

**Personality along the boldness-shyness axis in
*Psammophilus dorsalis***

Thesis submitted in partial fulfillment of the requirements of
Five Year BS-MS Dual Degree Program



Indian Institute of Science Education and Research, Pune

By

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At

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Under the guidance of

Dr. Kavita Isvaran

Certificate

This is to certify that this dissertation entitled “Personality along the boldness-shyness axis in *Psammophilus dorsalis*” towards the partial fulfilment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research, Pune represents original research carried out by Rachana Bhave at the Indian Institute of Science, Bangalore, under the supervision of Dr. Kavita Isvaran during the academic year 2014-2015.

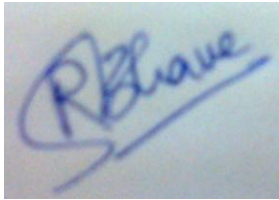


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Declaration

I hereby declare that the matter embodied in the report entitled “Personality along the boldness-shyness axis in *Psammophilus dorsalis*” are the results of the investigations carried out by me at the Centre for Ecological Science, Indian Institute of Science, Bangalore, under the supervision of Dr. Kavita Isvaran and the same has not been submitted elsewhere for any other degree.

A handwritten signature in blue ink, appearing to read 'Rachana Bhawe', is shown on a light-colored background. The signature is written in a cursive style with a horizontal line underneath.

Rachana Bhawe

26th March, 2015

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Abstract

Studies of personality, consistent behavioural differences between individuals, in animal behaviour reflect a paradigm shift in our understanding from the classical view of animals behaving optimally at all times. A wide range of studies in the past decade have described the existence of personality in animals across varied taxa. Nevertheless, studies measuring personality in wild populations, under their natural ecological and social contexts have been rather scarce. In addition, few empirical studies address the underlying drivers which can maintain personality, lesser so in the wild. As part of this thesis, I looked at the influence of state variables on personality using a novel study system the sexually dimorphic rock agama, *Psammophilus dorsalis*. I tagged and measured wild lizards and repeatedly assayed their response to a simulated threat within their natural home ranges and over a large part of their breeding lifespan. My study found substantial consistency in inter-individual differences in risk-taking, both in the short term, and over long term encompassing a large part of their breeding lifespan. Of all state-variables, sex and body condition seemed to be the most significant variables predicting differences in average risk-taking, but most of the measured state-variables were only weakly related to personality. The existence of clear personality variation in this wild lizard population, detectable even under typically variable and complex ecological and social conditions, opens a plethora of interesting opportunities to gain a better understanding of the adaptive role of personality in animal ecology.

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Next I would like to thank Rishi Valley School for providing me with the most luxurious field station I shall probably ever be in. The amazing time I had with the school kids and teachers alike shall always be remembered. The tranquil surroundings, hospitality and community at the school have been very enriching.

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especially like to thank Manvi, for keeping me such good company at times when it got too lonely and monotonous in the field station.

With this project comes the end of five exhilarating and fun-filled years that I have spent as a student in IISER-Pune. The end seems all too soon and the times spent too good to be true. Every interaction I have had with my professors, friends and colleagues alike has shaped me into the person I am today. There is almost a reluctance to finish this work because it would mean letting go of the wonderful environment at IISER that has nurtured me personally and professionally at every step. Needless to say, ecology and evolution classes shall sorely be missed. More than anyone else, I thank all my friends for always being there for me, keeping the madness and enthusiasm alive through the time that we have known each other .A special mention for those, who literally dragged me to the finish line with this one.

In the end I would like to thank my mother for her unending love and support throughout my endeavours. I wish to dedicate my work to the memory of my father and my beloved sister. In spite of their absence, they have given me immense strength and courage to pursue what I like doing.

Introduction

Personality in animals has, for long, been a well known but less accepted idea in the field of animal behaviour. Researchers in the past mostly focused on mean values of behaviours without formally addressing variance around the mean (Sih et al., 2004a). Theoretical and empirical work in animal behaviour has typically evaluated the average optimal behaviour, with the expectation that all individuals behave in a way that maximises net benefit. However, there has been increasing awareness of the fact that individuals often behave in ways which are consistently different from the expected optimal behaviour. This consistent inter-individual variation in behaviour is called personality (Carter et al., 2013). Other terms in literature such as behavioural types (Bell, 2007), coping styles (Koolhaas, 1999) or temperament (Boissy, 1995) also refer to personality. While personalities have been studied in humans primarily, there is mounting evidence about the existence of personalities in other animals as well. Several studies have reported the occurrence of personalities not only in domesticated and lab reared animals, but those in the wild too (Réale et al., 2010; Sih et al., 2004a). In addition, researchers have shown how in some cases consistent inter-individual differences can occur, in seemingly uncorrelated behaviours. For example, in some species, individuals that are aggressive to conspecifics are also bold in the face of a threat. This correlation of different behavioural types is referred to as behavioural syndromes. The field of behavioural syndromes and personality has caused a paradigm shift in our understanding of animal behaviour in the past couple of decades. It challenges the view that animals have an infinitely plastic behavioural response which is optimal in all situations (Sih et al., 2004b). Instead, the focus has now shifted on trying to understand the nature of variation in individual behavioural responses and the possible underlying factors which evolve and maintain these differences (Bell, 2007).

There is growing interest in personality research because of its ecological and evolutionary implications on behaviour (Réale et al., 2007; Sih and Bell, 2008). Studies have shown how being a certain behavioural type, can influence the dynamics of ecological variables in a population such as the anti-predator response, dispersal patterns, foraging, habitat usage as well as mate choice in a non-random fashion (Réale

et al., 2010; Sih and Bell, 2008). Individuals who are more bold or exploratory are the ones to first disperse in a population of great tits (Dingemanse et al., 2002). Further, social groups or foraging groups in some species may consist of assortative behavioural types which may lead to increased group benefit. In addition, personality can change fitness dynamics in a population. A study on great tits showed that fast explorers were selected for, in a resource poor habitat, however with increased predation risk slow explorers did better in the same habitat (Dingemanse et al., 2004). The correlation of behavioural traits can also impose an evolutionary constraint on the ability of animals to achieve optimality in each behavioural type independent of the other (Dochtermann and Dingemanse, 2013; Sih and Bell, 2008). For example, exploratory behaviour can help an individual gather more information about the resource structure of the habitat, but can also make it more prone to predation if boldness and exploratory behaviour are correlated.

Framework for understanding evolution and maintenance of personality

In the past decade, there have been a plethora of studies describing the existence of personalities in diverse behavioural contexts for several species across different taxa. However, empirical studies addressing the underlying proximate and ultimate causes of personality traits have been conducted only recently (Dall and Griffith, 2014; Dingemanse and Wolf, 2010). The reaction norm framework is a good conceptual tool to understand how various drivers affect the mean (intercept) and variation (slope) of behavioural responses, thus shaping personality (Dingemanse et al., 2010; Sih and Bell, 2008). This would involve addressing two fundamental questions (Schuett et al., 2010; Stamps, 2007):

1. Why is there inter-individual variation in behavioural response if, individuals experience the same set of environmental conditions by virtue of belonging to the same population?
2. Why are between individual differences in behaviour consistent across time and varied contexts?

The theoretical and conceptual framework to understand the possible drivers of personality and its adaptive role has been well-laid in published literature (Réale et al., 2010; Sih et al., 2004a; Wolf and Weissing, 2010). Some suggest that multiple behavioural types within the same population can arise if individuals differ in some state variable such as body condition, or hormonal levels, which in turn might be a result of genotype by environment interactions. If these differences in state remain stable over the lifetime of an individual, it could explain consistency in inter-individual variation as well (Wolf and Weissing, 2010). In some other cases, behavioural types in a population may be a result of negative frequency dependence where the rare behavioural type is advantageous and thus stably coexists. Stable differences in behavioural types can arise if the cost of plasticity in behaviour is very high as is the case in a stochastic environment. Of the proposed explanations about the evolution and maintenance of personality traits, for the purpose of the thesis, I decided to focus on understanding personality from a state-dependent perspective.

State-dependent mechanisms of maintaining personality

State variables refer to any condition of an individual with respect to its environment, relevant to increasing its fitness (Dingemanse and Wolf, 2010). It can include features of the focal individual such as its body size, age, morphology or body colour at the individual level and body temperature, hormone levels or parasite load at the physiological level (Dingemanse and Wolf, 2010). Since the condition of an individual can be relatively stable over a long period of time, it can also explain the existence of consistency in inter-individual variation. Till date there have been few empirical studies that have examined whether differences in a behavioural type are correlated with the state of an individual and the evidence is mixed. There are some cases in which state is strongly correlated with personality. It has been shown that body size and body condition of an individual is a good predictor of the anti-predator behavioural response in Iberian rock lizards, where poor body condition lizards are shy whereas lizards with a better body condition are bold (López et al., 2005). However, effect of state variables on differences in personality, have been shown to be specific to the species as well as to the particular behaviour (Bell et al., 2009; Fernández-Juricic et al., 2006). For example,

while studies have shown females to be more consistent than males in mate-choice, with respect to other behaviours such as anti-predator response, exploratory behaviour etc., males are more consistent than females (Bell et al., 2009).

Most other studies however, merely report if there are inter-individual differences in behaviour and propose correlations with state-variables without measuring or testing the correlations (Montiglio et al., 2015; Wolf and Weissing, 2010). In spite of a well worked out theoretical model, predicting the role of state-dependence in maintaining personality, there is little empirical evidence for it (Dall and Griffith, 2014; Luttbeg and Sih, 2010; Nussey et al., 2007).

Personality and plasticity

A relevant aspect of personality is the extent to which there is consistency in inter-individual differences. Varying levels of consistency in personality can possibly indicate how plastic an individual is. Studying plasticity in a behavioural type, can thus help gain some insights into the evolution of plasticity itself, in animals (Sih and Bell, 2008). It can indicate not only how genotypes interact with the environment as has been classically studied in evolutionary biology, but also unravel the nature of Individual x Environment interactions (I X E). Since personality itself may constrain the range of plasticity, reporting the range of variation in personality has gained importance. A study on exploratory behaviour of great tits (*Parus major*) has shown that individuals who are exploratory are also very plastic compared to less exploratory individuals (Dingemanse et al., 2012). Since state variables are predicted to co-vary with personality, it is hypothesised that state variables may also determine how plastic individuals are (Brommer, 2013; Dingemanse et al., 2010). Empirical studies examining these relationships have, however been fairly scarce.

Objectives of Thesis

The first step, before evaluating the possible drivers of personality in any system, is to establish if personality exists at all in a given population (Sih et al., 2004b). This requires that individuals be repeatedly sampled for a particular behavioural response (Bell et al., 2009; Wolf and Weissing, 2010). Most studies which do report inter-individual variation in behaviour have observational data collected only for a few days. Long term studies demonstrating personality are relatively few in number (Dingemanse et al., 2002) and typically involve performing experiments and observations on either lab-reared individuals or individuals brought from the wild and assayed in strictly controlled conditions in the lab. It is still not known how clear and strong personality variation is, in the typically variable and complex ecological conditions that a wild population experiences. Furthermore, since the environmental and social context itself can shape the behavioural responses of individuals, there lies merit in carrying out long term behavioural studies in the wild to assess personality (Archard and Braithwaite, 2010).

Thus, the broad goal of the thesis was to evaluate the nature of variation in individual behavioural responses, and its correlation with differences in individual state, in a wild population. For addressing this question, it was important to use a study system in which adults could be uniquely identified and observed repeatedly over a considerably long period of time. Hence, I studied *Psammophilus dorsalis*, an Indian rock lizard which shows sexual dimorphism and is spread across open rocky habitats in Southern India.

