to identify behaviours used in competitive

signalling in male *Psammophilus dorsalis* and to compare their behavioural response to varying levels of intruder threat. 3D printed plastic models of sizes approximately similar to that of the focal lizard were used as intruders. Adult individuals of *Psammophilus dorsalis* appear to show site-fidelity, with females occupying a small home range and males having a much larger home range, overlapping multiple female home ranges (Ranade, in prep). Both males and females spend a lot of time on rock perches, which is expected to allow better opportunity for spotting mates and intruders. Male-male encounters are rare, and most of them are quickly resolved, with one male fleeing from the spot (Pers. Observation). Based on pilot studies and studies from other species (Driessens et al., 2014; Martins et al., 2005; Ord et al., 2002), few behaviours like push up and gular extension are believed to be involved in aggression and are directed towards intruders. Also, we think it is highly likely that intruders at different locations in the home range of residents represent different levels of threat, and based on other studies (Scharf et al., 2011; Swierk and Langkilde, 2013), we suspect that individuals should respond differently to different threat levels .

Objectives:

To describe how male *Psammophilus dorsalis* signal and display aggression to varying levels of intruder threat. Plastic lizards were used as intruders. We have measured aggressive behaviour in the absence of an intruder, presence of a novel object and presence of intruder on the perch, and presence of an intruder on the ground. Based on our knowledge of the level of threat in each type, we expected maximum level of aggressive behaviour when the intruder is on perch, followed by presence of an intruder on the ground. Since the novel object does not indicate any danger to the resident, we predicted a lack of aggression. Similarly, no aggressive behaviour was expected in the absence of an intruder.

Materials and Methods:

Study species:

Psammophilus dorsalis is a lizard belonging to the family Agamidae. Found mostly in the rocky hills of southern India, it is a generalist species, found in urban as well as rural areas. It feeds mainly on ants, but eats other insects and small reptiles as well (Balakrishna et al., 2016; Sreekar et al., 2010). It is sexually dimorphic, with males being brightly coloured and bigger in size (mean SVL 10.15 ± 2.23 cm) and females being smaller (mean SVL 7.47 ± 3.12 cm) and camouflaging against the background (Deodhar, in review). The sex ratio in this species is skewed towards females (Deodhar, in review). The breeding season is typically from May to September. It is a largely annual species and a majority of the individuals disappear after the breeding season and most likely die (Deodhar, in review). Both males and females are found perching on rocks and males occupy higher perches as compared to females (Radder et al., 2005). There can be multiple reasons as to why these lizards perch on rocks. It allows greater visibility to spot potential mates, intruders and predators and it also serves as a good basking site. Breeding males have yellow or orange colour on the back and a jet black colour on their lateral side. Males have the ability to show dynamic colour change, requiring only a few seconds to change their colour (Pers. Observation). They change their colour based on the local environment. For example, they assume yellow red coloration when they encounter an intruder in their home range (Deodhar, in review). During the non-breeding season, males are typically pale yellow in colour and can look like females. Previous observation has shown that males change to orange colour when females are around (Deodhar, in review). Males have big home ranges overlapping multiple female home ranges. Mating system in this species appears to be polygynous, with males mating with the females residing in their home ranges.

Figure 1: Image with Male *Psammophilus dorsalis* on top of a rock perch

Study Site Description:

The study was performed in Rishi Valley, Madanpalle, which is located in Chittoor district of Andhra Pradesh (13.634°N, 78.454°E, 750 m elevation). It is surrounded by granite hills which have conspicuous gneissic rocks and boulders. Even though the surrounding regions are sparsely vegetated, with thorny plants and scrubs comprising a majority of the flora, Rishi Valley is rich in vegetation. Rainfall is inconsistent and hence, it is a drought prone region. The temperature ranges from around 12-14°C at night to around 40°C during the day in summer months. In the hills of Rishi Valley, there are patches of rocks surrounded by vegetation and these patches are referred to as sheet rocks. There are numerous species of birds, insects and reptiles which inhabit Rishi Valley. *Psammophilus dorsalis*, or the Indian Rock Agama, is a lizard which is seen around in this region. *P. dorsalis* (Gray, 1831) is sympatric with a related species, *Psammophilus blanfordanus*. But these two species are spatially segregated, with *P. dorsalis* occupying the sheet rocks and *P. blandfordanus* mostly populating the regions between sheet rocks (Personal

Observation).

This study was performed in 5 different sheet rocks in Rishi Valley: Boda Bunda 2 (BB2), Bodi Paina (BP), Gyadi Dona Bunda (GDB), East wall (EW) and Tent Rock (TR). Field work was carried out from May to September 2016, which corresponds to the breeding season of *P. dorsalis*.

Figure 2: Map of India. + mark indicates the study site, Rishi Valley.
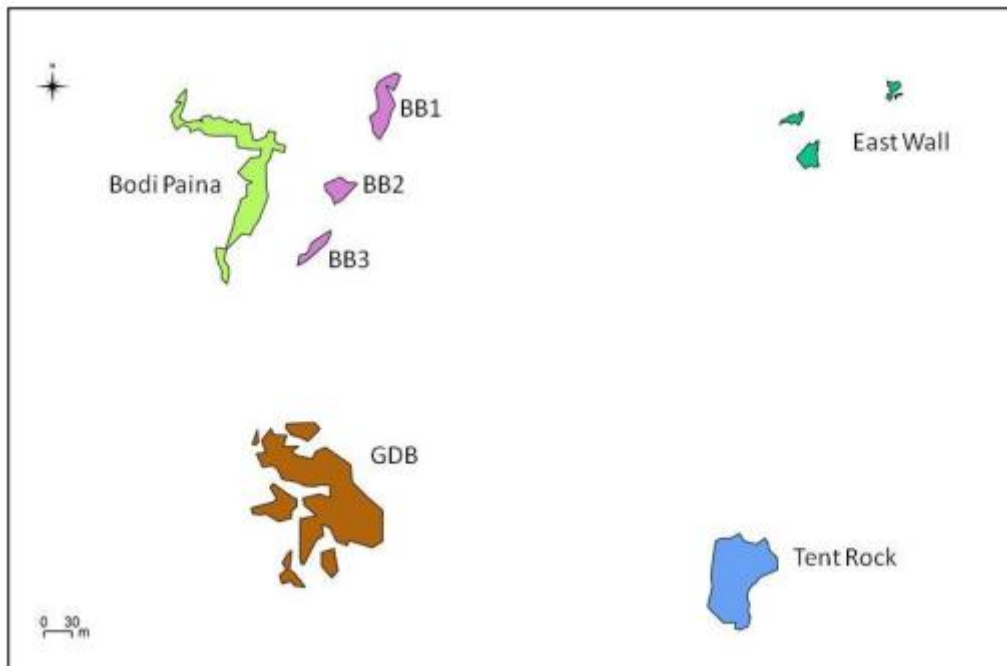
Figure 3: Sheet rocks and their sizes in comparison to each other.

Figure 4: Image representing one of the sheet rocks

Overview of study design:

In order to test the response of male *P. dorsalis* to intruder threat, I used plastic models as intruders. These models were of various sizes similar to the focal males. Tagged lizards of known body size were identified and their home ranges were tracked for the experiment. Prior to presentation of the model, each lizard was observed and video recorded for 30 minutes. To introduce an intruder threat, a model of the same size as the focal lizards was kept on a rock perch occupied by the lizard. Individuals spend most of their time on rock perches and they are expected to be valuable to them as they offer a better visibility with regard to mates and competitors. To check response to varying level of intruder threat, response to model presentation on perch was compared with the response towards a model kept on the ground, within his home range. This on perch and off perch model presentation was done for 20 tagged males of known body sizes and home ranges. To control for the possibility that the lizard's observed response towards the model is a response to a novel object, and not an intruder, a PVC pipe of size around 19 cm was used as a

novel object. PVC pipes were presented to 5 of these 20 tagged males and were kept on perch during presentation.

Tagging Lizards:

At the start of the breeding season, lizards were captured, measured and tagged in order to identify all individuals in the sheet rocks. Nooses were used to catch lizards from their home ranges. Once captured, the Snout-Vent Length (SVL), Inter-Limb Length (IL), Head Height (HH), Head Width (HW), Head Length (HL), Tail Base Width (TB) were measured using a vernier calliper with least count 0.1 mm and Tail length (TL) was measured using a 30 cm ruler with least count 1 mm. Weight of the lizard was calculated by putting it in a cloth bag and weighing the bag using a spring balance.

In order to tag the lizards, they were anesthetized by placing the cloth bag containing the lizard in an ice box for around 3-4 minutes. Ceramic beads of different colours were used to tag the individuals. A needle was inserted near the tail base and the string containing the beads was firmly tied. Every lizard was given a unique id, based on the sheet rock on which it was tagged, and had a unique bead combination for identification. After tagging the lizard, it was released at the exact location from where it was first seen prior to capture. After an individual was captured, no models were presented to him for at least 2 days.
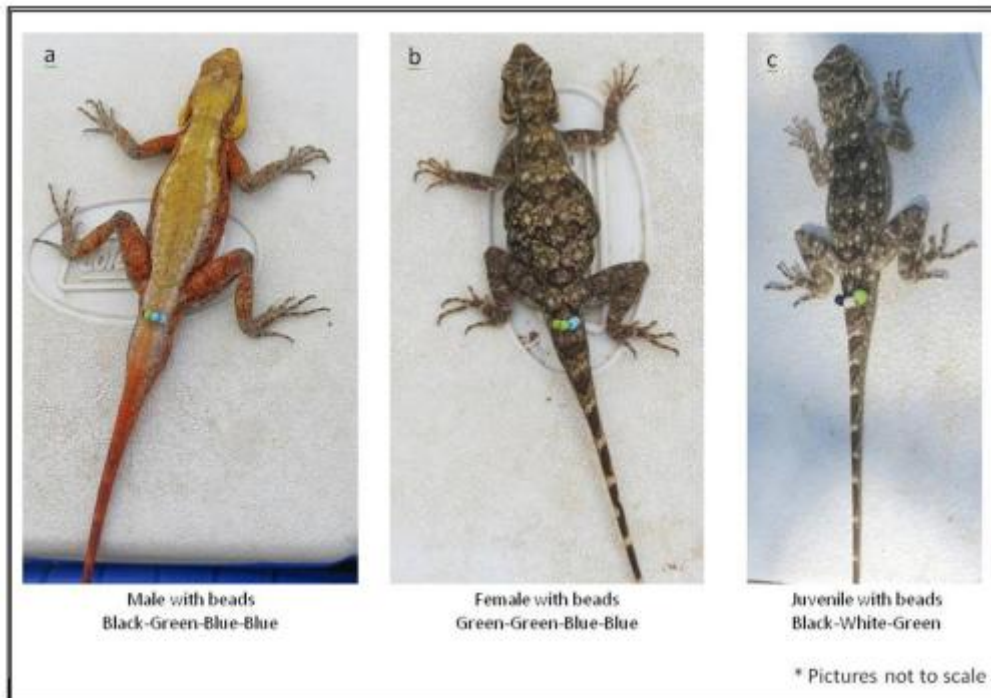
Figure 5: Tagging a) Males, b) Females, c) Juveniles with beads of different combinations.

