

## Chapter 4.4 Reproductive and Mating Behaviour

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### 1 INTRODUCTION

The sexual behaviour of tephritid fruit flies is interesting for several reasons. As far back as 1862, entomologists spoke of tephritids' 'graceful behaviour' (Loew, quoted in Zwölfer, 1974). More recently, entomologists such as Prokopy (1980) and Burk and Calkins (1983) have suggested that an increased comprehension of tephritid sexual behaviour could lead to more effective tephritid control. This upturn in interest in the behaviour of fruit flies has coincided with the growth of the branch of biology known variously as behavioural ecology or animal sociobiology, and there has been a cross-fertilization of ideas between entomologists and behavioural ecologists that has resulted in satisfying increases in our knowledge. In this chapter, our aim is to present an ecological framework for understanding tephritid sexual behaviour, to review some recent studies in the context of that framework, and to illustrate the depth of understanding that is potentially available by referring in some detail to results from a series of studies of one tephritid species. We will concentrate on studies not covered in the recent reviews by Prokopy (1980) and Burk (1981); for our detailed example, we have chosen the Caribbean fruit fly, *Anastrepha suspensa* (Loew).

### 2 CONCEPTUAL BACKGROUND

The general ecological framework for discussing the variety of tephritid sexual behaviour was provided by Bateman (1972). He divided the tephritids into r-selected and K-selected species; this distinction cut across the gall-former vs. fruit-infester spectrum, and was based mainly on climatic consideration (e.g., tropical vs. temperate species), especially as climatic and other ecological factors affected the distribution and availability of hosts in time and space. Bateman was able to correlate a variety of factors, such as dispersal abilities, with a species' r or K classification. Prokopy (1980) and Burk (1981) independently applied Bateman's model to explain the variety of mating encounter sites and behaviour in tephritids. Each suggested that, in tropical species, widely dispersed hosts would fruit asynchronously, leading to the evolution of fruit fly species that were multivoltine, polyphagous and good dispersers. In temperate species, short, synchronous host seasonality would

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lead to the evolution of univoltine, monophagous species. Both authors predicted that monophagous species, especially those whose hosts were somewhat patchily distributed, would mate directly on the oviposition substrate. In polyphagous species, decreased likelihood of male-female encounters at the oviposition site would allow the evolution of non-resource-bound mating systems, especially lek mating systems (leks are male communal display aggregations that are visited by receptive females).

Burk (1981) went on to attribute differences in the type and complexity of sexual signals in tephritids to these differences in their mating systems. He argued that species that mated directly on oviposition substrates, at least when hosts were patchily distributed, would have simple signalling systems. Such species would lack long-distance attractants, would exhibit male territoriality centered on the oviposition site, and their courtship signals would be simple, usually species-identifying wing waving. Males successful at establishing territories on such female-required resources would be assured of a steady supply of arriving females, and would be able to force copulations on arriving females in return for access to the oviposition substrate. However, in many monophagous or oligophagous species, the host plant is extremely abundant and evenly distributed, as is sometimes the case for gall-forming species. In such cases, females can be considered to have a choice of flying to a host with or without a resident male. In these situations, males would evolve more complex signalling systems to attract females and induce them to mate. In many such species, males supplement close-range wing waving with long-distance sex pheromone attractants. Females may still be willing to swap a copulation for access to a host plant, if response to a male pheromone allows her to more quickly and efficiently locate a suitable oviposition site. A further incentive to females is provided in the relatively small number of species in which the male offers a salivary secretion as a nutritional offering to a female prior to or during mating. Most of the species that are currently known to produce such nutritional offerings are gall formers whose hosts are abundant and widespread (see review in Dodson, 1978).