I focused on personality along the boldness-shyness axis which has been one of the most studied in personality research (Sih and Bell, 2008). A proxy to the level of boldness of an individual is its risk-taking behaviour or anti-predator response, which can be quantified by measuring the Flight Initiation Distance (alternatively, FID) for each individual. A term taken from studies first done on birds (Frid and Dill, 2002), FID is the least distance from an approaching observer at which, the animal flees from its perch. Thus, individuals which are bolder are expected to have a shorter FID when compared with shy individuals (Samia et al., 2015). Frid and Dill (2002) suggest that since anti-predator responses can change depending on the nature of the habitat (available refuge

for the individual), distribution and abundance of predators as well as the behaviour of the predator, response to non-lethal stimulus in the form of human-disturbance should also follow the same decision rules. Further, since the cost of underestimating danger has far more severe consequences than overestimating it, decision rules with respect to predation risk can prevail in an artificial scenario as well. I examined the existence and degree of personality variation in risk-taking behaviour in a wild population of a sexually dimorphic rock lizard and evaluated potential factors, environmental as well as state-dependent, which could influence this variation in personality.

Specifically, the major objectives of the thesis were to:

- 1) Describe the general patterns in risk-taking behaviour at a population level with respect to:
 - a) Environmental factors, such as temperature and climate
 - b) State variables of individuals such as sex, body size, body condition and parasite load.
 - c) Habitat features such as perch height and distance to nearest refuge
- 2) Describe the personality in risk-taking behaviour and possible state-variables that might be correlated with it.
- 3) Describe the plasticity in personality within an individual and identify state-variables which might be correlated with it.

Hypotheses and predictions

I. Factors influencing average risk taking behaviour in *P.dorsalis*

Focusing on average patterns in risk-taking behaviour, I considered several primary state variables that might affect flight initiation distance in lizards. The state variables included sex of the individual, body size, body condition, and parasite load as well as

habitat features such as distance to nearest refuge and height at which an individual was perched (perch height). In all of these cases though, I have assumed that there is a certain cost associated with initiating flight and leaving its location, such as loss of territory or foraging benefit. My predictions regarding the average pattern in risk-taking with respect to each predictor are as follows:

- a) Sex: Based on the hypothesis that males of *P. dorsalis* face a sufficiently higher predation risk, owing to their conspicuous coloration, I predicted that males should have a higher FID than females. Since females are cryptically coloured, they are expected to minimise movement to avoid detection, unless the predator is threateningly close (Ydenberg and Dill, 1986).
- b) Body Size:- Studies have shown that larger sized individuals have a slower sprint speed flee earlier than individuals with small body size (Fernández-Juricic et al., 2006). I thus predicted that FID should increase as body size of individuals increases.
- c) Body Condition:- Body condition can be an indicator of an individual's reproductive potential (Wolf et al., 2007). Individuals with low body condition might have a low future reproductive potential and thus are predicted to stay on the perch, rather than risking possible loss of status in terms of access to mates or better territory by leaving early which may not be compensated in the future. Thus, as body condition increases, FID is expected to increase.
- d) Escape distance: With respect to refuge use, a study on gray squirrels shows that if the nearest refuge is farther away, animals escape earlier (Dill, 1989). Similarly I predicted that, individuals should show greater FID as escape distances increase
- e) Perch height: The height at which an individual is perched, can affect the accuracy of information it can gather about an approaching predator. Thus, individuals perched at a lower height were expected to leave the perch only if the threat was very close, irrespective of the distance to refuge. However at high perch heights, FID was expected to scale proportionately with escape distance. Thus, an interaction effect was also included in the model.

- f) Temperature and climate: Environmental factors such as temperature and climate were expected to affect flight initiation distance since these lizards are ectothermic. I predicted that decrease in temperature would co-vary with decrease in FID, since the lizards would be less responsive at low body temperatures. (Cooper and Frederick, 2007). Similarly, local climatic variables such as increased cloud cover were expected to reduce the FID.
- g) Season: Moving from May to November, the overall temperatures as well as reproductive potential of individuals decrease as the end of the breeding lifespan approaches (Cooper and Frederick, 2007). I expected average FID to gradually decrease later in the breeding season.

II. Factors correlated with personality

Understanding how different state variables co-vary with personality can reveal the possible mechanisms involved in the maintenance of personality. Since males and females in *P.dorsalis* are subjected to differential selection pressures, I expected sex-specific patterns in personality. Repeatability(R) is a measure used to evaluate the presence of personality, i.e., consistent inter-individual differences, in a population and refers to the proportion of variance in a behaviour that can be attributed to between-individual variance alone. It ranges from 0 to 1 where R=0 means there are no distinct inter-individual differences or personality, whereas R=1 indicates highly consistent inter-individual differences.

Sexual selection theory predicts that repeatability in a behavioural type can act as a reliable cue for individuals to evaluate mate quality, thus acting as an honest indicator (Schuett et al., 2010). This cue may be useful not only for females but other males to assess the quality of a male, thus signalling to a female while deterring competition with lower quality opponents. Strong sexual dimorphism in this species may indicate sexual selection acting on males; I thus expected males to be more repeatable than females in the breeding season. Differences in state variables such as body condition, body size or parasite load between individuals can also co-vary with personality. Asset protection principle is derived from life-history studies suggesting that individuals, who possess

resources that can increase their fitness, should be more cautious and take lesser risks. Thus, individuals with a better body condition, bigger body size or higher residual reproductive value (RRV) are predicted to be shyer than individuals with poor body condition (McElreath and Strimling, 2006; Wolf et al., 2007). However, asset protection principle alone predicts a negative feedback loop between state and behaviour (Sih and Bell, 2008). As assets diminish over time, shy individuals may become bold, thus leading to a possible convergence of behavioural types in the population. Based on this hypothesis, I predicted the presence of a negative correlation between body condition and boldness. Body size too was expected to be negatively correlated with boldness.

Personality traits can be maintained in a particular species by parasite load of an individual as well (Barber and Dingemanse, 2010). Parasites are known to cause behavioural manipulations in the host to increase their own fitness. Thus, if a particular behavioural type is beneficial to parasites, it can manipulate the behavioural type of individuals to its own benefit. For example, malaria infection in great tits (*Parus Major*), increased exploratory behaviour of the infected birds in turn risking more infection (Poulin, 2013). Thus, parasitism can maintain personality acting via a positive feedback loop. If parasitism played a role in maintaining personality in *P.dorsalis*, I would expect individuals who are bold to have a higher parasite load than shy individuals.

III. Factors affecting variation in personality within an individual

Not all individuals may be equally consistent in their behavioural type. It is possible that some individuals are more plastic in their choice of behavioural type across time or contexts while others are less so (Gherardi et al., 2012). Since plasticity, always has an associated cost to it, I expected that individuals which were of higher quality would be more adept at bearing the cost than low quality individuals. Thus, males who have high body condition should show high plasticity in behaviour than individuals with low plasticity. Further, males with larger body size and lower parasite load were expected to be more plastic than their counterparts. However, if asset protection principle holds true then, I expect shy and bold individuals to be equally plastic (Dingemanse and Wolf, 2013).

Materials and methods:

All individuals were handled in accordance with the rules laid out by the Animal Ethics committee of IISc and necessary permissions were taken to carry out experiments on focal species.

1) Study site

Rishi Valley, Madanapalle is nestled within the Rishikonda hills of Chittoor district, Andhra Pradesh. The hills, which are an extension of the Peninsular Gneissic complex, consist of rock formations dating to the Archaen Eon which is said to have occurred about 3.4 billion years ago. The sheet rocks have either granodiorite or hornblende biotite rock (Geological Survey of India, 2008) giving it a greyish black appearance interspersed by reddish bands (See Figure 1). Rainfall is scanty averaging around 400-450mm per year. Vegetation consists primarily of thorn and scrub forests. There is high seasonal variation in temperature with summer temperatures from March-June ranging from 34-38 °C whereas in winters the temperatures fall in the range of 14 to16 °C . The local livelihoods depend on agriculture and animal husbandry. Grazing is prevalent in these hills and so is mining of stones to some extent (pers. observation).

I worked in the hills bordering the 400 acre campus of the Rishi Valley School (RV) run by the Krishnamurti Foundation of India (13.634°N, 78.454°E). These hills are under the RV Special Development Area and have a relatively rich green cover compared with other hills of the same complex away from the school campus. The terrain supports a diverse range of bird species as well as various reptiles which are well suited to the dry conditions (Rangaswami, S., 1993; RVSDA). The region supports populations of two closely related species of agamid lizards namely *Psammophilus dorsalis* (Gray, 1831) and *Psammophilus blanfordanus* (Stoliczka, 1891). Field work was carried out from May to November, a period which spans the breeding season of these lizards (Deodhar, S., in prep). All behavioural observations were mainly carried out at 6 sites DH, BB1, BB2, BB3, GDB, East Wall and Tent Rock. Since these sites are part of the same hill range

and all lie within a range of 1 km from each other, it is safe to assume that lizards at the focal sites constitute one population.



Figure 1: Image representing one of the field sites

2) Study Species

I chose *Psammophilus dorsalis* as my study species. The Indian rock agama, *Psammophilus dorsalis* is mostly found in the rocky habitats of scrub forests spread across different parts of India (Radder and Saidapur, 2005). They are typically an annual species in which majority of individuals breed during only one breeding season (Deodhar S., in prep). However, few individuals in the wild do live upto 3 years (Mahapatro et.al, 1989) Thus ,we can say that their lifespan ranges between 1-3 years. Adults exhibit sexual dimorphism with the males being much bigger in size when compared with females. These lizards have a distinct breeding season that lasts for about 6-7 months between the months of May –November. During the breeding season, males develop a bright coloration extending to the entire length of the body. Receptive females, on the other hand are more cryptically coloured. Males are suspected to be territorial in nature (Deodhar, S., In prep), with many females present within the territory. Females typically lay clutches of 6-8 eggs, with some females laying more than one clutch per season. The adult sex ratio is female biased and this species exhibits a

polygynandrous system of mating. Common predators of the lizards include raptors, snakes and monitor lizards.



Figure 2: Image showing adult breeding pair: male (left) and female (right) in species *P.dorsalis*

3) Tagging focal species

In any long term behavioural study, it is important to be able to identify individuals. The use of coloured beads to tag lizards is a well-established cost-effective method of assigning lizards a unique identity (Fisher, M. and Muth, A., 1989). The first part of the project included tagging as many lizards as possible, since past studies from the lab have shown that there is a lot of turnover among individuals present at the site at any given time (Deodhar, S., in prep). Adult lizards were first captured using a noose made of fishing line. Once captured, the lizards were kept in a box of crushed ice to lower their body temperature. This was done to make them relatively immobile and numb before tagging them. The duration of time for which the lizards were kept on ice varied depending on the size of the lizards. The tag constituted of 4 plastic beads, which was a unique combination from the 256 possible permutations of the colours green, white, blue and black. The colours of the bead were chosen such that they were similar to the body colour of the lizards and thus did not increase their chances of predation. The tag

was tied on the base of the tail, by stitching a nylon thread through the muscle of the tail. This ensured that even if the lizard moulted, the tag would remain intact over the season. The lizard was released back at the site of capture only after it had regained a moderately active state. Care was taken not to keep the lizards on ice for too long, as very low temperatures can potentially lead to the death of these lizards.

4) Morpho-metric Measurements

With the help of a pair of Vernier callipers, a foot ruler and spring balance, the following measurements were made at the time of capture- Snout to vent Length(SVL), Interlimb distance(IL), Head height(HH),Head Width(HW), Head Length(HL), Width of tail base(TB), Tail Length (TL) and body weight(Wt). A rough estimate of ectoparasite load was also noted for each individual by counting all visible ectoparasites on the body. Individuals were identified as males or females of either species (*P.dorsalis* or *P.blanfordanus*) based on reference photographs (See Figure 2 and 3) and pattern of scales on the body of the individual. Gravidity status of females was noted as well. In addition, the location from which the lizard was captured was noted using a GPS machine.



