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Unraveling The Behavioral Ecology Of The Western Diamond-Backed Rattlesnake (crotalus Atrox) Through The Lenses Of Personality, Predator-Prey Interactions, And Crypsis

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UNRAVELING THE BEHAVIORAL ECOLOGY OF THE WESTERN DIAMOND-BACKED RATTLESNAKE (*CROTALUS ATROX*) THROUGH THE LENSES OF PERSONALITY, PREDATOR-PREY INTERACTIONS, AND CRYPSIS

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DEDICATION

Pour mon père qui m’a apprit que le savoir est le pouvoir.

UNRAVELING THE BEHAVIORAL ECOLOGY OF THE WESTERN DIAMOND-BACKED RATTLESNAKE (*CROTALUS ATROX*) THROUGH THE LENSES OF PERSONALITY, PREDATOR-PREY INTERACTIONS, AND CRYPSIS

by

OCÉANE DA CUNHA, M.SC.

DISSERTATION

Presented to the Faculty of the Graduate School of
The University of Texas at El Paso
in Partial Fulfillment
of the Requirements
for the Degree of

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ABSTRACT

To thrive in an environment, individuals need to be able to forage efficiently and acquire mates. These resources are limited, and their acquisition depends upon the energy and time an individual chooses to allocate to each activity and the environmental conditions, leading to behavioral trade-offs. Different species, or even different individuals within the same population, respond to these trade-offs by employing contrasting strategies, leading to differential life-history outcomes. The overarching goal of this dissertation is to gain a better understanding of the trade-offs cryptic ambush mesopredators are facing using the western diamond-backed rattlesnake (*Crotalus atrox*) as a model species. Each chapter of this dissertation focuses on different aspects of these trade-offs: personality, predator-prey interactions, and camouflage strategies.

In Chapter 1, I investigated personality in wild western diamond-backed rattlesnakes (*Crotalus atrox*) across five axes: activity, exploration, boldness, sociability, and reactivity. The objectives of this chapter were to develop a protocol to successfully test personality traits in rattlesnakes following these axes and to determine whether *Crotalus atrox* exhibits repeatable personality traits and behavioral syndromes. To do so, 22 wild rattlesnakes were captured and submitted to a series of captive behavioral trials. *Crotalus atrox* exhibited individual differences that were repeatable through time across the five previously mentioned axes. Activity was the only axis that was sex-dependent, with males moving more than females on average. Moreover, these axes were grouped into three personality dimensions: reactivity, exploration, and activity-boldness-sociability. This last personality dimension provides evidence for the presence of a behavioral syndrome (i.e., correlation between several personality axes) within this species. This chapter provides a repeatable and ecologically relevant protocol to study personality in rattlesnakes. *Crotalus atrox* exhibits individual behavioral differences consistent through time and behavioral syndromes comparable to other species. This chapter provides a baseline to answer questions pertinent to personality in rattlesnakes such as conflict management and will help provide insights into the secretive life of serpents.

In Chapter 2, I investigated the effect of personality on the spatial ecology of the western diamond-backed rattlesnake (*Crotalus atrox*) and tested the predictions that bolder, more active and exploratory individuals will move more and have larger territories compared to shyer and less active individuals. I tracked 14 rattlesnakes for one year and then I assessed their personality in captivity across four different axes: activity, boldness, exploration, and reactivity. Bolder and more active individuals traveled more than shy, less active individuals, but only during the non-mating season. Shy individuals increased their movement rate significantly more than bold individuals during the mating season, thus leading to no significant difference in movements between shy and bold individuals during the mating season. Moreover, less bold and less active individuals were more responsive to the change in reproductive status. These results suggest the existence of two different strategies for resources acquisition within the same population, indicating that the pace-of life-syndrome hypothesis (i.e., species or individuals exhibit distinct set of physiological and behavioral traits that evolved with their specific life-history requirements) may be context-dependent. Ultimately, my results show that the existence of different life-history strategies within the same population are dependent upon the reproductive status of these individuals.

In Chapter 3, I researched how the landscape of fear affects the foraging decisions of *Crotalus atrox* by investigating factors influencing detection risk and prey availability. To do so, 30 biologically accurate 3D-printed snake replicas, each associated with a game camera, were deployed at Indio Mountains Research Station for two years to estimate the spatiotemporal factors affecting prey availability and predation risk. Concurrently, 25 *Crotalus atrox* were radiotracked at the same site to gather activity and microhabitat selection data regarding this species. Random-forest algorithms were trained using data obtained from the game camera and applied to predict the probability of predation and the probability of prey encounter for each radiotracking event. Time of the day, month, vegetation structure, and concealment percentage all had a significant effect on the probabilities of predation and prey encounters. Overall, rattlesnakes chose to be active when and where the probability of prey encounters was significantly higher than the probability of detection by predators, thus following optimal foraging theory. In conclusion, this study showed that the combination of 3D-printed models, game cameras, and telemetry provided effective and non-invasive methods to study predator-prey dynamics.

In Chapter 4, I investigated the trade-offs between background matching and thermoregulation in western diamond-backed rattlesnakes (*Crotalus atrox*). Rattlesnakes were predicted to better match selected microhabitats in terms of color, luminance, and pattern than random microhabitats within their home range. Body temperature was predicted to influence their body coloration with higher temperatures favoring lighter colors. Pictures of 14 radiotracked western diamond-backed rattlesnakes were taken in situ with a full spectrum camera (UV/VIS) and body temperature was recovered from internal temperature-datalogging radiotransmitters. *Crotalus atrox* matched the color, luminance, and pattern of the background better than a randomly selected background, thus enhancing background matching. Additionally, rattlesnake coloration varied independently of temperature indicating that rattlesnakes are behaviorally modifying crypsis regardless of thermoregulation.

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GENERAL INTRODUCTION

Observation is the first step in all scientific processes and disciplines (Norris 1984). Scientists observe the world, creating hypotheses and collecting data to validate or invalidate these same hypotheses (Moore 1993; Mayr 1997). Observation is the catalyst for scientific discovery (Mayr 1997; Klahr and Simon 1999). When observing an animal in the wild, for example, a western diamond-backed rattlesnake (*Crotalus atrox*) waiting patiently in ambush for prey, a number of questions come to the mind of the observer: How far did this snake travel to reach this particular location? Why did it choose this specific spot to hunt? Can other animals perceive this individual in the same way I do? The field of behavioral ecology offers a foundation to answer these types of questions by combining elements of animal behavior, ecology, and evolution (Davies et al. 2012). To thrive in an environment, individuals need to be able to forage efficiently and acquire mates (Davies et al. 2012). These resources are limited, and their acquisition depend upon the energy and time an individual chooses to allocate to each activity, as well as the environmental conditions (Dunham et al. 1989). The environmental conditions, such as the presence of predators or the availability of resources, define when and where an animal can forage and find mates (Dunham et al. 1989; Stearns 1992). Because of these limitations, animals have to constantly adjust their behavior to fulfill conflicting requirements (Werner and Anholt 1993). Different species, or even different individuals within the same population, respond to these trade-offs by employing contrasting strategies, leading to differential life-history outcomes (e.g. Bonter et al. 2013; Patrick et al. 2017). Unraveling the mechanisms behind these strategies is essential to grasp concepts ranging from response to environmental stress (Schultner et al. 2013) to community assemblage (Zhu et al. 2018). However, knowledge about the relationship between ecological and evolutionary processes and the traits involved in these mechanisms is still limited and requires additional investigation (Réale, Garant, et al. 2010).

The development of life-history strategies in a population is generally influenced by environmental factors (Stearns 1992). According to the pace-of-life syndrome hypothesis, closely related species are expected to display distinct sets of physiological traits that have evolved together with their specific life-history characteristics (Ricklefs and Wikelski 2002; Wikelski et al. 2003). These suites of traits might be conjointly influenced by ecological conditions favoring distinct life-history strategies (Réale, Garant, et al. 2010). While the pace-of-life syndrome hypothesis has been verified in different species (Wikelski et al. 2003; Tieleman et al. 2005; Wiersma et al. 2007), behavioral traits, especially personality traits, have only been recently integrated within this hypothesis (Réale, Garant, et al. 2010). Personality traits are defined as inter-individual behavioral differences that are consistent through time (Réale et al. 2007a). Different personality types within a population could be maintained due to their involvement in life-history trade-offs (Biro and Stamps 2010). Life history can be seen as a set of rules governing three types of allocations: 1) energy to competing functions, 2) time to competing activities, and 3) reproductive energy to competing offspring (Dunham et al. 1989). Personality traits have the potential to influence each of these allocations and thus produce individuals with different life histories in a population. For example, personality has been linked to trade-offs regarding energy allocation to reproduction. A meta-analysis of the fitness consequences of personality showed that, in general, shy and bold (more prone to risk-taking behavior) individuals have the same overall fitness, but they allocate energy to reproduction in different ways (Smith and Blumstein 2008). In wandering albatrosses (*Diomeda exulans*), bolder individuals increase their resource intake by spending more time foraging to allocate more energy to reproduction later in life (Patrick and Weimerskirch 2014). Similarly, bold bighorn sheep rams (*Ovis canadensis*) survive longer and have a higher reproductive success later in life than shy individuals. On the other hand, aggressive rams have shorter lifespans than docile ones but allocate more energy to reproduction early in life (Réale et al. 2009). Docility and boldness are genetically correlated and highly heritable, suggesting that these personality traits could have an important function in the evolution of life-history strategies (Réale et al. 2009).

To be able to allocate energy to competing functions, animals must first acquire resources. The net resources available to an individual depend on several factors: time available to forage (influenced by environmental conditions), allocation of time to forage, foraging success (depends on resource availability), digestive performance, and storage (Dunham et al. 1989). Food acquisition has been shown to be influenced by the individual level of activity, aggressiveness, exploration, and boldness in various taxa in both juveniles and adults (reviewed in Biro and Stamps 2010). For example, aggressive individuals of *Boa imperator* present a higher rate of successful feeding trials (i.e. they accept prey more readily) in captivity (Šimková et al. 2017a). Moreover, activity level has been directly correlated to foraging activity with active individuals usually allocating more time to forage than non-active individuals (Sweeney et al. 2013). Personality traits lead to foraging specialization by affecting dispersal, migration tendency, and home range size (Fraser et al. 2001; Cote et al. 2010; Chapman et al. 2011a; Quinn et al. 2011; Cote et al. 2013). Foraging behavior is constrained by biological and environmental factors. Predation risk, defined as the probability for an individual to be predated by another organism (Pettorelli et al. 2015), can influence where and when animals forage. Prey can respond to predation risk by morphological adaptations (Tollrian and Harvell 1999) or by altering their behavior. For example, changes in habitat use (Creel et al. 2005) and movement patterns (Fortin et al. 2005) have been observed in response to predation risk, leading to changes in foraging strategies (Winnie and Creel 2007). In general, behavioral modifications in response to predation risk are costly for individuals as they require shifts in energy acquisition and allocation, which negatively impact survival, growth, and reproduction (Creel et al. 2007; Pangle et al. 2007). However, species and even individuals do not respond equally to predation risk, leading to differential costs (LaManna and Martin 2016). For example, bold individuals forage in habitats with higher predation risk while shy individuals stay in low-risk habitats (Griffen et al. 2012; Ward-Fear et al. 2018). Although predation risk could significantly impact biological and ecological processes, there have been limited efforts to understand these cost variations among species and individuals (LaManna and Martin 2016).

Not all species respond the same to predation risk and the associated costs of predation can differ based on the strategies utilized to mitigate this risk. Camouflage is one of the most commonly adopted morphological defensive strategies in nature to avoid predation (Cott 1940; Ruxton et al. 2019). While camouflage is used as a general term encompassing methods aiming to prevent detection and recognition, organisms employ various techniques to conceal themselves (Pembury Smith and Ruxton 2020). For example, crypsis relies upon body coloration hindering detection (Merilaita et al. 2017), and masquerade depends on morphological adaptations hindering recognition (e.g. caterpillars looking like bird feces or stick insects looking like vegetation) (Skelhorn 2018). Camouflage is an exceptionally effective defense against predation, prolonging the time predators spend searching for prey while reducing their attack rate (de Alcantara Viana et al. 2022). Camouflaged prey experience predation risk differently than visible prey, allowing them to access more resources by increasing their foraging activity spatially but also temporally (Steinhoff et al. 2020). As a result, prey relying upon camouflage may develop alternative foraging strategies, resulting in distinct life-history trade-offs. In the past, discoveries about the adaptative nature of camouflage have been limited by the lack of techniques producing objective color measurements (White et al. 2015). Studying animal coloration is complex because of the diversity of visual systems to model and the fact that cameras do not always capture the relevant biological information. However, the recent development of digital imagery has allowed researchers to overcome these problems and scientists can now answer questions about how animals perceive each other in the field, thus enabling accurate and precise studies of coloration. Digital cameras enable scientists to quickly collect a large quantity of data in a wide range of scenarios (Troscianko and Stevens 2015) and to utilize complex image processing algorithms (Stevens et al. 2007). Because of these technological advances, further insight into the evolutionary and functional significance of camouflage can be gained. While the benefits of camouflage against predation are recognized, there is a critical need for studies that test protective effectiveness of camouflage using real prey and predators under natural conditions (de Alcantara Viana et al. 2022).

Rattlesnakes serve as an ideal study system to study life-history trade-offs, especially through the lenses of personality, predator-prey interactions, and crypsis. The presence of personality has been recently described in western rattlesnakes (*Crotalus oreganus*), although no behavioral syndromes (i.e., correlated suite of personality traits) were observed (Gibert et al. 2022). In the field, individual differences in activity that do not seem to be explained by environmental factors have been recorded in the western diamond-backed rattlesnake (*Crotalus atrox*; DeSantis et al. 2020), offering a foundation to investigate the relationship between personality and spatial strategies. Rattlesnakes are mesopredators and thus, their foraging decisions are influenced by both apex predators (Haswell et al. 2018) and prey availability (Brown and Kotler 2004). Because of their ambushing foraging strategy, rattlesnakes spend extended periods of time exposed to predators (Klauber 1956a). Thus, rattlesnakes are likely under considerable pressure to decide when and where to forage, resulting in trade-offs between resource acquisition and predator avoidance. Rattlesnakes also face another trade-off because of their ectothermic nature. Although rattlesnakes need to avoid being detected by both predators and prey for their survival, they must also cope with the challenge of meeting their thermal requirements within their environment. To thermoregulate, ectotherms can select habitats to bask or alter their coloration to optimize dermal absorption (Dunham et al. 1989; Seebacher and Franklin 2005). Consequently, conflicts between thermoregulation and crypsis emerge, with morphology, especially coloration, being a central piece in this trade-off (Smith et al. 2016).

The overarching goal of this dissertation is to unravel the behavioral ecology of the western diamond-backed rattlesnake (*Crotalus atrox*) by focusing on personality, predator-prey interactions, and camouflage strategies. Answering questions regarding these topics will allow a better grasp of the trade-offs this species faces in the wild, thus helping in the broader understanding of the life-history of cryptic ambush mesopredators in general. To achieve this goal, the following objectives are addressed in the different chapters:

Chapter 1

1. Validate a protocol to successfully test personality in rattlesnakes following five axes of personality by using the framework of Carter et al. (2013).
2. Quantify behavioral inter-individual variation to determine the extent of personality in *Crotalus atrox.*
3. Investigate the potential presence of behavioral syndromes within this species.

Chapter 2

1. Investigate the effect of personality on the spatial ecology of *Crotalus atrox.*
2. Determine whether *Crotalus atrox* follows the pace-of-life syndrome hypothesis.

Chapter 3

1. Determine the main predators of *Crotalus atrox* and the main factors influencing detection risk.

2. Determine the main factors influencing prey availability.
3. Determine if *Crotalus atrox* forages according to optimal foraging theory.

Chapter 4

1. Investigate background matching of *Crotalus atrox* in situ by comparing its body coloration and pattern to selected or random microhabitats.
2. Examine the trade-off between thermoregulation and crypsis in this species.

CHAPTER 1

Personally Rattled: a Unique Protocol to Support the Presence of Personality and Behavioral Syndromes in Rattlesnakes

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INTRODUCTION

Historically, while studying animals, researchers have observed behavioral individual variations that were described as data noise and were not further explored (Pennisi 2016). Ivan Pavlov was one of the first scientist to try to integrate these differences in his study design, thus laying the foundation for categorizing individual animal behavior (Pavlov 1966; Vonk et al. 2017). One of the first empirical studies to specifically address individual differences was published in 1938 but did not trigger more publications in this field (Crawford 1938; Vonk et al. 2017). This discipline did not expand until the publication of the work of King and Figueredo (1997) on chimpanzees. This study combined the methods of two landmark publications to assess individual differences: the emotions profile index (Buirski et al. 1973; Buirski et al. 1978) and the Madingley questionnaire (Stevenson-Hinde et al. 1980). The work of King and Figueredo provided the baseline to investigate individual differences in animals and most modern studies still use these methods (Freeman et al. 2011). To be applicable across species, personality traits are nowadays defined as behavioral tendencies that are different among individuals but consistent within individuals through time (Réale et al. 2007). While most of the early studies focused on highly cognitively developed species such as non-human primates, the field of animal personality has been rapidly growing and expanding to other taxa (Vonk et al. 2017).

While personality studies have been growing in number for various animal taxa, some groups have been underrepresented. Reptiles represent one of the most ecologically, morphologically, and behaviorally diverse groups of vertebrates (Pincheira-Donoso et al. 2013; Waters et al. 2017). Despite this fact, reptiles have been severely overlooked for behavioral studies even if individuals differences have been acknowledged (Waters et al. 2017). Several reasons could explain why personality has been understudied in reptiles. Observations and interpretation of reptile behavior remains challenging as they are generally secretive and difficult to observe (Shaffer et al. 2015). Consequently, little is known about the life history of reptiles compared to other taxa, a prerequisite to designing appropriate laboratory experiments (Ford 1995). Despite this fact, the number of studies investigating personality in reptiles has been slowly increasing in recent years. Personality has been described in squamates, turtles, and crocodilians, and linked to evolutionary and ecological processes in these taxa, showing the importance of investigating these individual differences (reviewed in Waters et al. 2017). Among these groups, snakes might be the most problematic to study as they possess unique behaviors due to their general biology, e.g., chemosensory tongue-flicking, infrared-sensing pit organs, limbless locomotion, near lack of hearing, unique prey handling, sometimes venomous nature, etc. (Ford 1995). Nonetheless, personality has been investigated in snakes (i.e., Maillet et al. 2015; Šimková et al. 2017; Gibert et al. 2022) but the literature remains limited and important gaps of knowledge still exist.

Rattlesnakes are perhaps one of the most notable groups of snakes due to their defensive display. They represent a widespread group ranging from Canada to Argentina and comprise 56 species (Uetz et al. 2022). Like most snake species, they suffer from misconceptions and are heavily persecuted (Murphy 2017). However, rattlesnakes play important ecological roles (Nowak et al. 2008; Reiserer et al. 2018) and exhibit more intricate behavior than previously thought (Schuett et al. 2016). Moreover, rattlesnakes are venomous species with medical significance giving rise to human-wildlife conflicts throughout their range (Malhotra et al. 2021). Only one study has investigated personality in rattlesnakes and it found that they exhibited consistent individual differences but no behavioral syndromes (Gibert et al. 2022), or suites of correlated behaviors (Sih et al. 2004) . Examining personality patterns in rattlesnakes would allow for better testing of how behavior and ecology are connected for these species by directly integrating inter-individual differences into ecological studies rather than considering these differences noise (Réale, Dingemanse, et al. 2010). Furthermore, providing new insights into rattlesnake personality has the potential to help preserve them (MacKinlay and Shaw 2023) and mitigate the conflicts they are facing (Gibert et al. 2022). Indeed, personality can be a useful tool to estimate the survival of individuals in case of reintroduction or translocation, predict the response to habitat change, or evaluate the vulnerability of individuals to zoonotic disease (reviewed in MacKinlay and Shaw 2023).

This study investigated the personality of the western diamond-backed rattlesnake (*Crotalus atrox*) across five axes: activity, exploration, boldness, sociability, and reactivity. The objectives of this study were the following: 1) validate a protocol to successfully test personality in rattlesnakes following these axes and using the framework of Carter et al. (2013); 2) determine whether *Crotalus atrox* exhibits personality; 3) investigate the potential presence of behavioral syndromes within this species. Western diamond-backed rattlesnakes were expected to exhibit individual differences consistent through time as seen in the western rattlesnakes (Gibert et al. 2022). A behavioral syndrome between activity, exploration, and boldness was also predicted as seen in many other studies (Conrad et al. 2011; Bókony et al. 2012; Chock et al. 2017; Kelleher et al. 2018).

MATERIALS AND METHODS

Animal collection

Adult western diamond-backed rattlesnakes were collected from 2019 to 2021 in El Paso and Hudspeth Counties (Texas, USA) and in Sierra County (New Mexico, USA) by using opportunistic visual survey encounters. Once individuals were captured, they were brought back to the laboratory where their morphometrics were recorded and their sex identified. Sex was determined by inserting a probe in the cloacal opening of the snake. In total, 22 individuals were used for this study including 15 males and 7 females.

Animal housing

Each snake was housed individually in ventilated plastic boxes (839 x 457x 304 mm) lined with paper towels in a room maintaining a temperature of 25 °C for no more than eight weeks. To minimize stress, each snake had access to a plastic hide large enough to enclose its entire body. Water was provided *ad libitum* during the time of the study. Food was not offered throughout the captivity period as desert rattlesnakes eat infrequently and have minimal energy requirements (Taylor et al. 2005).

Personality assessment

The personality of each snake was assessed following five axes: activity, exploration, boldness, sociability, and reactivity. Before starting any behavioral trials, snakes were acclimated to captivity for a minimum of one week. On average, only one trial was conducted per day. Each trial was repeated once to assess repeatability and a duration of at least one week was maintained between repeats. A summary of each behavioral trial performed, and variables measured is available in Table 1.1. To eliminate bias, a single observer scored all of the videos without knowing the snake's identity.

Activity levels were assessed as the duration (in seconds) an individual spent moving during a 24-hour period in an enclosure. The enclosures used for these trials were the same as the ones used to house the snakes (see description above). The first trial was performed in the enclosure where the snake was acclimated to captivity. To control for habituation, the trial was repeated in a novel enclosure with the same configuration (Šimková et al. 2017b). Trials were recorded using a security camera with infra-red night vision. Activity was evaluated from video records. Researchers were not present during testing to avoid any potential disturbances.

Exploration was measured using two different open-field tests. Open-field tests entail recording the behavior of an individual in a novel environment (Perals et al. 2017). Open-field tests were performed in an arena (1.4 m x 1.7 m x 1.2 m) built with plywood and sealed with epoxy paint. The arena floor was lined with a plastic transparent tarp that was disinfected and deodorized with a 20% bleach solution between each trial. Trials were recorded with a security camera for later analysis and no researchers were present in the room while the trials were in progress. The first open-field test (Explo1) was used to measure the willingness of an animal to venture into a new area and was adapted from previously used protocol (Herzog and Bailey 1987; Šimková et al. 2017b). Individuals were gently placed in the center of a 112 cm diameter circle marked on the floor of the arena. The trial was stopped when the head of the individual crossed the circle boundary. If the individual did not move after 60 minutes, the trial was stopped. The latency to move and to leave the circle was recorded (in seconds) for each individual as a proxy for exploration. For the second open-field test, the propensity of each individual to investigate a novel space was measured. To do so, the arena floor was sectioned off into 100 rectangles (14 x 17 cm) following a modified version of the protocol of Chiszar and Carter (1975). Each individual snake was placed in the center of the arena and allowed to wander freely for 60 minutes. Recording started one minute after the individual was placed in the arena. During these 60 minutes, the number of tongue flicks and number of squares entered by the head was extracted from the video recordings.

Boldness is generally described as the individual propensity to take risks (Chapman et al. 2011b) and was assessed following a modified version of the protocol of Mayer et al. (2016). Individuals were placed in a plastic box (32 x 21 x 22 cm) with a trap door inside the arena. After two minutes of acclimation when the box remained closed, the lid and trap door were removed allowing the snake to freely exit the box. If individuals did not move after 120 minutes, the trial was stopped. The box and the arena were disinfected and deodorized with a 20% bleach solution between each trial. Researchers were not present in the room during these trials. The time for the snake's head to emerge and the time for the complete body to emerge from the box (in seconds) were extracted from recordings and used to assess individual boldness level.

Reactivity was defined for this study as the response to a simulated predator attack (Maillet et al. 2015) and was tested two different ways. For the first test, individuals were placed in the arena and left alone for a minute to acclimate. After one minute, a human-scented glove filled with warm water (37°C) attached to 102 cm long snake tongs was presented 10 cm in front of the individual's face for five seconds. Individual responses were recorded using a security camera and were scored following a binary scale (0 = no bite; 1 = bite). The second trial consisted of a restraint test where the individual snake was immobilized in a tight plastic tube for a maximum duration of 5 minutes. Tubing was done by the same person each time and variation in time spent tubing was minimal and therefore not recorded. The rattling duration (s) during the restraining process was recorded and used as a proxy for reactivity.

Sociability is commonly described as the inclination to be attracted to conspecifics (Cote and Clobert 2007) and was measured using two different tests. For the first experiment, individual snakes were placed in an unfamiliar enclosure (839 x 457x 304 mm) with a piece of paper towel containing the scent of a conspecific positioned at one side and one with distilled water (control) at the other side. A control individual that was not part of the test subjects was used as a conspecific throughout the tests and its scent was extracted by soaking it in an amount of water proportional to its body mass following the protocol of Clark (2004). Individuals were left undisturbed for 60 minutes in the enclosure. After this period, their location within the enclosure was recorded as follows: 0 when >50% of the body of the snake was in the side of the unscented towel, 1 when in the middle, and 2 when the snake was on the side of the scented towel. For the second experiment, the test individuals were placed in the arena with a control individual for 60 minutes. The trials were recorded in their entirety with a security camera while researchers were not present. Behavior was scored as follows: 0 when the two snakes did not make contact and 1 when they did make contact, thus resulting in one value per snake per trial. This score was used as a measure of sociability.

Table 1.1: Summary of all behavioral trials performed

Context	**Trial abbreviations**	**Type of trial**	**Trial duration**	**Variables measured**
Activity	Act	Activity in 24h	24 h	Time spent moving (s)
Exploration	Explo1	Open-field test	60 min	Latency to move (s) Latency to leave arena (s) Number of squares crossed Number of tongue flicks
	Explo2	Open-field test	60 min	
Boldness	Bold	Emergence from shelter	120 min	Latency for head to emerge (s) Latency for body to emerge (s)
Reactivity	Reac1	Anti-predatory behavior	3 min	Behavioral score
	Reac2	Restraining test	5 min	Time spent rattling (s)
Sociability	Soc1	Response to conspecific scent	60 min	Score
	Soc2	Response to conspecific presence	60 min	Score

Statistical analysis

All statistical analyses were performed in R (R Core Team 2022). Data were mostly used untransformed as they followed a Gaussian distribution. Data distributions were checked using Shapiro-Wilk tests. Rattling duration (s) was log-transformed to follow a Gaussian distribution.

The scores for reactivity 1 and sociability 2 were fitted to a binary distribution while the scores for sociability 1 were fitted to a Poisson distribution.

Repeatability corresponds to the consistency of a result through time (Carter et al. 2013) and is an essential criterion for a behavior to be considered a personality trait (Sih et al. 2004; Réale et al. 2007). Generalized linear mixed-effects models (GLMM) fitted by restricted maximum likelihood were used to estimate the repeatability between repetitions using the *rptR* package in R (Stoffel et al. 2017). For these models, repetition number was included as a fixed effect and individual identification as a random effect.

To identify possible behavioral syndromes, an agglomerative clustering method using Ward's minimum variance was performed on the dissimilarity matrix including all the trials using the package *cluster* in R (Gyuris et al. 2010; Maechler et al. 2012). The dissimilarity matrix was obtained by first calculating the correlation matrix of the trials using Kendall's rank correlation method (Kendall 1948) and then, subtracting 1 from the absolute values of this matrix. The optimal number of clusters was estimated using a silhouette plot. Further, to confirm these associations and assess convergent validity, Spearman's rank correlation was calculated for each cluster.

To investigate the potential effect of snout-vent length (SVL), mass, and sex on personality results, mixed models were used. Mass, SVL, and sex were fixed while individual identification was included as a random effect in the models. All mixed models were performed using the package *lme4* (Bates et al. 2015). Linear mixed-effects models (LMM) were used for untransformed and transformed data following a Gaussian distribution. GLMMs with a binomial distribution were used for binary data such as sociability and reactivity scores.

RESULTS

Repeatability

The results of the GLMMs fitted by restricted maximum likelihood used to estimate repeatability are presented in Table 1.2. All variables measured except Soc1 were significantly repeatable between repetitions. Because of this, Soc1 was removed from the following analyses. Repeatability coefficients were estimated between 0.486 and 0.999 indicating that trials were moderately to highly repeatable.

Table 1.2: Summary of repeatability estimates calculated via GLMMs fitted by restricted maximum. Bold values indicate statistical significance of the test (<0.01)

Trial	Type of results	Repeatability	Confidence intervals	Statistical significance
Act	Time spent moving (s)	0.7	0.439 - 0.867	**p < 0.001**
Reac1	Scored behavior	0.971	0.891 - 0.999	**p < 0.001**
Reac2	Time spent rattling (s)	0.486	0.125 - 0.754	**p < 0.001**
Bold	Latency for head to emerge (s)	0.612	0.294 - 0.818	**p < 0.001**
	Latency for body to emerge (s)	0.741	0.487 - 0.883	**p < 0.001**
Explo1	Latency to move (s)	0.565	0.243 - 0.799	**0.00148**
	Latency to leave arena (s)	0.549	0.202 - 0.79	**0.00202**
Explo2	Number of squares crossed	0.857	0.709 - 0.939	**p < 0.001**
	Number of tongue flicks	0.686	0.414 - 0.858	**p < 0.001**
Soc1	Score	0	0 - 0.233	0.5
Soc2	Score	0.999	0.823 - 0.999	**p < 0.001**

Behavioral syndromes

The agglomerative clustering method identified three clusters across the five axes tested: reactivity, exploration, and sociability, boldness, and activity (Fig. 1.1). The optimal number of groups for the agglomerative clustering method was verified using a silhouette plot. The first cluster was composed of variables related to reactivity (Rho = 0.34, p = 0.019). The second cluster corresponded to the exploration personality dimension as it grouped all exploration variables (see Fig. 1.2A). The final cluster combined variables for boldness (Bold), sociability (Soc2), and activity (Act) supporting the presence of a behavioral syndrome (Fig. 1.2B).

Effects of morphometrics and sex on personality levels

The results of the mixed models used to determine if sex, SVL, and mass influenced personality levels are presented in Table 1.3. Morphometrics (SVL and mass) did not have a significant effect on any of the behavioral results. Sex appeared to have a significant impact on activity levels (p = 0.0357). Males spent significantly more time moving in 24 hours than females (Fig. 1.3).

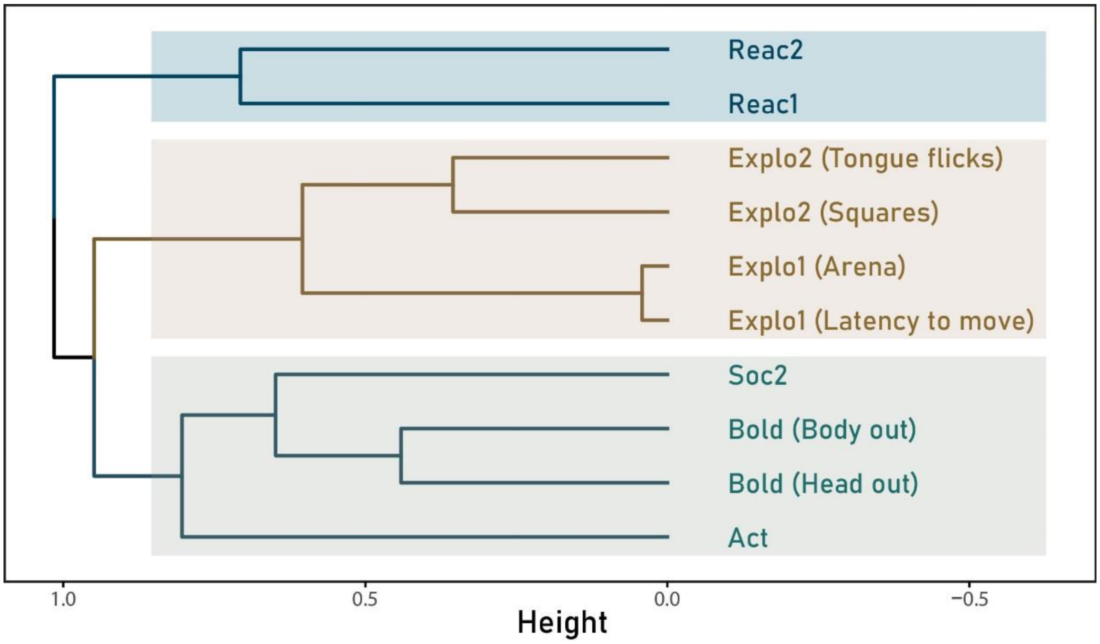

Fig. 1.1: Dendrogram resulting from agglomerative clustering analysis of the different behavioral variables tested. The agglomerative coefficient of the analysis was 0.553. Each box represents potential personality dimensions. Branch heights correspond to the similarity between variables.

