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PREDATION ON SOCIAL AND SOLITARY INDIVIDUALS OF THE SPIDER *STEGODYPHUS DUMICOLA* (ARANEAE, ERESIDAE)

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ABSTRACT. Encounters and effects of predators were examined for group-living and solitary dispersers of the spider *Stegodyphus dumicola* Pocock 1898 (family Eresidae) in Namibia. Birds and araneophagous spiders were major predators of solitary spiders; group members living in large, tough, complex nests were less vulnerable. Arboreal pugnacious ants *Anoplolepis steingroeveri* (Forel 1894) frequently attacked *S. dumicola* colonies of all sizes. As a means of defense against ants, the spiders produced copious amounts of sticky cribellar silk. Solitary spiders were incapable of sustaining this resistance for as long as groups could and usually died when ants attacked. Solitary individuals were, however, less likely to contract a contagious fungal disease that spread in large, old nests after rain. I conclude that the action of predators may explain why *S. dumicola* tend to be avidly social as well as prudently solitary.

Group living has behavioral, ecological and genetic consequences for spiders (Buskirk 1981; Rypstra 1993; Avilés 1993, 1996). The fundamental ecological reasons why some spiders spend their entire lives in groups may differ in different species. Safety from predators is often invoked as an explanation for grouping in animals (Inman & Krebs 1987). The encounter effect predicts that individuals encounter predators at a lower rate, due to foraging constraints by the predators. Once an encounter occurs, the dilution effect predicts that a member's probability of being captured decreases with group size.

Groups of non-territorial permanently-social spiders (hereafter referred to as social spiders) may have the possibility to lower their predation risk by using large, complex, communal retreats that provide physical protection. Cooperative defense is another possibility. The potential for cooperation is one of the distinguishing characteristics of social spiders (Avilés 1996), but its manifestations are not well-known. The suggested increased safety via communal fortification (Seibt & Wickler 1988a) and defense has not been confirmed.

Here I examine how *Stegodyphus dumicola* Pocock 1898 (Eresidae), living in groups or solitarily (Le Roy 1979; Seibt & Wickler 1988a; Henschel 1993), are affected by various kinds of predators (Meikle 1986; Seibt & Wickler 1988a; Griswold & Meikle 1990). In particular, I examined the roles of the silk and of defense in providing protection.

Stegodyphus dumicola occupy nests that are attached to tree branches at heights of 0.5–1.5 m. Cribellar sheet webs extend from the nests in different directions. Nest entrances point downwards and the tops are sealed. Colonies of *S. dumicola* are polydomous, i.e., different nests are interconnected with one web, or monodomous, i.e., having isolated nests, including founder colonies of solitary dispersing females. Generations are annual and the secondary sex-ratio is female-biased (12% males on average; Henschel, Lubin & Schneider 1995a). In Namibia, females mature from January onwards (mid-summer), produce eggs during February and March, care for offspring during March and April, and die during April to June when they are consumed by gerontophagous juveniles (Seibt & Wickler 1987). Most solitary dispersal by females occurs during January to March. Males mature in mid-summer, but are short-lived and apparently mate within the parent colony (Henschel et al. 1995a). Males that emigrate do not establish new nests, but perhaps join solitary females. The current study concentrates on females.

I examined (a) the predator encounter rates, vulnerability, and survival of *S. dumicola* individuals and colonies, and (b) the responses and anti-predator measures of *S. dumicola* towards each predator. These factors are discussed in terms of risk-related attributes of group-living and solitary dispersal by *S. dumicola*.

METHODS

Study area.—Most field work was conducted on the farm Christirina (23°25′S, 18°00′E), 170 km SE of Windhoek in Namibia, on the periphery of the Kalahari Desert. *Stegodyphus dumicola* were abundant (>100 nests per hectare) in an area of 20 × 20 km of moderately dense dwarf *Acacia* woodland surrounding Christirina. Intensive monitoring was carried out in an area of 35 × 45 m (referred to as the Windpump) that contained 122 trees. This area was surrounded by several hectares where all nests were marked and incidental observations and measurements were made (referred to as Christirina). Some field work was also conducted on farms near Christirina (Beenbreck, Nauas and Uhlenhorst), Windhoek (22°35′S, 17°05′E), Etendeka Mountain Camp (19°50′S, 14°00′E) and Hobatere Lodge (19°16′S, 14°25′E). The interior of Namibia is semi-arid with rainfalls being sporadic. The average summer rainfall recorded at Christirina is 250 mm, but in the dry summers of 1991/2 and 1992/3, less than 150 mm fell only late in the season.

