ABC 2025, 12(2):243-257
Animal Behavior and Cognition
DOI: https://doi.org/10.26451/abc.12.02.04.2025

Hide-And-Seek: Examining Hide Preferences And Behavior Patterns Of Reptiles Through 24-Hour Monitoring

Natasha Wierzal[1,*], Serena Seiler[2], Dan Boehm[3], and Jason Wark[1]

[1]Animal Welfare Science Program, Lincoln Park Zoo, Chicago, Illinois, USA
[2]Department of Biology, Western Kentucky University, Bowling Green, Kentucky, USA
[3]Animal Care & Horticulture Department, Lincoln Park Zoo, Chicago, Illinois, USA

*Corresponding author (Email: nkwierzal@lpzoo.org)

Citation – Wierzal, N., Seiler, S., Boehm, D., & Wark, J. (2025). Hide-and-seek: Examining hide preferences and behavior patterns of reptiles through 24-hour monitoring. *Animal Behavior and Cognition, 12*(2), 243-257. https://doi.org/10.26451/abc.12.02.04.2025

Abstract – Providing animals in zoos with private, out-of-view areas is a basic need for many species but has been rarely studied systematically. Recent research on reptiles has highlighted the welfare benefits of complex environments but, as these studies typically include private hide areas alongside other environmental complexity changes, the specific effects of hides have often not been isolated and their importance remains unclear. In this study, we evaluated artificial hides (PVC tube) for four reptile species: African rock python (*Python sebae* (n=1)); Rio Fuerte beaded lizard (*Heloderma exasperatum* (n=4)); West African Gaboon viper (*Bitis gabonica* (n=1)); Aruba Island rattlesnake (*Crotalus unicolor* (n=2)) Observations were conducted once per hour, each hour, for four weeks using a camera system (672 observations per species) to determine overall hide usage and preferences in hide height (ground-level or elevated), hide humidity (humid or dry), and time of day (day or night). Preferences in hide type were analyzed with chi-squared tests. Hide usage varied between species, with the African rock python observed rarely leaving the hide, and the Aruba Island rattlesnakes only entering hides twice during the entire study. Of the species that used hides, dry hides were preferred over humid hides. Hide usage based on height and time of day appeared to align with the natural history of each species. These results suggest that reptiles have a basic need for private spaces, and attention should be paid to the species' natural history when designing and placing hides. Future studies could improve understanding of species-specific hide needs.

Keywords – Animal Welfare, Reptile welfare, Exhibit design, Hides

Despite reptiles being commonly housed in zoos and aquariums, they have received comparatively less attention than other taxa, such as mammals and birds and, consequentially, our understanding of their welfare in these environments is limited (Binding et al., 2020). Historically, reptile care decisions have often been based on personal experiences and “folklore” that have been passed down in the pet trade and animal care fields that are rarely validated with empirical study (Eagan 2019; Mendyk & Warwick 2023; Warwick et al., 2013). Interpreting reptile behavior, the most commonly used indicator in welfare research (Binding et al., 2020), can be difficult when assessing reptile welfare as many reptile species display less activity compared to mammals and birds due to their physiology and natural history. Additionally, there is little information about the behavior patterns of reptiles in the wild on which to compare zoo-housed populations (Benn et al., 2019). Given these challenges and potential biases, welfare assessments for reptiles have emphasized input-based environmental parameters, such as temperature and humidity, over physical features that promote natural behaviors, like climbing structures, basking areas, soaking basins, and hides (Benn et al., 2019). Although meeting the environmental parameter needs for a reptile is critical for that animal's health, the behavioral needs of a reptile must also be considered for good welfare (Benn et al., 2019; Whittaker et al., 2021).

In recent years, as reptile welfare research has expanded, the understanding of how habitat design impacts reptile welfare has also expanded. Studies have assessed the impact of basic versus enriched housing on reptile welfare and have generally found reptiles seem to benefit from more complex spaces (Case et al., 2005; Hoehfurtner et al., 2021; Hollandt et al., 2021; Nagabaskaran et al., 2022; Spain et al., 2020). Other studies have described benefits of enrichment for reptiles (Bashaw et al., 2016; Zieliński 2023). Together, these studies highlight the importance of providing opportunities for natural behaviors (e.g., climbing features, water basins, substrates for burrowing/digging, basking opportunities, and hides/cover) rather than just biologically fit environmental parameters (e.g., exhibit temperature and humidity).

For many reptile species, one feature that likely benefits their welfare is access to hides or shelter (Azevedo et al., 2021; Pough 1991). In the wild, reptiles use shelter for many reasons, such as avoiding predators, thermoregulation, and assistance in ambushing prey (Kerr et al., 2003; Mendyk & Augustine, 2023). Hides are especially important in zoo settings because in addition to fulfilling the natural motivations for cover-seeking behavior, hides also offer security and privacy in their enclosures. In a study that evaluated enrichment for a variety of snake species, individuals spent approximately half their time during baseline conditions hiding, although differences between species were noted (Krishnan et al., 2022). Lack of hides/shelter could lead to chronic stress in reptiles, which could lead to severe health problems (Bonnet et al., 2013). Despite reptiles utilizing a variety of natural features for hides in the wild, little guidance is given on what these hides should look like in zoos. There are currently only two care manuals made by the Association for Zoos & Aquariums for reptile species (eastern indigo snake (*Drymarchon couperi*) and eastern massasauga rattlesnake (*Sistrurus catenatus*)), and both manuals mention that hides should be provided and that they should be dark, tight spaces. One study that examined hide usage specifically (Chiszar et al., 1987) found tight spaces, in which the reptile could touch at least three sides, and dark spaces with opaque sides were preferred in red spitting cobras (*Naja pallida*).

In this study, we evaluated the use of hides by four species of reptiles: African rock python (*Python sebae*); Aruba Island rattlesnake (*Crotalus unicolor*); Gaboon viper (*Bitis gabonica*); Rio Fuerte beaded lizard (*Heloderma exasperatum*). These four study species are found in a range of habitats, including tropical forests, grasslands, and desert climate zones. African rock pythons are found in tropical, semi-arid forests and grasslands across sub-Saharan Africa, typically near water (Antwi et al., 2019; Trape and Mané, 2006, Trape and Mané, 2015). They are opportunistic foragers, and as the largest snake in Africa, their diet comprises mammals and birds, including occasionally livestock (Antwi et al., 2019, Luiselli et al., 2001). African rock pythons are most active at night and are semi-arboreal (Trape and Mané, 2006). Aruba island rattlesnakes are found in the desert climates in Aruba, with steep, rocky hills and very sparse vegetation (Reinert et al., 2002). Aruba Island rattlesnake behavior is not well studied; however, rattlesnakes from similar rocky, hilly deserts (e.g., *C. scutulatus*, *C. viridis*, *C. cerastes*) tend to be nocturnal, though some species become crepuscular in slightly cooler spring and fall months (Maag et al., 2023, Webber et al., 2016). Rio Fuerte beaded lizards are found primarily in seasonal dry tropical forests around northwestern Mexico (Reiserer et al., 2013; Beck & Jennings, 2003). Their close relatives, Gila monsters (*Heloderma suspectum*), are most active April-November, especially after summer rains (Beck & Jennings, 2003). Though they use abandoned burrows when inactive, they are semi-arboreal, resting in trees, especially in the wet season, and foraging in trees for reptile and bird eggs (Beck 2005). Beaded lizards will share burrows, sometimes, at the same time as other beaded lizards (Carl et al., 2008). Beaded lizard activity patterns vary seasonally, with increased nocturnal activity during summer months and increased activity at dawn and dusk during cooler months (Beck 2005). Gaboon vipers are distributed across central Africa and, though found in tropical wet and dry forests, savanna, and anthropogenic habitats, they seem to rely on areas with some kind of plant cover, especially with leaf litter and shade (Marsh & Whaler 1984; Angelici et al., 2000). These vipers are primarily nocturnal and feed on small mammals, lizards, and birds at night (Angelici et al., 2000). We provided each species with a dry and humid hide located in various places in their habitats to determine whether the species natural history influenced their hide preference. Given the evolutionary importance of shelter, we predicted all species would use hides and that their hide usage would align with their natural history.

