

Does enclosure size influence the behaviour & welfare of captive snakes (*Pantherophis guttatus*)?

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ABSTRACT

There is much evidence in mammals and birds demonstrating the importance of providing sufficient space to allow captive animals to exhibit natural behaviours, however, little such evidence exists for reptiles. The aim of this study was to ascertain whether enclosure size impacted on the behaviour and welfare of captive corn snakes (*Pantherophis guttatus*). Snakes ($N = 12$) were housed in enclosures that were either $2/3$ their length (*small*) or longer than the length of the snake (*large*) for c.32 days. Their welfare was assessed through observations of the animals in their enclosure and behavioural tests; after completing these tests, each animal was switched to the other housing condition (order counterbalanced across individuals) and received the same welfare assessment. Following the second set of behavioural tests, all animals received a preference test. When housed in *large* enclosures, snakes were found to be more active and spent time stretched out - a behaviour that was not possible in the *small* enclosure. The behavioural tests revealed few effects of space provision; however, when given a choice, snakes showed a clear preference for the *large* enclosure whilst active, although this preference was not observed while resting. These findings suggest that providing a larger enclosure is beneficial to the behaviour and welfare of captive snakes. Not providing sufficient space to allow snakes to fully elongate appears to thwart a behavioural need and thus impacts negatively on their welfare. We therefore recommend that captive snakes be kept in an enclosure longer than their body length.

1. Introduction

Reptiles are popular pets, with an estimated 1.2 million being kept in the UK, substantially greater than the numbers of more traditional pets such as hamsters (600,000) and guinea-pigs (800,000, [PFMA, 2021](#)). Despite this popularity, there is much debate regarding appropriate housing and husbandry for reptiles in captivity, with vets attributing many health problems to improper care ([Loeb, 2018](#)). This appears to be due to lack of knowledge rather than a lack of attachment to pet reptiles ([Haddon et al., 2021](#)). One particular challenge is the limited information available on the specialist requirements of species that are commonly owned, reflecting a general shortage of underpinning scientific research both in captive and wild populations. There is also conflicting evidence on the uptake of this information, with some research finding that uptake of the information can be poor ([Howell et al., 2020](#)) whilst others have found that husbandry practices change and improve with the availability of information (e.g. [Bauer et al., 2018](#)) - highlighting the importance of a sound scientific evidence base.

One aspect of particular debate is the issue surrounding enclosure

size and the available space necessary for snakes. They are unusual in both their length relative to their overall size and the way in which they utilise their environment. Snakes are kept in varying conditions, ranging from a 'rack' style system, where they are kept in relatively small boxes to large vivaria that are of greater length than the snake itself, with no consensus on what is most suitable for good welfare. For example, in the *Licensing of Activities Involving Animals (LAIA) Regulations 2018 Guidance notes for conditions for selling animals as pets*, the minimum enclosure length for snakes is $2/3 \times$ snake length (i.e. less than the length of the snake), with many keepers housing their snakes in enclosures of this size or less ([Warwick et al., 2019](#)). However, it is also recommended (e.g. [PIJAC, 2016](#); [British Pet Insurance Services, 2019](#); [RSPCA, 2019](#) and as reviewed by [Warwick et al., 2021](#)) that snakes are given sufficient space within their cage to allow them to stretch to their full length and the potential to move lengthways (i.e. $>1 \times$ snake length). Given that many commonly kept snake species can grow to significant lengths (e.g. corn snakes (*Pantherophis guttatus*) grow to around 150 cm and sometimes larger – maximum recorded individual was 182.9 cm [Conant and Collins, 1998](#)), this recommendation requires substantial enclosure sizes

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that are often considerably larger than owners may provide.

Restricted movement due to confinement is considered to be a primary stressor for animals in captivity because it potentially results in the inability to escape from aversive stimuli such as light, sound, inappropriate climatic variables, as well as con- and hetero-specifics (Morgan and Tromborg, 2007). For animals more commonly kept as pets, such as rabbits, the importance of sufficient space to carry out normal behaviours, including a wide range of locomotory behaviour (e.g. rearing, stretching) and spatial usage (e.g. exploration), has been highlighted, and cages that inhibit these behaviours have a negative impact on welfare (Morton et al., 1993; Dixon et al., 2010). Similar findings have been demonstrated for a range of animals, including: chickens (Leone and Estevez, 2008); rats (Patterson-Kane, 2010); and primates (Buchanan-Smith et al., 2004). It is thought that insufficient space can lead to a number of health problems for reptiles, e.g. loss of bone density and muscle, and weight gain leading to obesity (Divers and Mader, 2005; Divers and Stahl, 2018).

In the wild, although snakes spend time resting hidden in a curled position to protect themselves from predators and to retain heat (Fitch, 1949), they may reach near to their full length while active (Jayne, 2020). Snakes have distinct locomotor patterns that are utilised to move effectively around their environment. For example, they move in a rectilinear motion (i.e. a caterpillar-like movement where the body is maintained in a straight line) when moving alongside a straight object or edge (Marvi et al., 2013; Newman and Jayne, 2018), and use concertina locomotion in arboreal habitats or when space to move laterally is limited, such as in tunnels (Gray, 1946; Astley and Jayne, 2007). All types of locomotion use some degree of body straightening, with this being particularly common in rectilinear, concertina and sliding motion (Jayne, 2020). These types of locomotion are key behaviours within the natural behavioural repertoire of a snake, and so providing an enclosure that thwarts the expression of these behaviours may compromise their welfare (e.g. Mason and Burn, 2011).