Procedures.—Christirina was visited 15 times during the mid to late summer seasons, January-May, of 1991–1993 at approximately monthly intervals for a total duration of 40 days. Data are based on these monthly spot checks of colonies and systematic observations were not conducted.

Many spiders were adult during the monitoring seasons. Group size was determined either directly by coercing spiders from small nests, or by applying the mark-recapture technique using the Lincoln index (Southwood 1978; the median of three counts for each colony correlates with known group size: $r^2 = 0.90$; n = 6; deviating by 4.7 ±SD 16.4% above actual counts). I marked 938 spiders; some of these served to identify the origin of new colonies.

Spider predators were identified by their presence at spider nests or by the type of damage. Indirect signs included tearing of nests by birds and the disappearance of *S. dumicola* that coincided with the appearance of araneophagous spiders at the *S. dumicola* nest. Wasp parasitoid attacks were recognized by the fact that paralyzed spiders were positioned by the wasp near the nest entrance (Ward & Henschel 1992). The history of an ant attack was revealed by the presence of numerous ant carcasses in the nest lining. Occasionally, direct observations of predation by all of these species were made, which confirmed their status as predators. Fungus was recorded as a cause of death when spiders became lethargic and died in nests overgrown with fungal hyphae. Detectability of predator signs may differ, as birds that snatch spiders outside the nest leave no conclusive signs, and signs of ant attacks disappear when the surviving spiders cover them with silk. Some of the foreign spiders could have been "boarders" and may not necessarily have been responsible for the disappearance of *S. dumicola*. In 53% of all cases, the cause of *S. dumicola* colony extinction could not be ascertained. These are excluded from the analyses.

The survival of dispersing spiders was tested by artificial relocation. Spiders (n = 497) were taken out of their nests and allowed to build new retreats in the laboratory in groups of 30 (n = 10), 5 (n = 21), 2 (n = 20) and 1 (n = 52). At night these were attached to different *S. dumicola*-free trees in the typical locations and positions of natural nests. All nests in a 100 m radius were monitored at monthly intervals to ascertain the survival of experimental spiders at the release site or elsewhere. Dispersal >100 m is not expected (Henschel et al. 1995b) and spiders that disappeared were assumed to be dead.

Stegodyphus dumicola that disappeared at the Windpump site were assumed to be dead if they could not be relocated nor traced by inference to new nests within a 100 m radius in all directions. All nests were marked in a 1 ha area surrounding the Windpump site; all new nests were easily detected and marked. Marked *S. dumicola* were observed to disperse over distances that were much shorter than the radius of the area monitored (Henschel, Schneider & Lubin 1995b). Therefore it is highly likely that disappearances were due to mortality. Furthermore, there was no evidence of individuals crossing among colonies except between interconnected polydomous nests. Movement between colonies is considered unlikely, as social spiders are highly inbred (Smith & Engel 1994; Avilés 1996; for *S. dumicola*: Wickler & Seibt 1993) and

Table 1.—Number of colonies, number of individuals in groups and solitary, and mean group size ±SD of *Stegodyphus dumicola* at Windpump at the beginning of three breeding seasons (1991–1993). Old groups were those that persisted from the previous generation, including group-living offspring of solitary females.

	1991	1992	1993	Total
Number of colonies (individuals)				
Old groups	9 (134)	20 (613)	2 (55)	31 (802)
New groups	45 (372)	4 (108)	0 (0)	49 (480)
Solitary	159 (159)	6 (6)	26 (26)	191 (191)
Total	213 (665)	30 (727)	28 (81)	271 (1473)
Mean group size (±SD)				
Old groups	14.9 ± 13.0	30.6 ± 28.1	27.5 ± 3.5	25.9 ± 24.5
New groups	8.3 ± 13.5	27.0 ± 16.5	0.0 ± 0.0	9.8 ± 14.5
Solitary	1.0	1.0	1.0	1.0
Total	3.1 ± 7.7	24.2 ± 26.2	2.9 ± 7.0	5.4 ± 13.0

group size did not increase, except by reproduction.