Methods

Ethics Statement

This study was approved by Lincoln Park Zoo's Research Committee (2018-019).

Subjects and Housing

In this study, the four study species (Table 1) were housed in adjacent habitats in the Regenstein Small Mammal and Reptile House in Lincoln Park Zoo (Chicago, IL, USA). All individuals were confirmed male, except for the beaded lizards. The beaded lizards are assumed male based on behavior, but it has not been medically confirmed. The venomous reptiles are not regularly measured – only weights are taken during annual veterinary exams.

Table 1

Study Animal Details

Subject	Species	Age (years)	Weight (g)	Time in Exhibit (years)
1	African rock python (*Python sebae*)	5.7	6660	0.5
2	Aruba Island rattlesnake (*Crotalus unicolor*)	0.7	616	0.5
3	Aruba Island rattlesnake (*Crotalus unicolor*)	12.6	647	7.0
4	Rio Fuerte beaded lizard (*Heloderma* exasperatum)	9.1	1480	7.1
5	Rio Fuerte beaded lizard (*Heloderma exasperatum*)	9.1	1480	7.1
6	Rio Fuerte beaded lizard (*Heloderma exasperatum*)	9.1	1442	7.1
7	Rio Fuerte beaded lizard (*Heloderma exasperatum*)	9.0	1576	7.1
8	West African Gaboon viper (*Bitis gabonica*)	8.6	3680	6.5

The habitats broadly reflected the natural habitat of each species (Figure 1). Each exhibit had a specific temperature set point (Table 2) but actual temperatures in the exhibits have been observed to range between 24-32˚C due to the heat lamps and hot rocks in the enclosure and the outside temperature fluctuations (i.e. slightly cooler at night with the lights off). Humidity stayed between 40-60% in all enclosures. In the African rock python habitat, there were a few rock ledges of varying elevations, along with tree branches, bushes, and a pool on the floor of the habitat. Two months prior to the start of the study, the African rock python had exhibited several behavioral and dietary concerns, so several habitat modifications were made, including raising the temperature of the habitat and adding an artificial hide (PVC tube) in an elevated location that he had previously shown a preference for. No other study species were provided an artificial hide prior to the start of the study. The two male Aruba island rattlesnakes were housed in a desert-style habitat, there were some boulders that provided a variation in elevation, along with some rocks, agave plants, and pieces of bark on the sand covered ground. The Rio Fuerte beaded lizard exhibit has two rock cliffs that they could climb up to using a branch. They also had a water feature and a covered area under a small deadfall tree that served as a naturalistic hide. The floor of their habitat was mainly mulch with some rocky surfaces in the back by the keeper entrance and by the water feature. The Gaboon viper exhibit has two rock cliffs on the left and right side of his habitat, with some foliage on both. The ground was mainly mulch with a small rock surface in the back by the keeper entrance. Originally, the male viper was housed socially, but for the duration of the study, the snake was independently housed.

Figure 1

Photos Of Study Habitats at Lincoln Park Zoo

Note. (A) African rock python. (B) Aruba island rattlesnake. (C) Rio Fuerte beaded lizards. (D) West African Gaboon viper.

Table 2

Study Species Exhibit Details

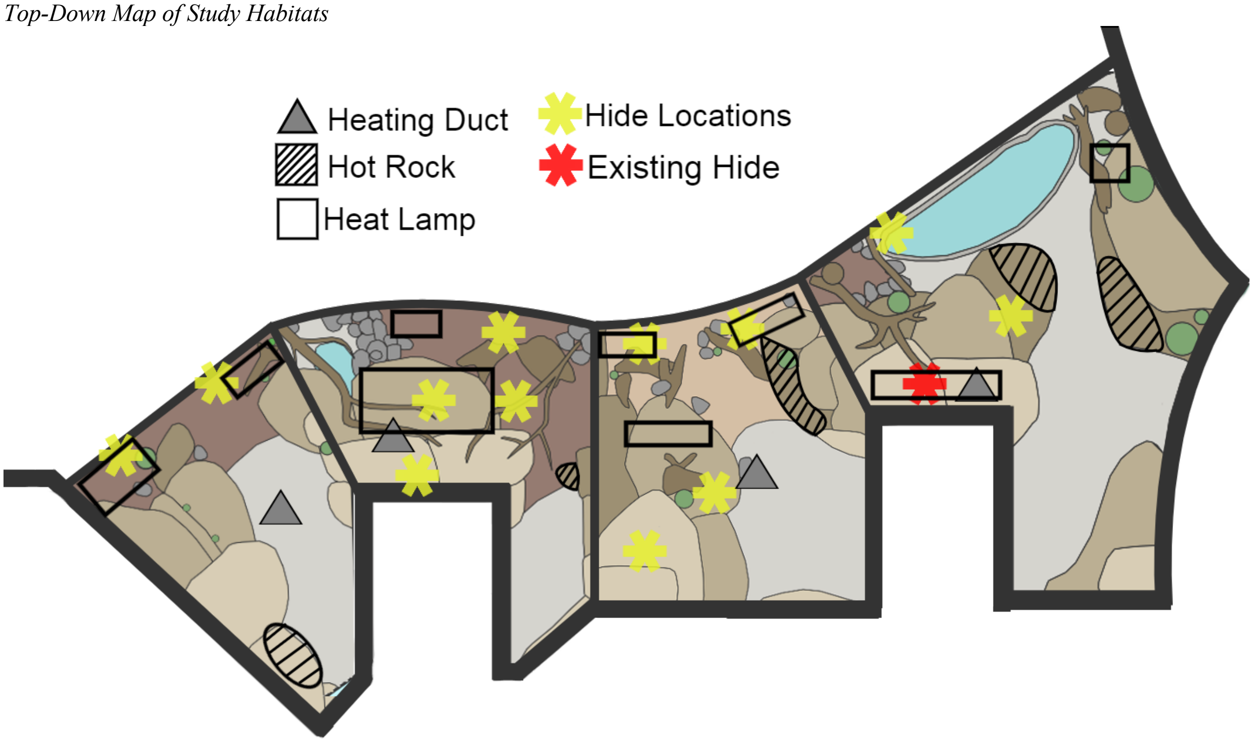
Species	Dimensions (m)	Temperature Set Point (˚C)
African rock python (*Python sebae*)	3.7 x 3.3 x 2.4	28.9
Aruba Island rattlesnake (*Crotalus unicolor*)	2.1 x 2.7 x 2.4	26.7
Rio Fuerte beaded lizard (*Heloderma exasperatum*)	3.0 x 3.0 x 2.4	27.8
West African Gaboon viper (*Bitis gabonica*)	2.7 x 3.0 x 2.4	27.8

Each habitat was equipped with various heating sources such as hot rocks with built-in heating elements, halogen heat lamps that provided basking hot spots, and heating ducts with hot, forced air (Figure 2). The reptiles also have UVB light available in their spaces (Mega-Ray 160-watt mercury vapor bulb).