Snakes' need for space provision has caused considerable debate (e.g. Newman, 2018; Warwick et al., 2019, 2021). The single study to date that has looked at the effect of enclosure size alone on snake behaviour investigated the impact of rearing rattlesnakes (*Crotalus enyo*) in two different sized enclosures (Marmie et al., 1990). No effect of enclosure size was observed on either their response to a novel environment or their persistence in following the scent of a prey item. However, this study was confounded by age and, crucially, with adult rattlesnakes of this species reaching a length of 89.8 cm (Klauber, 1956) even the large enclosure used in the study was substantially smaller than the length of an adult rattlesnake. As such, once fully grown, snakes would have been unable to stretch out in both conditions. Two recent studies have found that increasing environmental complexity and enclosure size together resulted in increased behavioural diversity and activity levels in two species of snake (Giant Hognose Snakes (*Leioheterodon madagascariensis*; Spain et al., 2020; Ball Python *Python regius* Hollandt et al., 2021). However, in these studies both enrichment and enclosure size were changed at the same time, making it difficult to determine what specific aspect influenced the snakes' behaviour – particularly given that the provision of enrichment alone impacts behavioural diversity and activity levels in snakes (Hoehfurtner et al., 2021). The aim of our study was therefore to fill this knowledge gap by comparing the impact of two different enclosure sizes on the range of behaviour exhibited by, and the overall welfare of, one of the most commonly kept captive snake species, the corn snake (*Pantherophis guttatus*), where the larger enclosure was longer than the maximum length of corn snakes.

2. Methods

2.1. Animals

Twelve captive-bred, adult corn snakes (*Pantherophis guttatus*), measuring ~118–157 cm, from a range of backgrounds and experiences,

were obtained from a reptile shelter. The snakes were housed at the University of Lincoln for the duration of the study and returned to reptile shelters for rehoming at the end of the study. Snakes were fed every two weeks on a Friday afternoon (~15:00). They were fed one dead (frozen and thawed) mouse, appropriate to their size. If the snake refused to eat another feeding attempt was made the following day, if at this point the food was still refused further attempts were not made until the next Friday.

Snakes were handled regularly for brief periods (2–5 min) each day to habituate them to the handling that they would experience when moved to the arena for testing, as well as that required for general husbandry purposes. Snakes were not handled for two days after feeding or during shed once their eyes turned 'milky' until 24 h after completing their shed.

2.2. Housing

Snakes were housed in one of two sizes of enclosure, a 'small' enclosure, measuring 83 × 35 × 39 cm (internal dimensions), approximately equal to two thirds of the snakes' lengths (to reflect LAIA guidance), or a 'large' enclosure, measuring 179 × 58 × 58 cm (internal dimensions), longer than the greatest length of any snake (to reflect guidance e.g. PIJAC, 2016; British Pet Insurance Services, 2019; RSPCA, 2019 and as reviewed by Warwick et al., 2021). Snakes were assigned to either a *small* or a *large* enclosure on their arrival, this was balanced for approximate size; all animals were housed individually. Six of the snakes were thus housed in the *small* enclosures, and the remaining six in the *large* enclosures.

The room lighting was on a 12-hour light/dark cycle (lights on from 07:00 till 19:00). All enclosures contained a 'natural' heat source, controlled by a HabiStat dimming thermostat (HabiStat, UK) that was also on a 12-h light cycle (on from 07:00 till 19:00) and a 'natural' light source, which was on four hours a day 10:00–14:00. The 'natural' light source took the form of a 60 cm UV tube located in the middle on the ceiling towards the back of the enclosure for both the *large* and the *small* enclosures. Both the heat lamp and the UV lamp were covered with a cage guard to prevent the snakes from coming into contact with the bulbs. All enclosures also contained the same enrichment in the form of a 'rock/cave' hide, a hanging hide, a 'humid' hiding place containing moistened moss and compost, a branch, a water bath, and a 'natural' substrate (Aspen shavings). All items were consistent in absolute size between the two sizes of enclosure. Snakes were housed in their respective enclosures for a minimum of 32 days before experiencing a series of behavioural tests of anxiety, after which they were housed in the size of enclosure that they had not previously experienced (i.e. from *small* to *large*, *large* to *small*), which they then also experienced for a minimum of 32 days before being presented with the same set of behavioural tests.

2.3. Welfare assessment

A series of measures were used to assess whether there was a differential impact on snake welfare between the two enclosure sizes. A combination of techniques were used: within-enclosure observation, to measure behaviours expressed and space utilisation; behavioural tests to measure response to a mild stressor; and preference tests after exposure to both enclosure types. The snakes were also weighed throughout the study. This approach allowed a comparison of how the animals behaved in, and interacted with, the enclosure, the impact of housing on their health and anxiety levels and their preference for the different enclosure sizes.

