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Tool Use by Spiders: Stone Selection and Placement by Corolla Spiders *Ariadna* (Segestriidae) of the Namib Desert

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Abstract

The corolla spider (Araneae: Segestriidae: *Ariadna*) of the Namib Desert gravel plains typically places seven or eight stones in a circle around its burrow entrance. It was examined whether the spider selects and places stones according to physical characteristics. Circle composition can be explained by the allometric scaling to spider size of the burrow entrance and the stones. The stones were usually placed with the narrowest side or point towards the burrow. Quartz crystals were preferred to four other stone types available. The spiders could detect prey brushing the outside of the circle stones that were about as wide as the spider's path of attack. I conclude that corolla spiders use the selected stones as tools to extend their foraging range.

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Introduction

Behavioural patterns of animals can confer numeric or geometric patterns on parts of their environment. For instance, orb web spiders apply silk into repetitive geometric patterns (VOLLRATH 1988; EBERHARD 1990). If building blocks are taken from the environment, it is unlikely that they will form consistent numeric and geometric patterns if their size and shape cannot be changed except by exchanging. When inanimate objects are, however, selected and rearranged to form such patterns, this may be incidental to their function, alone or combined.

The corolla spider *Ariadna* sp. (Segestriidae) of the Namib Desert gravel plains is conspicuous for its habit of placing stones in a single-layered circle around its burrow entrance (COSTA et al. 1993). The spider selects these stones from a

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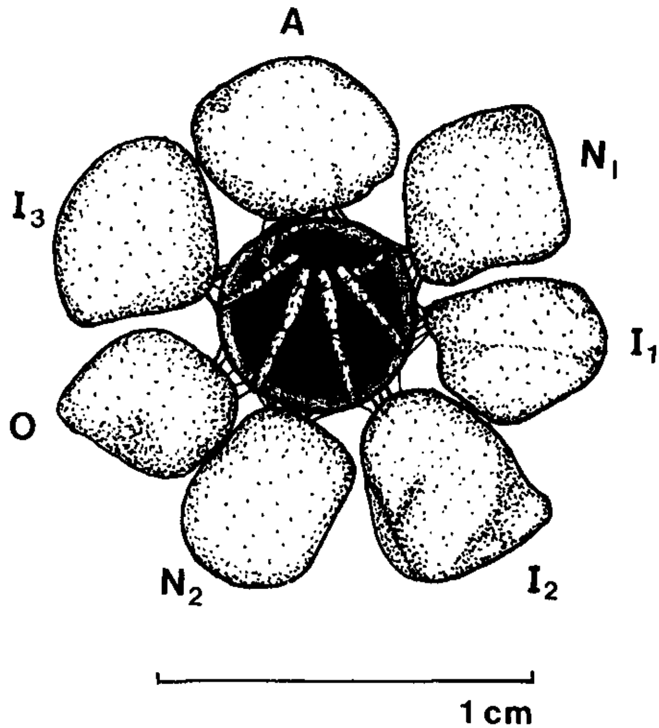

Fig. 1: Arrangement and orientation of stones in a stone circle of the corolla spider. The spider has positioned itself in the entrance with six feet on the burrow collar which is connected to the stones with silken threads. Letters indicate stone orientation: I_1, polar, pointed inwards; I_2, polar, narrow side inwards; I_3, wide triangle, pointed inwards; O, polar, pointed outwards; N_1, non-polar, pointed inwards and outwards; N_2, non-polar, not pointed; A, across

myriad of stones of many shapes and sizes littering the gravel plains and places them into a daisy-flower pattern around the lip of the burrow entrance (Fig. 1), hence the common name. The visual pattern suggests that selective mechanisms influence the size, shape, type and number of stones that the spiders use.