The most complex signalling systems in tephritids are found in the polyphagous fruit-infesting species (mainly tropical or subtropical in distribution, including such important pests as *Ceratitis capitata* (Wiedemann) and several *Dacus* and *Anastrepha* species). In such species, the females are liberated to a free choice of mate(s), and are expected from Darwinian sexual selection theory to have evolved highly discriminating mate choices. Sexual selection theory suggests that females should choose mates on the basis of material benefits offered or, failing any such benefits, on the basis of male vigour indicative of superior survival characteristics or the possession of characteristics that would make a female's sons attractive in turn to the next generation of females; see review of sexual selection theory as applied to insects in Thornhill (1980) and Thornhill et al. (1983). Males in these species will often aggregate in leks, and evolve elaborate sexual signalling systems for at least three reasons: (1) Males have to attract females to the communal display site, and they compete with each other to attract the most females; (2) Males also may compete aggressively to establish display territories in leks (perhaps in particularly favorable locations — see below for *A. suspensa*), leading to the evolution of male weapons and threat ornamentation and displays; (3) Females making discriminating mate decisions will become involved in a coevolutionary 'arms race' with displaying males (Dawkins and Krebs, 1979), leading to the open-ended evolution of ever-more-complicated courtship signalling interactions. In most lekking polyphagous species, we see the evolution of acoustic calling, courtship, and aggressive songs (Monro, 1953; Webb et al., 1976; Webb, unpublished data), which coexist in behaviour repertoires with long-distance, male-

produced sex pheromones and elaborate visual displays involving wing waving and dancing.

Burk (1981) produced the preceding generalizations based on a review of the pre-1981 literature and on preliminary observations of *A. suspensa*. With a few enlightening exceptions considered below, the scheme has been successful in predicting subsequent findings, some of which we now review.

### 3 MATING BEHAVIOUR

#### 3.1 Tephritids in General

Steck (1984) reported on the sexual behaviour of *Chaetostomella undosa* (Coquillett), which forms galls in seed heads of the thistle, *Cirsium cymosum*. Males alternately patrolled and sat in wait on the crown and upper leaves of the host. Males approached conspecifics and attempted to mount them. Males subsequently fought, while copulation ensued if the conspecific was a female. Steck reported, 'Precopulatory behavior was devoid of stylized wing movements or mouthpart contact . . .'. Dodson (1986a) observed two gall-formers associated with rabbitbrush (*Chrysothamnus* spp.), *Aciurina bigeloviae* (Cockerell) and *Valentibulla dodsoni* Foote and Blanc (see also Thornhill et al., 1983). Males established positions on host plants, and scanned for arriving conspecifics. If females were spotted, males walked along leaves and stems to intercept them. Mountings followed, with males using greatly enlarged front femora to gain a 'leglock'. Virgin females waved wings to attract the attention of males, while mated females seemed to resist male advances, so that only about 65% of interactions resulted in copulations. Courtship interactions involved only wing waving, although Dodson reports that this was often elaborate.

The papaya fruit fly, *Toxotrypana curvicauda* Gerstaecker, studied by Landolt and Hendrichs (1983), may offer some exceptions to the scheme given above. It is a tropical species, but nevertheless monophagous on papayas. At first, its sexual behaviour seemed to correspond to predictions based on its host specificity. Males were found to establish territories on papaya trees via overt aggressive interactions. Having done so, they positioned themselves on papaya fruit and 'puffed', expanding pleural membranes to release sex pheromone. Males approached arriving females from behind, and mounted them, often as they attempted to oviposit. However, Landolt et al. (1985) have since found a more complex courtship in the laboratory that takes place at a time flies are not normally on their host. They argue that as yet undiscovered lek sites exist (see Sivinski and Webb (1985a) for a description of the acoustic courtship signals). Hopefully, further field work will determine how well the papaya fruit fly fits into the Burk-Prokopy model.

Examples of recent studies of sexual behaviour in polyphagous lekking tephritids include those of melon flies (*Dacus cucurbitae* Coquillett) by Kuba et al. (1984) and of Mexican fruit flies (*Anastrepha ludens* (Loew)) by Robacker and Hart (1985). In *D. cucurbitae*, as in polyphagous *Dacus* species previously studied, males gather at specific times of day in aggregations or leks. Males do not reside on fruit, but set up single-leaf territories on leaves, from which they emit sex pheromone and produce calling songs. Females fly to such male aggregations to mate. In *A. ludens*, males establish single-leaf territories underneath leaves during a sexual activity period in the late afternoon. Male aggression is extensive, and the winning territory holders 'puff' to produce sex pheromone and also produce calling songs via rapid wing vibrations. Leks usually form in host trees, but away from the host fruit. Females approached

territory-holding males, and precopulatory orientation, approach, and wing-waving behaviour on the part of both sexes has been observed. Males mount females from a face-to-face orientation by flying over them and turning around to mount. As in *A. suspensa*, after mounting, males produce 'precopulatory' or courtship songs. Similar observations have been made for other *Anastrepha* species (*A. suspensa* — see below; *Anastrepha fraterculus* (Wiedemann), Morgante et al., 1983; Malavasi et al., 1983): we are now at the exciting point with this genus (the same applies to *Dacus*) where we can begin to perform careful comparative studies. Especially valuable would be studies of the monophagous species in the two very large genera, *Anastrepha* and *Dacus*.