In nine populations, all nests were counted, solitary individuals were counted and signs of ant attack were recorded. The populations were: Christirina in 1991, 1992 & 1993 (n = 213, 70 & 198 nests), Uhlenhorst (n = 48), Hobatere (n = 100), Windhoek (n = 31), Nauas (n = 20), Etendeka (n = 12) and Beenbrek (n = 54). Voucher specimens are deposited at the National Museum of Namibia in Windhoek. Means are given ± 1 SD; confidence limits were 95%, unless otherwise indicated.

RESULTS

Population.—The number of colonies and individuals present at Windpump varied among years by up to an order of magnitude (Table 1). New colonies were formed in each breeding season, mostly by solitary females, which, on average, comprised 13% of the population. This proportion differed between years ($\chi^2 = 148.8$; $df = 2$; $P < 0.001$) and was strongly reduced in 1992 (0.8%). New colonies were larger in 1992 than they were in 1991 (Mann-Whitney $U = 24$; $P = 0.016$), although in both years, old and new colonies did not differ significantly from each other (U-test; $P > 0.06$). Average colony size (including solitary spiders) was larger in 1992 than in 1991 ($U = 259.5$; $P < 0.001$). The 1993 population did not differ significantly from previous years in the above parameters.

Mortalities.—Colony extinction rate was high at Windpump (89% of 271 colonies in three years). Table 2 documents only the final causes of extinction of colonies at Windpump. For a founder inividual, one mortality event resulted in extinction of that colony, whereas a larger group only went extinct after several mortality events, of which only the final event is shown in Table 2. In spite of this, the overall survival rates between breeding seasons of solitary individuals and groups did not differ significantly ($\chi^2 = 0.28$; $df = 1$; $P = 0.59$). Table 3 shows the proportion of all encounters with predators observed for solitary-living and group-living individuals during the course of fieldwork at Christirina. Both measures of mortality, colony extinctions at Windpump (Table 2) and observed encounters of predators by *S. dumicola* individuals at Christirina (Table 3), are analyzed for each predator below.

Ants.—Ground-nesting diurnal ants *Anoplolepis steingroeveri* (Forel 1894) frequently encountered *S. dumicola* because both species had an affinity for trees. The spiders built their retreats against branches; the ants crawled up the branches to tend scale insects and aphids (Homoptera: Coccina and Aphididae) and repelled other fauna. When I checked all 122 trees at Windpump during one afternoon in February 1992, *A. steingroeveri* were present on every tree, of which 18 also contained *S. dumicola* nests. It is therefore not surprising that ants frequently encountered spider nests. Sometimes, the ants attacked *S. dumicola* by

Table 2.—Rate and cause of colony extinction of *Stegodyphus dumicola* at Windpump during three breeding seasons (1991–1993).

	1991	1992	1993	Total
Colony extinctions				
Groups	44/54	22/24	0/2	66/80
Solitary	149/159	6/6	20/26	175/191
Group extinctions				
Ants	1/44	17/22	0/0	18/66
Birds	0/44	0/22	0/0	0/66
Spiders	7/44	0/22	0/0	7/66
Other & unknown	36/44	5/22	0/0	41/66
Solitary extinctions				
Ants	13/149	6/6	3/20	22/175
Birds	24/149	0/6	10/20	34/175
Spiders	29/149	0/6	2/20	31/175
Other & unknown	83/149	0/6	5/20	88/175

gathering in large numbers (100s to 1000s) and invading the spider nests. At Christirina in 1992, about 5% of the spider nests (n = 70) were under attack by ants at any given time of observation. Over the season, 60% of the nests were attacked. The ants could continue attacks for several consecutive days and nests could be attacked repeatedly days or months later.

Ants dismembered the remains of spider prey, tore open cocoons to remove spider eggs, killed some spiders in the nest and killed those that dropped to the ground. Bites by only a few of these 1–2 mg ants killed even a 100–200 mg female. The ants transported their booty into their nest in the ground.

