

Crossley, S.A. Monash University, Clayton, Australia. Lek behaviour and its evolution in *Drosophila mycetophaga* (*Hirtodrosophila*).

Drosophila mycetophaga is a fairly large drosophilid (mean length, head to tip of wing: ♀ 4.5 mm, ♂ 4.0 mm). Male and females have picture wings (Fig. 1). The species is of particular interest because it is one of three Australian species reported to use a territory

or lek for courtship and mating (Parsons 1977; Parsons & Bock 1977). According to these workers the courtship territory is the horizontal undersurface of a bracket fungus (*Ganoderma applanatum*, Polyporaceae). This undersurface varies in colour according to the developmental stage of the fungus and flies are only found on it when it is in its white or grey stage. Courtship was briefly described as appearing "to conform with the general drosophiloid pattern" (Parsons 1977), and to include prominent wing display (Parsons & Bock 1977).

I attempted to confirm lek use by *Drosophila mycetophaga* in a field study (1981-1985). Approximately 32 hr of behavioural observations of *D. mycetophaga* were made each year. Five observers were used for this study, at least two in any year. In addition to behavioural observation and description, behaviour was also video recorded in the field.

Field work was in temperate rain forest in S.E. Australia. The fruiting bodies of *Ganoderma applanatum* were seen as hard wood-like brackets, growing out from the sides of fallen trees. Each year some brackets ripened and became covered ventrally with a pure white layer pierced by pores. Brackets occupied by *D. mycetophaga* were those which were ripe, discharging spores, and positioned where they reflected light penetrating the forest canopy.

To see whether individual flies selected and defended particular brackets, flies were aspirated from leks, sexed, marked with paint, and at dusk placed on a fern frond beside the capture site. Nine out of a total of ten marked individuals reappeared the next day, either on the same fungus, or on a neighbouring one that was in the same white phase of development. Therefore, flies did not return to exactly the same fungus from which they were taken, but on return they chose to land on a fungus which was equally conspicuous.

Field experimentation was hampered by difficult terrain, scarcity of *D. mycetophaga* and the fact that population density on accessible brackets was unpredictable from year to year. Eventually, success in culturing the species enabled detailed behavioural study and a re-interpretation of videotaped behaviors of flies on leks. Because of the difficulty of sexing and marking individuals in the field, any unmarked fly which wing displayed had been assumed to be male. This assumption was found to be wrong when flies of known sex were observed in the laboratory. The following account of behaviour is therefore based on laboratory studies and the behaviour of marked individuals of known sex in the wild.

The behaviour of males and females of *Drosophila mycetophaga* was more similar than for other drosophilids. Both sexes turned towards, oriented to, followed, bobbed the abdomen up and down, touched tarsi, and using the middle and fore legs stepped on (trampled) the fly oriented to. Females as well as males wing displayed by extending one wing to 90° and then turning the vane so that it was perpendicular to the substrate (wing extend, Fig. 2). Female wing display has only been reported previously for a "lesbian" mutant phenotype of *Drosophila melanogaster* (Cook 1975). Waving, which was a quick raising and lowering of one or of both wings alternately, was also shown by both sexes.

Behaviours unique to males were two additional wing displays in both of which the wings were vibrated, and chasing, which was distinguished from following by being faster. In vibration the wings separated 45° and in scissor the two wings were each held out to 90° to form a straight line across the body. Vibration occurred during approach and chase to both males and females, but scissor was only given, in long bouts at least, to females. Typically the male vibrated as he approached a female and scissored as he circled her. He paused and scissored in front, in long bouts, before moving behind and under her wings to make copulation thrusts. Copulation occurred when the male mounted the female and forced her wings apart. Copulation duration varied (17-22 min) and appeared to be terminated by female leg movements which dislodged the male.

Using a video-recording method (Crossley & McDonald 1980), sound emissions during courtship were matched to the displays which produced them. Wing extend was silent, vibration was accompanied by pulse song (interpulse interval 46 ms) and scissoring produced sine song, which had a carrier frequency of 180 Hz decreasing to 82 Hz as the wings closed in preparation for a copulation attempt.