Segestriid spiders typically construct silk-lined burrows with open entrances from which heavy silken threads radiate outwards (GERTSCH 1949; BEATTY 1970). These lines transmit vibrations of passing prey towards the edge of the burrow. In the ground-living Namib corolla spider, the silken trap-lines are very short (<1 mm) and terminate against stones lying against the lip of the burrow (Fig. 1). These spiders readily manipulate stones to build circles around their vertical burrows, and to close or open their burrows or to remove obstacles from the vicinity of their burrows.

In the current study, I tested the hypotheses: 1. that corolla spiders select stones based on physical characteristics; and 2. that they do so for a functional purpose. Indications of stone selection were sought by examining if the number, size, type and orientation of circle stones followed patterns that differed from those of other stones scattered in the vicinity. This was verified by removing stone circles and comparing the spiders' replacements with the originals. Finally, I examined how circle stones function in an attempt to explain why spiders select them.

Biology

Many ground-dwelling *Ariadna* of Namibia place circles of small stones around their burrow entrances (pers. obs.). Most stone circles other than those on the Namib gravel plains are composed of several layers of stones without the visual patterning seen for the corolla spiders.

The species investigated in the current study was identified as *Ariadna crf masculina* Lawrence 1928 by M. A. FERRANDEZ (pers. comm.) and its taxonomic status awaits a revision of the genus. Voucher specimens are kept at the State Museum of Namibia. In this paper, I refer to it as *Ariadna* or corolla spider.

These spiders weigh 1.2–63.8 mg and construct 4.5–13.4 cm deep, vertical burrows that are distributed unevenly on the gravel plains of the central Namib Desert and can reach high local densities (0.04–1.0 m^{-2}). Corolla spiders forage nocturnally by sitting and waiting at their burrow entrances. On a calm summer night, 95 % of the spiders forage, whereas none forage by day. At night and during early mornings, the spiders occasionally venture out of their burrows over short distances (<10 cm) to gather stones or to clear obstructions from their burrows. When clearing obstructions, they are capable of transporting stones that are 43–98 times their own mass over distances of 5–17 mm (n = 5). By day, some 20 % of the spiders close their burrows with stones that can be up to 20 times their own mass.

Materials and Methods

Fieldwork was conducted on several occasions between 1987 and 1993. The main study site was at Quartz Hill (23°32′S, 15°03′E), 5 km N of Gobabeb, described by WHARTON & SEELY (1982). It is situated on the Namib gravel plain, which was not vegetated during the study period.

The ground is scattered with fine gravel composed of quartz, schist, granite, feldspar, marble, gypsum, calcrete and garnet that are imbedded in or lie on top of fine sand. The stones of interest for this study are 0.2–400 mg in mass and 1–11 mm in diameter (range of sizes in circles). Stones of this size occur at densities of 3.0 ± SD 0.7 cm^{-2} (1.7–5.1 in 30 samples of 33 cm^2) on the surface of the study area. The distribution of stone sizes in this range is skewed towards the small end, with 68 % being <4 mm in diameter.

Potential prey include beetles, ants and thysanurans. Thirty-two species of tenebrionid beetles make up 90 % of the arthropods captured with pit traps at the study site (HENSCHEL, SEELY & POLIS, unpubl. data) with the most common small species being *Zophosis amabilis* and *Zophosis moralesi*. At least four species of ants frequent the site, namely *Tetramorium rufescens*, *Monomorium viator*, *Ocymyrmex turneri* and *Camponotus maculatus*. Other potential prey are crepuscular and nocturnal Thysanura. Potential predators of *Ariadna* are pompilid wasps, scorpions, solifugids, lizards, geckos and other spiders; the latter include *Orchestrella longipes* (Heteropodidae), *Asemesthes* sp. (Gnaphosidae), *Hermacha* sp. (Cyrtaucheniidae), *Uroctea* sp. (Oecobiidae) and several unidentified Salticidae.