Ant raids on colonies reduced spider group size. Spiders were counted in 11 colonies at Windpump in January, February and April 1992, yielding 22 records of group size changes. In the intervals between the monthly monitoring, ants raided the colonies 16 times. Ant-raided colonies declined by 57% ± 20, significantly more than the 15% ± 15 by those not raided (ANCOVA: F = 17.7, P = 0.0005; variable: final colony size; covariate: initial colony size; treatment: ant raid/no raid; there was no significant interaction between the treatment and the covariate: F = 0.13, P = 0.7). I estimated that if the ants appropriated all losses from ant-raided spider colonies, they would gain *ca.* 0.3–17 g of spiders as prey per raid.

Table 3.—Signs of encounters of various predators by groups and solitary individuals of *Stegodyphus dumicola* at Christirina made during the course of fieldwork (percent for columns).

Predator	Group	Solitary
Ants	79.3	28.5
Spiders	4.0	33.8
Birds	2.9	33.8
Wasps	8.0	2.6
Fungus	5.7	1.3
n	174	151

Ants could decimate *S. dumicola* populations. The 1992/3 cohort of spiders at the Windpump started with 20 colonies. Repeated ant attacks on spiders reduced them until only two colonies (10%) survived into the next breeding season. At another site within the same population, 54 colonies in one patch succumbed in a similar way resulting in the local extinction of the patch. By contrast, all 11 colonies survived in two other patches not frequented by ants.

The response of *S. dumicola* to *A. steingroeveri* was based on deterrence and evasion and never on counterattack (e.g., biting). The initial approach of single ants to the nest was prevented by sticky bands of cribellar silk (22.7 ± 8.4 mm wide; range 10–45) that the spiders laid around branches below the nest. These cribellar bands were laid only in three ant-frequented areas and were not present in four other areas where ant attacks were rare (< 10% of the colonies were attacked). Nonetheless, ants could cross the cribellar bands by swarming over each other. The spiders then left the nest, taking some egg cocoons with them. They positioned themselves below the nest in a portico of loosely-woven wide tunnels with porous walls bearing much cribellar silk. There they spun more layers of cribellar silk. Group members took turns in spinning at the ant front. This fresh silk hindered pursuit and many ants became permanently entangled. If ants continued swarming towards the spiders when they stopped spinning, the spiders then moved onto the capture web or dropped to the ground, where they were sometimes overcome by other *A. steingroeveri*.

Spiders did not escape to other branches or trees during ant raids. In polydomous colonies they abandoned nests that were under ant attack in favor of other connected nests. While ant raids took place, many *A. steingroeveri* were also active on surrounding trees, which could make the establishment of new nests difficult for spiders at such times.

Most of the predator encounters observed at spider groups were by ants, whereas other predators gained in relative importance for solitary individuals (Table 3; $\chi^2 = 84.7$, $df = 1$, $P < 0.001$). However, some individuals survived an ant raid in 85% of 20 groups at Christirina whereas all 28 solitary individuals died when ants attacked ($\chi^2 = 13.1$, $df = 1$, $P < 0.05$). Many groups even survived several ant attacks, although the extinction rate increased from 15% with the first attack on a colony to 24, 46 and 43% with the second, third and fourth attacks respectively. Four of 20 groups survived four attacks. Protection may be enhanced in polydomous colonies. At Christirina, a group of small *Acacia* trees that was festooned with webs of a polydomous colony comprising twelve nests, was free of ants throughout the study period, although ants frequented nearby *Acacia* trees.

The rate of solitary emigration by *S. dumicola* had an inverse relationship to the frequency of ant attacks. In nine populations, the proportion of nests with solitary individuals was negatively correlated to the extent of ant attack (Fig. 1) ($R_s = -0.78$; $P < 0.05$).

Araneophagous spiders.—Clubionidae, Gnaphosidae, Heteropodidae: *Olios* sp., Tetragnathidae: *Nephila senegalensis* (Walckenaer 1841), Salticidae, Thomisidae (listed by relative frequency) were implicated as predators of *S. dumicola*. All of these, except *N. senegalensis*, entered the nests. *Nephila senegalensis* attached its orb-web to the nest of *S. dumicola* and seized spiders that came to the attachment site.

