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SUPPRESSION OF *DROSOPHILA ANANASSAE* FLIES OWING TO INTERSPECIFIC COMPETITION WITH *D. MELANOGASTER* UNDER ARTIFICIAL CONDITIONS

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ABSTRACT. Interspecific competition between two species of *Drosophila: D. ananassae* and *D. melanogaster* was studied at the larval and adult stages. It was found that when *D. ananassae* and *D. melanogaster* adult flies were co-cultured, very few *D. ananassae* offspring could be recovered in the first generation. To investigate the reasons of *D. ananassae* apparent inhibition, mating behavior of *D. ananassae* in the presence of *D. melanogaster* was observed and it was found that the number of matings deviated significantly from those recorded when it was kept alone. To determine larval development of *D. ananassae* after being initially exposed to *D. melanogaster*, the females of the two species were separated in different food bottles after 3 days of being kept together. Good *D. ananassae* cultures could be recovered indicating that initial exposure of *D. ananassae* to *D. melanogaster* did not hamper its egg laying capacity or eclosion. However, if they remained together, no *D. ananassae* could be recovered from larval diet, suggesting that either *D. melanogaster* adults interfered with fertilization or egg-laying, or their larvae eliminated competitors. To see whether there is larval competition, polytene chromosomes of 54 third instar larvae were analyzed out of which only 5.56 percent were found to be *D. ananassae.* Thus, if a few eggs are laid by *D. ananassae* and they develop, all the while facing competition from *D. melanogaster* and till the third instar larval stage is reached, there is almost complete elimination of *D. ananassae*. Thus, interspecific competition exists at all stages of life cycle and few if any *D. ananassae* flies emerge.

Key words: Interspecific competition, mating propensity, co-culture, fecundity, larval competition, *D. ananassae*.

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RESUMEN. Se estudió la competencia interespecífica entre dos especies de *Drosophila*: *D. ananassae* y *D. melanogaster* en estado larvario y adulto. Se encontró que al criar simultáneamente adultos de *D.*

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ananassae y *D. melanogaster*, muy poca progenie de primera generación de *D. ananassae* podia recuperarse. Para investigar las causas de la aparente inhibición de *D. ananassae*, se observó el comportamiento de apareamiento de *D. ananassae* en presencia de *D. melanogaster* y se observó que el número de apareamientos se desvió significatívamente de aquel registrado cuando esta especie se mantuvo sola. Para observar el desarrollo larvario de *D. ananassae* después de la exposición a *D. melanogaster*, hembras de ambas especies fueron separadas en botes de alimento después de tres días de confinamiento conjunto. Se obtuvieron buenas crías de *D. ananassae*, indicando que la exposición de *D. ananassae* a *D. melanogaster* no afectó su capacidad de oviposición ni su fertilidad. Sin embargo, cuando ambas especies permanecieron juntas, no se recuperó *D. ananassae* de la dieta larvaria lo que sugiere que los adultos de *D.melanogaster* interfirieron con la fertilización u oviposición, o bien sus larvas eliminaron la competencia. Para establecer la existencia de competencia larvaria se examinaron los cromosomas polténicos de 54 larvas de tercer estadio entre las cuáles solo el 5.56 por ciento resultaron ser de *D. ananassae*. Por lo tanto, si algunos huevos son depositados por *D. ananassae* y se desarrollan, éstos enfrentan la competencia de *D. melanogaster* durante todo el desarrollo y hasta el tercer estadio, llegando a la casi total eliminación de *D. ananassae*. Existe competencia interespecifica en todas las etapas del ciclo de vida resultando en una casi nula emergencia de *D. ananassae*.
Palabras clave: Competencia interespecífica, co-cultivo, fecundidad, competencia larval, *D. ananassae*.

INTRODUCTION

Natural selection often operates through competition, allowing various forms to survive and establish under certain environmental conditions. It tends to eliminate, gradually or rapidly, forms exploiting identical niches. Charles Darwin (1859) in his book "Origin of species" stated that Intraspecific and interspecific competition among organisms are a part of natural selection. This competition can be the result of high reproductive potential of some species when compared to the environmental carrying capacity. The most severe form of interspecific competition exists when organisms of two species have the same requirements. On the basis of theoretical equations, Lotka (1925) and Volterra (1926) independently predicted that two species with identical needs and habits cannot survive in the same place if they compete for limited resources. If both types are found together in nature, they must differ in their ecology, or else there are fluctuations in the environment, favoring first one and then the other. Experiments on interspecific competition between similar species have also demonstrated the validity of this theory (Connell 1981; Crombie 1947; Denno *et al.* 1995; Gause 1934; Hochkirch & Groening 2012; Luan *et al.* 2012; Zhang *et al*. 2011; Zimmering 1948). Careful analysis of the instances in which both species survive has shown that they occupy slightly different niches (Gause 1934; Crombie 1947). According to Kohn and Orians (1962) competition between species reveals ecological differences permitting coexistence of stable populations of closely related species of various kinds of animals.