All 293 spider burrows found in a 30 × 60 m area were examined in detail during Sep. 1992. The following data were recorded: burrow entrance diameter, number of circle stones, the occurrence in the circle of large, fixed stones (wider than twice the burrow diameter or imbedded in the substratum) and gaps of dimensions greater than half the burrow entrance diameter. Stones abutting the burrow lip were defined as circle stones. The attachment of signal threads to them was not a useful field criterion, as the thin threads were often only visible under magnification or when the stones were lifted.

At approximately monthly intervals between Sep. 1992 and Aug. 1993, burrows were monitored in half of the above-mentioned area. The increases of burrow dimensions during this period were extrapolated to annual changes.

Forty-four burrows of approximately equal numbers of small, medium and large spiders were excavated in an adjacent area. Data recorded were number and size of circle stones (mass ± 0.1 mg directly; length and width ± 0.1 mm from 3 ×-magnified photographs), burrow entrance diameter and burrow depth. For 31 live spiders, body length and body mass were measured. For each stone in 26 of these circles, the first stone within the size range of 1–11 mm situated ≥1 cm distant perpendicularly away from the outer edge of the circle was selected for comparison (on photographs). These stones are referred to as scattered stones.

Stone type was identified from a reference collection at Gobabeb. Type frequencies in 50 circles were compared with those in matched samples of ≥1-cm-distant scattered stones within the size range of each circle.

Stone placement was analysed on photographs. Orientation was recorded as radial if the extension of the longest axis crossed the lip of the burrow entrance or as non-radial if it did not, except for those triangular stones where a corner pointed inwards or outwards (Fig. 1). Polarity of radial stones inwards or outwards was assessed depending on the orientation of the sharpest point or narrowest part. Ovals or equiangular polygons, except triangles, have no polarity.

Experiments were carried out on the spiders' stone-collecting performance. All stones were removed from 23 circles. Reconstruction of circles was recorded during the course of the following night; replacement stones were removed as soon as new circles were complete. This experiment was repeated with 26 spiders and monitored daily for a week. The stone sizes of the rebuilt circles were compared with those of the original circles.

To test whether circle stones transmitted information to spiders, the spiders' reactions to 13 ants *Tetramorium rufescens* that were released near burrows were noted. Another method was to use human hair to tap gently onto or next to stones.

I spent over 200 h in the field at night trying to observe spiders manipulating stones. When venturing out of their burrows, corolla spiders were extremely sensitive to minor disturbances such as light or movements and retreated as soon as I became aware of them. This explains why I did not see the method by which spiders moved stones.

Means are given with SD. Confidence limits are 95 % unless stated otherwise.

Results

Stone Circle Composition

The circles of stones around burrows were incomplete in 4 % of the 293 cases examined in Sep. 1992. Large fixed stones (diameter > twice burrow diameter), which the spider had probably not moved there, were present in 68 circles. The following is an analysis of the remaining 212 complete circles composed of stones lying loosely on top of the ground. Corolla spiders had evidently placed most or all of these stones there.

Stones were laid in a single layer around the silken collar of the burrow entrance (Fig. 1). Stone number ranged from six to 12, but the distribution was skewed to the left (Kolmogorov–Smirnov goodness-of-fit for normal distribution: $D = 0.247$, $df = 211$, $p < 0.01$), with the median being seven stones. Most (75 %) circles contained seven or eight stones (Fig. 2).

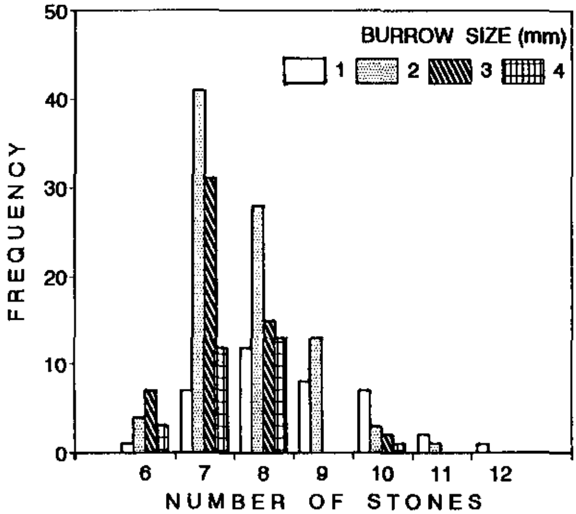

Fig. 2: Occurrence of stone circles with different stone numbers for four size classes of burrows. Data are from 212 complete circles in the main study area during Sep. 1992

