

17 • Mate choice and species isolation in swarming insects

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ABSTRACT

The term 'swarm' has been applied to a variety of aerial mating systems. All are supposedly non-resource-based, although their relationship to resources is sometimes ambiguous. There are several selective contexts for mate choice. The choice of swarm markers has been implicated in species isolation. However, certain swarm markers are used by multiple species, which suggests that qualities other than specificity are important. In some instances, species appear sequentially at a marker, and there is evidence that not all times of day are equally valuable for swarming. It is not clear whether species compete for a universally best time. Swarms themselves, as well as markers, can attract participants, and a swarm's size can contribute to its attractiveness. The position of an insect within a swarm might influence its sexual opportunities. In species where male size is positively correlated with reproductive success, there is an instance where larger individuals occupy certain parts of the swarm. There are more observations of homogeneous size distributions in swarms, although in some species from several families of Diptera, the smallest males swarm very little or not at all. Presumably, they lack the energy resources to compete with larger males. Swarming insects may emit sexual signals. Pheromones seem to be rarely used, perhaps because of difficulties in determining the source of the signal. Visual signals are the easiest to trace to their sender, and furthest projected. Vision seems to be the paramount sense in swarming species. However, there is a large amount of variance in the complexity among presumed visual signals. Some of this variation may be due to environmental limitations, such as light intensity, that are imposed on swarming species. Swarming may evolve when females are uniformly dispersed and unpredictably located in space and time. A comparison of swarming insects and their parasitoids is suggested as a means of examining the roles of dispersal and phylogeny. Body size relative to resource (marker) size might influence the ability of insects to control a territory.

It is suggested that when these ratios are large, insects are less able to expel rivals. Swarm formation then becomes more likely.

INTRODUCTION

Insects often occur in groups. These groups can be accumulations of individuals at resources, and may or may not have a sexual component (for contrasting examples see Robinson and Robinson 1977 and Sivinski 1983). In other aggregations mating is the sole function of gathering. A variety of such mating systems, including swarms, are clumped into the category of 'non-resource-based' (see, for example, Borgia 1979) (Fig. 17-1).

The distinction between resource- and non-resource-based is not always simple or clear. A few examples illustrate the difficulty of categorizing aerial mating systems (see Table 17-1). Male mayflies (Ephemeroptera) often gather above the water's surface or reeds. In either case they are aggregated over aquatic oviposition sites. There are instances in mayflies, as well as in caddisflies and chironomids, where there are sequences of species swarming at different distances inland, so that some are 40-50 m from the water (Savolainen 1978). Originally, in species with short-lived adults having no or little food demands, an oviposition site might have been selected by males as an encounter site. Females would be likely to emerge in these places, and both sexes would enjoy rapid mate selection and reduced travel costs. However, in the above instances, some aggregation sites have apparently been 'pushed' away from the aquatic resource. The reasons for these progressions are unknown, though interspecific competition for signaling sites is a possibility. If so, the onshore swarms may be as close to oviposition site resources as competition allows.

Campbell and Kettle (1979) observed that males of *Culexoides brevitaris* most frequently gathered on cattle pastures above shadows cast by clumps of fresh grass. Such markers

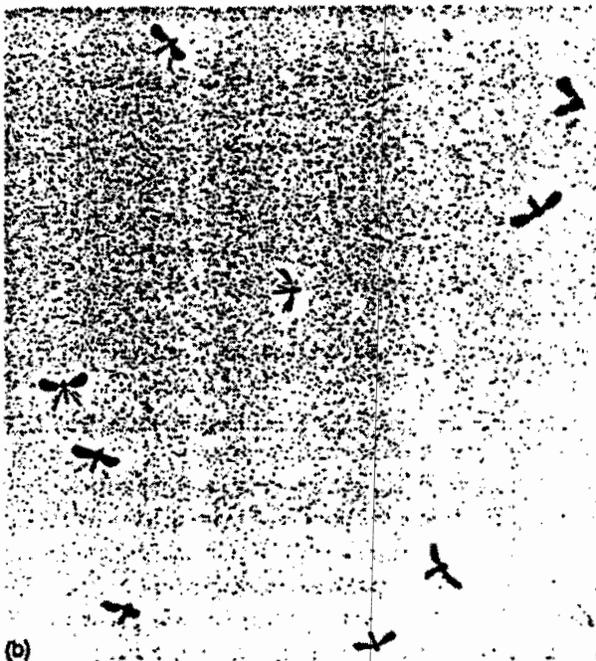


Fig. 17-1. (a) A swarm of unidentified male flies gathered above a swarm marker. The marker is not an oviposition, feeding or adult emergence site. Because of this, the aggregation is considered to be non-resource-based. We suggest that non-resource-based aggregations of flying insects are subject to unique selection pressures, and continue to make a distinction between aerial groups and those formed on a substrate (leks). The white lines in the photograph are due to the motion of the insects during the exposure period. The photograph is by J. E. Lloyd. (b) A female swarm of *Empis borealis*. Males bearing nuptial gifts choose mates from such aggregations. The photograph is by B. G. Svensson.

were common, but the swarms were not randomly distributed. The aggregates were significantly larger, closer together and more likely to contain females near cattle (female feeding site), although groups were formed in the absence of

cattle. Thus, within one species, the connection between aggregation site and a resource can vary considerably.

Finally, aggregations may also occur as side effects of mate-searching behavior. For example, male *Euphydryas* butterflies attracted to the movement of other nearby males, whom they appear to mistake for females, may attract still more males, resulting in what appears to be a classic non-resource-based aggregation (Odendaal *et al.* 1988).

