

WHAT DO FRUIT FLY SONGS MEAN?

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ABSTRACT

Many flies, including tephritid fruit flies, produce acoustic courtship signals; however, the message these signals transmit is not always clear. Courtship in general is often considered to be a mechanism for species recognition and the prevention of hybridization. Such a proposition suffers from the rarity of sympatric character displacement, the complexity of displays in some species with few close sympatric relatives and the simplicity of courtships in other species with many close sympatric relatives. The theory that displays are sexually selected advertisements of male qualities that females prefer in a mate faces none of these objections. The acoustic signals of male Caribbean fruit flies can be examined from a sexual selection perspective. Females appear to prefer large mates. Both the "calling" and "precopulatory" songs have characteristics that are correlated to male size and females are more likely to react to songs typical of large males. Studies of fruit fly acoustics may serve agriculture either in the development of attractants or by providing criteria to monitor the sexual competitiveness of insects reared for sterile release programs.

RESUMEN

Muchas moscas, incluyendo moscas tefriticas, producen señales acústicas de cortejo; sin embargo, el mensaje transmitido por estas señales no es siempre claro. En general, el cortejo es a menudo considerado ser un mecanismo de reconocimiento de especies y para prevenir la hibridación. Tal proposición sufre de la rareza de la destitución de la característica simpátrica, lo complejo de la demostración de algunas especies con pocos parientes cercanos simpátricos, y la simplicidad de cortejos en otras especies con muchos parientes cercanos simpátricos. La teoría que demostraciones del macho son un anuncio de sus selectas cualidades sexuales que las hembras prefieren en su consorte presenta ninguna de esta objeciones. Las señales acústicas de machos de la mosca del Caribe pueden ser examinadas desde una perspectiva de selección sexual. Las hembras parecen preferir machos grandes. Cantos "llamantes" y "precopulatorios" tienen características que están correlacionadas al tamaño del macho y es más probable que las hembras reaccionen al canto típico de machos grandes. Estudios acústicos de las moscas de fruta pudieran servir a la agricultura ya sea en el desarrollo de atrayentes o proporcionando un criterio para chequear la competitividad sexual de insectos esteriles criados para programas de liberaciones.

Many male flies, including tephritid fruit flies, make sexual courtship sounds. The contexts in which these songs are produced are often well described, but the information being transmitted to listening flies is less well understood. Acoustic and other courtship displays, such as wing waving, colors, and scents, are sometimes considered species isolating mechanisms, i.e., means by which creatures of the same species and opposite sex recognize each other. Calls in translation might be nothing more than, "I am a male species A—I am a male species B," etc.

A model for the evolution of such a song in a fruit fly might start with allopatric speciation (see Mayr 1963). First, a population of flies becomes geographically divided. Suppose, for example, that a fly cannot cross a mountain which arises to bisect its

range. Environments and, hence, selection pressures on the two sides of the mountain may not be identical; perhaps one is warmer or wetter or contains a novel predator. In addition, different mutations might arise in the separated regions from alleles whose frequencies differed in the first place because of genetic bottlenecks so that the raw material of evolution is also different. Over time, the genomes of the two populations diverge. When erosion breeches the mountain and the flies from the two sides mingle there are reproductive consequences arising from their previous isolation—hybrids between the two types may be less fit than offspring produced by same-type parents. Thus flies that only mate with members of their own isolate are at a reproductive advantage and will eventually replace those that do not. After all, the latter are spending time and resources on offspring (should zygotes even develop) that will bear fewer or no grandchildren. Flies that are clearly of a particular type and those that prefer mates that are clearly of their own type can “collaborate” in evolving features, *de novo* or through exaggeration, whose role is to explicitly say “I am a species A.”

