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Post-mounting courtship and the neutralizing of male competitors through “homosexual” mountings in the fly *Hydromyza livens* F. (Diptera: Scatophagidae)

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Abstract

Post-mounting courtship behaviour of a 6–8 mm long scatophagid fly *Hydromyza livens* which lays its eggs in yellow water lily (*Nuphar lutea*) is described and analysed. Enigmatic male–male encounters are described, along with lengthy “homosexual” mounting behaviour. A possible interpretation of both types of behaviour is given, with reference to their adaptive significance and the special problems encountered by males in locating females.

Keywords: Behaviour, courtship, Diptera, homosexual, post-mounting, Scatophagidae, water lily

Introduction

Post-mounting courtship has only rarely been noted within the Diptera. Examples which have been fully described occur in the Platystomatidae (McAlpine 1972) and Stratiomyidae (Eberhard 1988). Brief details of post-mounting courtship and puzzling “homosexual” behaviour in *Hydromyza livens* were given by Preston-Mafham and Preston-Mafham (1993, p 96–97). The present paper is intended to present an amplified account of the rather incomplete details given therein. Additional observations made in 1993 throw extra light on the possible reason for apparent homosexual behaviour.

Study area and methods

The study was carried out during August 1991 and 1993 on the slow-moving lowland river Arrow near Alcester in Warwickshire, England. Flies of this species were first noted walking around on leaves of the yellow water lily (*Nuphar lutea*), the larval food-plant. Several hours of observations were made from the bankside. Fortunately, many of the most interesting behaviours, including mating, took place on lily pads close beside the author on the bank.

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Mate-location and mating

What were, from their behaviour (see below), clearly males, appear to spend most of their time wandering around on lily pads or standing motionless on them. During 1991 males occurred at low densities relative to the abundance of floating leaves—estimated at no more than one male per 40–50 pads. In 1991 these pads, which are flat and measure 15–40 cm across, covered some 40% of the water-surface in the study area over a length of over 100 m. During 1993 this dropped to around 2–5% due to exceptionally high flood conditions earlier in the summer.

The males appear to work their way slowly across the pads searching for females more or less at random. Males pounce upon anything which remotely resembles a conspecific female, including two-dimensional natural features such as grey or yellowish blotches on the leaf surface, as well as the more obvious targets posed by water-strider bugs (Gerridae) and small dolichopodid flies. Only the latter resemble *H. livens* females to any extent.

Mating was noted on two occasions, being broadly similar each time. When a female alighted on a leaf, a nearby male instantly jumped on to her back. She shook her body slightly, but did not put up a noticeable struggle. Instead, she raised her wings up at an angle of approximately 45° and directed slightly outwards to form a V. The male then pushed his forelegs horizontally forwards under the female's wing-bases so that his tarsi rested on either side of her head. The pair then began rocking violently from side to side. At first this seemed to indicate that the female had ceased to co-operate and was trying to throw the male off her back. However, it proved possible to discern that it was in fact the male which, by lifting each anterior leg alternately, rocking the female from side to side. This lasted for several minutes (estimated) and the pair then remained in copula for approximately 10–15 min, during which time the female remained quiescent. She then walked suddenly to the edge of the lily leaf and kicked the male briefly with her hindlegs. He responded instantly by stepping backwards off her back, precisely as she stepped off the edge of the leaf and disappeared into the water.

In the first observed mating the female re-emerged back on the leaf just over 40 s later. The male, who had meanwhile waited on the leaf, immediately pounced on to her back and attempted to re-establish genitalic contact. The female's reaction now differed greatly from her initial one. Instead of raising her wings to 45° she kept them fully closed, while bucking violently and kicking out with her posterior legs. In the absence of the secure foothold formerly obtained by "threading" his forelegs under the female's wing-bases, the male was thrown off within a few seconds. He made several more attempts to mount but was easily rebuffed.

In the second observation of a complete mating sequence, copulation only lasted a few minutes and the female reappeared after spending only a little more than 10 s below water. Attempted re-mounting by the male followed the same unsuccessful pattern outlined above.

