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Hunger-induced convergence of personality traits towards ambush-predatory behavior in ball pythons (*Python regius*, Shaw 1802)

Octavian Craioveanu[1], Elisabeth Spataro[2], and Cristina Craioveanu[2,3]✉

[1]Academic Cultural Heritage Department – Vivarium, Babeş-Bolyai University, Clinicilor 5-7, Cluj-Napoca, Romania; [2]Department of Taxonomy and Ecology, Faculty for Biology and Geology, Babeş-Bolyai University, Clinicilor 5-7, Cluj-Napoca, Romania; [3]Babeş-Bolyai University, Centre 3B, Sociobiology and Insect Ecology Lab, Clinicilor 5-7, Cluj-Napoca, Romania
✉***Corresponding author, E-mail: cristina.craioveanu@ubbcluj.ro***

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Abstract. Personality traits have been shown to be influenced by environmental and internal factors, hunger being one of the most important. The resulting behavior fluctuates greatly depending on the feeding ecology of the different species and intraspecific individual variation.

In this study, we used eight captive-born juvenile ball pythons to examine the relationship between personality traits, namely shyness and exploratory tendencies, and the chronological postprandial-induced psychobiological effects on a seven-day interval that concluded with the installation of hunger.

We found a strong correlation between shyness and hunger. Regarding exploratory predispositions, we found high individual variation at the beginning and middle of the postprandial cycle that evened out as hunger's influence started to be perceived.

Notably, this study's outcomes have the potential to enhance our understanding of captive animal management techniques and contribute to improving zoo animal welfare.

Keywords: juvenile ball pythons, behavior experiment, reptile welfare, feeding strategy

Introduction

Although concepts like animal personality and animal personality traits are nowadays widely accepted as cutting-edge topics of the behavioral sciences (Gosling, 2001; Thaler *et al.*, 2022; Knight *et al.*, 2013; Wilson *et al.*, 2019; Stamps and Groothuis, 2010), reptiles and particularly snakes have seldom received the attention of the scientific community. This gap in the literature contains only a few existing studies (Thaler *et al.*, 2022; Skinner *et al.*, 2022; Waters *et al.*, 2017; Šimková *et al.*, 2017), all of which suggest that snakes display consistent personality differences that profoundly affect their behavior. However, empirical documentation about the personality trait-behavior relation is extremely sparse. Beyond its fundamental approach, the potential application of this research topic in conservation management and captive animal welfare (Nagabaskaran *et al.*, 2022; MacKinlay and Shaw, 2022) makes it even more relevant in the future.

Due to its high adaptability, relaxed temper, and low aggressiveness, *Python regius*, Shaw 1802, is one of the most popular snakes in the pet trade and has long been kept and bred in captivity (Toudonou *et al.*, 2022). In addition, the ball python is an important species for teaching, education, and raising awareness about herpetofauna conservation.

A personality trait can be considered a relatively consistent bias, habit, or disposition that, when combined with various environmental factors, causes individuals to behave in a certain way (Skinner *et al.*, 2022). However, these traits can sometimes be challenging to comprehend in terms of variation and evolution, as they may consistently differ on individual and group levels. Stamps and Groothuis suggest (2007) that a better way to understand these variations is to consider the functional connections between those traits and physiological processes.

The foraging behavior of snakes is typically predatory, and their individual and species-specific personality is highly affected by intrinsic physiological factors. Of these physiological factors, hunger is one of the more important (Perry and Pianka, 1997; Vitt and Pianka, 2007).

Studies on the postprandial behavior of snakes are rare and are mostly field experiments (*Crotalus spp* - Beck, 1996; *Elaphe obsoleta* - Blouin-Demers and Weatherhead, 2001; *Boiga irregularis* - Seirs *et al.*, 2018). In addition, we are unaware of any study that has formally examined post-prandial personality trait variation and its expression in behavior. Given the strong psychobiological effect of hunger (Beaulieu and Blundell, 2020; Ramond, 1954; Cooper, 2000), we expect to see a consistent correlation between hunger and behavior, especially in the risk aversion/risk tolerance region.