Few attempts have been made to theoretically analyze the whole spectrum of non-resource-based mating aggregations. An exception is Bradbury (1985) who suggested that the best way to fit mating aggregations into a common theoretical framework is to treat characteristics such as territoriality, male investment and female choice as continuous variables instead of discrete alternatives, and to accept that they may vary independently of each other. This perspective suggests that we should not be too concerned with fitting mating systems into clearly defined categories. However, because we shall argue that location influences sexual behavior, we continue to make the commonly used distinction between 'leks' (generally aggregations touching a substratum and having a territorial component) and 'swarms' (aerial aggregations; see Shelly and Whittier, this volume). It should be kept in mind that leks and swarms may share certain characteristics in varying degrees and that the boundary between the two can be indistinct. For example, the male establishment of territories, apparent in many leks, may not distinguish them from all swarms. Maynard Smith (1974) showed theoretically that territory size should be smaller when territories are settled synchronously, as would often be the case in swarms, than when settled over a period. Pajunen (1980) suggested that swarming behavior can be derived from territoriality. Some factors, e.g. high population densities, are assumed to have decreased the aggressiveness of the participants, leading to the 'breakdown' of territories and giving rise to a 'scramble-competition' aggregation. Svensson and Petersson (1992) showed that hypotheses for the evolution of leks can successfully be adopted to insect mating swarms.

We concentrate our discussion on adaptations in swarming species to the problems of species isolation and mate choice. In particular, we address (1) the selection of location, i.e. the place at which a swarm occurs; (2) characteristics unique to swarms themselves, e.g. numerical size, that influence sexual opportunities; and (3) the advantages for and limitations on communication among members of an aerial aggregation. In our concluding section we

Table 17-1. The distribution among 'encounter sites' in insect species with aerial mating aggregations

The table is based on 178 papers; the relevant references can be provided by E. Petersson upon request. We do not claim that this table is complete. Nevertheless, we think it gives a good view of the large variety of insect mating aggregations and how they are distributed within and among the orders. 'Classic swarms', as addressed in this chapter, do not occur over obvious resources. G, swarming above spots on ground; L, swarming close to or above landmarks; D, swarming occurs in a defined area, but no marker has been recognized; G/L, D/L, G/D, both types of behavior noted for a single species; H, swarming in vicinity of host or food plant; A, swarming in vicinity of animal host; E, swarming at (female) emergence site; O, swarming at oviposition site; S, 'summit swarmer' or hilltoppers; N, no information about orientation, but the species do aggregate.

Order/suborder	No. of species aggregating											
	C	L	D	G/L	D/L	G/D	H	A	E	O	S	N
Ephemeroptera	1	12	25	2	3	—	—	—	—	—	—	11
Odonata	—	1	—	—	—	—	—	—	—	—	—	—
Heteroptera	—	—	5	—	—	—	—	—	—	—	—	—
Neuroptera	—	1?	—	—	—	—	—	—	2	1?	—	2
Trichoptera	—	6	14	—	2	—	—	—	—	—	—	—
Lepidoptera	—	—	9	—	—	—	—	—	6	—	50	—
Coleoptera	—	—	1	—	—	—	—	—	—	—	1	—
Hymenoptera												
Symphyta	—	1	—	—	—	—	—	—	—	—	1	—
Parasitica	—	6	—	—	—	—	—	—	—	—	2	—
Other Aculeata	1	7	4	1	—	—	—	—	1	—	14	3
Diptera												
Nematocera	11	102	32	5	2	2	7	13	9	—	—	26
Brachycera	—	10	7	—	—	—	1	—	—	—	30	2

examine the evolution of swarms and consider the ecological and morphological factors that may influence their phyletic distribution (see Shelly and Whittier, this volume).

SWARM FORMATION AND ORIENTATION TO AGGREGATION SITES

Typically, but not universally, insect mating aggregations are formed by males. Swarms are usually found above contrasting spots on the ground or objects higher than their surroundings. In both cases, the object that serves as an orientation point is called a 'swarm marker'. The size and form of the marker can influence the size and form of male swarms (see, for example, Chiang 1961; Savolainen 1978; Allan and Flecker 1989) and female swarms (Svensson and Petersson 1992). Campbell and Kettle (1979) did not find such a relationship in *Culiseta brevitarsis*; the proximity to cattle was more important. There may be intraspecific variation in site preferences. In the leptocerid caddisfly *Mystacides azurea*, two types of swarm site have been reported: one over reeds, forming typical marker

swarms (Solem 1978), the other over the water surface, without any obvious landmarks (dispersed swarming, *sensu* Sullivan 1981; Petersson 1987; Gullefors and Petersson 1993). A mayfly, *Leptophlebia marginata*, swarms either over trees or horizontally over the ground (Savolainen *et al.* 1993). The latter swarm form appears to be better protected from winds. The insects that practice the different types of swarming have diverged morphologically and genetically. Speciation through specialization for particular modes of swarming may be underway. Swarming insects are often 'generalists' when choosing a marker. Many observers have reported chironomids and other nematocerans swarming above cattle, bushes, humans or any other object higher than its immediate surroundings (see Sullivan 1981). Some species are more specific in their site choices. The simuliid *Austrosimulium pestilens* is only found swarming over *Callistemon viminalis* (red bottlebrush) plants (Moorhouse and Colbo 1973). Most species use fairly simple visual cues to find an aggregation site within their habitat. Not all hilltop aggregations are the result of visual orientation; the insects may be guided uphill by wind currents (Alcock 1987).

In the following subsections we first describe the most common type of swarm, single-species swarms, and apparent adaptations for species isolation. Then we review the rarer occurrences of multiple-species swarms. Finally, we consider what the use of a site by several species reveals about the nature of swarm markers and the interspecific competition for their use.

Single-species swarms

In many insect groups, closely related species differ in their site preferences. This might contribute to species isolation. Downes (1958) reported that in Britain and Manitoba, there were seven to ten species of *Culicoides* (Diptera) and nine species of *Aedes* mosquito, respectively, that swarmed simultaneously. No mixed swarms could be observed. Hunter (1979) found three species of blackfly to have some overlap in site preferences, but they were rarely seen swarming together. Savolainen (1978) noted that mayflies in Finland swarmed at species-specific sites, and species-mixing did not seem to occur. A similar pattern is found in north European leptocerid caddisflies. Males of swarming species fly above the water surface at different distances from shore (Solem 1978, 1984; Gullefors and Petersson 1993; cf. Mori and Matubani 1953). Usually, several species are swarming simultaneously (Petersson 1989). Only during evenings with gusty wind conditions do swarms of different species occasionally become mixed.