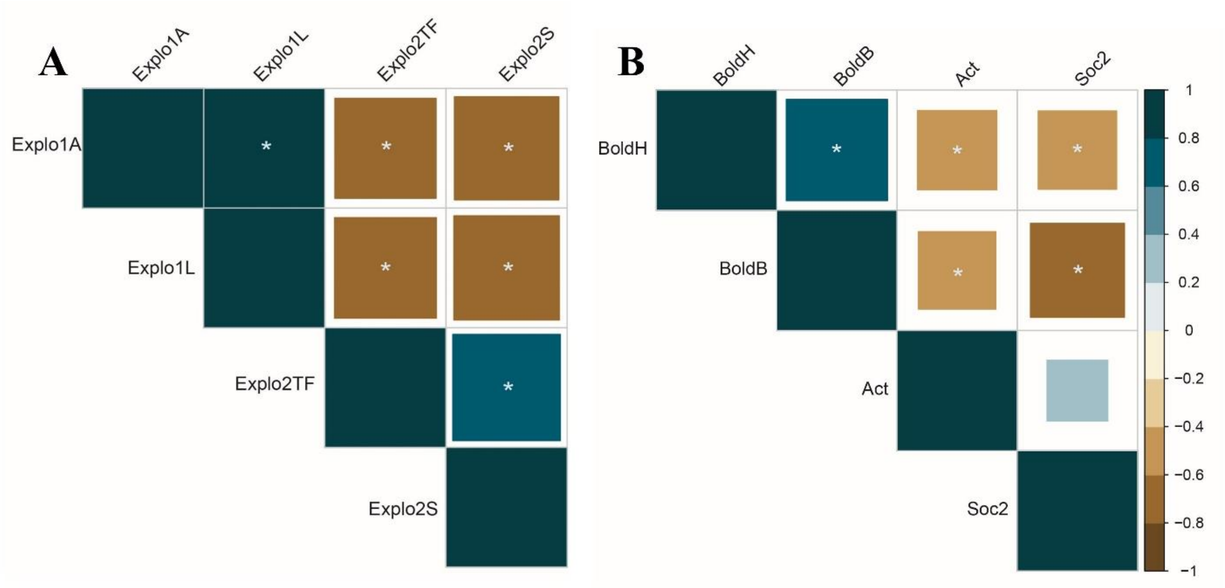

Fig. 1.2: Spearman's correlation matrix investigating the strength of the exploration dimension (A) and the behavioral syndrome (B) observed in Fig.1. The size and color of each squares denote the strength of the correlation (rho), and the star indicated the significance of the relationship ($p < 0.05$).

Table 1.3: Summary of mixed models results used to investigate the effects of sex and morphometrics on personality levels. In this Table, LMM stands for linearized mixed-models while GLMM stands for generalized linear mixed-models. T-value applies to LMM while z-value applies to GLMM. SE stands for standard error and DF for degree of freedoms. Significant p-values (<0.05) are bolded.

Source	**Type of model**	**Estimate**	**SE**	**DF**	**t/z**	**p**
(a) Activity	*LMM*					
Intercept		3791.121	2225.97	19	1.703	0.1048
Sex		2677.979	1184.68	19	2.261	**0.0357**
SVL		-0.8119	3.3814	19	-0.24	0.8128
Mass		-2.0413	3.4806	19	-0.586	0.5645
(b) Reactivity 2	*LMM with log-tranformed data*					
Intercept		3.664115	1.10618	18.9	3.312	**0.00366**
Sex		-0.623479	0.58871	18.9	-1.059	0.30285
SVL		-0.000344	0.00168	18.9	-0.204	0.84018
Mass		0.001441	0.00173	18.9	0.833	0.41504
(c) Boldness_head out	*LMM*					
Intercept		1928.523	1632.99	19	1.181	0.252
Sex		-1473.343	869.084	19	-1.695	0.106
SVL		0.822	2.481	19	0.331	0.744
Mass		2.535	2.553	19	0.993	0.333
(d) Boldness_head out	*LMM*					
Intercept		2963.48	1951.31	19	1.519	0.145
Sex		-1261.51	1038.5	19	-1.215	0.239
SVL		0.4953	2.9642	19	0.167	0.869
Mass		3.5375	3.0511	19	1.159	0.261
(e) Exploration 1_Latency to move	*LMM*					
Intercept		680.6852	980.448	19	0.694	0.496
Sex		-652.4206	521.799	19	-1.25	0.226
SVL		1.6207	1.4894	19	1.088	0.29
Mass		0.4931	1.5331	19	0.322	0.751
(f) Exploration 1_Latency arena	*LMM*					
Intercept		659.7062	1002.21	19	0.658	0.518
Sex		-604.0163	533.382	19	-1.132	0.272
SVL		1.7931	1.5224	19	1.178	0.253
Mass		0.4411	1.5671	19	0.281	0.781
(g) Exploration 2_Squares	*LMM*					
Intercept		129.6038	82.2804	19	1.575	0.132
Sex		31.982	43.7901	19	0.73	0.474
SVL		-0.0946	0.125	19	-0.757	0.458
Mass		0.1609	0.1287	19	1.251	0.226
(h) Exploration 2_Tongue flicks	*LMM*					
Intercept		1727.786	532.213	19	3.246	**0.00425**
Sex		224.3597	283.247	19	0.792	0.43808
SVL		-0.9337	0.8085	19	-1.155	0.26243

Mass		0.2711	0.8322	19	0.326	0.7482
(i) Reactivity 1	*GLMM with binomial distribution*					
Intercept		18	3.18016	2.6539	1.198	0.231
Sex			-2.051	1.9561	-1.049	0.294
SVL			0.00248	0.0042	0.586	0.558
Mass			-0.0065	0.0045	-1.427	0.153
(j) Sociability 2	*GLMM with binomial distribution*					
Intercept		18	5.05675	7.2454	0.698	0.485
Sex			2.72569	5.8459	0.466	0.641
SVL			0.00533	0.0091	0.585	0.559
Mass			-0.0178	0.0145	-1.233	0.218

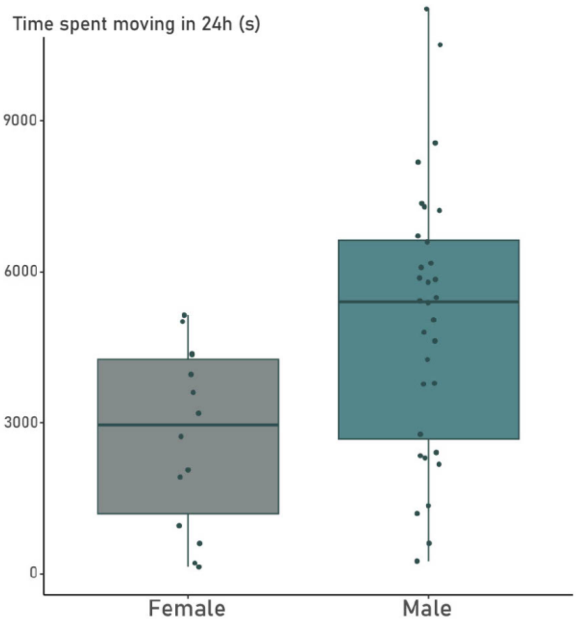

Fig. 1.3: Box plot showing activity levels of males versus females. The y-axis is expressed in seconds. Each dot represents one observation. Males were significantly more active than females. Boxes indicate the inter quartile range (IQR), with the central line depicting the median and the whiskers extending to the minimal and maximal observation.

DISCUSSION

The aims of this study were to develop a protocol to investigate the personality of western diamond-backed rattlesnakes (*Crotalus atrox*) and determine if they exhibit consistent individual differences and behavioral syndromes similar to other species.

Four criteria are taken into account to assess the validity of personality tests: ecological relevance, repeatability, and convergent and discriminant validity for each trial (Carter et al. 2013). Open-field tests were used to examine exploration in this species. Open-field tests have been shown to be powerful tests to quantify exploration as long as the recorded behavior is biologically relevant to the focal species (Perals et al. 2017). Squamates possess a unique olfactory system as it relies on the active stimulation of the vomeronasal organ by chemicals collected by the tongue (Daghfous et al. 2012). Tongue flicking is an easily quantifiable behavior that can be used as a proxy for exploration levels (Chiszar et al. 1976; Šimková et al. 2017b). Measure of tongue flicks in open-fields have been previously used in snakes and have been shown to be highly repeatable (Chiszar and Carter 1975). In this study, *Crotalus atrox* showed highly variable rates of tongue flicking between individuals, ranging from 0.85/min to 32.55/min and their numbers were highly consistent between trials (Table 1.2). The distance covered in a novel environment has also been used as a metric to quantify exploration in snakes (Chiszar and Carter 1975; Gibert et al. 2022). Similar to the findings of Chiszar and Carter (1975), distance covered (number of squares) was correlated to the number of tongue flicks (Fig. 1.1) demonstrating the convergent validity of these two metrics to measure exploration. Distance covered and tongue flick rate were also clustered with latency to move and latency to leave the arena of an open field (Fig. 1.1). These behaviors have also been used in the past to assess the exploration propensity of snakes (Šimková et al. 2017b; Gibert et al. 2022) and were significantly repeatable between trials in this study. Overall, open-field tests have been demonstrated to be suitable to measure exploration in the western diamond-backed rattlesnakes and all variables measured during these trials can be used to estimate exploration levels.

In this study, reactivity was defined as behavioral response to predators and was tested with a restraint test and with exposure to a simulated predator. Rattlesnakes evolved a unique communication signal, the rattle, believed to be used to warn off predators (Klauber 1956b; Allf et al. 2016). When threatened, rattlesnakes might choose to abandon their crypsis to rattle and potentially bite the aggressor (Greene 1988; Kissner et al. 1997). Variations in rattling have been observed between individuals (Atkins et al. 2021; Gibert et al. 2022) making it a biologically relevant character to test reactivity. Rattling behavior was significantly repeatable between trials in *Crotalus atrox* (Table 1.2) and was convergent with attacks of the simulated predators (Fig. 1.1). These two metrics have been previously used to measure reactivity in snakes (Herzog and Bailey 1987; Šimková et al. 2017b; Gibert et al. 2022). Rattling was also found to be repeatable between trials in *Crotalus oreganus* whereas striking rate was not consistent contrary to our findings (Gibert et al. 2022). Attack rate and rattling behavior are appropriate metrics to estimate reactivity in rattlesnakes and reactivity seems to represent its own personality dimension within *Crotalus atrox*.

Activity levels were estimated as the time spent moving over 24h for this study. Rattlesnakes are ambush predators known to be immobile for considerable amounts of time waiting for prey (Clark 2016). Because of this characteristic, measuring activity over an extended period was necessary to observe the full range of individual differences and make the test biologically meaningful. This test design was also utilized for another ambush snake species, the northern common boa (Šimková et al. 2017b). *Crotalus atrox* individual activity ranged in this study from two minutes to three hours per day demonstrating that 24-hour periods are of suitable length to measure activity in ambush pitvipers. The average daily activity for *Crotalus atrox* was 72 minutes which falls within the range of daily activity observed *in situ* with accelerometers. Indeed, individual diel activity was found to range from less than one minute to 90 minutes with considerable intraspecific variation observed (DeSantis et al. 2020). In this study, male *C. atrox* moved significantly more than females (Fig. 1.3). This trend was also observed with radiotelemetry studies for various species of rattlesnakes (Duvall and Schuett 1997; Glaudas and Rodríguez-Robles 2011; DeSantis et al. 2019a). Selection could be driving this difference as male rattlesnakes actively search for females and their success is directly correlated to their movements (Duvall and Schuett 1997; Glaudas and Rodríguez-Robles 2011). Increased reproductive success would then explain why higher activity levels are maintained in males as a result of this selection.

Boldness, or the propensity for an individual to take risks, was measured using an emergence test. Rattlesnakes spend most of their time hidden in burrows or vegetation to conceal themselves from predators (Gardiner et al. 2015; Maag et al. 2022) and predation risk seems to be the highest when they are moving on the surface (Maag and Clark 2022a). Consequently, emerging from a hide is a risky behavior for rattlesnakes and thus, emergence tests are biologically relevant when estimating their boldness levels. Emergence tests have been used to measure boldness in many taxa (see Carter et al. 2013), including snakes

(Mayer et al. 2016). Additionally, prey take longer to exit their shelters when they have been exposed to a predator beforehand (Bucklaew and Dochtermann 2021). In this study, emergence time was highly variable between individuals and the two variables used to measure emergence (head out and body out) were highly correlated (Fig. 1.1). Considering this, the emergence test is a valid experiment to measure boldness in rattlesnakes. Boldness was clustered with activity (Fig. 1.1) indicating the presence of a behavioral syndrome. As mentioned before, rattlesnakes appear to be rarely predated when concealed or coiled but are more likely to be killed while engaging in behavior such as mating or while moving across the landscape (Maag and Clark 2022a). Therefore, rattlesnakes are taking risks by being active and it seems to be consistent that boldness is correlated to activity.

Sociability is still understudied in reptiles, especially snakes, perhaps because of the lack of resemblance between humans and snakes (Lillywhite 2014; Schuett et al. 2016) or the technical difficulties to study the behavior of these cryptic species. However, rattlesnakes do exhibit social behaviors such as communal denning (Repp and Schuett 2008), kin recognition (Clark 2004), kin based aggregations (Clark et al. 2012), conspecific alarm signaling (Graves and Duvall 1988), and maternal attendance (Greene et al. 2002). Since rattlesnakes are known to aggregate and aggregation is easily quantifiable, this behavior presents an opportunity to measure sociability in these species. Rattlesnakes can recognize and follow conspecific scents (Clark 2007). Consequently, sociability was measured by exposing individuals to conspecific scent cues and recording whether or not they choose to position themselves near this cue. Even if this test was biologically relevant, the results were not repeatable (Table 1.2), making this sociability metric unusable as a personality trait. Inadequate test design, such as trial length or location, might be the cause of this inconsistency and should be investigated in future studies. In this study, sociability was also measured by exposing individuals to a conspecific and recording whether or not contact occurred between individuals. During trials, social behaviors were observed between snakes: individuals investigated, followed, or avoided each other in the arena, coiled near or fully on top of each other's, and rattled at each other. Individuals were also recorded rubbing their chins on each other, a behavior usually expressed during courtship (Schuett et al. 2016), but observed here with individuals of the same sex. Additionally, individuals were seen waving their tail at each other, a behavior that has been anecdotally recorded in the past (Schuett et al. 2016). Even if the biological meaning of these behaviors is not fully understood, contact between each individual was consistent between trials and thus, can be used to measure sociability in rattlesnakes.

Activity, boldness, and sociability were clustered together indicating a potential behavioral syndrome between these traits (Fig. 1). Individuals that were more active were also bolder and more social. The same observation was made for male guppies (*Poecilia reticulata*; Irving and Brown 2013). This behavioral syndrome is also found in three spined sticklebacks (*Gasterosteus aculeatus*) but only in populations were the predation pressure was high and thus, could be an example of adaptive evolution (Dingemanse et al. 2007). Several studies indicated that predation risk might be low for rattlesnakes as they exhibit high annual survivorship as adults (Diller and Wallace 2002; Jones et al. 2012). However, rattlesnakes have been noted to be preyed upon by many predator species (Klauber 1956b) and as they are elusive, as such it might be difficult to have an accurate estimation of predation risk. Predation risk might be one of the drivers for this behavioral syndrome, but further studies are required to investigate these results. Juvenile deccan mahseers (*Tor khudree*) were also found to be more social when they were bolder (Varma et al. 2020). The relationship between boldness and sociability has been found to be influenced by body condition in the social eider, *Somateria mollissima* (Öst et al. 2015). This observation was not verified in *Crotalus atrox*, as none of the morphometrics influenced boldness or sociability (Table 1.3). Boldness and sociability have been found to be genetically correlated (Mills and Faure 2000) and boldness is known to influence social organization (Öst et al. 2015). However, the rationale of this relationship remains to be investigated for rattlesnakes. There might be risk associated with rattlesnakes encountering each other thus, explaining why bolder rattlesnakes are more social. Rattlesnakes are known to fight each other, especially males during the breeding season. The main hypothesis to explain this behavior is that males fight for breeding opportunity, but females have been anecdotally observed to initiate fights. Fighting could also be a result of competition for resources such as food, shelter, or ambush sites (Hersek et al. 1992). Snakes cannot share food as they swallow their prey whole, and thus fights for food represent an immediate loss for the individual (Yeager and Burghardt 1991). When interacting with conspecifics, bolder snakes might have an advantage when competing for resources (Skinner et al. 2022) therefore promoting the correlation between boldness and sociability in rattlesnakes. Instances of cannibalism have been observed in several species of rattlesnakes and might be more common than previously thought (Prival et al. 2002). Because of this, approaching a conspecific could be dangerous hence explaining why bolder individuals are more likely to approach another individual. Rattlesnakes rely on crypsis as their main defense mechanism against predators (Maag and Clark 2022a). Detectability risk has been shown to increase with group size (Riipi et al. 2001) thus, making aggregated individuals easier to detect by predators. Consequently, being social might be risky for rattlesnakes explaining why individuals were more social when they were bolder.

To conclude, this study is one of the few studies to investigate personality across five axes in snakes and one of the only studies to examine personality in rattlesnakes. As with other organisms, *Crotalus atrox* exhibits individual behavioral differences consistent through time and behavioral syndromes comparable to other species. These preliminary results demonstrate that despite the lack of publications on their personality, snakes should be considered to further the comprehension of these individual differences. In this study, personality was measured in a controlled environment and future experiments should compare these results to *in situ* experiments to strengthen the validity of this protocol. This study provides a baseline to answer questions pertinent to personality in rattlesnakes such as its relationship with life history or ecology and will help gain insights in the secretive life of serpents.

CHAPTER 2

Insights into the Pace-of-Life Syndrome Hypothesis: Exploring the Influence of Personality on Movement Ecology in *Crotalus atrox*

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Contribution: conceptualization, data collection and analysis, preparation of original draft, manuscript submission

Contribution of other co-authors: data collection and manuscript editing

INTRODUCTION

To thrive within a given environment, individuals must efficiently gather food and find mates to reproduce (Davies et al. 2012). These resources are limited, and their acquisition depends on how individuals choose to distribute their energy and time among various activities, along with prevailing environmental conditions (Dunham et al. 1989). Because of these constraints, animals must continuously adapt their behavior to meet conflicting demands (Werner and Anholt 1993). Different species, or even different individuals within the same population, respond to these trade-offs by employing contrasting strategies, leading to differential life-history outcomes (e.g. Bonter et al. 2013; Patrick et al. 2017). Uncovering the mechanisms behind these strategies is essential for grasping fundamental concepts ranging from response to environmental stress (Schultner et al. 2013) to community assemblage (Zhu et al. 2018).

Life history can be seen as a set of rules governing three types of allocations: 1) energy to competing functions, 2) time to competing activities, and 3) reproductive energy to competing offspring (Dunham et al. 1989). In accordance with the pace-of-life syndrome hypothesis, closely related species are anticipated to exhibit distinct sets of physiological traits that have evolved in concordance with their specific life-history characteristics (Ricklefs and Wikelski 2002; Wikelski et al. 2003). These suites of traits are likely to be collectively influenced by ecological conditions thus favoring divergent life-history strategies (Réale, Garant, et al. 2010). While the pace-of-life syndrome hypothesis has been verified in different species (Wikelski et al. 2003; Tieleman et al. 2005; Wiersma et al. 2007), the integration of behavioral traits, particularly personality traits, within this hypothesis is a more recent development (Réale et al. 2010). Personality traits are defined as inter-individual behavioral differences that are consistent through time and these traits can be correlated, thus forming behavioral syndromes (Réale et al. 2007a). Personality traits have the potential to influence each rule governing life history, resulting in individuals with different life histories in a population.

To be able to allocate energy to competing functions, animals must first acquire resources. To acquire resources, most animals must move. The movement ecology paradigm hypothesizes that individual movement is controlled by three internal factors: navigation capacity (e.g. spatial information gathering and processing), motion capacity (e.g. means of movement), and internal state of the focal individual. These factors are themselves influenced by external factors such as biotic and abiotic components of the environment (Nathan et al. 2008). The internal state of an individual refers to the physiological and behavioral drivers of movements, determining the ultimate and proximate causes for movement (Nathan et al. 2008; Wilson et al. 2014). According to this definition, personality fits within the internal state of an individual and has the potential to lead to individual differences in movement strategies (Spiegel et al. 2017). Individual differences in behavior have been shown to influence home range size (Stiegler et al. 2022), habitat use (Schirmer et al. 2019), and local movement rate within species (Eccard et al. 2022; Michelangeli et al. 2022). This intraspecific variation in space use can lead to different life-history strategies, affecting individual fitness (Boyer et al. 2010; Nilsson et al. 2014). Additionally, the costs and benefits of these different space use strategies may fluctuate over time, depending on abiotic and biotic conditions (Dingemanse et al. 2004).

The connection between movement and personality has been primarily investigated in the context of dispersal, i.e. long-distance movements (Spiegel et al. 2017; Schirmer et al. 2019). Dispersal only constitutes a minimal fraction of an animal's lifetime movement, while local movements (i.e. small-scale movements) make up the majority of lifetime movement. Despite the importance of local movements, only a few studies focused on the relationship between personality and local movements (Kobler et al. 2009; Pearish et al. 2013; Spiegel et al. 2015; Schirmer et al. 2019; Stiegler et al. 2022). Local movements are important determinants of ecological interactions (Stamps 1995; Conner et al. 1999; Mettke-Hofmann et al. 2005; Morris 2005), the formation of individual niches (Schirmer et al. 2019; Schirmer et al. 2020), and thus, community dynamics and species coexistence (Kobler et al. 2009; Pearish et al. 2013; Best et al. 2015; Spiegel et al. 2015; Schlägel et al. 2020). Despite personality and movement ecology research focusing on the individual as the primary unit of study and how they react to environmental stimuli, these two fields have remained surprisingly separated (Nilsson et al. 2014). Combining movement ecology and personality will help illuminate the evolutionary implications of personality associated variation in animal movement driving that may impact, potentially leading to differences in life-history strategies (Sih et al. 2012; Wolf and Weissing 2012; Spiegel et al. 2017).

The main goal of this study was to investigate the effect of individual behavioral differences on the spatial ecology of the western diamond-backed rattlesnake (*Crotalus atrox*) by combining telemetry and behavioral assays. *Crotalus atrox* display variation in personality types (Da Cunha et al. 2023) and *C. atrox* individuals vary immensely in movement and territory size (DeSantis et al. 2019b; DeSantis et al. 2020). Therefore, *C. atrox* can be used as a model for examining the correlation between personality and spatial ecology. Moreover, as a mesopredator, rattlesnakes' foraging decisions are influenced by both apex predators (Haswell et al. 2018) and prey availability (Brown and Kotler 2004). Rattlesnakes are likely under considerable pressure to decide when and where to forage, resulting in trade-offs between resource acquisition and predator avoidance. *Crotalus atrox* was hypothesized to exhibit individual differences in space use and movement in the field that could be explained by individual differences in personality. Bolder, more active, more explorative individuals were predicted to have larger home ranges and higher movement rates than shy, less active, and less explorative individuals, thus following the pace-of-life syndrome hypothesis. To test these predictions, fourteen *C. atrox* were radio-tracked for a year to collect spatial data and then, their personality was assessed in captivity.

MATERIALS AND METHODS

Study site

Animal collection and fieldwork was conducted at the Indio Mountains Research Station (IMRS), a 161 km^2 property managed by The University of Texas at El Paso. IMRS is located within the Chihuahuan Desert approximately 42 km southwest of Van Horn in Hudspeth County (Texas, USA). The property includes most of the Indio Mountains and the southern spur of the Eagle Mountains, with an elevation ranging from 900 m to 1,600m. Within these elevations, the flora is classified as Chihuahuan Desert Scrub and is mostly represented by creosote bushes (*Larrea tridentata*), lechugillas (*Agave lechugilla*), black grama (*Boutela eriopoda*), and yuccas (*Yucca sp.*; Worthington et al. 2022).

Telemetry and field observations

Fourteen western diamond-backed rattlesnakes (*Crotalus atrox*) were captured on IMRS property and equipped with temperature-sensitive radiotransmitters (Holohil Systems Ltd., Carp, ON, Canada, SI-2T, 9.0 g). Radiotransmitters were surgically implanted into the coelomic cavity following a modified protocol based on Hardy and Greene (2000). Transmitters never exceeded more than 5% of the snake's body mass. Prior to surgery, the rattlesnakes were anesthetized with isoflurane using the open-drop method (Hardy and Greene 2000; Da Cunha et al. 2024). Surgical instruments were sterilized in a benzalkonium chloride solution for a minimum of 30 minutes, and benches were sanitized with 70% isopropyl alcohol. All procedures were conducted while wearing single-use sterile gloves. A 1.25 cm longitudinal incision was made into the coelomic cavity at two-thirds of the snout–vent length anterior to the cloaca, through which the transmitter was inserted. The transmitter antenna was then placed subcutaneously towards the head along the body, using a cannula that was subsequently removed (Hardy and Greene 2000; Da Cunha et al. 2024). Rattlesnakes were observed for 48 hours to monitor recovery before being released at the original capture site.

Rattlesnakes were radiotracked using an R-1000 telemetry receiver coupled with an RA-150 Yagi antenna (Communication Specialist, INC). Each rattlesnake was radiotracked for a full year with seven individuals radiotracked between 2020–2021 and seven others between 2021-2022 with the first tracking event being in June of 2020 and the last in August of 2022. Rattlesnakes were radiotracked twice a week during the active season (April–October) with a minimum of two days between tracking events. Rattlesnakes were only tracked once every two weeks during the inactive season (November–March) because previous studies have shown snakes to be inactive during this time (DeSantis et al. 2019b; DeSantis et al. 2020). As spatial strategies are known to vary between reproductive states for this species at this site (DeSantis et al. 2019b), the active season was split into non-mating season (April-July) and mating season (August-October). For each tracking event, the following data were recorded: date, time, GPS coordinates, behavior, microhabitat, and weather. After a year of being radiotracked and their personality assessed (see below), transmitters were removed, and snakes were released at their exact most–recent capture site.

Animal collection was authorized by the Texas Parks and Wildlife under permit number SPR-0290-019. All animal procedures adhered to the ethical guidelines of The University of Texas at El Paso and were pre-approved by the UTEP Institutional Animal Care and Use Committee (protocol number: A-201905-2_1447328-2).

Individual difference tests

After a full year of being radiotracked, all 14 rattlesnakes were brought to the laboratory at UTEP and were housed individually in ventilated plastic boxes (839 × 457 × 304 mm) lined with paper towels in a room maintaining a temperature of 25 °C for approximately eight weeks. To minimize stress, each snake had access to a plastic hide shelter and water was provided *ad libitum* throughout captivity. Food was not offered throughout captivity because desert rattlesnakes eat infrequently and have minimal energy requirements (Taylor et al. 2005).

The personality of each snake was assessed following four axes: activity, exploration, boldness, and reactivity following the protocol described in Da Cunha et al. 2023. Activity levels were evaluated by measuring the duration (in seconds) that an individual spent moving within an enclosure over a 24-hour period. Exploration, the propensity to venture into new areas, was assessed using two types of open-field tests. For the first test (Explo1), individuals were gently placed in the center of a 112 cm diameter circle marked on the floor of an arena. As a proxy for exploration (Explo1), the latency to move and leave the circle was extracted from video recordings (in seconds). For the second proxy of exploration (Explo2), each individual was placed in an arena where the floor was sectioned off into equal sized rectangles for 60 minutes. The number of tongue flicks and the number of squares crossed by the head were extracted from the video recordings (Explo2). Boldness, the propensity of an individual to take risk (Chapman et al. 2011b), was measured by using an emergence test. Each of these tests produced two variables that were used for statistical analysis. Snakes were placed in a plastic hide box in an arena for 120 min and the time for the snake's head to emerge and the time for the complete body to emerge from the box (in seconds) were extracted from recordings to assess individual boldness level. Finally, reactivity, defined as the response to a simulated predator attack (Maillet et al. 2015), was assessed using a restrain test. Individuals were immobilized (i.e. restrained) in a tight plastic tube for a maximum duration of five minutes and the rattling duration (in seconds) during the restraining process was recorded and used as a proxy for reactivity. Before starting any behavioral trials, snakes were acclimated to captivity for a minimum of one week. On average, only one trial was conducted per day. Each trial was repeated once to assess repeatability. To reduce bias, a single observer scored most of the videos without knowing the snake's identity. The activity trials were the only trials for which multiple observers scored the videos. To control bias between observers, different observers were tasked to score the same 24 h activity recording and it was ensured that the difference between observers was less than 5%.

Spatial metrics

All spatial metrics were calculated using the package *adehabitatHR* (Calenge 2006) and *move* (Kranstauber et al. 2018 Sep 11) in R (R Core Team 2023) for both non-mating and mating seasons using GPS points collected during radiotracking events. For each tracking event, we collected one GPS point within a 5-meter radius of the snake using a handheld GPS (Garmin Oregon 700), which has an accuracy of 3 meters. Home range size was estimated based on the 95% Minimum Convex Polygon (MCP) and the 95% kernel density (KD95). Core use area was based on the 50% kernel density (KD50). For all kernel estimators, the reference bandwidth selector was chosen as it is more robust to variations in sampling intensity (Bauder et al. 2015). Movement rate (meters/day) and total distance traveled (meters) for each individual were also calculated for each season.

Statistical analysis

All statistical analyses were performed in R (R Core Team 2023). To estimate the repeatability of behavioral traits between repetitions, generalized linear mixed-effects models (GLMM) fitted via restricted maximum likelihood were used via the *rptR* package in R (Stoffel et al. 2017). In these models, repetition number was treated as a fixed effect, while individual identification was considered a random effect.

To investigate the effect of behavioral traits on the spatial ecology of *Crotalus atrox*, linear models were used with spatial metrics included as response variables. Data distributions were verified using the Shapiro-

Wilk test on the residuals of the models. Data were mostly untransformed as they already followed a Gaussian distribution. When the residuals did not follow a Gaussian distribution, the response variable was log-transformed (see Table II for a list of variables that were log-transformed). Because of the small sample size (n = 14), only one behavioral trait was included in each model as a fixed effect. Sex was also included as a fixed effect. Some variables (latency to leave the circle, latency to move, and time for head to emerge) were not tested because they are highly correlated to the other exploration and boldness variables (Da Cunha et al. 2023). Because multiple linear models were performed on the same response variable, the level of significance was set to $\alpha < 0.01$ according to Bonferroni correction.

RESULTS

Repeatability of behavioral differences

The results of the generalized linear mixed-effects models (GLMM) fitted via restricted maximum likelihood that were used to test the repeatability of individual differences are presented in Table 2.1. All variables measured were significantly repeatable through time with repeatability coefficients varying from 0.586 to 0.848 (moderately to highly repeatable).

Table 2.1: Summary of repeatability estimates calculated via GLMMs fitted by restricted maximum.

Trial	**Variable measured**	**Repeatability**	**Confidence intervals**	**Statistical significance**
Activity	Time spent moving (s)	0.817	0.55 - 0.944	$p < 0.001$
Reactivity	Time spent rattling (s)	0.826	0.57 - 0.942	$p < 0.001$
Bold	Latency for head to emerge (s)	0.733	0.376 - 0.915	$p < 0.001$
	Latency for body to emerge (s)	0.593	0.139 - 0.855	$p < 0.001$
Explo1	Latency to move (s)	0.586	0.107 - 0.869	$p < 0.001$
	Latency to leave arena (s)	0.715	0.351 - 0.906	$p < 0.001$
Explo2	Number of squares crossed	0.847	0.589 - 0.955	$p < 0.001$
	Number of tongue flicks	0.848	0.6 - 0.953	$p < 0.001$

Influence of behavioral differences on spatial ecology

The results of the linear models used to test the relationship between behavioral differences and spatial metrics are presented in Table 2.2. For brevity, the influence of sex was only included in this table when personality scores had a significant effect on spatial metrics. Boldness had a significant effect on movement rate (m/day) during the non-mating season with bolder individuals traveling more per day than shy individuals (Figure 2.1a). Females travelled significantly less per day than males during the non-mating season (Table 2.2, Figure 2.1a). Activity did not have significant effect on total distance traveled (m) according to the Bonferroni's correction (p-value < 0.01; Figure 2.1b). Females travelled significantly less than males during the non-mating season (Table 2.2, Figure 2.1b). A linear model also showed that boldness had a significant effect on the difference in movement rate between season (Est. = 0.008, SE = 0.003, t = 3.039, p = 0.0113; Figure 2) with shy individuals increasing their movement rate more than bold individuals during the mating season.

