

## DISPERSAL IN THE SOLITARY *STEGODYPHUS AFRICANUS* AND HETEROSPECIFIC GROUPING WITH THE SOCIAL *STEGODYPHUS DUMICOLA* (ARANEAE, ERESIDAE)

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**ABSTRACT.** Mobility and dispersal of the solitary-living spider, *Stegodyphus africanus* Blackwall 1866, under laboratory conditions are described for the period from four months after hatching until death. Cohabitation with females of the social-living *S. dumicola* Pocock 1898, within the same experimental setup, reveals interspecific tolerance between both species.

Special attention has recently been paid to the cribellate eresid spider genus *Stegodyphus* Simon 1892 which contains both subsocial species with solitary adults, hereafter referred to as solitary, as well as permanently social species. A revision of the genus by O. & M. Kraus (1988) suggests three monophyletic subtaxa, or species groups, each of which includes a number of solitary as well as a single social species, proposing that sociality evolved independently three times. In view of the socially intolerant and aggressive lifestyle of the vast majority of spiders, the permanently and cooperatively social (Wickler & Seibt 1993) species form noteworthy exceptions. Unfortunately, up to now the biology of the social species' solitary sister species is practically unknown. On *S. africanus* in particular, nothing had been published except for the original description in 1866.

In Krüger Park, South Africa and in Swaziland we repeatedly found a fully-grown *S. africanus* female living parasitically in a colony of the social *S. dumicola* and even consuming individuals of the host species (Wickler & Seibt 1988). Therefore, we also wanted to confront the *S. africanus* under controlled laboratory conditions with *S. dumicola*, hoping for more data on interspecific behavior.

### METHODS

In February 1992, near Nshawu-Dam in the Krüger Park (South Africa, Transvaal; 23°29'S, 31°29'E) in dry, fairly flat grassland with squat *Colophospermum mopane* trees, we collected a *S. africanus* silk nest, 8 cm in diameter, situated about two meters high in a

mopane bush, containing a dead adult female with 82 living spiderlings, of 3–4 mm body length (= prosoma + opisthosoma, measured to  $\pm 0.1$  mm with a vernier calliper). We took the sponge-like nest to our laboratory to obtain data on the dispersal tendency of the growing spiderlings. Voucher specimens have been deposited in the arachnid collection of the Zoological Museum, Hamburg University.

We estimated that the *S. africanus* spiderlings had hatched from the cocoon at the beginning of January, about 30 days prior to collection. Four months after hatching, we placed the original nest with 54 surviving spiderlings into a 12-sided acrylic plastic (Plexiglas<sup>TM</sup>) container (Fig. 1) with a removable wire screen area in the floor for aeration, feeding and cleaning. Along the outer rim of the container's flat ceiling, 12 evenly spaced "houses" served as housing for emigrants; they consisted of a vertical Plexiglas "pipe" (C) which opened into a larger compartment, a Plexiglas cylinder (D) with a removable wire screen lid. The spiders were fed mostly flies, according to their sizes; and food was simultaneously supplied to all of them at their respective sites in order not to enforce feeding migrations and accumulations.

Within the Plexiglas container we identified 49 sites (see Fig.1): Twelve A, B, C, D locations, plus the central ground area where the original nest had been placed. At variable intervals (one day or more) we recorded the numbers of spider sightings at those sites (i.e., outside the original nest) starting on 29 April 1992. The observed number of animals varied because some returned to their non-transparent home nest or died.