Drosophila turns out to be the apt model system for studying interspecific competition, because in the genus *Drosophila* one finds a large number of species, some

showing high degrees of morphological and ecological similarities and also close genetical relationships (Tantawy 1964). No wonder, exhaustive studies have been done, especially involving sibling species of this genus to study interspecific competition (Nunney 1990). A practical way of studying interspecific competition in the laboratory is by co- culturing two species together in large population cages or in culture bottles. One may simply study the effect of co-culturing on the fecundity of the species involved or one can also check the effect of altering various ecological conditions such as larval density, temperature etc. on the fecundity of co-cultured populations of two species. Merrell (1951) cultured *D. melanogaster* and *D. funebris* together in food bottles and found that the proportion of *D. funebris* eggs reaching pupation decreased significantly in mixed larval populations. Interspecific competition between *D. melanogaster* and *D. simulans*, was studied in much detail by Barker & Podger (1970). They examined the effects of larval density and short-term adult starvation on fecundity, egg hatchability and adult viability. It was found that significant effect of larval density on fecundity was probably mediated through effects on adult body weight. *D. melanogaster* females raised in mixed species cultures were less fecund than those from pure cultures, while *D. simulans* showed the reverse effect. Increasing the larval density of the two species at 15 °C and 25 °C temperatures, causes a progressive reduction in per cent hatching (Tantawy & Soliman 1967; Miller 1964; Chiang & Hodson 1950; Birch 1955). Boggild & Keiding (1958) in their studies on house fly larvae found that harmful effects of crowding on adult emergence result from an increased incidence of collisions between larvae. This causes the metabolic rate to be increased and thus reduces the fraction of ingested food available for tissue formation. Tantawy & Soliman (1967) found that there was a gradual elimination of *D. simulans* by *D. melanogaster* in the two cages, irrespective of their initial percentage at 25 °C. These results also supported the results of Moore (1952) and Barker (1963). The results from cages kept at 15 °C indicate that the outcome of competition at 15 °C is completely different from that at 25 °C. At 15 °C there is an increase in *D. simulans* at the expense of *D. melanogaster*. A similar experiment was done by Montchamp-Moreau (1983) involving the same species. The optimum temperature for *D. simulans* was found to be 20 °C and for *D. melanogaster* it was 25 °C as while at 25 °C *D. melanogaster* eliminated *D.simulans* and at 20 °C the reverse occurred in mix culture cage populations. *D. pseudoobscura* and *D. subobscura*, two species sympatric in the west coast of North America exhibited competition in the laboratory to such an extent that *D. subobscura* was completely eliminated in just a few generations of their being co-cultured. The outcome was no different when they were reared at different temperatures (Pascual *et al*. 1998).

In nature two competing species do not face a straight battle and there may be other species too which have their own impact on the competition. For example it was

found that competition between two closely related species *D. melanogaster* and *D. hydei* was affected by a third distant species of an entirely different kingdom *Aspergilus niger* (Hodge *et al*. 1999). Not only other species but components of interspcific competition are also known to be affected under different environmental conditions, creating a geographic mosaic of outcomes (Joshi 2004; Joshi & Thompson 1995). Price *et al.* (2012) found that presence of mating rivals cause males of *D. pseudoobscura* to modulate sperm transfer through an increase in sperm transfer, alteration in ejaculate composition etc. In *D. melanogaster* Bretman *et al.* (2009) reported that males kept with rivals prior to mating, mated for a longer duration.

