

KLEPTOPARASITISM AND PHORESY IN THE DIPTERA

JOHN SIVINSKI¹, STEVE MARSHALL² AND ERIK PETERSSON³

¹USDA-ARS, Center for Medical, Agricultural, and Veterinary Entomology
P. O. Box 14565, Gainesville, FL 32604

²Department of Environmental Biology, University of Guelph
Guelph, Ontario, N1G 2W1, Canada

³Department of Zoology, Uppsala University
Villavagen 9, S-752 36 Uppsala, Sweden

ABSTRACT

Spiders, dung-feeding scarabs, social, and prey-storing insects provide predictable and concentrated sources of food for a variety of thief flies (kleptoparasites) and their larvae. Whenever waiting in the vicinity of the "host" for an opportunity to exploit its resources is more energy efficient and less dangerous than foraging among hosts, a number of intimate relationships between the fly and host may evolve. In extreme cases, flies may become long-term phoretic associates that travel with hosts even while the latter is in flight. The behaviors and ecologies of kleptoparasitic Diptera are

reviewed with special attention paid to the adaptations of Sphaeroceridae phoretic upon Scarabaeidae. The mating systems of kleptoparasitic flies are influenced by the type of resource that is stolen; flies associated with predators are mostly female, while those found on scarabs are of both sexes. These differences are discussed in terms of mate location, sperm competition, and mate choice.

Key words: Sphaeroceridae, Milichiidae, Chloropidae, mating system, mate choice

RESUMEN

Para una variedad de moscas ladronas (cleptoparasíticas) y sus larvas, las arañas, escarabajos peloteros, insectos sociales e insectos que almacenan sus presas son fuente de alimento predecible y concentrada. Siempre que sea más eficaz y menos peligroso el esperar en la cercanía del hospedero para aprovecharse de sus recursos en lugar de buscar alimento entre los hospederos, varias relaciones ecológicas íntimas entre la mosca y su hospedero podrían evolucionar. En casos extremos, las moscas pueden volverse socios foréticos, viajando con sus hospederos mientras éstos vuelan. Se examinan el comportamiento y la ecología de los dípteros cleptoparasíticos dándole atención especial a las adaptaciones de las moscas foréticas Sphaeroceridae en Scarabaeidae. El sistema de apareo de las moscas cleptoparasíticas es influenciado por el tipo de recurso que se robe; las moscas asociadas con depredadores son en su mayoría hembras, mientras que aquellas asociadas con escarabajos son de ambos sexos. Se discuten estas diferencias en cuanto a la localización de la pareja, competencia de la esperma, y la elección de la pareja.

*Thus what the world calls good business is only a way
To gather up the loot, pack it, make it more secure
In one convenient load for the more enterprising thieves.*

Chuang Tzu, 250 B.C.

In this unpredictable and competitive world, many arthropods have found it adaptive to sequester, and sometimes personally guard, resources for their future use or the use of their offspring. For example, some dung beetles spend many hours shaping, moving, burying, and shielding a fecal fragment they may either eat, or into which they may lay an egg (Halffter & Edmonds 1982). Caching results in a delay between taking possession of a resource and its final consumption, and during this period owners are vulnerable to thieves (kleptoparasites). Other invertebrates at risk from kleptoparasites simply take a relatively long time to consume their food; e.g., certain web-building spiders may take minutes to hours to masticate and preorally digest a victim. Again, delay exposes predators to thieves, and the robbers that exploit both cachers and slow-eaters are often small Diptera.

A number of these tiny kleptoparasitic flies have intimate relationships with their larger "hosts" (Table 1). Some are phoretic and spend hours or days upon the bigger animal, not feeding, but simply waiting for it to obtain the item the fly wishes to share. In such cases it is presumably more efficient and less hazardous to wait for a particular host to obtain something valuable than it is to search for a host that happens to be feeding or burying at that particular time. Other flies wait near their host and can join it in an instant. The reasons for closeness are similar to those that have led to phoresy, but perhaps the lack of mobility inherent in phoresy or the danger of continually clinging to a giant has resulted in a looser association. In still other instances kleptoparasites search out "wealthy" arthropods and contacts are brief and sporadic.

TABLE 1. REPRESENTATIVES OF VARIOUS FORMS OF KLEPTOPARASITIC FLIES AND WHETHER OR NOT THEY PRACTICE PHORESIS. P = PHORESIS, CA = CLOSE ASSOCIATION, I.E., FLIES REMAIN IN THE VICINITY OF THE "HOST" BUT NOT UPON IT, A "?" AFTER A NOTATION REFLECTS A BELIEF THAT EITHER PHORESIS OR CLOSE ASSOCIATION IS PRACTICED BUT THAT UNEQUIVOCAL OBSERVATIONS ARE MISSING, AND A "." REPRESENTS AN ABSENCE OF DATA.

Species	Host	Type of Association	Citation
Adult kleptoparasites of social insects (food thieves)			
<i>Braula coeca</i>	<i>Apis mellifera</i>	P	Askew 1971
<i>Vestigipoda myrmolarvoidea</i> (Phoridae)	<i>Aenictus</i> sp. (Formicidae)	CA	Disney 1996
<i>Termitophodrides heterospinalis</i> (Phoridae)	<i>Cornitermes similis</i> (Isoptera)	P	Bristowe 1924
Termitoxeniinae (Phoridae)	Isoptera	CA	Disney & Kistner 1997
<i>Malaya</i> spp. (Culicidae)	Formicidae	CA	Farquharson 1918
Adult kleptoparasites of predatory arthropods (food thieves)			
<i>Gaurax</i> sp. (Chloropidae)	Araneidae	P	Bristowe, 1941, Ismay 1977
<i>Phyllomyza</i> sp. (Milichiidae)	<i>Nephila clavipes</i> (Araneidae)	P	Robinson & Robinson 1977
<i>Phyllomyza</i> sp. (Milichiidae)	<i>Nephila clavipes</i> (Araneidae)	P (?)	Sivinski & Stowe 1980
	<i>Rhinocornis cuspidatus</i> (Reduviidae)		
	<i>Misumena vatia</i> (Thomisidae)		
<i>Desmometopa sorida</i> (Milichiidae)	<i>Argiope bruennichii</i> (Araneidae)	P	Richards 1953
	<i>Argiope argentata</i> (Araneidae)	P	Robinson & Robinson 1977
<i>Conioscinella</i> spp. (Chloropidae)	<i>Scolopendra veridis</i> (Scolopendridae)	P	Sivinski 1985
<i>Neophyllomyza wulpi</i> (Milichiidae)	<i>Ommatius minor</i> (Asilidae)	P	Biro 1899
<i>Anomoeceros punctulatus</i> (Chloropidae)	Araneidae	P/CA	Ismay 1977
	<i>Nephila clavipes</i> (Araneidae)		
<i>Olcella cinerea</i> (Chloropidae)	Reduviidae	CA	Sivinski 1985
<i>Olcella quadrivittata</i> (Chloropidae)	Asilidae		
	Mantodea	CA	Marshall 1998
<i>Olcella trigramma</i> (Chloropidae)	Reduviidae	.	Sivinski 1985

TABLE 1. (CONTINUED) REPRESENTATIVES OF VARIOUS FORMS OF KLEPTOPARASITIC FLIES AND WHETHER OR NOT THEY PRACTICE PHORESIS. P = PHORESIS, CA = CLOSE ASSOCIATION, I.E., FLIES REMAIN IN THE VICINITY OF THE "HOST" BUT NOT UPON IT, A "?" AFTER A NOTATION REFLECTS A BELIEF THAT EITHER PHORESIS OR CLOSE ASSOCIATION IS PRACTICED BUT THAT UNEQUIVOCAL OBSERVATIONS ARE MISSING, AND A "." REPRESENTS AN ABSENCE OF DATA.

