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Drosophila males provide a material contribution to offspring sired by other males

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Abstract. In *Drosophila mojavensis* (Patterson & Crow) the opportunity for cuckoldry is great due to female remating, storage of sperm and the transfer of a material donation from the ejaculate. Using a radioisotope and a genetic marker, it was possible to show that not only do first males provide an ejaculate benefit to progeny sired by subsequent males but that the first male's progeny also receive material from the second male.

Key-words: *Drosophila*, cuckoldry, parental contributions

Introduction

The reproductive behaviour of *Drosophila mojavensis* (Patterson & Crow) differs from that of *Drosophila melanogaster* (Meigen) in a number of ways. One striking contrast is the higher frequency at which *D. mojavensis* females have been observed to remate in the laboratory (Markow, 1982). *D. mojavensis* males provide a substantial material contribution to female somatic tissue and to developing oocytes through their ejaculate (Markow & Ankney, 1984). While a small amount of ejaculate-derived protein is also detectable in *D. melanogaster* females, its level is considerably less than that observed in *D. mojavensis* and it probably represents those peptides synthesized by male accessory glands which stimulate oviposition (Chen & Buhler, 1970). With *D. mojavensis* females remating frequently to males who provide nutrients to oocytes, the potential for cuckoldry is clearly high. The literature dealing with the delivery of material benefits by males focuses on the problem that female remating poses for the first male (Smith, 1984; Thornhill & Alcock, 1983; Borgia, 1979; Trivers, 1972). The experiments reported here concern two questions about mating in *D. mojavensis*. Does the first male contribute nutrients to progeny sired by subsequent mates? Do progeny from a first mating receive any contribution from non-parental males

that mate with their mother after their father had inseminated her? The results show that for *D. mojavensis* the first male definitely provides nutrients to oocytes that he does not fertilize. However, progeny sired by the first male may receive nutrients from subsequent male partners of the female, so that the first male's material contribution may be partially recompensed by donations to his offspring by other males.

Materials and methods

Flies utilized in this study were derived from a multi-female collection made at the Desemboque region of Sonora, Mexico, in 1980. Five-day-old females homozygous for a spontaneously arising recessive mutant causing dark eyes ('adobe'), were mated to two males 24 h apart. Both males were 9 days old. One male was wild-type and had been reared on medium containing ^{14}C amino acids by placing 50 eggs in shell vials containing 1.5 g of food medium made up with 70 Ci of a mixture of ^{14}C labelled amino acids (ICN10147). The other male was of the same mutant eye-color genotype as the female. In experiment 1, females were mated first to the wild-type ^{14}C labelled males and then to the mutant. In experiment 2, females were mated to the mutant male first and then to the ^{14}C labelled wild-type male. After the second mating, females in groups of five were allowed to oviposit on fresh medium supplied daily. Eggs were collected from four groups of females every 24 h for 5 days after the second mating. Each day all eggs from 20 females were pooled and from each collection, 100 eggs were selected at random and placed in a single scintillation vial containing 100 ml of ScintiGest tissue solubilizer. Eggs were crushed with glass rods and allowed to digest for 24 h at 50°C. Glacial acetic acid (2.5 ml) was added to neutralize the solution. Then 5 ml of ScintiVerse I scintillation fluid were added and each vial was allowed to sit for an additional 24 h prior to counting for 10 min/vial. The remaining eggs were allowed to develop into adults and their eye colour was scored to assess paternal genotype. Three replicates were made of each experimental group.

Table 1. Radioisotope levels in oocytes of twice-mated females and genotype of progeny. Mean disintegrations per minute (DPM) are from three replicates of 100 oocytes per replicate (a standard quench curve was prepared to enable the conversion of counts per minute [cpm] to disintegrations per minute).