Indirect evidence and anecdotal observations suggest that Boidae and Pythonidae are ambush-hunting predators. However, using a direct technique (radiotelemetry, videography) to prove that ambush hunting is their primary feeding strategy is a complicated process covered by only a few studies (*Morelia spilota* - Slip and Shine, 1988; *Corallus hortulanus* - Esberad and Vrcibradic, 2007; *Morelia viridis* - Wilson *et al.*, 2007). There is no extensive documentation to prove that the ball python is an exclusive ambush predator (Hanscom *et al.*, 2023), but according to Waas *et al.* (2010), the species is more on the sit-and-wait side of the specter. Therefore, a drop in activity levels with increasing hunger is expected as a sign of foraging activity initiation. However, ambush/active hunter is a broad behavioral classification; therefore, we would like to see if the ambush predation strategy is a strong, preprogrammed, instinctual behavioral pattern and it overwrites the individual personality trait variation or is more a personality-driven activity, with different personality individuals reacting in a slightly different manner to hunger (i.e., the reaction to hunger differs across individuals in the expression of the studied personality traits and the corresponding behaviors).

Therefore, the present study investigates the post-feeding personality trait variation of *Phyton regius* in controlled laboratory conditions, with the experiment focusing on two hypothetical questions:

1. Where is the ball python located on the ambush-active hunting scale? More precisely, we wanted to find out if hungry snakes are more prone to risky behavior or if they will lower their activity levels and go into ambush mode.

2. How flexible is the ball python´s hunting strategy? Is there a group-consistent, preprogrammed, instinctual behavioral response to hunger? And if there is one, to what extent will it take over the individual personality trait variation?

We conclude by discussing the results of the study and its possible applications in captive reptile management and welfare.

Materials and methods

The study was conducted between July and August 2023 in the herpetology laboratory of the Babeș-Bolyai University`s Vivarium. The study was conducted in accord with the highest humane and ethical principles, according to the ARRIVE guidelines for In Vivo Experiments and WAZA (World Association of Zoos and Aquariums, 2023) code of ethics and animal welfare.

To test our hypotheses, we used eight juvenile (2 months old) ball pythons (*Python regius*, IUCN near threatened, numbered P1-P8), a constrictor species native to West and Central Africa (D'Cruze *et al.* 2020), obtained by captive breeding.

To create a more compact experimental group, we used only females with no significant variation in size and weight (mean length ± SD = 528.50 ± 12.78 mm and mean mass ± SD = 64.12 ± 1.96 g).

For a seven-day acclimation period and during the next seven-day experiment, the subjects were housed separately in opaque, Tupperware-type plastic containers (27 cm x 17 cm x 8 cm) provided with bark mulch substrate, a hiding place, and a water bowl, indirect ambient sunlight illumination, and night-time/day-time temperature variation of 20/27° C (Westhoff, 2005).

Before the experiment and during the acclimation period, the snakes were fed once a week (Martinez, 2020) and provided with water *ad libitum*.

During the seven-day experiment, we performed four tests (on days 1, 3, 5, and 7) for two personality trait values: shyness and exploratory tendencies. Although these parameters are considered personality traits, in our experiment, they are foremost the expression of the measurement of a specific behavior.

The shyness test measured the time (seconds) the animals took to emerge from the shelter in a novel arena. Each animal was placed in a roughly 200 ml half-sphere shelter with a 2 x 2 cm covered opening on the side. The shelter was then positioned in the center of a 55 cm L x 45 cm W x 40 cm H arena, high enough so the snakes could not escape during testing. After a 1-minute settling period, the opening was uncovered, and the timing began while the experimenter quietly withdrew his hand from the test area.

The tests were filmed with a GoPro 7 camera placed 40 cm above the arena. Playing back the videos (Windows Media Player), we measured the elapsed time between the beginning of the trial and the complete emergence of the head from the shelter ("complete head out") – an indication of how soon the animal starts to investigate the arena.

The exploratory tendencies test used the open field method (Bergeron *et al.*, 2013; Montiglio *et al.*, 2010; Gould *et al.*, 2009) and was a continuation of the shyness test in which we examined a 10 minutes time-frame with the ”complete head out" being the T0 moment. With an alcohol-based permanent marker, we drew three concentric rectangles: 1, 2, and 3, so that we delimited four areas (the limit for area no. 4 was the external wall of the arena) in increasing order, with one being the closest and four the furthest from the shelter. The rectangles had the following dimensions: 10 cm x 25 cm, 20 cm x 33 cm, 27 cm x 42 cm, and 55 cm x 45 cm, respectively. We considered that the snake entered one area when the total length of its head was located inside that area.

To record and measure the snake`s exploratory tendencies, we recorded the distance covered in terms of all areas visited and the number of transitions between areas. For both variables, we computed their median. We used the median of the area numbers instead of their mean, because it is a better indicator for overall movement and for the distance traveled from the center.