Other recent studies of tephritid sexual behaviour have pointed out shortcomings of the generalizations mentioned above; but these exceptions are readily explainable from ecological or sexual selection considerations. For example, Dodson (1986b) has observed lekking-type aggregations in a monophagous gall-former, an unnamed *Procecidochares* species in the *minuta* species group. Males of this species aggregate on conspicuous nonhost saltbush plants in north central New Mexico. Males are alert and react quickly to incoming males or females, although signalling is simple (only wing-flicking was observed). The male aggregations on conspicuous objects are not uncommon in species whose population densities are low and whose adults are widely dispersed (this phenomenon is called 'hilltopping' by students of butterflies, wasps, and botflies). This situation seems to apply to the *Procecidochares* species, as Dodson points out.

A more general shortcoming of the simple scheme outlined above is that it underestimates the extent and importance of adaptive intraspecific variation in sexual behaviour. Behavioural ecologists in the last decade have extensively modeled the possibility of alternative male and female mating tactics, and many examples have been discovered in insects and other animals (see good reviews by Rubenstein, 1980; Cade, 1980). Even in 1980 and 1981, several examples of alternative sexual behaviour tactics were known in tephritids. Smith and Prokopy (1980) had discovered that early season matings in the apple maggot (*Rhagoletis pomonella* (Walsh)) took place in lek-type aggregations in host plant foliage and were female-initiated, while later in the season males defended host fruits and attempted to force copulations on arriving females. In the Mediterranean fruit fly, *C. capitata*, Prokopy and Hendrichs (1979) observed a within-day switch in location of sexual activities. Wing waving males chased and courted females on fruit in the morning and afternoon, but gathered in leks to display via sex pheromones and calling songs at midday. Similar patterns have been found in the most recent studies. Smith and Prokopy (1982) found an early-season late-season switch in *Rhagoletis mendax* Curran exactly like that in *R. pomonella*. Burk (1983) found that *A. suspensa* males engaged in on-fruit courtships early in the morning (the main female oviposition period), but formed leks in the late afternoon. However, the simple rule, 'monophagous species mate on fruit, polyphagous species mate on foliage in leks' perhaps can be defended even in such cases, when the relative success of various male tactics is examined. In *Rhagoletis*, male-initiated matings on fruit are usually successful, resulting in multiple matings by most females; so most matings probably do take place on fruit. In *Ceratitis* and *Anastrepha*, most courtships on fruit do not lead to copulation, and most matings therefore actually take place in the female-initiated interactions in leks. It seems likely (and some unpublished evidence by Hendrichs for *A. suspensa* supports the possibility) that on-fruit courtships in the polyphagous species are far less effective as a tactic than obtaining a display territory in a lek, and are probably performed by subordinate males unable to establish a lek territory. In Dawkins' (1980) terminology, these subordinate males are 'making the best of a bad job'.

So far, exploration of alternative tactics and their reproductive consequences has focused on male tephritids, but there are likely to be similar adaptive intraspecific female differences in mating behaviour (Thornhill, 1984). Students of tephritids, like other students of animal behaviour, need to pay much more detailed attention to female sexual behaviour.

### 3.2 *Anastrepha suspensa*

The generalizations and brief reviews given so far fail to give a real flavour of the types of questions being posed and answers being obtained in recent studies of tephritid sexual behaviour. To do that, we need to look in somewhat more detail at studies of a particular species. The one that has been examined most closely so far is the Caribbean fruit fly, *A. suspensa*.