2.4. Behavioural observations

Behavioural observations were performed twice a week (Tuesday and Thursday). Snakes were video recorded in their enclosures without

the observer present in the room to ensure their behaviour was not affected by human presence. Snakes were filmed for 30 min. After a snake was filmed the observer recorded the location of the snake within the enclosure so that this could be recorded if the snake was not visible in the video (e.g. in a shelter/hide). Filming was carried out at different times of the day spread over the full 12 h period that the lights were on, to take into account any effect on behaviour of the time of day. The order in which the snakes were recorded was pseudo-randomised to control for effects of observation order. Snakes were not handled for 2 h prior to recording to avoid any effects of handling. Behaviours analysed are in [Tables S1–S2](#).

2.5. Weight

Snakes were weighed every Friday (before feeding if on a feeding day), apart from when they were in shed. Snakes were weighed to the nearest 5 g. To overcome differences as a result of snakes not being present in the dataset for that day (when shedding) an average was calculated using values either side of the missing values, if multiple values were missing a moving average was calculated.

2.6. Anxiety tests

The snakes were given behavioural tests of anxiety to observe their response to novelty; novelty tests are a classic test for anxiety-like behaviour (e.g. [Prut and Belzung, 2003](#)) and have been demonstrated to be appropriate for reptiles ([Moszuti et al., 2017](#)). These were carried out on two occasions, once each time after the animals had experienced one of the two housing conditions for 32 days (order counter-balanced across individuals). On both occasions the snakes were given a novel environment test followed by a novel object test.

Two arenas were set up so that two snakes could be tested at a time, one in each arena. The snakes were returned to their home environments between trials and were given an inter-trial interval of 15–35 min. The arenas were cleaned with diluted disinfectant prior to and in between every trial. The temperature of each snake was measured using an infrared thermometer on the dorsal side at approximately the midpoint between head and tail before the start of each trial. Experimenters moved to the adjoining room for the duration of the trial and observed the trial on a monitor. Each trial lasted for ten minutes from the point at which the experimenter left the room. Trials were video recorded for later analysis using a video camera (Logitech C920 HD webcam) suspended above the centre of the arena. Behaviours analysed are in [Table S3](#).

2.7. Novel environment test

The snakes were assigned to one of two arenas, both arenas measured $86 \times 86 \times 75$ cm. The arenas were designed to contrast in texture, colour, pattern, and reflectiveness to enhance novelty ([Moszuti et al., 2017](#)). For the second test (after they had experienced the second size of enclosure) the snakes were exposed to the arena they had not yet experienced. Assignment of which arena was experienced first was evenly balanced across size of enclosure (i.e. half of the snakes that were in the *large* enclosure first experienced arena A first, and the other half arena B). The arena was covered with an acrylic lid. The snake was placed in the same location at the start of each trial.

2.8. Novel object test

The same arena was used for the novel object test as had been used in the novel environment tests. Each snake was habituated to the arena over a series of ten-minute habituation trials, snakes were considered habituated after they moved within ten seconds of the experimenter leaving the room and climbing within two minutes, or after eight trials, whichever occurred first. Each snake received a minimum of two

habituation trials, and no more than five trials in one day. The novel object test was carried out on the same day as the final habituation trial. Each snake received one novel object test per condition.

The 16 sections marked on the arena floor were grouped into quadrants. A novel object was placed in the centre of the top left or top right quadrant before the start of each trial. The snake was placed in the arena in the quadrant diagonally opposite to that containing the novel object. The novel object was counterbalanced across left and right quadrants between snakes, enclosure sizes and only one novel object test, per object, was carried out for each individual snake. The novel objects consisted of a range of similarly sized items (sizes varying from $5 \times 10 \times 7$ cm to $13 \times 14 \times 18$ cm) of different colours and shapes. The novel object was cleaned with diluted disinfectant between trials.

2.9. Motivational conflict tests

The snakes also received two different behavioural tests (emergence test and reverse emergence test) in which they were given the opportunity to select between two potentially conflicting motivations: to stretch out or to use a shelter ([Balasko and Cabanac, 1998](#); [Millsopp and Laming, 2008](#); [Appel and Elwood, 2009](#)). A long opaque arena was constructed out of polycarbonate sheets measuring 200×40 cm. An acrylic panel was placed on top of the arena and a grid dividing the arena into 10×10 cm squares was drawn on the floor of the arena. This arena was used for both conflict tests, both tests lasted for ten minutes from the point at which the experimenter left the room. Animals experienced both types of conflict test once after each housing condition (i.e. four conflict tests in total). Trials were video recorded for later analysis using a video camera (Logitech C920 HD webcam) suspended above the centre of the arena. Behaviours analysed are in [Table S4–S5](#).

2.10. Emergence test

Snakes were allowed to enter the hide of their own accord, this was achieved by holding them in front of the hide ($\varnothing \approx 28$ cm). Once fully inside the hide, the hide containing the snake was placed at one end of the arena. Each trial lasted 10 min. The position the hide was placed was counterbalanced across individuals and conditions.

2.11. Reverse emergence test

The following day the snakes were given the reverse of the above test in the same arena, with the empty hide placed at one end of the arena prior to the trial and the snake was placed at the opposite end (i.e. with the snake starting outside of the hide). The trial started with the snake being placed in the starting position, each trial lasted 10 min.

