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ORIGINAL ARTICLE

Investigating personality in vipers: individual rattlesnakes exhibit consistent behavioral responses in defensive and exploratory contexts

Ricardo G. Gibert[1] · Dylan W. Maag[1,2] · Lea N. Sanders[1] · Rulon W. Clark[1]

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Abstract

A burgeoning literature in animal behavior has demonstrated that most animals exhibit consistent individual variation in core behavioral traits or personality. However, the taxonomic spread of animal personality studies is uneven, with some ecologically important and diverse taxa still unstudied. Some of these understudied groups, such as venomous snakes, are also frequent targets of mitigation due to human–wildlife conflict, and conservation researchers have been increasingly focused on developing a general understanding of how individual personality, or temperament, mediates wildlife responses to management or mitigation actions. In this study, we used 20 captive Western Rattlesnakes (*Crotalus oreganus*) in standardized assays to test for repeatable behaviors (i.e., personalities) between individuals and examine possible relationships in personality traits across contexts (i.e., behavioral syndromes). Repeatability of behaviors was assessed over five repeated trials consisting of a handling assay, an open field test, and a threat assay. We found several behaviors related to exploration/avoidance, activity level, and boldness/shyness showed significant repeatability. However, we found no evidence for behavioral syndromes across contexts. Our analysis shows that, similar to many other species and taxonomic groups, viperid snakes also display individual personality traits when tested under standardized conditions, and we discuss the implications of this finding for mitigation, conservation, and comparative analyses across broadly similar species groups.

Significance Statement

It has now been well established that non-human animals exhibit individual behavioral traits similar to what humans term personality, and animal personality studies are becoming more important in the field of conservation and management. However, there are no previous personality/behavioral studies on venomous snakes, which are not only important predators in many ecosystems, but also a major source of human–wildlife conflict. We used a series of standardized behavioral tests to determine whether individual Western Rattlesnakes showed distinct personalities. We found that individual snakes did indeed exhibit repeatable behavioral traits consistent with personalities, but we did not find that these temperament traits were correlated across contexts. Our findings are important to developing a more nuanced view of the behaviors of venomous snakes and could aid in the development of more humane strategies to reduce human–wildlife conflict.

Keywords *Crotalus oreganus* · Western Rattlesnake · Aposematic display · Behavioral repeatability · Temperament · Behavioral syndrome

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✉ Ricardo G. Gibert
galaz.ricardog@gmail.com

✉ Rulon W. Clark
rclark@sdsu.edu

[1] Department of Biology, San Diego State University, San Diego, CA 92182, USA

[2] Department of Evolution, Ecology, and Organismal Biology, University of California, Riverside, 900 University Avenue, Riverside, CA 92521, USA

Introduction

In recent decades, behavioral ecologists have consistently found that many animal species, including various species of fish, birds, cephalopods, amphibians, and reptiles, exhibit individually repeatable suites of behavior, or personalities (e.g., Gosling 2001; Both et al. 2005; Wilson and Godin 2009; Harcourt et al. 2009). Animal personalities are typically defined as individual differences in suites of behaviors that remain consistent over time and context (e.g., Quinn and Cresswell 2005; Wilson and Godin 2009; Dingemanse et al. 2010). The term temperament is often used interchangeably with personality, but usually has a more restrictive definition focusing on differences in emotionality or traits that are shown very early on in life (Budaev 1997; Box 1999; Réale et al. 2007). Thus, both terms indicate individual differences in behaviors that are consistent over time and/or situations, but temperament typically indicates more core differences that are unlikely to change over an individual's lifetime (e.g., Budaev 1997; Box 1999; Lowe and Bradshaw 2001; Dall et al. 2004). Animal temperaments are frequently associated with five specific traits that are expressed along a continuum: shyness–boldness, exploration–avoidance, activity, aggressiveness, and sociability (e.g., Wilson et al. 1994; Reaney and Backwell 2007; Bell et al. 2009). Correlated suites of behaviors across these contexts are termed behavioral syndromes, which can be indicative of underlying constraints on behavioral expression within individuals related to plasticity and genetic linkages (Bell 2012; Réale et al. 2010; Sih et al. 2004).