Size Relationships between Spiders and Stones

The number of stones in circles tended to decrease with increasing spider size. Burrow entrance diameter served as index of spider size (correlation with spider mass: $r^2 = 0.95$, $n = 37$; with body length: $r^2 = 0.94$, $n = 37$). Burrows with complete circles ($n = 212$) were placed into four 1-mm-diameter size classes. The distribution of stone numbers differed with burrow size class (Fig. 2), significantly so for the two smallest classes compared with each other and with the larger class ($\chi^2 = 13$–40, $df = 6$, $p < 0.002$). Burrows of the 1–2 mm class tended to have more stones, with 47 % of 84 circles comprising 9–12 stones, compared with only 4 % in 84 of the 3–6 mm burrows. This was reflected in a negative correlation of stone number with burrow diameter ($r = -0.39$, $n = 212$, $p < 0.001$).

Stone size was related to spider size and to the spider's allometrically scaled burrow diameter. Stone width, which is singled out in further analyses due to its relationship to circumferential space around the burrow, was 0.80 ± 0.18 of the width of the burrow entrance (Fig. 3). Stone length was 0.68 ± 0.19 times the spider's body length ($r^2 = 0.79$, $n = 139$ stones from 19 circles). Stone mass was 2.4 ± 0.9 times the mass of the spider ($r^2 = 0.81$, $n = 234$ stones from 31 circles) and the total mass of the circle stones was 17.9 ± 6.9 times the spider's mass ($r^2 = 0.83$).

Circle Stones Compared with Scattered Stones

Reduced variability of stone width, length and mass provided evidence that spiders selected circle stones by size. Results are shown for width, as representative

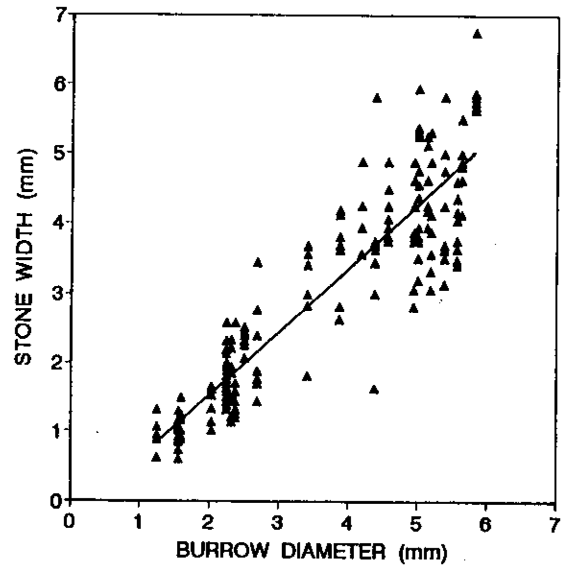

Fig. 3: Scatter plot and regression line ($r^2 = 0.84$) of stone width against burrow entrance diameter for 199 stones from 26 circles

