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Burrowing in captive juvenile Desertas wolf spiders *Hogna ingens*

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Abstract

The Desertas wolf spider *Hogna ingens,* endemic to Desertas Grande in Madeira, relies on burrows under rocks and crevices for protection. Studies at Bristol and Whipsnade Zoos investigated substrate preferences and various physical aspects of the environment that might promote burrowing behaviour. It is important that habitat preferences are understood for both captive husbandry and for future reintroductions. Two choice-experiments were conducted to separately investigate (i) preferences for types of soil substrate and (ii) the effect of the presence of burrow anchor points, which provide structural support for the burrow, on burrow location. In addition, the effects of the (i) type of substrate and (ii) depth of substrate on burrow occurrence were separately investigated. In each study the onset of burrowing and characteristics of the burrow were recorded. Results show that both the type and depth of substrate impacts the construction of burrows. Optimum substrate depth was over 50 mm and lighter, loosely packed substrates were favoured in both studies. The results of a binomial generalised linear model showed that the size of stones and the clutch the spider was born of significantly explained 76% (pseduo-R^2=0.76) of the variation in likelihood that a spider would use stones as structural supports (X^2; df=1, P>0.001). Husbandry guidelines for this species will be reviewed in the light of these results and evidence will be used to inform future in-situ conservation efforts.

Introduction

Habitat selection is a critical skill needed for survival during dispersal from natal areas and after habitat disruption in many species (Cote and Clobert 2006; Bond et al. 2016). Understanding species habitat preferences has important implications for captive husbandry as differences in enclosure design can have a significant effect on the survival and reproductive success of individuals. Information on habitat preferences and selection also assists conservation efforts, not only by aiding species distribution modelling, but by providing information on which areas or features need conservation prioritisation to provide suitable habitat for remaining wild populations and reintroductions.

Burrowing is a common behaviour in arachnids. Burrows can provide protection from predators, parasites or weather and can increase the animal's ability to hide thus increasing hunting success (Humphreys 1975; Hansell 2005). Spiders also use burrows for moulting, copulation, oviposition and care of egg sacs or young (Aisenberg et al. 2011). Excavating burrows below ground can reduce fluctuations of temperature and humidity within the burrow (Bulova 2002). Habitat selection in arachnids has been shown to be influenced by vegetation (Marshall and Rypstra 1999) and soil substrate (Rezáč et al. 2018). For example, a species of wolf spider, *Pardosa milvina,* exhibited a preference for soil types formed of more than one type of substrate, complex substances, over bare earth (Rypstra et al. 2007). These complex substrates have been found to offer protection and shelter from predators or cold weather (Kraus and Morse 2005; Voss et al. 2007).

Debris such as small rocks has also been found to influence habitat selection in spiders, most commonly by providing anchor points (a form of structural support) for burrowing (Canning et al. 2014). In these situations, a preference for stones with a larger surface area has been suggested (Van den Burg et al. 2015; Taucare Ríos et al. 2017). Additionally, spiders have been seen to place rocks near the entrances of burrows in order to extend their foraging range (Henschel 1995).

The Desertas wolf spider *Hogna ingens* (Blackwall 1857) is classified as Critically Endangered on the IUCN Red List (Cardoso 2014; Crespo et al. 2014). Originally described in 1857 and named *Lycosa ingens* Backwall 1857, the species has been re-described over the years (Kulczyniski 1899; Roewer 1960) but little is known about the species' behaviour and ecology. As an endemic of Vale de Castanheira on Desertas Grande Island, Portugal, *H. ingens* is particularly susceptible to habitat disturbance within its narrow range. A native species of grass *Phalaris aquatica* has become prolific within the range of *H. ingens*, a potential effect of the removal of native competitor grasses through selective grazing by feral goats which favour other grass species in their diet. The strong roots of *P. aquatica* prevent spiders from accessing potential habitat where burrows can be constructed, resulting in displacement. These spiders rely on burrows to facilitate hunting and for protection from predation, especially during the moulting process when they are vulnerable to both predation and disturbance (Cardoso et al. 2016).