While numerous studies have shown that individuals within species do indeed have consistent personalities, most species (and many larger taxonomic groups) have not yet been examined for these traits. Understanding the role of individual personality has an underappreciated, but expanding, role in conservation and management (Powell and Gartner 2011). This may be particularly true for species that are potentially dangerous to humans. Such species are often actively controlled or mitigated in areas where they are encountered by people, typically by translocation, harassment, euthanasia, or other direct interventions (Nyhus 2016). These management actions could be informed by a deeper understanding of individual personality and what role personality might play in mediating how individuals respond to mitigation or translocation (McDougall et al. 2006). However, taxon-specific research is necessary because the way in which personality influences behavioral responses varies widely across contexts and taxa. For example, individual tortoises with a stronger tendency to explore novel habitats were more likely to survive following translocation to a novel habitat (Germano et al. 2017), but captive-bred swift foxes (*Vupes velox)* that were less risk averse and more prone to exploration in personality tests were less likely to survive following release into the wild (Bremner-Harrison et al. 2006).

Venomous snakes are one of the most commonly encountered dangerous animals across the globe and can have a major impact on human health—especially in locations where humans do not have ready access to advanced medical services (Kasturiratne et al. 2008). As such, perhaps more so than any other vertebrate group, humans actively mitigate danger from snakes. If snakes encountered by humans are not immediately killed, they are typically translocated to an area away from human habitations (Malhotra et al 2021). Although more research is needed to understand the utility of this mitigation, translocated snakes often have low survival and frequently return to the site of capture, both of which are negative conservation outcomes (Cornelis et al. 2021). Understanding the nuances of behavior within and between species of venomous snakes mitigated in this fashion would be helpful in designing more effective management strategies. However, snakes are not often the subject of nuanced behavioral investigations. Relatively few species (primarily natricine colubrids) have been evaluated to determine whether they exhibit repeatable personality traits (Waters et al. 2017), and none that are venomous. Because venomous snakes frequently exhibit aposematic displays that humans perceive as dangerous, such as hooding by cobras or rattling by rattlesnakes, often entire species of snakes are qualitatively referred to as more or less "aggressive" (or similar terms) than other species. Although species differences in personality or temperament may exist it is also the case that the degree of intraspecific variation in such traits could be greater than interspecific variation between related species (Carter and Feeney 2012; White et al. 2020).

To understand how such traits might be expressed in a species dangerous to humans that exhibits specialized aposematic displays, we undertook the first such study on a venomous snake, the Western Rattlesnake (*Crotalus oreganus*). Our goal in the present study is to lay the groundwork for comparisons in temperament traits in rattlesnakes (*Crotalus* spp.), a clade of venomous snakes in North America that are often the focus of mitigation efforts. Rattlesnakes are widespread and abundant predators distributed throughout arid regions of North and Central America that are important for ecosystem functioning and also pose a medical hazard to humans (Beaupre and Duvall 1998; Nowak et al. 2008; Kasturiratne et al. 2021). These species readily exhibit defensive and exploratory behaviors that are easy to quantify and can be kept in captivity in large numbers, making them ideal candidates for studies of animal temperament. We used a handling test, an open field test, and a threat test to characterize the repeatability of behaviors in a captive sample of Western Rattlesnakes collected from local habitats (where they remain relatively abundant). We hypothesized that, similar to other animal species that have been assayed in temperament tests, individuals would display a set of repeatable behaviors in contexts relating to exploration/avoidance, activity, and boldness/shyness. Additionally, we hypothesized that a behavioral syndrome would exist between the behaviors associated with risk aversion (boldness/shyness) and exploration.

Methods

Study Animals/Animal Housing

Our test subjects consisted of 20 adult long-term captive *C. oreganus*. 17 males and three females. All individuals were caught as adults and had been in captivity for between two and nine years. Twelve individuals were “problem” snakes that were being translocated away from populated areas of Camp Pendleton Marine Corps Base in San Diego, CA, and 8 had been collected from other areas of San Diego County (California Fish and Wildlife Scientific Collecting Permit SC-9704). All snakes were kept and housed in individual containers in a secured room in a light (12:12 L:D)- and temperature (23–26 C)-controlled vivarium at San Diego State University. Housing containers were identical for each individual, consisting of paper substrate in a 50 × 30 × 20 cm plastic terraria, a hide box, and a water bowl that was regularly kept filled. Individuals were fed lab mice approximately once every month. After every behavioral assay, individual snakes were immediately placed back in its housing unit and not tested again for at least 14 days. This research was conducted under San Diego State University IACUC protocol 19–08-009C.