Table 2.2: Summary of linear models results used to investigate the effects of personality and sex on different spatial metrics. Sex is only included for significant relationships between spatial metrics and personality scores. MCP stands for Minimum Convex Polygon (95%), K95 for kernel density (95%), K50 for core use area (50%), MR for Movement Rate, and TDT for Total Distance Travelled. Significant results are in boldface (p < 0.01). * denotes when the response variable was log-transformed to follow a Gaussian distribution.

Response	Season	Personality score	Estimate	SE	t-value	df	p value
MCP	Mating	Exploration (tongue flicks)	0.000	0.004	0.069	11	0.947
		Exploration (squares)	-0.004	0.034	-0.119	11	0.908
		Boldness (body out)	0.001	0.001	0.797	11	0.442
		Activity	0.000	0.001	-0.443	11	0.666
		Reactivity	-0.080	1.590	-0.050	11	0.961
	Non-mating	Exploration (tongue flicks)*	0.000	0.000	-0.143	11	0.889
		Exploration (squares)*	-0.002	0.003	-0.508	11	0.622
		Boldness (body out)*	0.000	0.000	-0.718	11	0.487
		Activity*	0.000	0.000	1.460	11	0.172
		Reactivity	-0.019	0.019	-1.022	11	0.329
K95	Mating	Exploration (tongue flicks)	-0.026	0.029	-0.920	11	0.377
		Exploration (squares)	-0.265	0.225	-1.175	11	0.265
		Boldness (body out)*	0.000	0.000	-0.178	11	0.862
		Activity*	0.000	0.000	0.175	11	0.864
		Reactivity	0.266	0.160	1.658	11	0.126
	Non-mating	Exploration (tongue flicks)	0.010	0.220	0.469	11	0.648
		Exploration (squares)	0.137	0.174	0.799	11	0.448
		Boldness (body out)*	0.000	0.000	-1.921	11	0.081
		Activity*	0.000	0.000	1.218	11	0.249
		Reactivity	-0.162	0.125	-1.295	11	0.222
K50	Mating	Exploration (tongue flicks)	-0.004	0.005	-0.884	11	0.396
		Exploration (squares)	-0.037	0.037	-1.000	11	0.339
		Boldness (body out)	0.000	0.001	0.364	11	0.723
		Activity	0.000	0.001	-0.615	11	0.551

		Reactivity	0.040	0.027	1.499	11	0.162
	Non-mating	Exploration (tongue flicks)	0.001	0.003	0.242	11	0.813
		Exploration (squares)	0.008	0.228	0.364	11	0.723
		Boldness (body out)	-0.001	0.001	-1.968	11	0.075
		Activity	0.000	0.000	-0.058	11	0.954
		Reactivity	-0.027	0.015	-1.812	11	0.097
MR	Mating	Exploration (tongue flicks)*	0.007	0.008	0.886	11	0.394
		Exploration (squares)	0.044	0.069	0.645	11	0.532
		Boldness (body out)	0.002	0.002	1.039	11	0.321
		Activity*	0.000	0.001	-0.002	11	0.999
		Reactivity	0.014	0.052	0.264	11	0.797
	Non-mating	Exploration (tongue flicks)	0.000	0.000	0.521	11	0.613
		Exploration (squares)	0.111	0.888	1.250	11	0.237
		Boldness (body out)	-0.007	0.002	-3.463	11	**0.005**
		Sex (with boldness)	18.102	8.060	2.246	11	**0.002**
		Activity	0.000	0.000	1.870	11	0.088
		Reactivity	-0.058	0.069	-0.839	11	0.419
TDT	Mating	Exploration (tongue flicks)	0.310	0.711	0.436	11	0.671
		Exploration (Squares)	3.504	5.683	0.617	11	0.550
		Boldness (body out)	0.264	0.146	1.806	11	0.098
		Activity	0.042	0.093	0.445	11	0.665
		Reactivity	2.085	4.291	0.486	11	0.637
	Non-mating	Exploration (tongue flicks)	-0.335	0.604	-0.554	11	0.590
		Exploration (squares)	-1.934	4.899	-0.395	11	0.701
		Boldness (body out)	-0.213	0.126	-1.687	11	0.120
		Activity	0.149	0.067	2.239	11	0.047
		Sex (with Activity)	2435	485.6	4.914	11	**0.0005**
		Reactivity	0.139	3.702	-0.038	11	0.971

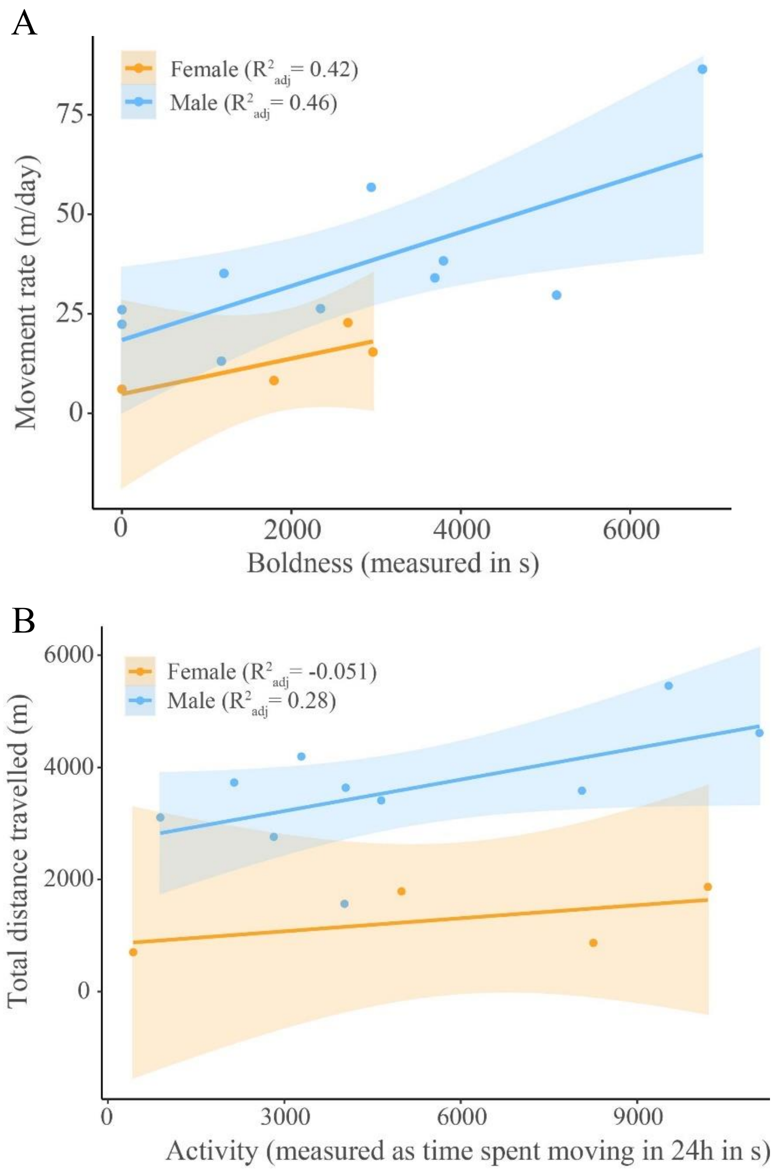

Fig. 2.1: Effect of personality on movements. (a) Effect of boldness on movement rate (m/day in the field) during the non-mating season on 14 radio-tracked *Crotalus atrox* (M = 10, F = 4). Boldness is measured here as the total length of the boldness trial (7200 s) minus emergence time, meaning that bolder individuals have larger scores in seconds. Results from linear model show that boldness had a significant effect on movement rate (see Table 2.2).

(b) Effect of activity (measured as time spent moving within 24 hours in seconds) on total distance traveled (m) during the non-mating season on 14 radio-tracked rattlesnakes (M = 10, F = 4). Results from linear model show that activity had a near significant effect on movement rate (see Table 2.2).

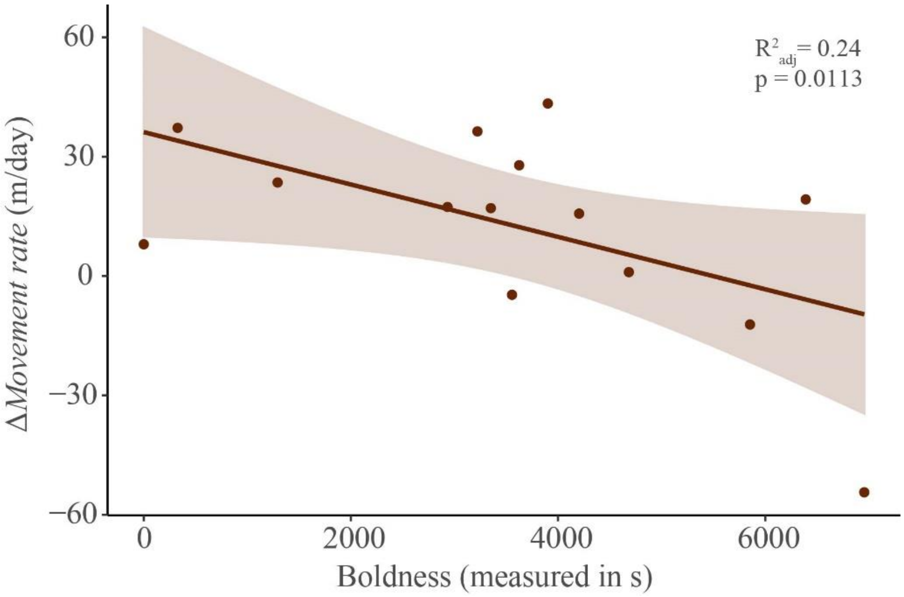

Fig. 2.2: Effect of boldness on *Δmovement rate* (m/day in the field) between non-mating and mating season 14 *Crotalus atrox* (M = 10, F = 4). Boldness is measured here as the total length of the boldness trial (7200s) minus emergence time, meaning that bolder individuals have larger scores in seconds. Individuals are considered bolder when they have a shorter emergence time. Results from the linear model shows that boldness had a significant effect Δ*movement rate* (p = 0.013).

DISCUSSION

The main goal of this study was to investigate the effect of individual behavioral differences on the spatial ecology of western diamond-backed rattlesnakes. The main hypothesis was partially supported as bolder and more active individuals traveled more than shy, less–active individuals during the non-mating season. Thus, shyer individuals increased their movement rate significantly more than bolder individuals during the mating season, resulting in no significant differences in movement between personality types during the breeding season. Generally, these results support the pace-of-life syndrome hypothesis only during the non-breeding season.

Boldness had a significant effect on movement rate (m/day) during the non-mating season. Indeed, bolder individuals moved more on average than shyer individuals. The same relationship has been previously described in other species (Eccard et al. 2022; Michelangeli et al. 2022). For most of their time, rattlesnakes stay hidden in burrows or within vegetation to stay concealed from predators (Gardiner et al. 2015; Maag et al. 2022). When hunting, rattlesnakes stay immobile for long periods of time (Clark 2016) rendering them difficult to spot by predators, even if the rattlesnake is not under the cover of vegetation (Da Cunha et al. 2024). Because of this, moving is risky for rattlesnakes as they are more likely to get killed while moving on the surface (Maag and Clark 2022b). Although boldness has been correlated with habitat use (Schirmer et al. 2019), dispersal rate (Chapman et al. 2011b), and home range size (Stiegler et al. 2022) in other species, no significant correlation between boldness and home–range size was found in this study. In the case of home range size, bolder individuals usually have larger home range and core use area (Spiegel et al. 2015; Schirmer et al. 2019) indicating a potential relationship between boldness and territoriality. Territoriality has been described in one species of snake (Webb et al. 2015), but generally snakes do not seem to be territorial. The lack of a relationship between boldness and home range size in the western diamond-backed rattlesnakes might be explained by their non-territorial nature.

Although activity did not have a significant effect on the total distance traveled according to the Bonferroni correction, the level of significance was still under 0.05. The Bonferroni correction has been subject to numerous critics, especially in the field of ecology (e.g. Moran 2003; García 2004). For this reason, the influence of activity is still discussed but these results must be interpreted with caution. Activity has been related to several spatial metrics in other species including core area size (Aliperti et al. 2021) and dispersal (Jokela et al. 2008; Thorlacius et al. 2015). In *C. atrox*, activity, boldness, and sociability form a behavioral syndrome (Da Cunha et al. 2023) meaning that in this study, bolder individuals are also more active. In this study, active and bold individuals tend to travel longer distances at a faster rate than less active and shy individuals. These characteristics are commonly found in superficial explorer (or fast) individuals (van Overveld and Matthysen 2009) showing that these results support the pace-of-life syndrome hypothesis (Réale, Garant, et al. 2010). Superficial explorers tend to move rapidly while being less sensitive to environmental stimuli and changes (Spiegel et al. 2017). Superficial explorers reduce their time at a specific spot, exploiting fewer resources (Wolf et al. 2007). Because of this, these individuals might need to travel longer distances to reach their resource requirements, even if that means taking more risks. However, less active and shy individuals are usually considered slow explorers, moving less and slower than fast explorers (van Overveld and Matthysen 2009). Slow explorers tend to carefully explore their environment, making them more sensitive to environmental variation (Spiegel et al. 2017). These different behavioral types are maintained in the population as they each perform better under different conditions (Wolf et al. 2007). Indeed, slow explorers might be more successful than fast explorers when resources are unequally distributed on the landscape, but they might be outperformed by fast explorers when resources are unpredictable (Spiegel et al. 2017). In general, boldness and activity are known to influence growth, survival, and reproduction success (reviewed in Réale et al. 2007). For example, bolder bighorn sheep (*Ovis canadensis*) males had higher lifetime reproductive success (Réale et al. 2009) and higher survival rates than shyer individuals (Réale and Festa-Bianchet 2003). Boldness also influenced positively body mass gain in several species (Ward et al. 2004; Westerberg et al. 2004). While individuals were found to move differently across the landscape based on their personality during the non-mating season in this study, the biological implications of this difference remains to be investigated.

In this study, personality influenced the movement ecology of *C. atrox* only during the non-mating season (April–July), showing that this relationship was dependent on the reproductive state of this species. The non-mating season represents four out of the seven active months of this species, and thus personality influences the majority of the active season. During the mating season, male rattlesnakes face a trade-off between searching for mates and hunting because of their ambush foraging strategy that requires them to remain sedentary (Tetzlaff et al. 2017). As a result, males usually choose to decrease their foraging activity to invest more in their reproductive output (Tetzlaff et al. 2017; Cochran et al. 2021). Rattlesnake males actively locate females and as a result, often travel more during the mating season (Glaudas and Rodríguez-Robles 2011; DeSantis et al. 2019b). The movement of males is closely linked to their reproductive success, and males who travel along straighter paths or longer distances tend to experience a higher frequency of mating events (Duvall and Schuett 1997; Glaudas and Rodríguez-Robles 2011). Therefore, increased movement of all males regardless of personality type during the mating season might be a result of sexual selection to increase reproductive success (Glaudas and Rodríguez-Robles 2011).

While on average, males increased their movement during the mating season, the difference in movement rate varied between individuals and was dependent on boldness. Shyer individuals increased their movement rate significantly more than bolder individuals during the mating season. According to the pace-of-life syndrome hypothesis, slow explorers should be more responsive than superficial explorers to environmental and social changes, such as reproductive status of other individuals (Ruiz-Gomez et al. 2011; Herborn et al. 2014; Spiegel et al. 2017). Thus, the results of this study support the pace-of-life syndrome hypothesis as slow-explorers responded more to a change in reproductive status. Slow-explorers tend to act based upon prior knowledge from personal and social origins whereas fast-explorers tend to make decisions independently from available information (Kurvers et al. 2010; Smit and van Oers 2019). These differences might be explained by variation in the incorporation of information based on personality type (Smit and van Oers 2019) with slow-explorers being more behaviorally flexible than fast-explorers when incorporating information (Mathot et al. 2009; Coppens et al. 2010). These contrasting strategies can be beneficial or maladaptive depending on the environmental context (Smit and van Oers 2019). Although using prior knowledge might generally be safer (Wolf et al. 2008), especially in a more constant or resource-scarce environment, ignoring prior knowledge might be more rewarding, particularly in more variable and higher–quality habitats (Herborn et al. 2010; Heinen and Stephens 2016). Male rattlesnakes are hypothesized to use three different strategies to find receptive females: 1) following scent-trails left by females; 2) using efficient search patterns to locate females; or 3) using prior experience to return to locations where females were previously found (Coupe 2002). Scent trailing does not seem to be an effective method to locate mates over extensive distances, as it largely relies on the chances of a male encountering the trail of a female. In line with evidence showing that slow-explorers tend to base their decisions on prior knowledge and social cues (Smit and van Oers 2019), slow-explorer rattlesnakes might use a combination of all three strategies to locate mates leading to an increase in movement rate during the mating season. However, fast-explorers are less accurate when incorporating information into their decision-making processes (Smit and van Oers 2019).

In conclusion, this study demonstrated that western diamond-backed rattlesnakes exhibit differences in their movement ecology according to their personality. The effect of behavioral differences on movement was dependent on the reproductive status of individuals. During the mating season, males adjusted their movements, with shy individuals showing a larger increase in movement rate than bold individuals. The results of this study suggest the existence of two different strategies for resource acquisition, thus supporting the pace-of-life syndrome hypothesis under specific contexts (i.e. non-breeding season; Réale, et al. 2010; Spiegel et al. 2017). While this study provides new insights into the relationship between personality and ecology, further research is required to validate and uncover the mechanisms and consequences of these strategies for this species.

CHAPTER 3

From Fear to Feast: Investigating Rattlesnake Foraging Strategies Under a Landscape of Fear by Combining 3D-Printed Snake Replicas, Telemetry, and Machine Learning

Will be submitted as Da Cunha, O., Dominguez, R. P., Horne, L.M., Mead J. J., Fournier, C., Johnson, J. D. & Seymoure, B. M. in a scientific journal to be determined.

Contribution: conceptualization, data collection and analysis, preparation of original draft, manuscript submission

Contribution of other co-authors: data collection and manuscript editing

INTRODUCTION

Survival ultimately comes down to interactions between predators and their prey. As such, predator-prey interaction studies have been foundational for understanding broad ecological themes such as community structure (Kneitel and Chase 2004), trophic cascades (Mooney et al. 2010), and biodiversity (Letnic et al. 2012). Overall, predator-prey interactions are pivotal in shaping ecosystem structures and functions (Berger et al. 2001; Hawlena and Schmitz 2010). Predator-prey interactions can be influenced by environmental factors such as temperature and habitat complexity (Wasserman et al. 2016). Moreover, the dynamics between predators and prey are influenced not only by behaviors during interactions (McGhee et al. 2013; Belgrad and Griffen 2016), but also by the isolated behaviors of prey and predators.

Generally, prey should minimize interactions with their predators and many prey modify their morphology, physiology, and behavior in response to predation risk (Lima 2009; Cresswell 2011; Kishida et al. 2014), defined as the probability of an individual to being predated by another organism (Pettorelli et al. 2015). For instance, changes in habitat use (Creel et al. 2005), foraging strategy (Winnie and Creel 2007), and movement patterns (Fortin et al. 2005) have been observed in response to predation risk. Such behavioral modifications are costly for individuals and have been found to negatively impact prey growth (Pangle et al. 2007), development (Skelly and Werner 1990), and fecundity (Peckarsky et al. 1993). Predation risk not only directly affects prey survival but also has the potential to alter community structure. For example, prey will shift their distribution and foraging activity in response to perceived predation risk (i.e. “fear”) leading to modifications in interspecific prey competition (Lima 1998) with cascading effects across trophic levels (Grabowski and Kimbro 2005). This “landscape of fear” proposes a model to explain these effects and how they cascade from individuals to ecosystems (Brown and Kotler 2004). This model measures how animals perceive their environment on a spatio-temporal scale based on trade-offs between perceived predation risk and activity patterns, thus creating a map of fear across the physical landscape (Bleicher 2017). Landscapes of fear continuously change and are shaped by a variety of biological, ecological and evolutionary factors (Bleicher 2017; Gaynor et al. 2019). The indirect effects of predation, such as predation risk, influence prey dynamics, sometimes even more than the direct effects of predation (Nelson et al. 2004; Cresswell 2011).

Mesopredators have a central role in predator-prey interactions by serving as both prey and predators within trophic systems (Mukherjee et al. 2009). Mesopredator foraging decisions are influenced by the presence of apex predators (Haswell et al. 2018) and by prey availability (Brown and Kotler 2004). Following from optimal foraging theory, mesopredators should forage when and where their prey are abundant while avoiding high predation risk (Pyke et al. 1977). However, studies investigating the foraging decisions of mesopredators in a context of predator-prey interactions are lacking, especially in natural settings. This paucity is partially due to the technical difficulty of observing instances of predation in the wild, particularly for cryptic mesopredators such as rattlesnakes. Nevertheless, rattlesnakes offer a good model to study predator-prey interactions as they are widespread and abundant mesopredators in North American ecosystems. Because of their ambushing foraging strategy, rattlesnakes spend extended periods of time exposed to predators (Klauber 1956). Thus, rattlesnakes and other mesopredators should face heavy pressure to decide when and where to forage, however, these pressures are not well-understood because of the lack of information regarding predation of rattlesnakes (Maag and Clark 2022a).

To gather information about predation, scientists have used rattlesnake replicas made of soft and malleable materials (e.g. Farallo and Forstner 2012; Harmel et al. 2020). However, these types of models present some disadvantages such as being time–consuming (Behm et al. 2018), relatively unrealistic, and limited in information provided about predation events. With the recent development of 3D-printing, models can be more biologically accurate and easy to build and manipulate (Bulté et al. 2018). The technology of 3D-printing offers opportunities to ask a wide array of behavioral questions (Igic et al. 2015), including reproduction, foraging, and predation behavior (Behm et al. 2018). While 3D-printing models have been slowly introduced into ecology, they have not been extensively used to study predation. Through combining the use of biologically relevant 3D-printed models with other technologies, such as radiotelemetry and camera trapping, the trade-off that mesopredators face involving foraging decisions can now be quantified.

Here, I aimed to investigate the foraging decisions of the western diamond-backed rattlesnake (*Crotalus atrox*) in natural settings by combining the use of 3D-printed biologically accurate snake replicas, camera trapping, and telemetry data. The main goal of this study was to determine how the landscape of fear affects the foraging decisions of *Crotalus atrox* by looking at factors influencing detection risk and prey availability. Predation risk and prey availability were hypothesized to influence diel activity patterns and micro-habitat selection with the prediction that *Crotalus atrox* choose to be active when and where prey availability is high and predation risk is low, consistent with the optimal foraging theory. To answer these questions, 3D-printed snake replicas associated with game cameras were deployed in the field to assess detection risk and prey availability. Concurrently, western diamond-backed rattlesnakes were radio-tracked and then the resulting telemetry data were compared to game camera observations to investigate individual rattlesnake foraging decisions.

MATERIALS AND METHODS

Rattlesnake 3D-printed model design

An adult male specimen of *Crotalus atrox (77.1cm SVL; 6.3cm TL)* from the UTEP Biodiversity Collections (UTEP 12333) was scanned with a modified Xbox Kinect© camera. The digital model created from the scan was then adjusted and printed with polylactic acid (PLA) using Ultimaker (New York, NY) 3D-printers. Models were printed in two different sizes: a smaller size (total length of 34.1 cm) to represent a juvenile *C. atrox* and a larger size (total length of 85.5 cm) to represent an adult *C. atrox*. Models were then painted according to the coloration and pattern of a western diamond-backed rattlesnake. To do so, the body coloration of a wild-caught *Crotalus atrox* was measured in the visible spectrum by placing it in a bucket with white, black, and grey (18%) standards to calibrate measurements. Pictures were taken with a Canon EOS REBEL T3i camera with a Canon EF 50mm f/1.4 USM lens. To control for light exposure, the bucket was illuminated by a light bulb presenting a spectrum close to natural sunlight (ExoTerra© halogen basking spot). Images were processed using Image J (Schneider et al. 2012) with the package micaToolbox (Troscianko and Stevens 2015). Blue, red, and green were measured for the following body parts: dorsum, diamonds, white outline of the diamonds, rattle, and black and white tail bands. Different paint mixes were applied to 3D-printed models and colors were measured with the same set-up as previously described. Paint mixes were considered satisfying for each body part when presenting a significant amount of overlap for blue, red, and green (see Appendix 1; Fig. S1). Then, paint (Vallejo© brand, Barcelona, Spain) was applied to the model using a combination of airbrushing and paint brushing. Snake scale pattern was created using fishnet stockings and one coat of varnish was applied to protect the paint from rain and sun damage (Liquitex professional matte varnish). Pieces of wood (1 cm x 0.5 cm x 0.5 cm) were glued under the models to limit their contact to the ground and protect them as ground temperature is known to reach over 60°C during the hottest part of the year.

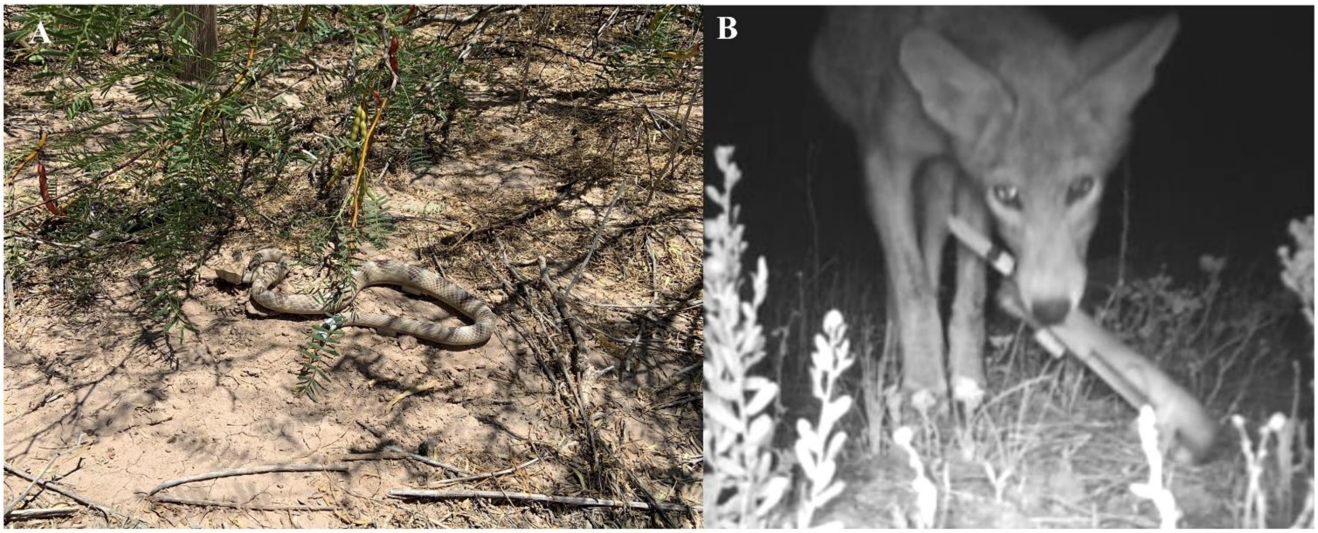

Fig. 3.1: Replicas in the field. **A**: A rattlesnake 3D-printed replica deployed in the field. **B**: A coyote (*Canis latrans*) predation observation.

Replica deployment

The replicas were deployed at Indio Mountains Research Station (IMRS) from June 2020 to December 2022 (Fig. 3.1). IMRS is a 161 km^2 research facility owned by the University of Texas at El Paso (UTEP). IMRS is located within the Chihuahuan Desert and the plant community could be mainly described as mixed desert scrub (Worthington et al. 2022). Remnant earthen cattle tanks can be found within the property from past ranching activities and tanks constitute an important landscape feature as they still collect water during the rainy season resulting in resource hot spots (DeSantis et al. 2019a). For this reason, two main habitats were identified for the purpose of this study: earthen tanks and desert scrub. Fifteen models were randomly distributed within two earthen tanks while fifteen others were randomly distributed within two plots of desert scrub. Each model was attached to a fishing line (to limit any displacement) and was positioned near a game camera (Stealth cam PX18FXCMO; Irving, TX) to record any interaction with the replicas. Cameras were set to record for 30 seconds when triggered. At each model location, environmental data about microhabitat was collected, with microhabitat defined as a one meter by one meter quadrat around the replica. The percentage of vegetation, exposed soil, and rock was recorded. Type of vegetation (species), vegetation height (recorded as a continuous variable), and distance to nearest vegetation (if no vegetation was within the microhabitat, continuous variable) were also recorded. Type of rock (sedimentary or conglomerate), distance to the nearest rock (if no rock was within the microhabitat, continuous variable), and type of soil (alluvial or sand) were also documented. Finally, concealment percentage, i.e. the percentage of the replica that was hidden from above, was recorded as a categorical variable (0%, less than 50%, or more than 50%). For each animal observed on camera, the following information was recorded: date, time, species, model detection, and model predation. Detection was considered to occur when an animal looked directly at the model or showed any behavioral reaction to the replica (e.g. bit, pawed the replica, ran or jumped). Predation was confirmed when a potential predator was attacking the model with its mouth or claws. Only records from April 1st to October 31st were used for analysis because these dates correspond to the activity period of *Crotalus atrox* at this field site (DeSantis et al. 2019a).

Radiotracking of rattlesnakes

Twenty-five western diamond-backed rattlesnakes were caught at IMRS from 2020 to 2023 and subsequently equipped with temperature-sensitive radiotransmitters (Holohil, Ontario, Canada, SI-2T, 9.0g) at an on-site surgery building. Following a modified protocol derived from Hardy and Greene (2000), transmitters were implanted in the snake coelomic cavity and never exceeded 5% of the snake's body mass. Rattlesnakes were sedated using isoflurane administered through an open-drop method within a transparent plastic tube. Benches were sterilized with isopropyl alcohol (70%), surgical instruments were sterilized in a solution of benzalkonium chloride for a minimum of 30 minutes, and procedures were conducted while wearing single-use sterile nitrile gloves. To insert the transmitter, a 1.25 cm longitudinal incision was made into the coelomic cavity, situated at two-thirds of the snout–vent length posterior to the head. Subsequently, the transmitter antenna was placed subcutaneously along the body towards the head using a cannula, which was then withdrawn. Following the surgery, the rattlesnakes were closely observed at the on-site facility for a period of 48 hours to monitor their recovery. Once environmental conditions were deemed favorable, they were released at the exact location where they had been captured. Each rattlesnake was radio-tracked twice a week during one active season at IMRS (April–October 2020, 2021, and 2022, and 2023). For each tracking event, the behavior of the rattlesnake was recorded as a categorical variable (tight coiled, moving, mating, non-visible). Rattlesnakes were considered active when they were visible and non-active when non-visible (usually in burrow underground). Moreover, the same microhabitat data as for 3D-printed replicas were collected for each event (see previously described).

Random forest models

Random forest models (R package *randomForest*; Liaw and Wiener 2002) were used to investigate which predictors were the most important for model detection by predators or prey encounters and to ultimately determine if rattlesnakes occupied space and time to increase prey interactions while decreasing predator encounters. Random forest models are machine learning algorithms in which classification trees are built on bootstrap samples from the data. Each tree uses a subset of randomly selected variables at each node for splitting. Out-of-bag observations, which are not included in a bootstrap sample, are used to evaluate the performance of each tree. The final prediction for each observation is determined by majority voting among the predictions of the trees, with ties being resolved randomly (Cutler et al. 2007). Variable importance can be estimated by looking at the mean decrease in accuracy. The mean decrease in accuracy for a variable is determined by comparing the classification accuracy of out-of-bag data when the variable is observed versus when the variable's values in the out-of-bag data are randomly permuted. A higher mean decrease in accuracy signifies greater importance of the variable in classification.