In 2017 Bristol Zoo Gardens (BZG) successfully bred *H. ingens* as part of an ex-situ conservation programme, the first recorded captive breeding of this species. Juvenile spiders were then raised at several zoological institutions. This paper addresses four studies (A, B, C and D) conducted on these juvenile spiders while in captivity at BZG (Studies A and B) and Whipsnade Zoo (WZ; Studies C and D). Each study addressed separate aspects of the aim to determine the effect of environment on *H. ingens* burrowing behaviour. Study A aimed to establish burrowing preferences for different soil substrates using choice-experiments. Here, it was hypothesised that *H. ingens* would show a significant preference for burrowing in mixes of soil substrate types, as this provides a more complex and physically stable substrate. Study B aimed to ascertain if the presence and size of a stone on the substrate surface influenced location and construction of burrows. It was hypothesised that the presence of stones would increase the probability of burrow construction, with increases in stone size having a positive effect on likelihood of burrow construction. Study C investigated the effects of substrate depth on both the construction and size of burrows, hypothesising that burrows would be more likely to be built and would be larger in deeper soils. Finally, Study D aimed to understand whether substrate type affected likelihood of burrow construction, hypothesising that spiders would be more likely to build a burrow in complex substrate types.

Materials and methods

Animals

All spiders were from four clutches of eggs produced by spiders held at BZG, which had hatched in the summer of 2017. On 8 September 2017, 25 spiders were transferred to WZ. At the start of the study period, mean spider size for BZG spiders from pedipalps to spinnerets was 6.90 mm (SD 0.44) and at the end of the study period mean size was 11.04 mm (SD 1.01). At WZ mean spider diagonal leg span size at the start of the study was 12.6 mm and mean spider diagonal leg span size at the end of the study was 39.08 mm. All spiders were housed individually within climate-controlled rooms maintained between 22 and 24°C at BZG and 21 and 25°C at WZ and were fed approximately once per week on small invertebrate prey items. The following studies were conducted using 120 spiders at BZG (60 for each study) and 25 spiders at WZ (all used for both studies).

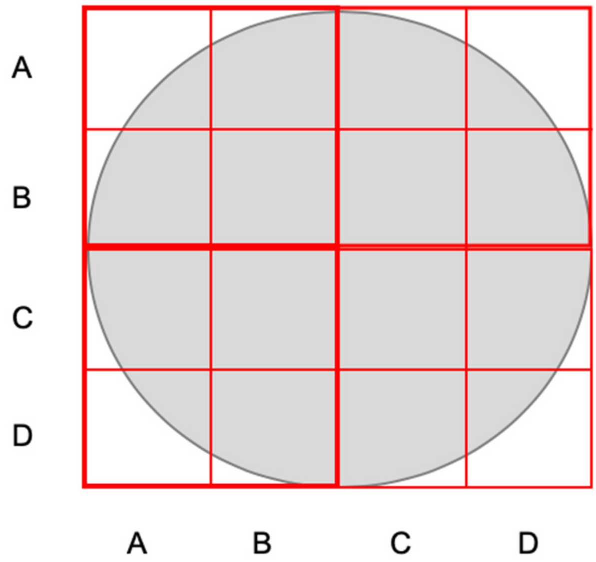

Figure 1. Layout of grid used to define locations of burrows (in Study A) and stones and burrows (in Study B). In Study A the substrate divider was along the midline vertically, in Study B all stones were placed equally in squares BA and CA. At the substrate depth of 35 cm enclosure diameter was 97.50 mm.

General

Study A was conducted between 5 January and 27 February 2018, Study B between 28 February and 1 May 2018, Study C between 17 September and 30 November 2017 and Study D between 30 November 2017 and 20 June 2018. Throughout this period both institutions undertook burrow observations, which included noting the construction of any new burrows, destruction of old burrows and taking burrow dimension (length and width) measurements of the burrow cross section visible through the translucent enclosure walls. This occurred twice weekly at BZG and once per week at WZ. Burrows were measured using Marathon CO030003 Vernier Callipers (WZ) and unbranded LCD digital Vernier Callipers (BZG). However, burrow dimensions were not recorded if the resident was in the burrow in order to prevent undue disturbance. A burrow was defined as an excavated crevice or hole made under the substrate surface by physical disturbance of the substrate, often lined with silk webbing. Abandoned burrows were defined as those that were actively destroyed by the spiders or left unused for a period of 48 hrs (instead being replaced by a newly constructed burrow). Husbandry data on feeding, growth and moults were also recorded but are not presented here.