Species	Host	Type of Association	Citation
<i>Trachysiophonella pori</i> (Chloropidae)	<i>Zodarium frenatum</i> (Zodariidae)	CA	Harkness & Ismay 1975
<i>Paramyia nitens</i> (Milichiidae)	<i>Argiope aurantia</i>	CA	Sivinski & Stowe 1980
	<i>Nephila clavipes</i> (Araneidae)	(?)	Eisner <i>et al.</i> 1991
<i>Neophyllomyza</i> spp. (Milichiidae)	<i>Nephila clavipes</i> (Araneidae)	.	Robinson & Robinson 1977
	<i>Zelus trimaculatus</i> (Reduviidae)	.	Sivinski & Stowe 1980, Eis- ner <i>et al.</i> 1991
<i>Milichiella</i> sp. (Milichiidae)	<i>Nephila clavipes</i> (Araneidae)	CA (?)	Sivinski 1985 Eisner <i>et al.</i> 1991
<i>Desmometopa m-atrum</i> (Milichiidae)	Araneida	.	Mik 1898
	Reduviidae	.	Biro 1899
<i>Desmometopa</i> <i>singaporensis</i> (Milichiidae)	Araneida	.	Mik 1898
	Reduviidae	.	Biro 1899
<i>Desmometopa m-nigrum</i> (Milichiidae)	<i>Thomisus onuustus</i> (Thomisidae)	.	Knab 1915
<i>Desmometopa latipes</i> (Milichiidae)	<i>Phidippus multiformis</i> (Salticidae)	.	Frost 1913
<i>Desmometopa</i> sp. (Milichiidae)	<i>Nephila clavipes</i> (Araneidae)	CA (?)	Eisner <i>et al.</i> 1991
<i>Didactylomyia longimana</i> (Cecidomyiidae)	<i>Nephila clavipes</i> and other Araneida	CA	Sivinski & Stowe 1980
<i>Culicoides bauri</i> (Ceratopogonidae)	<i>Nephila clavipes</i> (Araneidae)	.	Sivinski & Stowe 1980
<i>Atrichopogon</i> sp. (Ceratopogonidae)	Araneidae	.	Downes & Smith 1969
<i>Microphor obscurus</i> (Empididae)	Araneidae	.	Downes & Smith 1969
<i>Microphor crassipes</i> (Empididae)	Araneidae	.	Laurence 1948
<i>Megaselia</i> sp. (Phoridae)	<i>Nephila clavipes</i> (Araneidae)	.	Sivinski & Stowe 1980
<i>Lonchaea chorea</i> (F.) (Lonchaeidae)	<i>Enoplognatha ovata</i> (Clerk) (Theridiidae)	.	Dobson 1992

TABLE 1. (CONTINUED) REPRESENTATIVES OF VARIOUS FORMS OF KLEPTOPARASITIC FLIES AND WHETHER OR NOT THEY PRACTICE PHORESIS. P = PHORESIS, CA = CLOSE ASSOCIATION, I.E., FLIES REMAIN IN THE VICINITY OF THE "HOST" BUT NOT UPON IT, A "?" AFTER A NOTATION REFLECTS A BELIEF THAT EITHER PHORESIS OR CLOSE ASSOCIATION IS PRACTICED BUT THAT UNEQUIVOCAL OBSERVATIONS ARE MISSING, AND A "." REPRESENTS AN ABSENCE OF DATA.

Species	Host	Type of Association	Citation
<i>Lonchaea laticornis</i> Meig. (Lonchaeidae)	<i>Enoplognatha ovata</i> (Theridiidae)	.	Dobson 1992
<i>Setisquamalonchaea fumosa</i> (Egger) (Lonchaeidae)	Araneida	.	Dobson 1992
Larval kleptoparasites of oviposition ingress (thieves of developmental resources)			
<i>Taeniostola limbata</i> Hendel (Tephritidae)	<i>Cyrtotrachelus</i> sp. (Curculionidae)	P	Kovac & Azarae 1994
Larval Kleptoparasites of social insects (thieves of developmental resources)			
Myrmecophilous Phoridae	Formicidae	CA	Disney 1994
<i>Cataclinusa pachycondylae</i> (Phoridae)	Formicidae	P	Wheeler 1910
Larval kleptoparasites of prey storing insects (thieves of developmental resources)			
Miltogrammine (Sarcophagidae)	Sphecidae, Vespidae	CA	Evans 1966
<i>Lepidophora</i> spp. (Bombyliidae)	Sphecidae, Vespidae	.	Hull 1973
<i>Lasiopleura grisea</i> (Chloropidae)	<i>Bembix cameroni</i> (Sphecidae)	.	Evans 1973
Larval kleptoparasites of dung-feeding scarabs (thieves of developmental resources)			
<i>Ceroptera rufitarsis</i> (Sphaeroceridae)	<i>Scarabaeus sacer</i> (Scarabaeidae)	P	Lesne 1896
<i>Ceroptera sivinskii</i> (Sphaeroceridae)	<i>Geotrupes egeriei</i> and others (Scarabaeidae)	P	Sivinski 1983
<i>Ceroptera longicauda</i> (Sphaeroceridae)	<i>Pelotrupes pofundus</i> <i>Mycotrupes gaigei</i> (Scarabaeidae)	P	Marshall & Montagnes 1988 J. S., pers. obs.
<i>Ceroptera longiseta</i> (Villeneuve) (Sphaeroceridae)	<i>Pachylomera</i> sp. (Scarabaeidae)	P	Roubaud 1916
<i>Ceroptera nasuta</i> (Villeneuve) (Sphaeroceridae)	<i>Catharius</i> sp. (Scarabaeidae)	P	Roubaud 1916
<i>Ceroptera equitans</i> (Collin) (Sphaeroceridae)	<i>Scarabaeus gangeticus</i> (?) (Scarabaeidae)	P	Fletcher 1909, Collin 1910
<i>Biroina myrmecophila</i> (Sphaeroceridae)	<i>Cephalodesmius armiger</i> (Scarabaeidae)	P	Montieth & Storey 1981
<i>Norrbomia lacteipennisi</i> (Sphaeroceridae)	Scarabaeidae	P	Steyskal 1971

TABLE 1. (CONTINUED) REPRESENTATIVES OF VARIOUS FORMS OF KLEPTOPARASITIC FLIES AND WHETHER OR NOT THEY PRACTICE PHORESIS. P = PHORESIS, CA = CLOSE ASSOCIATION, I.E., FLIES REMAIN IN THE VICINITY OF THE "HOST" BUT NOT UPON IT, A "?" AFTER A NOTATION REFLECTS A BELIEF THAT EITHER PHORESIS OR CLOSE ASSOCIATION IS PRACTICED BUT THAT UNEQUIVOCAL OBSERVATIONS ARE MISSING, AND A "." REPRESENTS AN ABSENCE OF DATA.