Game camera observations associated with their microhabitat data were used to train random-forest algorithms to evaluate the importance of spatiotemporal variables for prey availability and predator detection. After training the models with this game camera dataset, the same random-forest models were applied to the radio-tracking dataset to estimate the probability of detection by predators or prey encounter for each tracking event. For each random forest algorithm, the number of trees were set to 500 and the best *mtry* (i.e. the number of variables randomly sampled at each split) parameter was determined based on accuracy and Kappa estimates. To verify variable importance, a variable with randomly generated numbers was included in each random forest model. If the mean decrease accuracy of a variable was below the mean decrease accuracy of the randomly generated variable (which should be the lowest), this variable was removed from further analysis as it can be assumed to contribute randomly to the model.

Statistical analyses

All statistical analyses were performed in R (R Core Team 2022). A t-test was performed on the number of recording days per camera to verify that camera trapping effort was the same between the desert scrub and earthen tank habitats. Wilcoxon signed-rank tests were used to compare the number of game camera observations of prey and predators between habitats. Wilcoxon signed-rank tests were also utilized to investigate the differences in detection and predation between replica sizes.

Further exploration of the predictors associated with prey encounters and detection risk was conducted using Kruskal-Wallis tests and generalized-mixed models (*lme4;* Bates et al. 2015). Differences between groups were analyzed using pairwise Wilcoxon post-hoc test. Wilcoxon signed-rank tests were used to compare the probability of detection by predators and prey encounters between tracking events where snakes were active or not (in burrows). Game camera observation data and telemetry data (for rattlesnakes) were used to obtain activity overlaps (Δ) between rattlesnakes and other species. Activity overlaps between organisms were calculated by measuring the similarity between the two Kernel density activity curves (Ridout and Linkie 2009) using the R package *Overlap* (Meredith and Ridout 2018). Different activity overlap coefficients were calculated depending on the number of observations: Δ_1 was used to calculate the overlap coefficient when there were less than 50 observations, while Δ_4 was used when there were more than 50 observations (see Ridout and Linkie 2009 for formulas). To assess the significance of the activity overlap, a Mardia-Watson-Wheeler test of homogeneity was performed for each overlap coefficient (Zar 2010). Activity overlap was calculated for predators and prey for the entire active season (April–November) and also divided per season: spring (April–May), summer (June–July), and fall (August–October) by combining all years together (2020-2023).

RESULTS

This study included 8,315 recordings days spread over thirty game cameras. In total, the game cameras captured 5,944 observations of more than 70 species. A summary of these observations can be found in Table 3.1. Collared peccaries (*Dicotyles tajacu*), greater roadrunners (*Geococcyx californianus*) and coyotes (*Canis latrans*) represented most of the predation attempts. Rock pocket mice (*Chaetodipus intermedius*), Merriam's kangaroo rats (*Dipodomys merriami*), and northern mockingbird (*Mimus polyglottos*) were the most commonly observed prey.

Table 3.1: Summary of game camera observations.

Group	Number of observations	Number of species	Number of detections	Number of predation attempts
Prey	2353	56	208	NA
Predator	701	11	196	69
Others	2889	12	98	NA

Difference between habitats and model size

Predator observations were significantly greater in earthen tanks than in desert scrub habitats (W = 0; p-value = 6.302e-05). Prey observations were also significantly higher in earthen tanks (W = 21; p-value = 0.00046). Large 3D-printed models were detected significantly more often than smaller models (W = 135; p-value = 0.03423) but the predation rate did not differ between the two (W = 33.5; p-value = 0.221).

Probability of detection by predators

A random forest model was performed with data collected from the game cameras to identify which variables were influencing the detection of a model by predators. The number of trees was set to 500 and the best *mtry* was determined to be 2 based on accuracy and Kappa estimates. For this model, the out-of-bag accuracy was estimated at 65.15%. A breakdown of the variable importance is presented in Fig. 3.2A. This same random-forest model was then utilized to estimate the probability of detection for each relocation when the snake was visible (N = 490). Month had a significant effect on detection risk (Kruskal-Wallis' chi-squared = 133.5, p-value < 0.001; Fig. 3.2C) as well as time (Kruskal-Wallis' chi-squared = 62.787, p-value < 0.001; Fig. 3.2B). Concealment percentage also had a significant effect on detection risk and the probability of detection was higher when the rattlesnake was not concealed (Kruskal-Wallis' chi-squared = 133.14, p-value < 0.001; Fig. 3.2F). Finally, a summary of a generalized linear mixed model testing the effect of continuous variables on detection risk is presented in Table 3.2.

Probability of prey encounter

A random-forest algorithm was used to determine which predictors influenced rattlesnake prey encounters. The number of trees was set to 500 and *mtry* parameter was set to 10 as it was determined to be the best based on accuracy and Kappa estimates. The out-of-bag accuracy for this model was estimated to be 74.99%. Predictors and their respective importance are presented in Fig. 3.3A. This model was used to obtain the probability of prey encounter for each snake relocation when the snake was visible. Time of day had a significant effect on the probability of encountering prey (Kruskal-Wallis' chi-squared = 75.849, p-value < 0.001; Fig. 3.3B). Pairwise Wilcoxon post-hoc analysis showed that month also had a significant effect on the probability of encountering prey (Kruskal-Wallis' chi-squared = 146.162, p-value< 0.001; Fig. 3.3C). Soil type did not have a significant effect on the probability of prey encounter (Kruskal-Wallis' chi-squared = 0.15778, p-value = 0.6912). Concealment had a significant effect on probability of prey encounter (Kruskal-Wallis' chi-squared = 9.8948, p-value = 0.007; Fig. 3.3E). Lastly, a summary of a generalized linear mixed model testing the effect of continuous variables on the probability of prey encounters is presented in Table 3.3.

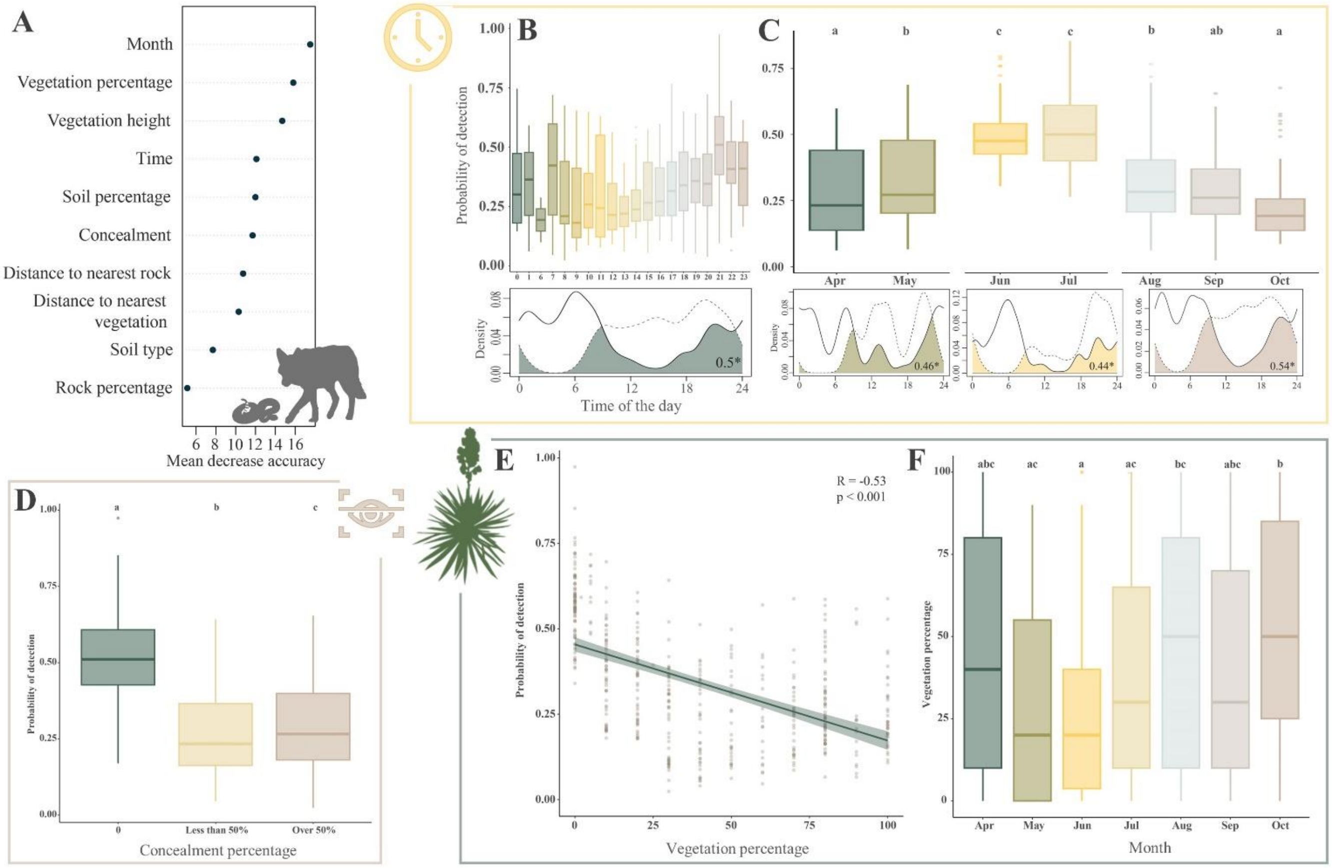

Fig. 3.2: Factors influencing probability of detection.

A: Importance of predictors associated with detection risk obtained through random-forest algorithm.
B: Box plots showing the probability of detection per hour of day. Time of day had a significant effect on detection risk (Kruskal-Wallis' chi-squared, $p < 0.01$). Activity overlap between predators (solid line) and *Crotalus atrox* (dashed line) is represented below and the coefficient was 0.5.
C: Box plots showing the probability of detection per month. Month had a significant effect on detection risk (Kruskal-Wallis' chi-squared, $p < 0.01$). Activity overlap between predators (solid line) and *Crotalus atrox* (dashed line) is represented below per season (April–May; June–July; Aug–Oct). Activity overlaps differed across seasons and thus, seasonal activity overlap figures have different Y-axis scales.
D: Linear regression between the probability of detection per predator and vegetation percentage. The linear regression model (line) was significant ($p < 0.001$) with a coefficient of -0.53. The dots represent observations.
E: Box plots showing vegetation percentage used per month. Month had a significant effect on detection risk (Kruskal-Wallis' chi-squared, $p < 0.01$).
F: Box plots showing the probability of detection per concealment (percentage of the snake hidden from above) category. Concealment had a significant effect on detection risk (Kruskal-Wallis' chi-squared, $p < 0.01$).
Boxes indicate the interquartile range (IQR), with the central line depicting the median and the whiskers extending to the minimal and maximal observation where outliers are represented by dots. Letters indicate significant differences between groups.

Table 3.2: Summary of generalized mixed model results used to investigate the effects predictors on detection risk. SE stands for standard error and DF for degree of freedoms. Significant p-values (<0.05) are in boldface.

Source	**Estimate**	**SE**	**z**	**p**
Probability of detection				
Intercept	0.0308	0.2218	0.130	0.8896
Vegetation height	-2.8845	0.5268	-5.475	**<0.01**
Vegetation percentage	-0.0194	0.0072	-2.705	**<0.01**
Distance to nearest vegetation	0.6801	0.2039	3.334	**<0.01**

Activity overlap

The activity period between *Crotalus atrox* and species of interest were all significantly different from each other. Overlap density plots for prey and predators are presented in Fig. 3.2 and Fig. 3.3 for the overall active seasons and per season (spring, summer, and fall).

Optimal foraging: Detection risk vs. probability of prey encounter

The probability of prey encounter (0.49) was on average significantly higher than the probability of detection by predators (0.38; W = 148263; p-value < 0.001). The probability of prey encounter and detection risk by predators was also estimated with random-forest algorithms when rattlesnakes were not active (i.e., hiding in a burrow) and compared to when they were active using Wilcoxon sum-rank tests. Detection risk did not significantly change based on the behavior of the rattlesnake (Kruskal-Wallis' chi-squared = 341.25; p-value = 0.6354; Fig. 3.4A). The probability of encountering prey varied significantly depending on the behavior of the snake (Kruskal-Wallis' chi-squared = 377.43; p-value = 0.04326; Fig. 3.4B).

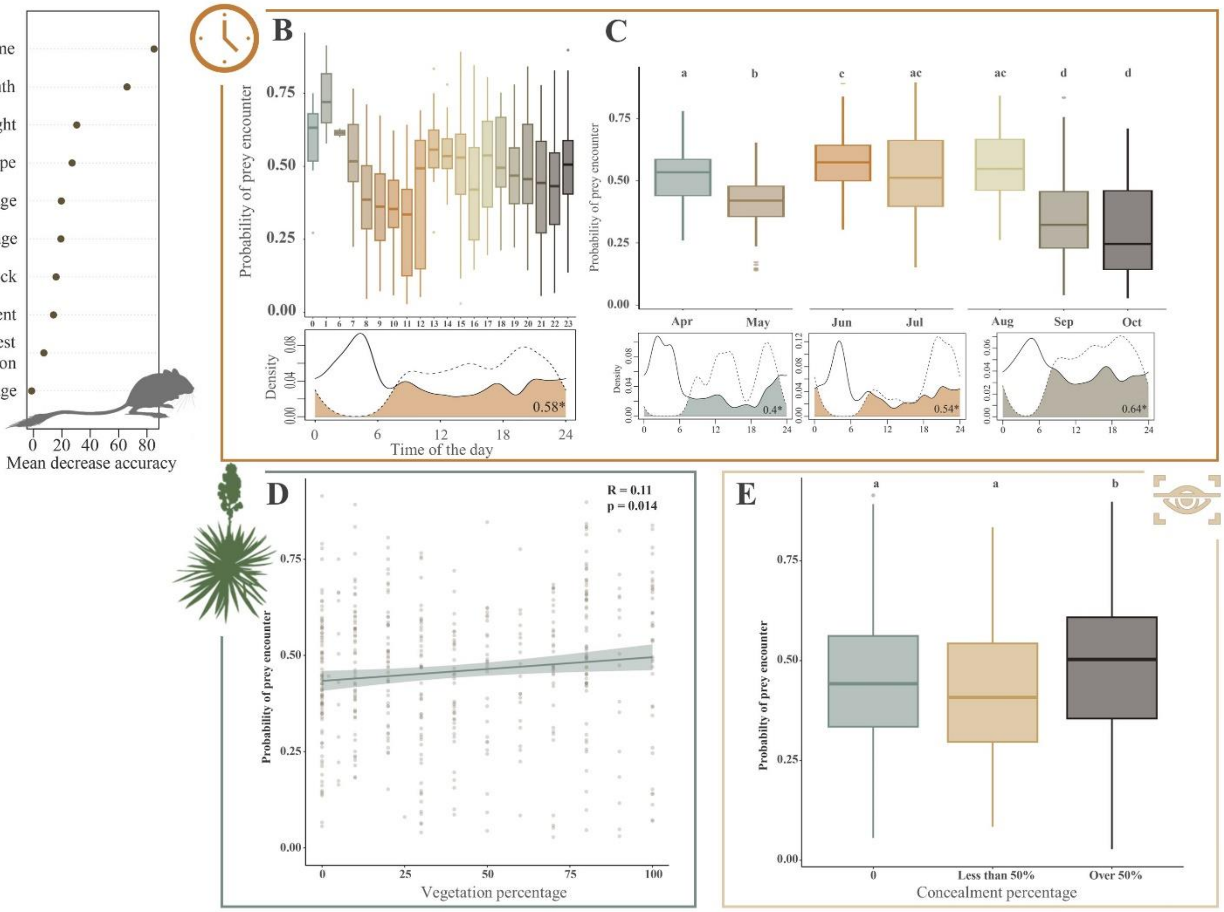

Fig. 3.3: Factors influencing probability of prey encounter.

A: Importance of predictors associated with the probability of prey encounter obtained through random-forest algorithm.

B: Box plots showing the probability of prey encounter per hour of day. Time of the day had a significant effect on detection risk (Kruskal-Wallis' chi-squared, $p < 0.01$). Activity overlap between prey (solid line) and *Crotalus atrox* (dashed line) is represented below and the coefficient was 0.58.

C: Box plots showing the probability of prey encounter per month. Month had a significant effect on the probability of prey encounter (Kruskal-Wallis' chi-squared, $p < 0.01$). Activity overlap between preys (solid line) and *Crotalus atrox* (dashed line) is represented below per season (April–May; June–July; Aug–Oct).

D: Linear regression between the probability of prey encounter and vegetation percentage. The linear regression model (line) was significant ($p = 0.014$) with a coefficient of 0.11. The dots represent observations.

E: Box plots showing the probability of detection per concealment category. Concealment had a significant effect on detection risk (Kruskal-Wallis' chi-squared, $p = 0.007$).

Boxes indicate the interquartile range (IQR), with the central line depicting the median and the whiskers extending to the minimal and maximal observation where outliers are represented by dots. Letters indicate significant differences between groups.

Table 3.3: Summary of generalized mixed model results used to investigate the effects predictors on probability of prey encounter. SE stands for standard error and DF for degree of freedoms. Significant p-values (<0.05) are in boldface.

Source	Estimate	SE	z	p
Probability of detection				
Intercept	-0.650	0.1742	-3.735	**<0.01**
Vegetation height	0.0537	0.1763	0.305	0.7606
Vegetation percentage	0.0069	0.0033	2.113	**0.0346**
Distance to nearest rock	0.0017	0.002	0.847	0.3967
Distance to nearest vegetation	0.1557	0.1342	1.160	0.2459

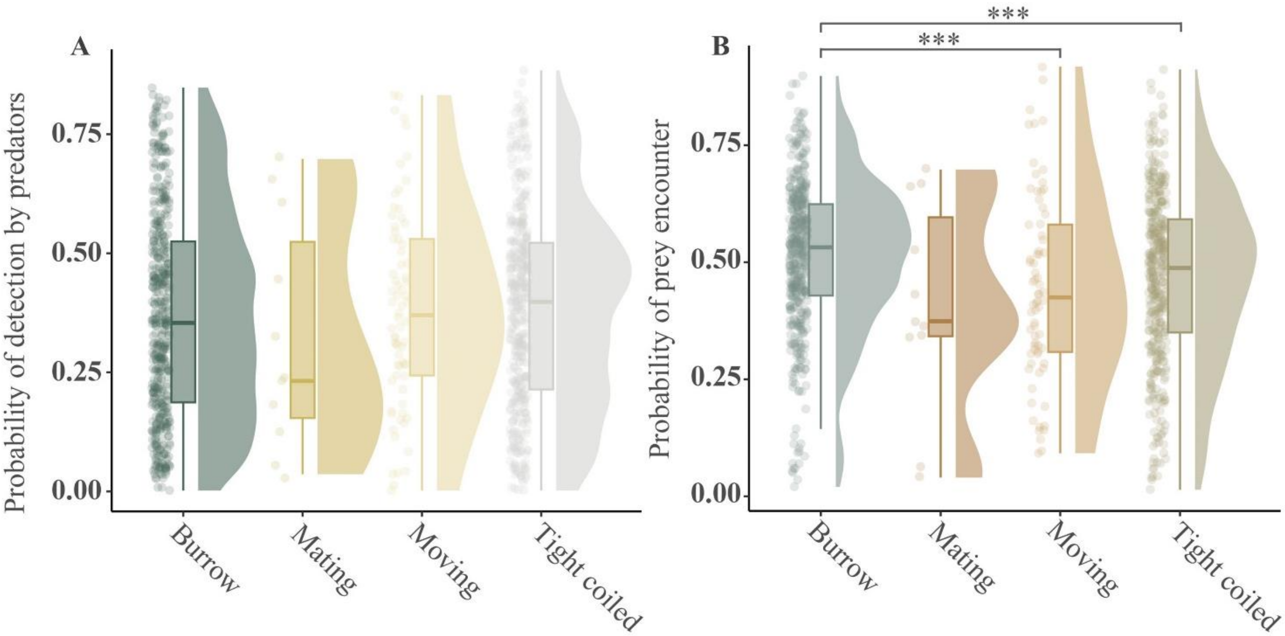

Fig. 3.4: Rain cloud plots representing the probability of detection by predators (A) or the probability of prey encounter (B) according to rattlesnake behavior. Each dot represents one observation. Boxes indicate the inter quartile range with the central line depicting the median. Half violin plots show the distribution of the probability for each observation. Statistical significance between groups is denoted by ***.

DISCUSSION

This study aimed to determine how the landscape of fear affects the foraging decisions *of Crotalus atrox* by looking at factors influencing detection risk and prey availability using 3D-printed biologically accurate snake replicas, camera trapping, and telemetry data. Key factors influencing detection risk and prey encounters were identified using comprehensive random-forest models and were then applied to test the optimal foraging theory. Rattlesnakes were active in the same spatiotemporal location as their prey and predators, but on average, chose spatiotemporal locations that had significantly higher probabilities of prey encounter than predator detection, supporting optimal foraging theory. This study demonstrated the effectiveness of using 3D-printed snake replicas paired with game cameras and associated with telemetry data and machine learning to test predator-prey interactions.

The probability of detection by predators varied temporally throughout the active season (April-October). First, detection probability fluctuated daily with higher probability to be detected by predators from 21:00 to 23:00 hours. This timeframe corresponds partially to the time interval in which rattlesnakes and their predators were the most active. Predators were mostly active from 20:00 to 06:00 hours which was also observed in similar studies conducted in the Chihuahuan Desert (Bissonette 1978; Durán-Antonio et al. 2020). Rattlesnakes were mostly active from 18:00 to 23:00. The activity period of rattlesnakes and their predators were significantly different, suggesting that rattlesnakes might temporally avoid predators as a strategy to decrease their risk of predation (Creel 2018). However, the diel activity pattern of rattlesnakes might be skewed in this study because of the lack of sampling effort between 01:00 and 06:00 hours. Indeed, *C. atrox* has been reported to mostly move between 18:00 and 06:00 hours at the same study site (DeSantis et al. 2020). Rattlesnakes might also be more active during the day when their predators are not, because of their thermal requirements. Collared peccaries and coyotes tend to avoid being active during the day and switch to a more nocturnal lifestyle when the temperatures rise above a certain threshold (Bissonette 1978; Melville et al. 2020). Rattlesnake activity is directly correlated to ambient temperature with the proportion of time hunting on the surface decreasing when average daily air temperatures are increasing (Putman and Clark 2015). Nevertheless, rattlesnakes also need to engage in basking during the day when their predators might not be active, to attain a specific temperature to facilitate essential physiological processes (Huey 1982). Even if a significant difference in activity periods between rattlesnakes and their predators was maintained throughout the year, predator detection varied significantly per month with higher probability to be detected in June and July. These results were not explained by the number of predator detections observed or the number of rattlesnakes observations per month. However, the vegetative structure utilized by rattlesnake, including both microhabitat percentage and vegetation height, exhibited significant monthly variation with June recording the lowest percentage and height, and April and May the highest. Conversely, probability of detection significantly increased when the percentage of vegetation decreased, meaning that variations in vegetative cover might explain the monthly difference in detection probability. Vegetation provides concealment to rattlesnakes, which was also linked to a decrease in the probability of being detected in this study. Habitat structure and complexity have been linked to predation risk in other studies (Denno et al. 2005; Gigliotti et al. 2020; Duchesne et al. 2022). Complex habitat structure provides shelter for organisms (Stellatelli et al. 2015; Worthington-Hill and Gill 2019), hinders the movements of predators (Ferreira et al. 2018), and decreases the visual detection of prey (Allen et al. 2013; Law et al. 2020), resulting in an overall decrease in predation success.

The probability to encounter prey also varied temporarily with a significant effect of time of the day and month. *Crotalus atrox* are known to prey upon rodents, passerine birds, and lizards (Beavers 1976). In this study, rodents, mostly represented by rock pocket mice (*Chaetodipus intermedius*) and Merriam's Kangaroo rats (*Dipodomys merriami*), exhibited a nocturnal activity period. The activity period of passerine birds followed a bimodal distribution with peaks around sunrise and sunset. *Crotalus atrox* activity followed the same bimodal distribution as birds during the spring and summer. It is unlikely that *Crotalus atrox* matches its activity pattern to those of birds because they only constitute a small portion of their diet (Beavers 1976). Birds show a crepuscular activity pattern to reduce predation risk (Bednekoff and Houston 1994; McNamara et al. 1994; Reyes-Arriagada et al. 2015), but also to avoid high temperatures (Silva et al. 2015). *Crotalus atrox* likely shows the same bimodal distribution to also avoid high temperatures in the middle of the day. Because of the lack of sampling effort between 01:00 and 06:00 hours, the activity overlap between rattlesnakes and rodents is expected to be much higher during the night as both rodents and rattlesnakes are known to be active throughout the night (DeSantis et al. 2020). The month of the year also had a significant effect on the probability of encountering prey, which did not seem to be caused by seasonal changes in activity overlap. September and October showed the smallest probability to encounter prey, which corresponds mostly to the mating season of *Crotalus atrox* at this field site (DeSantis et al. 2019a). Because of their ambush foraging strategy, rattlesnake males face a trade-off between hunting and searching for mates (Tetzlaff et al. 2017). Consequently, male snakes often decrease their foraging behavior (Slip and Shine 1988; Daltry et al. 1998; Glaudas and Alexander 2016; Tetzlaff et al. 2017; Cochran et al. 2021) to increase their reproductive output (Tetzlaff et al. 2017), as potentially observed in this study (see Fig. 3.3C). Vegetation percentage also had a significant positive effect on the probability of prey encounter. Vegetation structure and community are predictors of both rodent abundance (Kluever et al. 2016) and birds (Macías-Duarte et al. 2018). Vegetation also provides concealment from predators (as shown previously in this study) and thus, might offer shelter and foraging opportunities for rodents and birds. In fact, concealment had a significant effect on the probability of encountering prey, with a higher chance when concealment was 50% or more.

As discussed previously, rattlesnakes seemed to be active where and when both predators and prey were also active. However, the probability of encountering prey for rattlesnakes was significantly higher than being detected by a predator. This result could be explained by the higher density of prey compared to predators at our field site, or because rattlesnakes select less risky microhabitats with a higher chance of encountering prey. Because of the cryptic nature of rattlesnakes (Da Cunha et al. 2024), the predation pressure exerted on them is relatively low when they are tightly coiled on the surface (Maag and Clark 2022a). Instead, predation likely happens when rattlesnakes are performing risky behavior such as moving (Maag and Clark 2022a). However, the effect of movement could not be considered in this study as the 3D-printed replicas, despite mimicking a moving rattlesnake, were static. Because of the low predation pressure rattlesnakes face, predation risk might not influence their decision making. In this study, microhabitat variables were considered to investigate detection risk but not macrohabitat type. Two macrohabitats were selected in this study: Chihuahuan desert scrub and earthen tanks. Earthen tanks had significantly more predator and prey observations than the Chihuahuan desert scrub habitat. Macrohabitat type has been found to have an effect on predation risk (Mysterud and Ims 1998; Taylor et al. 1999), but it was not included in the final model of this study as its importance was very low and thus, unlikely to modify the probability of detection. Prey encounter probability varied significantly based on the behavior of the rattlesnake observed. The highest probability of encountering prey was when rattlesnakes were underground in burrows. Burrows used by rattlesnakes were mostly built by rodents, and thus it would be expected that the probability of encountering prey would be the highest by them, as predicted by this random-forest model. Rattlesnakes usually ambush prey in front of their burrow (Clark 2016), but rarely strike prey directly in burrows (Putman and Clark 2015). Instead, rattlesnakes retreat in burrows to avoid extreme temperatures and predators (Gardiner et al. 2015; Maag et al. 2022). In this study, detection risk was not significantly smaller in burrows than when the rattlesnakes were aboveground. This result might be biased as no 3D-printed models were placed underground, and thus the detection risk could not be exactly modeled when rattlesnakes were in burrows. Rattlesnakes use various cues to select ambush sites such as chemical signals (Clark 2016) or thermal backgrounds (Schraft et al. 2019). In this study, only spatiotemporal cues were considered to look at site selection, which could explain why the probability of encountering prey was not significantly higher when rattlesnakes were in ambush.

Finally, this study demonstrated the effectiveness of using 3D-printed snake replicas paired with game cameras and associated with telemetry data and machine learning to investigate predator-prey interactions. 3D-printed snake replicas are suitable to study predation in situ. Snake replicas resisted the environmental conditions of the Chihuahuan Desert for two years as well as the mechanical pressures exerted by the jaws of collared peccaries, horses, and coyotes. 3D-printed replicas offered an efficient alternative to the traditional plasticine models (Behm et al. 2018; Bulté et al. 2018) as they did not require frequent checks for predation marks while enabling the identification of predators down to the species level when paired with a game camera. These 3D-printed models were successfully used to determine the main predators of *Crotalus atrox* at this field site: collared peccaries, greater roadrunners, and coyotes. Greater roadrunners and coyotes have been previously reported as predators of rattlesnakes (Klauber 1956b; Maag and Clark 2022a). Surprisingly, collared peccaries accounted for most of the predation events. When encountering a rattling rattlesnake, collared peccaries tend to withdraw quickly, but are known to kill snakes (Neal 1959). While collared peccaries may not primarily eat rattlesnakes, they may occasionally consume them, particularly if the snakes are found dead. Thus, the high number of recorded instances of predation by collared peccaries on the 3D models could be attributed to the possibility that the peccaries perceived the rattlesnake models as lifeless, given their static nature. The combination of 3D-printed models and a game camera proved to be effective not only in identifying species that predate *Crotalus atrox,* but also in determining the primary factors influencing predation and predator detection rates. Overall, the detection rates for all animals were affected by the size of the 3D-printed models, with larger models being detected more frequently than smaller ones. However, the predation rate between small and large models did not significantly differ.

In conclusion, this study showed that the combination of 3D-printed models, game cameras, and telemetry provided efficient and non-invasive methods to study predator-prey dynamics. This study identified key factors influencing predation risk and foraging success using comprehensive random-forest models, shedding light on the complex interplay between rattlesnake behavior and predator-prey behavior. Future research should explore additional factors, including climate data and specific behaviors, such as movement, to further refine our comprehension of rattlesnake foraging strategy. Overall, this study provides valuable insights into the ecological nuances of rattlesnake behavioral ecology in the context of predator-prey interactions.

CHAPTER 4

You Can't See Me: Background Matching is Independent of Body Temperature in the Western Diamond-Backed Rattlesnake

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Contribution of other co-authors: data collection and manuscript editing

INTRODUCTION

The study of coloration and its evolutionary significance has been a major topic in biology for over a century (Poulton 1890; Cuthill et al. 2017). Coloration has been linked to broad biological functions such as sexual selection (Cooney et al. 2019), communication (Hutton et al. 2015), thermoregulation (Smith et al. 2016) and camouflage, i.e. morphological adaptations that inhibit detection and recognition by prey (Smithers et al. 2018; Cuthill 2019). Crypsis, defined as when body coloration hinders detection, is the most studied form of camouflage (Endler 1978; Stevens and Merilaita 2011; Merilaita et al. 2017). Crypsis can be divided into several subgroups but perhaps the most prevailing one is background-matching. Background-matching is when an organism's color and pattern is similar to its surroundings (Stevens and Merilaita 2011). Background matching has been documented in a large array of species (i.e. Stuart-Fox et al. 2006; Marshall et al. 2016; Robledo-Ospina et al. 2017; da Silva et al. 2020; Nokelainen et al. 2021, 2022; Liedtke et al. 2023) and depends on the interactions between the organism's coloration, its environment, and the visual system of the observer (Stevens and Merilaita 2009).

Each organism possesses specific neural connections and photoreceptors allowing the comparison of local features (i.e., color, luminance, texture) leading to the discrimination of two objects, i.e. figure-ground separation (Stevens and Merilaita 2011). Background matching is an adaptation to counteract this process (Stevens and Merilaita 2011). Mesopredators are in the middle of the trophic web, and they exert strong selection pressures on their prey as well as are strongly influenced by predation risk (Mukherjee et al. 2009). Ambush mesopredators hunt by waiting until their prey is within striking distance, and thus crypsis is crucial for their survival as they depend on it simultaneously to hunt and avoid predator detection (Pembury Smith and Ruxton 2020). To determine how accurately ambush mesopredators match their background, a trade-off between the visual system of their prey and predators must be considered (Stevens and Merilaita 2011). Background matching strategies depend on the type of habitat (homogeneous or heterogenous). In a homogeneous habitat, i.e. a background consisting of one color such as tan sand or green vegetation, an animal's coloration should be selected to represent the dominant background color. On the other hand, background matching in heterogeneous habitats is more challenging. Species can adapt by being polymorphic or by displaying compromise coloration that is an average coloration amongst the variable habitat coloration (Merilaita et al. 1999; Sherratt et al. 2007; Stevens and Merilaita 2011; Hughes et al. 2019). In heterogenous habitats, background matching can also be achieved through: 1) physiological color changes (Smith et al. 2016; Stevens 2016); 2) the behavioral choice of microhabitat similar in coloration to an individual (Marshall et al. 2016; Stevens and Ruxton 2019); 3) or a combination of both strategies (Smithers et al. 2018).