2.12. Preference Test

After the second set of behavioural tests had been completed, snakes were given a preference test between the *large* and the *small* enclosures. Each snake therefore received just one preference test after it had experienced being housed in both sizes of enclosure. The test set up was created by cutting a hole in the back of one *small* and one *large* enclosure and joining them together with a plastic T-tube ($\varnothing = 11$ cm) with an insert for the T-junction to create a straight tube and a screw cap for the access point ([Fig. 1](#)). The top of the enclosures were removed and replaced by a 4 mm sheet of acrylic to allow viewing from above. The original vivarium glass was covered with opaque sticky back plastic to create a visual barrier between the snake being tested and the other snakes in their home enclosures.

The snake was placed in the T-tube at 16:00 and removed the following day at 10:00 h. A camera (Raspberry Pi 3 Model B+, camera V2.1) was placed directly above the set up. The camera recorded a time lapse at 2 s intervals from 16:00 to 10:00. An infra-red light was placed above the setup to allow viewing in the period in which the room lights

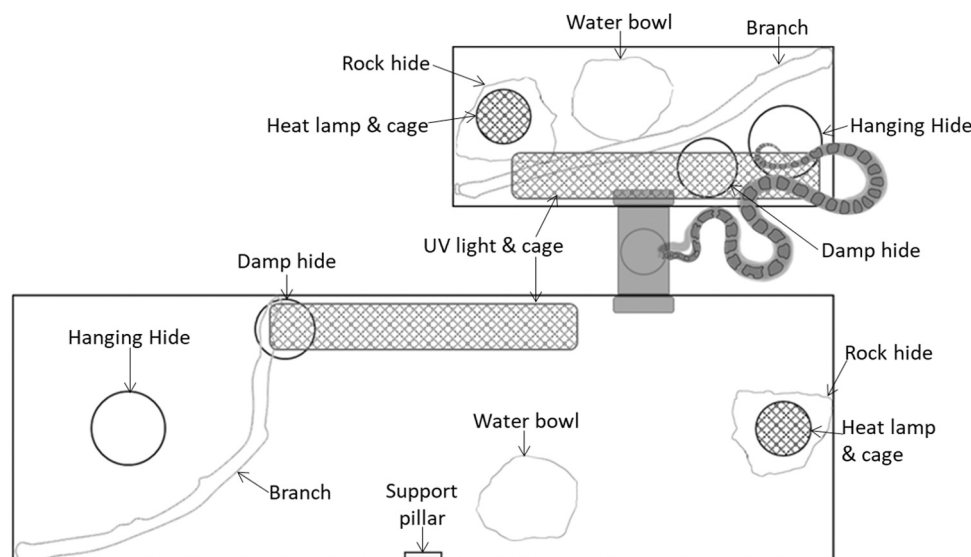


Fig. 1. Aerial view of the preference test set up.

and heat lamps were off. As the snakes were recorded over an 18-h period under both light and dark conditions during which their activity levels varied, we assessed their preferences both when active and when resting.

3. Data analysis

3.1. Behavioural observations

All videos were coded using BORIS (Friard and Gamba, 2016). Location within the home environment was sampled every 2 min starting at 0 and finishing at 30 min. Location was calculated as proportion of observations for which the snake was 'visible'. Other behaviours within the home environment were continuously recorded for 1 min at 5 min intervals, with the first recorded minute starting at 5 min, and the last minute starting at 25 min. If the snake was not visible for the entirety of the video the location was taken from the notes taken by the experimenter to ascertain the location of the snake for that video. Resting and visibility were calculated as a proportion of total duration of the video. Locomotory behaviours (Full Locomotion, Partial Movement and Stationary) were recorded as a proportion of the total time these behaviours were recorded. Nose rubbing was calculated as a proportion of active time i.e. when the snake was not recorded as 'resting', but was visible. 'Stretch' was calculated as a proportion of time spent resting outside of the hide. No instances of drinking or excreting were recorded and only one instance of submersion in the water bowl was observed, thus these behaviours are not reported. Nose rubbing and gaping occurred too infrequently in either condition to allow for statistical analysis.

3.2. Novelty tests

Behaviours were recorded continuously during the novelty tests. Duration of behaviour was extracted for all behaviours, so that each snake had a *large* and a *small* value for each behaviour. Durations were converted to proportions of observed time. Latency was also extracted for movement and object related behaviours. For object related behaviours frequency data was also extracted.

3.3. Motivational conflict tests

Behaviours were recorded continuously during the motivational conflict tests. Durations were converted to proportions of total time,

latencies are given in seconds and lengths measured from the snake were calculated as proportions of the snake's total length. Snake lengths were calculated from images taken of the snakes from directly above and measured in ImageJ (Rasband, 1997), three images were taken during the study and an average calculated to give a single measurement for each snake.

3.4. Statistical analysis

The study was designed as a within-subjects design so that each snake experienced both enclosure sizes (balanced for order) to account for individual differences, thus a mixed effects model using the function 'lmer' in the package lme4 (Bates et al., 2015) was used to investigate differences in behaviour between the *large* and *small* enclosures. For each behaviour, a linear model was specified with enclosure size (*large/small*) as the fixed effect, snake (individual) specified as a random effect, and behaviour as the outcome variable. P values were calculated using lmerTest (Kuznetsova et al., 2017). In the body weight analysis, enclosure size was included as a fixed effect, week as a covariate, and body weight as the outcome variable. One third of the videos from the novelty tests were second coded and a Spearman's rank correlation revealed a strong positive correlation between observers (novel environment test: $\rho = 0.99$, $p < 0.001$, novel object test: $\rho = 0.99$, $p < 0.001$). Choice in the preference test was analysed using a paired Wilcoxon signed rank test using the function 'wilcox.test' in the stats package (R Development Core Team, 2020) and the z value calculated using the function 'wilcoxonZ' in the package rcompanion (Mangiafico, 2021). All statistical analysis was carried out in R (version 4.0.2, R Development Core Team, 2020).