This model is appealing because the signals of so many species are recognizably different, even to humans. One can easily assume that these signals are different *because* species are different. However, the argument faces objections when applied to male-produced displays. First, it makes the largely unmet prediction of sympatric character displacement. That is, animals sometimes have similar signals in the parts of their ranges that do not overlap. Where the ranges do overlap, the need for species recognition should force the signals to diverge. Such cases of character displacement are rarely found (e.g. Walker 1974). Second, some of the most complex and elaborate courtships occur in species that have few close relatives and who would have little chance to err by choosing an almost, but not quite, proper mate (Otte 1972, Alcock & Pyle 1979, Thornhill & Alcock 1983, West-Eberhard 1984). A mirror image phenomenon can be observed by anyone watching the flies on a fresh pat of dung or other resource that concentrates insects. Closely related species can often be seen in great density on the fecal surface. The opportunity for error seems quite high, yet the courtship of these insects tends to be relatively simple. (see for example phoretic sphaerocerids of the genus *Borborillus*, Sivinski 1983, 1984, or many of the dung breeding Sarcophagidae, pers. obs.).

If it sometimes seems that species isolation is an insufficient explanation for the variety and complexity of male courtship, what does all its behavioral sound and fury signify? An alternative explanation arises from how much the sexes invest in their offspring. Females produce large gametes. The number of offspring they can have is largely limited by the number of eggs they can generate. Males make small, cheap gametes and the scope of their paternity is largely a function of how many females can be mounted and eggs fertilized. While number of matings is generally important to males, copulatory quantity is often of little concern to females. Rather, females can enhance their success at reproduction by choosing quality mates, i.e., by incorporating the best available genes into their offspring or by obtaining a valuable resource, such as ejaculate-borne proteins from the “wealthiest” male they encounter (Trivers 1972, Thornhill 1976, Sivinski & Smittle 1987).

Assume, then, that at least some courtship displays are advertisements that males produce to convince females that they have the qualities females prefer in a mate. One might imagine that females would be very discriminating, looking for relatively small differences among suitors. Species could be kept separate incidentally by females engaged in making minute distinctions among a subset of males of her own species. Hence the lack of large scale character displacement is less surprising. The elaborate courtship of isolated species poses no difficulty to the female choice/male advertisement model. If there were only one species in the world, it might still evolve complex communications between the sexes. The variety and species-uniqueness of signals may simply be due to

the improbability of selection ever repeating itself exactly during the evolution of independent displays.

There is profit in examining fruit fly songs as "intersexually selected" instruments of persuasion (Sivinski & Burk 1988). In the Caribbean fruit fly, *Anastrepha suspensa* (Loew) (Caribfly), there are two male sexual sounds, both produced by wing movement (Webb et al. 1976, Sivinski & Webb 1985a). The "calling song" is made up of repeated bursts (pulse trains). It is sung by males on the leaf territories they defend against interloping males and coincides with the release of pheromone from abdominal glands and everted anal membranes (Burk 1983, Nation 1972, Sivinski 1988, Chuman et al. 1988). Calling song may be sung in the absence of other flies, although it can be continued in the presence of a visiting fly. The "precopulatory song" is a continuous sound made as the male mounts the female and typically lasting until the male genitalia are completely threaded through the female ovipositor, a period averaging a minute and a half (Webb et al. 1984).

What qualities might such songs advertise? One trait that is preferred by females is large size (Burk & Webb 1983). Big males are more likely to mate than smaller rivals in many species of flies (e.g. Sivinski 1984). It is often unclear, however, if bulk wins out in competition with other males for access to females or if it is something favored by females or both. In Caribbean fruit flies the problem is simpler. Females go to males to initiate courtship and so must either prefer big males or be more likely to sense them.

Are there characteristics of the signals that are correlated to large size? In the calling song, the interval between pulse trains is such a correlate. Larger males tend to have shorter intervals (Burk and Webb 1983, see however Webb et al. 1984). The reason is unknown; perhaps with size come greater resources to sustain what must be a more expensive signal. The sound pressure level (SPL) of the precopulatory song is also related to male size, big males being louder (Webb et al. 1984).