Home Range Data Collection:

After tagging the lizards, their movements were observed and tracked, till they disappeared. Each sheet rock was surveyed at least once in 3 days, either from 0700 to 1200 hrs or from 1600 to 1800 hrs, and the location of the lizards was noted on the map of that sheet rock. All the sheet rocks had marked perches which serve as points of reference to locate the lizard on the map. This allowed us to identify the home range for every tagged individual and track the changes in home range, if any.
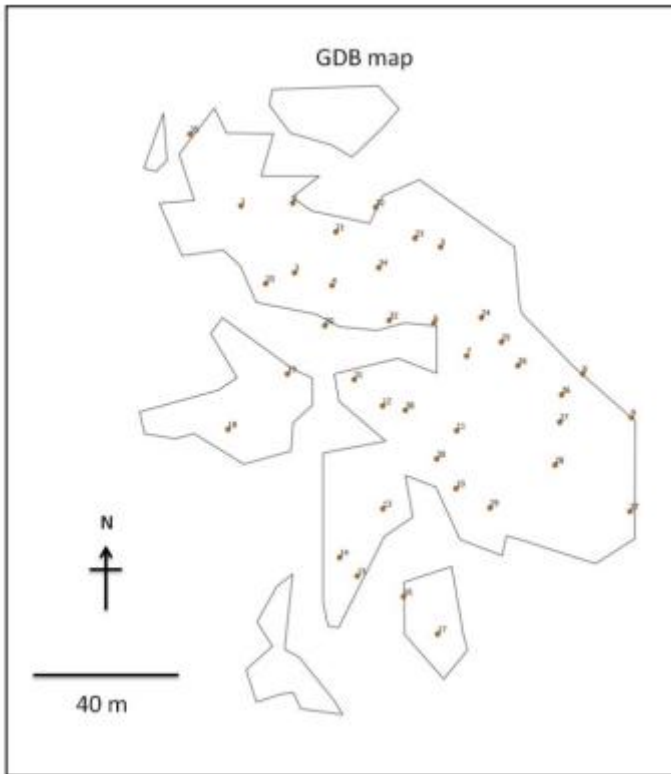
Figure 6: Map of sheet rock GDB with regularly used marked perches

Figure 7: Image showing one of the marked perches in GDB.

Description of Model:

Plastic models, resembling the males were used to simulate an intruder threat for the males. These models were 3D printed and painted using oil paints. The dorsal side of the model was bright yellow, while the lateral side was black. The colour of the model was chosen to be yellow as it is the breeding coloration of male *P. dorsalis* and most of the time during the breeding season is spent in yellow color (Deodhar, in review). There were 11 models of different sizes, with the smallest having a Snout Vent length (SVL) of 6 cm and the largest model having an SVL of 16 cm. A model of SVL closest to the size of focal male was used for the presentations so that the intruder was matched in size with the resident male. Grey coloured PVC pipes were used as novel objects.

Figure 8: Image of a model which was used as an intruder (SVL = 12 cm)
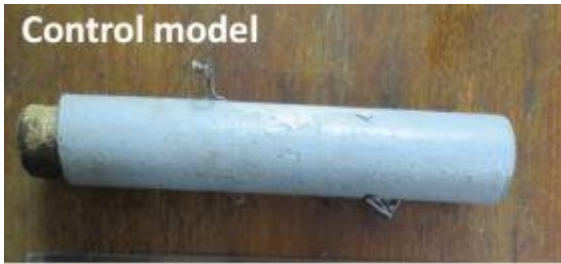
Figure 9: Image of the PVC pipe used as Control model

Model Presentation:

There were 3 types of model presentations: On perch (NP), Off-Perch (FP) and novel object (CONTROL). NP models were presented on the rock perch occupied by the male, and FP models were presented on the ground next to the perch. A gap of 2 days was maintained between successive model presentations to minimise habituation. CONTROLS were also presented on the perch, in order to facilitate comparison with NP. The order of presentation (NP, FP, CONTROL) for a particular male was randomised. On perch and off perch models were presented to 20 males and Control was presented to 5 of the 20 males.

Focal males were decided before every visit to the sheet rocks and appropriately sized models were taken to the field site. After spotting the male of interest, a camera and tripod was set up and the individual was observed and video recorded for 30 minutes. During the 30 minute natural observation focal (regular focal), the number of individuals within 10-15 m from the male was noted, along with the position of the focal male (ground, on perch). If the individual was on a perch, the height from ground was recorded. Approximate distance of movement was recorded if the animal moved. Weather, time of the day and temperature were also noted down.

After the 30 minute regular focal, I moved towards the male with the model and placed it near the position where the male was present during the last 5 minutes of the regular focal. Video recording started as soon as I came back to the position where the camera was kept. In addition to the previously recorded parameters, distance from model was approximated at the start and as the male moved during

the focal. Model presentations were also video recorded for 30 minutes.

Transcribing the Videos:

After data collection in Rishi Valley, the videos were transcribed using BORIS (Behavioral Observation Research Interactive Software) version 2.72 (Friard et al., 2016). 90 videos were transcribed, out of which 20 were NP, 20 were FP, 5 were CONTROL and 45 Regular.

For each video, all occurrences of the following behavioural events were noted while transcribing the videos:

Behaviour	Notation used	Description
Approach a male	app.m	Moved towards another male
Approach a female	app.f	Move towards a female
Bite	Bite	Bite another individual
Lower posture	body.down	Lowering the body posture
Raise posture	body.raise	Raising the body posture
Chase	Chase	Chase another individual
Crouch and Shudder	Cns	Move head up and down rapidly in flat posture
Defecate	defecate	Defecate
Forage	food.grab	Catch food using mouth
Ground Lick	gr.lick	Lick the surface of the ground
Ground Touch	gr.touch	Touch the ground without using the tongue
Head Bob	h.bob	Up and down motion of the head
Head Duck	h.duck	Duck the head
Head Move	h.move	Move the head sideways
Head Raise	h.raise	Raise the head

Head Turn	h.turn	Move the head sideways more than 45°
Head Scrape	h.scrape	Scrape head against the ground
Half Head Bob	half.h.bob	Partial up and down motion of the head
Half Push up	Hp	Partial up and down motion of the front part of the body
Jump	Jump	Jump towards prey
Mouth Scrape	m.scrape	Scrape mouth against the ground
Move	Move	Move from one location to the other
Out of refuge	out.refuge	Come out from a refuge site
Pounce	Pounce	Pounce on an intruder
Push Model	push.mod	Push an intruder
Push up	push.up	Up and down motion of the front part of the body
Scratch	Scratch	Scratch the body using forelimbs or hindlimbs
Shift	Shift	Shift the body without moving any distance
Shudder	shudder	Rapid up and down motion of the head in normal posture
Yawn	Yawn	Open the mouth and close it immediately

Table 1: Description of male behavioural events recorded during the focal observations

For each video (observation session) the time spent in the following behavioural states was noted while transcribing the videos:

Behavioral State	Levels	Description
Gape	Small/Large	Mouth open for a long duration
Gular Extension	Tiny/Small/Large	Extension of the gular pouch present on the throat
Lateral Compression	Small/Large	Body is laterally flattened with dorsal and nuchal crest extended
Tail Raise	Small/Half	Raising the tail

Table 2: Description of male behavioural states recorded during the focal observations

Following were the comparisons done for analysis:

Regular Vs NP:

Comparing the behaviours displayed in the regular focal and on perch presentation will allow us to discover the effect of an intruder on the focal male. The regular focals will inform us about the behaviours that are naturally observed in male *P. dorsalis* and the on perch presentation can help identify behavioural responses specific to an intruder threat.

NP vs Control:

Controls were used to check if the lizard models were treated as just a novel object or an intruder. Comparing the response to the two types of model presentations can help us understand if lizard models were in fact treated as intruders.

NP vs FP:

In this part, we varied the intruder threat by placing the models in different locations with respect to the rock perches. We expect that the perches are more valuable to the lizards, as they offer better visibility and are ideal basking spots. Comparing the response to NP and FP will tell us if the level of intruder threat influences how the resident male reacts.

Behavioural events were represented as rates (number of occurrences of a behavioural event per 5 minutes), and states were represented as the proportion of time spent in a state out of 5 minutes (time spent in a state divided by the total observation time in seconds multiplied by 300 sec).

Following were the behavioural events and states selected for comparison between types of focals:

1. Rate of Head Bob

2. Rate of Push Up

3. Rate of Head Move

4. Proportion of time spent in gular extension

5. Proportion of time spent in gular extension small

6. Proportion of time spent in lateral compression

7. Proportion of time spent in raised tail

8. Number of times the model was bitten

9. Number of times the model was pushed

10. Number of times the male gaped

11. Number of times the male came within 1 m from the model

8-11 were calculated as the number of model presentations in which these behaviours were observed.

Gular extension small was used as a parameter separate from gular extension because of its high frequency.

Analysis:

All analysis was performed using R version 3.2.1 (R Core team, 2015).