Male-male interactions

During 1991 males actively quartered the lily pads, often encountering one another. In most cases males either ignored one another, or veered away when still at some distance (e.g. 15–20 cm). However, on three occasions a male headed directly towards a second male and engaged in an apparently ritualized behaviour. While standing face-to-face, but at a slight angle to one another, the two males gently pushed with their anterior legs in a strange slow-motion "fending off" action. They then stood "head-by-head", yet with no obvious indication that any pressure was being applied which could be construed as

pushing. This interaction did not therefore seem to parallel the ritualized face-to-face “pushing matches” seen in other flies such as tephritids (Moulds 1977), drosophilids (Spieth 1981) and neriids (Preston-Mafham 2001). After engaging in this ritual, the two male *H. livens* always separated and went their separate ways. In 1991 a single example of homosexual mounting was noted which lasted for at least 22 min. During 1993 several examples were seen, including two “pairs” present simultaneously on adjacent leaves. It was not possible to know precisely how long these pairings had endured, as they were established before they were first noted. However, one of them lasted for a further 37 min. During such homosexual pairings the lowermost male struggled violently, and at frequent intervals, to unseat his rider, but without success (by contrast, uncooperative females are easily able to unseat an unwanted male). There were no copulatory efforts by the uppermost male that might have indicated that the attempted pairing had occurred through “mistaken identity”. Instead, the “rider” put all his effort into staying in place throughout his mount’s struggles to unseat him.

Discussion

The probable significance of post-mounting courtship

Although only two examples of successful mating were observed, it is possible to construct a plausible theory explaining the observed behaviours, although further research is needed in order to test and confirm this theory. It seems likely that females only visit the food-plant in order to mate and lay eggs. They probably always accept the first male to mount them. This behaviour is not as “unfussy” as it seems, because two methods of ensuring a mate’s fitness are available. Firstly, females are more likely to be pounced upon by a large male than a small one, for reasons explained below. Females of a number of insects have been shown to prefer larger males over small ones (e.g Borgia 1981; Simmons 1986) while intrasexual rivalry often leads to the largest males monopolizing most of the females (Cade 1979; Johnson 1982; Brown et al. 1985; Crespi 1986; Bartlett 1988; Hissmann 1991). Upon being mounted for the first time a female *H. livens* does not struggle, but co-operates by raising her wings and allowing her mate to rock her. It is possible that this rocking behaviour conveys vital information about the size and strength of the male, as small or weak males would lack the vigour typical of larger and stronger individuals. Feed-back derived through rocking would presumably allow the female to adjust accordingly the duration of copulation. She clearly has complete control over this because the male dismounts at her signal (by kicking) as she steps into the water.

It is possible that females which only permit brief copulations go on to lay fewer eggs fertilized by that particular mate. This could explain the considerable disparity in time spent below water in the two observed mating episodes. However, in view of the small sample size this must remain speculative until it can be tested on a larger sample. The female’s clear ability to rebuff an erstwhile mate when he tries to re-mount indicates that her initial willingness to accept him without preliminary courtship was not merely because she lacked the ability to reject him.

The possible significance of homosexual behaviour

Homosexual mounting behaviour is seen in a wide variety of insects, even where marked sexual dichromatism would appear to render it less likely, as in the Odonata (Preston-Mafham and Preston-Mafham 1993, p 36). It is usually a case of mistaken identity and as

such is normally very brief, often because the male being mounted objects violently to what is happening. However, at least one alternative reason for protracted male–male mounting has been suggested in a tephritid fly (Preston-Mafham and Preston-Mafham 1993, p 92–93).

Males of *H. livens* are faced with a difficult problem when seeking to encounter females. The food-plant, yellow water lily, is widely spread and often abundant. Males cannot therefore economically defend discrete areas against other males in an effort to monopolize egg-laying females (resource defence polygyny). In order to be economically defensible, a resource of use to the female has to be distributed in discrete patches (Emlen and Oring 1977). If individual specimens of the food-plant demonstrate certain qualities which are of extra attraction to the females, such as a low concentration of defensive chemical compounds in the leaves, then this could provide an alternative route for male monopolization of a “sure bet” rendezvous point. This indeed happens in certain grasshoppers (Otte and Joern 1975). However, there is no evidence for this in *Nuphar lutea* in which many of the surface leaves probably arise from chemically identical rhizomatous clones on the river-bed. An alternative strategy for the *H. livens* males could be to locate females in feeding or resting areas. However, what little evidence exists suggests that females of scatophagid species which lay their eggs in living plants tend to spend much of their time skulking among leaves, where it would be virtually impossible for males to locate them on any kind of economically feasible basis. If females ever feed on flowers, it seems unlikely that these would be restricted to any one type, thus ruling out yet another possible predictable rendezvous point.

The only remaining option is for the males to loiter on the food-plant in the certain expectation that sooner or later females will be sure to show up. In years when leaves of the food-plant cover a high percentage of the water-surface, a male’s best strategy may be to maintain a slow but steady search of the leaves in the hope of encountering a female who is moving from leaf to leaf. Interactions with other males could be mainly confined to rituals designed to maintain at least some discrete area of operation, i.e. the face-offs described above.