Animal keepers entered habitats daily for servicing (e.g., watering and maintaining plants, cleaning debris, etc.). All of the spaces except for the Aruba island rattlesnake exhibit have automatic misters. These run year-round in the python space but imitate seasonal rainy seasons for the Gaboon viper and Rio Fuerte beaded lizards. During the study, only the rock python and Gaboon viper spaces were getting misted – the misters would spray the habitat for 30 s, every 10 min. Humidity in each exhibit was measured every 12 hr using a SensorPush HT1 Wireless Thermometer/Hygrometer for iPhone/Android. The feeding schedule varied by species, with all individuals fed weekly with the exception of the Aruba island rattlesnake, who were fed every other week.

Figure 2

Top-Down Map of Study Habitats



Note. Hide locations and heating elements (heating duct, hot rock, and heat lamp) are indicated. From left to right: Gaboon viper, Rio Fuerte beaded lizard, Aruba island rattlesnake, African rock python.

Hide Design

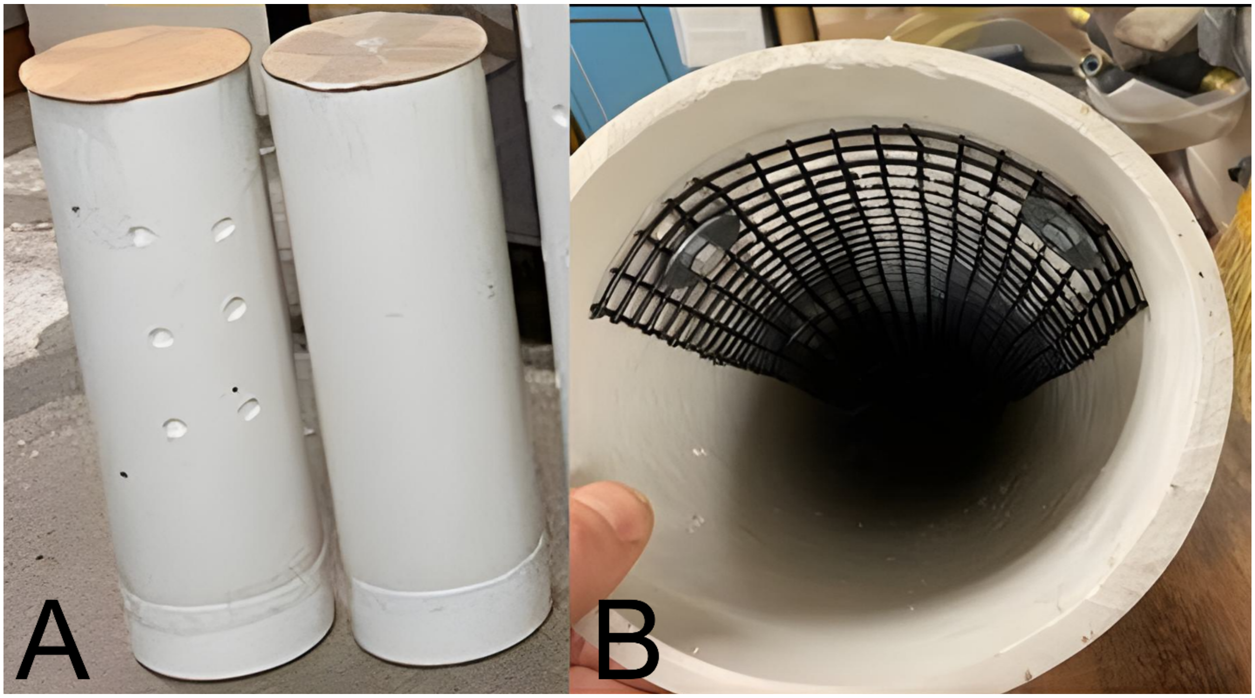
Hides were created using modified PVC tubes that varied in length and diameter based on species (Figure 3). The lengths of the PVC tubes were approximately 58 cm for the rattlesnake, to 61 cm for the rock python, 76 cm for the beaded lizard, and 91 cm for the Gaboon viper. The diameters of tubes were 10 cm for the rattlesnake and 15 cm for the python, beaded lizard, and Gaboon viper.

To create the humid hide, holes were drilled into the top of the designated hide and a towel was attached (Figure 3B). These hides were watered daily by keepers to maintain consistent humidity levels throughout the study. Humidity levels of a control hide located behind-the-scenes was measured using a SensorPush HT1 Wireless Thermometer/Hygrometer for iPhone/Android. Humidity levels ranged from 60%-70% humidity, which was 30-40% higher than the control room humidity.

Habitats with one individual (African rock python and Gaboon viper) had one dry and one humid hide added, and habitats with multiple individuals (beaded lizard and Aruba island rattlesnake) were provided with two dry and two humid hides. Hide locations were dependent on heat sources and the animals' baseline space use trends based on previous data. For each habitat, one type of hide was randomly selected and would be placed in an elevated location, while the other hide type would be on a lower, ground level. The only exception to this was the Gaboon viper as this habitat did not have a sturdy, elevated location to be able to place a hide safely for the animal or the keepers.

Figure 3

Humid Hide Design



Note. (A) A side view of the PVC tubes used for artificial hides. The humid hides have holes in the side to allow keepers to remoisten the towel secured to the inside. (B) A towel was secured to the inside of the tube with a piece of mesh. The towel was watered regularly by keepers to create humidity inside the tube.

Study Design

Three days prior to data collection, the hides were placed in predetermined locations to reduce the novelty of the objects, and the entrances were blocked to limit entry to the hides until data collection started. Data collection was planned to run for four weeks and was divided into two 2-week study phases (phase 1 and 2), where the humid and dry hide locations were swapped to minimize any individual spatial preferences from influencing hide preferences (Table 3). Midway through each study phase (i.e., phase 1A vs 1B and 2A vs 2B), ground-level hides were rotated 180° (this was not possible for elevated hides). Due to the venomous nature of these species, hides were not able to be moved or rotated when the animals were in the hides. As such, some phases lasted longer than others, but every phase lasted a minimum of five days (Table 3).