Species	Host	Type of Association	Citation
<i>Norrbomia frigipennis</i> (Sphaeroceridae)	Many species of Scarabaeidae including the genera <i>Canthon</i> , <i>Phanaeus</i> , and <i>Onthophagus</i>	P	Sivinski 1983
<i>Norrbomia singularis</i> (Sphaeroceridae)	<i>Canthon</i> spp. and <i>Copris</i> spp. (Scarabaeidae)	P	Sivinski 1983
<i>Pterogramma</i> sp. (Sphaeroceridae)	<i>Canthon pilularius</i> , <i>Phanaeus</i> spp. and others (Scarabaeidae)	CA	Sivinski 1983

In this examination of thievery and phoresis we first review the various forms of kleptoparasitism, and make a distinction between flies that feed upon the resources of the host (adult kleptoparasites) and those who put their offspring in a position to steal (larval kleptoparasites). Particular attention is called to those species that practice phoresis and other forms of close association, and the advantages and difficulties of staying near the host are discussed. We point out that phoretic kleptoparasites sometimes accumulate in high densities on hosts, and that this intimacy has affected other parts of the flies' natural history, notably their sexual behaviors. The various mating systems of phoretic kleptoparasites are compared and contrasted, and hypotheses are offered about the roles of mate searching, mate choice, and sperm competition in their evolution. Finally, we consider the vulnerability of different types of resources, and whether accessibility has influenced the diversity of various kleptoparasite guilds.

Adult Kleptoparasites (Particularly of Predaceous Arthropods)

Certain invertebrate predators are untidy eaters whose insect prey may be dripping with hemolymph and digestive secretions, and torn open to expose organs and fats. Such soups are repasts for various milichiid and chloropid flies, who lick up fluids either from the surface of the prey or from the predator's jaws (Fig. 1).

Spiders are the most commonly noted mounts of phoretic kleptoparasites. The chloropid *Guarax* sp. has been collected from orb-web spiders (Bristowe 1941, Ismay 1977), and a group of eleven Panamanian milichiids, *Phyllomyza* sp., was observed on the cephalothorax of the araneid *Nephila clavipes* (L.) over a period of four days (Robinson & Robinson 1977). Another (?) *Phyllomyza* sp., was found upon *N. clavipes* in Florida (Sivinski & Stowe 1980).

Other phoretic associations include the milichiid *Desmometopa sorida* (Fallén) which rides the backs of reduviids (Richards 1953) and a Florida chloropid, *Conioscinella* sp. mounted on the scolopendromorph centipede, *Scolopendra veridis* Say (Sivinski 1985). Biro (1899) observed up to three individuals of the New Guinean milichiid



Fig. 1. Acalypterates feeding on the hemipteran prey of the large spider *Nephila clavipes*. One individual is perched upon the chelicera of its host, while another can be seen with a fluid droplet in its mouthparts. Kleptoparasitic flies often imbibe considerable amounts and swell up to a substantial girth. (Photograph by J. S.)

Neophyllomyza wulpi Hendel (as *Desmometopa minutissima* Wulp) perched on the thoraxes of the asilid *Ommatius minor* Doleschall. By removing and marking phoretics, he discovered that they quickly remounted hosts from distances of up to 12 paces. Pairs of riding milichiids were common and they would take a position between the robber fly's wings, one facing forward and the other back (see also Kertész 1897, Mik 1898).

The majority of adult food-kleptoparasites are not phoretic, but many seem to be closely associated with hosts nonetheless (Table 1, see Sivinski 1985 and cit.). Some species appear to wait near predators and gather at a kill in a matter of seconds. For example, the Floridian chloropid *Olcella cinerea* (Loew) can instantaneously arrive on the freshly captured prey of *Nephila clavipes* (Sivinski 1985), and *Olcella quadrivittata* (Sabrosky) can quickly find certain kinds of prey items being consumed by mantids and asilids (Marshall 1998). The cecidomyid *Didactylomyia longimana* (Felt) consumes the liquified prey of spiders and is one of the rare instances of adult feeding in the family (Sivinski & Stowe 1980). It also rests in spider webs, hanging by its front legs with its tarsi placed between adhesive droplets. While nonkleptoparasitic cecidomyids also hang in webs, the habit might have additional advantages for a kleptoparasite.

Still other kleptoparasites appear to forage widely and may not be "waiters" at all. At least some of these flies use volatiles from the defensive compounds of the prey to locate a meal. Coreiidae and Pentatomidae trapped by spiders are particularly attractive to milichiids such as *Paramyia nitens* (Loew), *Neophyllomyza* sp., *Milichiella* sp., and *Desmometopa* sp. (Eisner et al. 1991, Aldrich & Barros 1995). One component of the defensive sprays of these bugs, trans-2-hexanol, attracts kleptoparasites when applied to dead moths whose bodies are not normally fed upon by the flies (Eisner et al. 1991). Other kinds of prey items, including Acanthosomatidae and Staphylinidae,

with strong defensive chemicals have also been associated with kleptoparasitic flies (Marshall 1998), but most species of kleptoparasitic acalypterates have been collected from aculeate Hymenoptera carcasses in the process of being eaten. There is also some evidence that predator digestive secretions are attractive to *Didactylomyia longimana*, and a phorid and a ceratopogonid species (Sivinski & Stowe 1980). Much remains to be discovered about chemical cues and the foraging of thief flies.

In addition to specialized kleptoparasites there are instances of certain Empididae, Anthomyiidae, and Sarcophagidae feeding in spider webs, but this feeding may be opportunistic (Irwin 1978). Recently, several species of lonchaeids have been seen partaking of spider's prey in English gardens and doing so in a careful and methodical manner that suggests specialization (Dobson 1992).

Caution is an admirable quality in a kleptoparasite that has to deal with the formidable dangers of a gargantuan predator and perhaps an entangling web. The empidid *Microphor crassipes* Macquart is a frequent prey of its spider host (Laurence 1948, see also the toll spiders take of kleptoparasitic panorpids, Thornhill 1978). *Paramyia nitens*, in spite of extremely elongate mouthparts that should aid it to safely sup between a spider's jaws, is sometimes captured and killed by its host (Sivinski & Stowe 1980). McCook (1889) found a similar fly "trussed up near the spot where it had lately fed."

The threat posed by a predator may dictate the degree of intimacy between the kleptoparasite and its host. While phoresy might allow the quickest response to a capture and be competitively superior to waiting farther away from a limited resource, it could also be more perilous. A sort of compromise may occur in the Ugandan chloropid *Anomoeceros punctulatus* Becker which hovers, even in strong winds, directly below the chelicerae of web-building spiders (Ismay 1977).