Figure 3: Image showing adult breeding pair male:(left) and female (right) in species *P. blanfordanus* (courtesy: Shreekant Deodhar)

During the study period, morphometric data were gathered for 150 tagged individuals, with maximum tagging done on individuals at the start of the breeding season from mid-April to May.

5) Measuring risk-taking

In order to measure the Flight Initiation Distance (FID), any tagged lizard was spotted from as far as possible using a pair of binoculars and/or a camera. The position from which the lizard was first spotted was marked as point A. I walked towards the lizard at a constant pace, in a straight line with direct gaze. I stopped walking as soon as the focal lizard left its perch (i.e. initiated flight) and marked that position as point B. The position at which the lizard was perched was noted as point C. The point to which the lizard first escaped to was marked as point D. Spotting distance or intruder starting distance (SD) referred to the total distance between point A and C. The distance between point B and point C constituted the Flight Initiation Distance (FID). The distance from the perch of the lizard to the first place it escaped to i.e. point C to D, was measured as escape distance (ED). The height at which the individual was perched was noted as perch height (PH). All distances were measured to the precision of 0.01 m using a 30 m long tape. Care was taken to make all measurements parallel or perpendicular to the ground. However, given the nature of the terrain, this was not always possible. For each trial, the air temperature was recorded using a mercury thermometer (Precision=0.05 degree Celsius). The climatic conditions were noted on a scale of 1 to 5 with 1 assigned if the sky was clear and 5, if the sky was heavily overcast with clouds. Both these measurements were taken to gain an estimate of the relative temperature of the individual since they are poikilothermic. Further, if females seemed gravid it was noted down. The context at the time of the study, such as direction of approach, disturbance due to other human-associated activities at the hillock such as grazing by cattle, or villagers collecting wood etc. was duly noted.

Attempts were made to get at least 2 separate trials within a week for the same individual. These trials were separated by a period of at least 16 hours to discount the effect of the previous trial on the current observation. Repeated trials performed within 10 days constituted one cycle of observations. Subsequently, each cycle of observation taken for an individual was separated by one month, as long as it was observed within the study area. FID data were collected for 74 tagged individuals over 370 trials from June- November, 2014.

6) Analysis

All analyses were performed using R statistical software (R Core Team 2014). Since the sample size of FID data on *P. blanfordanus* was very low (12 individuals, 42 trials), subsequent analyses were focussed on understanding patterns in risk-taking behaviour and personality in *P.dorsalis*. Dates were formatted using lubridate package in R (Grolemund and Wickham, 2011)

6.1) Effect of state and environmental variables on average risk taking

The effect of state and environmental variables on FID was analysed using a mixed effects model approach which accounted for pseudo replication in the data due to repeated measures on the same individual. The fixed effects included a mixture of continuous as well as categorical explanatory variables spanning both the state-dependent effects as well as environmental effects on Flight Initiation distance. The following variables were included as explanatory variables based on apriori hypotheses. Studies have shown that intruder starting distance or spotting distance itself affects flight initiation distance such that with increase in spotting distance, flight initiation distance also increases (Blumstein, 2003) in most species. Since the intruder starting distance can confound our interpretation of the risk assessment of the individual, it is recommended to include it as one of the covariates in the model (Blumstein, 2003). The variables included were:

- Sex – 2 categories(M or F)
- Snout to Vent Length(svL) *– continuous variable denoting body size
- Standardised weight (sw) **– continuous variable denoting body condition
- Perch Height(PH) - continuous variable denoting visibility
- Escape distance(ED)- continuous variable denoting distance to a refuge
- PH:ED- Interaction effect of Escape distance and Perch Height
- Spotting distance(SD)-continuous variable denoting first encounter with predator
- Temperature(temp)-continuous variable
- Climate(climate)-5 categories 1= Clear sky ,2= Hazy, 3= Partly Cloudy, 4= Cloudy, 5=Overcast

- Time in breeding season(season)-3 categories
 - Early breeding season=June-July
 - Mid- breeding season=August-September
 - Late breeding season=October- November

Individual ID was included as the random effect in the model. To reach a minimal model which would include only informative variables, I used backward simplification methods (Crawley, M.J. 2007) and compared models having different sets of fixed effects using likelihood ratio tests. To assess the significance of each of the variables in the final model on FID, I calculated 95% confidence intervals of all estimates using parametric bootstrapping. Since mixed effect models assume normality of error distribution and constancy of variance, I used quantile-quantile plots to test these assumptions. Preliminary analysis on the data showed that using a log transformation of the response variable FID, reduced the level of heteroscedasticity and ascribed to the assumption of constancy in variance. Thus, all further analysis was carried out using log-transformed values of FID. The maximal model was fitted using the lme4 package (Bates et.al. 2014) in R. The model was as follows:

$$\log_e(\text{FID}) \sim \text{sex} + \text{spotting distance}(\text{SD}) + \text{snout to vent length}(\text{svl}) + \text{standardised weight}(\text{sw}) + \text{perch height}(\text{PH}) + \text{escape distance}(\text{ED}) + \text{climate} + \text{season} + \text{PH:ED} + (1|\text{ID})$$

I plotted model predictions using the effects package (Fox, J 2003) in R.

*Snout to vent length (SVL): This was used as a measure of body length/body size. Since svl was correlated with all other morphometric measurements, it was used as a measure of body size. The correlations were visually analysed from the pair plots of morphometric measurements in R.

**Standardised weight: Since, weight is highly correlated with body length (SVL), I decided to use residuals from a regression of weight with a quadratic function of snout to vent length to obtain an index for body condition. Negative residuals denoted those individuals who had a body condition that was poorer than average at the time of capture. Positive residuals on the other hand denoted those individuals having a better

than average body condition (Fig. 4). The following equation was used to get residual values from the regression. Here a, b are parametric estimates of the slope and e is the estimate of the intercept from the regression:

$$\text{Weight} = a \cdot (\text{svl}) + b \cdot (\text{svl})^2 + e$$

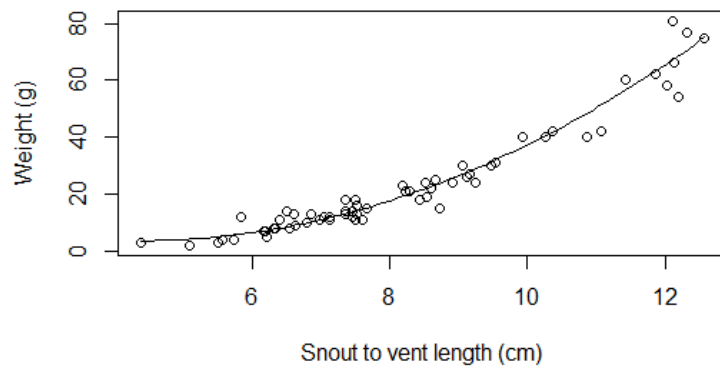


Figure 4: Plot showing relationship between body weight and body length in *P. Dorsalis*. Y-axis shows the weight of each individual and X-axis shows the snout-to-vent length which is representative of the body length of the individual (curve depicts fitted regression line).

6.2) Quantifying personality in risk-taking behaviour

To estimate repeatability or consistency of between-individual variation in risk taking behaviour, I used a linear mixed effects model based repeatability estimate as described by Nakagawa and Schielzeth (2010). Repeatability is defined as the proportion of variance in behavioural type that can be attributed to the between-individual variance alone. It is calculated as the ratio of between-group variance and the sum of between and within group variance, where group refers to the assigned random effect. Thus, if within-group variance is high and/or between-individual variance is low, the behavioural type will show less repeatability symbolising no personality:

$$R = \sigma_{\alpha}^2 / (\sigma_{\alpha}^2 + \sigma_{\epsilon}^2)$$

where, σ_{α}^2 = between group variance

σ_{ϵ}^2 = within individual variance

Adjusted repeatability measures were used so that factors whose effect on variance of FID was not of interest could be controlled for (Nakagawa and Schielzeth, 2010). These factors included Spotting distance (SD), Escape distance (ED), Perch Height (PH), Temperature as well as Season and were included as fixed effects in the model. Individual IDs were included as a random effect/grouping variable. As before, log_e-transformed FID was used as the response variable.

6.2.1) Repeatability across cycles

A cycle of measures, as mentioned before, consists of at least 2 repeated trials within a 10 day period. The repeatability estimate for one cycle of observations represents short term repeatability. Each cycle of observations was at least a month apart allowing one to estimate long-term repeatability, since no. of cycles of observation are representative of the tenure of individuals at the site. Thus, repeatabilities were estimated for each cycle as well as across cycles to assess if personality in individuals was short or long term. 95% confidence intervals for all estimates were obtained using parametric bootstrapping, to assess the significance of estimates. The estimates were plotted using ggplot2 package (Wickham, H. 2009) in R

As another measure of repeatability, the mean boldness score (see next section for calculation details) from one cycle was plotted against the mean boldness score of an individual in the subsequent cycle. Pearson correlation test was used to estimate correlation between the two cycles. Only those individuals were considered for whom I had more than 2 observations in each cycle.

Since the number of males sampled for 2 cycles or more was fairly low (7 individuals), comparisons between males and females were made only for the first cycle. The repeatability for all individuals across all cycles gave an estimate of the average repeatability for males and females respectively.

6.3 Estimating the relationship of personality with state-variables

The behavioural type, i.e., boldness score, of an individual was a measure of how consistently bold or shy it is. The mean FID estimate specific for each individual represented the boldness score of that individual. This was calculated using the random effects from a linear mixed effects model in which spotting distance, temperature, distance to nearest refuge, perch height, interaction term of escape distance and perch height as well as season were controlled for by denoting them as fixed effects. Only individuals with at least two FID measurements were included and FID values across cycles were pooled for each individual. Since no. of repeated measures per individual can potentially affect the boldness score, boldness scores were plotted against state variables for each cycle separately as well. However, the correlation coefficients for each cycle were not significantly different from those calculated when data across cycles was pooled. A review (Bell, 2009) also showed that no. of repeated measures per individual do not significantly affect the boldness score repeatability estimates, thus distinction between cycles was not made. I then used a linear model with boldness scores as the response variable and body size, body condition and parasite load as predictors, to test the significance of correlation between state- variables and boldness.

6.4. Estimating the relationship of plasticity with state-variables

Plasticity denoted how varied the individual behavioural response was from its mean behavioural type in each trial. Thus, I measured the standard deviation of the FID estimates from individual means for each individual. Confounding variables were adjusted for by using a mixed effects model with spotting distance , escape distance perch height etc as fixed effects. The plasticity score of each individual was given by the standard deviation of the residuals from mixed effects model. I then used a linear model with plasticity scores as the response variable and body size, body condition and parasite load as predictors, to test the significance of state- variables on plasticity for males and females. I used a Pearson correlation test, to identify the relationship between individual behavioural type and plasticity.

Results

1. Tagging, morphometric and FID measurements

42 males and 61 females of *P.dorsalis* species were tagged. The mean body length of males was 10.11 cm (SD =1.85, Range = 6.2 - 13.57, N =42), and of females was 7.13 cm (SD =1.14, Range = 4.39 - 9.24, N =61). The mean weight of males was 38.90 g (SD=22.25, Range= 6 - 90, N=42) and of females is 13.28 g (SD =6.98, Range =2 - 33, N =61), Parasite counts on individuals varied from a mean of 93.65 in males (SD = 96.02, Range = 8 - 582, N =42) to a mean of 58.73 in females (SD = 60.04, Range = 2-380, N = 61). The Flight Initiation Distances were measured for 21 tagged males and 41 tagged females from May to November and varied from 0.35 m to 30 m.