Study A: Choice tests on substrate type

A total of 60 *H. ingens* juvenile spiders were housed individually in clear plastic pots (115 mm diameter at the top and 80 mm diameter at the bottom × 80 mm deep) filled with 35 mm substrate and tamped down. Each spider was assigned to one of five substrate types, with 12 spiders for each condition. For each condition, coir (coconut fibre) substrate filled one side of the treatment pot with a plastic partition dividing the substrate vertically into two equal

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Figure 2. Study A enclosures with vertical division between two substrate types, coir on the left and a coir/sand mix on the right.

Figure 3. Enclosures used in Study D.

areas (Figure 2). The other side was filled with either coir, sand or a mix of the two in different ratios (1:3 coir:sand; 1:1 coir:sand; 3:1 coir:sand).

The case where both sides of the treatment pot contained coir was treated as a control. Coir was chosen as the control substrate as it is the standard substrate used in routine husbandry within both zoos. Whether burrows were made in the coir or the test substrate side of treatment pots was recorded. Additionally, the locations of burrows were noted according to the grid square layout in Figure 1. A Fisher's exact test was conducted on the results.

Study B: Testing effects of presence of an anchor point

For Study B, an additional 60 individuals, housed in the same style pots as the first study on 35 mm of coir substrate, were divided into five groups of 12. Of these, four groups had a small stone placed in the enclosure between grid squares BA-CA (Figure 1) while the fifth, control, group had no stone. Stones were approximately the same shape and had an area of 2 cm^2 (group 1), 4 cm^2 (group 2), 6 cm^2 (group 3) or 8 cm^2 (group 4).

Stones were recorded as being used as anchor points if the burrow touched the stone or incorporated it as part of the structure. To test if stones were more likely to be used as anchor points when they had a larger surface area, a binomial generalised linear model (glm, family=binomial, link=logit) was fitted. The response variable was whether the stone was used as an anchor point or not. The area of enclosure available for burrowing varied for different stone sizes; therefore, this was controlled for in the model by including the remaining exposed substrate surface area as an offset variable. The retained model was selected from a full model (which included stone area, spider clutch, date of data collection and spider size as explanatory variables) following Akaike's Information Criterion (AIC). The retained model was tested for over/under-dispersion and residual plots were assessed to ensure model assumptions were not violated. A X^2 test was conducted on the retained model and results were reported as statistically significant if the p-value was equal or less than 0.05.

Study C: Testing effects of substrate depth

Translucent plastic tubes (44 mm wide × 170 mm deep) were used to individually house 25 *H. ingens* juveniles. The 25 juveniles were divided into five groups of five, with each group assigned a different depth of coir substrate (15-, 20-, 30-, 40- or 50-mm depth). Burrow presence, dimensions and abandonment data (whether previous burrows had been abandoned and/or a new burrow built) were recorded weekly. Effect of substrate depth on burrow volume was analysed using a two-way ANOVA.

Study D: Testing the effects of substrate type

The spiders from Study C were also used in Study D, with four groups of five juveniles being rehoused into translucent plastic containers measuring 185 mm × 125 mm with a depth of 75 mm with 35mm depth of substrate (Figure 3). Each group was assigned either coir, sand, 1:1 coir:sand mix, leaf litter or chalk. The group of five that had been exposed to the shallowest substrate (15 mm) were rehoused in glass tanks 255 × 150 × 210 mm filled with 100 mm of coir substrate. Mid study, the group on chalk substrate was transferred to leaf litter substrate following the death of one juvenile found mid-moult (thought to be attributed to humidity issues related to the chalk substrate). The results from the investigation into the effect of substrate type will only be included in general terms.

All data handling and analyses were conducted in excel and RStudio statistics version 3.3.1 (R Core Team 2018) using packages plyr (Wickham 2011), dplyr (Wickham et al. 2018), lme4 (Bates et al. 2015), devtools (Wickham et al. 2020), tidyverse (Wickham 2019) and ggplot2 (Wickham 2016).

