EGG LAYING BEHAVIOR OF MEDITERRANEAN FRUIT FLIES (DIPTERA: TEPHRITIDAE): IS SOCIAL FACILITATION IMPORTANT?

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Abstract

In a set of three experiments, we were unable to verify earlier reports of social facilitation of oviposition-associated behavior in Mediterranean fruit flies, *Ceratitis capitata* (Wiedemann). In our first 2 experiments, we placed a focal fly on a kumquat (Experiment 1) or artificial fruit (Experiment 2) either occupied by an ovipositing resident fly or alone. The frequency of oviposition attempts by the focal fly was slightly, but not significantly, *lower* in the social than solitary case. In the third experiment, which was carried out in a large field enclosure, we found that focal flies did not prefer to alight on a kumquat occupied by an ovipositing fly compared with a similar but unoccupied kumquat. Our results suggest that social facilitation of oviposition-associated behavior may not be a ubiquitous phenomenon in medflies.

Key Words: Conspecific attraction, Mediterranean fruit fly, *Ceratitis capitata,* Fruit flies, Egglaying behavior

Resumen

En una serie de tres experimentos, no pudimos verificar reportes previos de la facilitación social del comportamiento asociado con la oviposición en la mosca frutera del Mediterráneo, *Ceratitis capitata* (Wiedemann). En los 2 primeros experimentos, colocamos a una mosca focal en una fruta kumquat (Experimento 1) o en una fruta artificial (Experimento 2) ya sea ocupada por una mosca residente ovipositante o sola. La frecuencia de los intentos de oviposición por la mosca focal fue ligeramente, pero no significativamente, más baja en el caso social que en el caso solitario. En el tercer experimento, el cual se llevó a cabo en un cercado grande de campo, encontramos que las moscas focales no prefirieron posarse en una kumquat ocupada por una mosca ovipositante en comparación con una kumquat similar pero no ocupada. Nuestros resultados sugieren que la facilitación social del comportamiento asociado a la oviposicion tal vez no sea un fenómeno ubicuo en la mosca del Mediterráneo.

The presence and behavior of conspecifics sometimes enhances an individual's likelihood of exploiting resources such as feeding grounds, hosts or mates. For example, hunters and wildlife managers have successfully employed conspecific decoys or playback-audio-tapes to attract individuals of various bird and mammal species at their feeding or breeding grounds (Reed and Dobson 1993). Further, Alatalo et al. (1982), using taped playback of pied flycatchers, demonstrated that these birds preferentially settled in areas where songs were played even though the species is strongly territorial. Other examples include tendencies of various insects to lay more eggs per female when held in groups than alone (Hilker 1989; Chess et al. 1990; Abernathy et al. 1994), and increases in time spent per host patch and amount of superparasitism with increasing numbers of female *Leptopilina* and *Asobara* parasitoids in patches of host *Drosophila* larvae (Visser et al. 1900, 1992a,b; van Alphen et al. 1992).

Recently, it has been reported that female Mediterranean fruit flies, *Ceratitis capitata* (Wiedemann), are more likely to alight on fruit occupied by conspecific females (Prokopy et al. 2000) than on unoccupied fruit and to express heightened propensity to oviposit in the presence than absence of an ovipositing conspecific female on a fruit (Prokopy and Duan 1998). Moreover, other reports have suggested that other species of tephritid flies also are more likely to oviposit in host fruit when in the presence than absence of a conspecific ovipositing fly (Robertson et al. 1995; Prokopy and Reynolds 1998; Prokopy et al. 1999). These studies are of ecological interest because social facilitation of egg laying can create non-linear patterns of individual distribution with far reaching effects on population dynamics (Fretwell

1972; Reed and Dobson 1993; Sutherland 1996; Stephens and Sutherland 1999; Courchamp et al. 1999). For tephritid flies, a thorough understanding of such non-linear population dynamics may also be of economic importance.

Our intent here was to verify the phenomenon of socially facilitated oviposition-associated behavior in medflies reported by Prokopy et al. (2000) and Prokopy and Duan (1998) in experiments conducted under a broader range of conditions than characterized in these previous reports.

MATERIALS AND METHODS

We conducted all experiments at the University of Hawaii Research Center in Kauai, Hawaii. Prior to the experiments, we initiated a colony of wild medflies from infested coffee berries collected from a commercial grove. All flies used in the experiments developed as larvae in papaya in the laboratory. Following eclosion, adults of both sexes were held together in groups of about 50 females and 50 males at about 25°C, 60% relative humidity and natural day length of 13 hours in 30 × 30 × 30 cm screen cages supplied with water and food consisting of a mixture of enzymatic yeast hydrolysate and sucrose. All flies tested were 1 to 3 weeks old, sexually mature, presumably mated, and carried a moderate egg load of 20-30 eggs (see below). Except for the "experienced" flies in experiment 2, the flies were not exposed to fruit prior to testing. A fly was used only once in the experiments.