3. Factors affecting average- risk-taking behaviour

The following minimal model was arrived at using a backwards deletion approach (Table 1):

$\log_e(\text{FID}) \sim \text{sex} + \text{sw} + \text{SD} + \text{PH} + \text{PH} : \text{ED} + \text{season} + (1|\text{ID})$ where,

sex= Sex of the individual (Male or Female)

sw= Standardised Weight

SD= Spotting Distance

PH= Perch Height

ED=Escape Distance

season= Time in breeding season (Categorised as early, mid and late)

1|ID denotes the random effect of individual

Table 1: Statistical significance of those variables included in the analyses of average FID. A linear mixed-effects modelling approach was used with \log_e FID as the response variable. Likelihood ratio tests were used to test the significance of fixed effects. For variables in the minimal model, likelihood ratio test statistics from comparison of minimal model with a model without the specified variable are shown. For variables excluded from the minimal model, likelihood ratio test statistics from comparing the minimal model with a model containing the specified variable are shown; sw=standardised weight, svl= Body size, PH =Perch Height, ED=Escape distance.

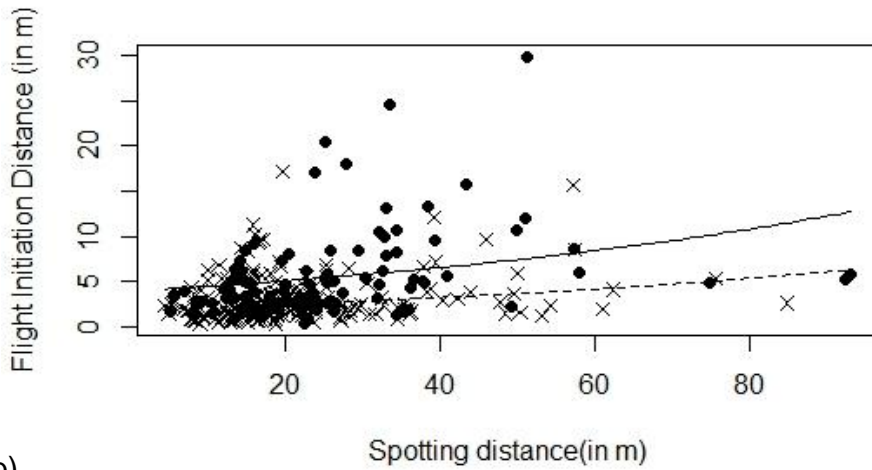
Variable	Likelihood Ratio statistic	df	p-value
<u>Included in minimal model</u>			
sex	17.632	1	2.68e-05
sw	5.882	1	0.0152
SD	25.117	1	5.394e-07
PH:ED	5.687	1	0.0170
Season	6.881	2	0.0324
<u>Excluded from minimal model</u>			
Temp	0.485	1	0.486
Climate	0	3	1
Svl	0	1	1

Among the predictors included in the minimal model, sex and spotting distance most strongly affected FID (Figure 5). On average, males had twice as high an FID as females (Table 2, Figure 6a). Increase in spotting distance was correlated with increase in FID (Table 2, Figure 5a & 7a). Body condition also had a significant effect on FID but it was not as large in magnitude as other effects. With an increase in body condition, FID also increased (Figure 5b, Figure 7b). The interaction term between escape distance and perch height was significant and positive (Table 2). Thus, as PH increased from low to high, the slope between FID and ED became more positive. At low perch height, $\log_e(\text{FID})$ decreased with increase in escape distance (estimated slope is -0.438). With increase in perch height, the slope of $\log_e(\text{FID})$ and ED changed by a magnitude of 0.145 (Figure 8). Season also had a significant effect on FID. FID in mid and late season was lesser than that in early season on average; however only FID in late season was significantly different than FID in early season (Figure 6b).

Table 2: Parameter estimates for fixed effects from the mixed effects model (minimal model) with \log_e -transformed FID as a response variable and sex, spotting distance, escape distance, perch height, body condition and season as explanatory variables. Confidence intervals not containing zero denote significant effects.

Parameter	Estimate	Std. Error	Lower CI	Upper CI
Intercept	0.799	0.109	0.585	1.014
sex(M)	0.696	0.154	0.38	1.023
SD	0.013	0.002	0.007	0.017
ED	0.002	0.028	-0.056	0.059
Sw	0.044	0.017	0.009	0.079
PH	-0.438	0.114	-0.663	-0.211
season: mid	-0.160	0.077	-0.316	0.006
season: late	-0.251	0.112	-0.463	-0.030
ED:PH	0.145	0.060	0.022	0.263

a)



b)

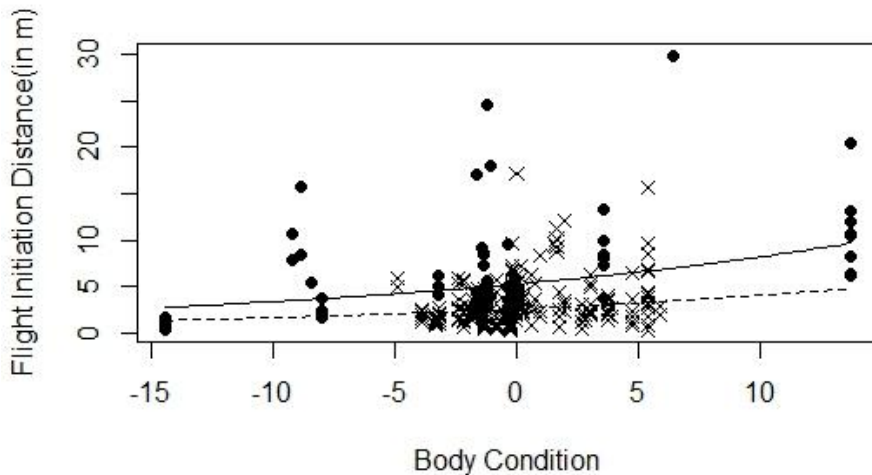
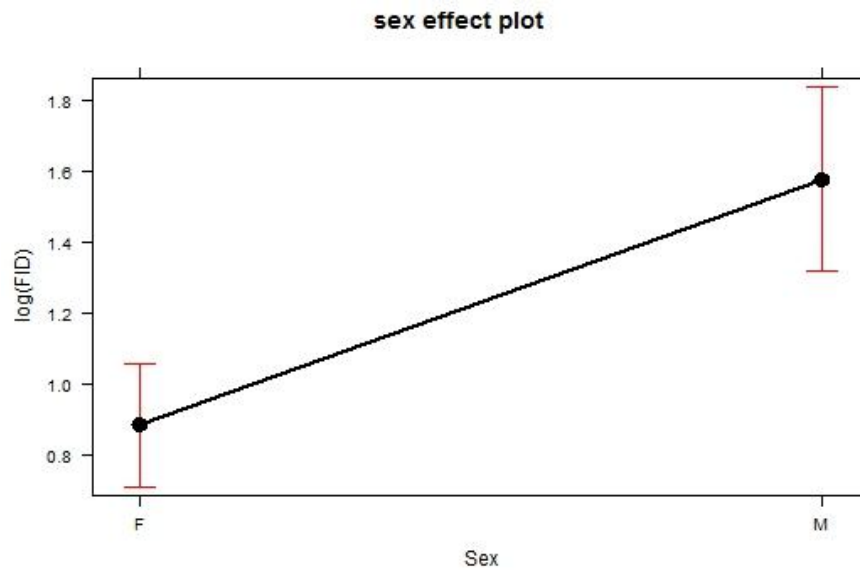


Figure 5: Scatterplots depicting general patterns between predictor variables and FID. (x) denote actual FID values for females, (•) denote FID values of males. (- - -) is the predicted curve of females as spotting distance increases and (—) is the predicted curve for males from mixed effects model estimates. Log_e -transformed FID was the response variable in the mixed-effects model. Model predictions have been back-transformed to visualise them on the original scale. Y-axis denotes the Flight initiation distances from data (in metres) plotted against: (a) Spotting distance on X-axis (b) Body condition calculated using standardised weight on X-axis. Low values denote poor body condition

a)



b)

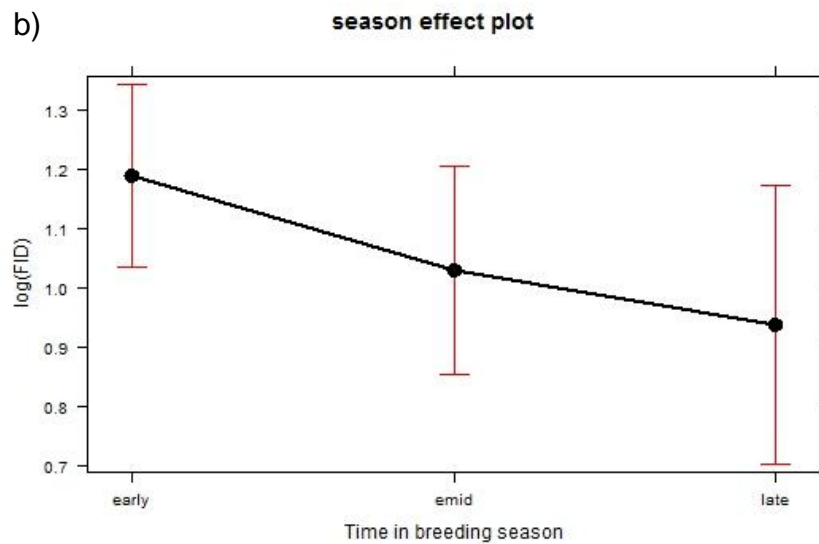
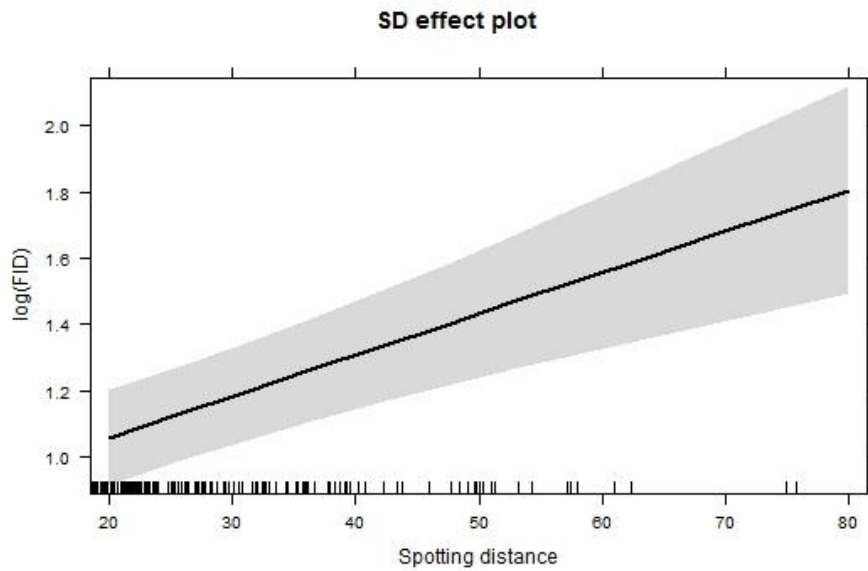


Figure 6: Summary of model predictions of Flight Initiation distance (FID) for the different categorical predictors in the mixed-effects model. Y-axis is the log transformed average FID estimate as predicted by the model showing effect sizes for (a) Sex on X-axis; M=Males, F=Females (b) Time in breeding season on X-axis; early = early breeding season (June-July), emid = mid breeding season (Aug-Sept), late = late breeding season (Oct-Nov). The error bars denote 95% confidence intervals of parameter estimates.

a)



b)