In order to visualise the behaviours displayed by the males under different

conditions, a boxplot of rates of behaviours was made using the count function and the melt function under the packages dplyr and reshape2 respectively.

Once the rate of behaviours and proportion of time spent in different behavioural states were calculated, mixed effects models were run using the functions glmmadmb and glmer using package glmmADMB and lme4 respectively. The behavioural events head bob, push up and head move were used as response variables and the error structure was negative binomial. Behavioural states gular extension, lateral compression and tail raise were also used as response variables and the error structure for these variables was binomial. In the abovementioned models, type of focal, i.e., Regular or NP or FP or CONTROL, was the fixed effect, and individual id was the random effect. The presence of neighbouring individuals was also included as the fixed effect. Rates of following behaviours which were similar to each other were combined for analysis: Head bob and Half Head Bob, as head bob, Push up and Half Push up, as push up and Head move and Head Turn, as head move. Proportion of gular extension tiny, small and large, and lateral compression small and large, and tail raise small and half were also combined. Gular extension small, GES which was seen more often as compared to gular extension large and tiny was used as a separate response variable.

As another way to compare behavioural responses between different contexts (e.g., NP versus FP), the difference in rates of behavioural events and proportions of behavioural states between the different types of focals being compared was calculated along with differences in log transformed proportions. For example, consider the behavioural event push up. Following are the values calculated for push ups: i) Rate of push up NP – Rate of push up FP and ii) log(Rate of push up NP/Rate of push up FP). Since in many scenarios the denominator can be zero, I added 1 to both numerator and denominator for behavioural events and 0.005 for behavioural states. If there is no consistent difference in rate or proportion of behaviour between two types of focals, then the values for the two parameters are expected to be close to zero. The two parameters were calculated for each individual and the mean, standard deviation, standard error and 95% confidence interval were calculated.

We had calculated the number of sessions in which bite, pushing of model, gape and the male coming within 1 m from the model was observed. Comparison of these

numbers between Regular and NP (only gape), CONTROL and NP, FP and NP was done using the prop.test function in R.

Results:

I presented NP and FP models to 20 males and CONTROL to 5 of those 20 individuals. Prior to every model presentation, I took a regular focal for 30 minutes. Thus, I measured male signalling and aggression under four contexts: natural ecological and social conditions (regular focal), simulated intruder threat on perch (NP), simulated intruder threat off perch (FP), and exposure to novel object (Control). Based on the videos, I calculated the rate for all behavioural events seen in each context in order to ascertain the common behaviours seen in male *P. dorsalis* under different threat conditions. The behaviours chosen to compare response to varying levels of intruder threat were based on existing literature about aggressive behaviour in lizards and on frequency of occurrences of behavioural events during a focal observation (very rare behaviours were excluded). Estimating the rates of behavioural events in different contexts can help us find out if there are behaviours not seen in other species which might be involved in aggression in *Psammophilus dorsalis*.

Context	Regular (n=45)	NP (n=20)	FP (n=20)	CONTROL (n=5)
Mean Duration of focal (in seconds)	1627.73 ± 201.62	1027.85 ± 212.74	990.55 ± 248.23	1068.4 ± 130.83

Table 3: Average duration of focals taken in different contexts

Broad patterns in behavioural events

A total of 30 behavioural events were observed in all the focals, with most of them being rare, and only a few being common. Head move was the most frequent behaviour observed in all contexts. Pattern among other behavioural events was not discernible due to high frequency of head move. Hence, I removed it and constructed another plot in order to facilitate the comparison of other behaviours. In all contexts, head bob, half head bob, head turn, move and shift were the most

common behaviours. Head bob and half head bob, head move and head turn, and push up and hp were clubbed together because of their similarity and these behavioural events were later used to compare response towards intruder threat.