However, in years when leaves of the food-plant only reach the surface in small numbers, the chances of being on a particular leaf when a female shows up are enormously increased. This reduces or eliminates the need for the males to move around in an active search for females. Similarly, the waiting males will also be far more concentrated in time and space. If a female is willing to mate with the first male who leaps on to her back, and males do not need to move around to locate a mate, then the most sensible strategy for beating a competitor in the race to an arriving female would be to mount him and remain in situ for as long as possible. The lowermost male is thereby denied the opportunity to leap upon an arriving female, while his rider can do so unhindered.

In order to be successful this strategy must rely on two conditions. Firstly, a newly arrived female must always be willing to mate with the first male who pounces upon her. From the limited evidence available at present, this clearly seems to be the case. Secondly, a mounted male must not be easily deposed. Mating males appear to be securely fixed to their mounts via their threaded front legs, more or less ruling out the second eventuality.

The above factors probably explain why homosexual mounting was much more common and lasted longer in 1993 than in 1991. Large fit males will probably be better at staying on board the bucking lowermost male than small males. The latter will be correspondingly less able to retain “top spot” upon a large rival and less able to throw off a large rival when mounted by one. Females are therefore more likely to end up with a large mate than a small

one. This would also be the case if the function of face-offs is to establish exclusive use of large areas of water lily leaves.

Statistical evidence to test the theory outlined above is clearly highly desirable. It would be difficult to obtain, given the difficulty of making sufficiently numerous and detailed observations over a broad area of deep water, but would certainly be possible given enthusiasm and dedication in any would-be researcher.

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References

- Bartlett J. 1988. Male mating success and paternal care in *Nicrophorus vespilloides* (Coleoptera: Silphidae). *Behavioural Ecology and Sociobiology* 23:297–303.
- Borgia G. 1981. Mate selection in the fly *Scatophaga stercoraria*: female choice in a male-controlled system. *Animal Behaviour* 29:71–80.
- Brown L, Macdonnell J, Fitzgeralds VJ. 1985. Courtship and female choice in the horned beetle *Bolitotherus cornutus* (Panzer) (Coleoptera: Tenebrionidae). *Annals of the Entomological Society of America* 78:423–427.
- Cade WH. 1979. The evolution of alternative male reproductive strategies in field crickets (*Gryllus integer*). In: Blum MS, Blum NA, editors. *Sexual selection and reproductive competition in insects*. London: Academic Press. p 343–379.
- Crespi BJ. 1986. Size assessment and alternative fighting tactics in *Elaphrothrips tuberculatus* (Insecta: Thysanoptera). *Animal Behaviour* 34:1324–1335.
- Eberhard WG. 1988. Paradoxical post-coupling courtship in *Himantigera nigrifemorata* (Diptera: Stratiomyidae). *Psyche* 95:115–122.
- Emlen ST, Oring LW. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197:215–222.
- Hissmann K. 1991. Phonotaxis of male crickets (*Gryllus campestris*) in a field population as an indication of territoriality (Orthoptera: Gryllidae). *Journal of Insect Behavior* 4:675–681.
- Johnson LK. 1982. Sexual selection in a brentid weevil. *Evolution* 36:251–262.
- McAlpine DK. 1972. Observations on the sexual behaviour of some Australian Platystomatidae (Diptera, Schizophora). *Records of the Australian Museum* 29:1–9.
- Moulds MS. 1977. Field observations on behaviour of a north Queensland species of *Phytalmia* (Diptera: Tephritidae). *Journal of the Australian Entomological Society* 16:347–352.
- Otte D, Joern A. 1975. Insect territoriality and its evolution: population studies of desert grasshoppers on creosote bushes. *Journal of Animal Ecology* 44:29–54.
- Preston-Mafham K. 2001. Resource defence mating system in two flies from Sulawesi: *Gymnomerius fuscus* Wiedemann and *Telostylinus* sp. near *duplicatus* Wiedemann (Diptera: Neriidae). *Journal of Natural History* 35:149–156.
- Preston-Mafham R, Preston-Mafham K. 1993. *The encyclopedia of land invertebrate behaviour*. London: Blandford Press. 320 p.
- Simmons LW. 1986. Female choice in the field cricket *Gryllus bimaculatus* (De Geer). *Animal Behaviour* 34:1463–1470.
- Spieth HT. 1981. *Drosophila heteroneura* and *Drosophila silvestris*: head shapes, behaviour and evolution. *Evolution* 35:921–930.