Table 1. Summary of the Akaike Information Criterion retained model predicting the likelihood of a *Honga ingens* juvenile spider using a stone as an anchor point depending on the area of the stone (cm^2) and the clutch of the spider (Study B).

	Estimate	Standard Error	z value	P value
Intercept	-749.85	1.12	-671.15	<2e-16
Area of Stone (cm^2)	1.55	0.18	8.56	<2e-16
Clutch B	1.27	1.03	1.22	0.22
Clutch C	0.13	1.06	0.12	0.92
Clutch D	-2.37	1.42	-1.67	0.10

Results

Study A: Choice tests on substrate type

Of the total 60 juveniles, 34 (56.67%) made a burrow in the 7-week observation period, 13 (38.24%) of these in the coir substrate. There were only two cases of burrow abandonment; typically, once a burrow was made it was continuously used for the whole observation period.

The condition in which the largest proportion of juveniles burrowed, regardless of the substrate in which the burrow was made, was the '1:1 coir to sand vs. coir' condition (83.33% of spiders burrowed). In the 'all-sand vs. coir' condition, all eight spiders which made a burrow burrowed on the coir side of the treatment pots, whereas in the '3:1 coir:sand' condition all burrows were made in the test material (Figure 4). A significant difference in the number of burrows constructed across substrate types was observed (Fisher's exact test, P=0.020). Two spiders in the 3:1 coir:sand group were found dead during the data collection period.

Study B: Testing effects of presence of an anchor point

Of the 48 spiders in Study B with a stone in their enclosure, 26 (54.17%) built a burrow without an anchor point, 16 (33.33%) built with an anchor point and six (12.50%) did not build a burrow.