Figure 10: Rate (Number of times the behaviour was seen per 5 mins) of all behavioural events seen during Regular focals (n=45) a) with and b) without head move. Refer to Table 1 in the methods section for explanation of these behaviours.
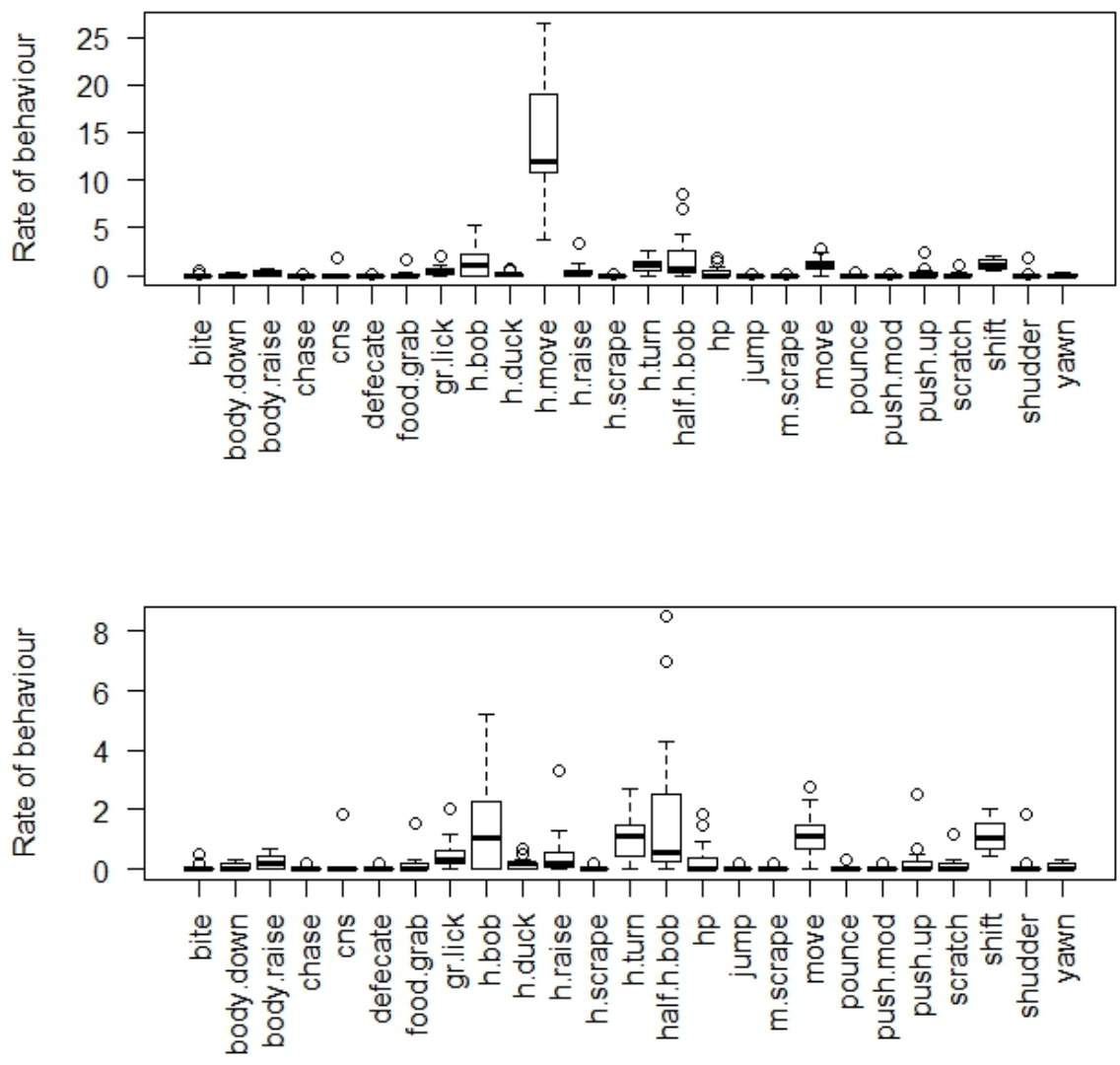
Figure 11: Rate (Number of times the behaviour was seen per 5 mins) of all behavioural events seen during NP focals (n=20) a) with and b) without head move. Refer to Table 1 in the methods section for an explanation of these behaviours.
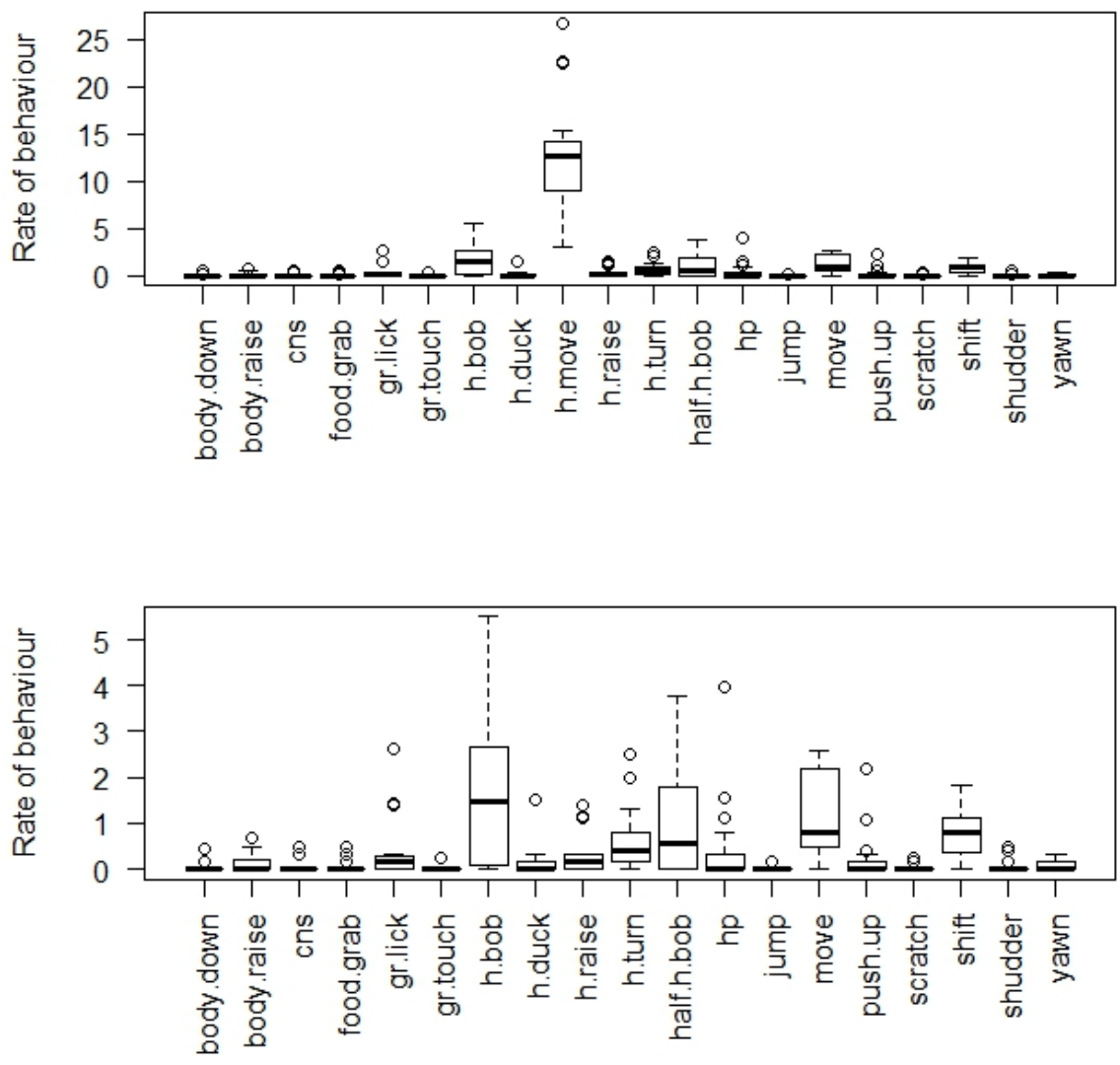
Figure 12: Rate (Number of times the behaviour was seen per 5 mins) of all behavioural events seen during FP focals (n=20) a) with and b) without head move. Refer to Table 1 in the methods section for an explanation of these behaviours.
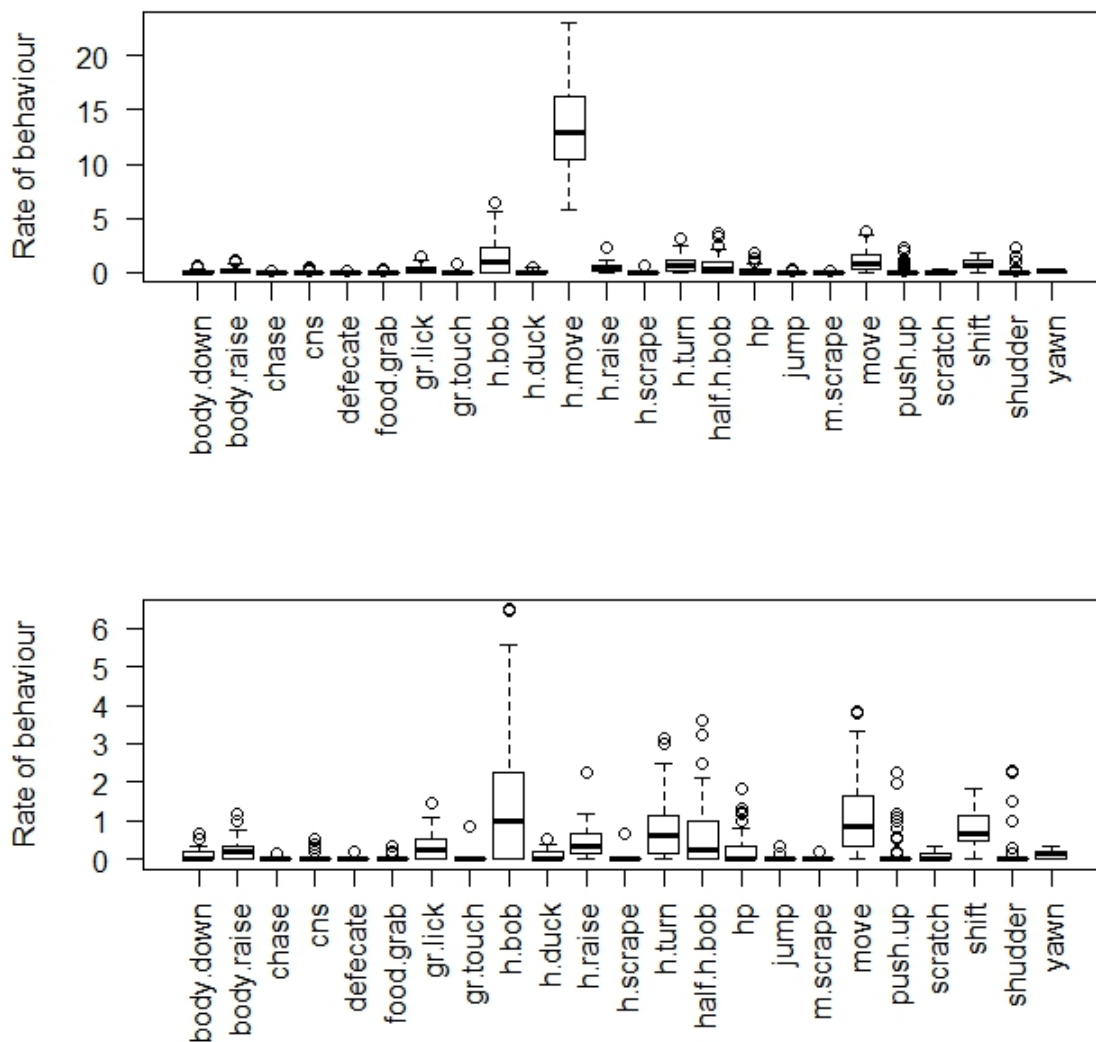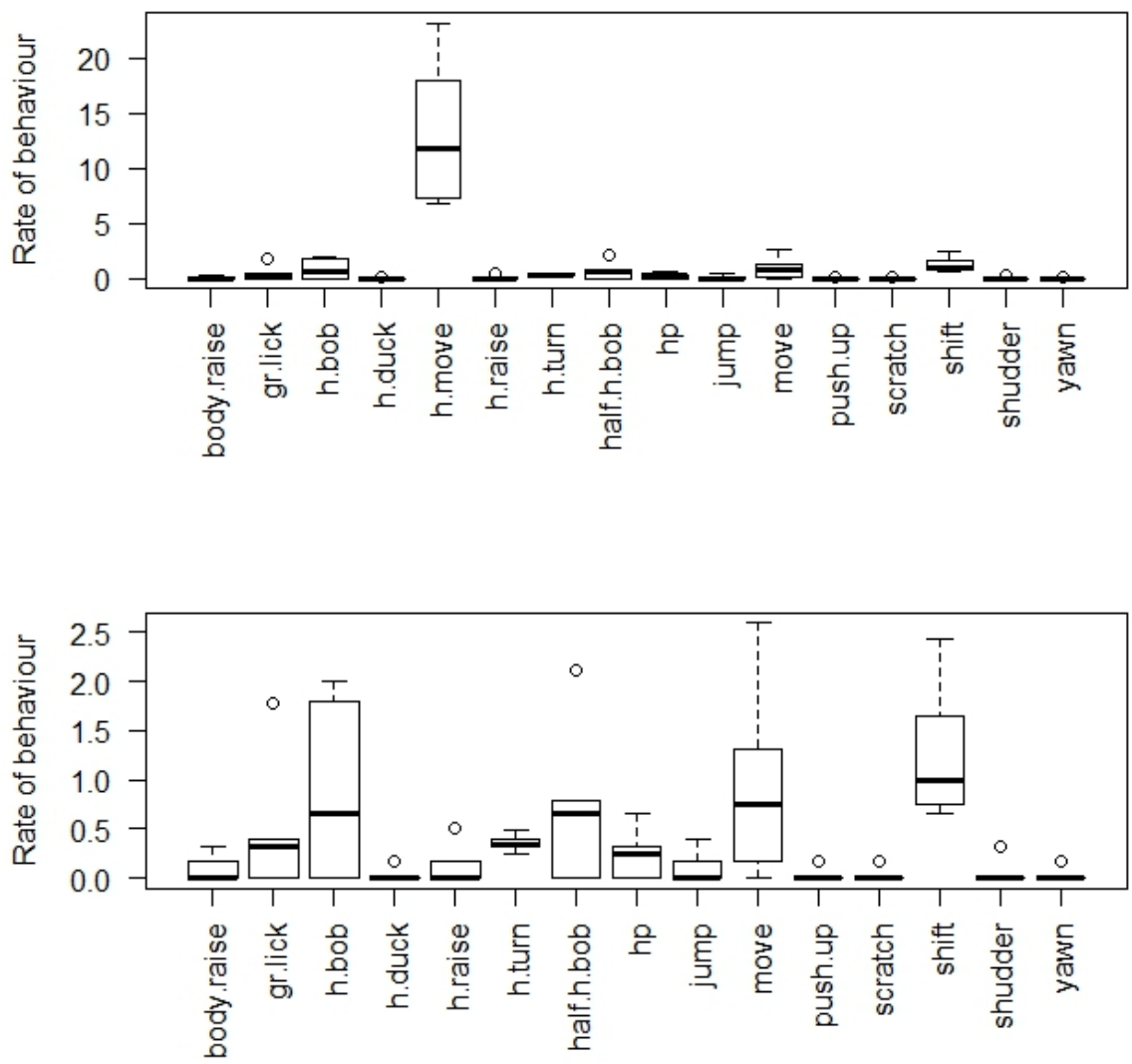
Figure 13: Rate (Number of times the behaviour was seen per 5 mins) of all behavioural events seen during CONTROL focals (n=5) a) with and b) without head move. Refer to Table 1 in the methods section for an explanation of these behaviours.