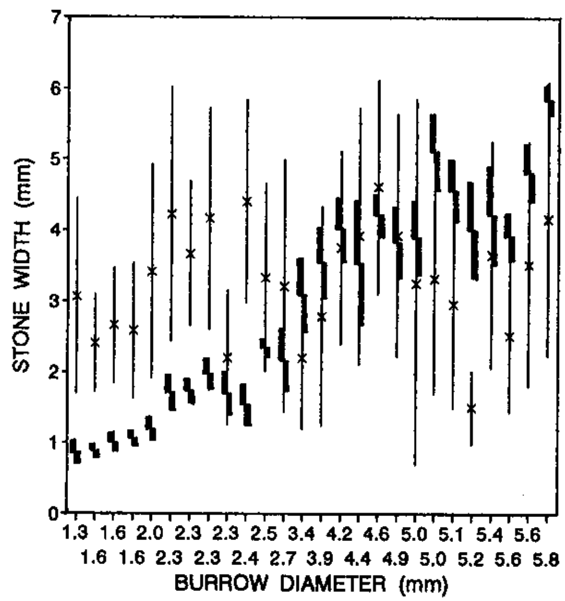

Fig. 4: $\bar{X} \pm 95$ % CL of the width of circle stones (bold staggered bar; n = 199, 26 circles) and matched samples of scattered stones (X ± vertical line). The x-axis is a non-continuous sample sequence. Note the differences between circle stones and scattered stones for each set

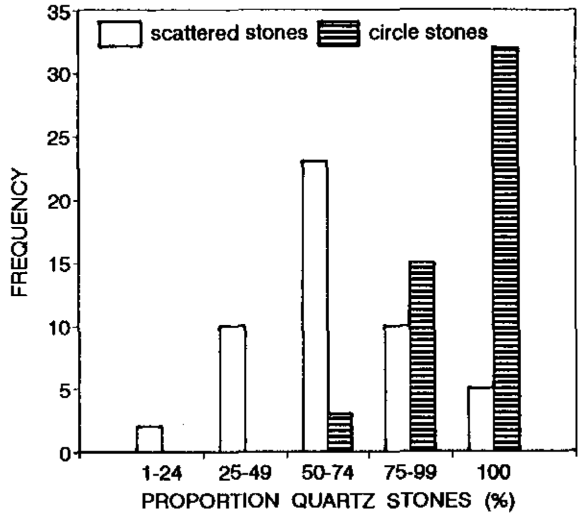

Fig. 5: Frequency of occurrence of various proportions of quartz stones in 50 circles (n = 371 stones) and matched samples of scattered stones

of these three correlated size parameters ($r^2 > 0.89$). When the widths of stones in 26 circles were compared with those of matched samples of scattered stones, the mean differed for small spiders (Fig. 4). The samples of scattered stones did not differ significantly from each other (bar one exception; t-test), but their variance was significantly higher than that of circle stones in all but three cases ($F = 5.4–107.6$; Fig. 4).

The shape of stones in circles differed slightly from that of similar-sized scattered stones. The slopes of regressions of width versus length differed significantly for 199 circle stones from 26 circles compared with matched samples of scattered stones ($r^2 = 0.89$ and 0.91 respectively; $t = 3.77$, $df = 394$, $p < 0.001$). On average, circle stones were 7 % wider than scattered stones of similar length.

Spiders preferred quartz stones over granite, schist, feldspar and marble stones. While 94 % of 371 circle stones from 50 burrows were quartz, only 63 % of the same number of similar-sized scattered stones were quartz. For each circle, the mean proportion of quartz was higher ($t = 8.78$, $df = 98$, $p < 0.001$) and less variable ($F = 4.54$, $df = 50$, $p < 0.001$) than in the samples of scattered stones. The frequency distribution of the proportion of quartz in the two samples differed significantly (Fig. 5; $\chi^2 = 180$, $df = 3$, $p < 0.001$). Most (64 %) of the circles were pure quartz, compared with only 10 % of the samples of scattered stones.

