Does group-living or aggregation of spiders of the genus *Stegodyphus* affect parasitism by pompilid wasps?

J. R. Henschel
Desert Ecological Research Unit of Namibia,
P.O. Box 1592,
Swakopmund, Namibia

J. Schneider
Max-Planck-Institut für Verhaltensphysiologie,
Seewiesen,
D-82319 Starnberg, Germany

and

T. Meikle
Natal Museum,
Private Bag 9070,
3200 Pietermaritzburg, South Africa

Summary

The hypothesis that risk of predation is inversely related to dispersion was examined for the subsocial spider *Stegodyphus lineatus* being parasitised by the pompilid wasp *Pseudopompilus humboldti* and the social *S. dumicola* parasitised by *P. funereus*. The only difference when comparing scattered individual spiders with aggregations and with social groups, was that spiders in aggregations experienced lower parasitism rates than did scattered spiders. This could be due to the escape response of spiders that detected attacks on nearby neighbours. Parasitism rates of social groups were influenced by conflicting factors, including intervention by ant predators. We conclude that the action of wasp parasitoids favours aggregation in *S. lineatus*, but probably did not affect the evolution of sociality in *S. dumicola*.

Introduction

Restricted dispersal is characteristic of cribellate spiders of the genus *Stegodyphus* (Araneae: Eresidae). Of 19 species, three are non-territorial, permanently social (Kraus & Kraus, 1988). The remaining 16 asocial or subsocial species live solitarily with scattered or aggregated dispersion patterns. Nevertheless, some individuals of all three social species also occasionally live solitarily (Jacson & Joseph, 1973; Seibt & Wickler, 1988; Henschel, 1993).

One hypothesis to explain grouping is lowered risk of predation (Inman & Krebs, 1987). Seibt & Wickler (1988) suggested that this applies to *Stegodyphus*, although the opposite has been shown to occur in colonial spiders that have territorial orb webs on common frame webs (Uetz & Hieber, 1994).

Here we focus on wasps of the genus *Pseudopompilus* (Hymenoptera: Pompilidae) that are specialised parasitoids of *Stegodyphus* (El-Hennawy, 1987; M. C. Day, pers. comm.). With each individual of *Stegodyphus* that a female *Pseudopompilus* captures, it provisions one of its own offspring (El-Hennawy, 1986; Griswold & Meikle, 1990; Ward & Henschel, 1992). Our spider-parasitoid pairs were the subsocial *S. lineatus* (Latreille, 1817) with *P. humboldti* (Dahlbom, 1845) and the social

S. dumicola Pocock, 1898 with *P. funereus* (Arnold, 1932).

To address the question of whether the dispersion pattern of spiders affects risk of wasp parasitism, we compared *S. lineatus* in high- and low-density areas. To determine whether risk differs for solitary and social spiders, we compared foundresses of *S. dumicola* with social groups.

Methods

Wasp-spider interactions were recorded and wasp grubs or pupal cocoons were counted on spider nests. Parasitoids can be readily seen, because female wasps position their victims at the spiders' nest entrance (El-Hennawy, 1987; Ward & Henschel, 1992). All nests occurring in local populations were monitored before and during the breeding seasons. For *S. lineatus* the breeding season is May–July (Schneider, 1992; Ward & Lubin, 1993) and for *S. dumicola* it is February–May (Seibt & Wickler, 1988; Henschel, 1995).

JS conducted intensive observations of 181 *S. lineatus* on the Greek island of Karpathos during February–July 1991. The spider dispersion was aggregated at two of the study sites and scattered at two other sites (median ± interquartile of the number of neighbours in a 50 cm radius of each nest: aggregated=3 ± 1; scattered=0+1). JS also examined an aggregated population near Sede Boqer, Israel, during February–July 1993 (n=268 spiders). The latter were compared with data from a nearby scattered population in Israel recorded by Ward & Henschel (1992) during May–July 1990 (n=54). TM observed *S. dumicola* occurring at one site at Spioenkop, Natal, South Africa, during monthly 2-day visits between October 1985 and October 1986 (n=59 nests; 27 solitary, 32 social colonies comprising 353 spiders). JH conducted observations over 2–3 days on a monthly or twice-monthly basis in a local population of *S. dumicola* on the farm Christirina near Uhlenhorst in Namibia during January–May of 1991–1993 (n=249 nests; 191 solitary, 58 social colonies comprising 1282 spiders).

For *S. dumicola*, social groups were compared with solitary dispersers, and for *S. lineatus*, aggregated populations were compared with scattered populations. These comparisons and that between species were made on the basis of individual rates of parasitism, i.e. the proportion of spiders in a given sample and dispersal class that were parasitised.

JS conducted an experiment in Israel to observe the reaction of aggregated *S. lineatus* to the presence of a foraging wasp. A female *P. humboldti* was released into

Locality	Individual rate	
	Scattered	Aggregated
Greece	0.287 (108)	0.151 (73)
Israel	0.256 (54)	0.138 (268)

Table 1: Individual rate of wasp parasitism (*n*) of solitary *Stegodyphus lineatus* occurring in aggregated or scattered dispersion patterns in Greece and Israel.

a cage containing four adult females of *S. lineatus* that occupied nests in the cage. The wasp and spiders were monitored until the wasp ceased to forage.