Although ectothermic ambush mesopredators need to avoid being detected by both predators and prey for their survival, they must also contend with variable temperatures in their environment. Ectotherms then must thermoregulate to reduce heat stress and desiccation. To thermoregulate, ectotherms can select habitats to bask or can change their coloration to maximize dermal absorption (Dunham et al. 1989; Seebacher and Franklin 2005). Indeed, dermal absorption of solar energy is dependent on body coloration and directly influences body temperature (Barlett and Gates 1967). Reptiles are known to modify their coloration to meet thermal requirements. For example, they might become darker to increase dermal absorption when cold (Smith et al. 2016). Consequently, conflicts between thermoregulation and crypsis arise with coloration being a central piece of this trade-off (Smith et al. 2016). In this context, the understanding of how animals employ color to address conflicting demands of thermoregulation and crypsis is limited.

As ectothermic species and ambush predators, rattlesnakes rely heavily upon their coloration making them excellent models to study background matching. Rattlesnakes possess a unique visual system allowing them to potentially perceive a wide range of colors (Gower et al. 2019). Specifically, the western diamond-backed rattlesnake (*Crotalus atrox*) has two types of cones and one type of rod in its retina resulting in dichromatic color vision under bright conditions (Gower et al. 2019). Cones operate in bright conditions enabling color perception (Lamb 2013) while rods are essential for dim light vision, perceiving size, shape, movement, brightness and in some instances, can contribute to color vision in low light conditions (Buck 1997; Sillman et al. 1999). Furthermore, *Crotalus atrox* is sensitive to ultraviolet light and can perceive infrared with its heat sensing pits (Gower et al. 2019). Images produced by the pit organs overlay with images produced by their visual system, thus combining into a single representation of their environment (Bothe et al. 2019). Due to its wide range, the visual system of rattlesnakes overlaps significantly with its prey and predators. Coyotes are a known predator of rattlesnakes (Goode and Duvall 1989). Birds act as prey and predators for rattlesnakes and can be divided into two groups based on their visual system: species with shortwave cones mostly sensitive in the ultraviolet (UV/VIS) and species with shortwave cones with sensitivity shifted towards violet (V/VIS; Ödeen and Håstad 2003; Hart and Hunt 2007). Raptors have been reported to prey on rattlesnakes (Klauber 1956a; Steenhof and Kochert 1985; Vanderpool et al. 2005) and passerine birds have been reported in their diet (Beavers 1976). Because of this, rattlesnakes might select microhabitat or change its body coloration to match better its surroundings according to the vision of its prey and predators.

This study had two aims: 1) investigate background matching of *Crotalus atrox* in situ by comparing its body coloration and pattern to selected or random microhabitat. And 2) examine the trade-off between thermoregulation and crypsis. *Crotalus atrox* was predicted to better match its selected microhabitat than random microhabitats. Body temperature was also predicted to influence body coloration with higher body temperatures favoring lighter colors and lower body temperature favoring darker colors due to dermal absorption. To address these aims, we compared the coloration matching of snakes to their selected backgrounds and to random backgrounds in the field. We also measured internal body temperature to determine if body coloration and body temperature correlated.

MATERIALS AND METHODS

Field observations

To test if rattlesnakes are choosing microhabitat based on background matching or thermoregulatory constraints, 14 rattlesnakes were radio-tracked with temperature-sensitive transmitters across natural habitats and visual contrasts of snakes against their chosen background and randomly selected background nearby were compared. All field observations were conducted at the Indio Mountains Research Station (IMRS). IMRS is a 161 km^2 research facility controlled by the University of Texas at El Paso (UTEP) and located approximately 42 km southwest of Van Horn (Hudspeth County, Texas). Animal collection was approved by Texas Parks and Wildlife (permit number: SPR-0290-019). All animal procedures were following the ethical standard of the University of Texas at El Paso and were approved beforehand by UTEP Institutional Animal Care and Use Committee (protocol number: A-201905-2_1447328-2).

Fourteen western diamond-backed rattlesnakes were captured on IMRS property and implanted with temperature-sensitive radiotransmitters (Holohil Systems Ltd., Carp, ON, Canada, SI-2T, 9.0g). Radiotransmitters were implanted in the coelomic cavity following a modified protocol of Hardy and Greene (2000) and never exceeded more than 5% of the snake body mass. Prior to the surgery, rattlesnakes were anesthetized with isoflurane via the open-drop method in a clear plastic tube. Surgical instruments were sterilized in a solution of benzalkonium chloride for a minimum of 30 minutes, benches were sterilized with isopropyl alcohol (70%), and procedures were conducted while wearing single-use sterile nitrile gloves. A 1.25 cm longitudinal incision was made into the coelomic cavity at two thirds of the snout-vent length, and the transmitter was inserted. The transmitter antenna was then inserted subcutaneously toward the head along the body using a canula that was then removed. Rattlesnakes were kept in observation for 48 hours to monitor recovery and then released at the exact capture site.

Rattlesnakes were radio-tracked twice a week during the active season at IMRS (April-October 2022; on average 26 tracking events per snake). For each tracking event when the individual was found coiled, a picture was taken of the snake and its immediate background. If the individual was found moving, no picture was taken. Pictures were taken using a Samsung NX1000 converted to full spectrum by removing the UV/IR filter inside the original camera. The camera was equipped with a Nikon El-Nikkor lens (80 mm), a Baader IR/UV cut filter, and a Baader Planetarium 1.25" U-Filter to produce visible and UV spectrum pictures, respectively. All pictures were taken in RAW format with the same ISO (800) and the same aperture (f/32). The shutter speed was the only factor adjusted according to light exposure. To control light exposure, a UV-suitable gray standard (Spectralon; Labsphere; 40% reflectance) was used for every picture. The gray standard was gently positioned near the rattlesnake by using a telescopic rod and was placed under the same light conditions as the individual photographed (see appendix 2, figure S1).

Rattlesnakes never reacted to the gray standard, i.e., did not change position. For each picture taken, a picture of a randomly chosen background was taken within the home range of the focal individual. To determine the location of the random background, a cardinal direction was randomly selected using a phone application and the background picture was taken 150 meters in this direction, away from the original rattlesnake picture. The distance of 150 meters was chosen with prior knowledge of *Crotalus atrox* home range and movements at this field site (DeSantis et al. 2019a) as it allowed for movement away from the snake location while staying within the home range, and thus usable habitat, for the specific rattlesnake. For each picture, GPS coordinates, sky condition (sunny; cloudy; sunny with clouds), and ground condition (sunny; shade; sunny with shade) were recorded. For sky conditions, it was considered sunny when the sun was completely exposed (0% cloud cover), cloudy when the sun was completely masked by clouds (50-100% cloud cover), and sunny with clouds when the sun was half masked by clouds (1-50% cloud cover). For ground conditions, it was considered sunny when the rattlesnake had 0% shade, shade when the rattlesnake was completely in the shade (100% shade), and sunny with shade when the rattlesnake was partially in the shade (1-99% shade). The distance and angle at which pictures were taken was not controlled between pictures due to the uneven nature of the ground at the field site making it challenging to adjust for when using a tripod. Moreover, movements around focal rattlesnakes were limited to minimize disturbances. Rattlesnake body temperature was extracted by fitting the radiotransmitter pulse interval recorded during each relocation to its specific 4th degree polynomial equation. Then we investigated the correlation between body temperature and body coloration.

Image analysis

Before any processing, the exposure of each picture was checked for proper exposure using the software RAWtherapee. Picture with inadequate exposure were removed from this study. Once assessed, multispectral images were created for each picture using *MICA toolbox* (Troscianko and Stevens 2015) with ImageJ (version 1.53k; Schneider et al. 2012). Using the same software, these multispectral images were then converted to the cone-catch models, i.e., predicted photoreceptor responses (Troscianko and Stevens 2015), of different species: domestic dog (*Canis familiaris*), human (*Homo sapiens*), peafowl (*Pavo* *cristatus*), and blue tit (*Cyanistes caeruleus*). The domestic dog visual model was chosen to represent the visual system of the coyote (*Canis latrans*) since visual pigments are conserved across all canids species (Jacobs et al. 1993; Jacobs 1993; Mowat and Peichl 2022). The human visual system was added as a reference to our own visual system. Humans can also be considered predators of rattlesnakes and rattlesnakes modify their defensive strategy due to human presence (Atkins et al. 2021). Peafowls and raptors are both part of the VS group and have similar pigments suggesting that the peafowl visual model can be used as an approximation for raptor visual models (Stevens and Cuthill 2007). The visual model of the blue tit was selected to represent UV sensitive passerine birds since most of them share the same sensitivity to UV (Hart 2001). Moreover, blue tits and western diamond-backed rattlesnakes are both maximally sensitive to UV around 370 nm (Hart 2001; Gower et al. 2019). A summary of the cone ratio used for each species is presented in appendix 2 (Table SI). Cone ratios correspond to the abundance of photoreceptors in the retina expressed as a ratio relative to the least abundant type of cones. Spectral sensitivity curves were obtained from the *MICA toolbox* plugin (Troscianko and Stevens 2015). To select the regions of interest, a polygon was drawn to encompass the body of the rattlesnake present on the picture (usually a quarter of a coiled snake). A rectangle was used to select a region of interest including most of the background present in the picture. The size of the region of interest was not controlled and chosen to encompass as much as possible of the object of interest to account for variations within object. Moreover, controlling the size of region of interest or snake body part selected would be challenging due to technical difficulties in the field.

To assess the color and luminance differences between rattlesnakes, selected backgrounds, and random backgrounds, the log version of Vorobyev and Osorio's receptor noise model was used (Vorobyev and Osorio 1998) with a Weber's fraction of 0.05 for each species using MICA toolbox (Troscianko and Stevens 2015). The receptor noise model calculates just noticeable differences (JNDs) to predict whether two objects are discriminable or not. Objects are typically undifferentiable when JNDs are below one and larger values are increasingly likely to be discriminable (Siddiqi et al. 2004). JNDs depend on estimates of the receptor noise, light conditions, and animal cognition, and thus, must be interpreted with caution. In this study, a broader region of uncertainty in discrimination thresholds (JNDs <3) is considered following previous studies (Nokelainen et al. 2019). Moreover, the Vorobyev and Osorio's receptor noise model was designed to handle chromatic signals, thus achromatic JNDs also need to be interpreted carefully (Olsson et al. 2018). However, the fundamental aspect of JNDs is that smaller JNDs values are synonymous with better camouflage (Nokelainen et al. 2019).

Color matching between rattlesnakes and either selected or random backgrounds, was also investigated by comparing color spaces within each visual model using the package *pavo* (Maia et al. 2019) in R (R Core Team 2022) and using the cone catch values calculated with *MICA toolbox* (Troscianko and Stevens 2015). As the dog visual color space is linear, the Euclidean distances between rattlesnakes and backgrounds were calculated to estimate color overlap. On the other hand, the human color space is triangular and the avian color spaces are tetrahedral. Thus, volume overlaps were calculated for these visual systems to estimate color overlap between rattlesnakes and backgrounds. A smaller Euclidean distance or bigger volume overlap means that the two color spaces are more similar.

Pattern matching between rattlesnakes and habitat background was assessed using granularity analysis conducted in ImageJ with the package *MICA toolbox* (Troscianko and Stevens 2015). Granularity analysis has been recently used to directly compare organism's pattern to their substrate using a measure of pattern energy difference (PED; Stevens *et al.*, 2017; Smithers *et al.*, 2018; Price *et al.*, 2019). Briefly, pattern differences were generated with Fast Fourier Transformation using the standard deviation of the luminance values at each spatial scale to derive the 'energy' at that spatial scale and then overall energy differences across all spatial frequencies were calculated, *sensu* Stevens et al. 2017. Thus, PED quantifies how closely rattlesnake coloration matches the size and contrast of background features (Stevens et al. 2017). Lower PED values indicate a closer match between the organism's pattern and its background's pattern.

Finally, hue, which is a measurement of the dominant wavelengths contributing to the color (Montgomerie 2006), was calculated as a ratio between the different color channels of *Cyanistes caeruleus* to represent photoreceptor stimulation by rattlesnakes, their backgrounds, and random backgrounds. A model developed for the European starling (*Sturnus vulgaris*) was used as *Cyanistes caeruleus* and *Sturnus vulgaris* possess similar pigments absorbance (Hart 2001). The following equation was utilized to calculate hue: *(LW+SW)/(MW+UV*) where LW is the value for the long-wave cone catch, SW for the short wave, MW for the medium wave, and UV for the UV sensitive cone (Komdeur et al. 2005; Stevens, Lown, and Denton 2014).

Statistical analysis

All statistical analysis were performed in R (R Core Team 2022). To test the difference in chromatic and achromatic JNDs, as well as PED between rattlesnake/selected background and rattlesnake/random background, paired Wilcoxon signed-rank tests were used for each visual system. For this specific statistical test, each observation was treated as independent as they were temporally and spatially isolated for each individual. Linear mixed-effects models were utilized to investigate the relationship between rattlesnake hue or rattlesnake luminance, selected background hue, random background hue, body temperature, sky condition (sunny; cloudy; sunny with clouds), and ground condition (sunny; shade; sunny with shade) as described above, using the package *lme4* (Bates et al. 2015). To control for repeated measures between individuals, rattlesnake identity was included in each model as a random factor.

RESULTS

Forty-two pictures of snakes and their backgrounds, and forty-two pictures of random backgrounds were collected and used in our analysis. Observations of individual snakes varied from one to six (see appendix 2; figure S3). Body temperature observed during this study averaged 29.96 (±5.82) within a range of 19.6°C to 42.8°C.

JNDs between rattlesnakes and backgrounds

Significant differences in achromatic JNDs were found between selected and random backgrounds for all visual systems (Fig. 4.1). On the other hand, differences in chromatic JNDs between rattlesnakes, their selected background, or random backgrounds were only significant for the blue tit visual system (Fig. 4.2). All JND summary statistics can be found in table 4.1.

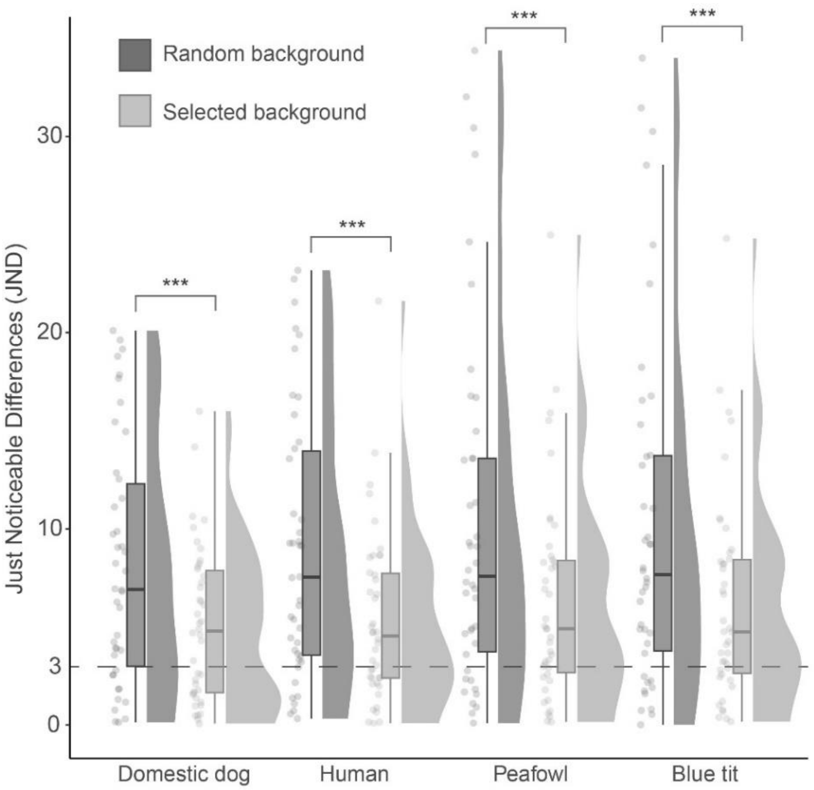

Fig. 4.1: Rain cloud plots representing the achromatic JNDs between rattlesnakes/selected backgrounds versus rattlesnakes/random background for each visual system tested. Each dot represents one observation. Boxes indicate the inter quartile range with the central line depicting the median. Half violin plots show the distribution of the JNDs for each observation. Statistical significance between groups is denoted by ***. The dotted line (JND =3) represents the threshold for visual system to be able to distinguish two objects.

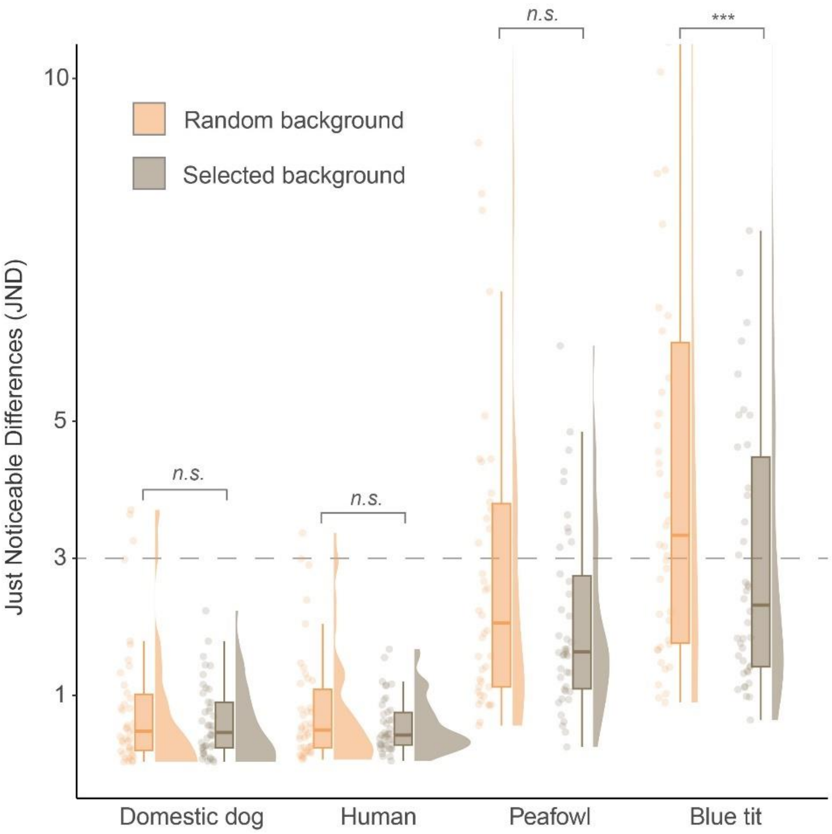

Fig. 4.2: Rain cloud plots representing the chromatic JNDs between rattlesnakes/selected backgrounds versus rattlesnakes/random background for each visual system tested. Each dot represents one observation. Boxes indicate the inter quartile range with the central line depicting the median. Half violin plots show the distribution of the JND for each observation. Statistical significance between groups is denoted either by *n.s.* (non-significant) or *** (significantly different). The dotted line (JND =3) represents the threshold for visual system to be able to distinguish two objects.

Colorspace analysis

For the dog visual system, the Euclidean distance between rattlesnakes and their selected background was 0.498 while between rattlesnakes and random background was 0.757. A smaller distance indicates that the color spaces are more similar. The percentage of volume overlap between rattlesnakes and selected backgrounds was greater than the overlap between rattlesnakes and random backgrounds for all the visual models tested, i.e. human, peafowl, and blue tit (Table 4.2).

Table 4.1: Summary of Wilcoxon signed-rank tests for achromatic and chromatic JNDs between rattlesnakes, their selected background, or random backgrounds. Bold p-value indicates significance.

Visual system	*Type of JNDs*	*Mean JNDs between rattlesnake and selected background*	*Mean JNDs between rattlesnake and random background*	*Wilcoxon signed-rank V*	*Wilcoxon signed rank p-value*
Domestic dog	achromatic	5.08 ± 3.92	8.17 ± 6.16	634	**0.02176**
Human	achromatic	5.35 ± 4.36	8.94 ± 6.76	659	**<0.001**
Peafowl	achromatic	6.28 ± 5.30	10.31 ± 9.12	651	**0.01177**
Blue tit	achromatic	6.24 ±5.28	10.25 ± 9.04	652	**0.01135**
Domestic dog	chromatic	0.62 ± 0.53	0.83 ± 0.97	493	0.6117
Human	chromatic	0.55 ± 0.39	0.79 ± 0.83	663	0.1668
Peafowl	chromatic	2.06 ± 1.33	2.98 ± 2.66	663	0.0992
Blue tit	chromatic	3.13 ± 2.42	4.72 ± 4.01	615	**0.0118**

Table 4.2: Volume overlaps for rattlesnakes, their selected backgrounds, and random backgrounds calculated for each visual system. Percentage overlap was calculated as the quotient of the overlap volume divided by the smaller volume (see appendix 2; table SII).

Visual model	*% overlap between rattlesnake and selected background*	*% overlap between rattlesnake and random background*
Human	84.91%	56.80%
Peafowl	81.41%	55.89%
Blue tit	78.17%	58.31%

Pattern analysis

For each visual system, the PED between rattlesnakes, selected background, and random backgrounds are presented in Fig. 4.3. While PED was on average smaller between snakes and their selected backgrounds than with a random background, the difference was only significant for the dog visual system (V = 619, p-value = 0.03584).

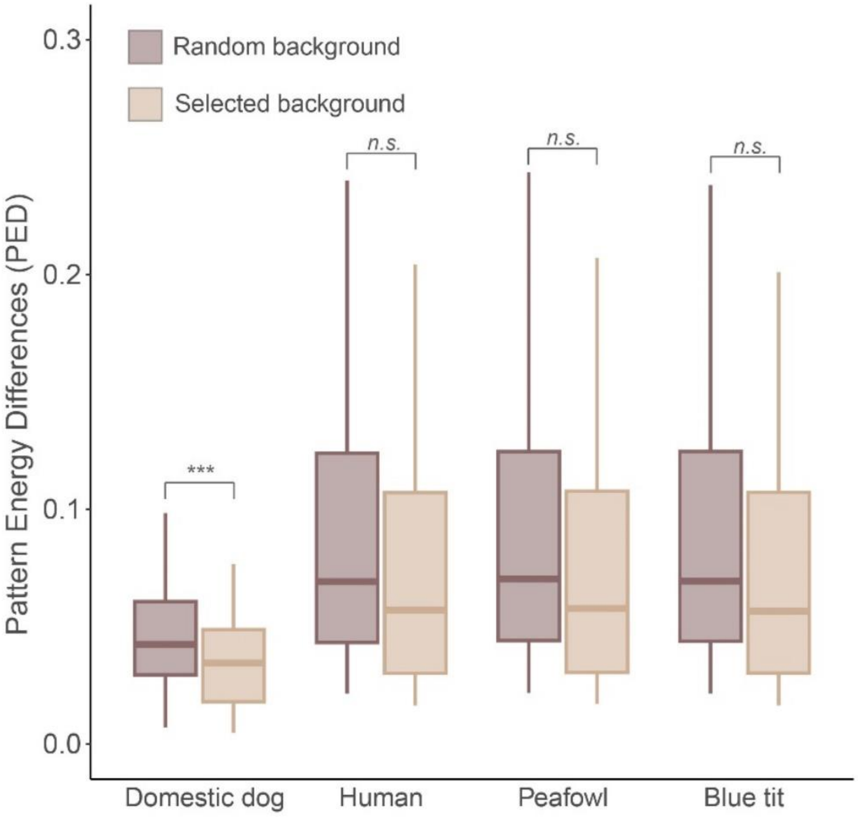

Fig. 4.3: Boxplot showing the pattern energy difference between rattlesnake body and selected background or with random background. *** represent significant differences between groups while *n.s.* non-significant differences. Boxes indicate the inter quartile range (IQR), with the central line depicting the median and the whiskers extending to the minimal and maximal observations.

Effects of the biotic and abiotic factors on hue and luminance

The results of the linear mixed-effect models to determine the relationship between hue, luminance, biotic factors, and abiotic factors are presented in Table 4.3. Rattlesnake hue only had a significant relationship with the selected background hue (t = 4.248, p-value < 0.001). Luminance was log-transformed to follow a gaussian distribution. As for luminance, the only significant relationship observed with the LMM was between rattlesnake luminance and selected background luminance (t = 5.113, p-value < 0.001). Body temperature did not have a significant relationship with hue or luminance (see table 4.3 and appendix 2 figure S2).

Table 4.3: Summary of mixed models results used to investigate the effects of biotic and abiotic factors on rattlesnake hue and luminance. In this table, LMM stands for linearized mixed models. SE stands for standard error and DF for degrees of freedom. Significant p-values (<0.05) are bolded.

Source	**Type of model**	**Estimate**	**SE**	**DF**	**t value**	**p-value**
(a) **Hue**	*LMM*					
Intercept		0.828758	0.424625	29.99893	1.952	0.060360
Hue selected background		**0.656809**	**0.167514**	**29.50796**	**3.921**	**0.000485**
Hue random background		-0.214301	0.233295	29.50731	-0.019	0.365763
Body temperature		-0.001944	0.004522	28.41865	-0.430	0.670577
Sky condition (Sunny)		-0.107879	0.074335	29.07782	-1.451	0.157415
Sky condition (Sunny with clouds)		-0.053898	0.066407	29.99718	-0.812	0.423401
Ground condition (Shade)		-0.103888	0.154179	29.15941	-0.674	0.505734
Ground condition (Sunny with shade)		-0.106489	0.157941	29.98402	-0.674	0.505327
Ground condition (Sunny)		-0.000394	0.170765	28.71709	-0.002	0.998175
(b) **Luminance**	*LMM with log-transformed data*					
Intercept		0.59682	0.60353	29.89967	0.989	0.331
Luminance selected background		**0.69081**	**0.13512**	**28.84224**	**5.113**	**1.88E-05**
Luminance random background		-0.02882	0.16715	27.72412	-0.172	0.864
Body temperature		-0.62429	0.35869	29.9556	-1.74	0.092
Sky condition (Sunny)		-0.06586	0.0856	26.72658	-0.769	0.448
Sky condition (Sunny with clouds)		0.05384	0.10669	28.85588	0.505	0.618
Ground condition (Shade)		0.06549	0.18224	29.98018	0.359	0.722
Ground condition (Sunny)		0.18881	0.20486	29.97526	0.922	0.364
Ground condition (Sunny with shade)		0.02839	0.18451	29.33122	0.154	0.879

DISCUSSION

This study aimed to investigate the relationship between *Crotalus atrox* body coloration, crypsis, and body temperature by analyzing digital images taken in the field. Achromatic JNDs were always significantly lower between the snake and its selected background than with a randomly selected background for all visual systems tested (dog, human, peafowl, and blue tit). Achromatic cues are used by organisms to help in the detection of movements, patterns, and texture (Kemp et al. 2015). Pattern matching between rattlesnakes and habitats was tested using PED as a proxy. Similarly to achromatic JNDs, PEDs were always lower between the snake and its selected background than with a randomly selected background, but the difference was only significant for the dog visual system. Pattern energy difference has been linked to the detection time of cryptic bird nests by predators (Troscianko et al. 2016) and hidden computer targets by humans (Troscianko, Skelhorn, et al. 2017). Achromatic cues might be especially useful for dichromatic animals as it might assist them in the perception of camouflaged objects by better discerning edges (Regan et al. 2001; Troscianko, Wilson-Aggarwal, et al. 2017). Moreover, birds seem to use achromatic signals to detect small objects and discriminate different textures (Osorio et al. 1999). The main predators of rattlesnakes consist of dichromatic mammals (Goode and Duvall 1989) or tetrachromatic birds (Klauber 1956a; Steenhof and Kochert 1985; Vanderpool et al. 2005) and thus, it can be assumed that these predators use achromatic cues to detect cryptic rattlesnakes. Because of this, it would be advantageous for *Crotalus atrox* to be achromatically and chromatically cryptic to avoid predation.

Several studies have shown that prey rely more on chromatic than achromatic crypsis to stay camouflaged (Théry et al. 2005; Stuart-Fox et al. 2006). In this study, chromatic JNDs were smaller between rattlesnakes and their selected background compared to rattlesnakes and random backgrounds, but the difference was only statistically significant for the blue tit visual system. For the dog and human visual systems, chromatic JNDs were mostly below 3 for selected or random backgrounds meaning that rattlesnakes are almost always chromatically cryptic to these species (Siddiqi et al. 2004). For the peafowl visual system, chromatic JNDs were also clustered around 3 indicating that snakes are for the most part camouflaged on a random or selected background under non-ideal visual conditions. These results might explain why statistical significance was not observed for these species as rattlesnakes appear to be chromatically cryptic for the most part regardless of the background. On the other hand, rattlesnakes were not always camouflaged for blue tits, especially when compared to a random background. Contrary to the other visual systems used in this study, blue tits are UV-sensitive (Hart 2001) and thus, might be able to more efficiently distinguish rattlesnakes from their backgrounds. Western diamond-backed rattlesnakes are also sensitive to UV similarly to blue tits (Gower et al. 2019) and might use this sensitivity to enhance their crypsis. Even if chromatic JNDs were not always statistically significant between selected and random backgrounds, calculated color spaces presented more overlap between the rattlesnake and its selected background than with a randomly selected background for all visual systems tested, showing that rattlesnakes chromatically match their selected background better than a random background. Moreover, rattlesnake hues only had a significant relationship with the selected background and not with random backgrounds, also demonstrating chromatic background matching. These results suggest that *Crotalus atrox* uses both chromatic and achromatic matching to enhance its crypsis. These results fit with previous findings showing that animals use a mixture of chromatic and achromatic cues to detect camouflaged objects (Kelber 2005; Stobbe et al. 2008).

This study provides evidence that *Crotalus atrox* strengthens its crypsis by matching its background. Background matching is a widespread strategy among organisms for defense or ambush. Background matching has been observed in arthropods (Stevens, Lown, and Wood 2014; Kang et al. 2015; Robledo-Ospina et al. 2017), mollusks (Josef et al. 2012), fishes (Stevens, Lown, and Denton 2014; da Silva et al. 2020), amphibians (Liedtke et al. 2023), reptiles (Stuart-Fox et al. 2006; Smith et al. 2016), birds (Nokelainen et al. 2022), mammals (Nokelainen et al. 2021), as well as other taxa. Background matching can occur through physiological color changes as observed in the bearded dragon (*Pogona vitticeps*) and the dwarf chameleon (*Bradypodion transvaalense*; Stuart-Fox et al. 2006; Smith et al. 2016) or through the behavioral choice of microhabitat with similar coloration as seen in the Aegan wall lizard (*Podarcis erhardii*; Marshall et al. 2016). In some instances, organisms use a combination of both color change and microhabitat selection to enhance their camouflage (Smithers et al. 2018). Even if this study showed that

Crotalus atrox matches its background to some extent, the mechanisms by which it does so remain undetermined and need to be further investigated. Intra-individual color and luminance variations were observed in the field showing that *Crotalus atrox* can modify its coloration to some extent (see appendix 2; figure S3). Color change has also been observed in response to stress level in the western rattlesnake (*Crotalus oreganus* ; Stepanek et al. 2019). However, in that study and the one presented here, the mechanisms involving color changes were not investigated. Coloration can change morphologically by a modification of the number and quality of chromatophores in the dermis or physiologically due to the movement of pigments within chromatophores. Physiological color change can happen instantly while morphological color change usually takes place over several days or months (Stuart-Fox and Moussalli 2009). *Crotalus atrox* and *Crotalus oreganus* have been observed to modify their coloration within the day (Personal observation; Stepanek et al. 2019) indicating a potential for physiological color changes. Physiological color change has been documented in several species of snakes, including viperids (McAlpine 1983; Hedges et al. 1989; Boback and Siefferman 2010). Western diamond-backed rattlesnakes might use physiological color change to adjust their coloration to better match their surroundings. They might also select specific microhabitats that match their own coloration. Behavioral background matching has already been observed in snakes. Corn snakes (*Panterophis guttatus*) choose more complex substrate and tend to avoid plain background in laboratory settings (Kravchuk and Watson 2020). Moreover, western terrestrial garter snakes (*Thamnophis elegans*) have been shown to choose basking sites matching their coloration, thus enhancing their crypsis (Isaac and Gregory 2013). Further investigations are required to determine if *Crotalus atrox* uses morphological or physiological color changing, or a mixture of both.

