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SHORT COMMUNICATIONS

Drosophila Larval Foraging Behaviour: Digging

A *Drosophila* larva feeds by shovelling food with its mouth hooks and moves by alternately extending its anterior and retracting its posterior end. Foraging behaviour reflects the relative amounts of feeding (shovelling), and locomotor (crawling) behaviour performed. Sokolowski (1980) identified a behavioural polymorphism in *Drosophila melanogaster* larval foraging patterns: A 'rover' larva had a high crawling score and covered a large area while foraging on a yeast-covered petri dish, whereas a 'sitter' larva had a low crawling score and covered a relatively smaller area. Genetic analysis showed that differences in these forager types could be attributed to the second pair of chromosomes.

Drosophila larvae do not only travel in a horizontal plane, they may also move downward through the medium. The tunnelling of larvae has been thought to be a measure of microdispersal. Barker (1971), in studying the dispersal of *D. melanogaster* and *D. simulans* larvae during competition, showed that *D. simulans* larvae used the lower portion of the medium, whereas *D. melanogaster* larvae used the upper portion. Differences in dispersal through the medium may exemplify niche separation in these sibling species, which are commonly known to coexist in nature (Parsons 1975).

The crawling component of locomotor behaviour has been shown to have a genetic basis (Sewell et al., 1975; Sokolowski 1980). Polygenic control of digging behaviour has been shown by Godoy-Herrera (1977, 1978) who studied variation in digging behaviour in strains of *D. melanogaster* and successfully selected for low digging activity.

Although strong evidence for the genetic control of crawling and digging behaviours has been previously cited, no study has ever shown joint genetic influences on these foraging behaviours. It is of interest to determine whether the 'rover' and 'sitter' larval foragers show differences in their tendency to dig into the medium.

The four stocks used in this study were designated W2W3, E2E3, E2W3 and W2E3. A breeding scheme that utilizes the presence of cross over suppressors to permit substitutions of intact second or third chromosome pairs from one stock into another is described in Sokolowski (1980). The use of this chromosome assay technique in behaviour genetic analysis is described in Hirsch & Ksander (1969). The reconstructed stocks were W2E3 and E2W3. The latter stock would have the same second chromosome pair as E2E3 but the same third pair as W2W3.

The method developed by Godoy-Herrera was employed to study digging behaviour. His technique is to divide the medium into two layers, the lower one darkened with charcoal and the upper one left undarkened. Larvae that dug as deep as the charcoal medium ('diggers') exhibited a stained digestive tract compared with larvae that stayed in the upper layer of regular medium ('non-diggers'). Two categories of larvae were distinguished, 'diggers' or stained larvae and 'non-diggers' or unstained larvae. The division of digging behaviour into morphs ('digger' and 'non-digger') involves an arbitrary, operational point of separation to facilitate the discussion of correlations, if any, between digging and crawling behaviour in the 'rover' and 'sitter' stocks.

Test vials, 2 cm in diameter and 9.5 cm high were filled with 4 ml of dead-yeast agar culture medium that was darkened with finely powdered charcoal using a concentration of 3 g of charcoal/400 ml of medium. After the darkened medium had hardened, 2 ml of undarkened medium was added.

Fifty 5–10-day-old flies of each stock (W2W3, E2E3, W2E3 and E2W3) were allowed to lay eggs on circular plugs (2.4 cm in diameter and 0.7 cm high) of medium for a period of 5 h beginning at 1200 hours. After this period a dissecting needle was used to transfer 10 eggs to each test vial. Eggs were placed at random on the surface of the test medium. The test vials were maintained at 22 ± 1 C and under a light cycle of 12 L : 12 D; the lights were turned on at 0800 hours. Ninety-six hours after hatching, the larvae were separated from the medium, washed in distilled water, and scored as either stained or unstained. A larva was scored as stained if any darkened medium could be seen along any section of the digestive tract.

All data in the form of percentages were transformed using an arcsine $\sqrt{}$ transformation. After the transformation, a test for the equality of percentages (Sokal & Rohlf 1969), was performed to compare the percentage of larva surviving and the percentage of stained larvae in the four stocks (Table I).