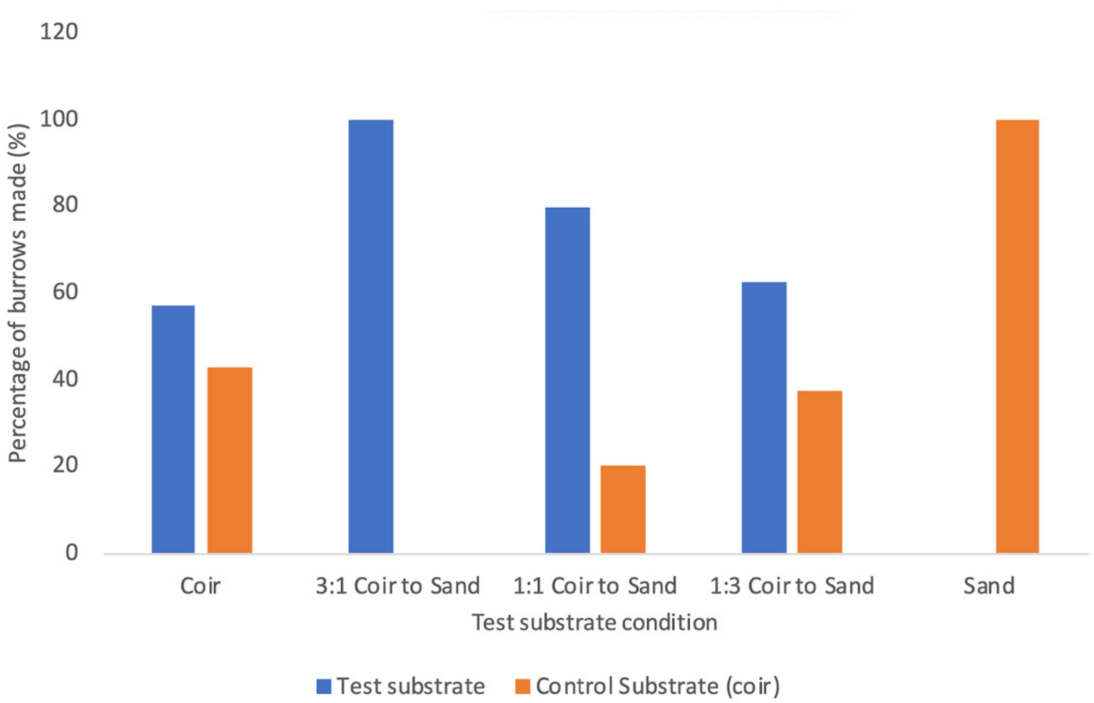

Figure 4. Percentage of burrows made in either the control substrate (coir) or test substrate in Study A. X-axis labels describe the test substrate condition provided alongside the control (coir). As only a proportion of spiders made a burrow, sample sizes for each condition vary: Coir (n=7); 3:1 Coir to Sand (n=4); 1:1 Coir to Sand (n=10); 1:3 Coir to Sand (n=8); Sand (n=5). Percentages of burrows made in the test substrate are shown by the blue bars and percentages of burrows made in the control substrate (coir) are shown by the orange bars.

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Table 2. Number of burrows and average burrow dimensions in different substrate depths (Study C).

Depth of substrate (mm)	Number of burrows started	Number of burrows abandoned	Mean burrow length (mm)	Mean burrow width (mm)	Median burrow depth (mm)	Mean burrow volume (mm3)
15	21	16	20	11	12	2432
20	13	8	20	10	14	2950
30	14	10	25	11	16	4279
40	15	10	23	13	14	3912
50	6	1	26	13	14	4702
100	6	0	26	26	26.5	17914

The AIC retained model contained stone area and spider clutch as explanatory variables, selected from the full model. Spiders with larger stones were significantly more likely to build with an anchor point than those with smaller stones ($X^{2;}$ df=1, P>0.001). The likelihood that a stone would be used as an anchor point increased by 82% per log cm increase in stone size (Figure 5; Table 1). Additionally, a weakly significant effect of clutch was found on the likelihood of anchor point use (X^2; df=3, P=0.020). The retained model explained 76% of the variation of the data (pseduo-R^2=0.76).

Study C: Testing effects of substrate depth

A negative correlation was found between the depth of the substrate and the number of abandoned burrows (linear regression R^2=0.66; Table 2). At the extremes, 16 burrows were abandoned in the 15 mm substrate-depth, whereas only one burrow was abandoned in the 50- and 100-mm substrate-depth conditions combined (Table 2). In general, where burrow parameters could be measured, the lengths and depths of burrows were greater than the widths (Table 2). There was no significant difference in burrow volume at different depths of substrate (ANOVA f=0.845, P=0.503).

Study D: Testing the effects of substrate type

In both the '1:1 coir to sand' and the 'chalk' test condition no spiders constructed burrows. Similar to the findings in Study A, only one spider built a burrow in the sand condition (Figure 6). Additionally, the sand condition had the longest latency to burrow construction.

Discussion

Substrate preferences (Study A and D)

Overall, results from Study A suggest *H. ingens* show a preference for substrates of coir/sand mixes in any ratio over 'all sand' or 'all coir' as a higher percentage of burrows were made in the test substrate than the control substrate in all conditions other than

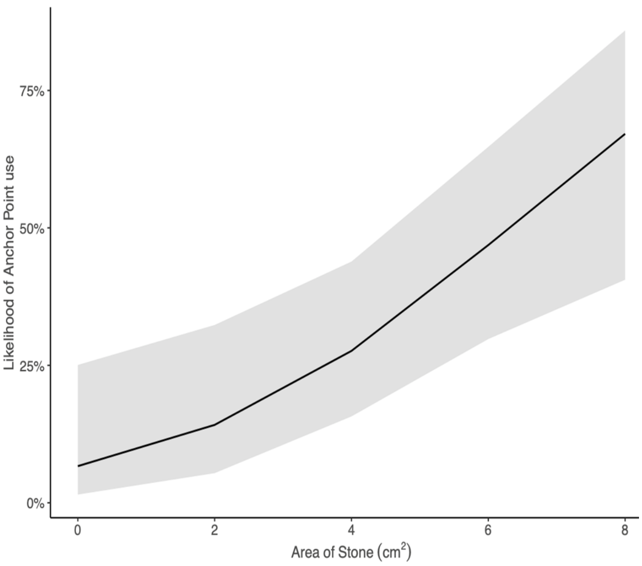

Figure 5. Likelihood of stone being used as an Anchor Point in Study B depending on stone area (cm^2) (n=12 for each stone area) according to retained binomial generalised linear model prediction. Grey shaded area represents 95% confidence intervals around this prediction.