While designing the arena, we faced the problem of arena size. Theoretically, we should have used an arena as large as the distance a snake would cover in a straight line at maximum speed within 10 minutes (testing time). However, such an area is technically impossible to provide in laboratory conditions. To compensate for this shortcoming, we introduced a variable – total time spent in area 4 (TR4). We considered a high value of this variable to be a strong indicator that the test animal would have gone further than the limits of the arena and has a greater propensity for exploration. The arena was cleaned with water and soap to remove the scent and thoroughly rinsed after each trial.

Both personality trait value tests were repeated four times, at two-day intervals, to allow the changes in the animal`s motivational state to impact their reaction. Day one of the experiment was the first day after feeding, and the snakes were considered satiated. Seven days after their last meal (in test no. 4 – day seven of the experiment), the animals were considered hungry but not post-absorptive (McCue, 2007; Spencer *et al.*, 2020).

Data analyses

First, we tested the distribution of the four variables we recorded: shyness (s), distance covered – D (median of areas visited), number of transitions between areas, and time spent in area 4 – TR4 (s), with the help of the Shapiro-Wilk test. We subsequently used non-parametric comparison methods for variables that were not normally distributed. We log-transformed the values for shyness and obtained a normal distribution. For all normally distributed values, we subsequently used one-way ANOVA.

To check for the influence of hunger on shyness, we checked for the influence of trials (equivalent to time since the last feeding) with the help of a linear mixed effect model (lmer, RStudio 2023). We tested the effect of the trial (time since feeding, corresponding to day 1, 3, 5, or 7 after feeding) on shyness as a fixed effect and “individual” as a random effect.

To analyze the exploratory tendencies in terms of distance covered, the number of transitions between areas, and the time spent in the fourth area (TR4), we used the Kruskal-Wallis rank sum test (Kruskal.test, RStudio 2023), followed in case of significant differences by a Dunn-test (dunnTest, RStudio 2023) with P-values adjusted with the Benjamini-Hochberg method to compare trials and individuals separately. All analyses and plots were performed in RStudio (RStudio, 2023).

Results

Shyness significantly increased with time in each of the four trials. The mixed effect model indicated that the fixed effect trial (time) had a strong influence on the shyness parameter ($Estimate_{23}$ = 0.17, SE = 0.07, t = 2.64, P = 0.015, Fig. 1), and the random effect explained only 5.49% of the total variation in the shyness-value (Variance Random Effect „Individual" (intercept) = 0.04, SD = 0.21; Variance Random Effect of residuals = 0.79, SD = 0.83).

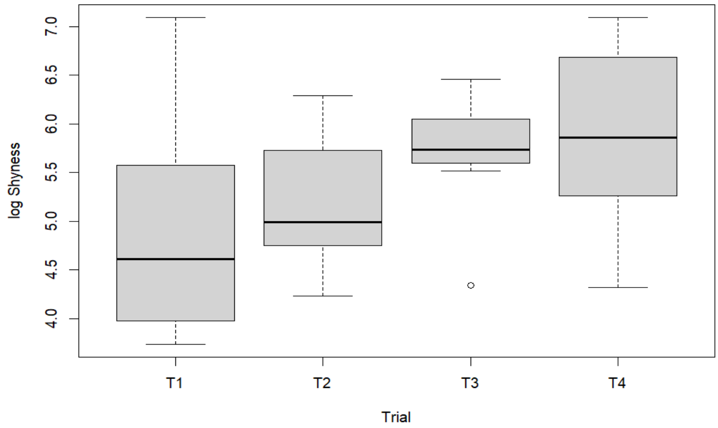

Figure 1. Log-transformed values of the Shyness parameter (time the animals took to emerge from the shelter) in each experimental trial (T1-T4). Boxplots represent median values (thick line inside the box), interquartile range (the box), maximum and minimum values (whiskers), and outliers (empty circles).