Several species may use a single marker, but at different times. Swarm initiation is often triggered by highly species-specific illumination thresholds (see, for example, Nielsen and Nielsen 1962). Yuval and Bouskila (1993) consistently found a series of species at the same swarm markers. The focus of their study, the mosquito *Anopheles freeborni*, began to swarm 5–10 min after sunset and continued for 30–35 min until the end of twilight. Attacks by dragonflies were more numerous at the beginning of this period because the visually foraging predators became less efficient with the deepening dusk and roosted 20–25 min after sunset. Why has *A. freeborni* not moved its mating period to a later time and escaped its enemies entirely? Yuval and Bouskila argue that the visibility of swarm participants to potential mates is declining over time as well. *Anopheles freeborni* is thus forced to expose itself to both mates and foes. But the higher copulation to predation ratio in the latter part of *A. freeborni*'s swarming period also raises the question of how swarming time over a marker is partitioned among species.

If not all times are equally valuable, then how do certain species secure particularly good periods? Perhaps a robust insect species can physically displace a smaller one, as larger males displace smaller ones within species. Adults of a more abundant species might simply arrive in greater numbers at a site during the optimal time, and due to their presence *en masse*, make finding a mate a confusing process for less numerous insects. The notion of competition for a single best time may be an oversimplification. Fewer predators may be present at dusk, but there will also be less heat, light and perhaps more confusion from the swarms of other species. Poor visibility at twilight could constrain mate choice. The different physiologies of different species might divide time into a sequence of species optima. If so, the historical displacement of one species by another may never have occurred. Time-sharing of sites, however, does imply that certain sites are particularly valuable as swarm markers, a point pursued in the following subsection.

Multiple-species swarms

Some records of multiple-species swarms (Gibson 1944; Usinger 1945; Hubbard and Nagell 1976) are too scant to evaluate the degree and persistence of mixing. However, there are a few swarm systems where mixing seems to be the rule. Most have been observed in tropical or subtropical areas and contain up to nine species of mosquito or midge (Provost 1958; Cunningham-van Someren 1965, 1973). Haddow and Corbet (1961) reported on swarms that almost invariably consisted of more than one mosquito species. Mayflies and various families of Diptera, notably Tipulidae, Chironomidae and Stratiomyiidae, were also represented.

Mixed swarms might come about in at least two ways. First, for one reason or another, some sites may be better than others and in short supply. In areas with high species diversity, many species may share these limited locations, e.g. a hilltop (cf. Parker 1978). Choice habitats may be safer to swarm in. Anisopteran dragonflies prefer open spaces (cit. in Yuval and Bouskila 1993). Thus male *Anopheles freeborni* mosquitoes swarming in areas sheltered by trees have higher copulation to predation ratios than those that swarm in open areas (Yuval and Bouskila 1993). Still, swarms are persistently formed in dangerous, open areas. Females that risk joining such aggregations may obtain mates that have demonstrated an ability to survive under perilous conditions.

What constitutes a favorable swarming site is sometimes mysterious. Even different forms of mating system, which might be thought to have different environmental requirements, can occur in the same spot. For example, two species of 'lekking' phorid, a territorial dolichopodid and two species of swarming chironomid all shared mating sites on a Florida floodplain (Sivinski 1988b). Replacement of swarm marker foliage with different vegetation did not influence the extreme site specificity. In a somewhat similar situation, two sympatric south European polistine wasps use the same landmarks, but have different mating systems. *Polistes gallicus* males form ordinary marker swarms, whereas *P. dominulus* males establish territories at the same site and try to chase away other males of both species (Beani and Turillazzi 1990; see also Frohne and Frohne 1952).

Second, multiple-species mating aggregations may be defensive adaptations, reducing the risk of predation through dilution (selfish-herd, cf. Hamilton 1971). The probability of predation per male in the chironomid *Chironomus plumosus* decreases with increased swarm size (Neems *et al.* 1992). With more eyes for surveillance the average vigilance of birds decreases with increasing flock size (cf. Pulliam 1973; Inglis and Lazarus 1981; see, however, Pulliam *et al.* 1982). In insect non-mating aggregations the distance at which a threat is discovered increases with group size (Treherne and Foster 1980, 1981, 1982; Vulinec and Miller 1989). However, it is not known whether greater awareness of predators is an advantage to individuals in multiple-species mating aggregations; i.e. whether different species can interpret each other's avoidance behavior. Predation pressure on swarms is considered to be more intense in tropical, as opposed to temperate, regions (Edmunds and Edmunds 1980). As noted, mixed swarms appear to be more common in the tropics.

ORIENTATION TO SWARMS BY POTENTIAL MEMBERS

It can be difficult to determine whether the site or the swarm attracts other insects. In some species, the visiting, non-swarming sex occasionally arrives at empty sites (Dahl 1965; Savolainen and Syrjämäki 1971; Savolainen 1978; Svensson and Petersson 1992). Savolainen and Syrjämäki (1971) reported that if a lone crane fly female flies above an artificial swarm marker, she always follows it if it is moved along the ground, i.e. she behaves as the swarming males do. Such observations suggest that both sexes are using

the same cues to find the aggregation sites and have the same site preferences ('encounter site conventions' *sensu* Parker 1978).

There are, however, aggregations for which this hypothesis appears to be unsatisfactory. Some *Chaoborus* (Diptera) (Downes 1958) and mayflies (Spieth 1940) form swarms above the water surface, sometimes kilometers offshore. These swarms often move as a unit. A similar pattern has been observed in lonchaeid flies (McAlpine and Munroe 1968). The swarms split and reform higher from the ground when disturbed by wind or the researchers. In such cases, females might be attracted to the swarm alone.

In the following subsections we examine the possibility that a characteristic unique to groups, i.e. the number of members, may make certain swarms more attractive than others. We also consider whether position within a swarm influences the reproductive success of its members and what influence this factor might have on the form of a swarm.

Are some swarms more attractive than others?