The present study aimed at comparing the viability of two species of *Drosophila, i.e*. *D. ananassae* Doleschall and *D. melanogaster* Meigen when they are cultured together in food bottles. Taxonomically both species belong to the *melanogaster* species group of the subgenus *Sophophora*. *Drosophila ananassae* falls in the *ananassae* subgroup and the *ananassae* complex and *D. melanogaster* belongs to the *melanogaster* subgroup (Bock & Wheeler 1972). Distribution wise both species are cosmopolitan. *D. melanogaster* being semi-domestic, occurring in orchards and gardens and *D. ananassae*, a domestic species is found at a closer proximity to human habitation, such as fruit markets, kitchens etc. It occupies a unique status among the *Drosophila* species because of certain unusual genetical features (Singh 2010). The morphological features of the two species enable easy distinction of the two species and their sexes as males of *D. melanogaster* possess black abdominal tip and a characteristic pattern of sex comb. The females of *D. melanogaster* are larger in size with more swollen abdomen and black thin stripes at abdominal segment junctions. *Drosophila ananassae* males do not possess black coloration at the abdominal tip and they have a number of thick hairs on the first and second tarsal segments forming a diffused sex comb pattern. The females of *D. ananassae* are light in color as they lack black abdominal stripes. Earlier experiments on interspecific competition involving *D. melanogaster* have been done with its sibling species. However, *D. ananassae* and *D. melanogaster* are quite distinct. Therefore, it would be interesting to see the degree of competition that exists between the two, and whether they are able to thrive in presence of each other. Experiments were conducted to determine at which stage(s) of the life cycle interspecific competition occurs between the two species.

MATERIAL AND METHODS

This study was done by taking two wild type species of *Drosophila*, *D. ananassae* and *D. melanogaster*. These two stocks have been reared in our laboratory for the last three years. *D. ananassae* was originally collected from Ranchi (Jharkhand state) and *D. melanogaster* was collected from Varanasi (Uttar Pradesh), as adult forms by net sweeping. The stocks of both species were maintained in the laboratory on simple

yeast-agar culture medium at 24ºC with a 12 hours cycle of light and darkness.

Virgin male and female flies from both species were collected and aged. Twenty pairs (ten pairs from each species) of seven day-old flies were then kept together in 250 ml cylindrical culture bottles (height 15 cm, base diameter 5 cm, mouth diameter 2.5 cm) containing 50 ml of food. After three days, all flies were discarded. Flies emerging from the bottles were separated according to species and sex and counted. Pure cultures were established to serve as controls. The number of progeny emerging from such control cultures were also counted. The experiment was repeated five times.

Mating behavior of *D. ananassae* and *D. melanogaster* flies was observed in the presence of each other. Ten pairs of seven day-old virgin male and female flies of both species were kept in an Elen-Wattiaux mating chamber and observed for one hour. When a pair commenced mating it was aspirated out. As a control, 10 pairs of *D. ananassae* and 10 pairs of *D. melanogaster* were observed separately in the mating chamber. The total number of matings (formed couples) and the time interval in minutes from release to pair formation was recorded. Six replicates of each mating combination were carried out. All mating experiments were done between 6:00 am to 11:00 am, as *Drosophila* exhibits peak mating activity during the morning hours. One way ANOVA was done to test whether there was any difference in the mean number of matings among the four groups, (*D. ananassae* alone, *D. ananassae* in presence of *D. melanogaster*, *D. melanogaster* alone and *D. melanogaster* in presence of *D. ananassae*). Bonferroni t- test were used for pair wise comparison between the groups.

Ten pairs of seven day-old virgin male and female flies of both the species were kept together in culture bottles (as described above). After three days males were discarded and females of each species were kept separately in fresh culture bottles, and allowed to lay eggs. They were not exposed to males of their own species so that the progeny produced was only the outcome of matings that occurred when both the species were housed together. Also the effect of initial exposure of the two species to each other, on their progeny recovery could be determined.

The two species were also co-cultured in the food bottles to study larval competition. Ten pairs of seven day-old virgin male and female flies of both species were kept in fresh food bottles for three days, after which the flies were discarded. Polytene chromosome preparations of the third instar larvae were made by lacto-aceto-orcein method, to identify whether the larvae were *D. ananassae* or *D. melanogaster*.

RESULTS

Drosophila ananassae flies were almost eliminated in number during the first generation itself, when reared in culture bottles along with *D. melanogaster* adults as very few *D. ananassae*, males could be recovered. The numbers of *D. melanogaster* (both

males and females) counted in the bottles are given in **Table 1**. Also, the numbers of flies counted in the control sets are shown.