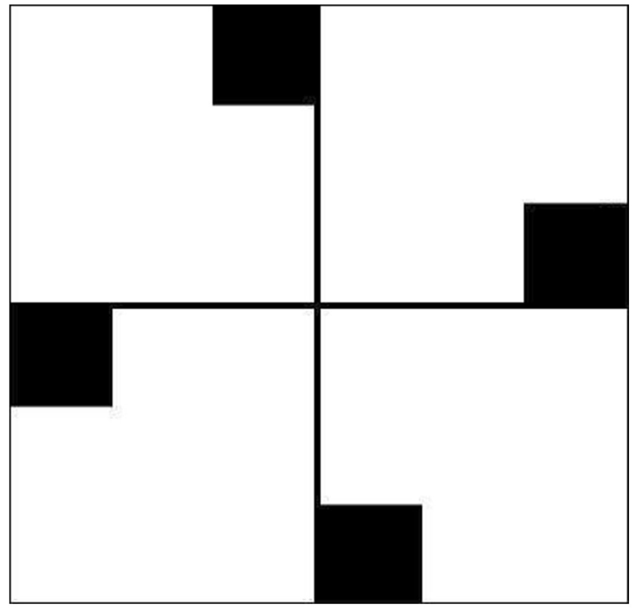

Fig. 1 Schematic showing top-down view of the arena (1.2 m×1.2 m×1.2 m) used for the open field test, illustrating the relative position of quadrants and hide boxes. The black squares represent hide boxes which were large enough to allow the snake to completely conceal itself. Thick lines represent the black tape on the floor of the arena splitting it into four equal quadrants

Experimental Design

In a separate isolated room from where the snakes were housed, a 1.2 × 1.2 × 1.2 m four-walled arena was constructed from polyvinyl sheeting. Black tape was used to create four quadrants on the floor of the arena, and a 10 × 5 × 3 cm black plastic hide box was placed in each quadrant (Fig. 1). The room was lit with the same lighting as the housing room and kept at a temperature of 23–24 C. Prior to any individual being tested, the arena was cleaned with commercial cleaner (Lysol®), and hide boxes were washed with soap and water and dried before being placed back in the arena. A video camera (PatrolMaster model PMD5) was mounted above the arena to record trials. Each trial was conducted by two people and consisted of three behavioral assays: handling, exploratory, and threat. Every individual snake received a total of five trials, with each behavioral assay conducted on each snake during each of the five trials.

Handling Assay

For the handling assay, snakes were taken from their housing unit and into the adjacent procedure room housing the arena. Snakes were handled using metal snake tongs and held at midbody for a total of 30 s over the center of the arena about 1 m from the floor, directly under the camera lens. After the initial 15 s, snakes were gently shaken back and forth twice. After the assay was complete, the snake was then lowered to the center of the arena floor with the tongs and released. During this assay, we recorded the latency to rattle, the total time spent rattling, the number of defensive strikes, and the latency to strike (if any occurred).

Exploratory Assay

After releasing the snake into the center of the arena, the two observers left the testing room and allowed the overhead video camera to record the exploratory behavior of the snake while it remained undisturbed for the next 60 min. These recordings were then reviewed to quantify the latency for the snake to move after release, total time spent moving during the 60 min period, total number of times crossing into a new quadrant, total number of times entering a hide box, total time spent in a hide box, and total time spent exposed (not in hide box) but not moving (time spent frozen). Latency to move and the onset of a bout of moving were only measured when the center of the snake’s body could be seen moving from its original spot in the arena. Entering a hide box and crossing a plane were counted when the front half of the snake entered a hide box and could no longer be seen by the camera, or when the front half of the snake broke the plane of a quadrant created by the black tape. Time frozen was counted when a snake was completely still (no detectable movement of head, body, or tail). When snakes were in motion, we categorized their movement as either lateral undulation (snake moving forward by propagating wave down body) or rectilinear (straight-line movement achieved by lifting of ventral scutes).

Threat Assay

The threat assay was used to quantify the tendency of snakes to strike defensively when confronted with a threatening stimulus. To elicit defensive strikes, following the 60 min exploratory assay, researchers reentered the room and used snake tongs to first remove all the hide boxes from the arena (including any that snakes were in) and then to maneuver the snake into one corner of the testing arena. The researchers then "threatened" the snake with an inflated balloon (to create a large visual looming stimulus) on the end of a wooden stick. Initially, the balloon stick was tapped in the center of the arena five times, approximately 80 cm from the cornered snake. It was then moved approximately 40 cm closer and tapped five times again. The balloon was then moved directly toward the snake and was used to tap the snake on the head five times. Head-hiding incidents were counted if the snake was seen hiding its head under any part of its body at any point during the assay. Time spent exhibiting escape behavior was counted as the time snakes spent moving rapidly away from the balloon. Time spent frozen in this assay was only counted while the snake stopped all movement (including rattling and head movements) and remained completely still. Individual defensive strikes were also counted, if exhibited, and the latency to strike was quantified. The threat assay was ended either as soon as the snake struck defensively at the balloon or after the last set of taps on the head with the balloon during the threatening approach.