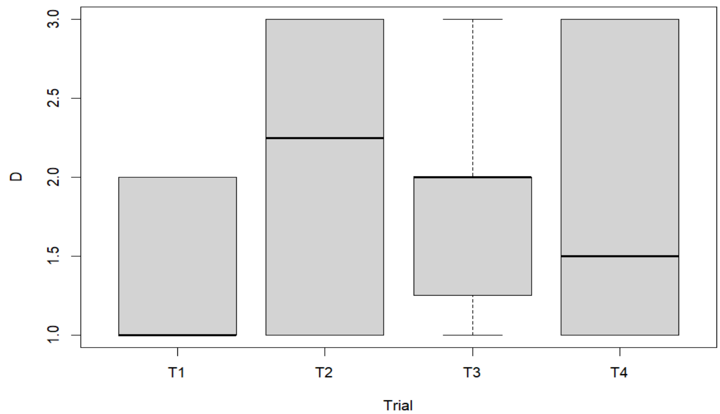

Figure 2. Median distance covered by individuals in different areas of the arena during the four Trials. Boxplots represent median values (thick line inside the box), interquartile range (the box), maximum and minimum values (whiskers), and outliers (empty circles).

We found no significant differences between the distances covered by the individuals in the four trials (Kruskal-Wallis test: χ^2_3= 1.85, P = 0.603). However, the median distance covered in the first trial by all individuals was shorter than the distance covered in the following two trials. In trial T4, the distance was slightly longer than in T1 but shorter than in T2 and T3, indicating a tendency to decrease from T2 towards T4 (Fig. 2).

We found significant differences between distances covered by individuals in the first three trials but not in the fourth (Table 1). However, when Benjamini-Hochberg-adjusted P-values were consulted, only the second trial showed a truly high variation of distances covered by each individual (Fig.3.). Some individuals tended to explore only the first area of the arena most of the trials, whereas others were more explorative. Individuals P6, P7, and P8 did not leave the shelter for the whole length of two trials (P8 in T1 and P6 and P7 in T4).

Table 1. Results of the comparisons between median distances (D) covered by individuals in each trial (individual Pythons are numbered P1-P8).

Trial	Kruskal-Wallis test result	Significant differences in D found between individuals Benjamini-Hochberg-adjusted *P*-values of the Dunn posthoc test
T1	χ^2_7 = 22.02 *P* = 0.003	-
T2	χ^2_7= 31.37 *P* < 0.001	P1-P2: *P* = 0.012 P1-P5: *P* = 0.010 P1-P7: *P* = 0.011 P1-P8: *P* = 0.010 P2-P4: *P* = 0.009 P3-P5: *P* = 0.009 P3-P7: *P* = 0.018 P3-P8: *P* = 0.011 P4-P7: *P* = 0.011 P4-P8: *P* = 0.014
T3	χ^2_7 = 19.09 *P* = 0.008	P2-P4: *P* = 0.016
T4	χ^2_7 = 13.57 *P* = 0.059	-

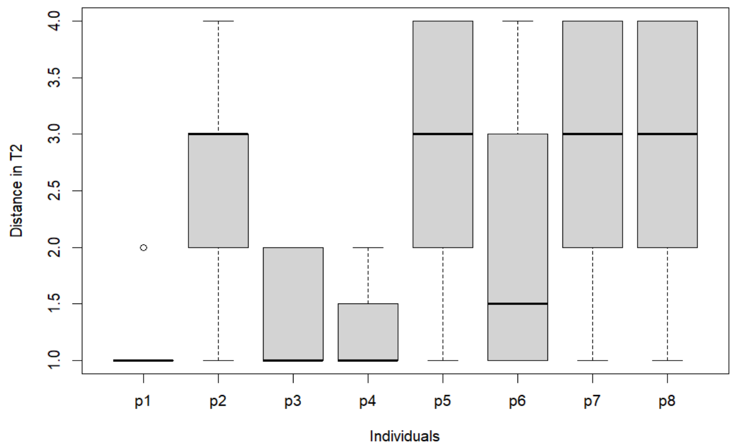

Figure 3. Distances covered by individual pythons in the second trial (T2). Boxplots represent median values (thick line inside the box), interquartile range (the box), maximum and minimum values (whiskers), and outliers (empty circles).

The number of transitions between areas of the arena did not differ significantly between trials (one-way ANOVA: $F_3 = 2.22$, $P = 0.108$) and between individuals (one-way ANOVA: $F_7 = 0.47$, $P = 0.844$). However, in the fourth trial, the individuals tended to make fewer transitions between areas (Fig. 4).