	Day after second mating	Total number of adult offspring	% wild type	% dark	$\bar{x} \pm \text{SE DPM}$ in eggs
Experiment 1	1	291	21.6	78.4	89.5 \pm 7.8*
1st ^{14}C wild type	2	268	38.8	61.2	106.4 \pm 5.1*
2nd dark eye	3	275	36.4	63.6	71.3 \pm 6.8*
	4	283	37.1	62.9	57.3 \pm 10.0
	5	149	47.7	52.3	44.4 \pm 8.1
Experiment 2	1	247	80.6	19.4	111.2 \pm 8.8*
1st dark eye	2	282	70.2	29.8	122.5 \pm 8.8*
2nd ^{14}C	3	187	67.9	32.1	103.4 \pm 7.8*
	4	160	63.1	36.9	87.6 \pm 8.2*
	5	126	55.5	44.5	95.5 \pm 10.0*

* $P < 0.01$, significantly different from unlabelled control eggs, $\bar{x} \pm \text{SE DPM} = 43.2 \pm 6.0$.

Results and discussion

The amounts of male-derived label and the proportion of progeny sired by the first and second males are reported in Table 1. From experiment 1, it is clear that males mating first contributed labelled material to eggs fertilized by second males; i.e. eggs collected prior to the second mating had the same amount of label ($\bar{x} \pm \text{SE DPMs } 102.9 \pm 7.1$) as day 1 and 2 eggs which consisted largely of the second males progeny. The contribution was highest to eggs ovipositioned during the first 2 days after the second mating in contrast to the suggestion by Wickler (1985) that in all insects, male-derived material requires 3 days to appear in any female tissues. However, by the fourth day, the amount of label in eggs was no longer significant. In experiment 2, a significant amount of label from the second male appeared in the first eggs, even though 20% of these eggs were fertilized by the first male. This same level of radiolabel appeared in eggs from the second and third day's collection, when an even greater proportion (30%) of the eggs were fertilized by the first male.

Male *Drosophila mojavensis* provide a material contribution in their ejaculate that is used by females to produce oocytes. Females mate several times and progeny sired by the second male receive nutrients from the first male. But progeny sired by the first male also receive a contribution from the second male and this tends to reduce the 'losses' experienced when one male's donations are used for eggs fertilized by other males. This finding might mitigate the importance assumed for cuckoldry as a selective force in mating system evolution.

Male donation in *D. mojavensis* may constitute a mating effort that is incidentally used by the female in manufacturing oocytes. The distinction between donations which constitute mating effort vs parental effort has not yet been critically evaluated in *Drosophila* but is being considered for katydids (Gwynne, 1986). Males mating first clearly donate material to progeny sired by males mating later. Males that provide material to offspring should display adaptations that improve the probability of their donation being utilized by their biological descendants. For *D. mojavensis* the male ejaculate contributes to the formation of a copulatory plug known as the 'insemination reaction' (Patterson & Stone, 1952) and physically impedes remating and oviposition for about 10h. Mating behaviour is strongly diurnal and the mass disappears by the following morning at which time, in the laboratory, females are observed to remate. If no plug is formed, females will remate sooner and the first male's fitness will decrease. Inducing the formation of a copulatory plug increases the refractory period and thereby increases the probability that a male will fertilize more eggs.

An additional 'paternity' adaptation is suggested by laboratory studies in which males presented with virgin and mated females preferentially courted the virgins, unless the mated female had copulated sufficiently long ago to ensure that her new mate would sire over 95% of subsequent progeny (Markow, 1982). The second male benefits by early discrimination between potentially desirable or undesirable matings and as an effect, this behaviour benefits the first male by reducing the probability that the female will

remate before utilizing his sperm. Despite these apparent adaptations, most male *D. mojavensis* probably become 'stepfathers' during their lives, i.e. contribute to offspring sired by other males (Wickler, 1985), because females remate frequently and store sperm. However, the impact of this problem for males mating earlier is lessened by the fact that, contrary to previous expectations (Borgia, 1979; Thornhill & Alcock, 1983), the eggs fertilized by first males receive a contribution from males mating later.

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