In this study, temperature did not have a significant effect on rattlesnake coloration. In ectotherms, coloration is under heavy selection as it is linked to two essential functions for survival: thermoregulation and crypsis (Smith et al. 2016). Coloration can thus lead to a trade-off between reaching a suitable body temperature or staying hidden from predators (Endler 1978; Dunham et al. 1989; Seebacher and Franklin 2005). Color change is used in a wide range of organisms for thermoregulation (Stuart-Fox and Moussalli 2009; Umbers et al. 2014; Smith et al. 2016). Rattlesnakes can modify their coloration (Stepanek et al.

2019) and might use this aptitude to thermoregulate. However, in this study, temperature did not affect rattlesnake coloration whereas coloration of the background did, showing that crypsis takes precedence over thermoregulation. Similarly, bearded dragons modify their coloration for thermoregulation but mainly adjust for crypsis (Smith et al. 2016). Just like bearded dragons, crypsis might be more important for western diamond backed rattlesnakes' survival than thermoregulation (Smith et al. 2016). Western diamond-backed rattlesnakes might not adjust their coloration to thermoregulate as temperature might not be a limiting factor in this specific study site. Indeed, this study took place in the Chihuahuan Desert from April to October where temperatures average 22°C and commonly go above 40°C (US Department of Commerce). These temperatures are sufficient for rattlesnakes to carry out biological activities and when temperatures are not ideal, they use refugia (Beck 1995). Moreover, color change abilities have been found to vary between populations in other organisms. Atlantic sand fiddlers (*Uca pugilator*) from different populations exhibit differential color change in response to temperature (Munguia et al. 2013). Because of this, replicating this study in a different population of *Crotalus atrox* living where temperatures are lower might yield opposite results.

This study used several theoretical models to estimate the level of crypsis in *Crotalus atrox*. These models are approximations of the animal vision as it depends on a large array of factors and results need to be interpreted carefully (Olsson et al. 2018). However, this study combined different models and comparatively tested differences between rattlesnakes, a selected background, and a random background. These models altogether showed that rattlesnakes match their background better than a random background. A comparative approach like the one used in this study allows for hypothesis testing even if models are approximations (Renoult et al. 2017). Through this thoughtfully chosen suite of models, this study provides evidence that rattlesnakes enhance their crypsis, specifically through background matching. Additionally, temperature does not seem to be a key factor determining coloration as is seen in some animals (Stuart-Fox and Moussalli 2009; Umbers et al. 2014; Smith et al. 2016). The mechanisms by which rattlesnakes match their background are still unknown and should be investigated in future studies to fully understand background matching in these species.

GENERAL CONCLUSION AND FUTURE DIRECTIONS

The overarching goal of this dissertation was to unravel the behavioral ecology of *Crotalus atrox* by focusing on personality, predator-prey interactions, and camouflage strategies. To achieve this goal, this dissertation was split into four chapters that each addressed specific underlying questions.

This dissertation is one of the few studies to investigate personality across five axes in snakes and one of the only studies to examine personality in rattlesnakes. *Crotalus atrox* was found to exhibit individual behavioral differences consistent through time (i.e. personality) and behavioral syndromes comparable to other species. This dissertation provides a baseline to answer questions pertinent to personality in rattlesnakes such as its relationship with life history or ecology and will help gain insights into the secretive life of serpents. These results demonstrate that despite the lack of publications on their personality, snakes should be considered as a model system to further the comprehension of individual differences.

This dissertation demonstrated that *Crotalus atrox* exhibit differences in their movement ecology according to their personality. The effect of behavioral differences on movement was dependent on the reproductive status of individuals. During the mating season, males adjusted their movements, with shy individuals showing a larger increase in movement rate than bold individuals. The results of this study suggest the existence of two different strategies for resource acquisition, thus supporting the pace-of-life syndrome hypothesis under specific contexts (i.e. mating versus non-mating season). While this dissertation provides new insights into the relationship between personality and ecology, further research is required to validate and uncover the mechanisms and consequences of these strategies for this species.

This dissertation showed that the combination of 3D-printed models, game cameras, and telemetry provided efficient and non-invasive methods to study predator-prey dynamics. Here, I identified key factors influencing predation risk and foraging success using comprehensive random-forest models, shedding light on the complex interplay between rattlesnake behavior and predator-prey behavior. Future research should explore additional factors, including climate data and specific behaviors such as movement, to further refine our comprehension of rattlesnake foraging strategy. Overall, this study provides valuable insights into the ecological nuances of rattlesnake behavioral ecology in the context of predator-prey interactions.

Finally, this dissertation used several theoretical models to estimate the level of crypsis in *Crotalus atrox* and provided evidence that rattlesnakes enhance their crypsis, specifically through background matching. Additionally, body temperature did not seem to influence the coloration of *Crotalus atrox* in the field. The mechanisms by which rattlesnakes match their background are still unknown and should be investigated in future studies to fully understand background matching in these species.

In conclusion, this dissertation revealed that *Crotalus atrox*: 1) exhibits personality traits that influence its spatial ecology; 2) optimally forages by selecting habitats with higher probability of prey encounter than predation risk; and 3) that they enhance their crypsis through background matching. While this dissertation provided novel insights regarding the behavioral ecology of a cryptic ambush mesopredator, further studies need to be conducted to understand the link between personality, predator-prey interactions, and crypsis. For example, personality is known to influence the outcomes of predator-prey interactions by affecting the foraging performance and survivorship of both prey and predators (Chang et al. 2017). Bolder predators tend to forage more successfully than shyer predators (Sundström et al. 2004). Bolder prey exhibit higher growth rates but lower survivorship than shyer prey (Biro and Stamps 2010). Bolder individuals might find more resources than shy individuals by being active during risky times or in risky habitats, but they might experience higher mortality rates because of the increased predation pressure. On the other hand, shyer individuals might have less opportunities to forage as they are active when and where predators are less abundant, thus presenting a higher survival rate than bolder individuals (Mangel and Stamps 2001; Belgrad and Griffen 2016; Ward-Fear et al. 2018). Moreover, predator foraging success and prey survival depend on predator-prey personality types (Chang et al. 2017). In general, bolder and more active predators capture shy and less active prey and vice versa (Huey and Pianka 1981; Belgrad and Griffen 2016; Chang et al. 2017). Despite this body of evidence, the connection between personality and predator-prey interactions remains largely unexplored. Understanding this relationship could help unfold the different life-history strategies and differential survival existing within a population while shedding light on the maintenance of personality type within a population.

Personality traits have also been found to covary with morphological traits, including coloration. For example, personality traits such as aggressiveness, boldness, exploratory, and reactivity, have been found to be correlated with melanic coloration in several taxa (e.g. Kittilsen et al. 2009; Costanzo et al. 2018), including non-avian reptiles (Cooper and Burns 1987; Mafli et al. 2011). Generally, darker individuals are more proactive (i.e. more active, reactive, bolder) than lighter individuals (Ducrest et al. 2008). For example, the size of the black bib of male Eurasian siskins (*Carduelis spinus*) is correlated to their personality and anti-predator behavior: males with larger bibs are more proactive and more vigilant than males with smaller bibs (Pascual and Senar 2014). Personality and morphology traits might have evolved together to fit sociosexual communication or natural selection scenarios, such as predator-prey interactions (Schuett et al. 2010; Costanzo et al. 2018). Cryptic animals rely on their coloration to stay hidden from prey and predators (Merilaita et al. 2017). Moreover, coloration is linked to two essential functions for survival: thermoregulation and crypsis in ectotherms (Smith et al. 2016). As coloration is so tightly linked to survival in cryptic ectotherms, it is counter-intuitive to expect variations within the same population. However, individual variation has been observed in cryptic ectotherms within the same species or population (Andrén and Nilson 1981; Allsteadt et al. 2006; Farallo and Forstner 2012; Brooks et al. 2022). Maintenance of these different morphs within a population could be explained by the thermoregulatory advantage of some morphs compared to others, sexual selection, or predation pressure (Andrén and Nilson 1981; Clusella Trullas et al. 2007; Farallo and Forstner 2012). If a correlation between coloration and personality traits exists within these species, it might explain why different life–history strategies are observed within the same population. For example, bold individuals might be darker than shy individuals, making them cryptic in different habitats. Because of this, the spatial strategy of the two different personality types might be different (i.e. habitat selection and movements). Moreover, bold individuals generally exhibit higher metabolism (Réale, Garant, et al. 2010), which could be enabled by their darker coloration. The relationship between personality traits, thermoregulation, and coloration in cryptic ectotherms remains unclear, and future studies should focus on unraveling the links between these different components.

In conclusion, this dissertation provided new insights into the behavioral ecology of an ambush mesopredator, shedding light on the relationship between personality and spatial ecology, predator-prey interactions, and crypsis. While I hope this dissertation provides a strong foundation for future studies, my work also highlights the need for further research to elucidate the connections between personality, predator-prey interactions, and crypsis. New insights into these relationships will further our understanding of the different adaptive strategies of *Crotalus atrox*, and potentially other cryptic ambush mesopredators, and their persistence through time.

LITERATURE CITED

de Alcantara Viana JV, Vieira C, Duarte RC, Romero GQ. 2022. Predator responses to prey camouflage strategies: a meta-analysis. Proceedings of the Royal Society B: Biological Sciences. 289(1982):20220980. doi:10.1098/rspb.2022.0980.

Aliperti JR, Davis BE, Fangue NA, Todgham AE, Van Vuren DH. 2021. Bridging animal personality with space use and resource use in a free-ranging population of an asocial ground squirrel. Animal Behaviour. 180:291–306. doi:10.1016/j.anbehav.2021.07.019.

Allen WL, Baddeley R, Scott-Samuel NE, Cuthill IC. 2013. The evolution and function of pattern diversity in snakes. Behavioral Ecology. 24(5):1237–1250. doi:10.1093/beheco/art058.

Allf BC, Durst PAP, Pfennig DW. 2016. Behavioral Plasticity and the Origins of Novelty: The Evolution of the Rattlesnake Rattle. Am Nat. 188(4):475–483. doi:10.1086/688017.

Allsteadt J, Savitzky AH, Petersen CE, Naik DN. 2006. Geographic variations in the morphology of Crotalus horridus (Serpentes: Viperidae). Herpetological Monographs. 20(1):1–63. doi:10.1655/0733-1347(2007)20[1:GVITMO]2.0.CO;2.

Andrén C, Nilson G. 1981. Reproductive success and risk of predation in normal and melanistic colour morphs of the adder, Vipera berus. Biological Journal of the Linnean Society. 15(3):235–246. doi:10.1111/j.1095-8312.1981.tb00761.x.

Atkins MCP, Howarth CR, Russello MA, Tomal JH, Larsen KW. 2021. Evidence of intrapopulation differences in rattlesnake defensive behavior across neighboring habitats. Behav Ecol Sociobiol. 76(1):3. doi:10.1007/s00265-021-03100-6.

Barlett PN, Gates DM. 1967. The Energy Budget of a Lizard on a Tree Trunk. Ecology. 48(2):315–322. doi:10.2307/1933120.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw. 67(1):1–48.

Bauder JM, Breininger DR, Bolt MR, Legare ML, Jenkins CL, McGarigal K. 2015. The role of the bandwidth matrix in influencing kernel home range estimates for snakes using VHF telemetry data. Wildl Res. 42(5):437–453. doi:10.1071/WR14233.

Beavers RA. 1976. Food Habits of the Western Diamondback Rattlesnake, Crotalus atrox, in Texas (Viperidae). The Southwestern Naturalist. 20(4):503–515. doi:10.2307/3669867.

Beck DD. 1995. Ecology and Energetics of Three Sympatric Rattlesnake Species in the Sonoran Desert. Journal of Herpetology. 29(2):211–223. doi:10.2307/1564558.

Bednekoff PA, Houston AI. 1994. Avian daily foraging patterns: Effects of digestive constraints and variability. Evol Ecol. 8(1):36–52. doi:10.1007/BF01237664.

Behm JE, Waite BR, Hsieh ST, Helmus MR. 2018. Benefits and limitations of three-dimensional printing technology for ecological research. BMC Ecol. 18(1):32. doi:10.1186/s12898-018-0190-z.

Belgrad BA, Griffen BD. 2016. Predator–prey interactions mediated by prey personality and predator hunting mode. Proceedings of the Royal Society B: Biological Sciences. 283(1828):20160408. doi:10.1098/rspb.2016.0408.

Berger J, Stacey PB, Bellis L, Johnson MP. 2001. A Mammalian Predator–Prey Imbalance: Grizzly Bear and Wolf Extinction Affect Avian Neotropical Migrants. Ecological Applications. 11(4):947–960. doi:10.1890/1051-0761(2001)011[0947:AMPPIG]2.0.CO;2.

Best EC, Blomberg SP, Goldizen AW. 2015. Shy female kangaroos seek safety in numbers and have fewer preferred friendships. Behavioral Ecology. 26(2):639–646. doi:10.1093/beheco/arv003.

Biro PA, Stamps JA. 2010. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? Trends in Ecology & Evolution. 25(11):653–659. doi:10.1016/j.tree.2010.08.003.

Bissonette JA. 1978. The Influence of Extremes of Temperature on Activity Patterns of Peccaries. The Southwestern Naturalist. 23(3):339–346. doi:10.2307/3670240.

Bleicher SS. 2017. The landscape of fear conceptual framework: definition and review of current applications and misuses. PeerJ. 5:e3772. doi:10.7717/peerj.3772.

Boback SM, Siefferman LM. 2010. Variation in Color and Color Change in Island and Mainland Boas (Boa constrictor). hpet. 44(4):506–515. doi:10.1670/09-026.1.

Bókony V, Kulcsár A, Tóth Z, Liker A. 2012. Personality Traits and Behavioral Syndromes in Differently Urbanized Populations of House Sparrows (Passer domesticus). McGraw K, editor. PLoS ONE. 7(5):e36639. doi:10.1371/journal.pone.0036639.

Bonter DN, Zuckerberg B, Sedgwick CW, Hochachka WM. 2013. Daily foraging patterns in free-living birds: exploring the predation–starvation trade-off. Proceedings of the Royal Society B: Biological Sciences. 280(1760):20123087. doi:10.1098/rspb.2012.3087.

Bothe MS, Luksch H, Straka H, Kohl T. 2019. Neuronal Substrates for Infrared Contrast Enhancement and Motion Detection in Rattlesnakes. Current Biology. 29(11):1827-1832.e4. doi:10.1016/j.cub.2019.04.035.

Boyer N, Réale D, Marmet J, Pisanu B, Chapuis J-L. 2010. Personality, space use and tick load in an introduced population of Siberian chipmunks Tamias sibiricus. Journal of Animal Ecology. 79(3):538–547. doi:10.1111/j.1365-2656.2010.01659.x.

Brooks J, Rohrer J, Beck DD. 2022. Color Variation, Tail Banding, and Sexual Dichromatism in Washington Populations of Northern Pacific Rattlesnakes, Crotalus oreganus. Herpetologica. 78(3):192–200. doi:10.1655/Herpetologica-D-20-00042.

Brown JS, Kotler BP. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters. 7(10):999–1014. doi:10.1111/j.1461-0248.2004.00661.x.

Buck SL. 1997. Influence of rod signals on hue perception: evidence from successive scotopic contrast. Vision Research. 37(10):1295–1301. doi:10.1016/S0042-6989(96)00276-3.

Bucklaew A, Dochtermann NA. 2021. The effects of exposure to predators on personality and plasticity. Ethol. 127(2):158–165. doi:10.1111/eth.13107.

Buirski P, Kellerman H, Plutchik R, Weininger R, Buirski N. 1973. A field study of emotions, dominance, and social behavior in a group of baboons (Papio anubis). Primates. 14(1):67–78. doi:10.1007/BF01730516.

Buirski P, Plutchik R, Kellerman H. 1978. Sex differences, dominance, and personality in the chimpanzee. Anim Behav. 26:123–129. doi:10.1016/0003-3472(78)90011-8.

Bulté G, Chlebak RJ, Dawson JW, Blouin-Demers G. 2018. Studying mate choice in the wild using 3D printed decoys and action cameras: a case of study of male choice in the northern map turtle. Animal Behaviour. 138:141–143. doi:10.1016/j.anbehav.2018.02.018.

Calenge C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling. 197(3):516–519. doi:10.1016/j.ecolmodel.2006.03.017.

Carter AJ, Feeney WE, Marshall HH, Cowlishaw G, Heinsohn R. 2013. Animal personality: what are behavioural ecologists measuring? Biol Rev. 88(2):465–475. doi:10.1111/brv.12007.

Chang C, Teo HY, Norma-Rashid Y, Li D. 2017. Predator personality and prey behavioural predictability jointly determine foraging performance. Sci Rep. 7(1):40734. doi:10.1038/srep40734.

Chapman BB, Hulthén K, Blomqvist DR, Hansson L-A, Nilsson J-Å, Brodersen J, Anders Nilsson P, Skov C, Brönmark C. 2011a. To boldly go: individual differences in boldness influence migratory tendency. Ecology Letters. 14(9):871–876. doi:10.1111/j.1461-0248.2011.01648.x.

Chapman BB, Hulthén K, Blomqvist DR, Hansson L-A, Nilsson J-Å, Brodersen J, Anders Nilsson P, Skov C, Brönmark C. 2011b. To boldly go: individual differences in boldness influence migratory tendency. Ecology Letters. 14(9):871–876. doi:10.1111/j.1461-0248.2011.01648.x.

Chiszar D, Carter T. 1975. Reliability of individual differences between garter snakes (Thamnophis radix) during repeated exposures to an open field. Bull Psychon Soc. 5(6):507–509. doi:10.3758/BF03333315.

Chiszar D, Carter T, Knight L, Simonsen L, Taylor S. 1976. Investigatory behavior inthe plains garter snake (Thamnophis radix) and several additional species. Learn Behav. 4(3):273–278. doi:10.3758/BF03214049.

Chock RY, Wey TW, Ebensperger LA, Hayes LD. 2017. Evidence for a behavioural syndrome and negative social assortment by exploratory personality in the communally nesting rodent, Octodon degus. Behav. 154(5):541–562. doi:10.1163/1568539X-00003433.

Clark R. 2016. Hunting and feeding behavior in free-ranging snakes. In: Rattlesnakes of Arizona. Vol. 2. GW Schuett, MJ Feldner, CF Smith, and RS Reiserer (Eds). Rodeo, New Mexico: Eco Publishing, Rodeo, NM. p. 91–118.

Clark RW. 2004. Timber Rattlesnakes (Crotalus horridus) Use Chemical Cues to Select Ambush Sites. J Chem Ecol. 30(3):607–617. doi:10.1023/B:JOEC.0000018632.27010.1e.

Clark RW. 2007. Public information for solitary foragers: timber rattlesnakes use conspecific chemical cues to select ambush sites. Behav Ecol. 18(2):487–490. doi:10.1093/beheco/arm002.

Clark RW, Brown WS, Stechert R, Greene HW. 2012. Cryptic sociality in rattlesnakes (Crotalus horridus) detected by kinship analysis. Biol Lett. 8(4):523–525. doi:10.1098/rsbl.2011.1217.

Clusella Trullas S, van Wyk JH, Spotila JR. 2007. Thermal melanism in ectotherms. Journal of Thermal Biology. 32(5):235–245. doi:10.1016/j.jtherbio.2007.01.013.

Cochran C, Edwards KL, Travis ZD, Pompe LR, Hayes WK. 2021. Diet and Feeding Frequency in the Southwestern Speckled Rattlesnake (Crotalus pyrrhus): Ontogenetic, Sexual, Geographic, and Seasonal Variation. hpet. 55(1):77–87. doi:10.1670/19-144.

Conner M, Plowman B, Leopold BD, Lovell C. 1999. Influence of Time-in-Residence on Home Range and Habitat Use of Bobcats. The Journal of Wildlife Management. 63(1):261–269. doi:10.2307/3802508.

Conrad JL, Weinersmith KL, Brodin T, Saltz JB, Sih A. 2011. Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. Journal of Fish Biology. 78(2):395–435. doi:10.1111/j.1095-8649.2010.02874.x.

Cooney CR, Varley ZK, Nouri LO, Moody CJA, Jardine MD, Thomas GH. 2019. Sexual selection predicts the rate and direction of colour divergence in a large avian radiation. Nat Commun. 10(1):1773. doi:10.1038/s41467-019-09859-7.

Cooper WE, Burns N. 1987. Social significance of ventrolateral coloration in the fence lizard, *Sceloporus undulatus*. Animal Behaviour. 35(2):526–532. doi:10.1016/S0003-3472(87)80277-4.

Coppens CM, de Boer SF, Koolhaas JM. 2010. Coping styles and behavioural flexibility: towards underlying mechanisms. Philosophical Transactions of the Royal Society B: Biological Sciences. 365(1560):4021–4028. doi:10.1098/rstb.2010.0217.

Costanzo A, Romano A, Ambrosini R, Parolini M, Rubolini D, Caprioli M, Corti M, Canova L, Saino N. 2018. Barn swallow antipredator behavior covaries with melanic coloration and predicts survival. Behavioral Ecology. 29(6):1472–1480. doi:10.1093/beheco/ary102.

Cote J, Clobert J. 2007. Social personalities influence natal dispersal in a lizard. Proc R Soc B. 274(1608):383–390. doi:10.1098/rspb.2006.3734.

Cote J, Clobert J, Brodin T, Fogarty S, Sih A. 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. Philosophical Transactions of the Royal Society B: Biological Sciences. 365(1560):4065–4076. doi:10.1098/rstb.2010.0176.

Cote J, Fogarty S, Tymen B, Sih A, Brodin T. 2013. Personality-dependent dispersal cancelled under predation risk. Proceedings of the Royal Society B: Biological Sciences. 280(1773):20132349. doi:10.1098/rspb.2013.2349.

Cott HB. 1940. Adaptive coloration in animals. Methuen&Co, London. London, Methuen.

Coupe B. 2002. Pheromones, search patterns, and old haunts: how do male timber rattlesnakes (Crotalus horridus) locate mates. In: Biology of the Vipers. Gordon W. Schnell, Mats Hoggren, Michael E. Douglas, and Harry W. Greene. 7705 North Wyatt Earp Avenue, Eagle Mounlain, Utah 84043, USA: Eagle Mountain Publishing. p. 139–148.

Crawford MP. 1938. A behavior rating scale for young chimpanzees. J Comp Physiol. 26(1):79–92. doi:10.1037/h0054503.

Creel S. 2018. The control of risk hypothesis: reactive vs. proactive antipredator responses and stress-mediated vs. food-mediated costs of response. Ecology Letters. 21(7):947–956. doi:10.1111/ele.12975.

Creel S, Christianson D, Liley S, Winnie JA. 2007. Predation Risk Affects Reproductive Physiology and Demography of Elk. Science. 315(5814):960–960. doi:10.1126/science.1135918.

Creel S, Winnie Jr. J, Maxwell B, Hamlin K, Creel M. 2005. Elk Alter Habitat Selection as an Antipredator Response to Wolves. Ecology. 86(12):3387–3397. doi:10.1890/05-0032.

Cresswell W. 2011. Predation in bird populations. J Ornithol. 152(1):251–263. doi:10.1007/s10336-010-0638-1.

Cuthill IC. 2019. Camouflage. Journal of Zoology. 308(2):75–92. doi:10.1111/jzo.12682.

Cuthill IC, Allen WL, Arbuckle K, Caspers B, Chaplin G, Hauber ME, Hill GE, Jablonski NG, Jiggins CD, Kelber A, et al. 2017. The biology of color. Science. 357(6350):eaan0221. doi:10.1126/science.aan0221.

Cutler DR, Edwards Jr. TC, Beard KH, Cutler A, Hess KT, Gibson J, Lawler JJ. 2007. Random Forests for Classification in Ecology. Ecology. 88(11):2783–2792. doi:10.1890/07-0539.1.

Da Cunha O, Fournier C, Horne LM, Seymoure BM, Johnson JD. 2024. You can't see me: Background matching in the Western diamond-backed rattlesnake (Crotalus atrox). J. Zool. doi:doi:10.1111/jzo.13167.

Da Cunha O, Horne LM, Johnson JD. 2023. Personally rattled: a unique protocol to support the presence of personality and behavioral syndromes in rattlesnakes. Behav Ecol Sociobiol. 77(10):115. doi:10.1007/s00265-023-03391-x.

Daghfous G, Smargiassi M, Libourel P-A, Wattiez R, Bels V. 2012. The Function of Oscillatory Tongue-Flicks in Snakes: Insights from Kinematics of Tongue-Flicking in the Banded Water Snake (Nerodia fasciata). Chem Senses. 37(9):883–896. doi:10.1093/chemse/bjs072.

Daltry JC, Wüster W, Thorpe RS. 1998. Intraspecific Variation in the Feeding Ecology of the Crotaline Snake Calloselasma rhodostoma in Southeast Asia. Journal of Herpetology. 32(2):198–205. doi:10.2307/1565297.

Davies NB, Krebs JR, West SA. 2012. An introduction to behavioral ecology. Nicholas B. Davies, John R. Krebs, and Stuart A. West. West Sussex: John Wiley & Sons, Ltd.

Denno RF, Finke DL, Langelloto GA. 2005. Direct and indirect effects of vegetation structure and habitat complexity on predator-prey and predator-predator interactions. In: Ecology of predator-prey interactions. Oxford, UK: Oxford University Press. p. 211–239.

DeSantis DL, Mata-Silva V, Johnson JD, Wagler AE. 2020. Integrative Framework for Long-Term Activity Monitoring of Small and Secretive Animals: Validation With a Cryptic Pitviper. Frontiers in Ecology and Evolution. 8. [accessed 2022 Sep 17]. https://www.frontiersin.org/articles/10.3389/fevo.2020.00169.

DeSantis DL, Wagler AE, Mata-Silva V, Johnson JD. 2019a. Effects of human-made resource hotspots on seasonal spatial strategies by a desert pitviper. Sci Rep. 9(1):16690. doi:10.1038/s41598-019-52957-1.

DeSantis DL, Wagler AE, Mata-Silva V, Johnson JD. 2019b. Effects of human-made resource hotspots on seasonal spatial strategies by a desert pitviper. Sci Rep. 9(1):16690. doi:10.1038/s41598-019-52957-1.

Diller LV, Wallace RL. 2002. Growth, reproduction, and survival in a population of Crotalus viridis oreganus in North Central Idaho. Herpetological Monographs. 16(1):26–45. doi:10.1655/0733-1347(2002)016[0026:GRASIA]2.0.CO;2.

Dingemanse NJ, Both C, Drent PJ, Tinbergen JM. 2004. Fitness consequences of avian personalities in a fluctuating environment. Proceedings of the Royal Society of London Series B: Biological Sciences. 271(1541):847–852. doi:10.1098/rspb.2004.2680.

Dingemanse NJ, Wright J, Kazem AJN, Thomas DK, Hickling R, Dawnay N. 2007. Behavioural Syndromes Differ Predictably between 12 Populations of Three-Spined Stickleback. J Anim Ecol. 76(6):1128–1138.

Duchesne T, Graitson E, Lourdais O, Ursenbacher S, Dufrêne M. 2022. Fine-scale vegetation complexity and habitat structure influence predation pressure on a declining snake. Journal of Zoology. 318(3):205–217. doi:10.1111/jzo.13007.

Ducrest A-L, Keller L, Roulin A. 2008. Pleiotropy in the melanocortin system, coloration and behavioural syndromes. Trends in Ecology & Evolution. 23(9):502–510. doi:10.1016/j.tree.2008.06.001.

Dunham AE, Grant BW, Overall KL. 1989. Interfaces between Biophysical and Physiological Ecology and the Population Ecology of Terrestrial Vertebrate Ectotherms. Physiological Zoology. 62(2):335–355.

Durán-Antonio J, González-Romero A, Sosa VJ. 2020. Activity overlap of carnivores, their potential wild prey, and temporal segregation, with livestock in a Biosphere Reserve in the Chihuahuan Desert. Journal of Mammalogy. 101(6):1609–1621. doi:10.1093/jmammal/gyaa120.

Duvall D, Schuett GW. 1997. Straight-line movement and competitive mate searching in prairie rattlesnakes,Crotalus viridis viridis. Anim Behav. 54(2):329–334. doi:10.1006/anbe.1996.0418.

Eccard JA, Herde A, Schuster AC, Liesenjohann T, Knopp T, Heckel G, Dammhahn M. 2022. Fitness, risk taking, and spatial behavior covary with boldness in experimental vole populations. Ecology and Evolution. 12(2):e8521. doi:10.1002/ece3.8521.

Endler JA. 1978. A Predator's View of Animal Color Patterns. In: Hecht MK, Steere WC, Wallace B, editors. Evolutionary Biology. Boston, MA: Springer US. (Evolutionary Biology). p. 319–364. [accessed 2023 Aug 18]. https://doi.org/10.1007/978-1-4615-6956-5_5.

Farallo VR, Forstner MRJ. 2012. Predation and the Maintenance of Color Polymorphism in a Habitat Specialist Squamate. PLOS ONE. 7(1):e30316. doi:10.1371/journal.pone.0030316.

Ferreira AS, Peres CA, Bogoni JA, Cassano CR. 2018. Use of agroecosystem matrix habitats by mammalian carnivores (Carnivora): a global-scale analysis. Mammal Review. 48(4):312–327. doi:10.1111/mam.12137.

Ford NB. 1995. Experimental Design in Studies of Snake Behavior. Herpetological Monographs. 9:130–139. doi:10.2307/1467001.

Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS. 2005. Wolves Influence Elk Movements: Behavior Shapes a Trophic Cascade in Yellowstone National Park. Ecology. 86(5):1320–1330. doi:10.1890/04-0953.

Fraser DF, Gilliam JF, Daley MJ, Le AN, Skalski GT. 2001. Explaining Leptokurtic Movement Distributions: Intrapopulation Variation in Boldness and Exploration. The American Naturalist. 158(2):124–135. doi:10.1086/321307.

Freeman H, Gosling SD, Schapiro SJ. 2011. Comparison of Methods for Assessing Personality in Nonhuman Primates. In: Weiss A, King JE, Murray L, editors. Personality and Temperament in Nonhuman Primates. New York, NY: Springer. (Developments in Primatology: Progress and Prospects). p. 17–40. [accessed 2023 Mar 21]. https://doi.org/10.1007/978-1-4614-0176-6_2.

García LV. 2004. Escaping the Bonferroni iron claw in ecological studies. Oikos. 105(3):657–663. doi:10.1111/j.0030-1299.2004.13046.x.

Gardiner LE, Somers CM, Parker DL, Poulin RG. 2015. Microhabitat Selection by Prairie Rattlesnakes (Crotalus viridis) at the Northern Extreme of their Geographic Range. J Herpetol. 49(1):131–137. doi:10.1670/12-266.

Gaynor KM, Brown JS, Middleton AD, Power ME, Brashares JS. 2019. Landscapes of Fear: Spatial Patterns of Risk Perception and Response. Trends in Ecology & Evolution. 34(4):355–368. doi:10.1016/j.tree.2019.01.004.

Gibert R, Maag D, Sanders L, Clark R. 2022. Investigating personality in vipers: individual rattlesnakes exhibit consistent behavioral responses in defensive and exploratory contexts. Behavioral Ecology and Sociobiology. 76. doi:10.1007/s00265-022-03239-w.

Gigliotti LC, Slotow R, Hunter LTB, Fattebert J, Sholto-Douglas C, Jachowski DS. 2020. Habitat complexity and lifetime predation risk influence mesopredator survival in a multi-predator system. Sci Rep. 10(1):17841. doi:10.1038/s41598-020-73318-3.

Glaudas X, Alexander GJ. 2016. Food supplementation affects the foraging ecology of a low-energy, ambush-foraging snake. Behav Ecol Sociobiol. 71(1):5. doi:10.1007/s00265-016-2239-3.

Glaudas X, Rodríguez-Robles JA. 2011. Vagabond males and sedentary females: spatial ecology and mating system of the speckled rattlesnake (Crotalus mitchellii). Biol J Linn. 103(3):681–695. doi:10.1111/j.1095-8312.2011.01677.x.

Goode MJ, Duvall D. 1989. Body temperature and defensive behaviour of free-ranging prairie rattlesnakes, Crotalus viridis viridis. Animal Behaviour. 38(2):360–362. doi:10.1016/S0003-3472(89)80100-9.

Gower DJ, Sampaio FL, Peichl L, Wagner H-J, Loew ER, Mclamb W, Douglas RH, Orlov N, Grace MS, Hart NS, et al. 2019. Evolution of the eyes of vipers with and without infrared-sensing pit organs. Biological Journal of the Linnean Society. 126(4):796–823. doi:10.1093/biolinnean/blz003.