Statistical Analyses

We recorded 5 separate trials for all 20 individuals for a total of 100 trials. Sex of the test subjects was not considered due to the sample size and inconsistencies which would arise from the insufficient sample. There were not an equal amount of males vs females and not enough overall to warrant a focus on sex.

All behaviors were scored by reviewing video recordings after trials. Reviewers were blind to the identity of the snake and trial number. All behavior scoring was done using the event-recording program BORIS v.7.10.2 (Friard and Gamba 2016). Two individuals scored all behavioral trials independently in order to correct for data recording mistakes and reduce observer bias. If the two observers noted very different behaviors (> 10% difference), the video was rescored a third time and the outlying score was eliminated. The mean of the two measures (rounded to whole numbers to retain integer values) was taken for statistical analysis.

All statistical analyses were done in R using R Studio (Version 1.4.1103). To reduce collinearity, we generated a correlation matrix for the responses within each behavior assay to identify highly correlated variables, and then chose only one of any highly correlated set to retain for analysis. In order to test for repeatability of behaviors, we used the rptR package (Stoffel et al. 2017), which provided repeatability (R value) and its 95% confidence interval (if repeatable and not binary) and statistical significance (p value) for each behavior. After examining data distributions, we chose to collapse the following variables into binary scores: rattle duration and latency to strike during the handling assay, and escape behavior, head-hiding, and latency to strike during the threat assay. In most trials snakes either exhibited these behaviors or did not. We used Poisson models for behaviors scored during the exploratory assay and binary models for yes/no variables (rattled or not, struck or not, escape behavior, and head hiding). Finally, in order to identify potential behavioral syndromes, we used GLMMs to analyze the dependence of repeatable defensive behaviors (propensity to rattle in handling assay, propensity to strike in threat assay) on repeatable exploration/activity behaviors (time spent frozen, time in hide box, quadrants crossed). We used this logistic regression approach rather than correlation because defensive behaviors were binary, whereas the exploratory behaviors were continuous (e.g., Johnson et al. 2015). We used GLMMs with scaled repeatable exploratory behaviors as predictor variables, and the binary defensive behavior as the response variable, with separate models for propensity to strike and propensity to rattle. These models included data from all trials, with individual identity of snakes included as a random factor.

Results

In examining for collinearity among variables, we found that lateral undulation was highly correlated with quadrant crossing ($r = 0.87$, $p < 0.001$) and moderately correlated with total time spent in a hide box ($r = -0.63$, $p < 0.001$), so we removed lateral undulation from analysis. Our repeatability analysis of other response variables indicated that some behaviors in each context were repeatable within individuals. Rattling, total time in hide box, time spent frozen, quadrants crossed, and defensive striking in the threat assay were all significantly repeatable (Table 1).

Additionally, we plotted key repeatable behaviors across all 20 individuals to elucidate typical values for personality traits. The majority of snakes exhibited limited exploration behaviors (quadrant crossing), but 6 of the 20 individuals exhibited relatively high (and variable) rates of quadrant

Table 1 Results of repeatability analysis of behaviors that individual *Crotalus oreganus* expressed in defensive and exploratory contexts. Behaviors that showed significant repeatability within individuals are shown in bold. See text for details of models implemented in *rptR* package

	Repeatability (R)	Confidence Interval (95%)	Significance (*p*)
Handling assay			
Rattled	**0.61**	**NA**	**< 0.0001**
Struck	0.08	NA	0.18
Open field test			
Latency to move	0.06	NA	0.23
Time spent frozen	**0.55**	**[0.29,0.68]**	**< 0.0001**
Time in hide box	**0.60**	**[0.36,0.74]**	**< 0.0001**
Quadrants crossed	**0.46**	**[0.19,0.67]**	**< 0.0001**
Rectilinear motion	0.13	NA	0.08
Threat assay			
Escape behavior	0.28	NA	0.08
Head hiding	0.13	NA	0.06
Defensive strike	**0.50**	**NA**	**< 0.0001**

crossing (Fig. 2). Half of the snakes rattled throughout the handling assay for all trials, but 6 of 20 individuals did not rattle at all during the majority of their handling trials with one individual never rattling during any of the trials (Fig. 3). Only four of the 20 snakes struck defensively during a majority of their threat trials, and 11 individuals never struck defensively (Fig. 4).