Particular aggregations can have characteristics that are more attractive to potential participants than others groups, regardless of whether the insects are originally attracted to the site or to the aggregation. For instance, a larger swarm represents a greater pool of potential mates. In the dance fly *Empis borealis*, females swarm and males come to swarms carrying nuptial gifts (Svensson and Petersson 1987). Once in the swarm males tend to choose the larger, more fecund, females as mates. Males stay longer in larger swarms (Svensson and Petersson 1987, 1988). The proportion of males leaving the swarms without mating decreases with swarm size (Svensson and Petersson 1992). In addition, males stay shorter times in swarms with greater variance in female size, perhaps because it is easier to discriminate among potential mates that differ remarkably in size (Svensson *et al.* 1989). Thus, individuals of both sexes are visually attracted to the site, but the characteristics of the group influence their behavior within the swarm. Female *Anopheles freeborni* mosquitos are most likely to join a particular swarm at the time of its peak size (Yuval and Bouskila 1993). They may gain protection from dragonfly predation by a 'dilution effect' (Foster and Treherne 1981; Wrona and Dixon 1991).

When swarm size is an important component of its attractiveness, there might be 'runaway' growth of a group. If one aggregation is larger by chance it will recruit more

members, which in turn increases its potential for further growth. Such a process would produce a highly skewed distribution of swarm sizes forming at random over various markers. Among lekking species and species aggregated at a resource, group size can also influence female arrival rates (for example, in *Drosophila conformis*, (Shelly 1989; Shelly and Whittier, this volume); and the sphaerocerid *Norrbomia frigipennis* (E. Petersson and J. M. Sivinski, unpublished)).

Position within swarms and mating success

Certain positions within an aggregation may be of different value when they are safer or because females prefer males in particular locations. For example, a central position may be attractive because it might be sheltered from predators. On the other hand, a peripheral position in a swarm could provide better access to females approaching the aggregation. If so, this would create a selective conflict in males between predator-avoidance and sexual success (Hamilton 1971). Alternatively, females might seek the relative safety of the swarm's core before coupling. Males and females would then both try to surround themselves with their neighbors. Records of predation on insect swarms contain scant information about the relative dangers of the different portions of aggregations (Banks 1919; Rao and Russel 1938; Frohne and Frohne 1952; Brickle 1959; Downes 1970, 1978; Cunningham-van Someren 1973; Chandler 1978). Most insect predators seem to enter swarms, which would even the risks to the participants.

Being in the right place at the right time could result in more contacts with opposite sex. In the dance fly *Empis borealis*, a male approaches a female from below and takes off with her in an ascending flight. Sometimes the pair couples in the air, but often the male performs the ascending flight with several or all females in the swarm before mating. He may also leave the swarm without mating (Svensson and Petersson 1987). Obviously, the males choose among females, and in such a swarm position is not critical, because males may evaluate all swarming females.

In other aggregations, with a less universal form of mate comparison, competition for position could be of enough importance to influence the form and composition of the swarm. The bibionid *Plecia nearctica* ("lovebug") swarms in pastures where adults emerge from the turf. Males search the area for females. Larger males are found closer to the ground, and hence to newly eclosed

females emerging from the soil, whereas smaller males are at the top of the swarm (Thornhill 1980; see, however, Hieber and Cohen 1983). However, in other species, there are no such position effects. McLachlan and Neems (1989) made horizontal sweeps through male swarms of the chaoborid *Chaoborus flavicans*, but found no difference in male size between the tops and bottoms of swarms. Females seem to aggregate in the vegetation under the swarm, and might enter the swarm from below. McLachlan and Neems did not investigate whether males in the swarm center differed from those on the periphery. Flecker *et al.* (1988) studied the mayfly *Epeorus longimanus* and followed individual males during their nuptial display. Females probably approach the male swarms near their top (Brodsky 1973); larger males have higher mating success. Larger males were therefore predicted to be most abundant at the swarm top, but males from different sections of the swarms did not differ in body size (Flecker *et al.* 1988). It appeared that each male occupied the full vertical range encompassed by the swarm. Males of the leptocerid caddisfly *Mystacides azurea* swarm above the surface of lakes. Females approach the swarms from above, generally coming from their resting sites on the shore vegetation. The number of pair formations in different parts of the swarm do not differ (Petersson 1987). Larger male *Anopheles freeborni* mosquitoes also have greater mating success, but it is not known whether this is due to female mate choice or to the ability of large males to procure more favorable sites in the swarm (Yuval *et al.* 1993; see also Reisen *et al.* 1981). In general, position effects appear to be relatively uncommon in insect swarms.

Male mating success in the species mentioned above is mainly determined by their success in pursuing or attracting females as they approach or enter the swarms. In six species of Chironomidae, and a chaoborid, small males rarely swarm at all, but wait for females on nearby vegetation. They may exploit the attractiveness of the larger males flying above and simultaneously save energy (McLachlan and Neems 1989; cf. Arak 1988). Males of the mosquito *Anopheles freeborni* fall into three categories: (1) small, non-swarming males; (2) larger males that swarm early and for as long as their energy reserves last; and (3) the largest individuals, who fly when females are most likely to join the swarm (Yuval *et al.* 1993, 1994). In this case the energetic difficulties of swarming act as a filter. Only the larger males with the greater reserves participate in the sexual aggregation.

COMMUNICATION WITHIN SWARMS

There is a considerable range in the complexity of intraspecific communication in aggregated insects (Burk 1981; Shelly and Whittier, this volume). In particular, the often elaborate courtships of lekking species, with sometimes simultaneous acoustic, pheromonal, and visual broadcasts, have been contrasted with the seeming absence of self-advertisement in many swarming species. Yet the existence of mixed-species swarms suggests that choice of swarm site alone is not always sufficient to provide species isolation. Information is being passed between members of swarms. In this section we first address the limitations swarming might place on the type of signal produced, and conclude that vision is the most practical channel for communication. We then examine cases of apparent visual signaling within swarms and consider the role of the swarming environment on the evolution of both elaborate and relatively simple communicative organs and behaviors.