4. Results

4.1. Behavioural observations

Snakes were significantly more active when housed in the *large* enclosures, i.e. less time was spent resting ($t = 3.308$, $df = 203.00$, $p = 0.0011$, Fig. 2). Whilst resting, snakes in the *large* enclosure spent significantly more time loosely coiled ($t = -5.260$, $df = 98.81$, $p < 0.001$), and snakes in the *small* enclosure spent significantly more time partially coiled ($t = 3.771$, $df = 97.25$, $p < 0.001$) and tightly coiled ($t = 3.326$, $df = 94.96$, $p = 0.0013$, Fig. 2). Snakes also spent on average approximately 19% of their time 'stretched' while resting in the *large* enclosure; however, this was not compared statistically because

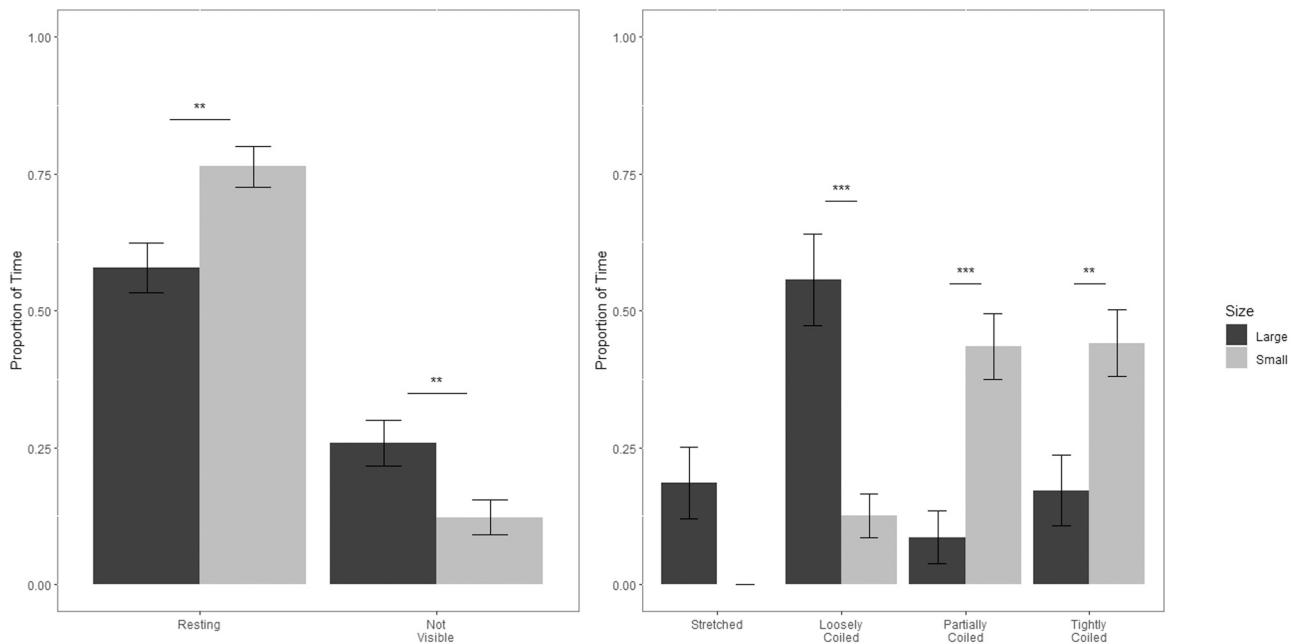


Fig. 2. Proportion of time spent resting and not visible in the two enclosure sizes (left) and proportion of time spent resting outside of the hide in various degrees of elongation (right). Note: It is not possible for snakes in the small enclosure to be 'Stretched out' (defined as 'Snake is in a straight or near straight line posture, with a mostly continuous portion of the snake being straight, (i.e. no lateral bending) with no self-contact. Cannot be going round corners to be defined as stretched.').

snakes in the *small* enclosure were not able to exhibit this behaviour. Snakes spent significantly more time visible when in the *small* enclosures ($t = -2.697$, $df = 203.00$, $p = 0.0080$, Fig. 2). There were no significant differences between any of the other behaviours (Table S6).

Snakes in the *large* enclosures spent significantly more time in hides ($t = -3.191$, $df = 203.00$, $p = 0.0016$), particularly the hanging hide ($t = -2.961$, $df = 203.00$, $p = 0.0034$), whereas in the *small* enclosures snakes spent more time on the substrate ($t = 2.022$, $df = 203.00$, $p = 0.0445$) and on the branch ($t = 3.319$, $df = 203.00$, $p = 0.0011$, Fig. 3).

