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Obligate Kleptoparasitic Behaviour of Female Flies at Spider Webs (Diptera: Empidoidea: Microphoridae)

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Abstract

Female *Microphor anomalus* hover in large numbers very close to orbwebs of spiders, land on entangled prey items and steal food. The regular structure of an orbweb facilitates the orientation of these small flies and prevents them from getting entangled in the sticky threads. Similar observations from several *Microphor* species suggest that females are obligate kleptoparasites in orbwebs. A review on kleptoparasitic Diptera at spider webs is given and discussed.

Introduction

The webs of spiders often catch much more insects than the resident spider is able to feed on. Especially during mass occurances of small insects like aphids or nematocerans, a spider's web can be covered with insects to which the web spider pays no attention. This food is used by a variety of predators which steal prey items from the web. They land on insects in the web and suck them dry or hover near the web and pick up the items. These kleptoparasites (for definition see Robinson and Robinson 1977, Vollrath 1984) belong to several vertebrate, insect and spider groups (panorpid scorpionflies, damselflies, several flies, wasps, mirid bugs, spiders, hummingbirds etc.; Thornhill 1975, Sivinski and Stowe 1980, Vollrath 1984, Nentwig 1985 and references mentioned there). They either visit a spider's web only occasionally or are closely linked with the life-cycle of their host. In most cases, however, kleptoparasitism and its influence on the host is poorly known. This paper deals with observations on an empidid fly which was numerously observed near spider webs in the Federal Republic of Germany.

Material and Techniques

Microphor (= *Microphorus*) *anomalus* Meigen 1824 (Empididae: Microphorinae = Empidoidea: Microphoridae) is a small 2-mm-fly, common in Europe. Larvae probably live in the detritus layer of forests or meadows. Adults can be found from June to August and are reported to probably be predacious or to feed on nectar or pollen (Chvala 1983 and pers. comm.).

In July 1981 and 1984 *M. anomalus* was observed at webs of *Zygiella x-notata*, *Meta* spec. (juv.), *Araneus diadematus* and *Nuctenea umbratica* (all Araneidae) in a mosaic landscape (pasture, crop fields, oldfields, forest edge) near Marburg, Federal Republic of Germany.

Results

On warm summerdays up to 15 *Microphor anomalus* females per orbweb were observed in or near the webs of several araneid spiders. No flies were observed near the three-dimensional space webs of Linyphiidae and Theridiidae in the same habitat. Typically, the flies approached the web and flew towards a prey item entangled in the sticky threads. This was inspected visually for a short moment, the flies than either landed on the carcass or flew to the next item. All dark objects in the web attracted the fly, whether seed, dirt or prey item. A fly approached several items successively, occasionaly landing and feeding on them.

On the average, *M. anomalus* females inspected 27 prey items per minute visually, they contacted only 4 items/min (= 14% of the items inspected) and fed on less than 2 items/min. Mean feeding time on a prey insect was 20 s. The standard deviation is high due to the wide range of all these values (Tab. 1). Since most orbwebs visited, contained only a few dozen prey items and since many flies flew in large groups of conspecifics for several minutes around each web, each *M. anomalus* inspected a given prey item several times. I observed that items previously rejected were accepted when inspected a second or third time.

Table 1. Activity of female *Microphor anomalus* on a warm summerday afternoon at orbwebs

activity	$\bar{x} \pm$ SD	range	*N*
prey items visually inspected/min	26.8 ± 9.4	(7–42)	20
prey items contacted/min	3.7 ± 1.9	(0–7)	20
prey items feeding on/min	1.7 ± 1.5	(0–3)	20
feeding time (s) per prey item	19.4 ± 40.9	(1–200)	35

The flies prefered to land on prey another fly was already feeding on. The invading fly tried to push the defending fly away and the latter tried to prevent the invader from landing. These fights last less than two second. *M. anomalus* females fed several times and even after long meals (more than 1 min) they continued to search for prey. After several minutes, a time in which they inspected hundreds of prey insects and had several meals, the flies flew away. No preference for a special kind of prey could be detected. The prey of the orbwebs consisted mainly of aphids (86%) and thysanopterans (10%) (Tab. 2).

Table 2. The prey composition of orb webs of *Nuctenea umbratica*

	N	%	size class (mm)
Diptera: Chironomidae	13	3.0	0.5–2.5
Limoniidae	1	0.2	2.5
Coleoptera: Staphylinidae	1	0.2	2.5
Nitidulidae	1	0.2	2.5
Aphidoidea, winged	363	84.4	0.5–3.5
not winged	7	1.6	0.5
Thysanoptera	44	10.2	0.5–1.5
total	430		

Microphor anomalus females fly in a relatively constant distance of approx. 1 cm from the web's plane. They obviously follow the spiral and radial threads of the orbweb. The resulting flight curve is therefore regular and consists of spiral and radial parts on which the fly "jumps" from one turn of the sticky thread to the next (Fig. 1). The flies stop at nearly all darker objects attached to the web. When such an object is close (not more than 1—1.5 cm) to the guiding web thread, the fly may leave its thread and fly across the open mesh of the orbweb.