Table 3

Number of Study Days per Phase for Each Study Species

	Number of Days in Phase[1]			
Species	1A	1B	2A	2B
African rock python	8	5	11	6
Aruba island rattlesnake	8	5	11	7
Rio Fuerte beaded lizard	8	5	11	7
Gaboon viper	13[2]	0[2]	12[2]	6

Note. [1]Location of dry and humid hides were swapped between phases 1 and 2 and ground hides were rotated 180° between phases A and B. [2]Hide was unable to be rotated on schedule due to the individual being in the hide.

Behavior Data Collection

A wireless IP camera (Wyze cam V3) was mounted on the roof of each study habitat to allow remote monitoring of behavior. Behavior was recorded for each study animal over an entire 24-hour period. Observations were made by a single observer at the top of every hour, every day for the duration of the study. There was a total of 672 scans per individual in this study. We recorded whether the individuals were using the hides and, when using a hide, we recorded hide type, location, and the estimated percentage of the animal's body in the hide rounding to the nearest third when a portion of the animal's body was in the hide. The animal had to be fully inside the hide to be marked as 100% coverage. When individuals were unable to be located, they were marked as not visible. Given the short duration of this study (1 month) and that animal locations could be reviewed multiple times in the camera footage, did not include individual identification, and were deemed less subjective than typical behavior observations, intra-rater reliability testing was not conducted in this study.

Statistical Analysis

As the number of individuals in each exhibit varied, hide usage was calculated per animal – taking the total count of hide usage divided by the number of animals per exhibit. It was not possible to recognize specific individuals through the cameras, so data are shown as a species usage, rather than individual. We examined hide humidity (wet or dry hide), hide height (ground-level or elevated hide), and time of day (using a hide at night or during the day). We defined time of day by the light cycles in the exhibits, with daytime hide usage as using a hide between 7AM to 7PM, and nighttime usage as using a hide between 7PM to 7AM.

For comparing hide usage across species, we present descriptive statistics of the percent of hourly scans using a hide (of any type of) per individual animal because there were varying numbers of animals per species. For within-species comparisons of hide types, we conducted chi-squared goodness of fit tests using the proportions of type of hide used out of the total number of scans a hide was used (e.g., comparing the proportion of scans a humid hide was used out of the total number of scans in a hide to the proportion of scans a dry hide was used out of the total number of scans in a hide). The phi metric was calculated as a measure of effect size, with a value of 0.1 indicating a small effect, 0.3 a medium effect, and 0.5 a large effect.

Data were analyzed with R statistical software (R Core Team, 2021). An alpha probability of .05 was used in all tests to determine significant effects.

Results

Overall Hide Usage

The overall hide usages of the study species are shown in Figure 4. Of the species assessed, the African rock python (n=1) used a hide the most often (556 times). This individual was observed using the dry hide that had been placed in the exhibit prior to the start of this study due to animal care needs. The beaded lizards (n=4) used hides next most often (260.5 times per individual). The Gaboon viper (n=1) infrequently used hides (107 times). The Aruba island rattlesnakes (n=2) were only observed using a hide on two occasions (1 time per individual).

Species Preferences

The African rock python was only observed using the elevated, dry hide (Figure 5). He was never observed using a ground-level hide or a wet hide, though this individual was noted investigating the hides occasionally at night. The rock python was not observed outside of the hide during the day and only exited the hide on occasion at night. Considering the full 24 hr cycle, the python demonstrated a slight preference for using hides during the day compared to at night (Day: 57.76%, Night: 42.24%; $\chi^2 = 15.53$, df = 1, $p < .001$, $\phi=0.15$).

Figure 4

Percent of Hourly Scans Occupying a Hide by Species During the Four-Week Study

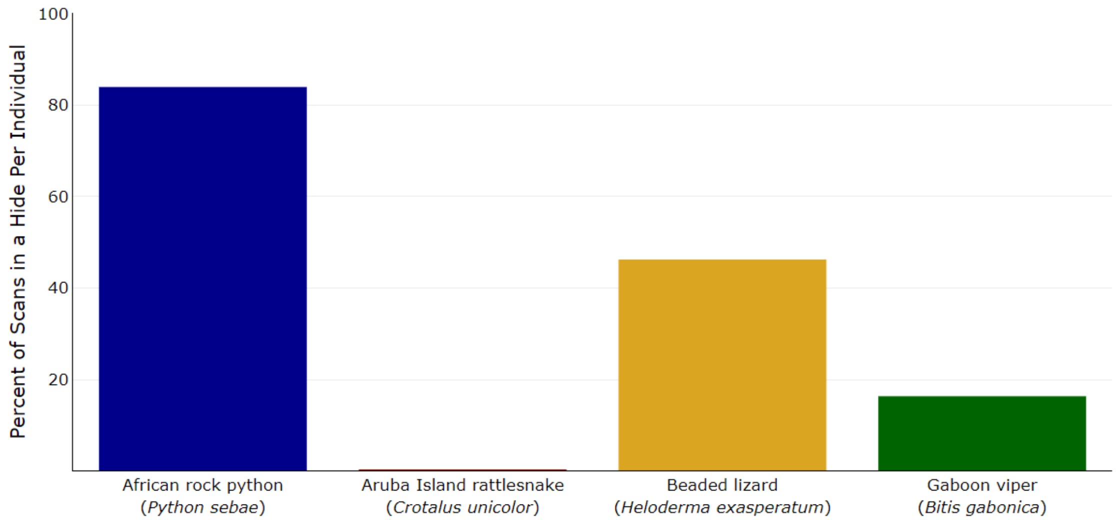
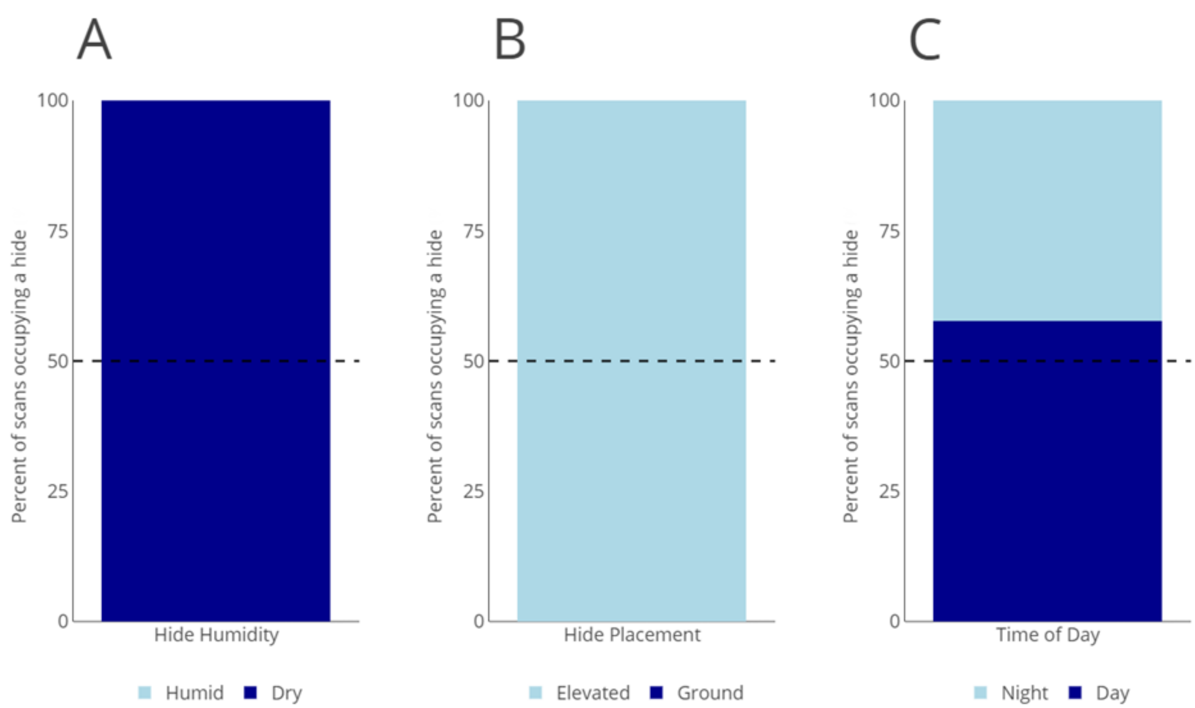