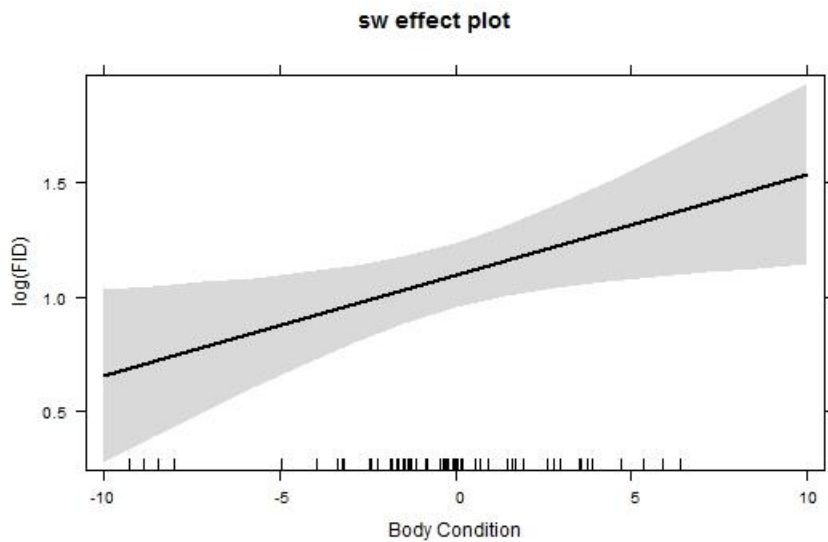


Figure 7: Summary of model predictions of Flight Initiation distance for the continuous predictors in the mixed - effects model of FID. Y-axis is the log transformed average FID estimate as predicted by the model with respect to (a) Spotting distance on X-axis. Black lines along the X-axis show the spotting distances from collected data which were used to predict the curve (b) Body condition on X-axis denoting standardised weight. Black lines along the X-axis show standardised weight of each individual from data collected which were used to predict the curve. Grey region=95% CI's

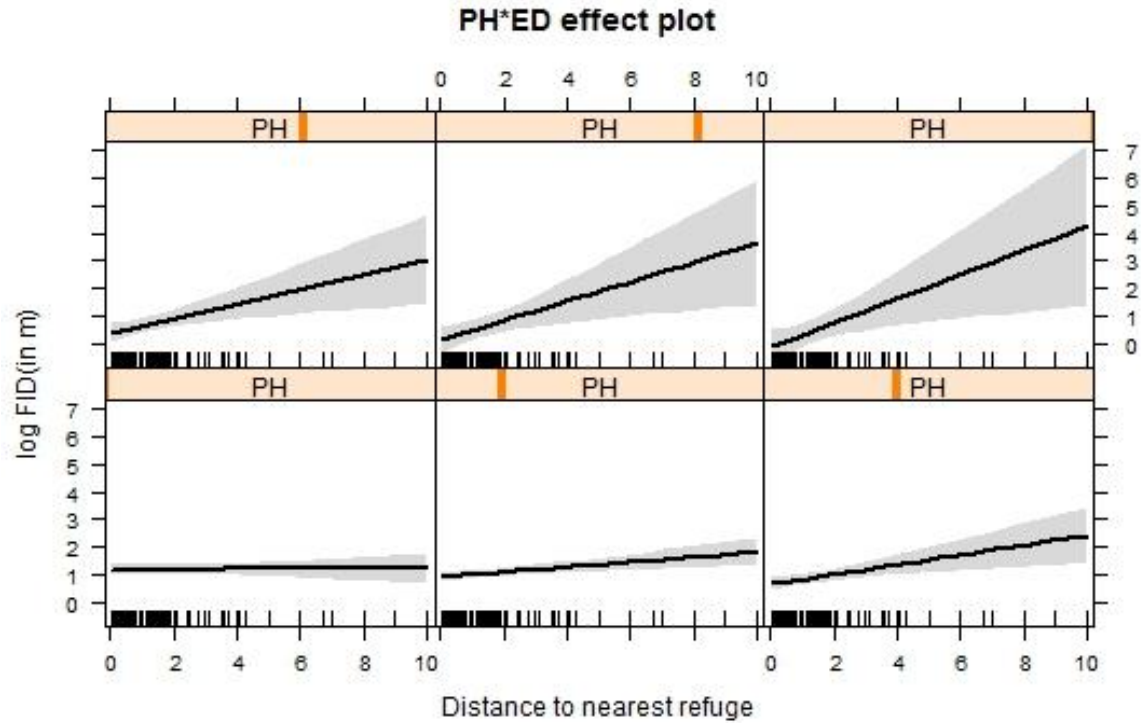


Figure 8: Summary plot showing the effect of interaction between Perch height and escape distance on average Flight Initiation distance (FID), as estimated from mixed effects model. Model predictions on the y-axis are on a log-scale. X-axis in each panel denotes distance to refuge (in metres). The black lines depict the values of refuge distance from the data which were used to predict the slopes. Panels moving from bottom right to top left describe the model predictions between FID and escape distance at perch heights, levels of which are denoted by yellow lines on the panel label. As Escape distance increases from left to right, the predicted slope between FID and Perch height becomes more positive. Grey areas around the curve denote 95% confidence intervals

Personality in risk taking behaviour

There were 16 males and 36 females for whom I had more than one FID observations. When all observations across all cycles were pooled, the repeatability estimate for females was 0.524 (N=36, 95% CI =0.32 - 0.66) and for males was 0.524 (N=16, 95% CI= 0.16-0.715) and were not significantly different.

a) Repeatability across cycles

Repeatability estimate for both males and females was 0.524. Repeatability although not uniform between cycles was not significantly different between short term or long term (Figure 9). Since I had more than 1 cycle of repeated observations for only 7 males and more than 3 cycles of repeated observation for only 4 females, repeatability could not be estimated for the 2nd cycle onwards for males and 4th cycle onwards for females. Average repeatability between males and females was not significantly different.

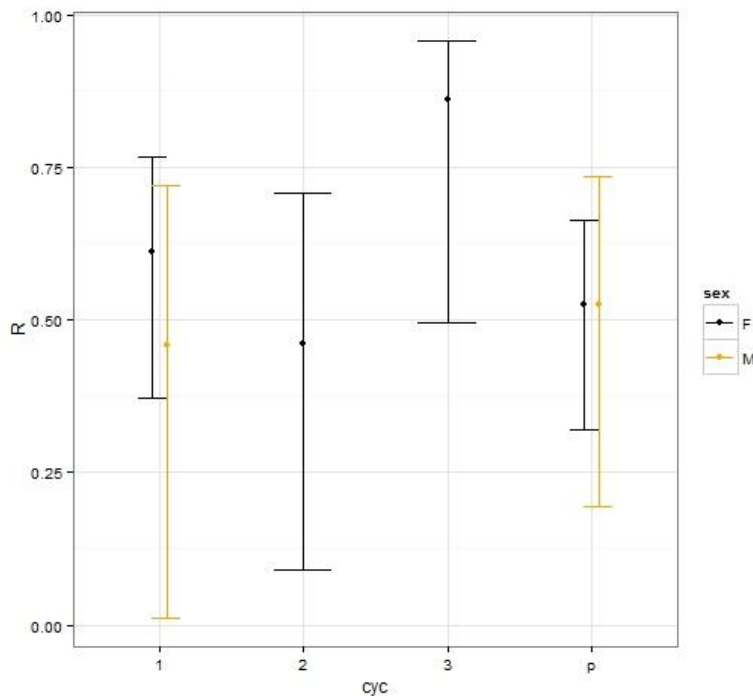


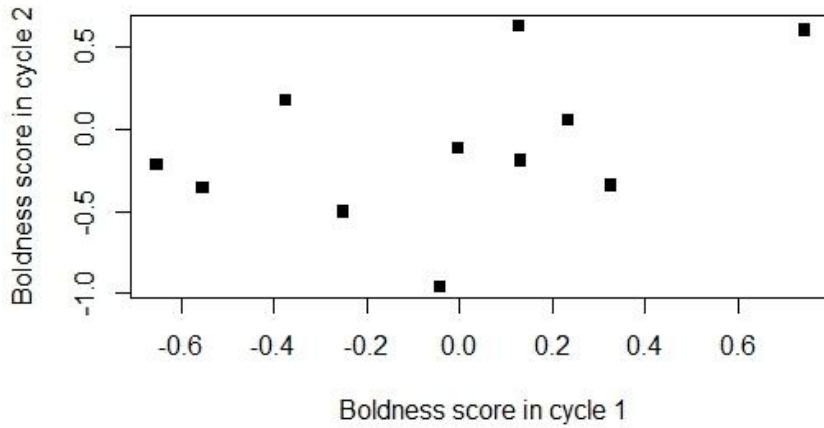
Figure 9: Repeatability estimates across cycles for males and females. X-axis denotes the cycle of observations for which repeatability was calculated. 1=1st cycle (N=31), 2=2nd cycle (N=12), 3 =3rd cycle (N=15) and P= Data pooled from all cycles (N= 36). Error bars show 95% confidence intervals.

c) Comparing boldness scores between cycles as a measure of repeatability

Boldness scores ranged from negative to positive values since the estimates were log-transformed values. A low score denotes smaller than average FID, therefore bolder individuals, and high score denoted individuals which had higher than average FID. The boldness score of females in cycle 1 was uncorrelated with their boldness score in cycle 2 (Pearson's correlation coefficient= 0.425, p-value=0.19, N =11). Similarly, the boldness

score of individuals between cycle 2 and 3 was uncorrelated (Pearson's correlation coefficient=0.311, p-value=0.497, N =7) (See Figure 10).

a)



b)

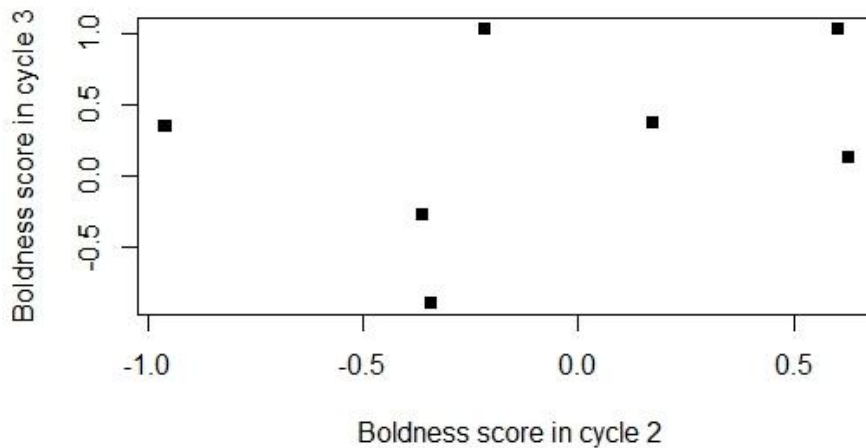


Figure 10: Relationship between boldness scores of females between consecutive cycles (a) Boldness score in cycle 1(X-axis) to Boldness score in cycle 2(Y-axis), N = 11 (b) Boldness score in cycle 2 (X-axis) to Boldness score in cycle 3(Y- axis), N=7

Factors affecting personality in risk-taking behaviour

Body condition was a significant predictor of male boldness (Table 3a). Body condition and boldness scores were positively correlated. Males having poor body condition were bolder (low score) than individuals with better body condition at the time of capture (Figure 11a). However, this effect was non-significant when the extreme values were removed. Body size and parasite load were not correlated with the boldness score of males (Figure 12a and 13a). The boldness score of females was uncorrelated with body condition (Figure 11b), body size (Figure 12b) as well as parasite load (Figure 13b) (Also see, Table 3b).