Stone Orientation

Circle stones were typically orientated radially with the sharpest point or narrowest part pointing towards the burrow. Of 371 stones from 50 circles, 92 % had radial orientation. Of these, 65 % were polar, i.e. were sharper or narrower

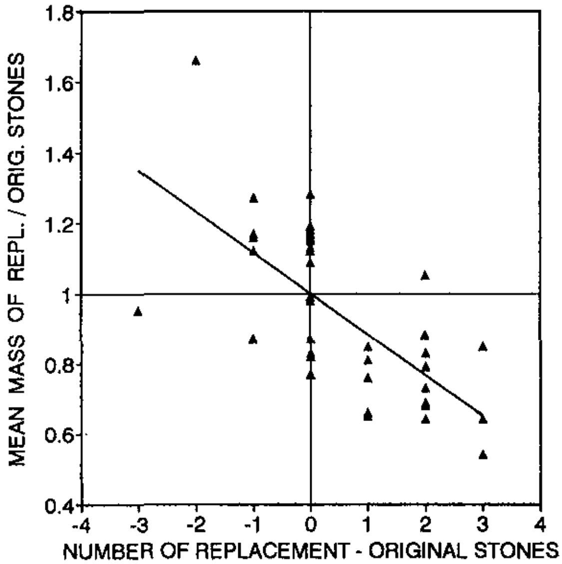

Fig. 6: Relationship between the difference in the number and the ratio of mean masses (mg) of replacement stones and original stones in 41 circles ($r = -0.52$, $p < 0.01$)

in one direction. Polar radial stones pointed inwards significantly more often (74 %) than outwards (26 %) (cross-tabulation of observed compared with equal frequencies: $\chi^2 = 51$, $df = 1$, $p < 0.001$).

Construction of New Circles

Spiders were usually quick to replace stone circles that were removed. Of 23 burrows from which circles were removed at 1800 h, 12 (52 %) had complete new stone circles by 2300 h. When these 12 replacement circles were removed, six (50 %) were again completely replaced by 0600 h and three were partly rebuilt. None of the spiders that did not begin construction early, did so later at night. In a second trial, circles were removed from 26 burrows and, at daily intervals, complete replacement circles were recorded and removed. Twelve (50 %) first replacement circles were finished in a day. When these were removed, nine (75 %) spiders rebuilt within a day. When data for first and second replacement circles are pooled ($n = 45$), 69 % of the spiders rebuilt circles within 2 d and 89 % within 1 wk.

The number of stones in replacement circles correlated weakly with the original number ($r = 0.35$; $p > 0.05$). Only 36 % of the replacement circles had the same number as the original. The total mass of stones in each circle was, however, remarkably constant (original mass/replacement mass = 1.03; $r = 0.96$, $p < 0.001$, $n = 41$ circles). Two spiders with the lightest and heaviest original circles were excluded from these calculations, as they changed replacement circle

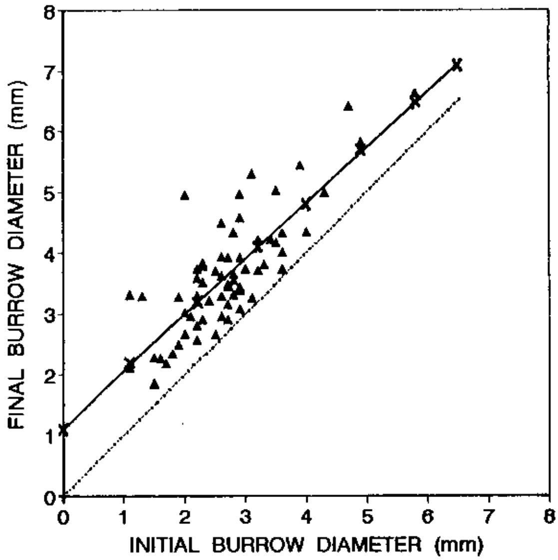

Fig. 7: Initial versus final burrow diameter of 69 immature spiders at the beginning and end of a year. The dotted line demarcates zero change, the solid line is the regression line ($r^2 = 0.65$) and 'X' indicates the successive annual increments of growth along this line. The regression line is extrapolated to 7.1 mm, the burrow size of an adult female

mass by a factor >2. The other 22 spiders tended to achieve constant total circle mass by picking more smaller stones or fewer larger ones (Fig. 6).