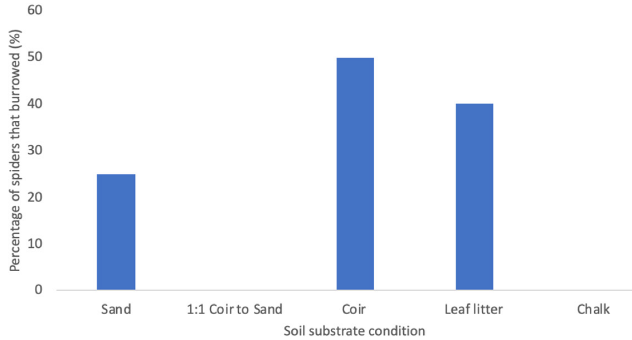

Figure 6. Percentage of spiders that made burrows for each soil substrate condition in Study D (Sand, n=5; 1:1 Coir to Sand, n=5; Coir, n=16; Leaf litter, n=10; Chalk. n=5). Spiders were considered to have burrowed whether their burrow(s) were utilised or abandoned.

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'all sand' (Figure 4). Study D results are consistent with that of Study A, also suggesting that pure sand is an unsuitable substrate, as the latency to burrows being constructed was longest in the pure sand condition. There were differences between the two studies' results with regards to preference for the 1:1 mix of sand and coir. Thus, it is not clear whether this is a suitable substrate and further research should be conducted.

The physical properties of the substrate influence the construction of burrows (Rypstra et al. 2007; Rezáč et al. 2018). Burrowing in sand may be limited by the 'free-flowing' quality of sand, as friction between particles is low, reducing structure stability. Burrowing behaviour was infrequent in the heavier substrates tested in Study D, such as sand and chalk. It should be considered that preferences may change over time; for example, Carrel (2003) found that a *Geolycosa* species of wolf spider changed its preference from barren sand to areas with more leaf litter coverage as they grew and their burrows were becoming larger.

A caveat of the substrate trials was that different soil types retain moisture to differing degrees, which may have biased burrowing. On Vale de Castanheira on Desertas Grande the soil is fine and dusty dirt, most similar to dried loam substrate. Although this might be expected to be a preferred substrate, when a similar soil was created it was found that the loam becomes sticky when moistened. Spiders initially exposed to this substrate were impeded by particles adhering to their legs so this was discontinued and not used in this investigation. Chalk has particle sizes similar to the Desertas soil, but was found to be unsuitable for similar reasons.

In both studies light, loose-packed substrates (i.e., mixes of substrates and leaf litter) were frequently selected by spiders and promoted high levels of burrowing. This may be explained by a trade-off between the energetic costs of burrowing in heavy material and the increased structural support of heavier substrates. Albín et al. (2018) found that a sand dune dwelling species of wolf spider *Allocosa senex* preferred digging in coarse sand over fine sand although rested longer when digging in coarse sand. This was attributed to the energetic costs of moving the grains. Suter et al. (2011) found similar results in *Geolycosa* species; more burrows were constructed and with shorter latencies in the lighter materials that also required less energy to move.

Some species of wolf spider make use of crypsis for protection against predators, for example, *Schizocosa ocreata* on leaf litter (Clark et al. 2011). Many wolf spiders are obligate sit-and-wait predators that rely on the same burrow for long periods, such as *Geolycosa* sp. (Marshall 1995). If *H. ingens* relies on camouflage, either as a sit-and-wait predator or as protection against predation, a preference for darker substrates might be expected. However, these mainly black and brown coloured spiders showed no affinity to the darker substrates when there was a choice, either for burrowing or where they were observed in the enclosures.

The death of a spider on the chalk substrate at WZ may have been associated with low humidity levels as high humidity with hygroscopic materials led to hardening of the substrate. This group was least likely to have burrowed and some individuals were repeatedly seen in the same corners of their enclosures rather than freely moving between different locations.