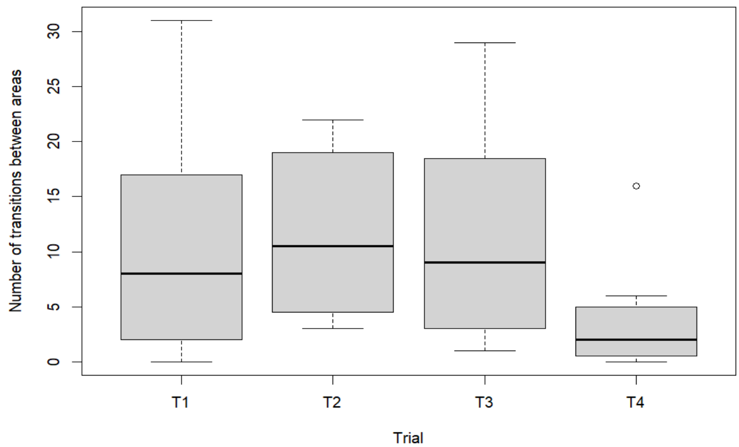

Figure 4. The number of transitions between areas of the arena recorded for all python individuals in the four trials. Boxplots represent median values (thick line inside the box), interquartile range (the box), maximum and minimum values (whiskers), and outliers (empty circles).

We found no significant differences between the times spent by all python individuals in the fourth area of the arena – TR4 (Kruskal-Wallis test: $\chi^2_3 = 4.28$, $P = 0.233$) per trial. We can, however, notice that most of the time spent by pythons in the fourth area of the arena was in the second and third trials (Fig. 5). Similarly, there were no significant differences detected between the time spent in the fourth area between individuals (Kruskal-Wallis test: $\chi^2_7 = 8.72$, $P = 0.274$). Considering individuals, we could notice that P1, P3, and P6 had a median of 0 time spent in the fourth region in all trials, whereas the other individuals spent between 25 and 444 s in the fourth region.

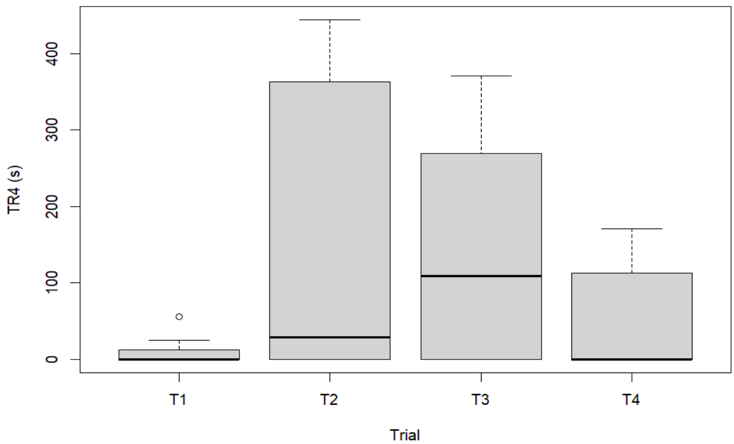

Figure 5. Time spent in the fourth area of the arena (TR4) by all python individuals in each trial. Boxplots represent median values (thick line inside the box), interquartile range (the box), maximum and minimum values (whiskers), and outliers (empty circles).

Discussion

Personality is what the animals are, behavior is what the animals do, and what they do is an intricate mesh between personality and the environment, internal or external. Therefore, we will interpret our results in behavioral terms primarily for practical purposes.

If we look at the statistical results, it becomes evident that there are two ways of interpretation.

First, if we consider only statistical significance, it is clear that shyness increases with time (Fig. 1) and consequently with hunger. Strictly speaking, animals take more and more time to stick their heads out of the shelter. This result describes the typical ambush predator behavior, in which the animals slowly and progressively adopt a sit-and-wait attitude perfectly correlated with hunger. This interpretation would also answer our initial hypothetical question No. 1. And we would more or less leave out of the discussion the exploratory tendencies of the animals (distance covered, number of transitions between areas of the arena, and time spent in the fourth area of the arena) because there were no statistically significant differences found between the four trials.

However, if we look beyond the statistical significance, it becomes evident that there are also important, even pattern-like, differences between the activity in the four testing sessions and that these should be addressed in this discussion.

So, in this alternative way of interpretation, we emphasize that shyness significantly increased with hunger, but the activity and exploration of the animals decreased. Not linearly, like shyness, but more like an unimodal distribution pattern found in all three measured exploratory variables (Fig. 2, 4, and 5). According to Hanscom *et al.* (2023), a true ambush-hunting snake has three distinct behavioral stages: 1) an initial search for an ambush site, 2) a prolonged wait while remaining cryptic, and 3) the actual targeting and striking of potential prey.