As noted, the Caribbean fruit fly is a polyphagous species that infests over a hundred hosts. In the morning, males are often found on fruit where they attempt, with relatively poor success, to mate with ovipositing/feeding females (Burk, 1983). In the afternoon, particularly late afternoon, males aggregate on host foliage and it is here that the complex sexual repertoire associated with polyphagy is performed. Males defend leaf territories with a mixture of postures, sounds, proboscis extension, and butting. Large size and prior residency are the major components of a successful defense (Burk, 1984). Females fly into leks and sometimes visit several leaf territories before mating or leaving the vicinity altogether. In the laboratory, females show a ca. 3/1 preference for larger males (Burk and Webb, 1983). The advantages of having a large mate are as yet unknown, but could include acquiring superior genes for offspring or obtaining greater material benefits from a more substantial ejaculate (see Sivinski, 1984). Besides mating more often, large males mate longer, perhaps passing more sperm, which could in turn lessen the possibility of remating (Webb et al., 1984; see Farrias et al., 1972 discussion of sperm transfer and mating duration in the Mediterranean fruit fly, Tzanakakis et al., 1968 for a positive relationship between coital and subsequent refractory period length in *Dacus oleae* (Gmelin)). Preliminary evidence in the field suggests that bigger males occupy more advantageous positions in leks. These sexual advantages to being large should be borne in mind, since the most attractive versions of some of the following displays are associated with greater size. We will argue that females use these displays not so much to determine males of the correct species as to find the best available mates within her species.

A number of signals and what appear to be signals are emitted by males on their leaves. The pleural abdominal glands are puffed and 'anal' pouch membranes everted to release a pheromone (discussed by Nation, Chapter 3.4.5). Initial data suggest that the pheromone plays a role in both long and short range communication with females and males. Certain pheromone components occur in the male head and it is possible that these are also used to communicate as the male intermittently dabs the female head with his mouthparts during mating (Sivinski, unpublished data). Wing waving, alternating movements of patterned wings reminiscent of semaphoring, is performed and its production increases in the presence of females (Sivinski and Webb, 1985b). These graceful wing motions accompany arcing sideways movements, the whole constituting a complex visual display. Periodically during the afternoon, puffing males produce a 'calling song' made up of repeated ca. 0.5 s bursts of sound at ca. 0.5 s intervals (bursts = pulse trains = PT; intervals = PTI, fundamental frequency = 149 Hz). The other principal part of the acoustic repertoire is the relatively continuous precopulatory song performed just after the male mounts the female for an average of ca. 150 s and at a slightly higher frequency ( $\bar{x}$  = 167 Hz) (Webb et al., 1976; Webb et al., 1984). These sounds are

generated by beating sexually dimorphic wings. Males have a more oval, surface area-boosting shape, as do males in the acoustically signalling tephritids *T. curvicauda* and *C. capitata*. The 'mute' *R. pomonella* has no such dimorphism (Sivinski and Webb, 1985c).

We have found that the relative form of acoustic displays influences the reproductive fate of their sender; that is, not all males sound alike, not all males have equal sexual success, and females in part choose males on the basis of the song they sing. Subsequently they offer a potential means for tephritid breeders to quantify the sexual competitiveness of their stock. Consider first the calling song. This sound is produced in the absence of another fly, although as we will see, it continues in a modified form in the presence of a conspecific (close neighbors also will sing earlier than isolated individuals; Burk, 1984). Under semi-natural conditions in field cages over guava host-trees, females are more likely to be caught in traps baited with recorded calling song than in silent controls (Webb et al., 1983). It is not clear how far calling song travels, but the acoustic morphology of the pulse train gives further evidence for a range beyond the immediate vicinity of the sender. *A. suspensa* pulse trains have two distinct frequencies, unlike the monotonic repeated pulse train songs of papaya fruit fly, *T. curvicauda*, and Mediterranean fruit fly, *C. capitata*, which are directed only at nearby individuals (Sivinski and Webb, 1985a). Frequency bimodality has been suggested to be a means of escaping filtering by vegetation in vibrational signals (Michelson et al., 1982), or to provide locational cues through the differential attenuation of the two frequencies (Morris et al., 1975). Either function is consistent with broadcasting toward a relatively distant receiver. Flies irradiated 48 h before eclosion (5 kR) lose much of their bimodality and may be less effective signallers (Webb et al., 1985).