Just as solitary predators obtain and hold desirable resources, so too do social insects which transport high-value foodstuffs from the field to their colonies. Like solitary predators, social insects also attract the attentions of kleptoparasitic flies. Phoretic adults of *Braula coeca* Nitzsch (the bee louse) feed on liquids taken from the mouths of honey bees (Askew 1971). The Brazilian phorid *Termitophodrides heterospinalis* Borgmeier is also phoretic and rides on the backs of worker termites (Bristowe 1924). Calliphoridae in the Old World genus *Bengalia* feed either as kleptoparasites or as facultative predators of various ant genera from which they snatch prey or brood (Maschwitz & Schonegge 1980). Mosquitoes in the genus *Malaya* also steal food from ants, hovering over their mouths and some cases even tapping the ant's antennae to solicit regurgitation (Farquharson 1918). Two phorid species are known to solicit food from ants (Disney 1994), and one milichiid feeds on the anal droplets of workers (Jacobson 1909). Perhaps the most remarkable association between an adult kleptoparasite and a social insect host is that of the recently discovered Malaysian phorid *Vestigipoda myrmolarvoidea* Disney and ants of the genus *Aenictus* (Disney 1996). Females of the fly are legless, wingless, larviform myrmecophiles which live in the ant colony, where they are apparently fed and cared for by the worker ants. Many Phoridae are larval kleptoparasites of ants and termites (e.g. Wilson 1971, Disney & Kistner 1997), and in many species females have greatly reduced wings, but no other phorid adults are known to be as integrated into the host social structure as is *V. myrmolarvoidea*.

Larval Kleptoparasites (Particularly of Aculeate Hymenoptera and Dung-feeding Scarabs)

Obtaining food for offspring, rather than for oneself, is the second great "motive" for kleptoparasitism by Diptera, and often for adult phoresy as well. This category is a complex one, and the nearly invariable relationship between phoresy and kleptopar-

asitism when only adults consume the resources of the host (phoretic adults are kleptoparasites) is not necessarily the case in instances where eggs are laid by phoretic adults in the vicinities of their associates (not all phoretic adults have kleptoparasitic larvae). The distinction requires some initial scrutiny, and we discuss flies that are phoretic but which probably take nothing of importance from their mounts nor compete with its offspring. Following this we examine the two best described forms of larval kleptoparasitism. First we review kleptoparasitism of aculeate Hymenoptera, and the sometimes close associations kept by the adults and larvae of such flies with their hosts. We then turn to some of the most common and easily observed kleptoparasites, the diverse and tenaciously phoretic Sphaeroceridae that ride upon dung beetles and lay eggs in the feces sequestered by their hosts.

The Reasons for Phoresy in Flies That Oviposit in the Vicinities of Other Arthropods (Kleptoparasitism vs Inquillinism). There are various "motives" for the phoretic relationships of adult flies who lay their eggs in the vicinities of other arthropods, and not all of these phoretic flies are kleptoparasites. However, in most cases of phoresy, whether involving a kleptoparasite or not, a larval resource associated with the mount is unpredictably available, and the best way to exploit it is to wait on the spot for its sudden appearance. One phoretic fly that is not a kleptoparasite is the sphaerocerid *Acuminiseta pallidicornis* Villeneuve, which rides on the backs of giant (20 cm) millipedes in West Cameroon (Disney 1974, Roubaud 1916). It apparently breeds in millipede droppings and mounted flies wait for their hosts to defecate (riding phorids on the same hosts may also lay their eggs in the feces, Schmitz 1939, see also phoretic insects that develop in the dung of sloths, Waage & Montgomery 1976, Ratcliffe 1980, and macropodids, Norris 1991). Some species of Sphaeroceridae and Drosophilidae are phoretic on terrestrial crabs for similar reasons, but lay eggs on the hosts and have larvae which stay on the host and develop in the microbe-rich waste material that accumulates on the "felt glands" (Gomez 1977, Carson 1967).

Alternatively, the medium in which the larvae of phoretic flies develop is not just a byproduct of the larger animal, but a valuable resource that has been sequestered or produced by the host. For example, a tephritid, *Taenioskola limbata* Hendel, lays its eggs in the oviposition holes bored by large weevils into bamboos (Kovac & Azarae 1994). One or two individuals will spend hours on the elytra of the beetle waiting for it to complete its laborious chore, then hop off and be the first to lay their eggs. If the fly larvae compete with the beetle grub for food or space, then *T. limbata* could be categorized as a kleptoparasite. The two major forms of larval kleptoparasitism are reviewed below.

Kleptoparasites of Aculeate Hymenoptera. Nests of social Hymenoptera and food stores of solitary Hymenoptera support a wide variety of kleptoparasitic larval Diptera, although it is sometimes difficult to distinguish between kleptoparasitic and scavenging habits among the former group. In some cases the association between the larval kleptoparasite and its host is quite close, as in the phorid *Cataclinusa pachycondylae* (Brues), which attaches itself to a host ant larva and steals food as its associate is fed masticated prey (Wheeler 1910). Other myrmecophilous phorid larvae are highly specialized, though not phoretic, and are groomed and fed by worker ants (Disney 1994).

Food stores of solitary aculeates are an obvious target for theft, and are attacked by a wide variety of specialized kleptoparasites. Both pollen-storing (Moradeshghi & Bohart 1968) and flesh-storing species are robbed by larval miltogrammine Sarcophagidae. Adult miltogrammines are usually closely associated with the nesting area rather than the adult host itself, typically mating nearby and larvipositing in or around the entrance to the host nest. Some miltogrammines, especially the genus *Senotainia*, are more closely associated with the adult host, and have earned the name

“satellite flies” for their habit of tracking foraging adult sphecids wasps. Satellite flies deposit larvae in the nest or on prey as it is being carried into the nest (Evans 1966). Other Miltogramminae (*Ptychoneura* spp.) deposit fully incubated eggs directly on the host (Day & Smith 1981). Larval kleptoparasites of solitary aculeates are also found in the Bombyliidae and Chloropidae. Species of the bombyliid genus *Lepidophora* develop on the provisions of Vespidae and Sphecidae (Hull 1973), and the chloropid *Lasiopleura grisea* Malloch has been reared from the nests of the sphecid *Bembix cameroni* (Evans 1966).

Kleptoparasites of Dung-feeding Scarabs. A diverse group of kleptoparasitic Sphaeroceridae ride upon dung-feeding scarabs in order to reach oviposition sites (Chobaut 1896, Roubaud 1916, Villeneuve 1916, Fletcher 1909, Collin 1910, Moulton 1880, Knab 1915, Steyskal 1971, Fig. 2). In fact, the term “phoresy” was coined by Lesne (1896) to describe the behavior of the sphaerocerid *Ceroptera rufitarsis* Meigen riding on the “Sacred Scarab”, *Scarabaeus sacer* L., in the sand dunes behind Algerian holiday beaches.

The clumped and ephemeral nature of dung and its often substantial food value (e.g., human feces are ~50% bacteria) can result in fierce competition among its consumers (Wilson 1971, Bartholomew & Heinrich 1979, Rabkin & Silverman 1979). A number of scarabs avoid such competition by burying caches of feces, both for their own consumption and as food for their larvae. Burials can occur either near the dropping, in which case the burrow may be relatively deep (e.g., *Phanaeus* spp.), or the feces can be shaped into a ball and rolled a considerable distance before being buried in a shallow burrow (e.g., *Canthon* spp.). In one Florida cattle pasture the feces cached by scarabs contained 11× fewer Nematocera, 7× fewer nonphoretic Sphaeroceridae, 4× fewer Cyclorrhapha, and 6× fewer predaceous insects than the above ground “pats” from which the buried dung had been detached (Sivinski 1983).