Results

Stegodyphus lineatus (Table 1)

All of the wasps' victims were adult females without young. The rate of parasitism was lower for high-density aggregations than for scattered spiders in Greece ($\chi^2=4.7$, $p<0.05$, df$=1$) and Israel ($\chi^2=4.6$, $p<0.05$, df$=1$).

On 13 occasions, one to six neighbouring spiders of a victim fled by dropping out of the retreat without using a dragline. Wasps sometimes waited in such abandoned retreats for over 24 h ($n=3$). Most (72%) of the spiders that had fled returned two days later, while the others disappeared. In the laboratory, a *P. humboldti* female released into a cage containing four *S. lineatus* females, succeeded in parasitising only one. The other three were alarmed, dropped out of their retreats, and survived. After inspecting the empty nests, the wasp ceased foraging and tried to leave.

Stegodyphus dumicola (Table 2)

Parasitism occurred only in colonies containing at least some mature females, but no spiderlings. The individual rate of parasitism of all *S. dumicola* was 13% of that of all *S. lineatus*. It was lower for *S. dumicola* in Namibia than in Natal ($\chi^2=43.2$, $p<0.001$). Of the 44 wasp grubs or pupae seen on *S. dumicola*, 86% were on spiders belonging to social groups. However, this difference appeared to be based merely on greater opportunities to parasitise enduring groups, as there was no difference in individual parasitism rate between the solitary and group-living spiders observed (Natal: $\chi^2=0.1$; Namibia: $\chi^2=1.1$; $p>0.1$, df$=1$).

On two occasions, we observed wasps making multiple captures of *S. dumicola* in colonies (4 and 8 captures in 2.0 h and 0.5 h from groups of 68 and 15 respectively). By contrast, a group of spiders once prevented a wasp from parasitising an immobilised group member. In a confrontation lasting 2.2 h, the wasp jabbed its sting at five other spiders that approached, but twice nearly fell prey to approaching spiders when it briefly became entangled in the web.

Discussion

Pompilid wasps appear to be a major mortality agent of *S. lineatus* that can affect up to 29% of a local

| Locality | Individual rate | | Colony rate |
	Solitary	Social	
Natal	0.074 (27)	0.068 (353)	0.375 (32)
Namibia	0.021 (191)	0.011 (1282)	0.069 (58)

Table 2: Individual and colony rates of wasp parasitism (*n*) recorded for solitary and social *Stegodyphus dumicola* in Natal and Namibia. Colony rates indicate the proportions of groups that contained affected individuals.

population of spiders. Other predators, such as birds, ants and araneophagous spiders, are less important (JS, pers. obs. in Israel: 12%, 6% and 4% respectively). For *S. dumicola*, wasp parasitism is far less important than other mortality agents. At the study site in Namibia, wasps only affected 1% of all *S. dumicola* compared with at least 45% that fell prey to ants and some 3% each taken by araneophagous spiders and birds (Henschel, 1995).

Aggregations of *S. lineatus* in separate webs appeared to be safer from wasps than were widely dispersed individuals. This could be due to wasp foraging behaviour, and/or because the spiders have a distinctive escape response to approaching wasps, which is particularly effective when the fleeing spider is not the first target. It is not known how spiders are alarmed; perhaps they are forewarned by the reaction of conspecifics that fall victim, although adult *S. lineatus* do not occupy common webs. In the colonial *Metepeira incrassata* F. O. P.-Cambr. (Araneidae), web signals appear to forewarn spiders of wasp attacks on other colony members (Uetz & Hieber, 1994). However, in the latter species, isolated individuals were safer from wasps than small colonies were, perhaps because the wasps foraged more intensively in spider groups.

By contrast, for *S. dumicola* in social groups, the individual rate of parasitism by wasps did not differ from that of solitary individuals. The drop-escape reaction may not be an effective way for group-living spiders to escape wasps, because mass exodus would probably expose rather than conceal many spiders. Furthermore, our observations of multiple-parasitism and group defence demonstrate the difficulty of interpreting grouping in this species as advantageous or disadvantageous in terms of risk of wasp parasitism.

Pompilid wasps appear to lack the destructive capabilities that pugnacious arboreal ants have on *S. dumicola* populations in Namibia (Henschel, 1995) and Natal (Meikle, 1986). Attacking ants also kill the stationary wasp grubs (Henschel, 1995), which are probably more vulnerable than non-parasitised spiders that actively use silk to defend themselves against ants. This could explain the low incidence of wasp parasitism in *S. dumicola* compared with *S. lineatus* where ant predation was less frequent (JS, pers. obs.). Wasps thus share with their hosts an enemy which may affect the parasitoid population more than that of the host species.