Communication channels in swarming insects

Although pheromones are important in many lekking species (e.g. tephritid fruit flies, Nation 1989), their role in swarms is less well understood. Females of the chironomid *Polypomyia brachialis* evert long glandular strings from their abdomens as they participate in sex-role-reversed female swarms (Edwards 1920). These have been interpreted as scent organs, but their bright orange color contrasting with a black body suggests a visual role as well (although the tubes are colorless in some other *Polypomyia* and species of the related *Bezyia*). Both sexes of the swarming caddisfly *Hydropsyche augustipennis* produce a chemical attractant, whereas only females of the non-swarming *Rhyacophila fasciata* emit a pheromone (Löfstedt *et al.* 1994). Thus, although pheromones do occur in swarming species, the act of swarming itself, where several insects move rapidly about in a common volume of air, would appear to limit their efficacy. It seems too difficult to track an odor plume to its producer and too simple to 'cheat' by saving the expense of producing a pheromone and exploiting the signal of a neighbor. Further exceptions tend to emphasize the dilemma. In the ghost moth *Hepialus humuli*, aggregated males hover 1–5 m apart, emitting pheromone from hind-tibial brushes (Mallet 1984). Although they bob up and down and swing 'like pendulums', they seem to be sufficiently stationary and separate to provide individual signals. Other related species are reported to loop back and

forth over the same spot, though some descriptions (cit. in Mallet 1984) give the impression of overlapping flight with more possibility of pheromone plume mixture (see also the occasionally stationary flight of the mayfly *Stenonema vicarium*; (Spieth 1940)). The limoniid fly *Erioptera gemina* mates both on the substrate and in swarms. Orientation on a substrate is mediated by a female pheromone and this pheromone is suspected to function in swarms as well (Savolainen and Syrjämäki 1971). If a female joining a swarm is not immediately mated, she hovers nearly motionless over the marker, a behavior that might better allow a male to track her scent.

Acoustic displays are common in some lekking taxa (again for example, tephritid fruit flies; see Sivinski and Burk (1989 and references) and Sivinski (1988a)); 'choruses' and 'sprees' of singing Orthoptera and cicadas have been widely studied (Bailey 1991). Many nematoceran males can recognize the flight tones of conspecific females (see, for example, Duhrkopf and Hartberg 1992; Ogawa 1992). Some mosquitoes are even capable of discriminating between virgin and mated females by their sounds (cf. Sotavalta 1974). Sexually dimorphic antennae, presumably specialized in males to detect sound, are well known in swarming mosquitoes and chironomid midges (see, for example, Roth 1948). However, there is little knowledge of, or even conjecture about, sexually selected acoustic displays in swarming species. Ewing (1989) has argued that flight tones would be of little use in attraction over a long distance (but see Bailey's (1991) discussion of near-field effects), although communication among nearby insects within swarms remains a possibility. Even a particular flight pattern, with changes in wing-beat frequency, might produce a sexually selected 'song' (J. E. Lloyd, personal communication). In tropical Mexico a large, unidentified non-swarming dipteran emits loud and dramatically modulated flight tones as it hovers (J. M. Sivinski, personal observation). The difference in intensity between pulses of sound and intervals was comparable, to my ear, to the songs of lekking tephritids (see Sivinski 1988a). However, an acoustic display, like a chemical one, might be difficult to identify with its sender in a swarm.

Visual signals seem to be the most individually recognizable, the most readily tracked, and the furthest projected of the options available to swarming insects. Not surprisingly, vision appears to be the dominant sense in swarm formation and sexual interactions within swarms. Petersson and Solem (1987) showed that males of two swarming caddisfly species are attracted to almost any object that is not too

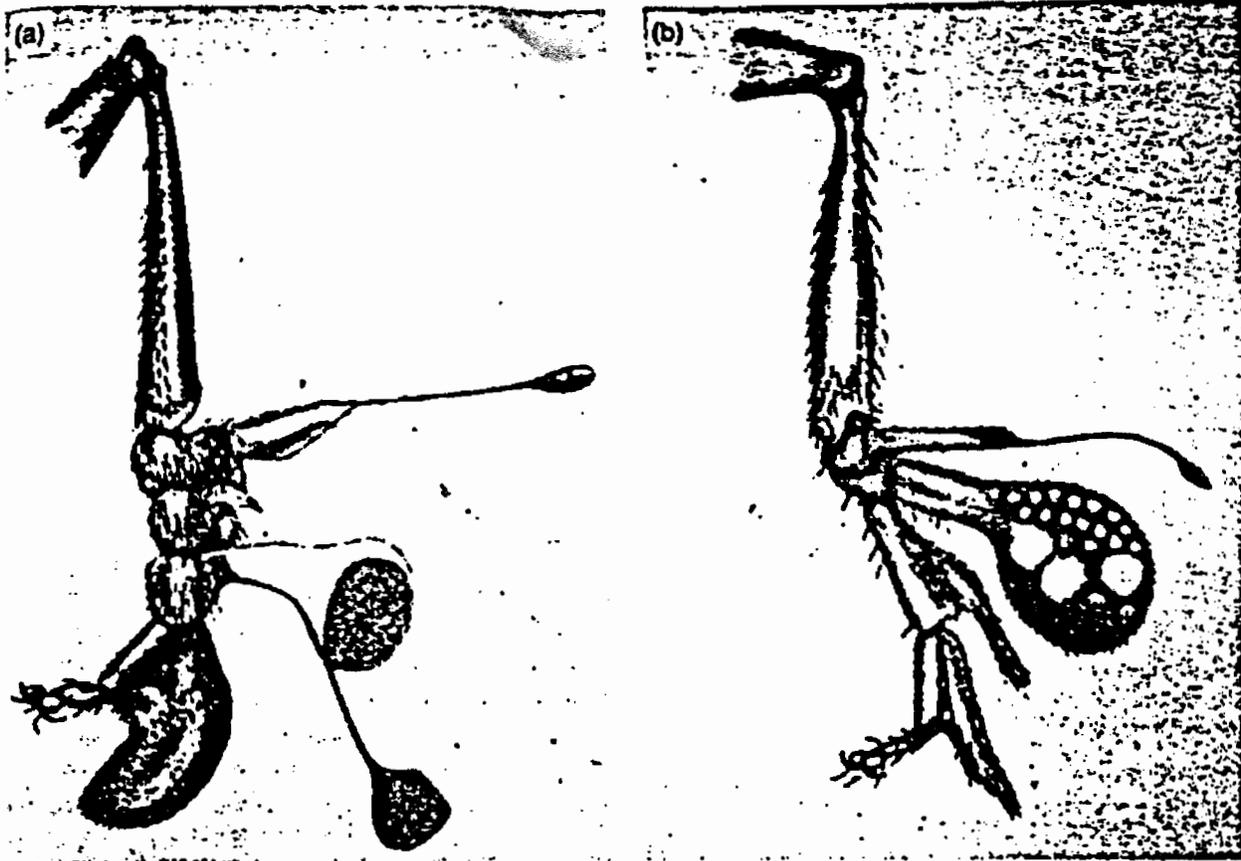


Fig. 17-2. Ornaments on the hind legs of the three allopatric species of *Calotarsa* (Platypezidae). All form swarms in widely separated regions of North America. (a) *C. pallipes*; (b) *C. calceus*; (c) (see p. 302) *C. insignis* (from Kessel and Maggioncalda 1968).