In the laboratory at 22°C the life cycle (egg - adult) is 17 days. Six-nine day old virgin females elicit persistent courtships from the same aged virgin males; courtship amongst 1-3 day old virgins is rare. The eggs are conspicuous being surmounted by four long filaments which protrude from the substrate (*Drosophila* medium plus commercial mushroom *Agaricus*). Newly eclosed flies dehydrate rapidly unless they are placed on fresh food within a day. Presumably, because their natural habitat is wet and humid, they are specially susceptible to desiccation.

In the field, once a male landed on a lek it usually remained there all day. It patrolled the lek, bobbing, holding its wings slightly apart, and orienting to small blemishes as if they were mistaken for

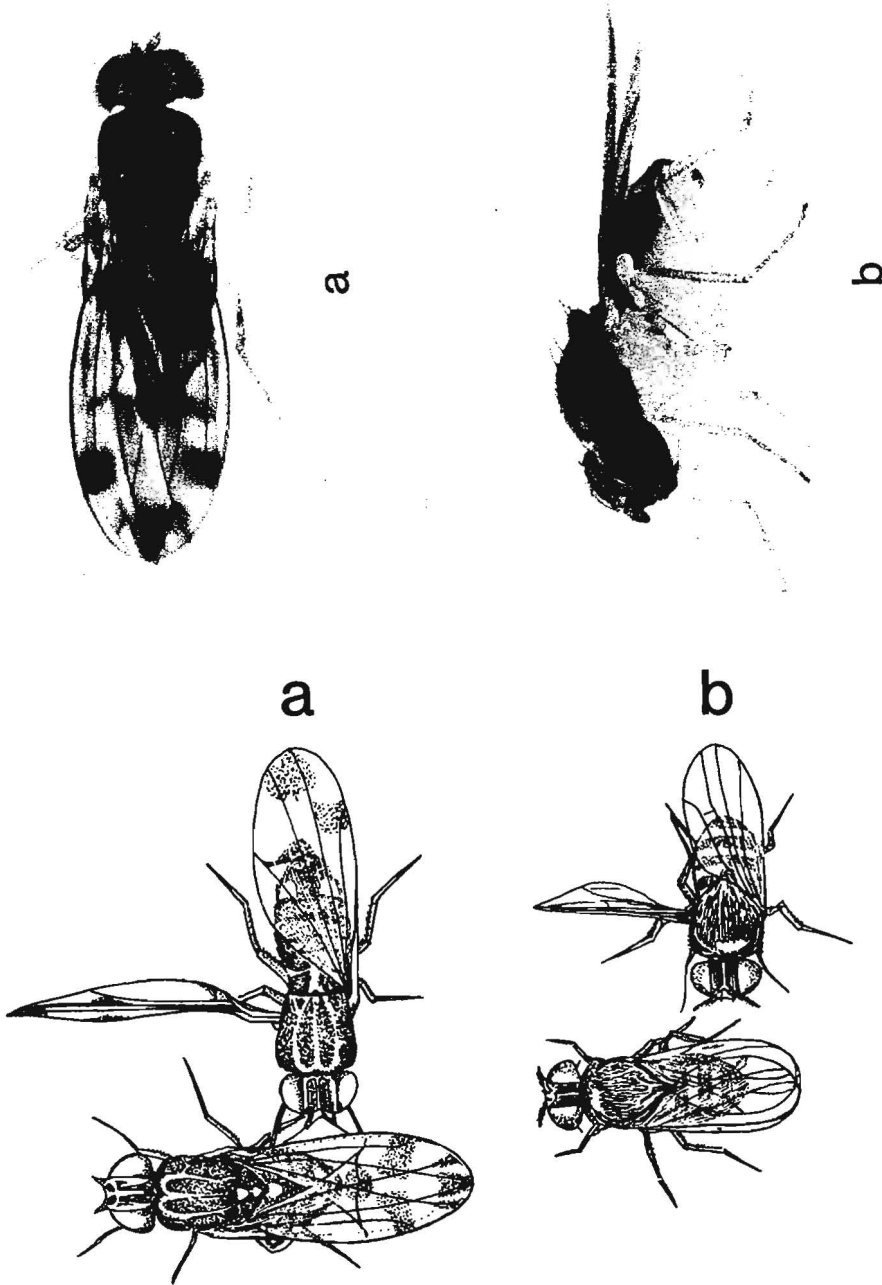


Figure 2. Wing extend in *D.mycetophaga* (a) compared with a similar display vibration in *D.melanogaster* (b). The wing vane does not extend into the partner's field of view in (b) as much as it does in (a).

tion sites of this species but the conclusion, from laboratory study and dissections of *Ganoderma applanatum* (decaying as well as fresh), was that soft fungi, as distinct from hard bracket fungi, are used. Soft fungi grow on almost every surface of the wet forest and favour the dispersal of the species. Bracket fungi showed no evidence of larval damage and no pupae were found, despite intensive searches of brackets and their surrounding decaying wood. Kimura (1980) reports that adult members of the subgenus *Hirtodrosophila* prefer fresh mushrooms in contrast to their larvae which prefer decaying fungi. Adult *D.mycetophaga*'s presence on ripe bracket fungi in nature and the utilisation of decaying mushroom as the larval food source in the laboratory, therefore agrees with Kimura's conclusions.

Figure 1. *Drosophila mycetophaga*. The sexes are similar with picture wings (a) and sharply contrasting dark upper and white lower body colouring (b). Differences between the sexes are the downturned genitalia of males and their shorter body length but these differences are not useful for distinguishing the sexes on the lek.