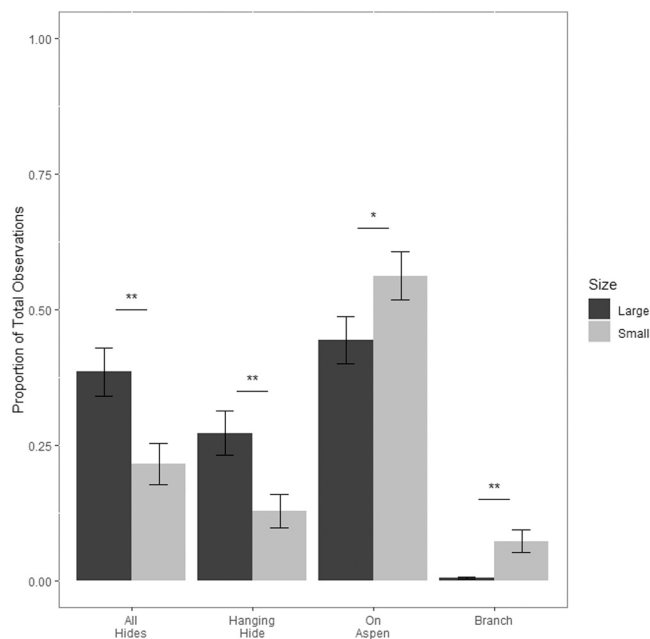


Fig. 3. Proportion of time spent in proximity with objects in the enclosure, only objects with significant differences are shown.

4.2. Weight

Weight did not significantly differ between enclosure sizes ($F_{1,121} = 0.547$, $p = 0.461$), throughout the study ($F_{5,121} = 1.035$, $p = 0.400$) or between enclosure sizes over time ($F_{5,121} = 0.532$, $p = 0.752$).

4.3. Behavioural tests

4.3.1. Anxiety tests

4.3.1.1. Novel environment test. Snakes had a similar range of body temperatures during the novel environment test ($23.9^{\circ}\text{C} \pm 0.3$). No significant differences were found in the novel environment test between snakes in *small* and *large* enclosures (Table S7).

4.3.1.2. Novel object test. Snakes had a similar range of body temperatures during the novel object test ($25.2^{\circ}\text{C} \pm 0.1$). Proportion of time the body (not inclusive of the head) was in contact with the object was significantly greater when the snakes were in *small* enclosures ($t = 3.086$, $df = 11$, $p = 0.0104$, Fig. 4). No other measures showed significant differences (Table S8).

4.3.2. Motivational conflict tests

4.3.2.1. Emergence test. Snakes had a similar range of body temperatures during the emergence test ($24.5^{\circ}\text{C} \pm 0.3$). There were no significant differences between the two conditions for any of the measures (Table S9).

4.3.2.2. Reverse emergence test. Snakes had a similar range of body temperatures during the reverse emergence test ($24.0^{\circ}\text{C} \pm 0.3$). Snakes in *large* enclosures spent more time outside the hide ($t = -3.198$, $df = 11$, $p = 0.008$) and were quicker to reach the hide ($t = -2.923$, $df = 11$, $p = 0.014$, Fig. 5).

There was no difference in maximum elongation between the two conditions (see Table S10 for details).

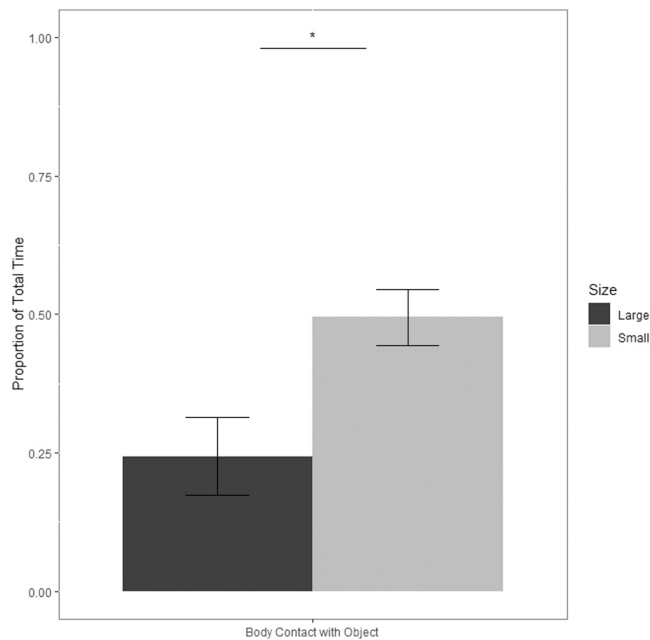


Fig. 4. Proportion of time that snakes spent in contact with the object with the body (not inclusive of the head).

4.4. Preference test

Snakes had to use the connecting tunnel in order to visit both enclosures, therefore, to ensure that the snakes were able to demonstrate a preference they had to visit both the *large* and the *small* enclosures at least once during the preference test. If this did not occur, they were retested and only results from tests where both enclosures were visited are included. 10/12 snakes completed on their first test, the remaining two on their second test. Analysis of the preference test data revealed that, when they were active, the snakes spent a significantly greater proportion of their time in the *large* enclosure ($z = -2.903$, $p = 0.001$, Fig. 6). When they were resting, they did not display a significant preference for either enclosure size ($z = -1.155$, $p = 0.267$).