We did not find statistically significant relationships between behaviors in different contexts (Table 2), indicating that there was not a strong relationship between traits expressed in defensive contexts with those indicative of increased exploration/activity.

Discussion

Our analysis of temperament in rattlesnakes indicated that, similar to many other species, individual Western Rattlesnakes exhibit consistent individual differences in behavior when tested under standardized conditions. Thus, these individuals can be characterized as having distinct personalities. The response variables in our study showed significant repeatability related to the general temperament traits of exploration/avoidance, activity, and risk aversion (boldness/shyness) in different ways. Because of the direct restraint or

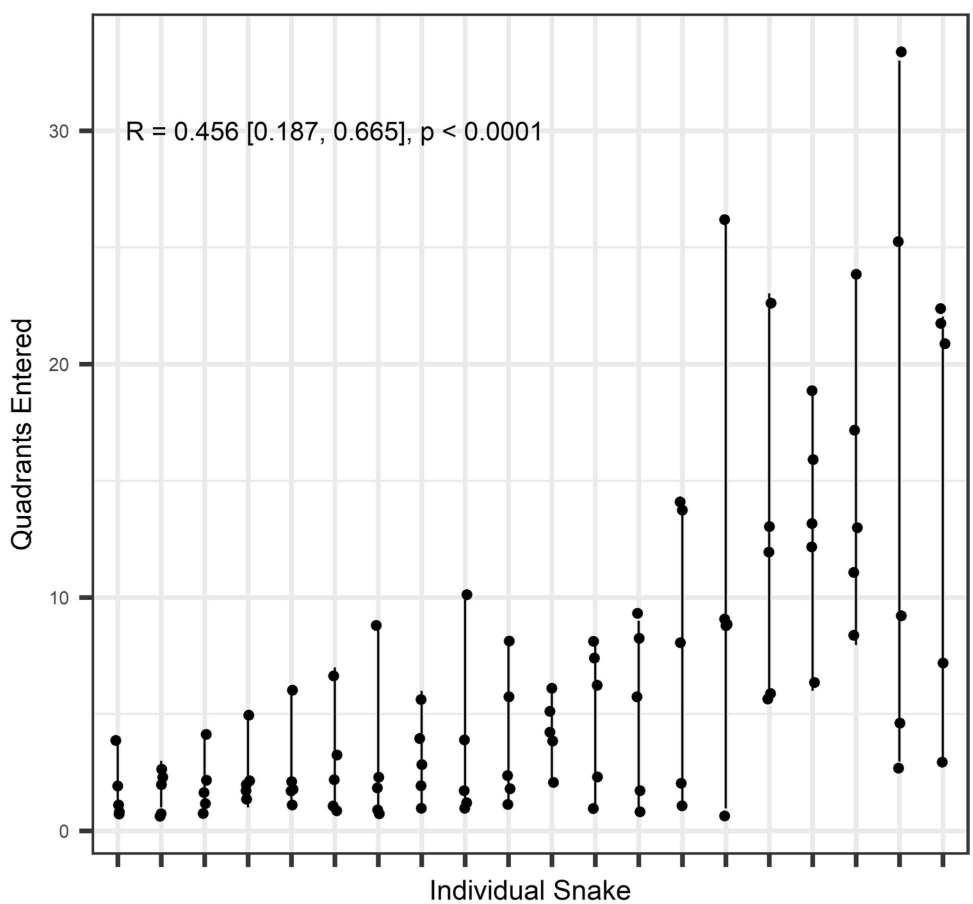

Fig. 2 Plot of individually repeatable exploration/activity (quadrants crossed during the open field test) values. Individual snakes are ordered from least to most active. Plot points indicate values of quadrants crossed during each of the 5 trials, with each individual plotted separately. Lines between points show the range of quadrant crossing across the five trials exhibited by each individual. R value refers to repeatability of quadrant crossing, with confidence interval and statistical significance

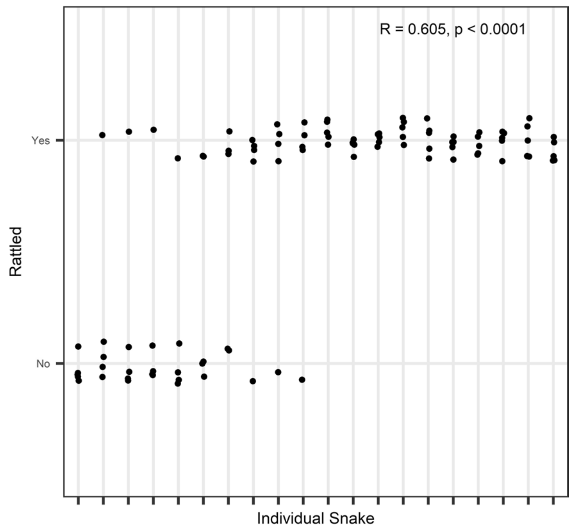

Fig. 3 Plot of individually repeatable defensive rattling (whether snakes rattled during the handling assay or not). Values are ordered from least to most defensive individuals. Jittered plot points indicate whether the snake rattled or not during each of five trials. R value refers to repeatability of rattling, with a 95% confidence interval and statistical significance