Comparison of behavioural events and states across the four contexts

To compare male behavioural responses to the four different contexts, I ran separate mixed effects models for each behavioural event/state with context as the fixed effect, individual identity as the random effect and with the error structure that

matched each response variable (for details, refer to the methods section). To complement the mixed effects models, I also compared male responses to the four different contexts by calculating differences and log-differences in behavioural responses between pairs of contexts. The results from these analyses are organised to answer the following questions:

1. Regular and NP: What is the effect of an intruder on the behaviour of the resident male?

2. Control and NP: Is the model treated differently as compared to a novel object?

3. FP and NP: How does the presence of an intruder at different locations with respect to the rock perch occupied by the male (i.e., different levels of threat) affect his response?

Behavioural events:

Males performed head bobs more frequently when exposed to an intruder on perch than when there was no intruder. Other behavioural events (head move and push up) did not show any difference in rates depending on presence or absence of an intruder.

Head move, head bob and push up did not differ when comparison of intruder and novel object was done (see Table 4). Even when the intruder threat was varied, the behavioural events did not show any detectable difference.

Behavioural states:

Compared to Regular, the proportion (amount of time the behavioural state was displayed, out of 5 minutes) of gular extension, lateral compression and tail raise was consistently higher in NP. Even in NP and Control, it was observed that gular extension and lateral compression is displayed consistently more when the intruder was present on perch. Varying the intruder threat lead the lizards to show gular extension, lateral compression and tail raise statistically significantly more when the threat was high, as compared to when the threat was low (Table 5). Gular extension

small was included as a separate dependant variable because it was much more common than the other levels of gular extension (refer to methods section for details) and we wanted to understand how it was used in different contexts.

Behaviour	Head Bob				Push Up				Head Move			
	Estimate	SE	Z value	p value	Estimate	SE	Z value	p value	Estimate	SE	Z value	p value
Intercept (Type : NP; Individuals around : Absent)	1.189	0.256	4.65	3.30E-06	-1.456	0.542	-2.68	0.0073	2.8	0.091	30.68	<2E-16
Type FP	-0.211	0.303	-0.7	0.487	0.365	0.465	0.78	0.4332	-0.0898	0.1138	-0.79	0.43
Type Regular	-0.619	0.26	-2.38	0.017	0.258	0.42	0.61	0.5388	-0.0555	0.978	-0.57	0.5708
Type CONTROL	-0.884	0.525	-1.68	0.092	0.869	0.877	0.99	0.3216	0.0533	0.1855	0.29	0.7737
MPRES	0.26	0.376	0.69	0.49	0.556	0.609	0.91	0.3617	0.3383	0.1225	2.76	0.0058
FPRES	0.594	0.361	1.65	0.1	-0.39	0.639	-0.61	0.5421	-0.3685	0.1287	-2.86	0.0042

Table 4: Effect of context on Behavioural Events. Results from modelling rate of behavioural events as a function of the social (presence of conspecific individuals) context and type of intruder using mixed effects model. See methods section for details. MPRES and FPRES is the average number of males and females seen near the focal individual.

Behaviour	Gular Extension				Gular Extension Small				Lateral Compression				Tail Raise			
	Est	SE	Z value	p value	Est	SE	Z value	p value	Est	SE	Z value	p value	Est	SE	Z value	p value
Intercept (Type : NP; Individuals around : Absent)	-2.32	0.54	-4.26	2.07E-05	-4.60	0.77	-6.00	1.96E-09	-3.47	1.03	-3.36	0.000793	-2.57	0.59	-4.31	1.61E-05
Type FP	-1.2	0.06	-18.24	<2E-16	-0.56	0.085	-6.59	4.16E-11	-2.303	0.079	-29.11	<2E-16	0.54	0.054	9.807	<2E-16
Type Regular	-1.32	0.05	-25.13	<2E-16	-0.59	0.078	-7.525	5.28E-14	-2.59	0.06	-40.67	<2E-16	-0.86	0.05	-16.92	<2E-16
Type CONTROL	-2.59	0.19	-13.63	<2E-16	0.79	0.24	3.36	0.000778	-2.83	0.14	-19.61	<2E-16	0.054	0.093	0.587	0.5631
MPRES	-0.877	0.12	-7.17	7.50E-13	-0.89	0.15	-5.84	5.34E-09	1.29	0.12	10.87	<2E-16	0.16	0.08	1.97	0.0491
FPRES	-0.052	0.087	-0.6	0.549	-0.86	0.11	-7.49	6.75E-14	-1.74	0.11	-15.47	<2E-16	-1.46	0.1	-14.01	<2E-16

Table 5: Effect of context on Behavioural States. Results from modelling rate of behavioural events as a function of the social (presence of conspecific individuals) context and type of intruder using mixed effects model. See methods section for details. MPRES and FPRES is the average number of males and females seen near the focal individual.

But all these models suffered from overdispersion, and therefore, the results from statistical hypothesis tests have to be treated with caution. One way to take care of the overdispersion problem is to carry out statistical null-hypothesis tests through permutation tests, which is beyond the scope of this thesis.

I subtracted the rates and proportions of behaviours between contexts and calculated the 95% confidence interval of all values. Comparing Regular and NP, I found that the proportion of time spent in lateral compression was consistently higher when the intruder was present than when it was absent. Presence of an intruder on the perch also led the lizards to have a higher proportion of lateral compression than when a novel object was present. Varying the intruder threat did not lead to any change in the rates or proportion of the behaviours.

Taking the log ratio of rates and proportions of behaviours and calculating the 95% confidence interval of all values, no difference was found in NP and Regular. However, gular extension and lateral compression was higher in NP as compared to Control. Again, varying the intruder threat did not have any effect on the rates and proportion of behaviours.

Figure 14: Resident male attacking the intruder present on perch.

Fig 15: Difference of rates of behaviours between contexts a) Regular and NP b) CONTROL and NP and c) FP and NP