These less-contested caches are in turn exploited by kleptoparasites, which include not only flies but even tiny phoretic Scarabaeidae (Hammond 1976). Of course by sidestepping many small competitors the kleptoparasite is confronted with a single very large one, the beetle itself. But scarabs are messy eaters, and there is often a good deal left over, some smeared into the burrow walls. In the laboratory, the numbers of offspring of the kleptoparasite *Norrbomia frigipennis* (Spuler) developing in food caches of the ball-rolling scarab *Canthon pilularius* (L.) decreased 63% when the beetle was also included (Sivinski 1983, the extraordinary range of adult size in this species may reflect some broods facing exceptional nutritional difficulties). A thief fly might also have the opportunity to oviposit in a more long lasting “brood ball” containing the offspring of the beetle, although there are special problems associated with this situation including parent beetles removing foreign insects from the dung mass and the encasing of the feces in soil (e.g. Halfter 1997).

In Florida there is a number of kleptoparasitic sphaerocerids, including a species with reduced eyes, *Ceroptera sivinskii* Marshall, that principally attaches itself to beetles that start their burrows under feces, and a mostly crepuscular species, *Norrbomia singularis* (Spuler) (Sivinski 1983, Marshall 1983). There is even a species, *Ceroptera longicauda* Marshall, that exploits a “non-dung beetle”, the scarab *Peltotrupis profundus* Howden which may bury decaying organic material or fungus (J. S., personal observation., see also the Australian scarab *Cephalodesmius armiger* Westwood which constructs brood masses from green leaves and its kleptoparasite *Biroina myrmecophila* (Knab & Malloch) [Montieth and Storey 1981]). The most abundant kleptoparasitic species in north Florida is the previously mentioned *Norrbomia frigipennis*, an attractive black fly with white wings and red eyes. It rides upon a broad range of “rolling” and “burying” scarab hosts (Sivinski 1983), although in the laboratory it has a slight preference for species of *Phanaeus*, which are among the larger of the available dung beetles (Pettersson & Sivinski 1997).



Fig. 2. The phoretic sphaerocerid *Ceroptera longicaudata* upon the geotrupid *Mycotrupes gagei* Olson & Hubbell. This fly rides on species of the related genus *Pelotrupes*. The burrows of these beetles are often very deep (sometimes 3>m), and at such depths their brood materials are likely to be safe from most other thieves and predators. (Photograph by S. M.)

The seasonal pattern of *N. frigipennis* abundance in north Florida may reflect the advantages of kleptoparasitism (Sivinski 1983). In late winter and early spring the community of Diptera developing in bovine dung undergoes a change. Nematocera, particularly Sciaridae and nonphoretic sphaerocerids, become less numerous while calypterates, principally Sarcophagidae, increase rapidly. It may be that the large, quick growing flesh flies competitively exclude most sphaerocerids. *Norrbomia frigipennis* is an exception to the trend, its numbers continue to expand, perhaps because it avoids contact with calypterates by ovipositing in scarab dung stores.

While kleptoparasitism appears to be a means of avoiding competition and unfavorable environmental conditions the benefits of phoresy are more obscure, especially in light of the considerable costs in terms of time. Mature adult sphaerocerids of many species, including *N. frigipennis*, ride their hosts underground and once buried cannot leave until they accompany the departing beetle to the surface (Sivinski 1983). Newly eclosed adults are prodigious diggers, but this does not seem to be the case once their exoskeletons harden. A fly can expect to spend a day, and perhaps several days or more, buried alive with its host, a sizable portion of a ~10-12 day life span.

Why stay with a particular scarab? Why not go from beetle to beetle depositing eggs in the dung that each is rolling or pushing into its burrow? In fact some kleptoparasites, *Ceroptera longiseta* (Villeneuve) and *C. nasuta* (Villeneuve) from central Africa, ride beetles as they move feces but oviposit as the balls are being buried and do not get trapped beneath the surface (Roubaud 1916). An unidentified Florida *Pterogramma* spp. follows scarabs rather than rides and appears to oviposit on dung as it

disappears underground (Sivinski 1983, see a Mexican species with similar following habits in Halfpeter & Matthews 1966). Why don't other kleptoparasites subscribe to this seemingly more sensible practice? Perhaps the eggs could be damaged as the feces are manipulated and packed into a burrow. Whatever the reason, *N. frigipennis* were only reared from dung caches that had been buried for at least 4 hours (Sivinski 1983).

When oviposition is best accomplished underground, flies need to stay close to a host that might dig out of sight at any second. Given the need to stay close, it is probably cheaper to ride the beetle than to walk behind it. It may also be safer to be attached to one of the larger and least vulnerable animals in the dung-feeding community. Predators abound around droppings, and some, such as the reduviid *Apiomerus crassipes* Fab., even appear to follow fecal odors in order to locate hunting grounds (Sivinski 1983; an African *Ceroptera* sp. rides underneath scarabs, suggesting a predator that can glean flies from a beetle's dorsum, [Hanstrom 1955-67]). When flies are committed to a beetle it might further be prudent to stay with it as it flies from one dropping to another and so avoid the risk of not finding a host in a new location. *Norrbombia frigipennis* clings to flying scarabs, particularly species of *Phanaeus*, and up to a dozen or so flies can be seen packed into forward-facing ranks on the great and glittering prothoracic shield of a male *P. vindex* MacLeay as it buzzes by (see Vulinec 1997).

The Distribution of the Sexes in Flies Phoretic upon Predators and Dung Beetles

With a few revealing exceptions to be discussed later, the flies from all six families that are found upon predators or their prey are females (Sivinski 1985 and cit.; see however records for occasional male milichiids and lonchaeids in Eisner et al. 1991, and Dobson 1992). Presumably it is only females that require proteins, probably for egg production. But why don't males take advantage of female concentrations in order to find mates?

There are two general reasons why males might not be found in the same places as females (Thornhill & Alcock 1983). The first is that the females in certain locations have no sexual value. Suppose females of a particular species control copulations and mate only once. As a consequence males will search for virgins and tend to accumulate at emergence sites (or swarm sites; see Sivinski & Petersson 1997). By the time females are feeding or ovipositing they are likely to have already been inseminated, making it too late for males to look for sexual encounters in such spots. Mosquitoes provide a commonly encountered example of this phenomenon (Sivinski 1984). For the most part the bloodthirsty legions hovering about our heads and the flanks of cattle are composed entirely of females that have copulated previously, over small water-filled containers, pond margins, or swarm markers.

The second reason males may not search for females at a feeding site is that the resources are too abundant relative to the numbers of females. The low probability that a female will be at any particular spot makes foraging among sites, or loitering at a site, an expensive and time-consuming business. Some of the predator kleptoparasites seem to be very rare (see Sivinski 1985), and males could search among spiders or wait around a particular web for a very long and unrequited time before encountering a mate. Presumably, males would instead either concentrate their efforts around oviposition/emergence sites (probably decaying vegetation and seeds or grass tillers in the case of milichiids and chloropids, Ferrar 1987, Teskey et al. 1976) or participate in swarms or leks at "encounter-convention" sites (e.g. Parker 1978).

