Panorpa scorpionflies foraging in spider webs — kleptoparasitism at low risk

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Summary

Males and females of *Panorpa vulgaris* and *P. communis* scorpionflies were observed to be frequent kleptoparasites of web-spinning spiders. In field studies they obtained a large proportion of their food from spider webs.

Even large spiders were sometimes attacked by the scorpionflies.

In contrast with North American *Panorpa* species, web-building spiders did not cause a high percentage of the mortality of the examined scorpionflies, and there was no indication that *P. vulgaris* males feeding in spider webs were the smaller and inferior males of the populations.

Introduction

Kleptoparasitism of scorpionflies in spider webs

Feeding of *Panorpa* scorpionflies in spider webs has been noted by many authors. Dixon (1881, cited by Jones-Walters, 1984) is believed to be the first to describe *P. communis* L. stealing prey in spite of two spiders trying to drive the scorpionfly out of the web.

Thornhill (1975, 1978) found that kleptoparasitism in spider webs is very common in North American scorpionflies. According to Thornhill, it is mostly small and contest-losing *Panorpa* males which have to look for insects or parts of arthropods which have become prey of spiders. Foraging in spider webs, however, is very risky: 65% of the observed mortality of adult scorpionflies in the field is caused by web-building spiders (Thornhill, 1975, 1978).

Nyffeler & Benz (1980), Locket (1983), Jones-Walters (1984), Jones-Walters & Locket (1985) and Greenwood (1989) observed European scorpionflies feeding in spider webs without identifying the *Panorpa* species. Nyffeler & Benz (1980) examined 3484 pieces of prey in 333 spider webs, but only 3 of these were *Panorpa*.

During investigations on the mating system of *P. vulgaris* Imhoff & Labram and *P. communis*, Bockwinkel (1990) collected field data concerning resource availability, foraging in spider webs, and predators of adult scorpionflies. In this paper we try to answer the following questions:

1. What significance has kleptoparasitism in spider webs for *P. vulgaris* and *P. communis*?
2. Are spiders important predators of these scorpionflies?
3. Is there a sex-specific risk for *P. vulgaris* males foraging in spider webs?

Biology of the examined scorpionflies

European scorpionflies live in moist woods, bushes, shrubs and late-successional grassland communities. Larval development occurs among litter covering the

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ground. Little is known about the food of *Panorpa* larvae. Adult *Panorpa* scorpionflies are very weak flyers. They are scavengers, feeding on carcases of insects and other arthropods (for further descriptions see Kaltenbach, 1978; Byers & Thornhill, 1983). Food is a highly limited resource for scorpionflies and there is severe inter- and intraspecific competition for dead arthropods (Thornhill, 1980a, 1981). Food limitations are important not only for survival rates, longevity and egg production, but also for mating of the scorpionflies: according to Thornhill (1981), male *Panorpa* exhibit a resource-dependent mating system.

Males of *P. vulgaris* and *P. communis* have two resource-dependent mating tactics: (a) offering dead arthropods or (b) offering salivary masses during copulation (Bockwinkel & Sauer, 1988; Bockwinkel & Sauer, in press). There is no resource-independent forced copulation in these species as described by Thornhill (1980b) for North American scorpionflies.

Methods

During May/June and August/September 1987 and 1988, i.e. at the times of the highest activity of the different *Panorpa* generations, field experiments were carried out near Freiburg i.Br. at the edges of late-successional shrub and bush communities (detailed description of the study area in Sauer & Hensle, 1977: sites IV and VI). Feeding activity and movements of scorpionflies in spider webs were recorded around plants of Stinging Nettles (*Urtica dioica* L.) for about 6 h every second day in an area of 60×2 m. As a measure of body size, the left forewing of scorpionflies feeding in spider webs was measured with vernier callipers while holding the wing between transparent PVC foil, and compared with the average wing length of the population.