Grabowski JH, Kimbro DL. 2005. Predator-Avoidance Behavior Extends Trophic Cascades to Refuge Habitats. Ecology. 86(5):1312–1319. doi:10.1890/04-1216.

Graves BM, Duvall D. 1988. Evidence of an Alarm Pheromone from the Cloacal Sacs of Prairie Rattlesnakes. Southwest Nat. 33(3):339–345. doi:10.2307/3671762.

Greene HW. 1988. Antipredator mechanisms in reptiles. In: Biology of the reptilia. Vol. 16. Alan R. Liss, Inc., New York. p. 1–152.

Greene HW, May PG, Hardy DL, Sciturro JM, Farrell TM. 2002. Parental behavior by vipers. In: Biology of the vipers. GW Schuett, M. Höggren, ME Douglas, and HW Greene, eds. p. 179–205.

Griffen BD, Toscano BJ, Gatto J. 2012. The role of individual behavior type in mediating indirect interactions. Ecology. 93(8):1935–1943. doi:10.1890/11-2153.1.

Gyuris E, Feró O, Tartally A, Barta Z. 2010. Individual behaviour in firebugs (Pyrrhocoris apterus). Proc R Soc B: Biol. 278(1705):628–633. doi:10.1098/rspb.2010.1326.

Hardy DL, Greene HW. 2000. Inhalation anesthesia of rattlesnakes in the field for processing and transmitter implantation. Sonoran Herpetologist. 13(10):109–113.

Harmel MV, Crowell HL, Whelan JM, Taylor EN. 2020. Rattlesnake colouration affects detection by predators. Journal of Zoology. 311(4):260–268. doi:10.1111/jzo.12786.

Hart NS. 2001. The Visual Ecology of Avian Photoreceptors. Progress in Retinal and Eye Research. 20(5):675–703. doi:10.1016/S1350-9462(01)00009-X.

Hart NS. 2002. Vision in the peafowl (Aves: Pavo cristatus). Journal of Experimental Biology. 205(24):3925–3935. doi:10.1242/jeb.205.24.3925.

Hart NS, Hunt DM. 2007. Avian Visual Pigments: Characteristics, Spectral Tuning, and Evolution. The American Naturalist. 169(S1):S7–S26. doi:10.1086/510141.

Hart NS, Partridge JC, Cuthill IC, Bennett ATD. 2000. Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine bird: the blue tit (Parus caeruleus L.) and the blackbird (Turdus merula L.). J Comp Physiol A. 186(4):375–387. doi:10.1007/s003590050437.

Haswell PM, Jones KA, Kusak J, Hayward MW. 2018. Fear, foraging and olfaction: how mesopredators avoid costly interactions with apex predators. Oecologia. 187(3):573–583. doi:10.1007/s00442-018-4133-3.

Hawlena D, Schmitz OJ. 2010. Physiological Stress as a Fundamental Mechanism Linking Predation to Ecosystem Functioning. The American Naturalist. 176(5):537–556. doi:10.1086/656495.

Hedges SB, Hass CA, Maugel TK. 1989. Physiological color change in snakes. J herpetol. 23(4):450–455.

Heinen VK, Stephens DW. 2016. Blue jays, *Cyanocitta cristata*, devalue social information in uncertain environments. Animal Behaviour. 112:53–62. doi:10.1016/j.anbehav.2015.11.015.

Herborn KA, Heidinger BJ, Alexander L, Arnold KE. 2014. Personality predicts behavioral flexibility in a fluctuating, natural environment. Behavioral Ecology. 25(6):1374–1379. doi:10.1093/beheco/aru131.

Herborn KA, Macleod R, Miles WTS, Schofield ANB, Alexander L, Arnold KE. 2010. Personality in captivity reflects personality in the wild. Animal Behaviour. 79(4):835–843. doi:10.1016/j.anbehav.2009.12.026.

Hersek MJ, Owings DH, Hennessy DF. 1992. Combat between Rattlesnakes (Crotalus viridis oreganus) in the Field. J Herpetol. 26(1):105–107. doi:10.2307/1565038.

Herzog HA, Bailey BD. 1987. Development of antipredator responses in snakes: II. Effects of recent feeding on defensive behaviors of juvenile garter snakes (Thamnophis sirtalis). J Comp Physiol. 101(4):387–389. doi:10.1037/0735-7036.101.4.387.

Hofer H, Carroll J, Neitz J, Neitz M, Williams DR. 2005. Organization of the Human Trichromatic Cone Mosaic. J Neurosci. 25(42):9669–9679. doi:10.1523/JNEUROSCI.2414-05.2005.

Huey RB. 1982. Temperature, physiology, and the ecology of reptiles. Physiological ecology.:25–95.

Huey RB, Pianka ER. 1981. Ecological Consequences of Foraging Mode. Ecology. 62(4):991–999. doi:10.2307/1936998.

Hughes A, Liggins E, Stevens M. 2019. Imperfect camouflage: how to hide in a variable world? Proceedings of the Royal Society B: Biological Sciences. 286(1902):20190646. doi:10.1098/rspb.2019.0646.

Hutton P, Seymoure BM, McGraw KJ, Ligon RA, Simpson RK. 2015. Dynamic color communication. Current Opinion in Behavioral Sciences. 6:41–49. doi:10.1016/j.cobeha.2015.08.007.

Igic B, Nunez V, Voss HU, Croston R, Aidala Z, López AV, Tatenhove AV, Holford ME, Shawkey MD, Hauber ME. 2015. Using 3D printed eggs to examine the egg-rejection behaviour of wild birds. PeerJ. 3:e965. doi:10.7717/peerj.965.

Irving E, Brown C. 2013. Examining the link between personality and laterality in a feral guppy Poecilia reticulata population. J Fish Biol. 83(2):311–325. doi:10.1111/jfb.12165.

Isaac LA, Gregory PT. 2013. Can snakes hide in plain view? Chromatic and achromatic crypsis of two colour forms of the Western Terrestrial Garter Snake (Thamnophis elegans). Biological Journal of the Linnean Society. 108(4):756–772. doi:10.1111/bij.12020.

Jacobs GH. 1993. The Distribution and Nature of Colour Vision Among the Mammals. Biological Reviews. 68(3):413–471. doi:10.1111/j.1469-185X.1993.tb00738.x.

Jacobs GH, Deegan JF, Crognale MA, Fenwick JA. 1993. Photopigments of dogs and foxes and their implications for canid vision. Visual Neuroscience. 10(1):173–180. doi:10.1017/S0952523800003291.

Jokela M, Elovainio M, Kivimäki M, Keltikangas-Järvinen L. 2008. Temperament and Migration Patterns in Finland. Psychol Sci. 19(9):831–837. doi:10.1111/j.1467-9280.2008.02164.x.

Jones PC, King RB, Bailey RL, Bieser ND, Bissell K, Campa III H, Crabill T, Cross MD, Degregorio BA, Dreslik MJ, et al. 2012. Range-wide analysis of eastern massasauga survivorship. J Wildl Manage. 76(8):1576–1586. doi:10.1002/jwmg.418.

Josef N, Amodio P, Fiorito G, Shashar N. 2012. Camouflaging in a Complex Environment—Octopuses Use Specific Features of Their Surroundings for Background Matching. PLOS ONE. 7(5):e37579. doi:10.1371/journal.pone.0037579.

Kang C, Stevens M, Moon J, Lee S, Jablonski PG. 2015. Camouflage through behavior in moths: the role of background matching and disruptive coloration. Behavioral Ecology. 26(1):45–54. doi:10.1093/beheco/aru150.

Kelber A. 2005. Alternative use of chromatic and achromatic cues in a hawkmoth. Proceedings of the Royal Society B: Biological Sciences. 272(1577):2143–2147. doi:10.1098/rspb.2005.3207.

Kelleher SR, Silla AJ, Byrne PG. 2018. Animal personality and behavioral syndromes in amphibians: a review of the evidence, experimental approaches, and implications for conservation. Behav Ecol Sociobiol. 72(5):79. doi:10.1007/s00265-018-2493-7.

Kemp DJ, Herberstein ME, Fleishman LJ, Endler JA, Bennett ATD, Dyer AG, Hart NS, Marshall J, Whiting MJ. 2015. An Integrative Framework for the Appraisal of Coloration in Nature. The American Naturalist. 185(6):705–724. doi:10.1086/681021.

Kendall MG. 1948. Rank correlation methods. Charles Griffin & Co. Ltd.

King JE, Figueredo AJ. 1997. The Five-Factor Model plus Dominance in Chimpanzee Personality. J Res Pers. 31(2):257–271. doi:10.1006/jrpe.1997.2179.

Kishida O, Costa Z, Tezuka A, Michimae H. 2014. Inducible offences affect predator–prey interactions and life-history plasticity in both predators and prey. Journal of Animal Ecology. 83(4):899–906. doi:10.1111/1365-2656.12186.

Kissner KJ, Forbes MR, Secoy DM. 1997. Rattling Behavior of Prairie Rattlesnakes (Crotalus viridis viridis, Viperidae) in Relation to Sex, Reproductive Status, Body Size, and Body Temperature. Ethol. 103(12):1042–1050. doi:10.1111/j.1439-0310.1997.tb00146.x.

Kittilsen S, Schjolden J, Beitnes-Johansen I, Shaw JC, Pottinger TG, Sørensen C, Braastad BO, Bakken M, Øverli Ø. 2009. Melanin-based skin spots reflect stress responsiveness in salmonid fish. Hormones and Behavior. 56(3):292–298. doi:10.1016/j.yhbeh.2009.06.006.

Klahr D, Simon HA. 1999. Studies of scientific discovery: Complementary approaches and convergent findings. Psychological Bulletin. 125(5):524–543. doi:10.1037/0033-2909.125.5.524.

Klauber LM. 1956a. Rattlesnakes: their habits, life histories, and influence on mankind. University of California Press, Berkeley.

Klauber LM. 1956b. Rattlesnakes. University of California Press, Berkeley.

Kluever BM, Gese EM, Dempsey SJ. 2016. The influence of wildlife water developments and vegetation on rodent abundance in the Great Basin Desert. Journal of Mammalogy. 97(4):1209–1218. doi:10.1093/jmammal/gyw077.

Kneitel JM, Chase JM. 2004. Disturbance, Predator, and Resource Interactions Alter Container Community Composition. Ecology. 85(8):2088–2093. doi:10.1890/03-3172.

Kobler A, Klefoth T, Mehner T, Arlinghaus R. 2009. Coexistence of behavioural types in an aquatic top predator: a response to resource limitation? Oecologia. 161(4):837–847. doi:10.1007/s00442-009-1415-9.

Komdeur J, Oorebeek M, van Overveld T, Cuthill IC. 2005. Mutual ornamentation, age, and reproductive performance in the European starling. Behavioral Ecology. 16(4):805–817. doi:10.1093/beheco/ari059.

Kranstauber B, Smolla M, Scharf AK. 2018 Sep 11. move: Visualizing and analyzing animal track data. R package version 3.1.0. [accessed 2024 May 23]. https://pure.mpg.de/pubman/faces/ViewItemOverviewPage.jsp?itemId=item_3012621.

Kravchuk L, Watson C. 2020. Corn Snakes Can Behaviorally Enhance Crypsis by Choosing Complex Backgrounds and Substrate. Animal Behavior and Cognition. 7:39–48. doi:10.26451/abc.07.01.04.2020.

Kurvers RHJM, Van Oers K, Nolet BA, Jonker RM, Van Wieren SE, Prins HHT, Ydenberg RC. 2010. Personality predicts the use of social information. Ecology Letters. 13(7):829–837. doi:10.1111/j.1461-0248.2010.01473.x.

LaManna JA, Martin TE. 2016. Costs of fear: behavioural and life-history responses to risk and their demographic consequences vary across species. Ecology Letters. 19(4):403–413. doi:10.1111/ele.12573.

Lamb TD. 2013. Evolution of phototransduction, vertebrate photoreceptors and retina. Progress in Retinal and Eye Research. 36:52–119. doi:10.1016/j.preteyeres.2013.06.001.

Law C, Lancaster L, Hall J, Handy S, Hinchliffe M, O'Brien C, O'Brien K, Watts S, O'Brien D. 2020. Quantifying the differences in avian attack rates on reptilesbetween an infrastructure and a control site. Eur J Wildl Res. 66(4):54. doi:10.1007/s10344-020-01393-y.

Letnic M, Ritchie EG, Dickman CR. 2012. Top predators as biodiversity regulators: the dingo Canis lupus dingo as a case study. Biological Reviews. 87(2):390–413. doi:10.1111/j.1469-185X.2011.00203.x.

Liaw A, Wiener M. 2002. Classification and Regression by randomForest. 2.

Liedtke HC, Lopez-Hervas K, Galván I, Polo-Cavia N, Gomez-Mestre I. 2023. Background matching through fast and reversible melanin-based pigmentation plasticity in tadpoles comes with morphological and antioxidant changes. Sci Rep. 13(1):12064. doi:10.1038/s41598-023-39107-4.

Lillywhite HB. 2014. How Snakes Work: Structure, Function and Behavior of the World's Snakes. Oxford University Press.

Lima SL. 1998. Nonlethal Effects in the Ecology of Predator-Prey Interactions. BioScience. 48(1):25–34. doi:10.2307/1313225.

Lima SL. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biological Reviews. 84(3):485–513. doi:10.1111/j.1469-185X.2009.00085.x.

Maag D, Clark R. 2022a. Safety in coils: predation rates of ambush hunting rattlesnakes are extremely low. Amphib-reptil. 43(4):425–430. doi:10.1163/15685381-bja10101.

Maag D, Clark R. 2022b. Safety in coils: predation rates of ambush hunting rattlesnakes are extremely low. Amphibia-Reptilia. 43(4):425–430. doi:10.1163/15685381-bja10101.

Maag DW, Maher SP, Greene BD. 2022. Spatial Ecology and Microhabitat Selection of the Pygmy Rattlesnake (Sistrurus miliarius) in Southwestern Missouri, USA. Herpetol Conserv Biol. 17(2):316–330.

Macías-Duarte A, Panjabi AO, Pool DB, Ruvalcaba-Ortega I, Levandoski GJ. 2018. Fall vegetative cover and summer precipitation predict abundance of wintering grassland birds across the Chihuahuan desert. Journal of Arid Environments. 156:41–49. doi:10.1016/j.jaridenv.2018.04.007.

MacKinlay RD, Shaw RC. 2023. A systematic review of animal personality in conservation science. Conserv Biol. 37(1):e13935. doi:10.1111/cobi.13935.

Maechler M, Rousseeuw P, Struyf A, Hubert M, Hornik K. 2012. cluster: Cluster Analysis Basics and Extensions. [accessed 2023 Feb 3]. https://lirias.kuleuven.be/3999459.

Mafli A, Wakamatsu K, Roulin A. 2011. Melanin-based coloration predicts aggressiveness and boldness in captive eastern Hermann's tortoises. Animal Behaviour. 81(4):859–863. doi:10.1016/j.anbehav.2011.01.025.

Maia R, Gruson H, Endler JA, White TE. 2019. pavo 2: New tools for the spectral and spatial analysis of colour in r. Methods in Ecology and Evolution. 10(7):1097–1107. doi:10.1111/2041-210X.13174.

Maillet Z, Halliday WD, Blouin-Demers G. 2015. Exploratory and defensive behaviours change with sex and body size in eastern garter snakes (Thamnophis sirtalis). J Ethol. 33(1):47–54. doi:10.1007/s10164-014-0416-2.

Malhotra A, Wüster W, Owens JB, Hodges CW, Jesudasan A, Ch G, Kartik A, Christopher P, Louies J, Naik H, et al. 2021. Promoting co-existence between humans and venomous snakes through increasing the herpetological knowledge base. Toxicon: X. 12:100081. doi:10.1016/j.toxcx.2021.100081.

Mangel M, Stamps J. 2001. Trade-offs between growth and mortality and the maintenance of individual variation in growth. Evol Ecol Res. 3(5):###-###.

Marshall KLA, Philpot KE, Stevens M. 2016. Microhabitat choice in island lizards enhances camouflage against avian predators. Sci Rep. 6(1):19815. doi:10.1038/srep19815.

Mathot KJ, Godde S, Careau V, Thomas DW, Giraldeau L-A. 2009. Testing dynamic variance-sensitive foraging using individual differences in basal metabolic rates of zebra finches. Oikos. 118(4):545–552. doi:10.1111/j.1600-0706.2009.17357.x.

Mayer M, Shine R, Brown GP. 2016. Bigger babies are bolder: effects of body size on personality of hatchling snakes. Behaviour. 153(3):313–323.

Mayr E. 1997. This is biology. Cambridge, Massachusetts: The Belknap Press of Harvard University Press.

McAlpine DF. 1983. Correlated Physiological Color Change and Activity Patterns in an Indian Ocean Boa (Casarea dussumeri). Journal of Herpetology. 17(2):198–201. doi:10.2307/1563469.

McGhee KE, Pintor LM, Bell AM. 2013. Reciprocal Behavioral Plasticity and Behavioral Types during Predator-Prey Interactions. The American Naturalist. 182(6):704–717. doi:10.1086/673526.

McNamara JM, Houston AI, Lima SL. 1994. Foraging Routines of Small Birds in Winter: A Theoretical Investigation. Journal of Avian Biology. 25(4):287–302. doi:10.2307/3677276.

Melville HIAS, Conway WC, Hardin JB, Comer CE, Morrison ML. 2020. Abiotic variables influencing the nocturnal movements of bobcats and coyotes. Wildlife Biology. 2020(3):wlb.00601. doi:10.2981/wlb.00601.

Meredith M, Ridout M. 2018. Overview of the overlap package. https://cran.r-project.org/web/packages/overlap/vignettes/overlap.pdf.

Merilaita S, Scott-Samuel NE, Cuthill IC. 2017. How camouflage works. Philosophical Transactions of the Royal Society B: Biological Sciences. 372(1724):20160341. doi:10.1098/rstb.2016.0341.

Merilaita S, Tuomi J, Jormalainen V. 1999. Optimization of cryptic coloration in heterogeneous habitats. Biological Journal of the Linnean Society. 67(2):151–161. doi:10.1111/j.1095-8312.1999.tb01858.x.

Mettke-Hofmann C, Wink M, Winkler H, Leisler B. 2005. Exploration of environmental changes relates to lifestyle. Behavioral Ecology. 16(1):247–254. doi:10.1093/beheco/arh159.

Michelangeli M, Payne E, Spiegel O, Sinn DL, Leu ST, Gardner MG, Sih A. 2022. Personality, spatiotemporal ecological variation and resident/explorer movement syndromes in the sleepy lizard. Journal of Animal Ecology. 91(1):210–223. doi:10.1111/1365-2656.13616.

Mills AD, Faure JM. 2000. Ease of capture in lines of Japanese quail (Coturnix japonica) subjected to contrasting selection for fear or sociability. Appl Anim Behav Sci. 69(2):125–134. doi:10.1016/S0168-1591(00)00126-X.

Montgomerie R. 2006. Analyzing Colors. In: Bird Coloration. Hill G. E. and McGraw K. J. Cambridge, Massachusetts: Harvard University Press. p. 90–148.

Mooney KA, Gruner DS, Barber NA, Van Bael SA, Philpott SM, Greenberg R. 2010. Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. Proceedings of the National Academy of Sciences. 107(16):7335–7340. doi:10.1073/pnas.1001934107.

Moore JA. 1993. Science as a Way of Knowing: The Foundations of Modern Biology. Cambridge, Massachusetts: Harvard University Press.

Moran MD. 2003. Arguments for Rejecting the Sequential Bonferroni in Ecological Studies. Oikos. 100(2):403–405.

Morris DW. 2005. Habitat-Dependent Foraging in a Classic Predator-Prey System: A Fable from Snowshoe Hares. Oikos. 109(2):239–254.

Mowat FM, Peichl L. 2022. Ophthalmology of Canidae: Foxes, Wolves, and Relatives. In: Montiani-Ferreira F, Moore BA, Ben-Shlomo G, editors. Wild and Exotic Animal Ophthalmology: Volume 2: Mammals. Cham: Springer International Publishing. p. 181–214. [accessed 2023 Jul 20]. https://doi.org/10.1007/978-3-030-81273-7_11.

Mukherjee S, Zelcer M, Kotler BP. 2009. Patch use in time and space for a meso-predator in a risky world. Oecologia. 159(3):661–668. doi:10.1007/s00442-008-1243-3.

Munguia P, Levinton JS, Silbiger NJ. 2013. Latitudinal differences in thermoregulatory color change in Uca pugilator. Journal of Experimental Marine Biology and Ecology. 440:8–14. doi:10.1016/j.jembe.2012.11.010.

Murphy JB. 2017. Rattlesnakes and Zoos. Herp Review. 48(4):887–898.

Mysterud A, Ims RA. 1998. Functional Responses in Habitat Use: Availability Influences Relative Use in Trade-Off Situations. Ecology. 79(4):1435–1441. doi:10.1890/0012-9658(1998)079[1435:FRIHUA]2.0.CO;2.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences. 105(49):19052–19059. doi:10.1073/pnas.0800375105.

Neal BJ. 1959. A Contribution on the Life History of the Collared Peccary in Arizona. The American Midland Naturalist. 61(1):177–190. doi:10.2307/2422349.

Nelson EH, Matthews CE, Rosenheim JA. 2004. Predators Reduce Prey Population Growth by Inducing Changes in Prey Behavior. Ecology. 85(7):1853–1858. doi:10.1890/03-3109.

Nilsson JÅ, Brönmark C, Hansson LA, Chapman BB. 2014. Individuality in movement: the role of animal personality. In: Animal movement across scales. Susanne Åkesson, Lars-Anders Hansson. Oxford University Press. p. 90–109.

Nokelainen O, Helle H, Hartikka J, Jolkkonen J, Valkonen JK. 2022. The Eurasian Treecreeper (Certhia familiaris) has an effective camouflage against mammalian but not avian vision in boreal forests. Ibis. 164(3):679–691. doi:10.1111/ibi.13056.

Nokelainen O, Maynes R, Mynott S, Price N, Stevens M. 2019. Improved camouflage through ontogenetic colour change confers reduced detection risk in shore crabs. Funct Ecol. 33(4):654–669. doi:10.1111/1365-2435.13280.

Nokelainen O, Scott-Samuel NE, Nie Y, Wei F, Caro T. 2021. The giant panda is cryptic. Sci Rep. 11(1):21287. doi:10.1038/s41598-021-00742-4.

Norris SP. 1984. Defining observational competence. Science Education. 68(2):129–142. doi:10.1002/sce.3730680206.

Nowak EM, Theimer TC, Schuett GW. 2008. Functional and Numerical Responses of Predators: Where Do Vipers Fit in the Traditional Paradigms? Biol Rev. 83(4):601–620. doi:10.1111/j.1469-185X.2008.00056.x.

Ödeen A, Håstad O. 2003. Complex Distribution of Avian Color Vision Systems Revealed by Sequencing the SWS1 Opsin from Total DNA. Molecular Biology and Evolution. 20(6):855–861. doi:10.1093/molbev/msg108.

Olsson P, Lind O, Kelber A. 2018. Chromatic and achromatic vision: parameter choice and limitations for reliable model predictions. Behavioral Ecology. 29(2):273–282. doi:10.1093/beheco/arx133.

Osorio D, Miklósi A, Gonda Zs. 1999. Visual Ecology and Perception of Coloration Patterns by Domestic Chicks. Evolutionary Ecology. 13(7):673–689. doi:10.1023/A:1011059715610.

Öst M, Seltmann MW, Jaatinen K. 2015. Personality, body condition and breeding experience drive sociality in a facultatively social bird. Anim Behav. 100:166–173. doi:10.1016/j.anbehav.2014.12.008.

van Overveld T, Matthysen E. 2009. Personality predicts spatial responses to food manipulations in free-ranging great tits (Parus major). Biology Letters. 6(2):187–190. doi:10.1098/rsbl.2009.0764.

Pangle KL, Peacor SD, Johannsson OE. 2007. Large Nonlethal Effects of an Invasive Invertebrate Predator on Zooplankton Population Growth Rate. Ecology. 88(2):402–412. doi:10.1890/06-0768.

Pascual J, Senar JC. 2014. Antipredator behavioural compensation of proactive personality trait in male Eurasian siskins. Animal Behaviour. 90:297–303. doi:10.1016/j.anbehav.2014.02.002.

Patrick SC, Pinaud D, Weimerskirch H. 2017. Boldness predicts an individual's position along an exploration–exploitation foraging trade-off. Journal of Animal Ecology. 86(5):1257–1268. doi:10.1111/1365-2656.12724.

Patrick SC, Weimerskirch H. 2014. Personality, Foraging and Fitness Consequences in a Long Lived Seabird. PLOS ONE. 9(2):e87269. doi:10.1371/journal.pone.0087269.

Pavlov I. 1966. Constitutional differences and functional disturbances: Experimental neuroses. In: Essential Works of Pavlov. M. Kaplan. New York: Bantam books. p. 261–267.

Pearish S, Hostert L, Bell AM. 2013. Behavioral type–environment correlations in the field: a study of three-spined stickleback. Behav Ecol Sociobiol. 67(5):765–774. doi:10.1007/s00265-013-1500-2.

Peckarsky BL, Cowan CA, Penton MA, Anderson C. 1993. Sublethal Consequences of Stream-Dwelling Predatory Stoneflies on Mayfly Growth and Fecundity. Ecology. 74(6):1836–1846. doi:10.2307/1939941.

Pembury Smith MQR, Ruxton GD. 2020. Camouflage in predators. Biological Reviews. 95(5):1325–1340. doi:10.1111/brv.12612.

Pennisi E. 2016. The power of personality. Science. 352(6286):644–647. doi:10.1126/science.352.6286.644.

Perals D, Griffin AS, Bartomeus I, Sol D. 2017. Revisiting the open-field test: what does it really tell us about animal personality? Anim Behav. 123:69–79. doi:10.1016/j.anbehav.2016.10.006.

Pettorelli N, Hilborn A, Duncan C, Durant SM. 2015. Chapter Two - Individual Variability: The Missing Component to Our Understanding of Predator–Prey Interactions. In: Pawar S, Woodward G, Dell AI, editors. Advances in Ecological Research. Vol. 52. Academic Press. (Trait-Based Ecology - From Structure to Function). p. 19–44. [accessed 2022 Sep 26]. https://www.sciencedirect.com/science/article/pii/S0065250415000021.

Pincheira-Donoso D, Bauer AM, Meiri S, Uetz P. 2013. Global Taxonomic Diversity of Living Reptiles. PLOS ONE. 8(3):e59741. doi:10.1371/journal.pone.0059741.

Poulton SEB. 1890. The Colours of Animals: Their Meaning and Use, Especially Considered in the Case of Insects. D. Appleton.

Price N, Green S, Troscianko J, Tregenza T, Stevens M. 2019. Background matching and disruptive coloration as habitat-specific strategies for camouflage. Sci Rep. 9(1):7840. doi:10.1038/s41598-019-44349-2.

Prival DB, Goode MJ, Swann DE, Schwalbe CR, Schroff MJ. 2002. Natural History of a Northern Population of Twin-Spotted Rattlesnakes, Crotalus pricei. J Herpetol. 36(4):598–607. doi:10.1670/0022-1511(2002)036[0598:NHOANP]2.0.CO;2.

Putman BJ, Clark RW. 2015. Habitat Manipulation in Hunting Rattlesnakes (Crotalus Species). swna. 60(4):374–377. doi:10.1894/0038-4909-60.4.374.

Pyke GH, Pulliam HR, Charnov EL. 1977. Optimal Foraging: A Selective Review of Theory and Tests. The Quarterly Review of Biology. 52(2):137–154. doi:10.1086/409852.

Quinn JL, Cole EF, Patrick SC, Sheldon BC. 2011. Scale and state dependence of the relationship between personality and dispersal in a great tit population. Journal of Animal Ecology. 80(5):918–928. doi:10.1111/j.1365-2656.2011.01835.x.

R Core Team. 2022. R: A Language and Environment for Statistical Computing.

R Core Team. 2023. R: A Language and Environment for Statistical Computing. https://www.R-project.org/.

Réale D, Dingemanse NJ, Kazem AJN, Wright J. 2010. Evolutionary and ecological approaches to the study of personality. Philosophical Transactions of the Royal Society B: Biological Sciences. 365(1560):3937–3946. doi:10.1098/rstb.2010.0222.

Réale D, Festa-Bianchet M. 2003. Predator-induced natural selection on temperament in bighorn ewes. Animal Behaviour. 65(3):463–470. doi:10.1006/anbe.2003.2100.

Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio P-O. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. Philosophical Transactions of the Royal Society B: Biological Sciences. 365(1560):4051–4063. doi:10.1098/rstb.2010.0208.

Réale D, Martin J, Coltman DW, Poissant J, Festa-bianchet M. 2009. Male personality, life-history strategies and reproductive success in a promiscuous mammal. Journal of Evolutionary Biology. 22(8):1599–1607. doi:10.1111/j.1420-9101.2009.01781.x.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007a. Integrating animal temperament within ecology and evolution. Biological Reviews. 82(2):291–318. doi:10.1111/j.1469-185X.2007.00010.x.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007b. Integrating animal temperament within ecology and evolution. Biological Reviews. 82(2):291–318. doi:10.1111/j.1469-185X.2007.00010.x.

Regan BC, Julliot C, Simmen B, Viénot F, Charles-Dominique P, Mollon JD. 2001. Fruits, foliage and the evolution of primate colour vision. Philos Trans R Soc Lond B Biol Sci. 356(1407):229–283. doi:10.1098/rstb.2000.0773.

Reiserer RS, Schuett GW, Greene HW. 2018. Seed ingestion and germination in rattlesnakes: overlooked agents of rescue and secondary dispersal. Philos Trans R Soc Lond, B, Biol Sci. 285(1872):20172755. doi:10.1098/rspb.2017.2755.

Renoult JP, Kelber A, Schaefer HM. 2017. Colour spaces in ecology and evolutionary biology: Colour spaces in ecology and evolutionary biology. Biol Rev. 92(1):292–315. doi:10.1111/brv.12230.

Repp RA, Schuett GW. 2008. Adult Western Diamond-backed Rattlesnakes (Crotalus atrox) gain water through harvesting and drinking rain, sleet, and snow. Southwest Nat.(53):109–115.

Reyes-Arriagada R, Jiménez JE, Rozzi R. 2015. Daily patterns of activity of passerine birds in a Magellanic sub-Antarctic forest at Omora Park (55°S), Cape Horn Biosphere Reserve, Chile. Polar Biol. 38(3):401–411. doi:10.1007/s00300-014-1596-5.

Ricklefs RE, Wikelski M. 2002. The physiology/life-history nexus. Trends in Ecology & Evolution. 17(10):462–468. doi:10.1016/S0169-5347(02)02578-8.

Ridout MS, Linkie M. 2009. Estimating overlap of daily activity patterns from camera trap data. JABES. 14(3):322–337. doi:10.1198/jabes.2009.08038.

Riipi M, Alatalo RV, Lindström L, Mappes J. 2001. Multiple benefits of gregariousness cover detectability costs in aposematic aggregations. Nature. 413(6855):512–514. doi:10.1038/35097061.

Robledo-Ospina LE, Escobar-Sarria F, Troscianko J, Rao D. 2017. Two ways to hide: predator and prey perspectives of disruptive coloration and background matching in jumping spiders. Biological Journal of the Linnean Society. 122(4):752–764. doi:10.1093/biolinnean/blx108.

Ruiz-Gomez M de L, Huntingford FA, Øverli Ø, Thörnqvist P-O, Höglund E. 2011. Response to environmental change in rainbow trout selected for divergent stress coping styles. Physiology & Behavior. 102(3):317–322. doi:10.1016/j.physbeh.2010.11.023.

Ruxton GD, Allen WL, Sherratt TN, Speed MP. 2019. Avoiding Attack: The Evolutionary Ecology of Crypsis, Aposematism, and Mimicry. Oxford University Press.

Schirmer A, Herde A, Eccard JA, Dammhahn M. 2019. Individuals in space: personality-dependent space use, movement and microhabitat use facilitate individual spatial niche specialization. Oecologia. 189(3):647–660. doi:10.1007/s00442-019-04365-5.

Schirmer A, Hoffmann J, Eccard JA, Dammhahn M. 2020. My niche: individual spatial niche specialization affects within- and between-species interactions. Proceedings of the Royal Society B: Biological Sciences. 287(1918):20192211. doi:10.1098/rspb.2019.2211.

Schlägel UE, Grimm V, Blaum N, Colangeli P, Dammhahn M, Eccard JA, Hausmann SL, Herde A, Hofer H, Joshi J, et al. 2020. Movement-mediated community assembly and coexistence. Biological Reviews. 95(4):1073–1096. doi:10.1111/brv.12600.

Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. Nat Methods. 9(7):671–675. doi:10.1038/nmeth.2089.

Schraft HA, Bakken GS, Clark RW. 2019. Infrared-sensing snakes select ambush orientation based on thermal backgrounds. Sci Rep. 9(1):3950. doi:10.1038/s41598-019-40466-0.

Schuett G, Clark R, Repp R, Amarello M, Smith C, Greene H. 2016. Social Behavior of Rattlesnakes: A Shifting Paradigm. Vol. 2. GW Schuett, MJ Feldner, CF Smith, and RS Reiserer (Eds). Rodeo, New Mexico: ECO Publishing. p. 161–244.

Schuett W, Tregenza T, Dall SRX. 2010. Sexual selection and animal personality. Biological Reviews. 85(2):217–246. doi:10.1111/j.1469-185X.2009.00101.x.

Schultner J, Kitaysky AS, Gabrielsen GW, Hatch SA, Bech C. 2013. Differential reproductive responses to stress reveal the role of life-history strategies within a species. Proceedings of the Royal Society B: Biological Sciences. 280(1771):20132090. doi:10.1098/rspb.2013.2090.

Seebacher F, Franklin CE. 2005. Physiological mechanisms of thermoregulation in reptiles: a review. J Comp Physiol B. 175(8):533–541. doi:10.1007/s00360-005-0007-1.

Shaffer HB, Gidiş M, McCartney-Melstad E, Neal KM, Oyamaguchi HM, Tellez M, Toffelmier EM. 2015. Conservation Genetics and Genomics of Amphibians and Reptiles. Annu Rev Anim. 3(1):113–138. doi:10.1146/annurev-animal-022114-110920.

Sherratt TN, Pollitt D, Wilkinson DM. 2007. The evolution of crypsis in replicating populations of web-based prey. Oikos. 116(3):449–460. doi:10.1111/j.0030-1299.2007.15521.x.

Siddiqi A, Cronin TW, Loew ER, Vorobyev M, Summers K. 2004. Interspecific and intraspecific views of color signals in the strawberry poison frog Dendrobates pumilio. Journal of Experimental Biology. 207(14):2471–2485. doi:10.1242/jeb.01047.

Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol Evol. 19(7):372–378. doi:10.1016/j.tree.2004.04.009.

Sih A, Cote J, Evans M, Fogarty S, Pruitt J. 2012. Ecological implications of behavioural syndromes. Ecology Letters. 15(3):278–289. doi:10.1111/j.1461-0248.2011.01731.x.

Sillman AJ, Carver JK, Loew ER. 1999. Photoreceptors and visual pigments in the ball python. J Exp Biol. 202(14):1931–1938.

da Silva CRB, van den Berg CP, Condon ND, Riginos C, Wilson RS, Cheney KL. 2020. Intertidal gobies acclimate rate of luminance change for background matching with shifts in seasonal temperature. Journal of Animal Ecology. 89(7):1735–1746. doi:10.1111/1365-2656.13226.

Silva JP, Catry I, Palmeirim JM, Moreira F. 2015. Freezing heat: thermally imposed constraints on the daily activity patterns of a free-ranging grassland bird. Ecosphere. 6(7):art119. doi:10.1890/ES14-00454.1.

Šimková O, Frýdlová P, Žampachová B, Frynta D, Landová E. 2017a. Development of behavioural profile in the Northern common boa (Boa imperator): Repeatable independent traits or personality? Lutermann H, editor. PLoS ONE. 12(5):e0177911. doi:10.1371/journal.pone.0177911.

Šimková O, Frýdlová P, Žampachová B, Frynta D, Landová E. 2017b. Development of behavioural profile in the Northern common boa (Boa imperator): Repeatable independent traits or personality? Lutermann H, editor. PLoS ONE. 12(5):e0177911. doi:10.1371/journal.pone.0177911.

Skelhorn J. 2018. Prey mistake masquerading predators for the innocuous items they resemble. Curr Biol. 28(14):R780–R781. doi:10.1016/j.cub.2018.06.022.

Skelly DK, Werner EE. 1990. Behavioral and Life-Historical Responses of Larval American Toads to an Odonate Predator. Ecology. 71(6):2313–2322. doi:10.2307/1938642.

Skinner M, Brown S, Kumpan LT, Miller N. 2022. Snake personality: Differential effects of development and social experience. Behav Ecol Sociobiol. 76(10):135. doi:10.1007/s00265-022-03227-0.

Slip DJ, Shine R. 1988. Feeding Habits of the Diamond Python, Morelia s. spilota: Ambush Predation by a Boid Snake. Journal of Herpetology. 22(3):323–330. doi:10.2307/1564156.

Smit JAH, van Oers K. 2019. Personality types vary in their personal and social information use. Animal Behaviour. 151:185–193. doi:10.1016/j.anbehav.2019.02.002.

Smith BR, Blumstein DT. 2008. Fitness consequences of personality: a meta-analysis. Behavioral Ecology. 19(2):448–455. doi:10.1093/beheco/arm144.

Smith KR, Cadena V, Endler JA, Kearney MR, Porter WP, Stuart-Fox D. 2016. Color Change for Thermoregulation versus Camouflage in Free-Ranging Lizards. The American Naturalist. 188(6):668–678. doi:10.1086/688765.

Smithers SP, Rooney R, Wilson A, Stevens M. 2018. Rock pool fish use a combination of colour change and substrate choice to improve camouflage. Animal Behaviour. 144:53–65. doi:10.1016/j.anbehav.2018.08.004.

Spiegel O, Leu ST, Bull CM, Sih A. 2017. What's your move? Movement as a link between personality and spatial dynamics in animal populations. Chase J, editor. Ecol Lett. 20(1):3–18. doi:10.1111/ele.12708.

Spiegel O, Leu ST, Sih A, Godfrey SS, Bull CM. 2015. When the going gets tough: behavioural type-dependent space use in the sleepy lizard changes as the season dries. Proceedings of the Royal Society B: Biological Sciences. 282(1819):20151768. doi:10.1098/rspb.2015.1768.

Stamps J. 1995. Motor Learning and the Value of Familiar Space. The American Naturalist. 146(1):41–58.

Stearns SC. 1992. The evolution of life histories. Oxford University Press.

Steenhof K, Kochert MN. 1985. Dietary shifts of sympatric buteos during a prey decline. Oecologia. 66(1):6–16. doi:10.1007/BF00378546.

Steinhoff POM, Warfen B, Voigt S, Uhl G, Dammhahn M. 2020. Individual differences in risk-taking affect foraging across different landscapes of fear. Oikos. 129(12):1891–1902. doi:10.1111/oik.07508.

Stellatelli OA, Block C, Vega LE, Cruz FB. 2015. Nonnative Vegetation Induces Changes in Predation Pressure and Escape Behavior of Two Sand Lizards (Liolaemidae: Liolaemus). Herpetologica. 71(2):136–142. doi:10.1655/HERPETOLOGICA-D-14-00026.

Stepanek J, Claunch NM, Frazier JA, Moore IT, Vernasco BJ, Escallón C, Taylor EN. 2019. Corticosterone and Color Change in Southern Pacific Rattlesnakes (Crotalus helleri). Herpetologica. 75(2):143–152. doi:10.1655/D-18-00008.

Stevens M. 2016. Color Change, Phenotypic Plasticity, and Camouflage. Frontiers in Ecology and Evolution. 4. [accessed 2023 Aug 9]. https://www.frontiersin.org/articles/10.3389/fevo.2016.00051.

Stevens M, Cuthill IC. 2007. Hidden Messages: Are Ultraviolet Signals a Special Channel in Avian Communication? BioScience. 57(6):501–507. doi:10.1641/B570607.

Stevens M, Lown AE, Denton AM. 2014. Rockpool Gobies Change Colour for Camouflage. PLOS ONE. 9(10):e110325. doi:10.1371/journal.pone.0110325.

Stevens M, Lown AE, Wood LE. 2014. Color change and camouflage in juvenile shore crabs Carcinus maenas. Frontiers in Ecology and Evolution. 2. [accessed 2023 Jul 10]. https://www.frontiersin.org/articles/10.3389/fevo.2014.00014.

Stevens M, Merilaita S. 2009. Animal camouflage: current issues and new perspectives. Phil Trans R Soc B. 364(1516):423–427. doi:10.1098/rstb.2008.0217.

Stevens M, Merilaita S. 2011. Animal Camouflage: Mechanisms and Function. Cambridge University Press.

Stevens M, Párraga CA, Cuthill IC, Partridge JC, Troscianko J. 2007. Using digital photography to study animal coloration. Biological Journal of the Linnean Society. 90(2):211–237. doi:10.1111/j.1095-8312.2007.00725.x.

Stevens M, Ruxton GD. 2019. The key role of behaviour in animal camouflage. Biological Reviews. 94(1):116–134. doi:10.1111/brv.12438.

Stevens M, Troscianko J, Wilson-Aggarwal JK, Spottiswoode CN. 2017. Improvement of individual camouflage through background choice in ground-nesting birds. Nat Ecol Evol. 1(9):1325–1333. doi:10.1038/s41559-017-0256-x.

Stevenson-Hinde J, Stillwell-Barnes R, Zunz M. 1980. Subjective assessment of rhesus monkeys over four successive years. Primates. 21(1):66–82. doi:10.1007/BF02383825.

Stiegler J, Lins A, Dammhahn M, Kramer-Schadt S, Ortmann S, Blaum N. 2022. Personality drives activity and space use in a mammalian herbivore. Mov Ecol. 10(1):33. doi:10.1186/s40462-022-00333-6.

Stobbe N, Dimitrova M, Merilaita S, Schaefer HM. 2008. Chromaticity in the UV/blue range facilitates the search for achromatically background-matching prey in birds. Philosophical Transactions of the Royal Society B: Biological Sciences. 364(1516):511–517. doi:10.1098/rstb.2008.0248.

Stoddard MC, Miller AE, Eyster HN, Akkaynak D. 2019. I see your false colours: how artificial stimuli appear to different animal viewers. Interface Focus. 9(1):20180053. doi:10.1098/rsfs.2018.0053.

Stoffel MA, Nakagawa S, Schielzeth H. 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods Ecol Evol. 8(11):1639–1644. doi:10.1111/2041-210X.12797.

Stuart-Fox D, Moussalli A. 2009. Camouflage, communication and thermoregulation: lessons from colour changing organisms. Philos Trans R Soc Lond B Biol Sci. 364(1516):463–470. doi:10.1098/rstb.2008.0254.

Stuart-Fox D, Whiting MJ, Moussalli A. 2006. Camouflage and colour change: antipredator responses to bird and snake predators across multiple populations in a dwarf chameleon. Biological Journal of the Linnean Society. 88(3):437–446. doi:10.1111/j.1095-8312.2006.00631.x.

Sundström LF, Petersson E, Höjesjö J, Johnsson JI, Järvi T. 2004. Hatchery selection promotes boldness in newly hatched brown trout (Salmo trutta): implications for dominance. Behavioral Ecology. 15(2):192–198. doi:10.1093/beheco/arg089.

Sweeney K, Cusack B, Armagost F, O'Brien T, Keiser CN, Pruitt JN. 2013. Predator and prey activity levels jointly influence the outcome of long-term foraging bouts. Behavioral Ecology. 24(5):1205–1210. doi:10.1093/beheco/art052.

Taylor EN, Malawy MA, Browning DM, Lemar SV, DeNardo DF. 2005. Effects of food supplementation on the physiological ecology of female Western diamond-backed rattlesnakes (Crotalus atrox). Oecologia. 144(2):206–213. doi:10.1007/s00442-005-0056-x.

Taylor JS, Church KE, Rusch DH, Cary JR. 1999. Macrohabitat Effects on Summer Survival, Movements, and Clutch Success of Northern Bobwhite in Kansas. The Journal of Wildlife Management. 63(2):675–685. doi:10.2307/3802657.

Tetzlaff SJ, Carter ET, DeGregorio BA, Ravesi MJ, Kingsbury BA. 2017. To forage, mate, or thermoregulate: Influence of resource manipulation on male rattlesnake behavior. Ecology and Evolution. 7(16):6606–6613. doi:10.1002/ece3.3193.

Théry M, Debut M, Gomez D, Casas J. 2005. Specific color sensitivities of prey and predator explain camouflage in different visual systems. Behavioral Ecology. 16(1):25–29. doi:10.1093/beheco/arh130.

Thorlacius M, Hellström G, Brodin T. 2015. Behavioral dependent dispersal in the invasive round goby Neogobius melanostomus depends on population age. Current Zoology. 61(3):529–542. doi:10.1093/czoolo/61.3.529.

Tieleman IB, Williams JB, Ricklefs RE, Klasing KC. 2005. Constitutive innate immunity is a component of the pace-of-life syndrome in tropical birds. Proceedings of the Royal Society B: Biological Sciences. 272(1573):1715–1720. doi:10.1098/rspb.2005.3155.

Tollrian R, Harvell CD. 1999. The Ecology and Evolution of Inducible Defenses. Princeton University Press.

Troscianko J, Skelhorn J, Stevens M. 2017. Quantifying camouflage: how to predict detectability from appearance. BMC Evolutionary Biology. 17(1):7. doi:10.1186/s12862-016-0854-2.

Troscianko J, Stevens M. 2015. Image calibration and analysis toolbox – a free software suite for objectively measuring reflectance, colour and pattern. Methods in Ecology and Evolution. 6(11):1320–1331. doi:10.1111/2041-210X.12439.

Troscianko J, Wilson-Aggarwal J, Griffiths D, Spottiswoode CN, Stevens M. 2017. Relative advantages of dichromatic and trichromatic color vision in camouflage breaking. Behavioral Ecology. 28(2):556–564. doi:10.1093/beheco/arw185.

Troscianko J, Wilson-Aggarwal J, Stevens M, Spottiswoode CN. 2016. Camouflage predicts survival in ground-nesting birds. Sci Rep. 6(1):19966. doi:10.1038/srep19966.

Uetz P, Freed P, Aguilar R, Reyes F, Hošek J. 2022. The Reptile Database. [accessed 2023 Mar 22]. http://www.reptile-database.org.

Umbers KDL, Fabricant SA, Gawryszewski FM, Seago AE, Herberstein ME. 2014. Reversible colour change in Arthropoda. Biological Reviews. 89(4):820–848. doi:10.1111/brv.12079.

US Department of Commerce N. Climate. [accessed 2023 Aug 18]. https://www.weather.gov/wrh/Climate?wfo=maf.

Vanderpool R, Malcolm J, Hill M. 2005. Crotalus atrox (western diamondback rattlesnake) predation. Herp Review.(36):191–192.

Varma V, Vasoya H, Jain A, Binoy VV. 2020. 'The Bold are the Sociable': Personality traits and laterality in an indigenous megafish, the Deccan Mahseer (Tor khudree). Ichthyol Res. 67(4):483–492. doi:10.1007/s10228-020-00744-8.

Vonk J, Weiss A, Kuczaj SA, editors. 2017. Personality in Nonhuman Animals. Berlin, Germany: Springer International Publishing. [accessed 2023 Feb 10]. http://link.springer.com/10.1007/978-3-319-59300-5.

Vorobyev M, Osorio D. 1998. Receptor noise as a determinant of colour thresholds. Proc R Soc Lond B. 265(1394):351–358. doi:10.1098/rspb.1998.0302.

Ward AJW, Thomas P, Hart PJB, Krause J. 2004. Correlates of boldness in three-spined sticklebacks (Gasterosteus aculeatus). Behav Ecol Sociobiol. 55(6):561–568. doi:10.1007/s00265-003-0751-8.

Ward-Fear G, Brown GP, Pearson DJ, West A, Rollins LA, Shine R. 2018. The ecological and life history correlates of boldness in free-ranging lizards. Ecosphere. 9(3):e02125. doi:10.1002/ecs2.2125.

Wasserman RJ, Alexander ME, Weyl OLF, Barrios-O'Neill D, Froneman PW, Dalu T. 2016. Emergent effects of structural complexity and temperature on predator–prey interactions. Ecosphere. 7(2):e01239. doi:10.1002/ecs2.1239.

Waters RM, Bowers BB, Burghardt GM. 2017. Personality and Individuality in Reptile Behavior. In: Personality in Nonhuman Animals. Springer International Publishing. p. 153–185.

Webb JK, Scott ML, Whiting MJ, Shine R. 2015. Territoriality in a snake. Behav Ecol Sociobiol. 69(10):1657–1661. doi:10.1007/s00265-015-1977-y.

Werner EE, Anholt BR. 1993. Ecological Consequences of the Trade-Off between Growth and Mortality Rates Mediated by Foraging Activity. The American Naturalist. 142(2):242–272. doi:10.1086/285537.

Westerberg M, Staffan F, Magnhagen C. 2004. Influence of predation risk on individual competitive ability and growth in Eurasian perch, *Perca fluviatilis*. Animal Behaviour. 67(2):273–279. doi:10.1016/j.anbehav.2003.06.003.

White T, Dalrymple R, Noble D, O'Hanlon J, Zurek D, Umbers K. 2015. Reproducible research in the study of biological coloration. Animal Behaviour. 106:51–57. doi:10.1016/j.anbehav.2015.05.007.

Wiersma P, Muñoz-Garcia A, Walker A, Williams JB. 2007. Tropical birds have a slow pace of life. Proceedings of the National Academy of Sciences. 104(22):9340–9345. doi:10.1073/pnas.0702212104.

Wikelski M, Spinney L, Schelsky W, Scheuerlein A, Gwinner E. 2003. Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. Proceedings of the Royal Society of London Series B: Biological Sciences. 270(1531):2383–2388. doi:10.1098/rspb.2003.2500.

Wilson RP, Grundy E, Massy R, Soltis J, Tysse B, Holton M, Cai Y, Parrott A, Downey LA, Qasem L, et al. 2014. Wild state secrets: ultra-sensitive measurement of micro-movement can reveal internal processes in animals. Frontiers in Ecology and the Environment. 12(10):582–587. doi:10.1890/140068.

Winnie J, Creel S. 2007. Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. Animal Behaviour. 73(1):215–225. doi:10.1016/j.anbehav.2006.07.007.

Wolf M, van Doorn GS, Leimar O, Weissing FJ. 2007. Life-history trade-offs favour the evolution of animal personalities. Nature. 447(7144):581–584. doi:10.1038/nature05835.

Wolf M, van Doorn GS, Weissing FJ. 2008. Evolutionary emergence of responsive and unresponsive personalities. Proceedings of the National Academy of Sciences. 105(41):15825–15830. doi:10.1073/pnas.0805473105.

Wolf M, Weissing FJ. 2012. Animal personalities: consequences for ecology and evolution. Trends in Ecology & Evolution. 27(8):452–461. doi:10.1016/j.tree.2012.05.001.

Worthington RD, Johnson JD, Lieb CS, Anderson W. 2022. Biotic Resources of Indio Mountains Research Station (IMRS) Southeastern Hudspeth County, Texas: A Handbook for Students and Researchers. https://www.utep.edu/science/indio/_Files/docs/Natural-Resources-New-2_uploaded-on-the-IMRS-website.pdf.

Worthington-Hill JO, Gill JA. 2019. Effects of large-scale heathland management on thermal regimes and predation on adders Vipera berus. Animal Conservation. 22(5):481–492. doi:10.1111/acv.12489.

Yeager CP, Burghardt GM. 1991. Effect of food competition on aggregation: Evidence for social recognition in the plains garter snake (Thamnophis radix). J Comp Psychol. 105:380–386. doi:10.1037/0735-7036.105.4.380.

Zar JH. 2010. Biostatistical analysis. 5th edition. Hoboken, New Jersey: Pearson Education, Inc.

Zhu Y, Queenborough SA, Condit R, Hubbell SP, Ma KP, Comita LS. 2018. Density-dependent survival varies with species life-history strategy in a tropical forest. Ecology Letters. 21(4):506–515. doi:10.1111/ele.12915.

APPENDIX 1

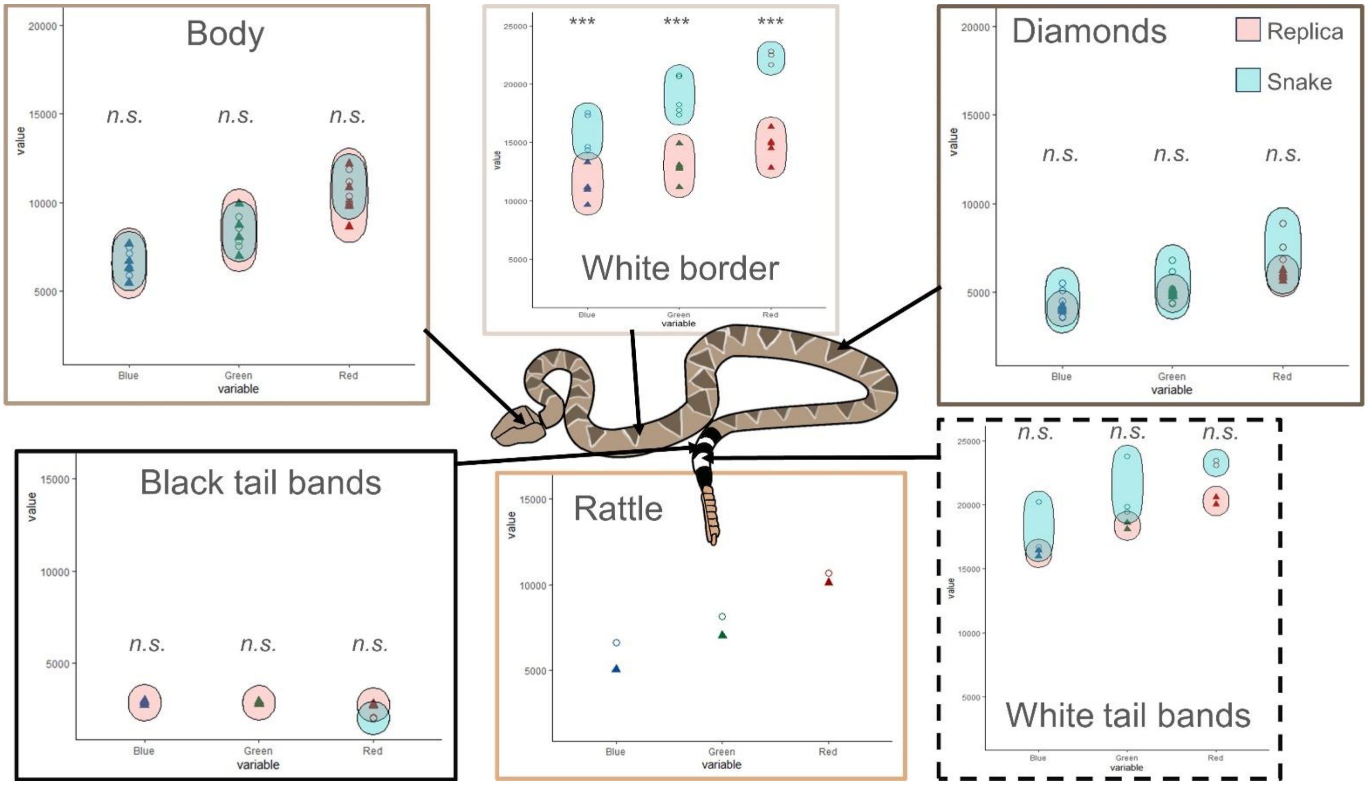

Figure S1: Coloration comparison between a *Crotalus atrox* live specimen and a replica. Significance was tested using Wilcoxon tests when possible. N.s. denotes no significant differences between the two groups, while *** denotes a significant difference between the two groups.

APPENDIX 2

Figure S1: Example of field setting when taking a picture of a rattlesnake and its background. The camera is on a tripod to limit movement between visible and UV pictures. The gray standard is positioned next to the snake with a telescopic rod.

Table SI: Cone ratio and their source used for this study.

Species	Cone ratio	Source of cone ratio
Canis familiaris	9 : 1	Stoddard et al. 2019
Homo sapiens	11.03 : 5.51 : 1	Hofer et al. 2005
Pavo cristatus	1 : 1.9 : 2.2 : 2.1	Hart 2002
Cyanistes caeruleus	1 : 1.92 : 2.68 : 2.7	Hart et al. 2000

Table SII: Volumes and volume overlap for rattlesnakes, their selected backgrounds, and random backgrounds calculated for each visual system. Percentage overlap was calculated as the quotient of the overlap volume divided by the smaller volume.

Visual model	*Volume C. atrox*	*Volume selected background*	*Volume random background*	*Overlap volume*	*% overlap*
Human	0.0008308973	0.001176634	-	0.0007055243	**84.91%**
Human	0.0008308973	-	0.0009448275	0.000471972	**56.80%**
Peafowl	6.696731e-05	5.27578e-05	-	4.295264e-05	**81.41%**
Peafowl	6.696731e-05	-	4.164338e-05	2.327596e-05	**55.89%**
Blue tit	0.0001991265	0.0001765359	-	0.0001380121	**78.17%**
Blue tit	0.0001991265	-	0.0001114216	6.497264e-05	**58.31%**

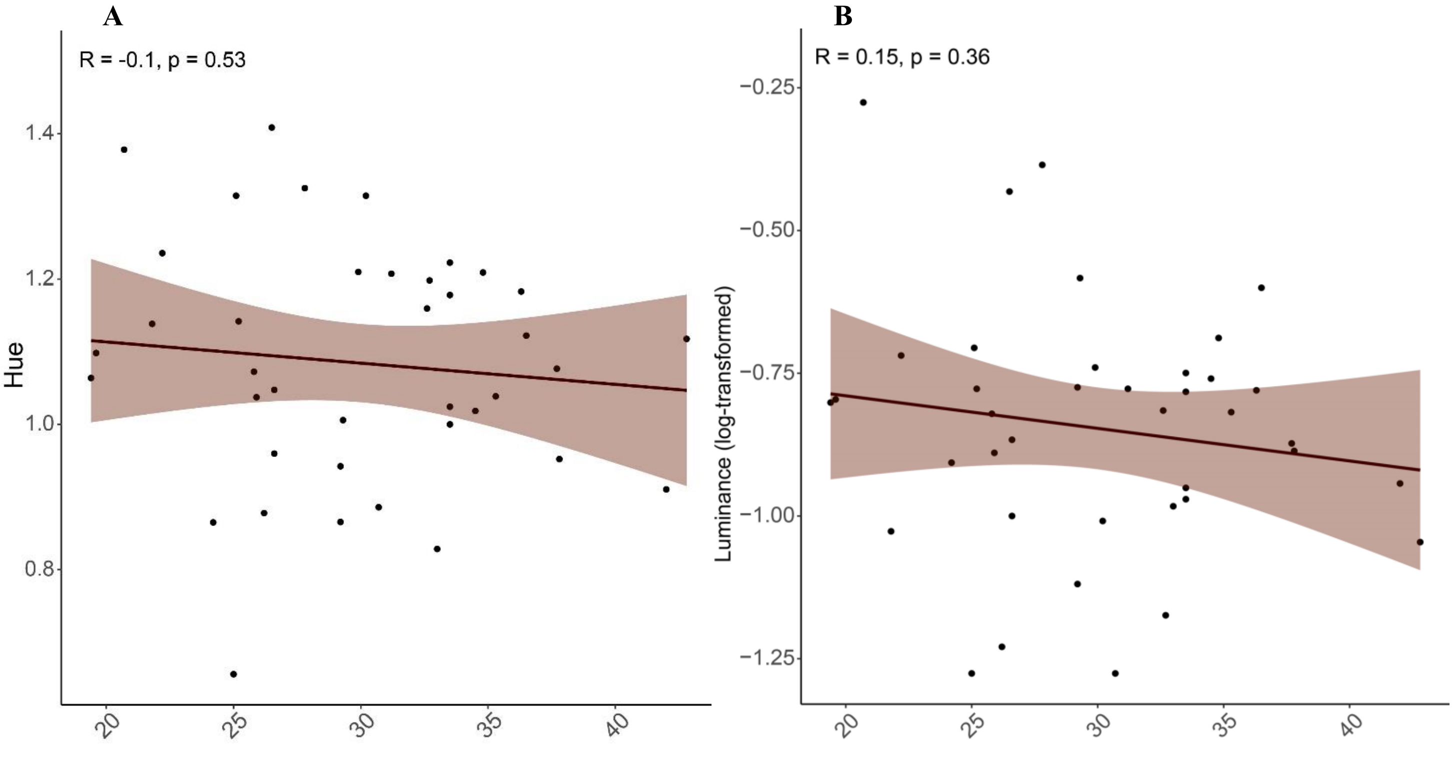

Figure S2: Linear regression between hue (A) or log-transformed luminance (B) and rattlesnake body temperatures. These relationships were not statistically significant.

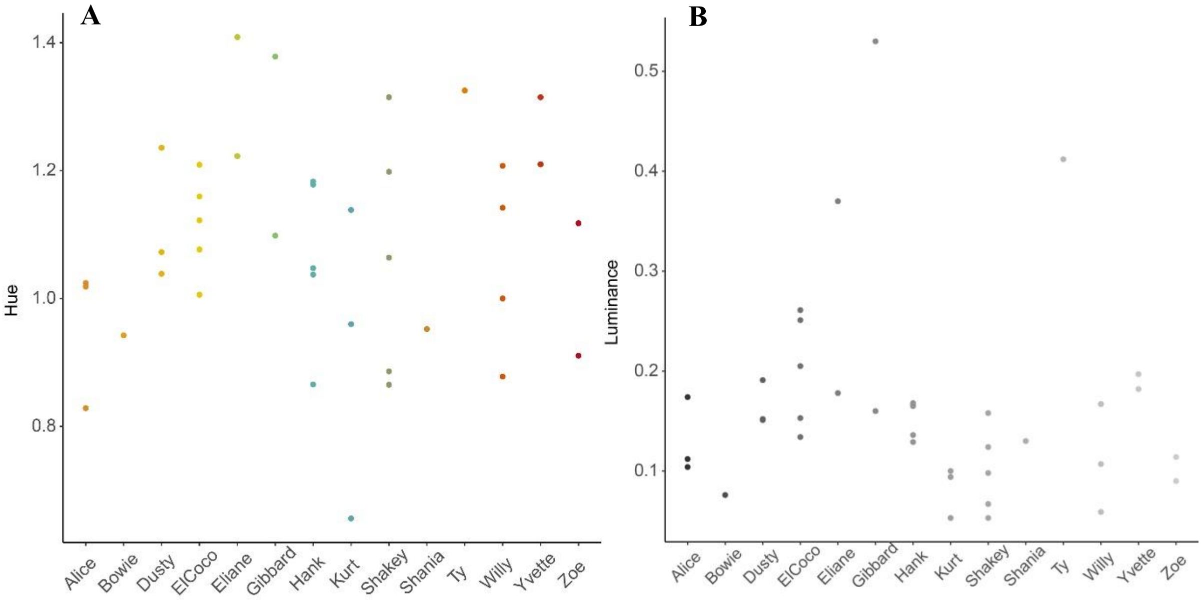

Figure S3: Dot plots showing the variation in hue (A) and luminance (B) observed for each snake during this study. Each dot represents one observation.

VITA

Océane Da Cunha graduated from the University of Lorraine with a bachelor in Biological Sciences in 2015. She then obtained a Master's degree in Ecophysiology and Ethology from the University of Strasbourg in 2017. Océane joined the UTEP Ecology and Evolutionary Biology PhD program in 2018.

During her Master's degree, Océane participated in the publication of a book chapter regarding animal ethics (see Chaussadas et al, 2017). Océane also conducted an internship during her Master's degree with Dr. Montgomery investigating the biology, movements, and habitat use of the Timber Rattlesnake (*Crotalus horridus*) using radiotelemetry in Missouri. Her collaboration with Dr. Montgomery led to several peer-reviewed journal articles, including a first-author publication (see Da Cunha et al., 2020). Océane's dissertation work investigating the behavioral ecology of the western diamond-backed rattlesnakes led to several first-author publications (see Da Cunha et al., 2023, 2024), conference presentations, and media coverages.

During her dissertation, Océane obtained fundings for her research from internal and external sources, including the Helen and Frederick Gaige Fund Award from the American Society for Ichthyology and Herpetology. Océane also was awarded the George Toland Award for Ecological Research on North American Herpetofauna for best student presentation at the Kansas Herpetological Society Meeting (2023). She was invited as a speaker for Truman State University Step Scholars seminars (2024) and for Biology of the Pitvipers 5 conference (2025).

Lastly, Océane was the teaching assistant for organismal biology, field biology, desert ecology, and vertebrate zoology and the course instructor for vertebrate zoology during her PhD. She also mentored nine undergraduate students and one graduate student from France during her dissertation. She also participated in numerous outreach activities in collaboration with the UTEP Biodiversity Collections, reaching approximately 8,000 people from the community.