large, especially if it is moving like a conspecific female approaching the swarm. Male lonchaeid flies are attracted by any moving object about the size of a small- or medium-sized fly (McAlpine and Munroe 1968). In many tabanids, the initial detection of females by males is also visual. Males pursue small objects such as stones thrown near them (Allan *et al.* 1987). Male *Aedes triseriatus* mosquitoes show a similar behavior (Loor and DeFoliart 1970).

Many swarming males possess larger eyes than conspecific females. These are generally adaptations for mate finding (cf. Thornhill and Alcock 1983). Within Diptera, sexual dimorphism in eye size with enlarged facets in the male's upper eye is common among swarming species (cf. Downes 1969; Zeil 1983). In leptocerid caddisflies males of some species have larger eyes than the females. Gullefors and Petersson (1993) found that this sexual dimorphism is less expressed in species where the females enter the male swarms, and more expressed in species where a female is detected by a male before reaching the swarm. Larger

male eyes have also been reported for the bee *Exoneura hamulata*, where males seem to scan an area for females (Michener 1974), and in a swarming hemipteran (Kritsky 1977). In mayflies of the family Baetidae, males may possess divided eyes. The lower part functions as an ordinary eye; and the part facing upwards is adapted for scanning for females approaching the swarm. Curiously, the upper eyes are covered in the male subimago. Species of some mayfly genera, such as *Ephoron*, *Campsurs* and *Palingenia*, emerge and mate during the night. Males have undivided eyes that are relatively small (Spieth 1940). Location and recognition of mates is probably not visual.

Variance in signal production among swarming species

Once an insect has joined a group, communication with its fellows is possible. Signals could be sent to sexual rivals or attract the scrutiny of the opposite sex. There appear to be

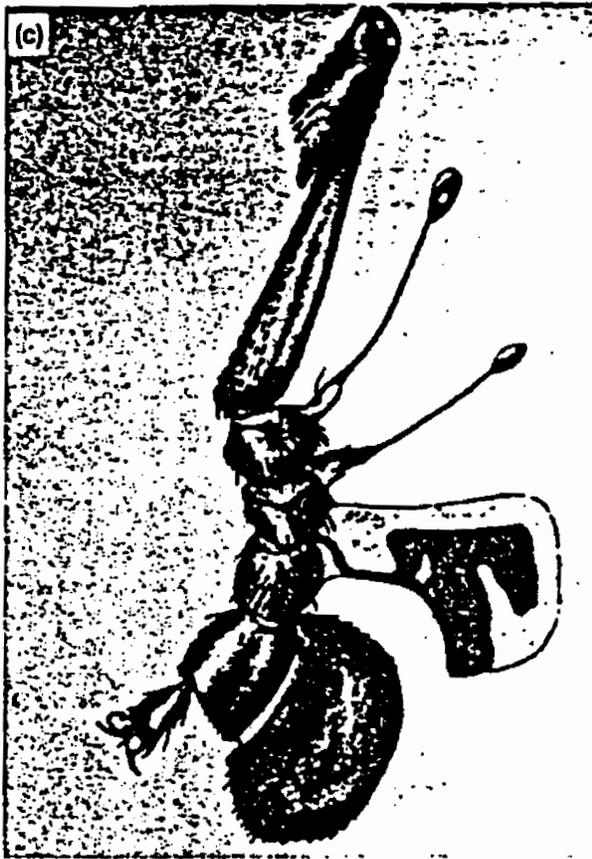


Fig. 17-2 (cont). For legend see previous page.

substantial differences among species in the amount of effort and materials put into visual and other signals. Some, but not all, of this variance can be accounted for by whether or not an aggregation has occurred at a resource (see, for example, Burk 1981). Before trying to explain the distribution of investment in communication, it would be useful to have some idea of what is being communicated, particularly between the sexes.

Displays by individuals have often been interpreted as species-isolating mechanisms (see, for example, Mayr 1963; Alexander *et al.*, this volume). One problem with this idea is that often the most elaborate signals occur in taxa where selection for species isolation seems weakest (at least given the present ranges of the species) (West-Eberhard 1984). An example from the swarming Diptera are the three species of the platypezid genus *Calotarsa*. All are rare and found in widely separated North American locations: California, New Mexico, and Eastern forests. Swarming males dangle their enlarged hind legs, which

bear a variety of curious projections and glittering aluminum-colored flags (Kessel 1961, 1963) (Fig. 17-2). Snow (1884) noted how they '...allow their hindfeet to hang heavily downward and look as if they were carrying some heavy burden'.

There is an alternative to species isolation that seems to better explain the variety of displays and has been adapted to aggregated flies (Burk 1981; Prokopy and Roitberg 1984). Signals are hypothesized to be sexually selected advertisements of male (more rarely female) qualities directed to females (occasionally males) who are choosing a mate. There are circumstances where an individual can profitably advertise and circumstances where it cannot. One place where there is little profit in making a signal is where resources used by females are discrete, scattered, and relatively rare. Males can become closely associated with the resource, and 'guard' or 'control' it. If a female attempting to use that resource is subject to the mating attempts of a resident male or males, it might be more beneficial for her to immediately mate rather than spending time and energy choosing a particular male (note the strong selection for postcopulatory mate choice in such a situation; see Ward 1993). In the absence of female discrimination, selection for male courtship display is also absent. An unusual example of this behavior pattern occurs in the phoretic dipteran *Norrbomia frigipennis*. Females copulate frequently, often several times an hour, while riding a beetle (the resource), and there is no obvious courtship or sexual dimorphism (Sivinski 1984; see, however, Lachmann 1990).