Figure 16: Difference in proportion of time spent in different behaviours between contexts a) Regular and NP b) CONTROL and NP and c) FP and NP (GE: Gular Extension, GES: Gular Extension Small, LC: Lateral Compression, TR: Tail Raise)
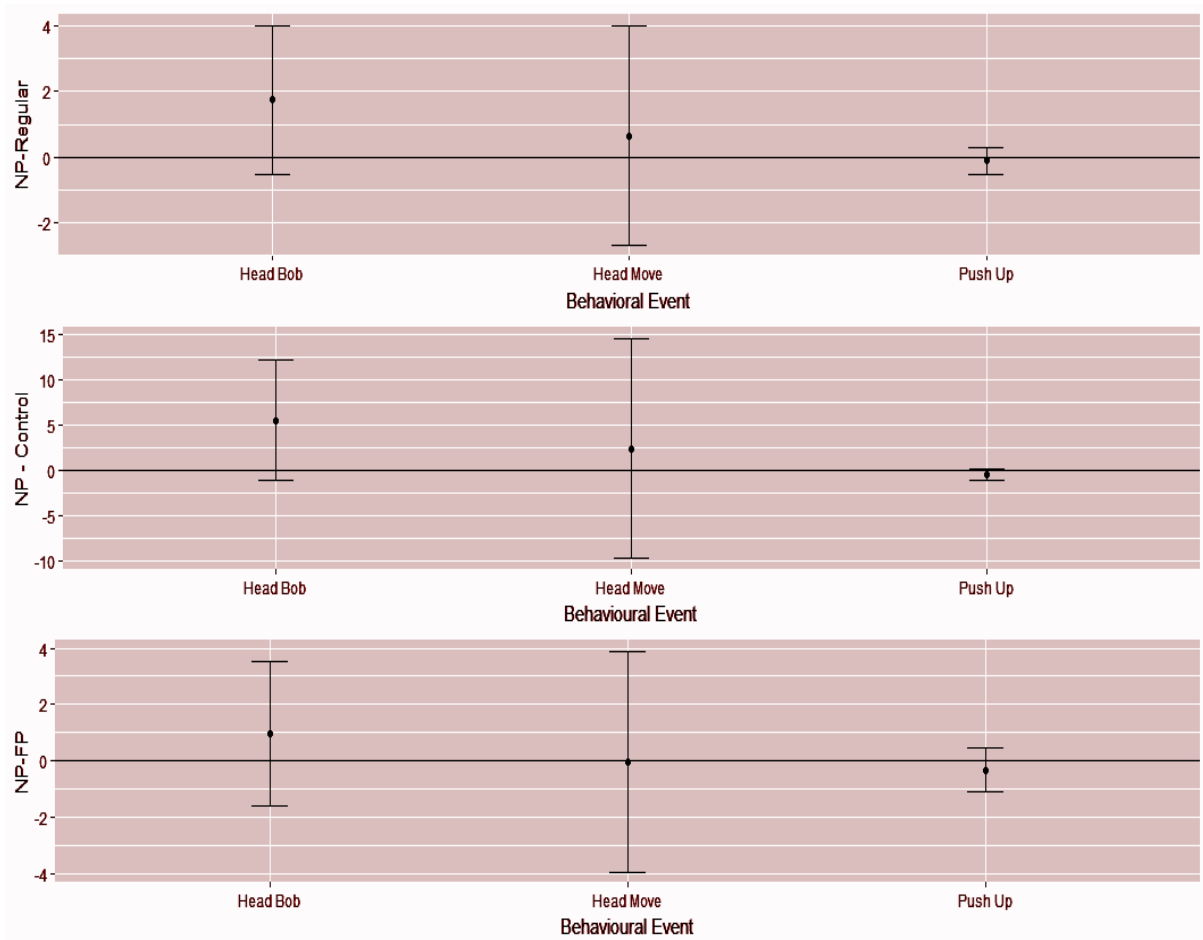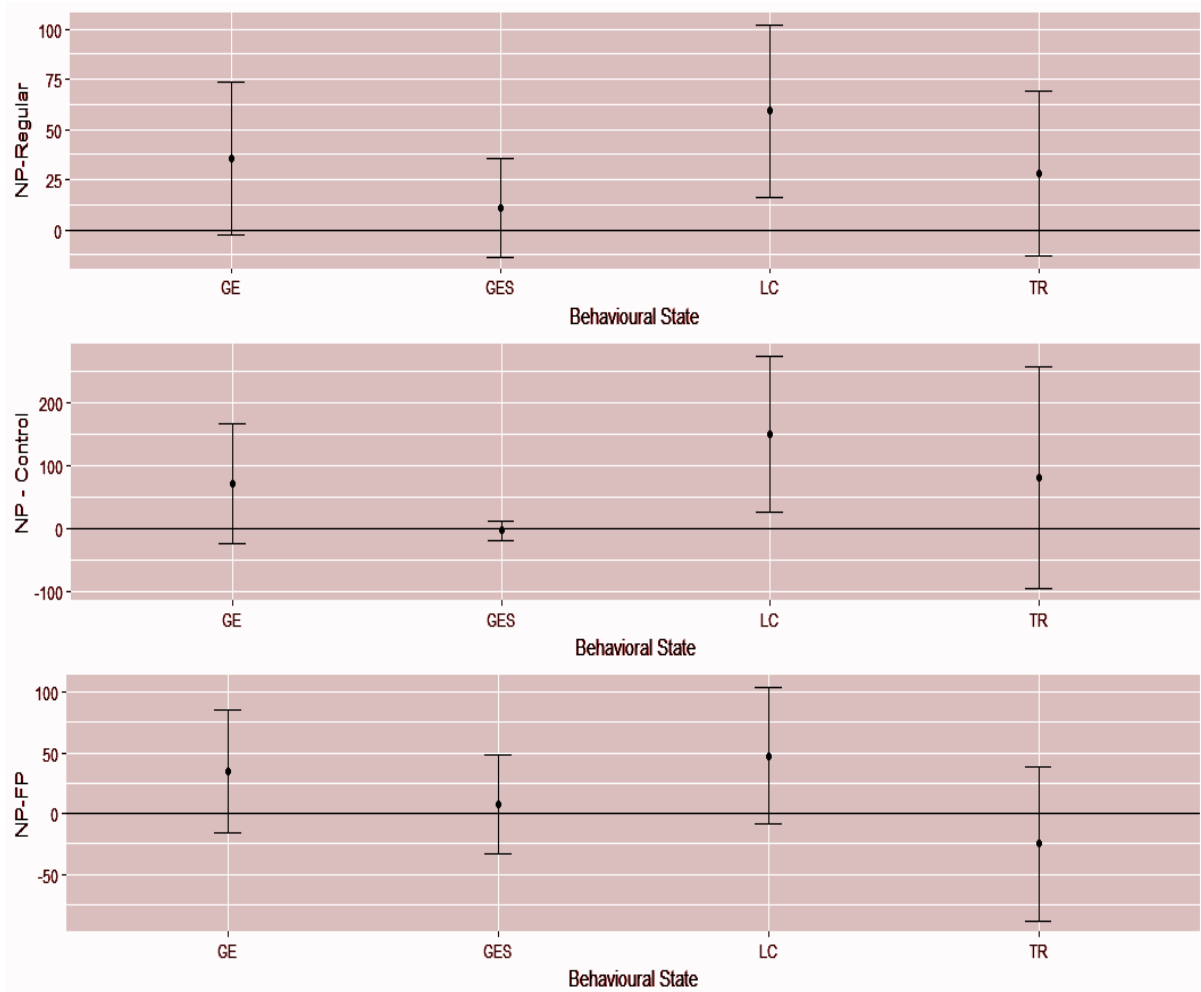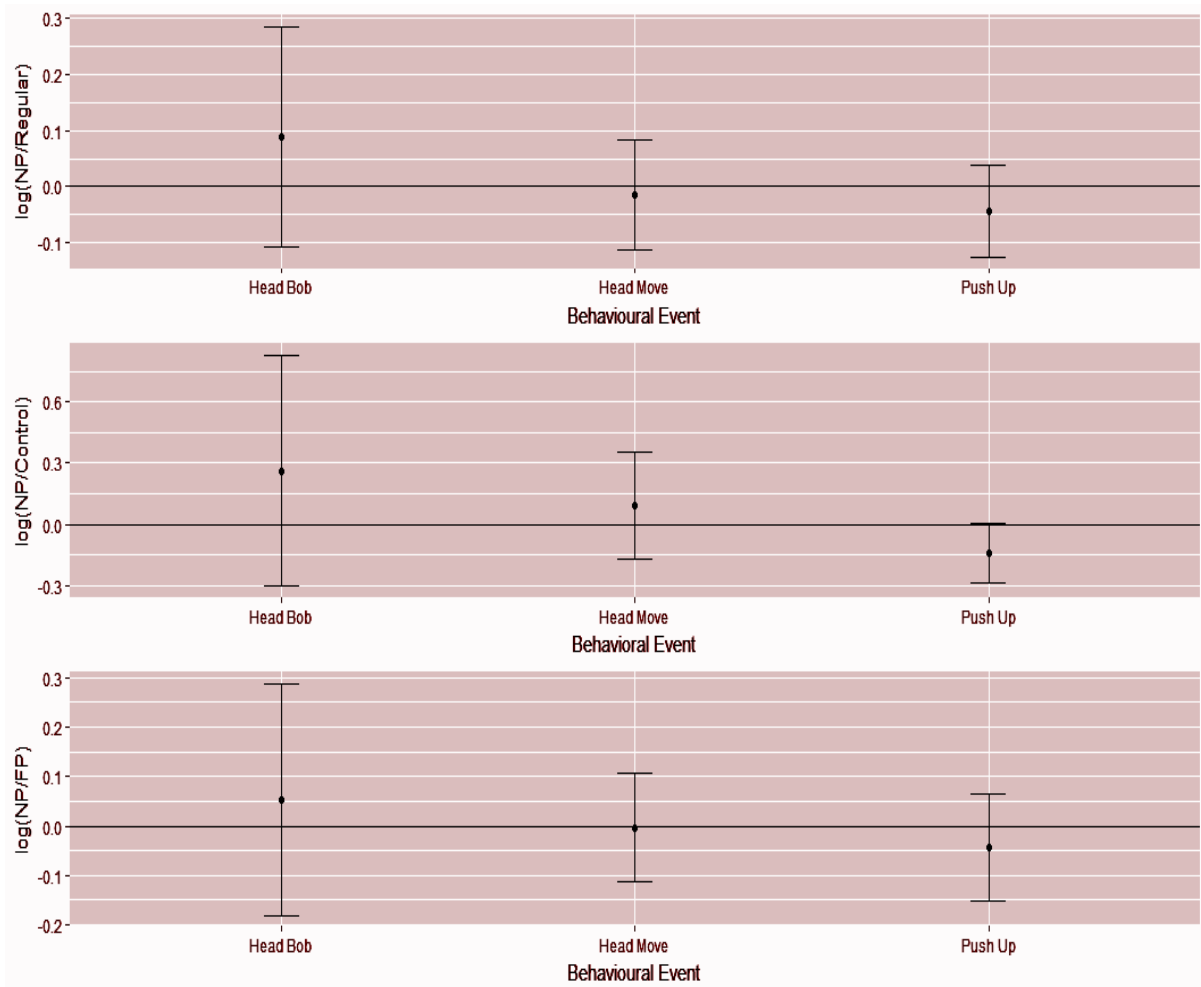
Fig 17: Log ratio of rates of behaviours between contexts a) Regular and NP b) CONTROL and NP and c) FP and NP
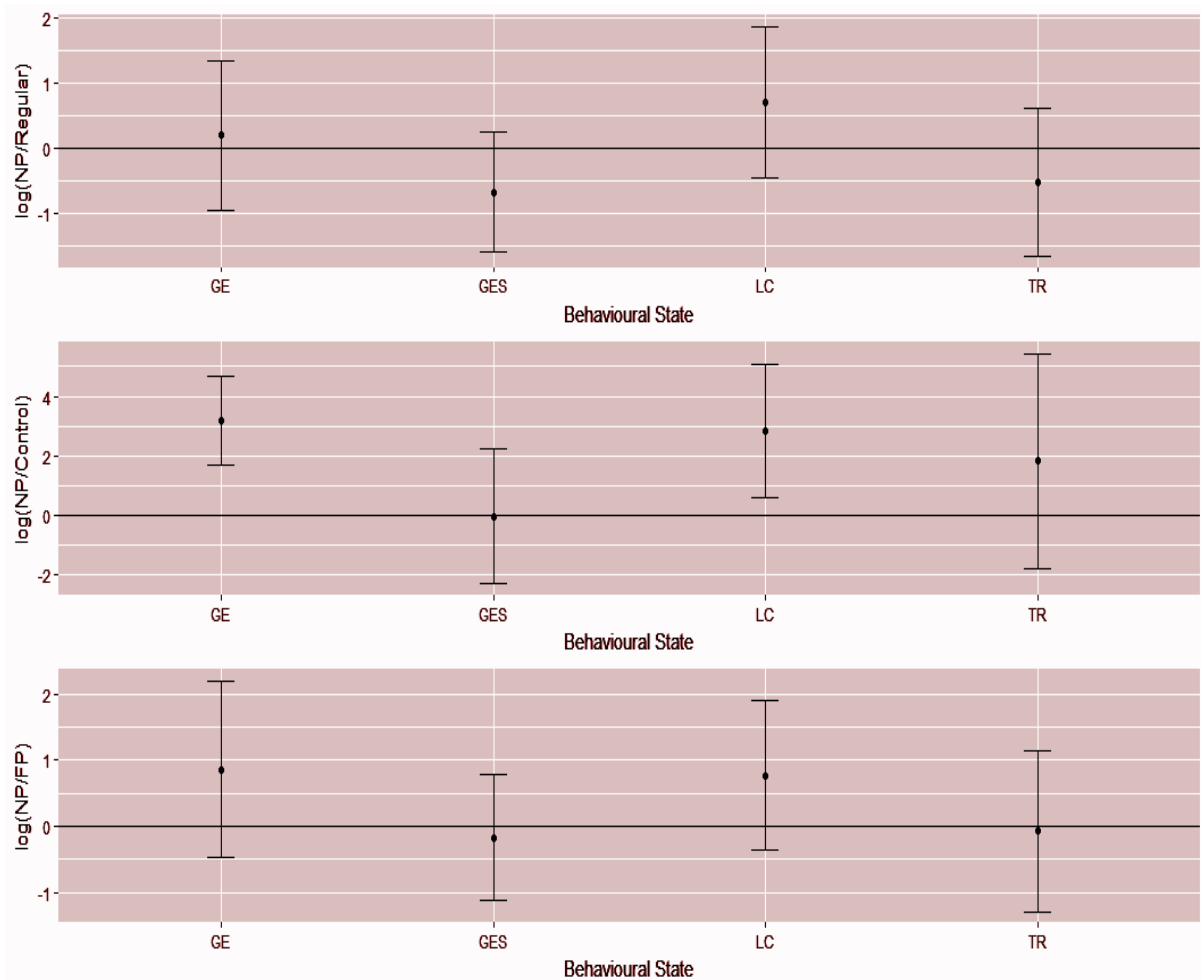
Figure 18: Log ratio of proportion of time spent in different behaviours between contexts a) Regular and NP b) CONTROL and NP and c) FP and NP (GE: Gular Extension, GES: Gular Extension Small, LC: Lateral Compression, TR: Tail Raise)

Proportion of times gape, bite, pushing of model, approaching within 1 m of the model and yellow red colouration was displayed was compared between contexts. It was found that gape was seen in NP consistently in a higher proportion as compared to Regular, and male came within 1 m from the model more during NP as compared to FP. Other comparisons between Regular and NP, Control and NP and NP and FP did not yield any statistically significant results.