In the second set of experiments, where males and females of both the species were observed in Elen-Wattiaux mating chamber, it was found that males of both species largely courted females of their own species. However, occasionally, *D. melanogaster* males would unsuccessfully court a *D. ananassae* female. It was also observed that *D. melanogaster* males would interfere with the courtship rituals of *D. ananassae* males and chased away a courting *D. ananassae* male. The results of one way ANOVA (**Table 2.**) show that there is a significant difference between the mean number of matings in *D. ananassae* and *D. melanogaster* when they are confined alone in the mating chamber and when they are kept in presence of each other. Bonferonni t-tests (**Table 3.**) proved that there are significant reductions in the number of *D. ananassae* matings, when it is kept with *D. melanogaster*. Therefore the presence of *D. melanogaster* affects the mating propensity of *D. ananassae*. **Figure 1** shows that as the number of *D. melanogaster* pairs decreases in the mating chamber after being aspirated out when a pair commenced mating, the number of matings of *D. ananassae* increases. The average data of the six sets of mating experiments with ten pairs of *D. ananassae* in the presence of 10 pairs of *D. melanogaster* was used. **Figure 2**

Table 1. Number of adult progeny recovered from pure and mixed adult cultures of *D. ananassae* and *D. melanogaster* in bottles containing 50 ml of diet. (Rows represent different replicates, N=5).

Pure culture				Mixed culture			
D. melanogaster		*D. ananassae*		*D. melanogaster*		*D. ananassae*	
♂	♀	♂	♀	♂	♀	♂	♀
84	28	65	112	103	62	18	0
72	80	150	105	125	136	0	0
114	90	40	34	94	75	0	0
188	85	260	167	250	203	0	0
314	85	473	339	289	101	25	2

Table 2. Results of one-way ANOVA comparing the number of matings among four mating combination groups of 7-day old adult flies i. e. *D. ananassae, D. melanogaster, D. ananassae in* presence of *D. melanogaster* and *D. melanogaster* in presence of *D. ananassae*

Source of variation	*df*	SS	MS	F
Between groups	3	70.79	23.59	21.61*
Within groups	20	21.83	1.09	
Total	23	92.62		

*P < 0.001

Table 3. Pair wise comparison of the number of matings, under different conditions in *D. ananassae* and *D. melanogaster* Bonferroni t-test

Bonferroni t-test		
ana(s) vs. *ana*(m)*	*ana*(s) vs. *mel*(s)	*ana*(s) vs. *mel*(m)
ana(m) vs. *ana*(s)*	*ana*(m) vs. *mel*(s)*	*ana*(m) vs. *mel*(m)*
mel(s) vs. *ana*(s)	*mel*(s) vs. *ana*(m)*	*mel*(s) vs. *mel*(m)
mel(m) vs. *ana*(s)	*mel*(m) vs. *ana*(m)*	*mel*(m) vs. *mel*(s)

*$P < 0.05$, *ana*(s) *D. ananassae* alone, *ana*(m) *D. ananassae* in presence of *D. melanogaster*, *mel*(s) *D. melanogaster* alone, *mel*(m) *D.melanogaster* in presence of *D. ananassae.*

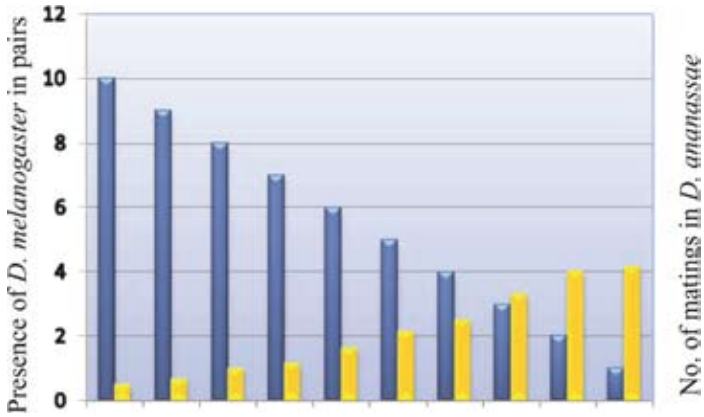

Figure 1. Number of formed couples of *D. ananassae* (yellow bars) according to number of *D. melanogaster* (blue bars) pairs (10 to 1) remaining in mating cages.

shows the effect of time on mating success in *D. ananassae* and *D. melanogaster* in different conditions. The graph was constructed with the pooled data of the six sets of mating experiments. It depicts that the number of matings in *D. ananassae* in first 10 minutes is very high, when they are alone in the mating chamber, compared to when they are confined with *D. melanogaster*. In the next 50 minutes, however, the number of matings remains almost the same under the two conditions. For *D. melanogaster,* the number of matings was found to be less when alone than when in the presence of *D. ananassae*.

Initial exposure of the two species to each other does not affect fecundity or larval development, as good *D. ananassae* and *D. melanogaster* cultures could be recovered from culturing females which had been exposed to males of the other species earlier.