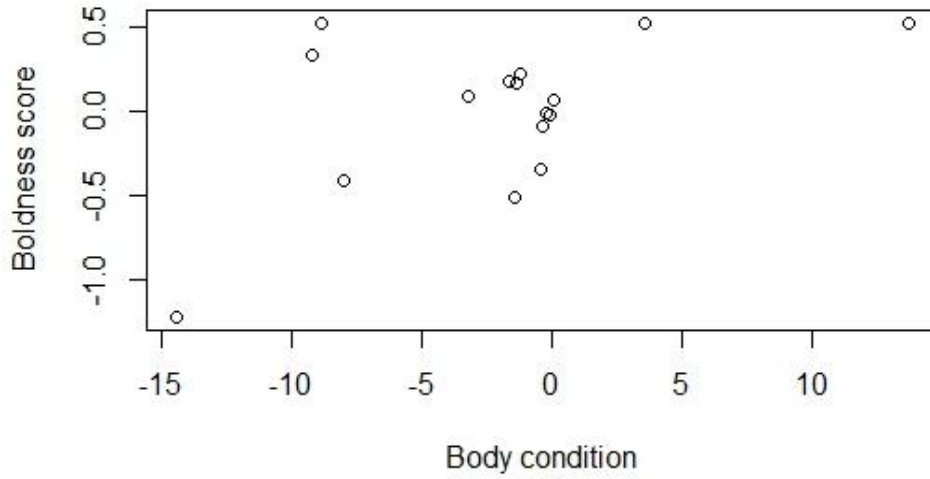
Table 3: Parameter estimates from a linear regression of boldness against state-variables for (a) males and (b) females.

Parameter	Estimate	Std. Error	t-value	p-value
Intercept	0.891	0.623	1.429	0.178
Body condition	0.045	0.017	2.512	0.027
Parasite Load	0.197e-2	0.018e-1	1.053	0.313
Body Size	-0.098	0.069	-1.423	0.180

b) For females

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	-1.100	0.543	-2.024	0.051
Body condition	0.023	0.001	-0.075	0.437
Parasite Load	-1.038e-4	0.029	0.786	0.941
Body Size	0.154	0.081	1.898	0.066

a)



b)

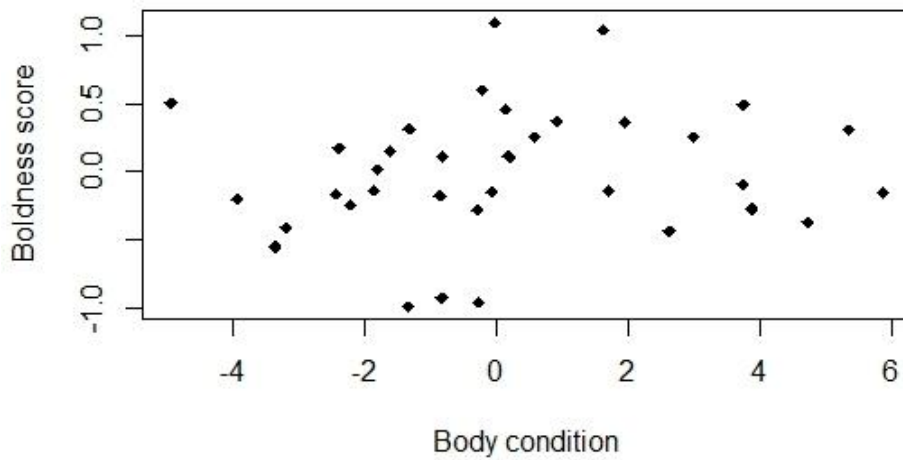
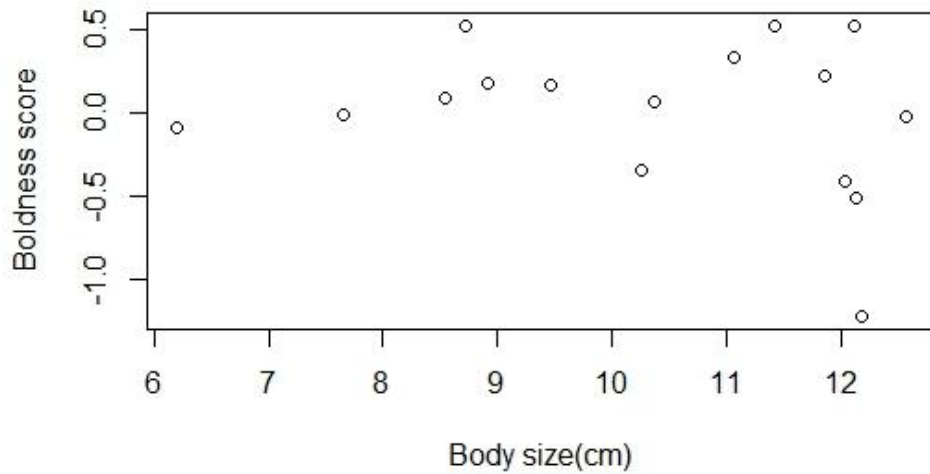


Figure 11: Plot showing relationship between boldness score and body condition (a) For males-(open circles) N=16 (b) For females (filled diamonds),N=36. Y-axis denotes the boldness scores as estimated from random effects of adjusted repeatability model : Low score indicates bold individuals and high score indicates bold individuals; X- axis denotes body condition of each individual given by the standardised weight, ranging from poor body condition to better body condition.

a)



b)

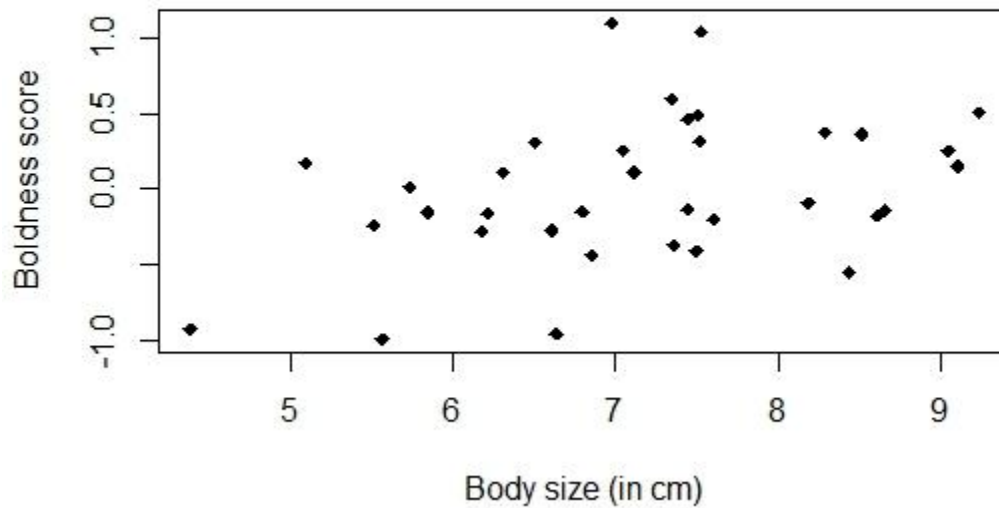
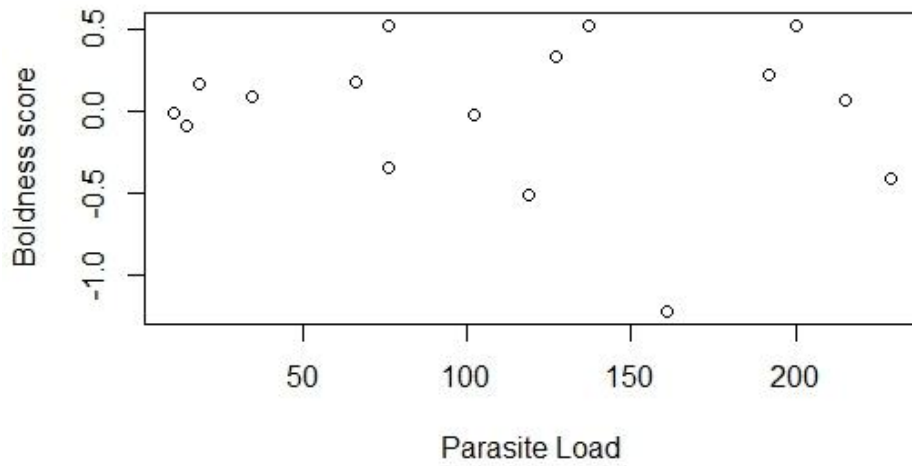


Figure 12: Plot showing relationship between boldness score and body size (a) For males-(open circles) (b) For females (filled diamonds).Y-axis denotes the boldness scores as estimated from random effects of adjusted repeatability model: Low score indicates bold individuals and high score indicates bold individuals: X- axis denotes body condition of each individual given by the body size (in cm).

a)



b)

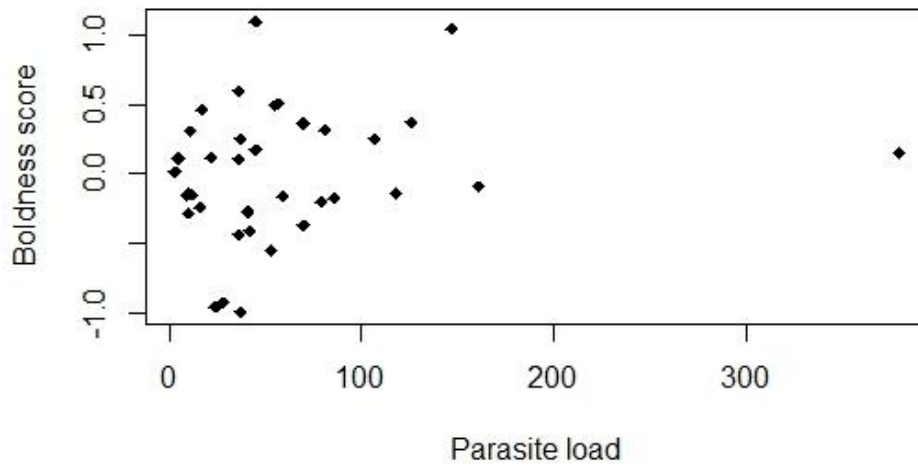


Figure 13: Plot showing relationship between boldness score and parasite load (a) For males (open circles) (b)For females (filled diamonds). Y-axis denotes the boldness scores as estimated from random effects of adjusted repeatability model. X- axis denotes parasite load for each individual.

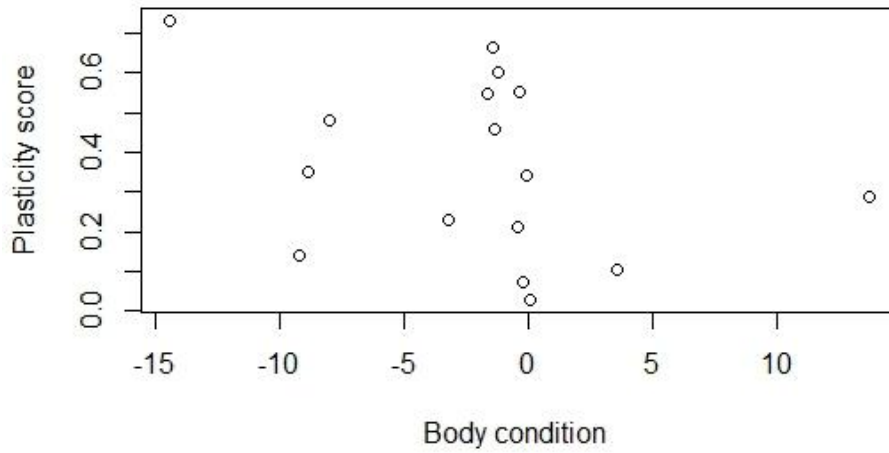
Factors affecting plasticity in personality

The plasticity score of females ranged from 0 to 1 whereas plasticity in males ranged from 0 to 0.8. Plasticity score was uncorrelated with body condition, body size or parasite load in females. Males showed a similar lack of pattern (See figures 14,15 &16, Table 4).