Figure 5

African Rock Python Hide Use by Type and Time

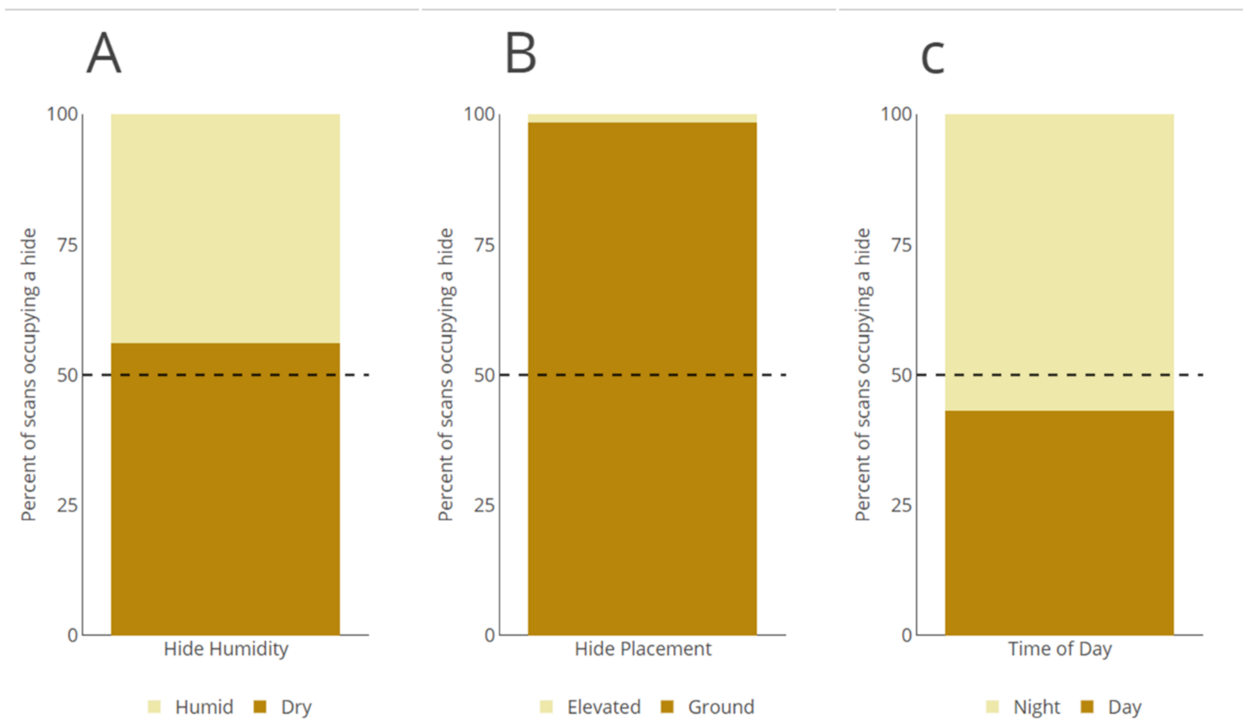


Note. The line represents the expected value if there was no preference between conditions. Figure 5A shows hide use based on humidity (humid vs dry). Figure 5B shows hide use based on hide placement (elevated or ground-level). Figure 5C shows hide use based on time of day (night vs day)

The Rio Fuerte beaded lizards showed a preference for ground-level hides (Ground: 98.46%; Elevated: 1.54%; χ^2 = 978.98, df = 1, p < .001, ϕ=0.61; Figure 6B). Although the lizards did show a slight preference for dry hides (Dry: 56.14%; Humid: 43.86%; χ^2 = 15.724, df = 1, p < .001, ϕ=0.07; Figure 6A), they used the humid hides more than any other species. The beaded lizards used more at night (Day: 43.09%; Night: 56.91%; χ^2 = 19.9, df = 1, p < .001, ϕ=0.0.09); however, this difference was slight (Figure 6C). This species also used a pre-existing ground-level, naturalistic hide (180 scans), albeit less than their use of the ground-level artificial, study hides (dry: 569 scans; humid: 457 scans).

Figure 6

Rio Fuerte Beaded Lizard Hide Usage by Type and Time

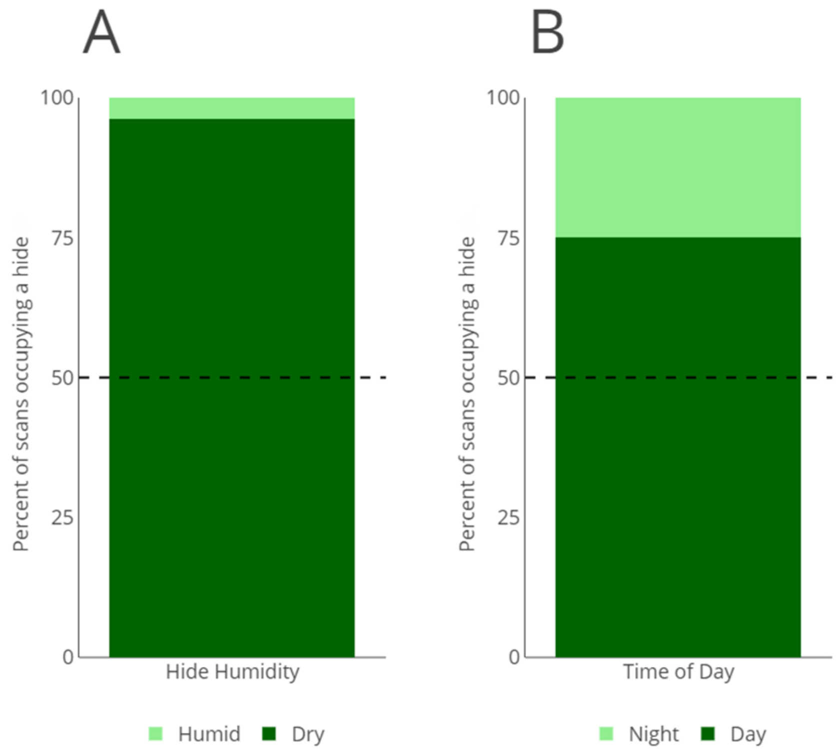


Note. The line represents the expected value if there was no preference between conditions. Figure 6A shows hide use based on humidity (humid vs dry). Figure 6B shows hide use based on hide placement (elevated or ground-level). Figure 6C shows hide use based on time of day (night vs day).