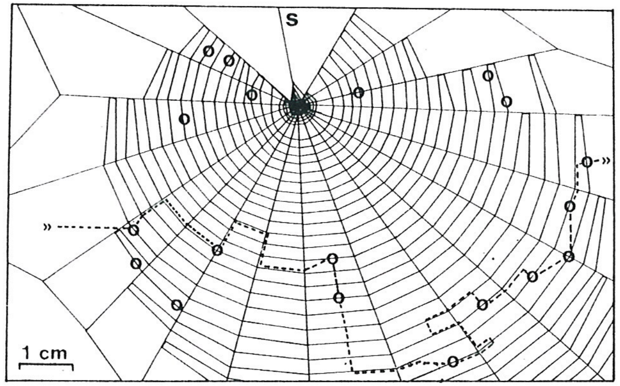

Fig. 1. The orb web of *Zygiella x-notata*; the signal thread (s) leads from the hub to the retreat where the spider sits. Broken line: Flight of one *Microphor anomalus* female (from left to right); flight duration 30 s. Open circles represent prey items (mainly aphids), scale 1 cm

Discussion

Observations of the flight behaviour of *M. anomalus* at orbwebs indicate that these small flies are able to detect the single thread of a spider's web. The thread functions as a guideline and probably "helps" the fly to orientate at orbwebs. I never saw a microphorid caught in a web, indicating that this method is rather secure. It explains as well, why no flies were found near three-dimensional space webs of linyphiids or theridiids, two common web-types in the same habitat. The irregular arrangement of threads in these webs probably prevents inspection flights, where the fly encounters a high risk of getting entangled.

Previously, insects avoiding spiders' webs have numerously be recorded, but most records concern large insects such as bees, bumble bees (Hymenoptera); syrphid, muscid, calliphorid, asilid and tipulid flies (Diptera); dragonflies and damselflies (Odonata) (Bristowe 1941, Nentwig in press b, unpubl.). Most of these optically orientated insects are pollinating insects or predators. The small kleptoparasitic flies may perhaps be compared with parasitic hymenopterans which sometimes show a considerable avoidance behaviour, too (Nentwig 1981, 1985, in press a).

The spiral threads of the orbweb of *Zygiella x-notata* (Araneidae) measures 0.15 µm in diameter (Lehmensick and Kullmann 1956). Considering the Minimum separabile or the Minimum visible of good insect eyes (Kaestner 1972, Penzlin 1977) the thread is by far too thin to be detected. Diffuse light reflections, how-

Table 3. Kleptoparasitic Diptera at spiders and their webs (taxonomy according to Sick 1977)

Diptera	spider	country	reference
Nematocera: Cecidomyiidae			
indet.	Araneidae	USA	McCook (1889)
Didactylomyia longimana (Felt)	Araneidae	USA	Sivinski and Stowe (1980)
Ceratopogonidae			
Atrichopogon spec.	orb web spider	USA	Downes and Smith (1969)
Culicoides bauri	Araneidae	USA	Sivinski and Stowe (1977)
Brachycera: Orthorrhapha: Empidoidea: Microphoridae			
Microphor vetulinus	web spider	GB	Morley and Atmore (1915)
M. crassipes Macq.	Araneidae	GB	Laurence (1948)
M. obscurus Coq.	orb webs	USA	Downes and Smith (1969)
M. anomalus Meig.	Araneidae	FRG	this study
Cyclorrhapha: Aschiza: Phoridae			
Megaselia spec.	Araneidae	USA	Sivinski and Stowe (1980)
Cyclorrhapha: Schizophora: Acalyptrata: Milichiidae: Madizinae			
Desmometopa m-nigrum Zett.	Thomisidae	Jugoslavia Sweden	Biro (1899), Lundström (1906)
D. sordida Fall.	Thomisidae	Jugoslavia Sweden Germany GB	Biro (1899) Lundström (1906) Kramer (1917) Richards (1953)
D. tarsalis Loew.	wandering spider	Singapore	Hennig (1937)
D. spec.	Araneidae	Australia	McMillan (1975)
Leptometopa latipes Meig.	Salticidae	USA	Frost (1913)
unident.	Araneidae	India	Champion-Jones (1937)
Phyllomyza spec.	Araneidae	Panama	Robinson and Robinson (1977)
		Panama	Nentwig, unpubl.
Neophyllomyza spec. a, spec. b	Araneidae	USA	Sivinski and Stowe (1980)
Paramyia nitens (Loew)			
Phyllomyza spec.			
Neophyllomyza spec.	Araneidae	Panama	Nentwig, unpubl.
Chloropidae			
Gaurax spec.	Araneidae	Uganda	Bristowe (1941)
Trachysiphonella pori	Zodariidae	Greek	Harkness and Ismay (1975)
Anomoeoceros punctulatus	Araneidae	Uganda	Ismay (1977)
Conioscinella spec.	Araneidae	Panama	Robinson and Robinson (1977)