From the mixed culture of the two species, larvae were also analyzed to identify which species they belonged to by observing their salivary gland chromosomes.

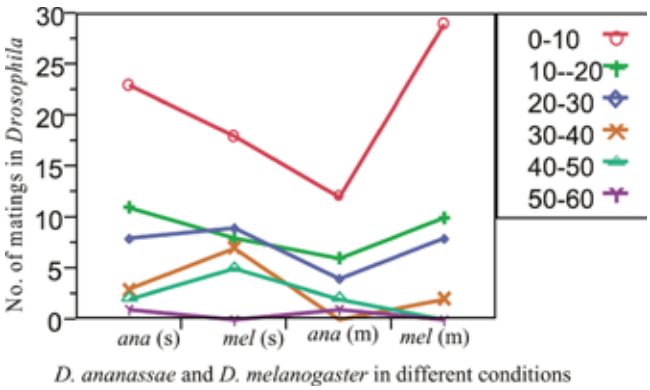

Figure 2. Total number of observed matings per species at different 10 min time intervals (colored lines) in cages of *D. ananassae* and *D. melanogaster* held alone (s) in pure specific cohorts or in competiton with each other (m) in mixed cohorts.

Out of fifty four larvae examined only three were found to be *D. ananassae* and the remaining larvae were all identified as *D. melanogaster*. Thus, bulk mortality of *D. ananassae* occurs in or before the third instar larval stage, with only a handful remaining alive to reach the pupal stage and even less if any emerging as adults.

DISCUSSION

Our experiments demonstrate that *D. ananassae* flies cannot thrive when confined in the small space of a food bottle with *D. melanogaster*. A finding consistent with observation of their habits in their natural habitat (Bock & Wheeler 1972), where in the presence of one, the other prefers another niche. It has also been observed by the authors that in nature when there is abundance of *D. melanogaster* in a certain place, *D. ananassae* is found fewer in number.

To go deeper into understanding the nature of interspecific competition that exists between the two species, we planned different experiments and found that competition starts right at the level of courtship rituals and matings and lasts until the late larval stages and perhaps beyond until *D. ananassae* is eliminated completely or its development severely hindered. Though, it is not sure what the outcome would have been if the two species were co-cultured in larger enclosures, one thing is certain, if *D. ananassae* is almost eliminated in the first generation in food bottles, in larger enclosures too it would not take a number of generations for it to disappear.

Fitness of *D. ananassae* is reduced in presence of *D. melanogaster* as *D. melanogaster* males interfere with the courtship rituals of *D. ananassae* males and prevent fertilization. Therefore in the presence of *D. melanogaster*, *D. ananassae* mates more infrequently than normal.

D. ananassae females which have succeeded in mating, may face competition from *D. melanogaster* females for egg laying sites. Given that when they were exposed initially to *D. melanogaster* and separated from them latter, their egg laying was normal and resulted in good larval recovery. Therefore, fitness of *D. ananassae* is affected only as long as *D. melanogaster* is present.

It was not possible for us to utilize the first and second instar larval stages for species identification, as they are small, present deep inside the food and their polytene chromosome preparations are not very good. However, the fact that a few *D. ananassae* third instar larvae could be identified through polytene chromosomes, indicates that some *D.ananassae* larvae are able to fight and withhold the battle until the third larval stage, facing a tough competition from *D. melanogaster*.

We observed that out of few progeny of *D. ananassae* reaching the third instar larval stage owing to larval competition, fewer pupate and lesser hatch as flies. Similar result was found by Merrel (1951) on *D. funebris* and *D. melanogaster*. This may indicate that individuals surviving to stage display lower survival probabilities than those stemming from pure cultures.

A very interesting observation was that while in *D. ananassae* the number of mating is reduced in presence of *D. melanogaster*, with *D. melanogaster* just the opposite occurs, that is *D. melanogaster* mates more rapidly in the presence of *D. ananassae* than when held alone at similar densities.

Both these behaviors are the outcomes of competition, a proof that both the species compete with each other. In the face of competition while *D. ananassae* may be conserving the energy required in courtship and matings (an important cost of reproduction) and invest it in survival waiting for less restrictive conditions, *D. melanogaster* increases its mating rate, perhaps to serve the purpose of ousting the competitor with the weapon of numbers. Under our experimental conditions the strategy displayed by *D. melanogaster* is perhaps better, as clearly it wins the battle. Yet *D. ananassae* might be more successful under different environmental conditions.

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