For the Gaboon viper, it was not possible to test preferences of hide height due to safety concerns for the animal and for care staff. The viper showed a moderate preference for dry hides (Humid: 3.70%, Dry: 96.30%; χ^2 = 92.59, df = 1, p < .001, ϕ=0.37; Figure 7A). The Gaboon viper used hides more during the day than at night (Day: 75.00%, Night: 25.00%; χ^2 = 27, df = 1, p < .001, ϕ=0.20; Figure 7B). The Aruba island rattlesnakes were only observed in hides on two occasions on different days. Both of these occasions were during the day and involved a humid hide located on the ground in the front right corner of their habitat, and both instances were very brief, less than 10 min each. Given this minimal hide use, it was not possible to determine any preferences for hide type during this study.

Figure 7

Gaboon Viper Hide Usage by Type and Time



Note. The line represents the expected value if there was no preference between conditions. Figure 7A shows hide use based on humidity (humid vs dry). Figure 7B shows hide use based on time of day (night vs day). Hide height level was not assessed for the Gaboon viper due to safety concerns.

Discussion

Sheltered areas, with the corresponding benefits of privacy, safety, thermoregulation, and humidity they confer, are a basic need for many species. For reptiles, hide shelters have been recommended as an important component of habitat design but, given the general paucity of research on reptile welfare, our understanding of the species-specific suitability of hides is limited (Azevedo et al., 2021; Pough 1991). Here, we evaluated the use of artificial hide shelters in the form of PVC tubes by several reptile species to better understand their importance and consideration in reptile habitat design. Use of hides varied greatly between species, with the African rock python rarely leaving a hide, and the Aruba island rattlesnake rarely using a hide. Due to the small sample size of this study, it difficult to determine if the differences in hide usage that we observed are actual species preferences, or just the preferences of the individual animals within the study. It should be noted that, even with a small sample size, our results did confirm the importance of hides for some individuals.

The African rock python used hides more than any other individual observed in this study. In a survey of snake habitat preferences in Nigeria (Oyeleye et al., 2021), pythons (*P. sebae* and *P. regius*) were encountered in holes (e.g., rock crevices and aardvark dens) more often than other snake species. In a study of snake enrichment, Krishnan et al. (2022) recorded the behavior of multiple snake species in a zoo setting during morning hours and noted two individuals, a ball python (*P. regius*) and Kenyan sand boa (*Gongylophis colubrinus*), were observed exclusively in hides during the duration of their study (with an additional individual of each species also demonstrating a similar proclivity for hiding). Although it is possible that pythons and boas, as constrictors with an ambush hunting strategy, may have a strong preference for hides, it should be noted that Krishnan et al. also observed a rosy boa (*Lichanura trivirgata*) that rarely hid during their study, highlighting the potential for individual differences. In this study, the python was observed to have only used the elevated, dry hide. African rock pythons are efficient climbers (Trape & Mané, 2006), which aligns with what we observed in the rock python's preference for the elevated hide location. As a nocturnal species, the preference to only leave the hide at night also aligned with natural history of African rock pythons and correspond to behavior patterns others have observed in managed care (Haagner, 1992). Given the wide range of habitats that African rock pythons inhabit, ranging from grassland to semi-arid tropical forest, it was challenging to predict one clear preference for hide humidity. While it is possible that the python's preference for the dry hide indicates a sufficient humidity level in the exhibit, the python was occasionally observed soaking in a pool in the exhibit overnight, so it is possible that humidity needs were being met through the python's behavioral patterns. Prior to the start of the study, this individual exhibited minimal interest during feeding events and was provided a dry hide in an elevated location to promote additional comfort in the space. This individual was observed during the study leaving the hide overnight and using lower areas of the habitat space, but the prior experience with the elevated, dry hide may have ingrained a bias towards that choice.

The beaded lizards showed a strong preference for the ground-level, dry hides and used those hides slightly more overnight than they did during the day. Rio Fuerte beaded lizards recycle old animal burrows to use as hides in the wild and display seasonal activity patterns (Beck 2009). In this regard, the beaded lizards' hide usage seems to align with the species' natural history. In Gila monsters (*Heloderma suspectum*), the types of shelters used varies seasonally (Beck & Jennings 2003). During the winter, Gila monsters used dry, rocky hides, which stay warmer, more often, but in summer months, they preferred more humid, softer shelters, which stay cooler (Beck & Jennings 2003). When weather conditions were more variable in the spring, the hide selected also varied more in temperature and humidity (Beck & Jennings 2003). While they still used dry hides more, the beaded lizards did use the wet hides more than any other species studied here. Given that the size of their habitat was only able to accommodate four hides for the four individuals, it is possible that lizards were choosing to use any hide that was available, even if it was not a preferred type (i.e., wet). There is evidence of Gila monsters sharing hides in the wild, though this trend appears to be seasonal as well, sharing hides more often during mating season and less often the rest of the year (Beck & Jennings 2003). In our study, we regularly observed multiple beaded lizards in a hide at one time, even when there were empty hides available. This could indicate that, at least for these animals, there is a stronger need to use any hide rather than a preferred hide type or environmental trait (i.e. humidity or aridity), even if that requires sharing a hide. This highlights the importance of considering social competition in an exhibit and providing an appropriate number of different kinds of hides to ensure that every animal in the exhibit is using a hide that is actually desirable, and not just using the only option available.

The Gaboon viper showed a strong preference for the dry hide over the humid hide and used the hides more during the day. As a nocturnal species, this pattern aligns with natural history; however, we did not expect the Gaboon viper, a species from wet, tropical rainforests, to prefer the dry hides. Overall, the Gaboon viper used the hides infrequently. A similar behavior pattern was observed by Augustine et al. (2022), where they observed Wagner's vipers (*Montivipera wagneri*) spent less than 10% of their time hiding in a zoo setting. Oleyeye et al. (2021) found vipers in Nigeria were most commonly exposed on the ground in their survey and rarely encountered using holes or dens. However, this study may have been limited by a detection bias, as they conducted their surveys during the morning and late evening, time periods that Gaboon vipers have been reported to be most active (Angelicci et al., 2000). Considering the full 24-hr cycle, Angelicci et al. (2000) followed radio-tracked Gaboon vipers in Nigeria and found those individuals spent a considerable amount of time underground, ranging from 44% to 71% of their location events across individuals, with a consistent peak in under-ground activity during the middle of the day for all individuals. Bonnet et al. (2013) demonstrated under controlled laboratory conditions that aspic vipers (*Vipera aspis*), when given a choice, showed a preference for sheltered areas, which the authors suggested was a key defensive behavior. It is possible that vipers living in a zoo setting with no risk of predation and minimal handling compared to laboratory settings may be less defensive. However, the design of hides may also warrant further attention. Both species with cryptic coloring, the Gaboon viper and the Aruba Island rattlesnakes, rarely used hides, which may have conflicted with the white PVC tube hides or allowed the animals to still "feel hidden" when not in an actual hide.