Table 3 (continued)

Diptera	spider	country	reference
Calyptrata: Scatophagidae			
Scatophaga stercoraria	Araneidae	GB	BRISTOWE (1941)
Calyptrata: Anthomyiidae			
unident.	Araneidae	GB	BRISTOWE (1941)

ever, enlarge the apparent diameter of silk threads, so that many insects are able to see them. The constant distance between *M. anomalus* and web probably indicates that the fly can neither fly much closer to the sticky threads (too dangerous) nor can it keep a wider distance (high probability to "loose" the thread). Experiments to keep *Microphor* females in cages or boxes with a spider web failed because the flies did not fly (LAURENCE 1948, own observations).

Only females of *Microphor* species and other kleptoparasitic flies were observed near spider webs (HENNIG 1937, BRISTOWE 1941, LAURENCE 1948, SIVINSKI and STOWE 1080 and references mentioned there) although the feeding habits of the two sexes are identical in most Empidoidea (DOWNES and SMITH 1969). Male microphorids gather at the tips of twigs or fly around branches but were never observed feeding. Females are larger and heavier, they need energy for the production of eggs and are obviously specialised on prey items caught in spider webs. The high intraspecific competition of females at spider webs and the lack of other detailed feeding records for this genus strongly suggests that this kleptoparasitism is the only way of food intake in *Microphor* females. Considering the relatively high abundance of web spiders and the average high amount of small prey insects in these webs, an obligate feeding on these items seems to be a very effective method.

LAURENCE (1948) observed *Microphor crassipes* on tipulids, small midges, aphids, psocids and parasitic hymenopterans. Own observations of *M. anomalus* females cover a wide range of mainly small insects. SIVINSKI and STOWE (1980) report on kleptoparasitic flies feeding on many large insects, especially Hymenoptera and discuss a possible specialisation in this group. This is probably due to the limited number of observations and certainly does not reflect a real food specialisation. Within their niche, kleptoparasitic flies are unspecialised and accept most (all?) kind of prey.

In the literature, I found approx. two dozen records of Diptera which steal prey from spiders (Tab. 3). These citations, however, are restricted to a few groups. In Nematocera, only Cecidomyiidae and Ceratopogonidae are known to feed on spiders' prey. In Brachycera, mainly three unrelated groups are kleptoparasites: *Microphor* species (Orthorrhapha: Empidoidea: Microphoridae), several genera of Madizinae (Acalyptrata: Milichiidae) and several chloropid genera (Acalyptrata: Chloropidae). In chloropids, the situation is less clear and needs further investigation. BRISTOWE'S (1941) observation on an unidentified chloropid from Uganda is probably a case of parasitism; the observation on *Conioscinella* spec. by ROBINSON and ROBINSON (1977) may be an occasional kleptoparasitic behaviour in a parasitic species because some *Conioscinella* species are known spider parasites (DUDA 1933). Records of Phoridae are probably a case of real parasitism rather than kleptoparasitism (SIVINSKI and STOWE 1980); scatophagids and anthomyiids at

spider webs (BRISTOWE 1941) are probably an exception. Both families are predacious or visit flowers, *Scatophaga* (= *Scopeuma*) *stercoraria* is a common species and certainly not specialised on spider webs.

Dipterans in two nematoceran families and three brachyceran groups are known to exhibit true kleptoparasitism at spider webs. In two cases (Ceratopogonidae, Chloropidae) this behaviour may have evolved via endo- or ectoparasitism, in Microphoridae via predation on flying insects. Kleptoparasitism has evolved several times independently and an increasing knowledge of the biology of small flies (e.g. many Acalyptrata) may probably enlarge the number of kleptoparasites.

Zusammenfassung

Die Weibchen von *Microphor anomalus* schweben in größerer Zahl nahe den Radnetzen von Spinnen, landen im Spinnennetz auf Beutetieren und saugen daran. Beim Suchflug orientierten sich die Fliegen an den Einzelfäden des Netzes, so daß ein Verfangen an den Klebfäden vermieden werden kann. Ähnliche Beobachtungen an anderen *Microphor*-Arten lassen den Schluß zu, daß die Weibchen dieser Gattung obligate Kleptoparasiten an Radnetzen sind. Eine Literaturübersicht über Beobachtungen von kleptoparasitischen Dipteren an Spinnennetzen wird gegeben und diskutiert.

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