When males do not control access to a resource, selection on signaling differs (see, for example, Headrick and Goeden 1994). For females the cost of mate choice is lower and they may be able to afford to discriminate among males; males in groups profit by appearing to be outstanding among their fellows (see, for example, Alexander 1975).

Even among non-resource-based aggregations, such as classic swarms, there is still a great deal of variation among species in displays (or markings and organs that can be interpreted as displays). At one extreme it has been noticed in both Brazil (Shannon 1931) and Africa (Haddow and Corbett 1961), that swarming mosquitoes are drab, but non-swarming species (e.g. *Toxorhynchites* spp.) are often strikingly colored. It was suggested by Shannon, Haddow and Corbet that because mosquito swarms were crepuscular, or nocturnal, there was little chance for visual communication, whereas non-swarming mating systems centered over 'small containers' were diurnal and took advantage of

the light to send visual signals (such as the blue leg 'paddles' of *Sabethes cyaneus* (Hancock *et al.* 1990)). There is at least one diurnal swarming mosquito, *Culex territans*, which is not unusually colored to our eye, even in the ultraviolet (although white markings on mosquitoes are often reflective in the ultraviolet (J. M. Sivinski, personal observations)). However, small species of Ephemeroptera with hyaline or semihyaline wings are generally diurnal swimmers (Spieth 1940). One such species was described as shining in the sun like falling snowflakes (Morgan 1911). Large dark species usually swarm just at sunset to darkness (Spieth 1940). Spieth suggests that bulky species escape predators by swarming in the dark and small ones take advantage of their relative safety to enhance their visual apparency. Note that large termites, which may be more vulnerable to predators, tend to have their mass dispersal flight at night, and small species fly in daylight (Banks and Snyder 1920).

At the other extreme of the display spectrum among swarming flies are the previously mentioned platypezids and a number of peculiarly ornamented empidids. We argued that pheromones could be difficult to track in species that move rapidly within swarms, and so rarely evolve. The same problem may confront certain types of visual signal. Brightly colored or ornamented swarming insects often have a 'dignified' floating flight that would aid a responder in orienting to the signal (see, for example, Kessel 1955, 1963). Famous examples occur among the empidids that bear nuptial gifts. Many carry a dead insect, which they present to females. Others are more exotic, and carry flower petals or prey wrapped in silky balloons or empty balloons (cit. in Downes 1969). These 'gifts' are often bright, shining even in twilight, and can be seen bobbing against the darkened foliage in an uncanny manner.

If slow-floating swimmers were to settle to the ground or foliage, the result would be a mating system like a lek (an actual example of an insect that 'swarms' then lands to lek is *Bactrocera tryoni* (Tychsen 1977)). From a stable platform, a lekking insect can generate elaborate signals in different channels that can be easily traced back to a relatively constant point. The opportunity exists for broadcasting, and many lekking species have fulfilled the potential.

The seemingly small step between small, slow-flying swarms and leks suggests an alternative evolutionary route for elaborate displays among swarming species. Given the limitation on aerial signaling, perhaps the more ornate appendages and colorations arose in species that originally signaled from the substrate. Predation may be

an important factor in the evolution of leks and the use of protected lekking sites (see, for example, Hendrichs and Hendrichs 1990). Predators may have pushed certain leks from vegetation entirely. One result could be swarms whose participants fly slowly or hover in order to better display ornaments that evolved under stationary circumstances on the 'ground'. A preswarming ancestor might have resembled certain dolichopodid flies, whose legs bear expansions similar to those illustrated in Fig. 17-2. However, these 'flags' are waved during courtships that occur on leaf surfaces (Oldroyd 1964). Dipteran taxa, such as Platypezidae, Phoridae and, to a lesser extent, Tephritidae, contain species that either swarm or lek, or display both behaviors under different circumstances, or simultaneously combine aerial and leaf-based aggregations (see, for example, Tychsen 1977; Sivinski 1988b). Examination of these groups might reveal the role of predation in the interface between leks and swarms.

The nature of sexually selected signaling information is a difficult problem that has occupied generations of biologists (see, for example, Fisher 1930; Hamilton and Zuk 1982; Alexander *et al.*, this volume). Occasionally, there are displays that offer what seems at least plausible 'translations' of the information. *Rhamphomyia longicaudata* is an empidid in which females swarm. Males provide a nuptial food-gift and may attempt to present the gift and their ejaculate to the female that can provide the most offspring. Females, when they swarm, swell up and give the impression of a flying abdomen (Steyskal 1941; Newkirk 1970). This may be an exaggerated promise of fecundity. Recently, body symmetry, as a reflection of genomic quality, has been found to play a role in female mate choice (Møller 1992; Thornhill 1992). The elaborate 'flags and feathers' that project from the legs of some swarming flies might be a difficult morphological test of the genome's ability to produce symmetry.

The plausibility of conjectures about the information content of displays depends on the mental capacity and range of experience of the choosing sex. Alexander *et al.* (this volume) propose that mate choice by insects is different from that by birds and mammals. The strongest form of their argument assumes that memory, experience with the opposite sex and individual recognition are all absent. It follows that comparisons can only be made among simultaneously encountered potential mates. There is no need for memory or experience when a choosing individual has innate minimum criteria, and the first mate to meet these standards is accepted. This, they suggest, is the typical

form of mate choice in insects. Limitations on intersexual selection due to limited abilities to compare has implications about how structures used for communication are interpreted. For example, 'Fisherian runaway selection' is more likely when females 'learn about male traits so as to compare the range of variation in any group of males and choose the extreme regardless of precisely where it might fall' (Alexander *et al.*, this volume). From this perspective, elaborate structures in insects are more likely to be due to armsraces between and within the sexes rather than 'ornamental' exaggerations that appeal to a preference for the extreme.