Results

Diet of P. vulgaris

Figure 1 shows the results of feeding observations of *P. vulgaris* in the field. Because there were no differences in the diet between the sexes (Chi-square test) all data are pooled in Fig. 1. Compared with the findings of Thornhill (1980a), whose nine *Panorpa* species in Michigan fed almost exclusively on dead insects and phalangiids (88.8–100%), *P. vulgaris* showed two important differences in our study: pollen and nectar of plants and excrements of birds and snails made up 33.6% of all feeding observations ($n = 467$). Besides this, *P. vulgaris* is a predator of small arthropods (Lachnidae, Aphidae, young spiders; 12%). The amount of feeding observations on large carrion (2.6%) and medium-sized insects (muscid flies) (1.5%) is quite low. Most of our feeding observations concerned parts of dead insects (wings, legs, parts of the exoskeleton) thrown out of spider webs (18.8%) and prey in spider webs directly (31.5%).

P. communis showed lower activity and a lower abundance (Bockwinkel, 1990) in the study areas than *P. vulgaris*. Therefore, we obtained fewer feeding observations of this species ($n = 79$), but no interspecific

differences in the food spectra were established (Bockwinkel, 1990).

Spiders as predators of Panorpa

In spite of the large amount of spider prey observed in the diet of the scorpionflies, predation by spiders did not play an important role in *P. vulgaris* and *P. communis*. Individuals of these species and of a co-occurring species, *P. germanica* L., moved around in webs of Araneidae, Linyphiidae, Tetragnathidae and Theridiidae without struggling in the webs. They fed on parts of dead insects, freshly caught prey and also young spiders. Often even large spiders (*Tetragnatha extensa* (L.), *Araneus diadematus* Clerck) were attacked by scorpionflies (males used their genital claspers and females their abdomens for fighting and striking spiders, as they do also in intra-specific aggressive interactions). Intra- and interspecific aggression between scorpionflies for food was observed in spider webs while the spiders had to wait at a distance. Once in a linyphiid web a pair of *P. vulgaris* even copu-lated, with the male offering spider prey as a nuptial gift to the female, without being disturbed by the displaced spider.

During 173 observations of *P. vulgaris* and *P. communis* individuals feeding in spider webs very few scorpionflies were found entangled in spider silk of araneids ($n = 2$) and a theridiid ($n = 1$). Also, one *P. vulgaris* male was caught by a *Pisaura mirabilis* (Clerck) female, one female of this species and another female of *P. germanica* were caught by *Xysticus* females in their hiding places. So the observed mortality in the field caused by web-building and hunting spiders was equal and was probably of little importance, as the population of *P. vulgaris* females in the study area reached about 2015 individuals in the first generation of 1987 (SD 636; mark/recapture experiment; Bockwinkel, 1990).
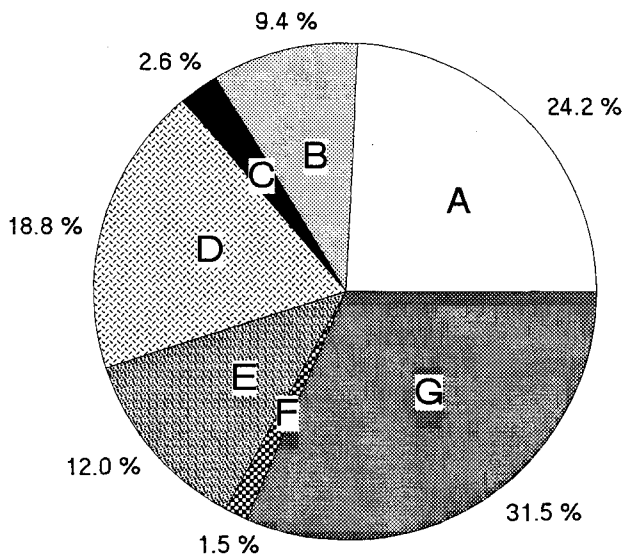

Fig. 1: Spectrum of 467 feeding observations of *Panorpa vulgaris* in the field in 1987 and 1988. A = nectar and pollen ($n = 113$); B = excrement of birds and snails ($n = 44$); C = large insect carrion ($n = 12$); D = parts of dead insects thrown out of spider webs ($n = 88$); E = small living arthropods ($n = 56$): F = muscid flies parasitised by fungi ($n = 7$); G = insects in spider webs ($n = 147$).