Table 4: Parameter estimates from a linear regression of plasticity score against state-variables for (a) males and (b) females.

a)Parameter	Estimate	Std. Error	t value	p-value
Intercept	0.078	0.357	0.219	0.831
Condition	-0.012	0.010	-1.263	0.231
Parasite	-3.72e-4	0.001	-0.346	0.735
Body Size	0.028	0.039	0.729	0.480
b) Parameter	Estimate	Std. Error	t value	p-value
Intercept	0.406	0.263	1.541	0.133
Condition	0.011	0.014	0.809	0.424
Parasite	-3.00e-4	6.73e-4	-0.445	0.659
Body size	0.002	0.039	0.056	0.956

a)



b)

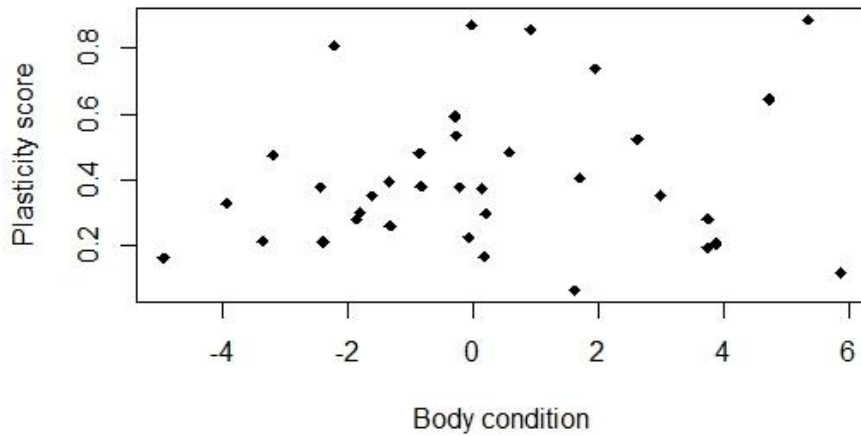
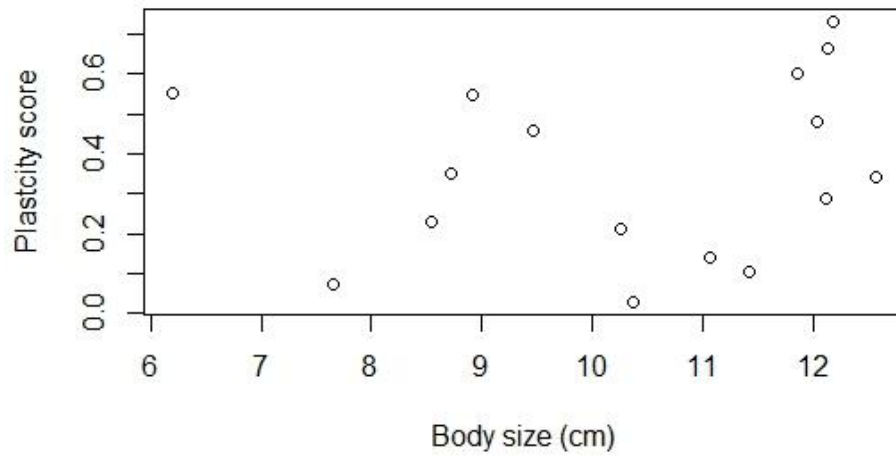


Figure 14: Plot showing relationship between Plasticity score and body condition (a)For males (b)For females. Y-axis denotes the plasticity scores as estimated from residuals of random effects from adjusted repeatability model. X- axis denotes body condition given by standardised weight

a)



b)

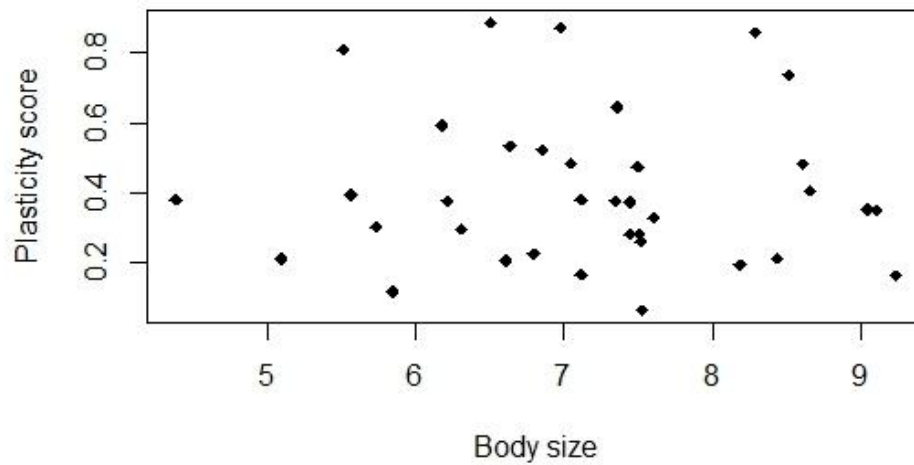
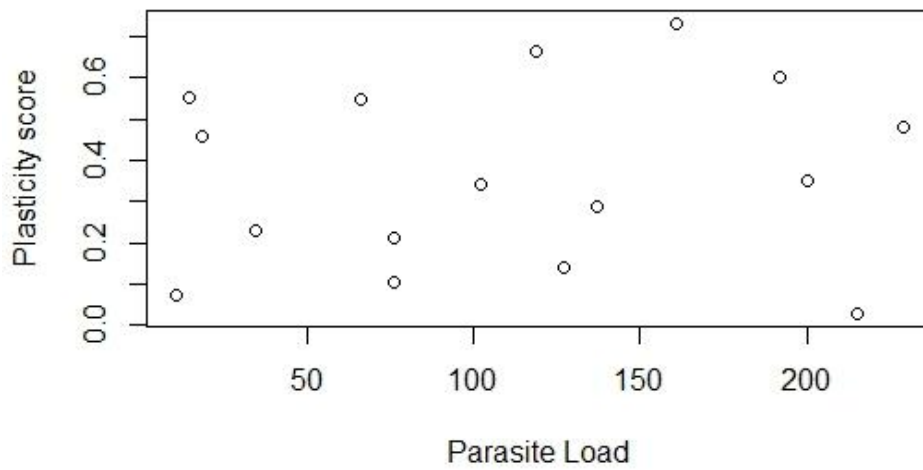
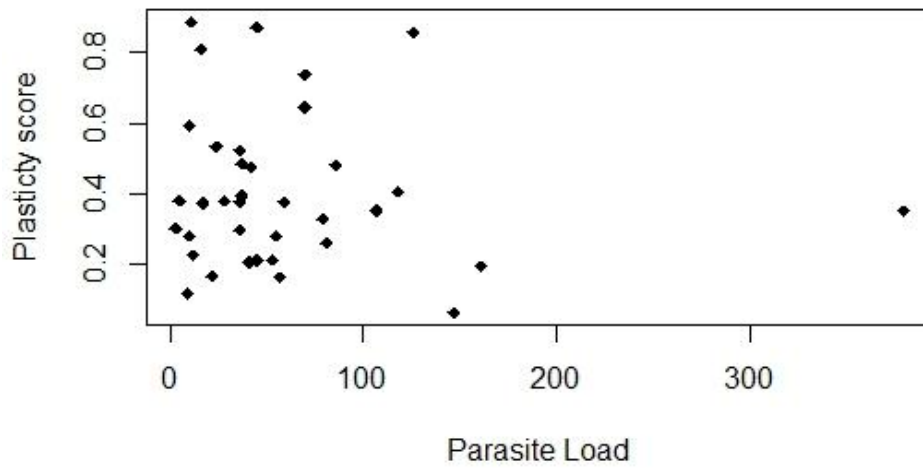


Figure 15: Plot showing relationship between plasticity score and Body size(a)For males (b)For females. Y-axis denotes the plasticity scores as estimated from residuals of random effects from adjusted repeatability model. X- axis denotes body size (in cm)

a)



b)



Relationship of plasticity with personality of an individual

Finally, the plasticity scores in males show a strong negative correlation with the boldness scores (Pearson correlation= - 0.51, p-value=0.023). Individuals who were less bold (high score) were also less plastic. However, upon removal of the extreme point (plasticity>0.7), this correlation weakened and became non-significant (Pearson correlation= - 0.36, p-value=0.223). Boldness and plasticity scores for females were uncorrelated (Pearson correlation=0.03, p- value=0.84) (See Figure 17).

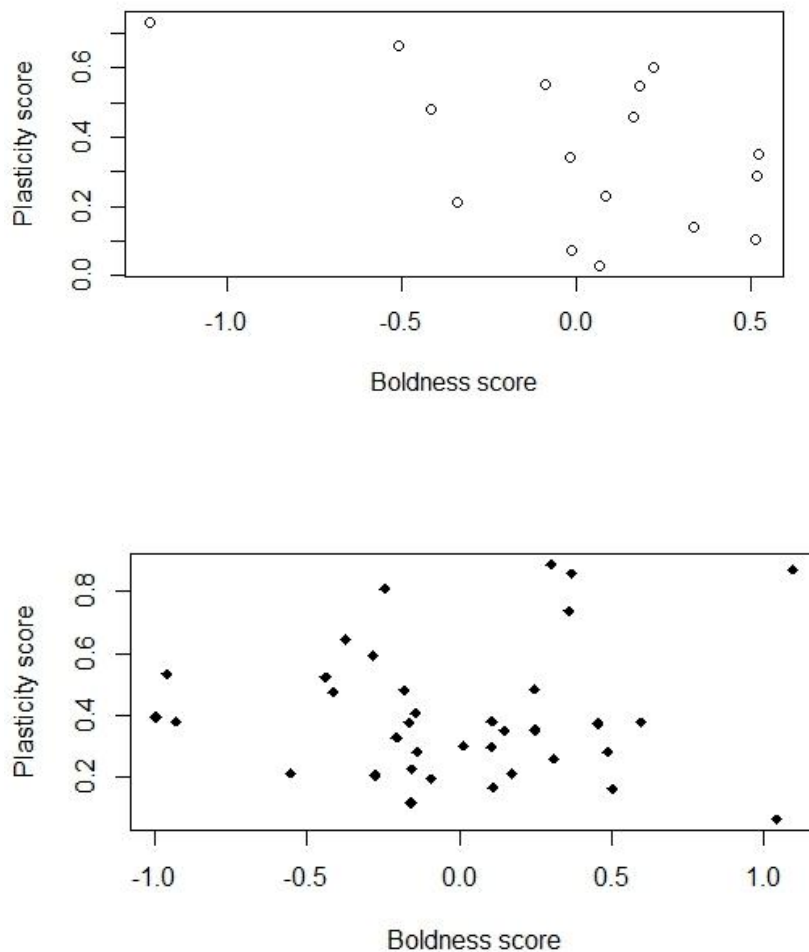


Figure 17: Plot showing relationship between plasticity score and Parasite load (a)For males (b)For females. Y-axis denotes the plasticity scores as estimated from residuals of random effects from adjusted repeatability model. X- axis denotes boldness score for each individual taken from the random effects of the model.

Discussion

My study provides strong evidence for animal personality in the wild, in the context of risk-taking behaviour. However, I did not find clear relationships between the measured state variables and personality variation. I also examined average or population-level risk-taking behaviour and report evidence to suggest that on average, lizards show state-dependent responses to a simulated threat, modulate their response depending on habitat features, specifically, visibility and their access to refuges, and take greater risks towards the end of their breeding lifespan.

Factors influencing average risk taking

I found that among all state variables, sex of an individual was the most important predictor of average risk-taking. Females were found to take more risk than males. In this species, sex is also associated with other differences in state such as differences in body size, colour and possibly hormonal levels. Thus, a combination of these state-variables could explain why males take lesser risk than females (Ydenberg and Dill, 1986). Males, being larger in size and more brightly coloured, may face a higher predation risk than females do. In response to differences in their phenotype and predation-risk, males and females seem to have evolved different strategies (Cooper and Frederick, 2007; Schuett et al., 2010). Previous studies have also shown that species that are not sexually dimorphic, show no significant sex specific difference in risk-taking behaviour (Qi et al., 2014). Another test of this hypothesis would be to compare risk-taking between breeding and non-breeding seasons. Since males and females in the non-breeding season are fairly similar in size and colour, we would expect sex-specific differences to be absent in risk-taking. However, published literature indicates that this may be species specific effect. A meta-analysis of risk-taking behaviour in lizards showed that sex-specific differences were found in only 6 out of 30 sexually dimorphic lizard species, excluding *P.dorsalis* (Fernández-Juricic et al., 2006).