Posture may have also influenced overall hide usage. For example, the Gaboon viper would typically adopt a "hairpin" coil when in the hides, given their size relative to the PVC tubes that were offered. However, outside of the hides, this individual was typically observed resting in an elongated rectilinear posture. Similarly, the Aruba island rattlesnake was commonly observed outside of hides in a tight circular coil that they may not have been able to adopt in the PVC tube hides. Previous research has highlighted the importance of considering body size and behavior when designing hides. In a study on blue-tongued skinks, researchers found that individuals would enter natural burrows headfirst and then reposition using larger chambers inside the burrow to have their head oriented out (Ebrahimi et al., 2012). However, for artificial burrows, skinks would enter headfirst, then be forced to reverse out of the artificial burrow and would then back into the burrow to maintain their outward facing posture. For these reasons, it is possible the tube hide design used in this study was not optimal for these species and resulted in less hide usage. Future studies are needed with a larger sample size and a greater diversity of hide designs to better understand the ideal hide type for these species.

Several limitations of the current study should be noted. As data were collected through a camera system, it was not possible to individually identify group-housed animals. Thus, while the camera system did make it possible to collect data over a 24-hour period, this system did limit our ability to detect individual preferences in some situations. This study was also conducted during winter, with lower seasonal crowd numbers. In 2023, visitor numbers ranged from 2200-2500 visitors per day on average in the winter, to 12000-13200 visitors per day on average in the summer. Although prior studies have demonstrated a mixed impact of zoo visitors on reptiles (Carter et al., 2021; Hamilton et al., 2022; Riley et al., 2021), it is possible the need for privacy from guests may have been relatively lower during the study period and resulted in less hide usage. Future studies should consider periods of high and low visitor levels to better understand if guests are a motivating factor for reptiles to use hides.

Although none of the species showed a clear preference for wet hides, it should be noted that none of the individuals were shedding during the study period. During a shedding cycle, many species of reptiles have additional needs for higher humidity to effectively shed their skin, thus the individuals in this study may not have had a need for the increased humidity of the wet hides. Offering wet hides again while these animals are shedding could offer more insight into the observed preference. For reptile species in more temperate climates, such as the beaded lizards, moisture needs will change throughout the year, thus requiring these species to be more active in either conserving their body water or seeking out humid environments. It is likely that if the exhibits were less humid, humid hide usage would have increased.

In this study, we observed several species of reptiles used novel, dedicated hides, highlighting the importance of providing these features when designing habitats. Although this study broadly supports past research that had demonstrated reptiles can benefit from "enriched" environments (Bonnet et al., 2013; Case et al., 2005; Hoehfurtner et al., 2021; Hollandt et al., 2021; Spain et al., 2020), what an "enriched" environment looks like will likely vary for different species of reptiles, making it important to evaluate the specific attributes of exhibit features that are ideal or preferred for a given species. Despite the general recommendation for hides to promote good welfare (AZA Eastern Massasauga Rattlesnake SSP 2013; AZA Snake Tag 2011; Case et al., 2005; Chiszar et al., 1987), our results showed that merely meeting guidelines for a dark and enclosed space may not be effective, and special attention should be paid to species-specific and animal-specific needs in hide placement and design.

Although concerns of exhibit naturalism may make PVC tubes an impractical hide choice for some, these elements can be camouflaged to blend into an animal's habitat to minimize any potential impact on guest perception. Furthermore, the use of plants and logs as an alternative to dedicated hides, although natural, may not provide the full suite of benefits conferred from hides that are "dark and enclosed", as recommended by care manuals (AZA Eastern Massasauga Rattlesnake SSP 2013, AZA Snake Tag 2011). Indeed, in this study we observed a preference for dedicated hides by most species over the existing foliage and deadfall in their habitats. As such, we recommend reptile habitats include dedicated hides in addition to existing foliage and deadfall. We hope that this study encourages additional work exploring the design of reptile habitats and provides a jumping off point for determining exhibit needs in other understudied taxa.

Acknowledgements

We thank the animal care staff of the Regenstein Small Mammal and Reptile House, Dave Bernier, Maureen Leahy, Lou Keeley, Katherine Cronin. We are also thankful for Adera Craig's help in building up the early stages of this research.

Author Contributions: NW, SS, DB, JW: conceptualization, writing – review & editing; SS, DB: data collection; NW, DB, JW: project administration, supervision, resources; NW, SS, JW: writing – original draft; NW, JW: data analysis, visualization

Funding: No external funding was used for this study.

Conflict of Interest: The authors declare no conflicts of interest.

Data Availability: Raw data analyzed for this study are available at: https://osf.io/cdp7j/

References

Angelici, F. M., Effah, C., Inyang, M. A., & Luiselli, L. (2000). A preliminary radiotracking study of movements, activity patterns and habitat use of free-ranging Gaboon vipers, *Bitis gabonica*. *Revue d'écologie*, *55*(1), 45-55.

Antwi, R., Ofori, B., Attuquayefio, D., & Owusu, E. (2019). Predation on the Kob (*Kobus kob*) by the African rock python (*Python sebae*) at Shai Hills Resource Reserve, Ghana. *Herpetology Notes*, *12,* 1181–1183.

Augustine, L., Baskir, E., Kozlowski, C. P., Hammack, S., Elden, J., Wanner, M. D., Franklin, A.D., & Powell, D. M. (2022). Investigating welfare metrics for snakes at the Saint Louis Zoo. *Animals*, *12*(3), 373.

AZA Eastern Massasauga Rattlesnake SSP (2013). Eastern Massasauga Rattlesnake (*Sistrurus catenatus catenatus*) Care Manual. Association of Zoos and Aquariums, Silver Spring: MD.

AZA Snake TAG 2011. Eastern Indigo Snake (*Drymarchon couperi*) Care Manual. Association of Zoos and Aquariums, Silver Spring, MD.

Azevedo, A., Guimarães, L., Ferraz, J., Whiting, M., & Magalhães-Sant'ana, M. (2021). Pet reptiles—Are we meeting their needs? *Animals*, 11(10), 2964.

Bashaw, M.J., Gibson, M.D., Schowe, D.M., & Kucher, A.S. (2016). Does enrichment improve reptile welfare? Leopard geckos (*Eublepharis macularius*) respond to five types of environmental enrichment. *Applied Animal Behaviour Science*, *184,* 150-160.

Beck, D. D. (2005). *Biology of Gila monsters and beaded lizards* (Vol. 9). Univ of California Press.

Beck, D. D. (2009). *Biology of Gila Monsters and Beaded Lizards*. University of California Press.

Beck, D. D., & Jennings, R. D. (2003). Habitat use by Gila monsters: the importance of shelters. *Herpetological monographs*, *17*(1), 111-129.

Benn, A. L., McLelland, D. J., & Whittaker, A. L. (2019). A review of welfare assessment methods in reptiles, and preliminary application of the welfare quality® protocol to the pygmy blue-tongue skink, *Tiliqua adelaidensis*, using animal-based measures. *Animals*, *9*(1), 1–27.

Binding, S., Farmer, H., Krusin, L., & Cronin, K. (2020). Status of animal welfare research in zoos and aquariums: Where are we, where to next? *Journal of Zoo and Aquarium Research*, *8*(3), 166–174.