Replacement stones were sometimes more variable in size than the original stones. Variance increased significantly in 16 % of the 45 replacement circles ($F > 5.0$, $p < 0.05$) and decreased in only 4 % ($F > 6.4$, $p < 0.05$). Incidental observations indicated that some of the stones that were first incorporated into circles, were later exchanged with others.

Long-term Changes

Most corolla spiders (54 %) remained in the same burrows for at least a year and widened their burrows by 0.95 ± 0.58 mm per annum (n = 69). From the size-dependent changes in burrow diameter (Fig. 7), I calculated that under the conditions prevailing during the current study, it took about 7 yr for the spiders to widen their burrows from an initial 1.1 mm to a final 7.1 mm. This indicates that these spiders are long lived.

Opportunities for allometric adjustments of stones following spider growth occur when circles are reconstructed after storms. For example, a storm in Mar. 1993 broke many stone circles. At 80 of 102 disturbed circles, reconstruction had commenced within 3 d; 36 % had 1–3 stones more, and 20 % had 1–6 fewer, sometimes with incomplete circles. On an annual basis, 69 reconstructed circles around continuously inhabited burrows had a temporary maximum of 1.0 ± 1.2

(range 0–6) stones more than the number recorded initially during Sep. 1992 (see above). Subsequent changes brought the numbers down again.

Response to Stimuli

Stones evidently transmit information to foraging spiders. At night, *Ariadna* typically position themselves at the burrow entrance with the three anterior pairs of legs resting on the silken collar that is connected to the inside of the circle stones with fine silken lines (Fig. 1). In this position, the spiders are very sensitive to the approach of small insects, even ants < 10 % of the spider's size.

To observe this, I released ants next to burrows (n = 13). When the ants brushed against the outside of circle stones, the spiders reacted instantly by pouncing onto the ants and snatching them into the burrow. Gentle stroking or tapping of a circle stone with a human hair elicited similar spider attacks. Stroking the surrounding ground within 1 mm of the circle elicited no reaction from the spider. This suggested that the ground was less effective in transmitting vibrations to the spider than stones were.

The role of stones was further demonstrated by using artificial stimuli (human hair) at six burrows with foraging spiders from which stone circles were removed. In each case, the spiders reacted (5 attacked, 1 fled) only when the hair touched the silken collar, but failed to react when the ground was scraped within 1 mm of the collar. Each of these spiders was again tested when it had rebuilt a complete stone circle 6 h later. All responded (5 attacked, 1 fled) when the ground-scraping hair touched the outside of a circle stone, demonstrating that stones increased the spider's range of sensitivity by up to 11 mm.

Discussion

Corolla spiders construct stone circles with consistent numeric and geometric patterns. The narrow, skewed distribution of stone number with a median of seven stones and absence of a distribution tail below six (in complete circles) suggest the existence of factors determining stone number. These factors or the spiders' experience may change with age, as the distribution of the number of stones becomes increasingly narrow with increasing spider size. The rapid replacement of removed circles suggests that the spiders require such circles.

The stones picked for the circle were considerably lighter, at 2.5 times their own mass, than the maxima that the spiders are capable of transporting. The load of 100 times their mass that corolla spiders can move compares with the feats of some ants (HÖLLDOBLER & WILSON 1990). This capability enables spiders to clear away relatively large stones that roll onto their burrows.

The relative constancy of the number and total mass of circle stones is evidently a consequence of corolla spiders picking stones on the basis of size and placing them around their burrows until there is no more room in the single-storeyed circles. They could select stones on the basis of any size parameters as these are highly correlated, although there is evidence that they prefer broad stones to narrow stones.

There is no evidence that corolla spiders use other than metrical cues to pick circle stones. It is therefore difficult to explain the spiders' strong preference for quartz. Geologists can differentiate quartz from feldspar, marble, granite and schist on the basis of mineral content, crystal shape and size, type of fracturing, electrical conductivity, density, colour, surface microtexture, and transmittability of vibrations. Among the stone types, quartz is of intermediate specific density. It is, however, unknown whether corolla spiders can detect any of the above properties.