Which, if either, of these explanations accounts for seldom seen predator-kleptoparasite males is unknown, although the second, an unfavorable ratio of females to feeding sites, has a shred of circumstantial support. Matings on the bodies of predators and on their prey have been observed in two species of the chloropid genus *Olcella*



Fig. 3. An unusual sight, mating by the predator-kleptoparasite *Ocella quadrivittata* on prey held by its robber fly host. Typically, only females of such flies are found on or near the “host”, and mating in association with a predator has only been observed in a few species of this genus. (Photograph by S. M.).

(Sivinski 1985, Marshall 1998, Fig. 3), both of which appear to be “waiters”, i.e., they instantly appear on prey captured by spiders, robber flies, and possibly mantids. Both species can be unusually abundant at certain times and places. Perhaps high populations of females make it profitable for males to also wait around large predators. A higher female to host predator ratio means males have a reasonable expectation that females will show up at any particular host.

Among dung beetle-kleptoparasites everything is different. Males are as common as females on the backs of scarabs and flies engage in repeated copulations both above and below ground (Fig. 4). In laboratory arenas female *N. frigipennis* spent an average of 25% of their time repeatedly mating (in one case 70%, Sivinski 1983). It is the potential for multiple inseminations that is probably responsible for males following a relatively few females underground and consequently diminishing their chances of finding new mates. Typically, sperm from the last of a series of inseminations are used to fertilize most of the eggs a female lays (Parker 1970). Because oviposition occurs underground, the opportunity for the valuable last mating is beneath the surface as well.

In some instances, large numbers of flies and hosts might even allow both male and female flies to choose a mount on the basis of its sexual opportunities, i.e., the prospective mates and sexual rivals already on board the scarab. These kinds of choices would be reflected in the composition of beetle-back groups. Large and small groups of *N. frigipennis* on the ball-rolling scarab *C. pilularis* tend to have female-biased sex ratios (Sivinski 1982, Petersson & Sivinski unpub.). When the patterns of male and female abundances are compared to random distributions, the sex ratio biases appear to be due largely to males being less numerous than expected in small groups and females being much more common in large groups than chance would predict. It is plausible that a male would avoid unoccupied beetles or those with a few other flies



Fig. 4. A group of *Norrbonnia frigipennis* wait and mate upon the head and prothoracic shield of a male of the dung feeding scarab *Phanaeus vindex*. This is a common association in Florida, and the fly can be found riding beetles as they walk on the surface, burrow in the ground, and fly through the air. (Drawing by Kevina Vulinec).

aboard, otherwise he could wind up underground without a sexual partner. On the other hand, a female, particularly a mated female, might benefit from belonging to a small group because her offspring would face fewer competitors. But, if this is the case, why are females "over represented" in large groups? Perhaps there are sexual reasons. Either virgin females or females seeking superior mates would have a greater pool of sexual partners to sample in larger groups.

There is some support for the notion that some mated females do not prefer large groups (Pettersson & Sivinski, unpub.). In a laboratory experiment where mated and virgin *N. frigipennis* of both sexes had a choice of mounting one of a pair of beetles with different numbers of freeze-dried conspecifics glued to the elytra, the only significant response was that mated females avoided large groups. In keeping with the argument that virgins would prefer larger groups, there was a significant positive

correlation between the proportion of virgin females in field collected groups and the size of the groups.

The notion that at least some females prefer a large sample of prospective mates supposes that they can choose from what is available or, in the absence of choice, that the “fittest” males on beetle-back have greater access to females. There is no obvious male courtship in *N. frigipennis* that would serve to advertise desirable characteristics. However, large size is an easily perceived trait that might indicate “genetic quality” or be advantageous in competitions between males. If so, it might also be a quality females would like to see inherited by their sons. In the laboratory where large and small males were placed with a single female, the proportion of large male encounters with females that lead to copulation was significantly higher than those involving small males (Sivinski 1984). It could be that females preferred large males and were more likely to acquiesce, or that large males were better able to force themselves onto uncooperative females. It also appears that male-male competition filters out the smaller males and makes them less likely to contact females. Small males are just as liable as large to initiate an interaction with another male, but they are much less likely than large males to encounter females. This suggests that the vicinities around females are “controlled” by large males who exclude smaller rivals. There is also a negative correlation between male size and the proportion of time actually spent on scarabs, as opposed to following behind them. Again, perhaps larger males are able to dispossess the smaller and keep them from locating mates.

Conclusion: Kleptoparasite Diversity

Flies are the master thieves of their world. Take for example the predictably located and exposed food-treasures suspended in a spider’s web. Only the formidable owner and her entangling snare stand in the way of a surfeit of protein, and a number of bold arthropods take the risk for the reward. Among these are other spiders (e.g. Vollrath 1979), a mirid bug (Davis and Russell 1969), scorpionflies (Thornhill 1975), damselflies (Vollrath 1977), fireflies (Provonsha 1998), and even Lepidoptera larvae (Robinson 1978). But no other kleptoparasitic group, of insects at least, seems to be as abundant, or as diverse, as the Diptera. Much the same may be said for the insects found infesting the dung-stores of scarabs, and flies, particularly species of Phoridae, are a major component of the “food-sharing” fauna living in the underground nests of social insects (e.g. Wilson 1971; Disney & Kistner 1997).

However, there appear to be differences in diversity within these various kleptoparasite guilds. For example, the symbionts of dung beetles are largely (entirely?) Sphaeroceridae, although flies of this family are certainly not the only Diptera found near feces. The only known exception in north Florida is a sort of proto-kleptoparasitism practiced by the sarcophagid *Ravinia derelicta* (Walker) which preferentially larviposits in the dung balls of *Canthon pilularis* and in the soft, moist “work faces” on the feces where the beetles labor (Sivinski 1983). On the other hand, the dipteran kleptoparasites of spiders include species of Milichiidae, Chloropidae, Lonchaeidae, Phoridae, Empididae, and even Nematocera in the families Ceratopogonidae and Cecidomyiidae.

The barriers these different types of hosts place around their resources must differ in permeability to the flies that prowl outside them. Perhaps the subterranean nature of food stores in scarabs and ground-dwelling social insects presents a more formidable problem to the typical fly than the open air exposure of prey held in jaws or suspended in a web. The above ground nests of social wasps and bees may be even more impenetrable. Only the tiny bee louse, apparently alone among all of the sugar-seeking flies, has been able to exploit the riches of the honeybee.

ACKNOWLEDGMENT

We thank Jim Lloyd, Denise Johanowicz, and Sid Mayer for many helpful comments on earlier drafts of the manuscript. Jim Lloyd deserves further gratitude for showing J.S. his first phoretic fly. Valerie Malcolm prepared the manuscript, and Gina Posey helped gather and organize the often obscure and peculiar literature of kleptoparasitism.