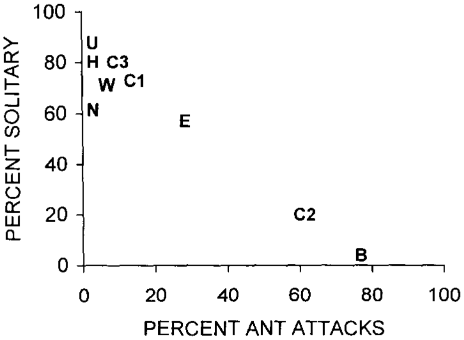

Figure 1.—Occurrence of solitary dispersal of *Stegodyphus dumicola* in populations that differed in the proportion of nests attacked by ants. Populations are Christirina in 1991 (C1), 1992 (C2) & 1993 (C3), Uhlenhorst (U), Hobatere (H), Windhoek (W), Nauas (N), Etendeka (E) and Beenbrek (B).

Stegodyphus dumicola did not appear to employ specific countermeasures against araneophagous spiders. They were either passive (towards Clubionidae, Thomisidae and Salticidae), attracted towards them (*N. senegalensis*), or helpless against them (Heteropodidae and Gnaphosidae).

Araneophagous spiders attacked mainly solitary-living or emigrating *S. dumicola* (Tables 2, 3). For example, as members of a domestic *S. dumicola* colony emigrated singly, they were seized by pholcid spiders *Smeringopus* sp. ($n = 11$) that surrounded but did not enter the social colony. Only eight non-emigrant *S. dumicola* survived out of a colony of 180 spiders. This suggests that the predation risk to solitary emigrant *S. dumicola* was not communicated to the parent colony.

Birds.—Any of the 30 insectivorous birds occurring at Windpump could have been predators of *S. dumicola*. Nine species were seen at spider nests. During ant raids, spiders could not retreat when birds approached. Gabar goshawks (*Micronisus gabar)* carried large *S. dumicola* nests onto their own nests in high trees ($n = 8$ colonies); however, goshawks are not regarded as true predators, although they removed spiders from the local population (see Henschel et al. 1992a,b).

During the heat of the day, *S. dumicola* sitting in the cool shade below the nest quickly retreated into the nest upon the approach of birds, often leaving their egg cocoons behind. After some minutes, they re-emerged cautiously. The location of nests against branches provided birds with convenient perches from which to attack *S. dumicola* nests. The nests of larger groupings, however, are made of tough multiple layers of silk, making it difficult for birds to extract the spiders. By contrast, birds were capable of tearing small nests of solitary spiders apart to extract the spiders.

Wasps.—Pompilid wasps *Pseudopompilus funereus* (Arnold 1932) lured *S. dumicola* out from the nest onto the web where they were captured and then positioned below the nest, as described for *S. lineatus* (Latreille 1817) by Ward & Henschel (1992). The spiders may mistake wasps for potential prey. Observations at Christirina, pooled with other data, showed that individual rates of wasp parasitism did not differ for groups and solitary individuals (Henschel et al. 1996).

Fungus.—Entire colonies of *S. dumicola* could die when unidentified fungi spread through wet nests. Inhaled spores appear to be harmful also to humans (pers. obs.). Exposed nests dried quickly in the sun, evidently preventing the growth of fungus. However, during two wet periods of several days each, 12 colonies at Christirina succumbed to fungus. None were affected during long dry spells or after brief rainstorms. At Windpump, all but 7 of 249 nests were exposed to the sun for at least several hours on typically sunny summer days. The relative susceptibility of spiders from the seven shaded nests to outbreaks of fungus could not be tested in the field, as all of these colonies died from causes other than fungus (ants, spiders, unknown) before the rains came. Fungus began to proliferate on large, wet nests (n = 21) that were taken indoors and did not dry within 1–2 days. Several spiders died before I removed others from the infested nests. By contrast, fungus did not grow in any of the 126 dry nests taken indoors for examination.

Large, spongy nests of groups appeared to retain water for longer than the single tunnels of solitary spiders, which may explain the higher susceptibility of fungal outbreaks in groups (Table 3).

Table 4.—Attributes of dispersal behavior of *Stegodyphus dumicola* that may enhance survival (+) when various predators are enountered.