In the laboratory, virgin females, but not mated females or males, increase their activity (flying and walking) during the broadcast of a recorded calling song (Sivinski et al., 1984). This increase is a plausible reaction for a mate-searching female to make toward a 'long range' attractant. The superficially similar song of the papaya fruit fly, *T. curvicauda*, results in great quiescence of its females, but here the song is sung only at close range and may hold a choosing female in place until she can further ascertain the quality of the singer (Sivinski and Webb, 1985a). Virgin female caribflies do not respond to either the song of *Dacus neohumeralis* Hardy or a caribfly song conspicuous for its long pulse train interval (Sivinski et al., 1984). Thus, sexually receptive females distinguish, and discriminate among conspecific signals. The stimulating character of short pulse train interval is correlated with the attractive quality of large male size (Burk and Webb, 1983, see however the weaker relation in Webb et al., 1984). Males tend to decrease their pulse train interval in the presence of females corroborating a female preference for short interval songs (Sivinski and Webb, 1985b). It is tempting to conclude that females try to judge male size/vigor by interval length and that males expend more energy in front of a female audience in order to appear as attractive as possible. If so, breeders should note the positive relationship between radiation dosage and pulse train interval (Webb et al., 1985).

Besides its role in female attraction and courtship, calling song plays a part in male-male encounters. Songs sung near other males have a higher frequency and longer pulse trains. Broadcasts of such modified songs have the same quieting effect on males as the clearly agonistic aggression song (Sivinski and Webb, 1985b).

Precopulatory song is sung by males as they mount the back of a potential mate. Often, but not always, the sound lasts until the aedeagus is completely threaded through the ovipositor. Similar sounds are produced if a female

becomes restless during copulation (Webb et al., 1984). The context of singing argues that the proximate role of the song is to quiet the female and maintain her cooperation in the insemination. We propose that its ultimate function is as a last and crucial display of fitness, i.e., the song will gain further cooperation if it demonstrates the quality of its singer. The power of precopulatory song, 3.3X that of the calling song, reflects the effort put into its production. A correlate of this power, sound pressure level (intensity of the sound) is an important attribute of a song. Dealtated, essentially mute, males placed with females are more likely to copulate if a precopulatory song is broadcast at 90 dB. The same song at 52 dB has no significant effect (Sivinski et al., 1984). This demonstrates the causality behind the finding that males who mate tend to have louder songs than those who fail, i.e., females prefer loud songs and are not choosing mates by criteria only incidentally correlated to volume (see Burk and Webb, 1983; Webb et al., 1984). Parenthetically, the lower sound pressure level of failed songs is not an artifact produced by the females' vigorous movements during the rejection. Males that both fail and succeed show no difference in the sound pressure level of their successful and unsuccessful efforts (Webb et al., 1984).

Sound pressure level is correlated to male size and so could be used by females searching for large mates (Webb et al., 1984). Interestingly, while size is inversely related to calling song fundamental frequency, there is no such correlation in precopulatory song. Perhaps females 'prefer' a particularly narrow range of sound and males have been strongly selected to perform it.

In addition to intensity, the form of the precopulatory song is important as well. Inappropriate calling song broadcast at 90 dB to females and dealtated males has no effect on rejection rate. There is considerable variance in the length of the precopulatory song, which can last from a second to 25 min. However, the longer the song, generally, the shorter the copulation. This inverse relationship between song length and mating duration may be due to a less attractive male having more difficulty eliciting female cooperation so that it takes him longer to insert his genitals and leaves him less able to maintain the coupling in the face of female 'restlessness' (Webb et al., 1984). Heavily irradiated males (10 kR) tend to have longer songs sung at a lower frequency (Webb et al., 1985). A few flies (3% of one large sample) mate without producing a song at all. These, likewise, have significantly shorter copulations (Sivinski et al., 1984).

#### 4 CONCLUSION

We hope that we have outlined something of the surprising breadth of fruit fly sexual behaviour. Males communicate to females in many 'media' and from a number of stages. Some of these advertisements appear to be both self-revealing and complicated by the possibility of deceit. Tephritid displays are all the more remarkable when one recalls the alternative behavioural suites males employ at different times and under different regimes of competition. Finally, it is satisfying to note an organizing generalization: that the richness of a species' courtship can be predicted from the distribution of its oviposition sites.

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