5. Discussion

Our findings suggest that housing captive corn snakes in *large* enclosures (longer than the length of the snake) was beneficial to their welfare. When housed in *large* enclosures, snakes were more active and spent time stretched out. In addition, when given the choice between the two sizes of enclosure, snakes exhibited a strong preference for the larger enclosure when active. However, the results of the behavioural tests were less clear, with no consistent indication of differences between the two enclosure sizes in the recorded anxiety measures.

When snakes were housed in the larger enclosures we observed greater activity, stretching and exploration; expressions of normal behaviour considered to be welfare-enhancing (Mellor, 2015). Snakes in

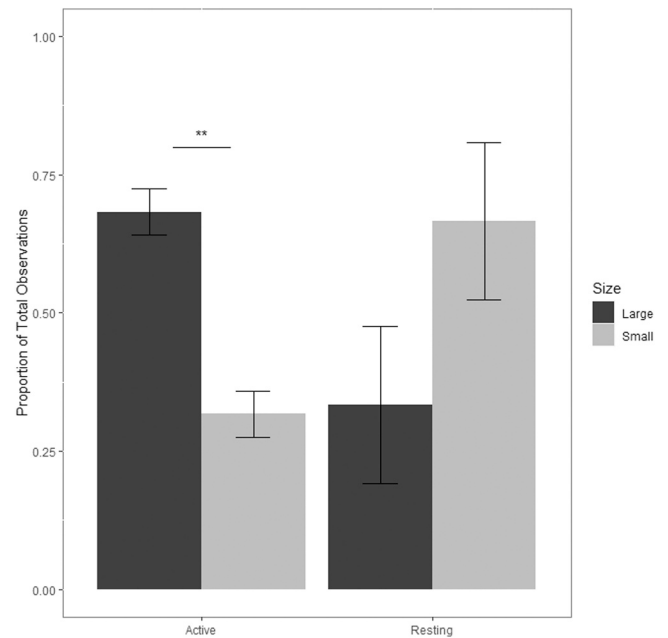


Fig. 6. Average proportions of observations snakes spent in the large or small enclosure in the preference test.

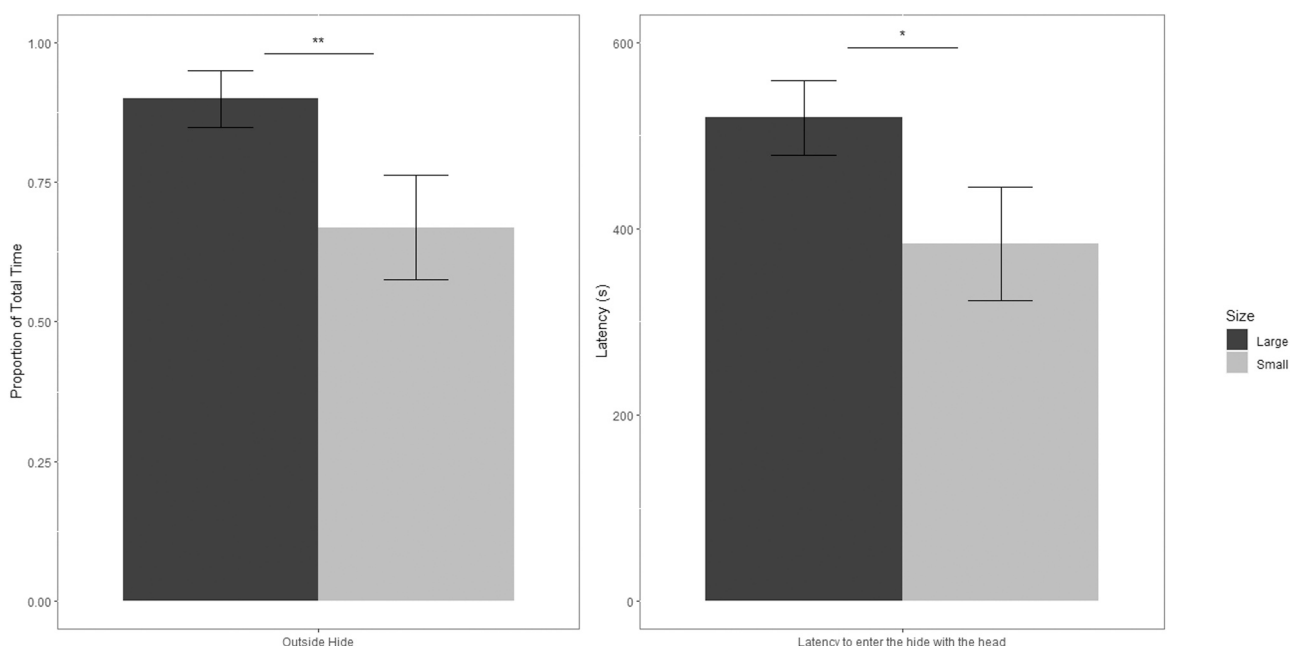


Fig. 5. Time spent outside of the hide (left) and latency to enter the hide with the head (right).

the *large* enclosure also spent significantly more time in the hides, whereas snakes in *small* enclosure spent more time on the substrate, resulting in more time spent visible. Eastern blue tongue lizards (*T. scincoides*) were also found to make more use of hides in larger enclosures. This highlights the importance of providing suitable hiding places and environmental complexity alongside additional space, improving the quality as well as the quantity of space (e.g. Buchanan-Smith et al., 2004), because corn snakes require a suitable selection of hides and other resources to meet their behavioural and cognitive needs (Hoehfurtner et al., 2021; Nagabaskaran et al., 2021).