threatening approach of a looming stimulus, rattling during the handling assay and the tendency to strike defensively are likely both indicative of boldness. More risk averse individuals would likely be less willing to draw attention to themselves and engage potential predators by rattling continuously and striking defensively (and thus exposing themselves to counterattack and making themselves vulnerable to attacks to the back of the head and/or neck). In our open field test, the number of quadrants crossed is indicative of high levels of exploration and/or activity, whereas the time spent hiding in the hide box or immobile while out of the hide box would both be indicative of a reduced tendency to explore novel environments.

Temperament traits can mediate important ecological and evolutionary processes like reproductive success, population dynamics, colonization of new habitats, and speciation (Réale et al. 2007). Similar to other species, it is likely that different temperaments in rattlesnakes would be favored under different contexts. For example, more risk averse individuals may be more likely to survive and reproduce under high predation pressure, but also less likely to obtain food or find mates when predation pressure was low (Smith and Blumstein 2008). Because we tested wild-caught adult individuals, we do not know how the expression of temperament might change over time or maturation. Studies in other species, however, have indicated that core temperament traits tend to be consistent within a life stage (such as sexually mature adults) (Šimková et al. 2017; Cabrera et al. 2021).

Although a very robust literature on temperament and animal personality has developed in recent decades, there is still only a limited number of studies on species that are frequent subjects of human–wildlife conflict mitigation, such as large carnivores and crop-damaging animals. This may be due to the fact that most such species (unlike viperids), are not tractable study subjects in behavioral trials requiring repeated testing of a fairly large sample of individuals. Blackwell et al. (2016) reviewed the use of behavioral principles in the literature on human–wildlife conflict and highlighted the importance of continued focus on individual variation in temperament traits for understanding responses to mitigation. Our results suggest that a comparative analysis across venomous snake species could similarly help understand the sources of variability in how these taxa are impacted by mitigation measures. For example, similar to the approach taken by Germano et al. (2017), assaying snakes for personality traits prior to translocation could help identify what traits (if any) are predictive of survival, and individuals could be treated accordingly. Current research indicates translocations do not work particularly well as a mitigation strategy for most snake species (Cornelis et al. 2021), so any changes that could improve outcomes should be explored. Additionally, our results could play a role in conservation messaging, as a recent study found that messaging focused on complex social behaviors that make rattlesnakes more empathetic to humans improved public perception of snakes (Allison et al. 2022).

Although data on these behaviors in free-ranging snakes are limited, a recent study on the propensity of *C. oreganus* to rattle after being disturbed by human handlers provides an intriguing example of how these temperament traits might be shaped by either individual experience or natural selection. Atkins et al. (2022) found that rattlesnakes inhabiting recreation areas with high levels of human activity were much less likely to rattle in response to human handling and disturbance than snakes occupying landscapes with restricted human presence. Their study indicated that defensive rattling, which we found to be a repeatable temperament trait indicative of increased boldness, may have been shaped by the relatively recent invasion of their habitat by large numbers of human "predators." Although Atkins et al. (2022) did not repeatedly test the same individuals, our results indicate that Western Rattlesnakes may develop fundamentally different temperaments in regions with high human disturbance. Thus, this may represent an example of how variation in temperament traits related to boldness could lead to a rapid population-level adaptation to a new ecological situation.