A common characteristic of the behavioral patterns found in our experimental lot is that in T1, T2, and T3, the animals were more prone to exploration (T1, however, with lower values). They were at peak energy after digestion and before hunger, and they became relatively familiar with the arena after the first trial. Even though they were shyer than in T1, they ventured further and explored more of the arena than in T1 and T4.

The behavior of our experimental animals in T2 and T3 contradicts Clark`s asset protection principle (Clark, 1994), so at high energetics, they do not exhibit low activity and high levels of shyness but rather the opposite. However, the behavior mentioned above corresponds with stage 1 of the ambush behavioral pattern (Hanscom *et al.*, 2023) and, most likely, has to do with an active search for a suitable ambush site (small mammal pathways and nodes in the pathway networks, Clark, 2004), with a high probability of predation success.

Another characteristic of this second way of interpretation is the further increase in shyness (Fig. 1) and the decrease in exploratory activities in T4, compared with T2 and T3 (Fig. 2, 4, and 5). Again, this behavior opposes Clark's asset protection principle, which stipulates that at a low energy budget, they should be very bold and embark on risky activities to avoid starvation. However, it corresponds fully with stage 3 of the ambush behavioral pattern described by Hanscom *et al.* (2023).

When analyzing the data, we noticed that the initial levels of exploratory behavior (particularly in T2, see Table 1) varied significantly between individuals. However, later in T4, it looks like suddenly, abruptly, all individual variation stopped, and they all became very shy. Although the name of the personality trait test is shyness, this is a manifestation of the species' ambush foraging behavior.

The values recorded in the first testing session, T1, turned out to be quite puzzling and challenging to explain in terms of this species' ecology and life history. The animals were freshly fed, so a typical digestion behavior was expected, with low exploratory activity and high shyness. The exploratory activity was indeed low (Fig. 2, 4, and 5), or at least lower than in T2 and T3, but also the levels of shyness were at the lowest level (fig 1). They were more curious but less explorative, a very counterintuitive combination. They were sticking their head out of the shelter quicker but staying close to the shelter. It was their first testing trial; they were in unknown territory; maybe they were curious, but not that curious to explore further than the immediate vicinity of the shelter. Overall, we found no reasonable explanation for this personality-trait value association in the formal or anecdotic literature and got stuck in the realm of speculation. Nevertheless, one thing is for sure: all eight experimental animals exhibited the same low shyness levels in the digestion stage.

Besides the fundamental aspect of our research, there are also practical ways in which our results can be helpful. The personality trait-based technique described here can be used as a complementary tool, besides the more direct but difficult ones (telemetry, videography), in assessing the feeding strategies applied by different snake species. More precisely, it can be a more accessible method of pinpointing the snake species´ location on the ambush-active hunting scale.

The ball python is one of the most popular pet reptiles, with many captive specimens and well-known captive management techniques. However, there is always room for continual improvement; this is where our study could have another practical use and make a significant difference. Concerning enclosure design, the low activity in T4 emphasizes the importance of a shelter so the animal can behave as closely as possible to its instincts. The presence of the shelter will not only increase the feeding/hunting efficiency but will most certainly be very beneficial for the psychological welfare of the animal. It is common knowledge that handling any snake species right after feeding is not recommended because of the risk of vomiting up the food. Our results propose that another such time is just before eating, at least in ambush species. Causing discomfort in the prandial cycle's ambush phase may easily detour the snake from eating. The stubborn refuse of food and lengthy fasts the ball pythons are known for (Barten and Mader, 2013) may also be a direct result of unrestricted handling. So, if the animal is shyer and less active than usual, we recommend disturbing it as little as possible. Besides solving some of the fasting issues, this will also decrease the risk of getting bit. Any ambush snake species in captivity can benefit from the information mentioned above.

Time spent in the outer ring of the experimental arena suggests that even if they seem to get by in a smaller enclosure (McCurley, 2006; Rizzo, 2014; Hollandt *et al.*, 2021), ball pythons have a higher exploratory inclination (Fig. 5) before entering the ambush foraging mode (T3 in our experiment). Setting up a larger terrarium is not always possible, so a multi-level enclosure design could be a solution to meet the animal´s exploration needs.

Conclusion

From the perspective of our starting hypotheses, there is a group-consistent response to hunger, and the significant personality trait variation between individuals is only visible in the satiated state. In other words, the feeding strategy is not driven by personality. Once hunger sets in, the ambush-foraging state of mind overrides all personality variation, and there is no individual inclination towards a more active hunting style.

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