1987		1988	
spider webs	aver. pop.	spider webs	aver. pop.
13.48 ± 0.32	13.52 ± 0.5	13.68 ± 0.46	13.64 ± 0.49
$n = 16$	$n = 146$	$n = 21$	$n = 126$

Table 1: Wing lengths (mean ± SD, mm) of males of *Panorpa vulgaris* feeding in spider webs compared with the average wing lengths of the populations.

Body size of foraging males and sex ratio in spider webs

According to Thornhill (1978, 1981), it is mainly small, inferior males which have to face the risk of foraging in spider webs.

Table 1 shows the wing lengths of *P. vulgaris* males of the first generations in 1987 and 1988 which were caught while feeding in spider webs, compared with the average wing lengths of the rest of the population (males caught out of spider webs). No differences in wing length between these two groups were found (Mann Whitney U-test). Moreover, there was no statistical difference between the numbers of males and females of this species foraging in spider webs: 78 males and 69 females were observed (binomial test).

Discussion

The spectrum of feeding observations (Fig. 1) indicates that there is a shortage of available insect carrion in the examined scorpionfly species. This interpretation is supported by the fact that only at the beginning of the first generation of a year, are males of *P. vulgaris* able to produce salivary masses as nuptial gifts (Bockwinkel & Sauer, 1988; Bockwinkel & Sauer, in press). At this time most copulations observed in the field were of males employing the saliva tactic. Later, males have not enough protein reserves stored in the salivary glands; therefore, the tactical options of the *Panorpa vulgaris* males are restricted and they are forced to use carrion as nuptial gifts (Bockwinkel & Sauer, in press).

Moreover, female fecundity under field conditions is diminished significantly by limited resource availability compared with well-fed control groups in the laboratory (Bockwinkel, 1990).

Under conditions of strong food limitation and severe intra- and interspecific food competition (Thornhill, 1980a, 1981; Bockwinkel, 1990), the examined *Panorpa* scorpionflies have to be kleptoparasites of spider prey. In contrast with North American species, however, which often become prey of araneid and tetragnathid spiders (Thornhill, 1978) the examined *Panorpa* species' foraging in spider webs seems to be almost risk-free, in spite of the adhesiveness of spider silk (Eisner *et al.*, 1964).

Therefore, both sexes of these species feed on spider prey equally, and instead of inferior males being forced to avoid aggressive interactions with larger competitors by foraging in spider webs, intra- and interspecific aggression of scorpionflies for food is frequent in spider webs, both within and between the sexes (Bockwinkel, 1990).

Obviously individuals of *P. vulgaris* and *P. communis* gain an important amount of their food resources in spider webs (Fig. 1) by usurping prey and striking the spiders with genital claspers or abdomens. This special fighting behaviour of the observed scorpionflies (Bockwinkel, 1990) is probably the main reason for the dominance of *P. vulgaris* and *P. communis* in aggressive interactions with spiders. Tipulidae and Rhagionidae, which are similar in body size but do not show such fighting behaviour, were frequently found entangled in spider silk.

The question of how *Panorpa* manage to forage in spider webs without becoming stuck to the adhesive silk cannot be answered now and may be of some interest for arachnologists. Apart from the possibility of morphological adaptations of the scorpionfly leg and tarsus, it may be significant that the *Panorpa* usually walked into the spider webs, so the wings did not touch the silk.

Acknowledgements

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