Our study examining the repeatability of behaviors in *C. oreganus* is the first quantitative analysis of personality traits in any viperid or elapid species, the two most diverse and medically significant families of highly venomous snakes. In general, our study design and findings are similar to those

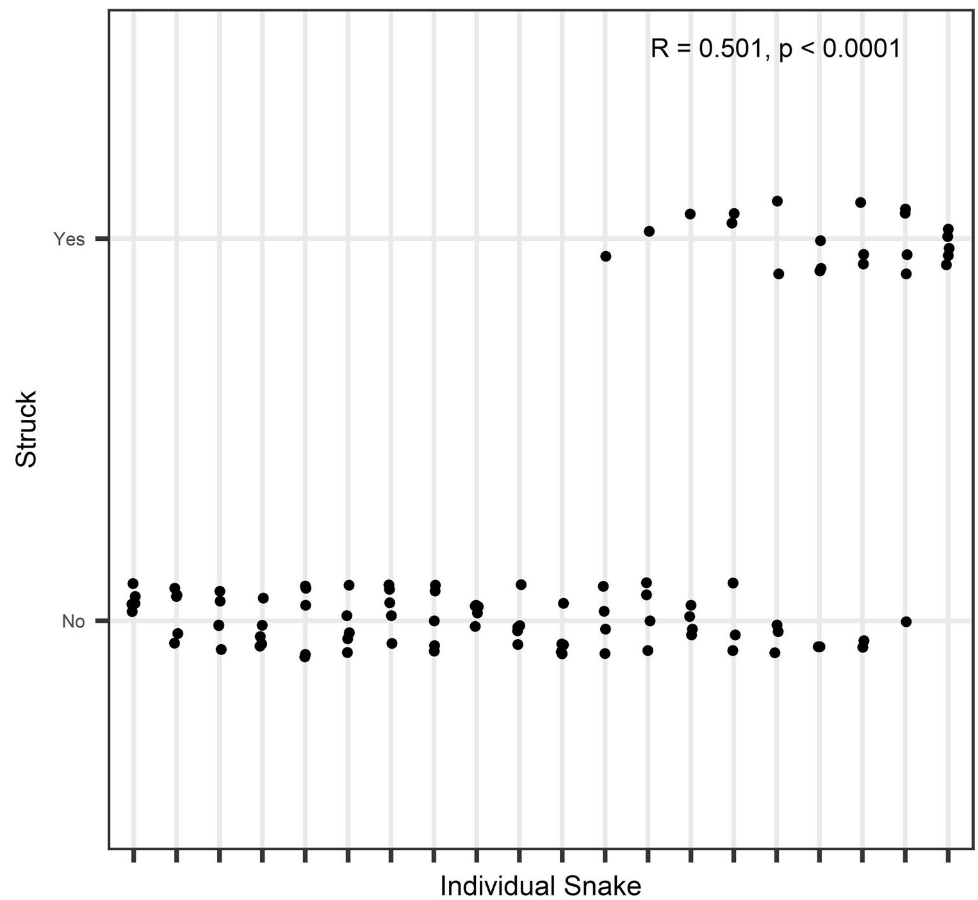

Fig. 4 Plot of individually repeatable defensive striking (whether snakes struck during the threat assay or not). Values are ordered from least to most defensive individuals. Jittered plot points indicate whether the snake struck or not during each of five threat trials. R value refers to repeatability of rattling, with a 95% confidence interval and statistical significance

Table 2 Results from GLMMs of relationship between repeatable behaviors that individual *Crotalus oreganus* expressed in the threat and handling assays (struck during threat assay, rattled during handling assay) with those expressed in the open field assay (time spent frozen, time in hide box, quadrants crossed). No statistically significant relationships across contexts were identified. All models included a random intercept for snake identity

	Estimate	SE	z	*p*
Struck during threat assay				
Intercept	-1.69	2.71	-0.62	0.53
Time spent frozen	-0.79	1.39	-0.57	0.57
Time in hide box	-0.99	0.67	-0.59	0.59
Quadrants crossed	0.33	0.98	0.34	0.74
Rattled during handling assay				
Intercept	-1.88	2.62	-0.72	0.47
Time spent frozen	1.81	1.36	1.33	0.18
Time in hide box	2.48	1.60	1.55	0.12
Quadrants crossed	1.24	0.96	1.29	0.20

conducted in other vertebrates, including other reptiles (reviewed in Waters et al. 2017). Previous studies of colubrid and boid snake species also consistently found that snakes exhibit repeatable traits indicative of boldness, exploration, and defensiveness (Maillet et al. 2015; Mayer et al. 2016; Šimková et al. 2017; Skinner and Miller 2020). Temperament traits have also been found in various other reptile taxa, including species of skinks, agamas, common lizards, and turtles (Carter et al. 2012; Le Galliard et al. 2013; Michelangeli et al. 2019; Pich et al. 2019; Roth et al. 2020). Overall, risk aversion (boldness) is among the most frequently supported temperament traits, but most studies also found support for repeatable levels of exploratory behavior in novel environments. These trends are mirrored in the personality literature focusing on birds (e.g., Dingemanse et al. 2002; Both et al. 2005), mammals (e.g., Réale et al. 2000; Myers and Young 2018), and arthropods (Mather and Logue 2013), and it is may be that canalization within individuals is an unavoidable byproduct of complex behavioral phenotypes that develop as iterative feedbacks between gene expression and environmental variability (Lewejohann et al. 2011; Trillmich and Hudson 2011).