Body condition was negatively correlated with risk-taking in the population. On average, individuals with better body condition took lesser risk than those having a poor body condition. This is in consensus with other studies which have shown body condition and size to affect risk-taking on an average (Samia et al., 2015) . As predicted from life-

history theory, a better body condition index of individuals can be an indicator of their reproductive potential (Wolf et al., 2007). Thus, individuals with high body condition could have a high future reproductive benefit and escape earlier to maximise this benefit. Individuals with low body condition however, may gain more by staying on the perch and retaining their current status (better territory/access to potential mates) rather than leaving.

Risk-taking was also correlated with habitat features, such as distance to refuges, indicated by escape distance. When individuals were perched at a relatively low height, individuals stayed on the perch until a potential threat was nearby, irrespective of distance to refuge. Another study has shown similar effects of low perch height on flight initiation (Cooper, W.E., 2010). Individuals may show this response because when perched lower than usual, individuals may have incomplete information about the approaching predator. Thus if the distance to refuge is farther away, individuals may stay on the perch to avoid the associated cost of leaving.

At a higher perch height however, we find that flight is initiated at a distance proportional to the proximity of nearest refuge. This could be because individuals with better visualisation of the predator may make a more informed choice based on the propensity of risk. Hence, if the refuge is nearby, individuals take more risk and stay on the perch whereas if the refuge is far off, individuals escape earlier (Dill, 1989).

I also found that the population on average became bolder later in the season. The theory of asset protection may provide a possible explanation for this increase in flight initiation distance. Early in the season, individuals have a higher residual reproductive value and can thus maximise future benefit by avoiding potential predation. Being an annual species, these lizards have little to gain by escaping early at the end of the breeding season. Thus, individuals may not escape until the predator is very close, to prevent loss of access to a better mate or territory. A study on Namibian rock lizards showed a similar change of FID with season. However, there was evidence of habituation in those lizards (Carter et al., 2012). I did not consider habituation to play a role in my study, on the other hand, because there was a huge turnover of lizards on the

field site. Thus, at any given point in the breeding season, the data sampled consisted of both experienced individuals and individuals novel to the stimulated predation risk.

As predicted, flight initiation distance increased with increase in intruder starting distance/spotting distance. This could be merely because larger starting distances allow for a larger range of distances at which flight is initiated by individuals (Cooper, Jr., 2005). It should be remembered here however that spotting distance is a proxy to the distance at which a predator is first noticed by the focal animal, a parameter that is nearly impossible to truly estimate. I expected decrease in temperature to decrease flight initiation distance, since lizards are ectothermal. Contrary to this, temperature and climatic variables showed no effect on average risk-taking. This could be because lizards can behaviourally compensate for decrease in external temperature by basking out for longer. However, note that air temperature may not be an accurate representative of the actual body temperature of lizards. Thus, future studies should involve tools to accurately determine body temperature by measuring the rock temperature instead, to understand its role in the risk-assessment of lizards.

Evidence for personality in *Psammophilus dorsalis*

I found that repeatability, which is a measure of personality, was high in short term and long term. Long term studies of personality in the wild are rare despite researchers highlighting the importance of such studies (Archard and Braithwaite, 2010). Repeatabilities in the wild are often greater than those in the lab (Bell, 2009) suggesting that the ecological and social context of the individual is important in shaping personality. Interestingly, vertebrate ectotherms show an average repeatability of about 0.2 - 0.27 in the lab. Contrary to this, I found that repeatability in *P.dorsalis* is almost twice as high. This seems to be a feature true for other agamids as well since a study on Namibian rock lizards also showed high repeatability estimates ($R=0.95$) in anti-predator behaviour. Repeatability is often considered to be an upper limit to heritability (but see Dohm, M.R, 2002) hence, it is important to look at the underlying drivers of personality and the possible adaptive role it might have. In this context I looked at different state variables that could be correlated with personality.

State-dependent correlates of personality

The state-variables I considered included, sex, body condition, body size and parasite load. Males and females were found to be similarly repeatable ($R=0.524$ for both males and females). This repeatability measure is similar to most other studies in the wild which report repeatability in the range of 0.48-0.52 (Bell et al., 2009). My finding is in accordance with the general pattern reported that sex-specific repeatability in the wild is non-significant (Bell et al. 2009). It is unclear why repeatability in behaviour is similar for the sexes even though they show differences in the average risk-taking pattern. It is likely that the underlying evolutionary mechanisms generating personality in the two sexes may be similar whether it be genetic, state-dependent, frequency dependent or otherwise.

Alternatively, the lack of effect could also be due to lack of power in the study to detect these differences since data from 16 males and 36 females was used to estimate repeatability through the breeding season. More recent studies have reported sex differences in repeatability of individuals with respect to exploratory behaviour and learning (Fresneau et al., 2014; Titulaer et al., 2012). Thus, repeating the study with a larger sample size may help detect sex-specific differences more clearly. Comparison of repeatability estimates between cycles for females hinted towards an increase in the repeatability with number of cycles; however the overlap in confidence intervals rendered these differences non-significant. An increase in sample size within each cycle will also clarify, what is the nature of personality in these lizards over short and long term of their lifespan.

While there were no significant differences in repeatability measures of males and females, some state-variables showed sex-specific correlation with personality and plasticity in personality. Body condition emerged as a significant covariate of degree of boldness in males. Boldness in females on the other hand, showed no correlation with any state-variables, be it body condition, body size or parasite load.

The relationship between boldness score and plasticity as well as boldness score and body condition however, became weaker and statistically non-significant, when the

extreme values were removed. This suggests that repeated sampling in the future for a larger number of individuals is needed to demonstrate if these patterns can be generalised for the species or not. Further, since the body condition score was taken at the time of capture, when some males were at a sub adult stage, this correlation may not be entirely representative of the role of body condition in personality variation. In spite of this, the correlation coefficients between body condition and personality are considerably higher than that for females, indicating that body condition of all other state variables may play a biologically significant role in explaining variation in personality. Further since the outliers are not biologically outliers in the population, I will be discuss briefly the possible implications of body condition on personality in males.

The few empirical studies that report state-dependence in personality have shown that, shy individuals have a better body condition and are less plastic. However, these effects are dependent on resource availability (Carter et al., 2012; Montiglio et al., 2015). In my study, I found that males which were of better body condition were indeed shyer than those with a poor body condition at the time of capture. Further, individuals with a high boldness score were more plastic in their behavioural type when compared to shy individuals. Quite a few studies on a range of species have documented that, shy individuals are less plastic as well (Carter et al., 2012; Dingemanse and Wolf, 2013; Verdolin and Harper, 2013).

This evidence suggests that there may be negative feedback acting between body condition and boldness in *P.dorsalis*. The asset protection principle (McElreath and Strimling, 2006) predicts that individuals having assets that can potentially increase the lifetime fitness of the individual should be shy especially in the face of a predation threat. This can result in a continuum of behaviour types along the boldness-shyness axis due to differences in body condition. Further, if assets diminish over time, individuals later in the season should be bolder leading to a convergence of behavioural types (Sih and Bell, 2008). In the mating context of *Psammophilus*, both residual reproductive value (RRV) as well as body condition is representative of individual assets. As predicted, we find that males with more assets (better body condition or high RRV), as is the case in early breeding season, are shy. In addition, individuals became

bolder by the end of the breeding season which might indicate diminishing assets. To the best of my knowledge only four other studies till date provide similar empirical evidence for the possible role of asset protection principle in explaining personality in the wild (Carter et al., 2012; Highcock and Carter, 2014; Montiglio et al., 2015; Nicolaus et al., 2012).

An individual's personality type seemed to also determine the consistency of personality itself, which was denoted by the plasticity of each individual. Individuals who were bold also showed more plasticity in risk-taking suggesting that they switch between behavioural types more often than the ones who are shy. Although, this is contrary from what I had predicted other recent studies have shown similar correlations to occur, for eg. in Namibian Rock agama in which bold individuals were more variable than shy individuals (Highcock and Carter, 2014).

In addition, I found that not all related state variables are correlated with personality. For example, body size and parasite load which can be related to body condition, showed no correlation with either boldness or plasticity in both males and females. Further, boldness as well as plasticity scores were uncorrelated with all measured state-variables in females, suggesting that mechanisms underlying personality in *P. dorsalis* are different for males and females. Clearly long term data, in combination with experimental manipulation is required to clearly understand the role of different drivers of personality

Conclusions and future directions:

My study revealed the influence of several state (e.g., body condition) and ecological (e.g., season, distance to refuge) variables on average risk-taking behaviour suggesting that behavioural responses to predation are costly and are sensitive to changing costs and benefits deriving from variation in state and in ecological conditions. Thus risk-assessment in these lizards does seem to be dynamic and can be predicted by the optimal escape theory. Comparison between populations facing differential predation pressure will help investigate if the patterns and underlying explanations about variation in risk-taking behaviour hold true or not (Dingemanse and Réale, 2005).

This study provides sufficient primary evidence for the presence of personality traits along the boldness-shyness axis (risk-taking) in *Psammophilus dorsalis*. In future studies, we can combine lines of evidence from parentage analysis and behavioural observations to understand if such personality traits might be heritable. Theoretically, repeatability estimates are considered to be upper limits of heritability (Dingemanse and Réale, 2005; Smith and Blumstein, 2007). Thus, a repeatability estimate of 0.52 suggests a promising role of this study system in understanding heritability of personality traits in the wild.

Females have been found to be more repeatable than males in most contexts other than mating (Bell, 2009). However I found no sex-specific differences in repeatability in risk-taking behaviour. Similar results have been reported in other studies on lizards, where repeatabilities were not sex-specific in 24 out of 30 species (Cooper et al., 2013). Note that due to a lack of a large sample size for males over a longer period, male and female repeatabilities were only compared in the short-term and further work is needed to test whether males and females are similar in repeatability over a significantly long period of their lifespan.

Although I present observational evidence for the presence of a negative correlation between state and behaviour in males, the next step would be to experimentally manipulate body condition and observe changes in behavioural traits to understand if personality is indeed condition dependent. However, more work needs to be done to confirm the nature of this correlation as removal of extreme points rendered the correlations statistically insignificant. This should include not only increasing sample size but also measuring body condition of individuals at a time closer to the assessment of their risk taking behaviour.

Given that personality in females was uncorrelated with the state variables measured, we still have little knowledge about the underlying causes affecting personality and variation in personality of *P.dorsalis* females along the boldness-shyness axis. Future studies need to be designed to assess if other state variables such as gravidity status might be correlated with risk-taking behaviour. It is also possible that the same state variables might actually explain variation in some other behavioural axis for females, a

potential candidate for which is mate choice (Brommer, 2013). Thus it is also important to look at multiple state variables across multiple contexts in order to uncover personality traits, as we see that not all state-variables have an equivalent effect on personality (Sih and Bell, 2008).

It is important to emphasise that most literature, theoretical as well as empirical, regarding personality in animals has thus far, focussed on understanding personality variation in males. Explicit state-dependent mechanisms which can underlie personality variation in females are absent. I hope that more studies in the future will look at the underlying mechanisms of personality in females, to get a better understanding of how personality evolves and is maintained in populations in the wild. On the whole, state-dependent mechanisms seem to be weakly correlated with personality. Thus, other mechanisms should be investigated to understand the drivers of high repeatability that this population shows.

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