Anchor points (Study B)

Results of the binomial generalised linear model support the hypothesis that as stone size increases there was a significant positive effect on the likelihood of burrow construction (X^2; df=1, P>0.001). This suggests that stones with larger surface areas provide more structural support for burrows than stones with smaller surface areas. The significant effect of clutch on likelihood of using an anchor point when burrow building suggests an influence of genetics upon burrow building behaviours (X^2; df=3, P=0.020). Genetic effects on wolf spider burrowing behaviours and burrow characteristics have previously been found; for example, Murphy et al. (2006) found phylogenetic variation between wolf spider species that permanently burrow and only burrow for brood-care and wolf spider species that build burrows with trap-doors compared with turrets. The effect of intraspecific genetic variation on burrowing strategies of *H. ingens* remains currently unstudied and is an area for future research.

Depth of substrate (Study C)

Abandonment of burrows was greater in substrates that were less than 50 mm deep. It is not clear whether this is as a result of burrows not providing appropriate shelter or security or if it was a maturational effect as, consistent with findings from Marshall (1995), there were greater rates of burrow abandonment at both institutions in early stages of the studies when the spiders were younger and smaller. The continual burrow making seen in the shallower substrate depths could indicate that the spiders are unable to produce a burrow that satisfies their requirements and may have implications for captive husbandry, such as requiring a minimum substrate depth limit for housing *H. ingens*.

No relationship was found between the depth of the substrate and the burrow volume, in contrast to the findings of Miller and Miller (1984). This may be an effect of either the low sample size or the developmental stage of the spider. Albín et al. (2016) showed that the number of entrances, branches and overall burrow dimension varied with life stage in the sand-dwelling wolf spider *Allocosa brasiliensis.* Therefore, as results from these studies relate to spiders at different life stages, results may explain behaviours unique to these life stages.

General observations

It is noted that results of these four studies may differ if spiders at different life stages were tested and, therefore, results are only generalisable to juvenile spiders. However, as each study consisted of spiders of same age as each other, and as results have been analysed within studies rather than across studies, the difference in ages between the four studies does not affect the accuracy of the results. The effect of age on the relationships identified in these studies could be investigated in the future.

The characteristic shapes of a range of wolf spider burrows are discussed by Uchman et al. (2018). In some species the shapes change at different times in the life cycle depending on whether the burrow is used primarily for shelter and defence or for mating and nurturing egg sacs. Burrow dimension data showed that juvenile Desertas wolf spider burrow size did not change over the relatively short periods of these studies. However, more research is needed on the characteristics and dimensions of Desertas wolf spider burrows at different spider life stages. Additionally, casts of burrows could be made in order to determine burrow size and structure under different conditions and life stages of this species.

Although the spiders were of similar ages and had undergone similar numbers of moults when transferred to the test conditions, not all created burrows within the 7–8-week period of data collection. The onset of a moult may trigger burrowing behaviour as spiders with burrows moulted within them. At BZG it was noted that burrows were initially built around the spiders without an entrance, sealing the animal in, before a moult. Once a moult had been completed an entrance was created. The second group in the BZG tests involved animals that were two to three months older than those at the start of the first experimental series and more created burrows within the timeframe of the second experiment. It is not clear whether this was stimulated by the presence of a small stone or a maturational effect.

Recommendations for captive husbandry

The results from these studies demonstrate the importance of the depth of substrate, the physical characteristics of substrates and the presence of anchor points in not only promoting burrowing behaviour, but the production of burrows that are occupied over an extended period. It is therefore recommended that captive populations of *Hogna ingens* of similar age (3–8 months) are housed on loosely-packed, light substrates of non-uniform particle size, that can retain some moisture, such as mixes of leaf-litter, coir and sand. The substrate should be at least 50 mm depth with an anchor point, such as a stone, of minimum 40 mm in diameter.

Implications for in-situ conservation

A better understanding of physical parameters that can promote burrowing behaviour is needed to aid identification of suitable reintroduction sites; additionally, insights into microhabitat requirements would also benefit identification of potential sites. Future research could investigate the effect of the provision of temporary (biodegradable) shelters that could impact the success of reintroductions.

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