Even though the processes leading to its development may still be unclear, individual variation in core temperament traits is widespread in animals, and we believe that this variation can result in humans ascribing specific behavioral characteristics to dangerous species that have robust or conspicuous defensive displays. This is evident in how people normally view rattlesnakes and other venomous species with aposematic displays. Humans often misunderstand defensive rattling and rearing displays as attacks or interpret them as displays of aggression (Werler and Dixon 2000; Campbell 2011), and so will characterize species as "aggressive" or "likely to attack" following encounters. Because our results indicate that individual rattlesnakes within a species or population can vary widely in the degree of defensiveness or boldness, anecdotal encounters with a few individuals would not be sufficient to characterize species-typical values. Moreover, our results actually highlight the reluctance (rather than the propensity) of most individual snakes to strike defensively, even while being handled or threatened. More than half of the individuals in our study (11 out of 20) never struck defensively in either context across all trials.

To date, among venomous snakes, this type of individual variation in distinct temperaments and behaviors has only been quantified in *C. oreganus* however. Although we believe it is likely that other viperids are similarly variable in personality types, more species need to be studied to verify this assumption. Even though other studies of viperid behavior have not explicitly assessed personality traits, there are several studies that have reported substantial intraspecific variability in similar traits (Gibbons and Dorcas 2002; Shine et al. 2002; Glaudas et al. 2005; Adams et al. 2020), and a study on defensive behaviors of Cottonmouth Snakes (*Agkistrodon piscivorous*) qualitatively reported high levels of individual variation in defensive displays and striking when threatened (Glaudas et al. 2006).

We did not find evidence for behavioral syndromes in *C. oreganus,* as there were no significant relationships between any of the repeatable temperament traits across contexts. This finding is similar to what has been reported in other snakes; Maillet et al. (2015) found no evidence of behavioral syndromes between boldness, exploration, and defensive behaviors in Eastern Garter Snakes. Results from studies of lizards are more mixed, with several studies finding no evidence for behavioral syndromes across these contexts, whereas others show significant correlations between some of the response variables (reviewed in Waters et al. 2017). Lizards are generally similar to other vertebrate groups that have been studied in detail, in that the majority of studies (but not all) find some evidence for correlated temperament traits across contexts (Sih and Bell 2008; Kelleher et al. 2018). It may be that temperament traits in snakes develop more independently than in other taxa, but additional comparative studies would be needed to evaluate this. However, it should be noted that our study and that of Maillet et al. (2015) were not optimally designed to characterize behavioral syndromes in that we could not control for carryover effects due to the order in which assays were conducted, as suggested by Dochtermann (2010). We conducted all three assays in the same order for each trial (handling, experimental, threat) because the snakes needed to be moved from their enclosures into the testing arena for the exploratory assay and doing so necessarily involved handling them with snake tongs. Thus, we incorporated the handling assay into this required transfer into the arena in order to minimize the overall impact of handling on study subjects. Additionally, the threat assay was potentially the most stressful, so we chose to always run this assay last to minimize the impact of stress on potential responses in other trials.

In conclusion, we found that *C. oreganus* individuals do in fact have distinguishable personalities as seen through their consistent behaviors over time and in context of boldness/shyness, exploration/avoidance, and activity. We believe *Crotalus* species are ideal for comparative analyses of the development and expression of temperament traits, as this diverse genus is abundant and widespread in North America, and yet exhibits conserved defensive and exploratory behaviors that are readily quantifiable. Additional studies could focus upon variables not considered here, such as sex, age, and body size, which could all play very important roles in what behaviors and temperaments are consistent in individuals (Kissner et al. 1997; Maillet et al 2015). Additionally, while using a captive population of snakes allowed for us to efficiently and repeatedly test for personalities, length of time in captivity (or other developmental differences) could affect the measurement of these traits (Glaudas et al. 2006). Thus, our study should be considered a starting point for evaluating temperament in viperid snakes, and we encourage further studies building on these findings.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-022-03239-w.

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Data availability The datasets analyzed during the current study are available as electronic supplementary material.

Declarations

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of San Diego State University, and methods were approved by the Institutional Animal Care and Use Committee (APF 09–08-009C) prior to data collection.

Conflict of interest The authors declare that they have no conflict of interest.

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