another fly. Females alighted on the edge of the lek, stayed for shorter periods than males, and were outnumbered by males. The nearest male rushed to a newly arrived female and scissored. If a second male approached, the first male chased the intruder away. Such chases were short and usually successful in repelling intruders. After a chase the victor rushed back to the female and resumed courtship. Females were more passive than males in that they did not move around the fungus as much. However, they did wing extend to other flies as well as following them and during courtship they turned to bring themselves into the copulatory position or avoided copulation by abdominal raising. When females were not present on the fungus, chases were rare. Males moved sideways to avoid each other during patrols, as if spatial positions had been learned in earlier interactions. The same males tended to occupy the edge of the lek where females landed. Individual males, therefore, differed in their access to females and females had the opportunity to select a mate.

Nothing is known of the natural feeding and oviposition

The use of a lek for mating may have evolved because sexual displays on the food source were not visible in the dimly lit forest. On the lek, visual displays and picture wings, enhanced by the white background, were selected for. The male wing displays and their accompanying sounds may be sexually stimulating as well as serving a sexually isolating function in the evolution of *Hirtodrosophila*, whereas the bisexual wing extend and wave may advertise presence on the lek. In *D.mycetophaga* the wing is brought further into the partner's view by wing extend than it is in *D.melanogaster* males which lack picture wings (Fig. 2). Perhaps wing length is implicated in the evolution of wing adornment. Olfactory stimuli may also be important for aggregation on leks and during courtship but the evidence, as a whole, supports the view that visual stimuli provide the greater component of total stimulation.

Spieth (1974) suggested that bird predation was the significant factor in the evolution of lek behaviour in Hawaiian *Drosophila*, but no predators are known for *D.mycetophaga*. This species is camouflaged, however, when viewed on the lek from the side (Fig. 1) so that protection against terrestrial predators, such as spiders and lizards, may have featured in its evolution once it began to use fungal leks.