Behaviour			Comparison of Regular and NP	Comparison of Control and NP	Comparison of FP and NP
Gape	Estimate	Prop1	0	0	0.05
		Prop2	0.1764	0.15	0.15
	95% CI		(-0.3982,0.0452)	(-0.4315,0.1315)	(-0.3333,0.1333)
	x^2		4.9525	0.0237	0.2777
	p-value		**0.026**	0.8777	0.5982
Yellow-Red Colouration	Estimate	Prop1	0.044	0	0.05
		Prop2	0.2	0.2	0.2
	95% CI		(-0.377,0.0659)	(-0.5003,0.1003)	(-0.3996,0.0996)
	x^2		2.3577	0.1674	0.9143
	p-value		0.1247	0.6824	0.339
Bite	Estimate	Prop1		0	0
		Prop2		0.1	0.1
	95% CI			(-0.3314,0.1314)	(-0.2814,0.0814)
	x^2			3.17E-31	0.5263
	p-value			1	0.4862
Pushing the Model	Estimate	Prop1		0	0
		Prop2		0.05	0.05
	95% CI			(-0.1955,0.0955)	(-0.1955,0.0955)
	x^2			3.68E-32	0
	p-value			1	1
Within 1 m	Estimate	Prop1		0.8	0.4
		Prop2		0.85	0.85
	95% CI			(-0.4839,0.3839)	(-0.7657,-0.1343)
	x^2			3.21E-31	6.8267
	p-value			1	**0.008981**

Table 6: Pairwise comparison of number of times the above-mentioned behaviours were seen across contexts.

Discussion:

In this study, I have compared behavioural responses of males across different contexts and examined a male's response to varying intruder threat. Most studies involving an intruder threat in lizards are performed in the lab or semi-captive conditions. Although they are important in ascertaining the behaviours that can be displayed by the lizards towards intruders, the ecological relevance of these behaviours in their natural habitat, which usually involves males displaying from established home ranges and territories, is lacking in such studies. I presented different types of models in the home ranges of these lizards, which represent different levels of threat, and compared their response to these models.

Comparison of Rate of Behavioural Events across contexts:

Comparing the rate of behavioural events in Regular, NP, FP and CONTROL, I observed that head move is the most common behaviour across all contexts, followed by head bob and one of its variations, half head bob. There was a huge variation in the frequencies of different behaviours, with a few of them being extremely rare.

Many such behaviours like head bob, push up and crouch and shudder, are observed in other species of lizards as well. Earlier studies have found that head bob display rate increases when another male is present nearby, as compared to male-alone contexts (Decourcy and Jenssen, 1994), and hence is used as both "assertion" and "challenge" display. In the sagebrush lizard, *Sceloporus graciosus*, push ups are used in multiple scenarios. During agonistic encounters in males, push-up displays expose their gular pouch and blue belly. But, this push-up display is also seen after bouts of locomotion, and hence, might perform multiple functions (Martins, 1993). In *Anolis carolinensis*, even recently hatched juveniles show head bob display after locomotion (Cooper Jr., 1971).

Crouch and shudder is also seen in many other lizard species, in the context of courtship. This behaviour has been named differently by different researchers, with some of them calling it "nod-sets", "courtship nods", "jiggling" or just "shudder".

Although courtship is the most widely assumed function of this behaviour, it has also been mentioned as an aggressive behaviour which signals social dominance. (Carpenter, 1962; Rothblum and Jenssen, 1978; Ruby, 1977; Smith and John-Alder, 1999)

Response to intruder threat across different contexts:

When presented with an intruder, the resident is expected to respond to the intruder based on the intruder's perceived capabilities, the resident's own abilities as well as the value of the contested resource (Swierk and Langkilde, 2013). The present study is ideal to examine response towards intruder when the value of contested resource is varied. In this experiment, no intruders were presented in the home ranges of lizards in Regular, a novel object was placed on a rock perch occupied by the lizard in CONTROL, an intruder was put on the perch (high value resource) in NP, and an intruder was presented on the ground (low value resource) next to the perch occupied by the lizard in FP. By comparing Regular and NP, we can quantify behavioural responses to an intruder at a highly valued resource. By comparing CONTROL and NP, we can verify if the model is indeed treated as an intruder, or just a novel object, and by comparing NP and FP, we can evaluate the response to varying values of the contested resource.

Comparing NP and Regular, it was found that the proportion of time spent in lateral compression is consistently higher in NP. Other behavioural events and states did not show any change from the basal level, where the intruder was absent. Lateral compression, or lateral display, is directed at the intruder and signals the motivation to attack the trespasser. In collared lizard, *Crotaphytus collaris*, lateral display rate and aggression are positively correlated (Husak, 2004). Also, gape was observed consistently more often in NP than regular. Gape is a behaviour which has been described as an aggressive behaviour used during agonistic encounters. In a parthenogenic lizard, *Cnemidophorus uniparens*, gape is observed in the presence of an intruder (Grassman and Crews, 1987). Gape might be an indicator that the individual is ready to escalate and bite the opponent (Godfrey et al., 2012). Therefore, it is very likely that it is the presence of the intruder that is causing the

lizards to gape more often. In this scenario, we do see that the residents respond to the intruder using at least two behaviours associated with aggression in lizards.

During NP focals, lizards showed consistently higher proportion of gular extension and lateral compression when compared with Control. This demonstrates that the model lizards are indeed treated differently than novel objects. Even though the function of gular extension remains equivocal, it is seen more frequently during male-male encounters, as compared to male-female encounters (Simon, 2011). Instead of a gular pouch, many lizards have dewlaps (skin folds hanging on the throat), which are extended during social encounters. It has been suggested that rival males elicit dewlap extension in the Brown Anole, *Anolis sagrei* (Scott, 1984). In *Psammophilus dorsalis*, it has been argued that gular extension displays are directed towards conspecific males (Radder et al., 2006). Combined with the information that lateral compression is also an aggressive behaviour, this suggests that intruders elicit more aggression than novel objects.

Residents did not show any difference in response when the intruder threat was varied. The rates of behavioural events and the proportions of behavioural states remained unchanged with the variation in threat. However, individuals approached the intruder more often when the threat was high (NP), than when the threat was low (FP). It is possible that the lizards attempt to collect more information about the intruder when it represents a higher threat. During the day, males spend most of their time on top of rock perches (Pers. Observation). During NP, the models were presented at the same location on the perch that they previously occupied. Hence, it is possible that rather than approaching the model, they are coming back to their original position and therefore individuals come within 1 metre from the model more often as compared to FP.

Contrary to what was expected, behavioural events like head bob and push up, which are used in agonistic encounters in other species, did not show any difference across the contexts which were compared. Tail raise display, which was among one of the behavioural states measured, does not seem to be common among male lizards. However, in an iguanid lizard, *Liocephalus carinatus coryi*, males raise their tails in the presence of an intruder (Evans, 1953). Previously, it was believed that in *Psammophilus dorsalis*, only females raise their tails, and it was suggested that it

signals receptivity to males (Radder et al., 2006). Our study demonstrates that tail raise is displayed by males as well, but it does not seem to perform any aggressive function. Tail raise did not show any significant difference across the contexts which were compared. It is possible that tail raise display plays a role in species recognition (Gibbons, 1979). Also, bite frequency and number of times the model was pushed was not different between contexts. This agrees well with our previous understanding that actual aggression might be rare among animals, as it can be extremely costly for them.

The finding that individuals do not change their display rates and proportions with varying level of threat is a little surprising as it is expected that individuals modulate their behaviour based on the threat. This has been shown in multiple other species, including the ant *Temnothorax longispinosus*, which attacks its slave-making species much more aggressively than its non-nestmate conspecific (Scharf et al., 2011). In sand fiddler crabs, males show higher intensity of aggression and escalate more frequently when encountered with an unfamiliar intruder as compared to a neighbour, which represents lesser threat than the unfamiliar conspecific (Pratt and McLain, 2006).

Following are the possible reasons why there was no difference in display rates and proportions between NP and FP:

●   More cues might be required from the intruder in order to respond differentially. Perhaps a robotic model can be used as an intruder.

●   It was expected that some regions within the home range of the lizard might be more important than others. However, that might not be the case in *P. dorsalis*, with the owners defending all regions within the home range equally. NP and FP may not actually differ in the level of intruder threat as believed earlier.

●   The presence or absence of other conspecific individuals is not incorporated into these results. It may be possible that including them might lead to some changes in the result.

Increase in lateral compression during NP as compared to Regular and CONTROL and gape during NP as compared to regular suggests that male *P. dorsalis* indeed act aggressively towards other males. Individuals modulate their signals based on

presence/absence of an intruder. Also, since NP vs FP may not actually be a change in level of threat, they do not alter their levels of signalling. Behaviours like head bob and push ups, which are considered aggressive in other species of lizards, may not be used in aggressive encounters in the case of *P. dorsalis*.