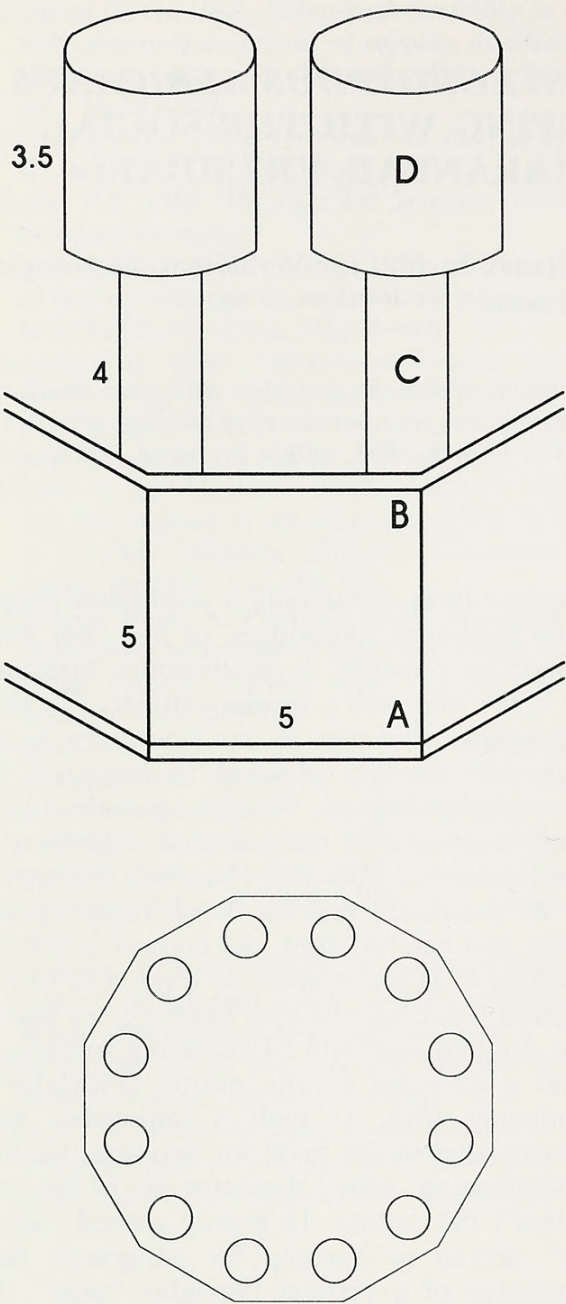


Figure 1.—Diagram of the acrylic plastic (Plexiglas<sup>®</sup>) apparatus (diameter = 19 cm): Face of one side with two of the twelve “houses”: A, B, C, D, observation sites; numbers, lengths in cm. Below: Cross-section at level C.

As numbers of spiders per site varied between records, pairs of records 24 h apart were chosen to estimate spider mobility. Due to ongoing asynchronous moltings, the individuals could not be marked without destructive interference. Therefore, we assumed no mobility if the number of spiders at a given site had not changed between successive records. A lower count in a second record gave the minimum number of spiders that had

Table 1.—Observation periods and *Stegodyphus* spiders observed.

| Species             | Period | Proto-                |                       | Sight-ings<br>(n) |
|---------------------|--------|-----------------------|-----------------------|-------------------|
|                     |        | Days<br>per<br>period | cols<br>per<br>period |                   |
| <i>S. africanus</i> | I      | 59                    | 28                    | 36                |
| <i>S. africanus</i> | IIa    | 113                   | 23                    | 32                |
| <i>S. africanus</i> | IIb    | 82                    | 10                    | 8                 |
| <i>S. africanus</i> | III    | 207                   | 68                    | 8                 |
| <i>S. dumicola</i>  |        |                       |                       | 21                |
|                     |        |                       |                       | 406               |

moved. In our system, these spiders turned up elsewhere; an increase of spider number at a given site from first to second record was therefore ignored.

The total observation time (461 days) was formally subdivided into three periods (Table 1): Period IIa began when the first adult *S. africanus* males appeared, and it ended when the last *S. africanus* male had died and only female *S. africanus* were left (Period IIb). Period III began when we added *S. dumicola* individuals from a colony that we had collected in December 1992 near the *S. africanus* locality. Thus, periods I and II deal with *S. africanus* only, while during period III the two species are mixed.

Young *Stegodyphus* tend to stay in the maternal web structure until a certain age, at which they begin to disperse. In our experimental setup spiders had the option to disperse, and to form groups or isolate themselves; we always found some (though different) “houses” empty (from 1–3 in period IIa to 2–7 in period III, with always 13–30 spiders present).

RESULTS AND DISCUSSION

On 28 April 1992 the *S. africanus* spiderlings had grown to a body length between 4.0–7.5 mm (mean  $\bar{X}$  = 5.4, SD =  $\pm$  0.8 mm;  $n$  = 54); their weight ranged from 7–49 mg. About four months later, adult males measured from 4–12 mm ( $8.3 \pm 1.6$  mm;  $n$  = 20) and weighed from 48–170 mg ( $73.8 \pm 41$  mg;  $n$  = 18). At the same time females measured from 8.4–16.0 mm ( $12.2 \pm 2.5$  mm;  $n$  = 17) and weighed from 79–545 mg ( $370 \pm 210$  mg;  $n$  = 24). As indicated by field data (Seibt & Wickler 1988), fully grown social *S. dumicola* females are much smaller ( $7.5 \pm 1.2$



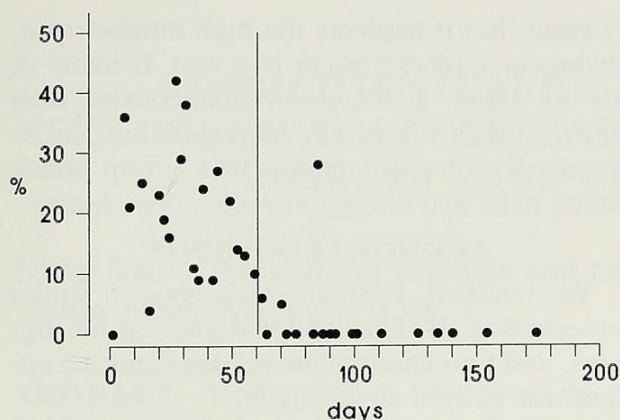


Figure 2.—Percent of recorded spiders in the ground region in 38 (independent) protocols over 173 days. The vertical line separates periods I and IIa.

mm,  $n = 877$ ;  $49.1 \pm 2.5$  mg,  $n = 848$ ) than *S. africanus*.