Do females use these correlates when choosing a mate? Virgin females are more responsive (i.e., increase movement) to shorter pulse train interval songs. Their activity increases when a recording of a short, but not a long, pulse train interval song is broadcast into their cage (Sivinski et al. 1984). This increased movement is a plausible response to a sound heard at some distance that directs the hearer toward an attractive goal. It is interesting that the papaya fruit fly (*Toxotrypana curvicauda* [Gerstäcker]) sings only as it approaches nearby females. These sounds quiet the female (Sivinski & Webb 1985b). Perhaps these females become still in order to access their approaching suitors. Also of note is a sexual dimorphism in the response of Caribflies to calling sounds. Males become quiet in the presence of the shorter pulse train interval songs, while mated females are not affected by differences in pulse train intervals. This makes it less likely that virgin females are simply startled by the short interval sound and so become agitated. If short pulse train interval songs are both more effective and more energetically expensive, it might be predicted that pulse train intervals would decrease when a male was "certain" a female was observing. This is the case. An individual male will shorten his pulse train intervals in the presence of a female. When another male is close by, the pulse trains themselves are longer in time, and made at a higher frequency, suggesting a between-male communication role for calling song as well (Sivinski & Webb 1986).

The precopulatory song is also an important component of courtship. Its absence in muted (dealated) males leads to a greater number of rejections by females. A calling sound reproduced by a tape recorder at a SPL of 90 dB (OdB re 20 μ pac) broadcast increases female acceptance, but a broadcast at 50 dB does not (Sivinski et al. 1984). Thus, females make sexual decisions on the basis of precopulatory SPL and that SPL is positively correlated to male size.

What agricultural purpose is served by studies of fruit fly sex sounds and an appreciation that not all males and their displays are equally attractive? Studies of this type,

not only on sounds but also visual and pheromonal displays, have at least two potential applications. The first, which is arguably more important in studies of chemical cues, is the manufacture of attractants and more efficient traps, either to monitor pests or to control them. Caribbean fruit fly calling sounds are attractive in themselves. Traps baited only with recorded songs are more effective than silent controls (Webb et al. 1983). It remains to be demonstrated that sounds and pheromone together, for example, can be more attractive than a more conventional chemical cue alone or, if they are, whether it is economically feasible to produce such a trap. The second use is in the quality control of reared insects. A major concern of sterile release programs is that their reared insects be sexually competitive with the wild rivals they encounter in the agricultural arena. While sterile releases are often a very efficient means of fruit fly control, there have been some less spectacular efforts where overflooding ratios have reached thousands of reared for every wild fly and still not succeeded (Burk & Calkins 1982). A possible reason for these expensive failures (and perhaps some overly expensive successes) is the inadequate courtships of the reared flies. A first step in ensuring that competitive flies are released is a description of sexual behavior in a species followed by periodic comparison of factory reared stock wild flies in mating compatibility and competitive tests. In this way, waste can be minimized and the efficiency of programs be enhanced. It may concern *A. suspensa* breeders, for instance, that radiation can increase the calling pulse train interval of irradiated males (Webb et al. 1987). On the other hand, years of domestication in Central American stocks have not dramatically influenced the acoustical signals of the Mediterranean fruit fly *Ceratitidis capitata* (Wied.) (Sivinski et al. 1988).

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REFERENCES CITED

- ALCOCK, J., AND D. W. PYLE. 1979. The complex courtship behavior of *Physiphora demandata* (F.) Diptera: Ottidae) Zeit. fur Tierpsychol. 49: 352-362.
- BURK, T. 1983. Behavioral ecology of mating in the Caribbean fruit fly, *Anastrepha suspensa* (Loew). Florida Entomol. 66: 330-344.
- BURK, T., AND C. O. CALKINS. 1982. Medfly mating behavior and control strategies. Florida Entomol. 66: 3-18.
- BURK, T., AND J. C. WEBB. 1983. Effect of male size on calling propensity, song parameters, and mating success in Caribbean fruit flies (*Anastrepha suspensa* (Loew)). Ann. Entomol. Soc. Am. 76: 678-682.
- CHUMAN, T., J. SIVINSKI, J. H. TUMLINSON, R. R. HEATH, AND C. O. CALKINS. 1988. Variation in the composition of volatiles produced by the male Caribbean fruit fly *Anastrepha suspensa* (Loew) (Tephritidae). J. Chem. Ecol. (in press)
- MAYR, E. 1963. Animal species and evolution. Belknap of Harvard University Press, Cambridge, Massachusetts.
- NATION, J. L. 1972. Courtship behavior and evidence for a sex attractant in the male Caribbean fruit fly, *Anastrepha suspensa*. Ann. Entomol. Soc. Am. 65: 1364-1367.
- OTTE, D. 1972. Simple versus elaborate behavior in grasshoppers: an analysis of communication in the genus *Syrbala*. Behavior 42: 291-322.
- 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 frugipennis* (Sphaeroceridae). Ann. Entomol. Soc. Am. 77: 232-235.