By concentrating on mature female spiders, wasps obtained the largest possible hosts. By avoiding parasitising females with young, wasps avoided having their grubs devoured by gerontophagous spiderlings. This could be achieved roughly by seasonal synchronisation, but the targeting of only one class of spiders from a variable population may indicate more precise selection based not only on body size (El-Hennawy, 1986), but also on other cues that may relate to female maturation or egg production. *Stegodyphus lineatus* females can protect themselves by sealing their nests after egg-laying (Ward & Lubin, 1993; JS, pers. obs.), but there are trade-offs with the need to thermoregulate in hot environments (Henschel, Ward & Lubin, 1992) and to forage.

Pompilid wasps appear to face many more trade-offs that relate to host procurement and the future welfare of the parasitoid grubs. For instance, *P. humboldti* is adept at dealing with the trade-off between the future thermal requirements and predation risk faced by the host (Ward & Henschel, 1992). The female wasp places the spider victim at the exposed nest entrance rather than in the protective nest tunnel. The increased risk of the spider and grub being discovered by a predatory bird in the cool nest entrance is preferable to certain death caused by overheating in the hot confines of the nest during a summer afternoon. Some other trade-offs may be more complex, e.g. those between spider dispersion, defensive and evasive behaviour, phenology and environment on the one hand and wasp foraging limitations and offspring survival-to-imago on the other hand. Our study indicates that these host-parasitoid relationships may involve some discrete factors, such as spider nearest-neighbour distances and specific cues that may alert wasps and spiders to the presence of each other. Further study is necessary to reveal the co-evolutionary processes involved.

Acknowledgements

References

EL-HENNAWY, H. K. 1986: On the relation between *Stegodyphus dufouri* (Audouin) 1827 (Araneae: Eresidae) and *Pseudopompilus humboldti* (Dahlbom) 1845 (Hymenoptera: Pompilidae). *In* W. G. Eberhard, Y. D. Lubin & B. C. Robinson (eds.), *Proceedings of the ninth international congress of arachnology, Panama, 1983*: 91–93. Smithsonian Institution Press, Washington, D.C.

EL-HENNAWY, H. K. 1987: Preliminary notes on the biology, distribution, and predatory behaviour of *Pseudopompilus humboldti* (Dhlb.) (Hymenoptera: Pompilidae). *Serket* **1**: 1–11.

GRISWOLD, C. E. & MEIKLE, T. C. 1990: Social life in a web. *Nat.Hist.N.Y.* **3/90**: 6–10.

HENSCHEL, J. R. 1993: Is solitary life an alternative for the social spider *Stegodyphus dumicola*? *J. Namibian Sci.Soc.* **43**: 71–79.

HENSCHEL, J. R. 1995: Group-living reduces risk of predation in the spider *Stegodyphus dumicola* (Eresidae). *Zool.J.Linn.Soc.*: submitted.

HENSCHEL, J. R., WARD, D. & LUBIN, Y. 1992: The importance of thermal factors for nest-site selection, web construction and behaviour of *Stegodyphus lineatus* (Araneae: Eresidae) in the Negev Desert. *J.therm.Biol.* **17**: 97–106.

INMAN, A. J. & KREBS, J. 1987: Predation and group living. *TREE* **2**: 31–32.

JACSON, J. J. & JOSEPH, K. J. 1973: Life history, bionomics and behaviour of *Stegodyphus sarasinorum* Karsch. *Insectes soc.* **20**: 189–204.

KRAUS, O. & KRAUS, M. 1988: The genus *Stegodyphus* (Arachnida, Araneae). Sibling species, species groups, and parallel origin of social living. *Verh.naturw.Ver.Hamb.* **30**: 151–254.

MEIKLE, T. 1986: Nest associates of two species of group-living Eresidae in southern Africa. *In* J. A. Barrientos (ed.), *Actas X congreso internacional de aracnologia, Jaca, 1986* **1**: 275. Juvenil Press, Barcelona.

SCHNEIDER, J. 1992: *Die Wurzeln des Soziallebens bei der subsozialen Spinne* Stegodyphus lineatus *(Eresidae)*. Ph.D. thesis, Ludwig-Maximillian-Universität, München, Germany.

SEIBT, U. & WICKLER, W. 1988: Bionomics and social structure of 'Family Spiders' of the genus *Stegodyphus*, with special reference to the African species *S. dumicola* and *S. mimosarum* (Araneida, Eresidae). *Verh.naturw.Ver.Hamb.* **30**: 255–303.

UETZ, G. W. & HIEBER, C. S. 1994: Group size and predation risk in colonial web-building spiders: analysis of attack abatement mechanisms. *Behav.Ecol.* **5**: 326–333.

WARD, D. & HENSCHEL, J. R. 1992: Experimental evidence that a desert parasite keeps its host cool. *Ethology* **92**: 135–142.

WARD, D. & LUBIN, Y. 1993: Habitat selection and the life history of a desert spider, *Stegodyphus lineatus* (Eresidae). *J.Anim.Ecol.* **62**: 353–363.