Many explanations can be suggested for ground-burrowing spiders constructing turrets. Such a turret may reduce flooding of burrows (MAIN 1982, 1986), reduce blocking of burrows by rolling stones or windblown sand, anchor the sides of open burrows, conceal spiders from predators or prey that wander about between stones, facilitate the accumulation of condensed water from fog, or attract prey that climb onto stones, e.g. thermoregulating ants (MARSH 1985). These speculations do not explain why corolla spiders select and place their building blocks so geometrically.

The current study indicates that the stones serve as foraging tools; the spiders extend their sensory range by monitoring vibration-transmitting stones. Use of long, silken trigger-lines as in other segestriids may not be possible on the Namib Desert plains because abrasive wind-blown sand makes web maintenance difficult (HENSCHEL & LUBIN 1992). Furthermore, scattered pebbles on the gravel plains may dissipate faint ground-borne vibrations that dune spiders and scorpions can use to detect prey (BROWNELL 1977; HENSCHEL 1994). Quality stones, positioned favourably, appear to be effective in directing prey-generated vibrations towards the spider. Gaps or no circle at all would give the spider no indication of approach and would pitch the spiders' reaction time against that of the prey; gaps may be dangerous if the interloper is an enemy. The use of stones by corolla spiders is akin to the use of twigs by Ctenizidae (COYLE 1986; J. HAUPT, pers. comm.).

Constant maintenance of a functional foraging-structure may be important for a predator inhabiting a hyperarid plain with very low productivity (SEELY 1978) where opportunities to capture prey are rare. The Namib dune spiders *Leucorchestris arenicola* and *Seothyra henscheli* normally capture prey every 5–7 wk, although they forage almost on a daily basis (HENSCHEL 1994; LUBIN & HENSCHEL 1995). Insect abundance appears to be much lower on the gravel plains than in the dunes (HENSCHEL, SEELY & POLIS, unpubl. data). It is thus not surprising that *Ariadna* are nearly constantly ready to capture prey at night. *Ariadna*'s estimated longevity of 7 yr during a dry period may be a function of low prey availability. Long life is a feature commonly found in desert spiders (CLOUDSLEY-THOMPSON 1983; HENSCHEL 1990).

The foraging-tool hypothesis explains why stone size should be important to corolla spiders. Large stones extend the foraging range, but do not provide precise information on prey locality. Small stones provide very precise information on direction, but cover only a small range and many are required to encircle a burrow. Stones that are as wide as the spider's path of attack, which is slightly less than the burrow diameter, are, conceptually, ideal, as they are the largest stones that would allow spiders to target accurately and thus take prey by surprise. Widths of 0.80 ± 0.18 times the burrow diameter, recorded for circle stones, fit this concept.

The observed number of stones and their placement are also consistent with the foraging-tool hypothesis. Around a circle of any size, there is room for 7.5 objects of 0.8 times its diameter. In addition, sometimes a few smaller stones fill the last gaps. The orientation of stones, usually with the sharpest point inwards, should direct vibrations from the wider outside arc towards the inside point. Because the spider monitors the silken collar, which is connected to the inside point, but does not appear to monitor the stones or their connecting threads directly, there is no reason to believe that an algebraic relationship exists between the number of stones and the number of spider legs. Smooth-surfaced crystals are better at transmitting directional vibrations than conglomerates are (R. SWART & B. ZIMANOWSKI pers. comm.). This may explain the spider's preference of quartz.

Tool selection by corolla spiders can serve as a good model to investigate decision-making by animals. Some variables involved, such as stone size, shape, position and orientation, are quite straightforward to determine and to manipulate experimentally. An important property involved, the transmittability of vibrations, is more complicated and requires knowledge of the spider's sensory physiology (BARTH 1982). However, the key property to understand the evolution of this geo-engineering, is the spider's assiduous maintenance of its stone web.

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