The mean percentage of stained larvae/vial within each 'rover' and 'sitter' stock was not significantly different at the $P = 0.001$ level. However, the mean percentage of stained larvae/vial between all but one comparison of 'rover' and 'sitter' stocks were significantly different ($P < 0.0001$), indicating that the second pair of chromosomes contributes significantly to the differences in digging behaviour in these stocks. The exception was the non-significant difference ($P = 0.1$) between the W2E3,

Table I. Digging Behaviour

Forager type	No. of vials	Total no. larvae counted / Total no. larvae added	% larvae surviving	Arcsine $\sqrt{}$ of % larvae surviving	Mean % stained larvae	Arcsine $\sqrt{}$ mean % stained larvae
Rover						
W2W3	23	173/230	75.2	60.1	73.0	58.7
W2E3	15	72/150	48.0	43.8	59.8	50.6
Sitter						
E2E3	21	125/210	59.5	50.5	32.7	34.9
E2W3	21	151/210	71.9	58.0	48.0	43.8

rover' and the E2W3, 'sitter' stocks. This result indicates that the third pair of chromosomes as well as the second pair influences 'digging' behaviour.

The numbers of vials sown for each stock is shown in Table I. Since each vial was sown with 10 eggs, stock 'survivorship' estimates (a composite of egg hatchability and larval survivorship) could be calculated. In all cases, stocks sharing the W3 chromosomes showed significantly higher 'survivorship' ($P < 0.008$) than stocks with the E3 chromosomes.

Godoy-Herrera suggested that inter-strain differences in digging patterns provide evidence for the genetic control of digging behaviour. Differences in the digging behaviour of the four stocks tested in this study were consistent with his interpretation. The tendency for 'rover' larvae to perform more digging and crawling behaviour than 'sitter' larvae reflects some joint genetic influences in crawling and digging behaviours that are to some extent caused by differences in the second pair of chromosomes. However, in contrast to crawling behaviour where major differences in this behaviour could be attributed to the second pair of chromosomes, the genetic control of digging behaviour is also affected by the third pair of chromosomes.

In a series of natural population studies, Sokolowski (1980, in press) showed that both 'rover' and 'sitter' forager types were found within a single pear. If natural populations of 'rovers' also tend to dig more than 'sitters,' then greater dispersal (both horizontal and downward) would be expected in larvae of the 'rover' morph. Because the adult female *D. melanogaster* lays her eggs on or close to the surface of the medium, the amount the larvae dig into the medium measures the microdispersal. The ability of a larva to utilize and compete for a distant food resource may depend on the amount of digging and crawling behaviour it exhibits.

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Mate Takeover and Possible Infanticide by a Female Northern Jacana (*Jacana spinosa*)

Birds in the pan-tropical family Jacanidae breed on floating vegetation in marshes. Female jacanas employ a suite of tactics that make their reproductive strategy unique among female vertebrates: attainment of larger body size than males, defence of limited breeding habitat, simultaneous reproduction with up to four mates, and lower investment in offspring care than males (Jenni 1974; Jenni & Betts 1978; Ridley 1978). Observations that I made during a study of northern jacanas (*Jacana spinosa*) in Costa Rica reveal that the reproductive strategy of female jacanas sometimes involves aggressive takeovers of mates from neighbouring territorial females and suggest that females may destroy the current offspring of mates acquired by takeovers, as detailed below.

At 0605 hours on 25 June 1981, a bigamous territorial female, here designated F1, landed within the territory of a bigamous neighbouring female (F2), who flew to the intruder and attacked her. The females beat each other with their wings and pecked with their bills. After two minutes of fighting, F2 retreated under water and swam away. F2 had fought with a third female in an adjacent territory just before this fight and perhaps had been weakened enough to enable F1 to defeat her.

One of F2's mates, male M2a, stood near F1 and F2 as they fought. He attacked F1 when his mate disappeared but failed to evict her. F1 only occasionally retaliated against M2a's attacks by attempting to peck him. In contrast to M2a's behaviour, F1 invited copulation from him and made nest-construction movements.

M2a had a nest with a full clutch of eggs. He increased the intensity of his attack as F1 wandered nearer his nest, but this had no effect. He then performed a distraction display: he crouched and drooped his wings (as if brooding), and slowly rocked the wings. This behaviour is easily distinguished from other displays of jacanas. M2a gave two more distraction displays to F1 during the two hours of observation; both occurred while F1 was near his nest. F1 appeared to ignore the display in all three instances.

The defeated female had one other mate (M2b), whose young offspring were concealed in emergent vegetation after the fight between F1 and F2. F1 encountered M2b during her inspection of F2's territory. M2b attacked F1 when she approached the vicinity of his offspring. His vocalizations apparently summoned his defeated mate, who reappeared and fought F1 again, only to retreat under water once again. M2b continued the attack without his mate but F1 retaliated by chasing him from his territory. He returned shortly thereafter, however, and was still present when observations were terminated at 0800.

F1 was at M2a's nest when observations began the following day at 0900, yet M2a was no longer hostile toward her. A check of the nest at 1100 revealed it to be empty. The pair courted on this day and F1 began laying