REFERENCES CITED

- ALDRICH, J. R., AND T. M. BARROS. 1995. Chemical attraction of male crab spiders (Araneae, Thomisidae) and kleptoparasitic flies (Diptera, Milichiidae and Chloropidae). *J. Arachnol.* 23: 212-214.
- ASKEW, R. R. 1971. *Parasitic Insects*. American Elsevier Pub. Co. Inc., New York.
- BARTHOLOMEW, G. A., AND B. HEINRICH. 1978. Endothermy in African dung beetles during flight, ball making and ball rolling. *J. Exp. Biol.* 73: 65-83.
- BIRO, L. 1899. Commensalismus bei flieggen. *Termes Fuzetek* 22: 196-204.
- BRISTOWE, W. S. 1924. XXI. Notes on the habits of insects and spiders in Brazil. *Trans. Entomol. Soc. London* 1924: 475-503.
- BRISTOWE, W. S. 1941. *The Comity of Spiders*, Vol. II. Ray Society, London.
- CARSON, H. L. 1967. The association between *Drosophila carcinophila* Wheeler and its host, the land crab *Gecarcinus ruricola* (L.). *American Midl. Nat.* 78: 324-343.
- CHOBOUT, A. 1896. Observations sur un diptere vivant les *Ateuchus*. *Bull. Soc. Entomol. de France* 1896: 166.
- COLLIN, J. E. 1910. New species of the dipterous genus *Limosina* MacQ. (Borboridae) from Ceylon, with habits similar to those of *L. sacra* Meig. *Entomol. Mon. Mag.* 46: 275-279.
- DAVIS, R. N., AND M. P. RUSSELL. 1969. Commensalism between *Ranzovius moerens* (Rueter) (Hemiptera: Miridae) and *Holoena curta* (McCook) (Araneidae: Agelenidae). *Psyche* 76: 262-269.
- DAY, M. C., AND K. G. V. SMITH. 1981. Insect eggs on adult *Rhopalum clavipes* (L.) (Hymenoptera, Sphecidae): a problem solved. *Entomologist's Gazette* 31: 173-176.
- DISNEY, R. H. L. 1974. Speculations regarding the mode of evolution of some remarkable associations between Diptera (Cuterebridae, Simuliidae and Sphaeroceridae) and other arthropods. *Entomol. Mon. Mag.* 110: 67-74.
- DISNEY, R. H. L. 1994. *Scuttle Flies: The Phoridae*. Chapman and Hall, London.
- DISNEY, R. H. L. 1996. A new genus of scuttle fly (Diptera: Phoridae) whose legless, wingless females mimic ant larvae (Hymenoptera: Formicidae). *Sociobiology* 27: 95-118.
- DISNEY, R. H. L., AND D. H. KISTNER. 1997. Revision of the Oriental Termitoxeniinae (Diptera: Phoridae). *Sociobiology* 29: 1-118.
- DOBSON, J. R. 1992. Are adult Lonchaeidae (Diptera) specialized kleptoparasites of spiders' prey? *British J. Entomol. Nat. Hist.* 5: 33-34.
- DOWNES, J. A., AND S. M. SMITH. 1969. New or little known feeding habits in Empididae (Diptera). *Canadian Entomol.* 101: 404-408.
- EISNER, T., M. EISNER, AND M. DEYRUP. 1991. Chemical attraction of kleptoparasitic flies to heteropteran insects caught by orb-weaving spiders. *Proc. Nat. Acad. Sci.* 88: 8194-8197.
- EVANS, H. E. 1966. *The Comparative Ethology and Evolution of the Sand Wasps*. Harvard University Press, Cambridge, Massachusetts.
- FARQUHARSON, C. O. 1918. *Harpagomyia* and other Diptera fed by *Crematogaster* ants in S. Nigeria. *Proc. Entomol. Soc. London* 1918: xxix-xxxix.
- FERRAR, P. 1987. *A Guide to the Breeding Habits and Immature Stages of Diptera Cyclorrhapha*. E. J. Brill/Scandinavian Science Press, Leiden, Denmark.
- FLETCHER, J. B. 1909. Beetle carrier of winged Diptera. *Entomol. Mon. Mag.* 26-26: 168.

- FROST, C. A. 1913. Peculiar habits of small Diptera, *Desmometopa latipes* Meig. Psyche 20: 37.
- GOMEZ, L. D. 1977. La mosca del cangrejo terrestre *Cardisoma crassum* Smith (Crustacea: Gecarcinidae) en la Isla del Coco, Costa Rica. Rev. Biol. Trop. 25(1) 59-63.
- HALFFTER, G. 1997. Subsocial behavior in Scarabaeinae, pp. 237-259 in J. C. Choe and B. J. Crespi [eds.] The Evolution of Social Behavior in Insects and Arachnids. Cambridge Univ. Press Cambridge, England.
- HALFFTER, G., AND W. D. EDMONDS. 1982. The Nesting Behavior of Dung Beetles (Scarabaeinae). Instituto de Ecologia. Mexico, D.F.
- HALFFTER, G., AND E. G. MATTHEWS. 1966. The Natural History of Dung Beetle of the Subfamily Scarabaeinae (Coleoptera: Scarabaeidae). Folia Entomol. Mexicana. Nombres 12-14.
- HAMMOND, P. M. 1976. Kleptoparasitic behaviour of *Onthophagus suturalis* Perringuey (Coleoptera: Scarabaeidae) and other dung beetles. Coleopt. Bull. 30: 245-249.
- HANSTROM, B. 1955-67. South African Animal Life; Results of the Lund Expedition in 1950-1951. Almqvist & Wiksell, Stockholm.
- HARKNESS, R. D., AND J. W. ISMAY. 1975. A new species of *Trachysiphonella* (Dipt.: Chloropidae) from Greece associated with the ant *Catalglyphis bicolor* (F.) (Hymen.: Formicidae). Entomol. Month. Mag. 111: 205-209.
- HULL, F. M. 1973. Bee Flies of the World. Smithsonian Institution, Washington D.C.
- IRWIN, A. G. 1978. Spiders (Araneae), pp 184-186 in A. Stubbs and P. Chandler [eds.] A Dipterist's Handbook. The Amateur Entomologist's Society, Middlesex, UK.
- ISMAY, J. W. 1977. *Anomoeoceros punctulatus* (Bekker) (Diptera: Chloropidae) associated with spiders. Entomol. Monthly Mag. 113: 248.
- JACOBSON, E. 1909. Ein Moskito als Gast und diebischer Schamarrotzer der *Crematogaster diffiformis* Smith und eine andere schmarzotzende Fliege. Tijdschrift voor Entomologie 52: 158-164.
- KERTESEZ, C. VON. 1897. Dipterologisches aus Neu-Guinea. Termes. Fuzetek. 20: 611-613.
- KISTNER, D. H. 1969. The biology of termitophiles, pp. 525-557 in K. Krishna and F. Weesner [eds.] Biology of Termites. Vol 1.
- KNAB, F. 1915. Dipterological miscellany. Proc. Entomol. Soc. Washington 17: 38-40.
- KOVAC, D., AND I. AZARAE. 1994. Depredations of a bamboo shoot weevil. Nature Malaysiana, December, 1994: 115-122.
- LAURENCE, B. R. 1948. Observations on *Microphorous carassipes* MacQuart (Diptera: Empididae). Entomol. Monthly Mag. 84: 282-283.
- LESNE, P. 1896. Moeurs de *Limosina sacra* Meig. (Famille Muscidae, tribu Borborenae). Phenomenes de transport mutuel chez les animaux asticales. Origines de parasitisme chez les insectes Dypteres. Bull. Soc. Entomol. de France 1896: 162-165.
- MCCOOK, H. C. 1889. American spiders and their spinning work. Vol. 1, Philadelphia.
- MARSHALL, S. A. 1983. *Ceroptera sivinskii*, a new species of Sphaeroceridae (Diptera) in a genus new to North America, associated with scarab beetles in the southwestern United States. Proc. Entomol. Soc. Washington 85: 139-143.
- MARSHALL, S. A. 1998. Kleptoparasitic Chloropidae (*Olcella quadrivittata* (Sabrosky)) feeding and mating on staphylinid prey of Asilidae and hemipteran prey of Mantodea. Studia Dipterologica 5(1): (in press).
- MARSHALL, S. A., AND D. J. S. MONTAGNES. 1988. *Ceroptera longicauda*, a second North American species in the kleptoparasitic genus *Ceroptera* Macquart (Diptera: Sphaeroceridae). Proc. Entomol. Soc. Washington 90(2): 189-192.
- MASCHWITZ, U., AND P. SCHONEGGE. 1980. Fliegen als Beue und Brutrauber bei Ameisen. Insectes Soc. 27: 1-4.
- MIK, J. 1898. Merkwürdige beziehungen zwischen *Desmometopa m-atrum* Meig. Aus Europa und *Agromyza minutissima* v.d. Wulp aus NeuGuinea. Wiener Entomol. Zett. 17: 146-151.
- MONTIETH, E. G., AND R. I. STOREY. 1981. The biology of *Cephalodesimius*, a genus of dung beetle which synthesizes "dung" from plant material (Coleoptera: Scarabaeidae: Scarabaeinae). Mem. Queensland Mus. 20: 253-277.