The behaviour of *D.mycetophaga* is consistent with the view that it is a "classical" lek species, as defined by Bradbury (1981), which evolved for different reasons from the Hawaiian lek species. Since the latter belongs to the subgenus *Drosophila* and *D.mycetophaga* to the subgenus *Hirtodrosophila* this is a case of convergent evolution (Parsons & Bock 1976). Choice tests are in progress to determine the perceptual abilities of *D.mycetophaga* and the stimuli underlying lek use. By combining field and laboratory studies, it is ensured that hypotheses tested relate to the species' naturally occurring behaviour.

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References: Bradbury, J.W. 1981, in: *Natural Selection and Social Behavior* (Alexander & Tinkle, eds.), Chiron Press Inc. 138-169; Cook, R. 1975, *Nature* 254:241-242; Crossley, S. & J. McDonald 1980, *DIS* 5:150-151; Kimura, M.T. 1980, *Evolution* 34(5):1009-1018; Parsons, P.A. 1977, *Evolution* 31:223-225; — & I.R. Bock 1977, *Nature* 265:48; Spieth, H.T. 1974, in: *Genetic Mechanisms of Speciation in Insects* (White, ed.), Australian & New Zealand Book Co., 94-101.

Demakova, O.V. and E.S. Belyaeva. *Inst. of Cytology & Genetics, Novosibirsk 630090 USSR.* Effect of mating direction on the position effect variegation of $T(1;2)dor^{var7}$ in *D.melanogaster*.

The influence of some external and genotypic factors on variegation is known to be one of the characteristics of position effect variegation (see, for review, Spofford 1976). For some rearrangements influence of parental genotype on variegation was demonstrated. These so called parental effects have

predominantly the maternal character (Hessler 1961; Cohen 1962; Spofford 1976; Khesin & Bashkirov 1979).

We started the investigation of position effect variegation of $T(1;2)dor^{var7}$, relocating the 1A-2B7-8 region of the X-chromosome to the 2L-chromosome 40A-F region (Zhimulev et al. 1986; Demakova et al., *DIS*:this issue). This note is devoted to revealing possible parental rearrangement source effect in this model system. The $dor^{var7}/FM6$ females or dor^{var7}/Y males from one stock were crossed to individuals, carrying different mutations in 1F3-4 - 2B7-8 region (see Demakova et al. *DIS*:this issue) at various temperatures (25°C, 18°C, 14°C). In F₁ the phenotypes and viability of daughters, heterozygous for rearrangement and mutations (B^+) were analysed.

The results of the analysis are given in Table 1. With the parental source of rearrangement variegation increases considerably, both in decrease of heterozygotes viability and in increase of abnormal flies number among B^+ females (Table 1, 25°C) or in stronger manifestation of mutant phenotypes:

swi - (a) Mosaics have crumpled, singed wings; (b) Most of mosaics have extremely reduced, singed wings. dor - (a) About 5% of B^+ females have dor-variegated eyes; (b) In dying pupae one can observe formed imago with eyes almost completely dor-coloured. Few surviving flies have eyes variegated in the same manner. sta - (a) Mosaics may have small rough eyes and some head macrochetes absent; (b) Besides these abnormalities mosaics may have roughly deformed heads, eyes, antennae and ocelli (3.3%). I(1)BA12 - (a) Some of B^+ females have reduced eyes or some have head macrochetes absent; (b) Abnormalities are numerous; about 8% of B^+ females have eyes and heads roughly deformed. I(1)BA11 - (a) Wings are slightly curled; (b) About 13% of B^+ females have curled and twisted wings. I(1)BA5 - (a) Mosaics have some macrochetes on heads and (rarely) palpus reduced in size; (b) Reduction of macro- and microchetes can be found on heads, palpus and thoraxes; sometimes eyes are deformed.

After combining 2 modifying factors (low temperature and paternal source), variegation enhanced more considerably (Table 1, 18°C and 14°C). Only in such "extreme" conditions the variegation expression appeared to be significant for some loci, inactivation of which after position effect was questioned in the other conditions: cwi - crumpled wings; I(1)BA1 - viability reduced, rough small eyes; I(1)BA9 - viability reduced. Thus, the enhancement of variegation is expressed in some lengthening of its spreading distance also.