Bonnet, X., Fizesan, A., & Michel, C. L. (2013). Shelter availability, stress level and digestive performance in the aspic viper. *Journal of Experimental Biology*, *216*(5), 815–822.

Carl, N. J., Paul, J. S., & Mendelson, J. (2024). Smell and Tell: Behavior Associated with Chemosensory Stimuli in Guatemalan Beaded Lizards (*Heloderma charlesbogerti*). *Herpetological Conservation and Biology*, *19*(1), 1–12.

Carter, K. C., Keane, I. A. T., Clifforde, L. M., Rowden, L. J., Fieschi-Méric, L., & Michaels, C. J. (2021). The Effect of Visitors on Zoo Reptile Behaviour during the COVID-19 Pandemic. *Journal of Zoological and Botanical Gardens*, *2*(4), 664–676.

Case, B. C., Lewbart, G. A., & Doerr, P. D. (2005). The physiological and behavioural impacts of and preference for an enriched environment in the eastern box turtle (*Terrapene carolina carolina*). *Applied Animal Behaviour Science*, *92*(4), 353–365.

Chiszar, D., Radcliffe, C. W., Boyer, T., & Behler, J. L. (1987). Cover-seeking behavior in red spitting cobras (*Naja mossambica pallida*): Effects of tactile cues and darkness. *Zoo Biology*, *6*(2), 161–167.

Eagan, T. (2019). Evaluation of enrichment forrReptiles in zoos. *Journal of Applied Animal Welfare Science*, *22*(1), 69–77.

Ebrahimi, M., Fenner, A. L., & Bull, C. M. (2012). Lizard behaviour suggests a new design for artificial burrows. *Wildlife Research*, *39*(4), 295–300.

Haagner, G. V. (1992). The husbandry and captive propagation of the southern rock python, *Python sebae natalensis*. *British Herpetoogical Society Bulletin*, *42*, 30-41.

Hamilton, J., Gartland, K. N., Jones, M., & Fuller, G. (2022). Behavioral assessment of six reptile species during a temporary zoo closure and reopening. *Animals*, *12*(8), 1–17.

Hoehfurtner, T., Wilkinson, A., Nagabaskaran, G., & Burman, O. H. P. (2021). Does the provision of environmental enrichment affect the behaviour and welfare of captive snakes? *Applied Animal Behaviour Science*, *239*(105324), 1–8.

Hollandt, T., Baur, M., & Wöhr, A. C. (2021). Animal-appropriate housing of ball pythons (*Python regius*)—Behavior-based evaluation of two types of housing systems. *PLoS One*, *16*(5), 1–20.

Kerr, G. D., Michael Bull, C. M., & Burzacott, D. (2003). Refuge sites used by the scincid lizard *Tiliqua rugosa*. *Austral Ecology*, *28*(2), 152–160.

Krishnan, S., Klaphake, E., Rao, S., & Sadar, M. J. (2022). The effect of varied enrichment types on snake behavior. *Journal of Zoo and Wildlife Medicine*, *53*(2), 266-274.

Luiselli, L., Angelici, F. M., & Akani, G. C. (2001). Food habits of *Python sebae* in suburban and natural habitats. *African Journal of Ecology*, *39*(1), 116–118.

Maag, D. W., Francioli, Y. Z., Shaw, N., Soni, A. Y., Castoe, T. A., Schuett, G. W., & Clark, R. W. (2023). Hunting behavior and feeding ecology of Mojave rattlesnakes (*Crotalus scutulatus*), prairie rattlesnakes (*Crotalus viridis*), and their hybrids in southwestern New Mexico. *Ecology and Evolution*, *13*(11), 1–19.

Marsh, N. A., Whaler, B. C. (1984). The Gaboon viper (*Bitis gabonica*): Its biology, venom components and toxinology. *Toxicon*, *22*(5), 669–644.

Mendyk, R. W., & Warwick, C. (2023). Arbitrary Husbandry Practices and Misconceptions. In C. Warwick, P. C. Arena, & G. M. Burghardt (Eds.), *Health and Welfare of Captive Reptiles* (2nd ed., pp. 561–582). Springer International Publishing.

Nagabaskaran, G., Skinner, M., & Miller, N. (2022). Western hognose snakes (*Heterodon nasicus*) prefer environmental enrichment. *Animals*, *12*(23), 1–9.

Oyeleye, D.O., Ajayi, S.R., Odebiyi, B.R., Jaiyeoba, W.A., Ironokhai, E.A., Alaye, S.A., & Kambai, C. (2021). Study of snakes behavior and habitat preferences in Kainji Lake National Park. Ethiopian *Journal of Environmental Studies & Management*, 14(6), 755-765.

Pough, F. H. (1991). Recommendations for the care of amphibians and reptiles in academic institutions. *ILAR Journal*, *33*(4), S1–S21.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Reinert, H. K., Bushar, L. M., Rocco, G. L., Goode, M., & Odum, R. A. (2002). Distribution of the Aruba Island rattlesnake, *Crotalus unicolor*, on Aruba, Dutch West Indies. *Caribbean Journal of Science*, *38*(1/2), 126-128.

Reiserer, R. S., Schuett, G. W., & Beck, D. D. (2013). Taxonomic reassessment and conservation status of the beaded lizard, *Heloderma horridum* (Squamata: Helodermatidae). *Amphibian & Reptile Conservation*, *7*(1), 74–96.

Riley, A., Terry, M., Freeman, H., Alba, A. C., Soltis, J., & Leeds, A. (2021). Evaluating the effect of visitor presence on Nile crocodile (*Crocodylus niloticus*) behavior. *Journal of Zoological and Botanical Gardens*, *2*(1), 115–129.

Spain, M., Fuller, G., & Allard, S. (2020). Effects of habitat modifications on behavioral indicators of welfare for Madagascar giant hognose snakes (*Leioheterodon madagascariensis*). *Animal Behavior and Cognition*, *7*(1), 70–81.

Trape, J. F., & Mané, Y. (2006). *Guide des serpents d'Afrique occidentale: savane et désert*. IRD éditions.

Trape, J. F., & Mané, Y. (2015). The snakes of Niger. *Amphibian & Reptile Conservation*, *9*(2), 39-55.

Warwick, C., Arena, P., Lindley, S., Jessop, M., & Steedman, C. (2013). Assessing reptile welfare using behavioural criteria. *In Practice*, *35*(3), 123–131.

Webber, M. M., Jezkova, T., & Rodríguez-Robles, J. A. (2016). Feeding ecology of sidewinder rattlesnakes, *Crotalus cerastes* (Viperidae). *Herpetologica*, *72*(4), 324–330.

Whittaker, A. L., Golder-Dewar, B., Triggs, J. L., Sherwen, S. L., & McLelland, D. J. (2021). Identification of animal-based welfare indicators in captive reptiles: A delphi consultation survey. *Animals*, *11*(7) 2010.

Zieliński, D. The effect of enrichment on leopard geckos (*Eublepharis macularius*) housed in two different maintenance systems (Rack System vs. Terrarium). *Animals*, *13*, 1111.