Dispersal	Ant	Spider	Bird	Wasp	Fungus
Leave natal colony	−	−	−	−	+
Emigrate at night	+	−	+	?	−
Short distance	+	+	−	−	−
Bridging lines	+	+	−	−	−
Group dispersal	+	+	+	−	−

Dispersal of *S. dumicola*.—Risk during dispersal was tested at Christirina by experimentally relocating 103 colonies of which 70% were solitary or pairs. A month later, all spiders had died in 94% of the nests, including all singles and pairs; another month later, the remaining spiders died. Spider groups survived significantly longer than singles or pairs (<1 month vs. >1 month: $\chi^2 = 14.8$, $df = 1$, $P < 0.05$). The final cause of extinction of all 103 colonies was known for 31 colonies: 77% were attacked by ants, 10% by other spiders, 6% by birds and 6% were dislodged and drowned in a storm.

Some behavioral attributes by naturally dispersing spiders may reduce the risk of predation (Table 4). By leaving the natal group, the spiders left old nests that often harbored lethal fungus. Spiders avoided encountering ants and birds away from their nest by dispersing at night, but may risk running into nocturnal wandering spiders (e.g., Heteropodidae). Short distances of dispersal should reduce the latter risk. Solitary emigrants typically did not move further than they could travel in an evening, and they established new nests by dawn (only 4 of 55 female dispersers were observed without nests). Dispersal distances were short (median = 4 m, quartiles = 3–8 m, n = 17). The maximum distance, 26 m, was much shorter than the area being monitored. None of the 938 spiders marked at Windpump appeared in the surrounding one hectare area, and there was no evidence that *S. dumicola* dispersed by ballooning (Henschel et al. 1995b; but see Wickler & Seibt 1986).

Dispersal was along bridging lines in all 48 cases where the method of dispersal could be established. Bridging lines enabled return to the parent colony if ants attacked; this was observed once, and the occurrence of interconnected empty nests was suggestive of similar attacks in at least a dozen cases. Bridging lines were in place for one day or longer; in 15% of the cases they were used by other colony members to form new groups.

DISCUSSION

The action of predators may explain why *S. dumicola* tend to be avidly social as well as prudently solitary. Risk of predation combines the effects of encounter rate with a predator and the spiders' vulnerability, which is affected by defense, nest impenetrability, avoidance and escape capabilities.

The poor defense of solitary individuals when faced with attacking ants made them highly vulnerable. By contrast, attacking ants had more difficulty penetrating colonies whose members kept them at bay by taking turns at spinning fresh silk. Araneophagous spiders could penetrate *S. dumicola* colonies of all sizes (see also Meikle 1986; Seibt & Wickler 1988a, 1988b; Wickler & Seibt 1988; Griswold & Meikle 1990), but groups may be less affected than solitary individuals, possibly due to the dilution effect or because emigrants were attacked more than residents. Birds other than the Gabar could more easily tear apart small nests of *S. dumicola* than large ones and could thus more easily capture solitary spiders than group members. Specialized pompilid wasps were potentially dangerous to all *S. dumicola* (Henschel et al. 1996), but their own populations were probably severely reduced by ants and birds preying on wasp larvae fixed beneath spider nests. The danger of fungus destroying colonies may grow with the age and size of the nests that accumulate spores. Furthermore, there could be a high risk of cross-infection among social group-members that frequently contact each other. During wet spells, groups of spiders in long-established nests may be in greater danger of contracting the disease than solitary spiders in new, small, clean nests.

There appear to be trade-offs for the spiders in reducing risk to specific predators. For example, nests in the sun build up heat loads in summer which may prevent fungal growth and deter ants and araneophagous spiders. However, sun-exposed nests also get too hot for *Stegodyphus* (Seibt & Wickler 1990; Henschel et al. 1992c), making it necessary for them to move out onto the web together with their egg cocoons during hot hours. There, spiders and eggs may be more vulnerable to birds and wasps, including egg parasites (the latter were present, but were not examined).

Another trade-off involves nest size and group size. The very factors that may reduce the risk towards some predators increase the risk of *S. dumicola* contracting fungal disease. Many spiders are susceptible to common pathogenic fungi that do not appear to be species-specific (Nentwig 1985; Greenstone, Ignoffo & Samson 1987). It is possible that the risk of mycosis contracted from wet nests confines the distribution of *S. dumicola* to hot, sunny regions. In India, social *S. sarasinorum* Karsch 1891 seal the tops of their nests with thick layers of water-repellent silk that render nests rain-proof during the monsoon season (Bradoo 1972).