- MORADESHAGI, M., AND R. H. BOHART. 1968. The biology of *Euphytomimma nomiivora* (Diptera: Sarcophagidae), a parasite of the alkali bee *Nomia melanderi* (Hymenoptera: Halictidae). J. Kansas Entomol. Soc. 41: 456-473.
- MOULTON, J. T. 1880. Flies riding on a tumble bug. American Entomol. 3: 226.
- NORRIS, K. R. 1991. General Biology in Insects of Australia, CSIRO, Melbourne, Australia.
- PARKER, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. Biol. Rev. 45: 525-567.
- PARKER, G. A. 1978. Evolution of competitive mate searching. Ann. Rev. Entomol. 23: 173-196.
- PETERSSON, E., AND J. SIVINSKI. 1997. Attraction of a kleptoparasitic sphaerocerid fly (*Norrbomia frigipennis*) to dung beetles (*Phanaeus* spp. and *Canthon* sp.). J. Insect Behav. 9: 695-708.
- PROVONSHA, A. 1998. Observations on *Photuris* feeding. Fireflyer Companion 1(4): 62-63.
- RABKIN, E. S., AND E. M. SILVERMAN. 1979. Passing gas. Human Nat. January: 50-55.
- RATCLIFFE, B. C. 1980. Scarabaeidae: sloth associates. Coleopt. Bull. 34: 337-350.
- RICHARDS, O. W. 1953. A communication on commensalism of *Desmometopa* with predacious insects and spiders. Proc. Roy. Entomol. Soc. London. (C) 18: 55-56.
- ROUBAD, E. 1916. Nouvelles observations de phoresie chez les Dipteres du groupe des Borboridae. Soc. Zool. de France. 41: 43-45.
- ROBINSON, M. 1978. Symbioses between insects and spiders: an association between Lepidopteran larvae and the social spider *Anelosimus eximius* (Araneae: Theridiidae). Psyche 84: 225-232.
- ROBINSON, M. H., AND B. ROBINSON. 1977. Associations between flies and spiders: bi-commensalism and dipsoparasitism. Psyche 84: 150-157.
- SCHMITZ, H. 1939. A new species of Phoridae (Diptera) associated with millipedes from the Yemen. Proc. Roy. Entomol. Soc. London (B) 8: 43-45.
- SIVINSKI, J. 1982. The Reproductive Biology of Sphaerocerid Kleptoparasites of Dung Beetles. PHD Disert., Univ. of Florida, Gainesville, FL.
- SIVINSKI, J. 1983. The natural history of a phoretic sphaerocerid Diptera fauna. Ecol. Entomol. 8: 419-426.
- SIVINSKI, J. 1984. Sexual conflict and choice in a phoretic fly, *Borborillus frigipennis* (Sphaeroceridae). Ann. Entomol. Soc. America. 77: 232-235.
- SIVINSKI, J. 1985. Mating by kleptoparasitic flies (Diptera: Chloropidae) on a spider host. Florida Entomol. 68: 216-222.
- SIVINSKI, J., AND E. PETERSSON. 1997. Mate choice and species isolation in swarming insects, pp. 294-309 in J. C. Choe and B. J. Crespi [eds.] The Evolution of Mating Systems in Insects and Arachnids. Cambridge Univ. Press, Cambridge, England.
- SIVINSKI, J., AND M. STOWE. 1980. A kleptoparasitic cecidomyiid and other flies associated with spiders. Psyche 87: 337-348.
- STEYSKAL, G. C. 1971. Notes on some species of the genus *Copromyza* subgenus *Borborillus*. J. Kansas Entomol. Soc. 44: 476-479.
- TESKEY, H. J., J. M. CLARKE, AND C. R. ELLIOTT. 1976. *Hylemya extremitata* (Diptera: Anthomyiidae) and species of Chloropidae associated with injury to bromegrass, with descriptions of larvae. Canadian Entomol. 108: 185-192.
- THORNHILL, R. 1975. Scorpionflies as kleptoparasites of web-building spiders. Nature 258: 709-711.
- THORNHILL, R. 1978. Some arthropod predators and parasites of adult scorpionflies (Mecoptera). Environ. Entomol. 7: 714-716.
- THORNHILL, R., AND J. ALCOCK. 1983. The Evolution of Insect Mating Systems. Harvard University Press, Cambridge, Mass.
- VILLENEUVE, J. 1916. Descriptions de Borboridae africains nouveaux. (Dipt.) Bull. Soc. Zool. de France. 41: 37-42.
- VOLLRATH, F. 1977. Zur Ökologie und Biologie von Kleptoparasitischen *Argyrodes elevatus* und synoken *Argyodes* arten. Dissertation, Univ. of Freiburg.

- VOLLRATH, F. 1979. Behavior of the kleptoparasitic spider *Argyodes elevatus* (Theridiidae). *Anim. Behav.* 27: 515-521.
- VULINEC, K. 1997. Iridescent dung beetles: a different angle. *Florida Entomol.* 80: 132-141.
- WAAGE, J. K., AND G. G. MONTGOMERY. 1976. *Cryptoses chloepi*: a coprophagous moth that lives on a sloth. *Science* 193: 157-158.
- WHEELER, W. M. 1910. *Ants: their Structure, Development, and Behavior*. Columbia Univ. Press, New York.
- WILSON, E. O. 1971. *The Insect Societies*. Harvard Univ. Press, Cambridge, MA.