In our apparatus, we found 24 young outside the maternal nest on the first observation day, 28 on the 8th, 36 on the 27th day. Many of them tended to stay within the ground region, i.e., next to the maternal nest. In order to test for independent data, an autocorrelation was run between successive protocols. We pooled all sites A and the central ground area into "ground region", and 12 times sites B, C, D into 12 house-regions. Autocorrelation analysis then left us with independent data from 20 protocols in Period I and 18 in Period IIa. No individual was found in the ground region in just one protocol in period I, but in period IIa, they were there in 15 protocols. The difference is significant ( $P < 0.001$ ,  $\chi^2 = 20.7$ ,  $df = 1$ ). This change in preference for the upper regions B, C and D coincides with the appearance of the first adult male on observation-day 61 (Fig. 2). Thereafter the home nest was no longer used. Spider sightings from the available 12 house-regions during all periods deviated significantly from uniformity. But no consistent preferences for specific house-regions over periods I and IIa were found.

During period I, *S. africanus* spiders formed close contact groups of up to 15 conspecifics in 66% of all sightings ( $n = 851$ ); in 34% they were seen singly. As long as males were present (up to 12 in period IIa), female spiders formed groups of maximally 5 females in 42% of 354 sightings, in 58% they were seen singly. After the males died (period IIb),

females were seen pairwise in 10% of all sightings ( $n = 79$ ), in 90% singly. The difference between periods IIa and IIb is significant ( $P < 0.001$ ,  $\chi^2 = 27$ ,  $df = 1$ ). This decreasing number of grouped animals over time could be due to an effect of male presence, of decreasing numbers, or of increasing age. As 58% of a total of 129 male sightings showed them without females, males do not seem to attract females or induce female groupings. To account for the decrease in number of animals and increasing age over time, a partial correlation was used: a series of 61 protocols over the successive periods I, IIa and IIb showed a significant ( $P < 0.05$ ; two-tailed, partial correlation coefficient = 0.31) age dependent increase in percent of animals seen isolated vs. grouped, proving an increase in isolation tendency with age. *S. dumicola* females formed close contact groups with up to 13 conspecifics in 77% of all 406 sightings (Table 1, period III). The grouping tendency was therefore most like that of *S. africanus* spiderlings.

In 49% of all protocols for periods II and III we found a single *S. africanus* in a previously unoccupied "house", proving that spiders did not just move between groups. In 21 of 24 cases where between two successive records only one spider had moved from one site to another it had covered the distances between 2, 3 or 4 "houses". We found no difference in the total rate of site-changes within 24 hours between *S. africanus* spiderlings (105 changes in 286 sightings in Period I) and females (24 changes in 65 sightings in Period IIa) ( $R^*C$  test,  $P = 0.91$ ,  $\chi^2 = 0.012$ ,  $df = 1$ ). The available settlement areas ("houses") were homogeneously designed, and there were no consistent preferences by the spiders for any one of them. Mobility of the spiders decreased over time, most likely as the individuals settled in separate nest tubes, as they would do in the field. Fully grown *S. dumicola* females (Period III) had changed location between records 24 hours apart in 41 of 86 sightings. There is no significant difference to *S. africanus* spiderlings (105 changes in 286 sightings, period I) ( $P = 0.09$ ,  $\chi^2 = 2.89$ ,  $df = 1$ ) and females (24 changes in 65 sightings, period IIa) ( $P = 0.25$ ,  $\chi^2 = 1.3$ ,  $df = 1$ ).

During period III the apparatus contained females of *S. africanus* and *S. dumicola*. In 69 cases females of both species were seen at the



same site, often even in body contact; 66 times there was a single *S. africanus* together with 1–5 *S. dumicola* individuals, and in three instances two *S. africanus* were found with 1–2 *S. dumicola*. Some of these heterospecific groupings lasted up to 18 consecutive days. In 12 cases we recorded which species came to meet the other at a given site; seven times it was *S. dumicola*, three times *S. africanus*, and two times females of both species met at a new site. In 13 cases (when twice as many *S. dumicola* than *S. africanus* females had been present) we recorded which species ended the heterospecific grouping; 10 times it was *S. dumicola*, two times *S. africanus*, and once all females separated. These results show that females of neither species avoid those of the other species. In the field we have found both sexes of *S. africanus* living in a *S. dumicola* nest. Thus, interspecific tolerance does not seem to be confined to the female sex.

No hostile or cannibalistic behavior between species was observed in the experimental setup. Such interspecific tolerance may be governed by a simple cost/benefit assessment, with the cost factor being most important for the socially-living animal. While even large prey as well as aggressive hymenoptera ensnared in the cribellate silk are attacked, the situation is very different with a congeneric spider that does not become ensnared and moves freely. Here attack will provoke counterattack, and the full risk of being severely damaged would fall upon the assailant, while costs arising from tolerance would be shared among all community members (Seibt & Wickler 1988). An alleged alternative explanation, "that the solitary spiders are much larger than the social ones, so that the costs of being aggressive are rather small for *S. africanus* but high for *S. dumicola*" (Schneider 1995) in fact uses the same cost/benefit ar-

gument; but it neglects the high number of *S. dumicola* spiders present in a nest. If many or all of them attacked simultaneously, they could defeat a larger *S. africanus*; but any *S. dumicola* not participating in a group attack saves risks and energy and thus does better.

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