Since the males use costly signals to communicate aggression towards intruders, this study demonstrates that male *P. dorsalis* indeed defend their home range. Preventing the home range from intrusion possibly allows the males to have access to females, as they overlap multiple female home ranges. Hence, home range defence can have potential fitness benefits.

Conclusion:

This study provides evidence for the existence of intrasexual competition among male *Psammophilus dorsalis*. I found that individuals signal more aggressively when an intruder is present than when it is absent or when a novel object is present. This indicates that intruders might possibly have negative fitness effects, leading the resident to display aggressively towards them. When the intruder threat was varied, residents displayed similarly to models in both scenarios, but they approached the model more often when the threat was high. We also report a new behaviour, lateral compression, which is not frequently found in the lizard literature, as an aggressive behaviour. Although there are many studies in lizards which indicate signalling and aggressive behaviour to an intruder, they are done in lab or semi-captive conditions, where the individuals are not in their "natural territories/home ranges", and ours is the first such study on a tropical lizard in the field.

References:

Alatalo, R. V., Lundberg, A., and Glynn, C. (1986). Female pied flycatchers choose territory quality and not male characteristics. *Nature 323*, 152–153.

Alberts, S.C., Altmann, J., and Wilson, M.L. (1996). Mate guarding constrains foraging activity of male Baboons. *Anim. Behav. 51*, 1269–1277.

Alvarez, F. (1993). Risks of Fighting in Relation to Age and Territory Holding in Fallow Deer. *Can. J. Zool. Can. Zool. 71*, 376–383.

Balakrishna, S., Batabyal, A., and Thaker, M. (2016). Dining in the city: Dietary shifts in Indian rock agamas across an urban-rural landscape. *J. Herpetol. 50*, 1–6.

Boesch, C., Kohou, G., Néné, H., and Vigilant, L. (2006). Male Competition and Paternity in Wild Chimpanzees of the Tai Forest. *Am. J. Phys. Anthropol. 130*, 103–115.

Briffa, M. (2008). Decisions during fights in the house cricket, *Acheta domesticus*: mutual or self assessment of energy, weapons and size? *Anim. Behav. 75*, 1053–1062.

Briffa, M., and Elwood, R.W. (2005). Rapid change in energy status in fighting animals: Causes and effects of strategic decisions. *Anim. Behav. 70*, 119–124.

Calsbeek, R., and Marnocha, E. (2006). Context dependent territory defense: The importance of habitat structure in *Anolis sagrei. Ethology 112*, 537–543.

Carazo, P., Font, E., and Desfilis, E. (2008). Beyond nasty neighbours and dear enemies? Individual recognition by scent marks in a lizard. *Anim. Behav. 76*, 1953–1963.

Carpenter, C.C. (1962). Patterns of Behavior in Two Oklahoma Lizards. *Am. Midl. Nat. 67*, 132–151.

Cooper Jr., W. (1971). Display behavior of hatchling *Anolis carolinensis. Herpetologica 27*, 498–500.

Cox, C.R., and Le Boeuf, B.J. (1977). Female Incitation of Male Competition: A Mechanism in Sexual Selection. *Am. Nat. 111*, 317–335.

Darwin, C. (1871). The Descent of Man, and Selection in Relation to Sex.

Davies, N.B., and Halliday, T.R. (1978). Deep croaks and fighting assessment in toads *Bufo bufo. Nature 274*, 683–685.

Decourcy, K.R., and Jenssen, T.A. (1994). Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis. Anim. Behav. 47*, 251–262.

Driessens, T., Vanhooydonck, B., and Van Damme, R. (2014). Deterring predators, daunting opponents or drawing partners? Signaling rates across diverse contexts in the lizard *Anolis sagrei. Behav. Ecol. Sociobiol. 68*, 173–184.

Evans, L.T. (1953). Tail display in an iguanid lizard, *Liocephalus carinatus coryi. Copeia 1953*, 50–54.

Fenner, A.L., and Bull, C.M. (2011). Central-place territorial defence in a burrow-dwelling skink: Aggressive responses to conspecific models in pygmy bluetongue lizards. *J. Zool. 283*, 45–51.

Friard, O., Gamba, M., and Fitzjohn, R. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol. Evol. 7*, 1325–1330.

Gibbons, J.R.H. (1979). The Hind Leg Pushup Display of the *Amphibolurus decresii* Species Complex (Lacertilia : Agamidae). *Copeia 1979*, 29–40.

Godfrey, S.S., Bradley, J.K., Sih, A., and Bull, C.M. (2012). Lovers and fighters in sleepy lizard land: Where do aggressive males fit in a social network? *Anim. Behav. 83*, 209–215.

Grassman, M., and Crews, D. (1987). Dominance and reproduction in a parthenogenetic lizard. *Behav. Ecol. Sociobiol. 21*, 141–147.

Hernandez-Jimenez, A., and Rios-Cardenas, O. (2012). Natural versus sexual selection: Predation risk in relation to body size and sexual ornaments in the green swordtail. *Anim. Behav. 84*, 1051–1059.

Hibbitts, T.J., Whiting, M.J., and Stuart-Fox, D.M. (2007). Shouting the odds: Vocalization signals status in a lizard. *Behav. Ecol. Sociobiol. 61*, 1169–1176.

Husak, J.F. (2004). Signal use by collared lizards, *Crotaphytus collaris*: The effects of familiarity and threat. *Behav. Ecol. Sociobiol. 55*, 602–607.

Martins, E. (1993). Contextual use push-up display by the sagebrush lizard, *Sceloporus graciosus. Anim. Behav. 45*, 25–36.

Martins, E.P., Ord, T.J., and Davenport, S.W. (2005). Combining motions into complex displays: Playbacks with a robotic lizard. *Behav. Ecol. Sociobiol. 58*, 351–360.

Martins, E.P., Ord, T.J., Slaven, J., Wright, J.L., and Housworth, E.A. (2006). Individual, sexual, seasonal, and temporal variation in the amount of sagebrush lizard scent marks. *J. Chem. Ecol. 32*, 881–893.

Ord, T.J., Peters, R. a., Evans, C.S., and Taylor, A.J. (2002). Digital video playback and visual communication in lizards. *Anim. Behav. 63*, 879–890.

Pandav, B., Shanbhag, B.A., and Saidapur, S.K. (2007). Ethogram of Courtship and Mating Behavior of *Calotes. Curr. Sci. 93*, 1164–1167.

Parker, G.A. (1974). Assessment Strategy and Evolution of Fighting Behavior. *J. Theor. Biol. 47*, 223–243.

Paterson, A. V., and McMann, S. (2004). Differential Headbob Displays toward Neighbors and Nonneighbors in the Territorial Lizard *Anolis sagrei. J. Herpetol. 38*, 288–291.

Pratt, A., and McLain, D.K. (2006). How dear is my enemy: Intruder-resident and resident-resident encounters in male sand fiddler crabs (*Uca pugilator*). *Behaviour 143*, 597–617.

R Core team (2015). R Core Team. R A Lang. Environ. Stat. Comput. R Found. Stat. Comput. , Vienna, Austria. ISBN 3-900051-07-0, URL http//www.R-Project.org/. *55*, 275–286.

Radder, R.S., Saidapur, S.K., and Shanbhag, B.A. (2005). Population density, microhabitat use and activity pattern of the Indian rock lizard, *Psammophilus dorsalis* (Agamidae). *Curr. Sci. 89*, 560–566.

Radder, R.S., Saidapur, S.K., Shine, R., and Shanbhag, B.A. (2006). The language of lizards: Interpreting the function of visual displays of the Indian rock lizard, *Psammophilus dorsalis* (Agamidae). *J. Ethol. 24*, 275–283.

Rothblum, B.L., and Jenssen, T.A. (1978). Display Repertoire Analysis of *Sceloporus undulatus hyacinthinus* from South-Western Virginia. *Anim. Behav. 26*, 130–137.

Ruby, D.E. (1977). The Function of Shudder Displays in the Lizard *Sceloporus jarrovi*. *Copeia 1977*, 110–114.

Ryan, M., Tuttle, M., and Rand, S. (1982). Bat predation and Sexual advertisement in a neotropical anuran. *Am. Nat. 119*, 136–139.

Scharf, I., Pamminger, T., and Foitzik, S. (2011). Differential Response of Ant Colonies to Intruders: Attack Strategies Correlate With Potential Threat. *Ethology 117*, 731–739.

Scott, M.. (1984). Agonistic and courtship displays of male *Anolis sagrei. Breviora 49*, 1–22.

Simon, V.B. (2011). Communication Signal Rates Predict Interaction Outcome in the Brown Anole Lizard, *Anolis sagrei. Copeia 2011*, 38–45.

Smith, J.M., and Parker, G.A. (1976). The logic of asymmetric contests. *Anim. Behav. 24*, 159–175.

Smith, L.C., and John-Alder, H.B. (1999). Seasonal specificity of hormonal, behavioral, and coloration responses to within- and between-sex encounters in male lizards (*Sceloporus undulatus*). *Horm. Behav. 36*, 39–52.

Sreekar, R., Deodhar, S., and Kulkarni, Y. (2010). Predation on *Hemidactylus treutleri* (Squamata: Gekkonidae) by the peninsular rock agama *Psammophilus dorsalis* (Squamata: Agamidae) in Rishi Valley, Andhra Pradesh, India. *Herpetol. Notes 3*, 33–35.

Swierk, L., and Langkilde, T. (2013). Sizing-up the Competition: Factors Modulating Male Display Behavior During Mate Competition. *Ethology 119*, 948–959.

Tibbetts, E.A., and Lindsay, R. (2008). Visual signals of status and rival assessment in *Polistes dominulus* paper wasps. *Biol. Lett. 4*, 237–239.

Vehrencamp, S.L., Bradbury, J.W., and Gibson, R.M. (1989). The energetic cost of display in male sage grouse. *Anim. Behav. 38*, 885–896.