Whilst resting, snakes spent significantly more time tightly or partially coiled when housed in the *small* enclosures, whereas snakes in the *large* enclosures were observed to spend significantly more time loosely coiled, reflecting the greater space availability but also a more positive welfare state of reduced anxiety and increased relaxation (Hoehfurtner et al., 2021). When housed in *large* enclosures that allowed them to stretch out, the snakes chose to do so, spending around 19% of their resting time in this position – an option that was not physically available to them when housed in the *small* enclosures that were ~2/3 of the snakes' body length. Housing a snake in a *small* enclosure would therefore thwart these strongly motivated natural behaviours, representing a significant welfare concern (Mason and Burn, 2011).

The results of the behavioural tests were less clear, with few indications of differences between the two enclosure sizes in the behavioural tests of anxiety or conflict. The small number of significant differences that were observed in these four tests (e.g. snakes in *small* enclosures spent more time with their body (not inclusive of the head) in contact with the novel object, and snakes in *large* enclosures spent more time outside of the hide in the reverse emergence test) were apparently contradictory. With so few significant results in the range of behavioural tests used here, and no significant effects at all for the novel environment test or emergence test, these results should be taken with caution. Marmie et al. (1990) similarly found no effect of enclosure size on the response of rattle snakes to a novel environment. Therefore, it may be that, although these kinds of test have been found to be effective in tortoises (Moszuti et al., 2017) and bearded dragons (Siviter et al., 2017; Stockley et al., 2020), they are less appropriate for snakes – either because individual differences potentially mask an effect, or, because any effects did not impact snakes in such a way that changed their behaviour under these conditions.

Preference and choice tests are thought to be an important measure of animal welfare and can be used as a benchmark against which other measures can be validated (Dawkins, 2008). The preference test results suggest that snakes strongly prefer to have access to an enclosure longer than their own body length when active, however, they exhibited no preference whilst resting, when they used both enclosures equally. This lack of preference is likely to reflect the snakes' natural behaviour in which they both rest in shelters and small spaces (Todd et al., 2016), and, when comfortable with the environment, rest elongated (Warwick et al., 2019). In contrast, they strongly preferred additional space when active within their environment. That snakes expressed a preference when given the opportunity indicates that housing them in smaller enclosures, where such behaviour is not possible, is likely to result in compromised welfare due to a lack of control over their environment (e.g. Buchanan-Smith and Badihi, 2012) and an inability to perform a behavioural need (Dawkins, 1988). Providing animals with the choice between resting in a suitable hide or elongating while active or resting, not only more closely imitates what is available in their natural environment, but also mimics behaviours observed in the wild (Arena et al., 2018).

Although there were clear welfare benefits to being housed in *large* enclosures, we observed no differences in bodyweight between the two housing conditions, and there were also too few examples of possible stress behaviours (e.g. nose rubbing, gaping) in either enclosure size to allow analysis. However, the study was conducted over a relatively short time period (c.32 days in each enclosure size) in comparison to the

potential life-span of a captive snake, and so may not have reflected any cumulative negative effect on welfare associated with longer-term exposure (Wolfensohn et al., 2015) including weight gain. It should also be noted that in our study the snakes had identical enrichment in both enclosure sizes, and, though there were some differences in the amount that they were used between conditions, all enrichment items were utilised in both environments – something that is important for the welfare of captive reptiles (Hoehfurtner et al., 2021). This enrichment provision might have mitigated the lack of space in the *small* enclosure to an extent – although without satisfying the important motivation for stretching out necessary for good welfare.

In addition to providing the necessary space in which to perform natural behaviour, larger enclosures allow greater scope for environmental enrichment and increased within-cage environmental complexity, with the aim of encouraging the amount and diversity of positive behaviours whilst reducing behaviours indicative of negative welfare (e.g. Mellor, 2015). This is thought to increase an animal's resilience and ability to cope with challenges that it may face (Young, 2003). Enrichment (e.g. branches and hides/shelters) should be provided alongside the additional space to give the snakes options for concealment, basking, climbing, exploring, bathing and other important behaviours, as well as to provide cognitive stimulation, which has been shown to improve snake welfare (Hoehfurtner et al., 2021) and even performance on a cognitive task (Nagabaskaran et al., 2021). However, it is important that the enclosure is sufficiently large for these resources to be present whilst still providing sufficient space on the floor to move about freely and occupy a rectilinear position.

In conclusion, when the snakes had more space available they chose to use it – both during phases of activity and to stretch out when resting – suggesting a clear and valued behavioural need (Dawkins, 1988) that should be met to maximise their welfare. It is important to emphasise that good animal welfare requires these kinds of positive rewarding experiences and opportunities, and not just the absence of suffering (Mellor, 2016). As such, based on the preferences of the snakes and the within-enclosure behavioural observations, it appears that the provision of additional space sufficiently large to allow stretching out to their full length – especially when snakes were active – was beneficial to the behaviour and welfare of captive corn snakes, and is a requirement that cannot be satisfied in smaller enclosures. Our recommendation would therefore be that an enclosure longer (at least) than a snake's body length is provided for captive snakes.

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Competing Interests

The authors confirm no competing interests.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2021.105435.

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