The ultimate ecological reasons for solitary dispersal have not been established. Dispersers reduce the static distribution pattern of colonies and may reach areas that are spared from catastrophes, such as outbreaks of fungal disease, escalating ant attacks, and, perhaps, major storms or fires. A more immediate reason for dispersal could be escaping intragroup competition for food, as has been suggested for *S. mimosarum* Pavesi 1883 (Ward & Enders 1985; Ward 1986; Seibt & Wickler 1988a). Surviving solitary females may have a higher reproductive output than they would have had if they had remained in groups (Wickler & Seibt 1993). Furthermore, their offspring grow up away from conspecific competitors. Henschel et al. (1995a) suggested that this may be how intermediate-sized, late-maturing female *S. dumicola* increase their fitness, as solitary emigrants that have removed their offspring from conspecific competitors may tend to have more fecund daughters than if they had not dispersed.

Increased overall safety from aggressive ants may be a reason for spiders not to disperse, though ants exert high direct and indirect tolls on *S. dumicola* of all group sizes. These include lost foraging time, greater exposure to birds, loss of eggs and of resources for their offspring, and, often, increased mortality. However, in addition to being predators, ants are cleaners in *S. dumicola* nests. They remove prey remains and kill parasitoid wasp larvae. In some other social spiders, ants appear to be exclusively scavengers/cleaners and do not disturb the spiders (Furey & Riechert 1989; Downes 1994).

Stegodyphus dumicola protect themselves from ants by employing silk. They deter approaching ants with sticky cribellar bands wrapped around the nest-supporting branches and they defend themselves against attacking ants by constructing fresh cribellar-silk shields. These anti-predator measures are adjusted to the degree of threat, but exceed the capabilities of solitary spiders. For breeding Gabar goshawks, a potential benefit of translocating colonies of *S. dumicola* onto their own nests (Henschel et al. 1992a,b) would be keeping ants away from their chicks.

Escaping from attacking ants does not appear to be a solution for *S. dumicola* because ants also frequent the surrounding terrain. This is different for *S. sarasinorum* in India (Bradoo 1972); when attacked by ants, these spiders left and established new nests elsewhere. Though a new nest and web may incur a higher overall cost of silken material than the cost of a defensive shield, emigrating *S. sarasinorum* are not required to produce this at such a high rate as defenders would be.

Anoplolepis ants are widely distributed in southern Africa; and in the areas studied in central Namibia, they frequent most trees daily (Prins 1982). Other genera of arboreally-foraging ants that attack *S. dumicola* include *Acantholepis*, *Crematogaster* and *Pheidole* (Meikle 1986 pers. comm.; Seibt & Wickler 1988a; Le Roy pers. comm.; pers. obs.). These ants seek food in trees, particularly honeydew from scale insects and aphids, and repel other animals by chemical and physical means (Hölldobler & Wilson 1990). The frequent confrontations of *S. dumicola* with ants are a consequence of the spiders' reliance on retreats built against solid objects and their chosen microhabitat in tree branches.

By contrast, the sympatric solitary *S. bicolor* (O. Pickard-Cambridge 1869) builds its nest against stalks of grass and herbs that do not appear to be frequented by aggressive ants (pers. obs.). The ephemeral nature of these substrata in the presence of large ungulates may pose different problems for *S. bicolor* that occur at low densities of three or more orders of magnitude less than *S. dumicola*. Nevertheless, ants pose a potential problem for other species of solitary-living *Stegodyphus*. Schneider (1992) reports that ants annually raided 3.6% of solitary *S. lineatus* in Greece. Although this is much less than the 23.2% incidence of wasp parasitism, the ability of ants to escalate their attacks would still appear to make them dangerous.

Arboreal ants may exert selective pressure on *S. dumicola* at the group level. All members of a colony under attack are affected. On the one hand, the actions of ants may restrict spider dispersal because ant encounters with groups provide potential emigrants a means to assess the danger of leaving the safety of the group. On the other hand, the ability of ants to eventually eliminate even the largest, resistant colonies, would place those spider demes with several dispersed sister/daughter colonies at a selective advantage. Dispersers that reach temporarily enemy-free sites can found new colonies that grow rapidly in the first few generations due to the high female productivity in small colonies (*sensu* Seibt & Wickler 1988a) and female-biased sex ratios (*sensu* Avilés 1993).

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