Are the explanations we have proposed for 'elaborate' displays (leg flags, silk balloons and air-filled abdomens) compatible with mate choice by minimum criteria? An adaptation like 'females exaggerate fecundity by swelling their abdomens' could be the result of a type of arms race. A small female that can appear larger might meet the standards of a gift-bearing male. As deceitful swelling spreads, higher minimum standards in males would become adaptive, and so on. However, a little relaxation of Alexander *et al.*'s assumptions in their strongest form allows Fisherian selection of 'ornaments' to occur in populations with limited mental abilities and sexual experience. Swarms are ideal places for simultaneous comparisons. This technique of mate choice requires less memory, individual recognition and experience than picking the most extreme of a sequentially encountered series of the opposite sex. A valued character, perhaps a leg plume, would be displayed by potential mates in a small area and at the same time. Individuals could be judged relative to one another, and extremes selected. One swarming insect suggests that Alexander *et al.*'s assumptions could be relaxed even further. As discussed earlier, males of the empidid *Empis borealis* bestow a nuptial gift and prefer large females (Svensson and Petersson 1987). They perform an 'ascending flight' with potential mates, presumably to judge their quality. A male may perform this flight with all the females in a swarm before mating; i.e. he appears to 'compare the range of variation' in female size.

CONCLUSIONS: THE EVOLUTION OF SWARMING AND SUGGESTIONS FOR FUTURE RESEARCH

We have reviewed the behaviors of insects as they approach and participate in swarms. We conclude by examining the evolution of the swarm mating system and its distribution

among insect taxa. We first discuss how female unpredictability can result in the use of navigational objects as primitive swarm markers, and ask why the phyletic distribution of swarming seems to be so remarkably patchy. We then revisit Pajunen's (1980) argument that swarms result from the 'breakdown' of territoriality into 'scramble competition' and consider a simple notion based on body size of why this might occur in some taxa and not others. These discussions will suggest future research into the relationships between swarming and morphology, phylogeny and resource distribution.

The phyletic distribution of swarming

The distribution of swarming is extremely patchy (Table 17-1). Many Diptera swarm; these species often develop in extensive, uniform habitats such as lakes and streams and their surrounding soil. Under these conditions females may be more concentrated over conspicuous objects used for navigation (swarm markers; see Parker 1978) than at emergence or oviposition sites. Males accumulating as they wait to intercept mates at navigational aids would constitute a simple type of swarm. Unlike flies, swarming beetles are seldom encountered (Table 17-1). Are there few beetles with population structures conducive to the evolution of swarming, or might the typically heavy exoskeleton of Coleoptera make swarming flight too expensive to perform? If it is robustness that constrains swarming, it is peculiar that swarming has been only sporadically described among parasitic Hymenoptera (with the exception of the braconid subfamily Blacinae (Southwood 1957; van Achterberg 1977)). There are a large number of small, lightly built species. Again, are population structures that result in female unpredictability at resources or emergence sites uncommon in parasitoids? Are there phylogenetic restraints on the evolution of swarming? These questions might be addressed through comparisons of parasitoid mating systems with those of their hosts. Adult solitary parasitoids may sometimes have distributions in time and space similar to their host's, particularly when parasitism levels approximate 50%. Their mating systems would, at least in part, be subject to similar selection pressures. An example may occur among the opiine braconid parasitoids of tephritids. *Diachasmimorpha longicaudata* and *Doryctobracon areolatus* often attack substantial proportions (ca. 50%) of the larvae of lekking fruit flies and also form leks in the trees infested by their hosts (J. M. Sivinski, personal observations). Similar convergence might also be possible

between hosts that swarm and their parasitoids. At present, the difficulty in testing the hypothesis is finding suitable sets of insects to compare. Aquatic Diptera and the Trichoptera, which commonly swarm, are rarely parasitized (Krombein *et al.* 1979; see, however, agriotypin ichneumonids that attack pupae of caddisflies (Goulet and Huber 1993)). Swarming Blacini attack Coleoptera, but we are unaware of any information on their spacial distribution (Krombein *et al.* 1979). A swarming nearctic chalcidoid, *Bothriothorax nigripes*, attacks the larvae of Syrphidae (Nadel 1987), a dipteran family which includes species that aggregate on hilltops. Another parasitoid of syrphids, the European ichneumonid *Diplazon pectoratorius*, forms unusual male aggregations that have characteristics of swarms (Rotheray 1981). Peculiar, mostly female, swarms of a torymid, *Torymus phillyrae*, have been observed in Europe (Graham 1993). This parasitoid attacks certain Chironomidae, a family containing many swarming species (Graham 1994). However, the sexual significance of these female hymenopteran swarms has yet to be demonstrated. We suspect that opportunities for comparative studies will arise as the sexual behavior of parasitoids in the field becomes better documented (see, for example, Smith 1994). An effort to describe the little-known mating systems of dipteran parasitoids (see, for example, Toft 1989), particularly those that share hosts with or are hyperparasitized by hymenopteran parasitoids, may be especially useful in illuminating the roles of resource distribution, body size and phylogeny in the evolution of swarming.

Intrasexual conflict and swarming

For whatever reason, once females (or more rarely males) arrive over or near a marker, the air above the marker is a sexual resource (Parker 1978). Large insects, certain syrphid flies for instance, might be able to defend a territory containing a marker either by forays from a perch or by continual aerial patrol (see, for example, Fitzpatrick and Wellington 1983). Small insects, when confronted with the same marker, face a relatively larger space, which they are less able to control. Sexual rivals could accumulate without restraint. The typical absence of size distribution in swarms implies that even larger individuals in species of small size are not able to control access to locations where mating is more likely to occur. The packing together of small insects in an indefensible space might be particularly prevalent in aerial aggregations because of certain qualities

of an aerial environment. First, these spaces are relatively large compared with substrate resources. The volume over a marker is considerable larger than the area of the marker itself. A lekking tephritid would have to defend a good deal more if it fought not only for a leaf but for the air above it as well. Second, air could be a difficult medium to fight in. The energetic cost of tracking and hitting an opponent in fast-paced three-dimensional combat may be prohibitive. Smaller individuals of some species do not swarm at all, presumably because of insufficient energy reserves. Aggression might weaken an already precarious ability to remain airborne during the period of female arrival. If this argument is correct, then the ratio of insect size to swarm volume should be greater than that of insect size to the defended space of an individually held territory, be it aerial or on a substrate. Exceptions might occur in female swarms or where males bear resources (as in some Empididae). If intrasexual competition between swimmers is less intense in these aggregations, then even large insects might find it more useful to coinhabit a volume they could potentially have defended as a territory (for advantages, see Svensson and Petersson 1992).

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