- SIVINSKI, J. 1989. Lekking and the small scale distribution of the sexes in the Caribbean fruit fly, *Anastrepha suspensa* (Loew). Florida Entomol. (in press).
- SIVINSKI, J., AND T. BURK. 1988. Reproductive and mating behavior. in A. Robinson and G. Hooper, eds. Fruit flies—their biology, natural enemies, and control. Elsevier, Amsterdam, The Netherlands.
- SIVINSKI, J., AND T. BURK. 1988. Reproductive and mating behavior. in A. Robinson and G. Hooper, eds. Fruit flies—their biology, natural enemies, and control. Elsevier, Amsterdam, The Netherlands (in press).
- SIVINSKI, J., AND B. SMITTLE. 1987. Male transfer of materials to mates in the Caribbean fruit fly, *Anastrepha suspensa* (Diptera: Tephritidae). Florida Entomol. 70: 233-238.
- SIVINSKI, J., AND J. C. WEBB. 1985a. Sound production and reception in the caribfly *Anastrepha suspensa*. Florida Entomol. 68: 273-278.
- , AND ———. 1985b. The form and function of th acoustic courtship signals of the papaya fruit fly, *Toxotrypana curvicauda*. Florida Entomol. 68: 634-641.
- SIVINSKI, J., AND J. C. WEBB. 1986. Changes in Caribbean fruit fly acoustic signal with social situation (Diptera: Tephritidae). Ann. Entomol. Soc. Am. 79: 146-149.
- SIVINSKI, J., T. BURK, AND J. C. WEBB. 1984. Acoustic courtship signals in the caribfly *Anastrepha suspensa*. Anim. Behav. 32: 1011-1016.
- SIVINSKI, J., C. O. CALKINS, AND J. C. WEBB. 1988. Comparison of acoustic courtship signals between wild and laboratory reared Mediterranean fruit fly. Florida Entomol. (in press)
- THORNHILL, R. 1976. Sexual selection and paternal investment in insects. Am. Nat. 110: 153-163.
- THORNHILL, R., AND J. ALCOCK. 1983. The evolution of insect mating systems. Harvard Univ. Press, Cambridge, MA.
- TRIVERS, R. L. 1972. Parental investment and sexual selection. Pages 136-179 in B. Campbell, ed. Sexual selection and the descent of man 1871-1971. Aldine-Alterton, Chicago, Illinois.
- WALKER, T. J. 1974. Character displacement and acoustic insects. Am. Zool. 14: 1137-1150.
- WEBB, J. C., T. BURK, AND J. SIVINSKI. 1983. Attraction of female Caribbean fruit flies *Anastrepha suspensa* (Loew) (Diptera: Tephritidae) to males and male-produced stimuli in field cages. Ann. Entomol. Soc. Am. 76: 996-998.
- WEBB, J. C., J. L. SHARP, D. L. CHAMBERS, J. J. MCDOW, AND J. C. BENNER. 1976. The analysis and identification of sounds produced by the male Caribbean fruit fly, *Anastrepha suspensa* (Loew). Ann. Entomol. Soc. Am. 69: 415-420.
- WEBB, J. C., J. SIVINSKI, AND C. LITZKOW. 1984. Acoustical behavior and sexual success in the Caribbean fruit fly, *Anastrepha suspensa* (Loew) (Diptera: Tephritidae). Environ. Entomol. 13: 650-656.
- WEBB, J. C., J. SIVINSKI, AND B. SMITTLE. 1987. Acoustical courtship signals and sexual success in irradiated Caribbean fruit flies (*Anastrepha suspensa*) (Diptera: Tephritidae). Florida Entomol. 70: 103-109.
- WEST-EBERHARD, M. J. 1984. Sexual selection, social communication, and species specific signals in insects. Pages 283-324 in T. Lewis, ed. Insect Communication. Academic Press, London.