We conducted Experiments 1 and 2 inside a large screen house with a transparent plastic roof, which provided ample natural light and protection from frequent brief showers. The test arena consisted of a 1 m tall, 70 cm wide and 50 cm deep screen enclosure, which contained a small potted non-fruiting coffee plant.

EXPERIMENT 1: THE TENDENCY TO BORE IN OCCUPIED KUMQUATS

In the first experiment, we followed the methods of Prokopy and Duan (1998). We hung a single kumquat fruit (*Fortunella japonica*, family Rutaceae) using a coated wire twist attached to the coffee plant. The kumquats were essentially the same size as those used by Prokopy and Duan (1998). On average, they weighed 13.5 ± 0.3 g (mean ± SE), were 35.8 ± 0.6 mm long and 25.3 ± 0.3 mm wide (n = 10). They were shipped from California, were uninfested, and were washed and dried prior to use. A fresh fruit was used for each trial. Because medflies cannot readily penetrate a kumquat skin, we followed Prokopy and Duan (1998) and used a pin to generate a single 0.5 mm diameter hole at the center of the kumquat prior to placing a fly on the fruit. The flies

used were 14 days old, with an average load of 22.9 ± 3.8 eggs (based on a sub-sample with n = 10 flies).

Each trial, we randomly selected a new, experimentally naïve focal fly from the cage, and using a small plastic cup, placed her on the fruit. To test whether a focal fly was more likely to oviposit or oviposited more quickly when another fly was present, we compared the behavior of focal flies in two treatments detailed below. We ran 50 trials of each treatment in haphazard order. We used chi square tests or log linear models to analyze frequency data and ANOVA's for latency data.

Treatment 1: Resident Present

A trial of this treatment began with puncturing a single hole in the fruit and then placing on the fruit a first fly, the resident. Shortly after the resident initiated oviposition, we punctured a second hole approximately 1 cm to her rear and placed the focal fly about 1.5 cm to her side. We recorded interactions between the flies, whether the focal fly initiated oviposition, and the latency from introducing the focal fly to initiation of oviposition.

Treatment 2: Resident Absent

Here we initiated a trial by puncturing the fruit and then placing the focal fly at the center of the fruit approximately 1.5 cm from the hole. We recorded whether or not the focal fly initiated oviposition, as well as the latency from introducing the focal fly to initiation of oviposition.

Based on the results of Prokopy and Duan (1998), we predicted that the frequency of boring by focal flies would be higher, and the latency to bore would be shorter in the resident present than resident absent treatment.

RESULTS

In the 'resident present' treatment, the resident and focal flies were within less than fly length in 80% of the trials, but we observed clear interactions between the flies only in 20% of the trials. Such interactions typically involved head waggling and wing waving, and sometimes also head butting and foreleg kicking. Following such an exchange, focal and resident flies departed the fruit in 4% and 2% of the trials respectively.

The presence of an ovipositing resident fly did not affect the propensity of focal flies to initiate an oviposition bout: focal flies started boring in 74% of the 'resident present' trials and in 84% of the 'resident absent' trials ($\chi^2 = 0.5$, df = 1, P > 0.4), and their latency to bore was similar in either treatment, 55.7 ± 6.7 s in the 'resident present' trials and 53.6 ± 9.1 s in the 'resident absent' trials ($F_{1,77} = 0.03$, P > 0.5).

EXPERIMENT 2: THE TENDENCY TO BORE IN OCCUPIED ARTIFICIAL FRUITS

Focal flies in the 'resident absent' treatment of Experiment 1 bored in 84% of the trials compared to only 34% in the comparable treatment of Prokopy and Duan (1998). One may argue that in our experiment, there was relatively little opportunity for a resident to facilitate the boring propensity of the focal fly, which was already very high in the absence of a resident. Hence we conducted a more elaborate experiment, using a less acceptable 'fruit' and a variety of resident and focal flies. Our general motivation was to try to generate a favorable condition for the expression of social facilitation.

We created spherical artificial fruits 30 mm in diameter by mixing 6% agar and 1% green food coloring in water, boiling the mixture and pouring into spherical molds (Boller, 1968). After the spheres cooled, we wrapped them with parafilm, leaving a short 'stem' used to hang the sphere with a plastic coated wire twist from the coffee plant.

We used two types of flies in this experiment: naïve flies, which were 8-10 days old with no prior exposure to fruit; and experienced flies, which were 3 weeks old and had been exposed to artificial fruit in their cage for 2 days. The average egg load of a sample cohort of naïve flies was 31.9 ± 5.8 and that of a sample cohort of experienced flies was 26.1 ± 2.9 (n = 10) for each sample. Overall, there were 3 conditions of the resident fly (resident absent, naïve resident, or experienced resident), and 2 conditions of the focal fly (naïve or experienced). We ran trials of the 6 combinations in haphazard order within blocks of 6 trials for a total of 180 trials. Here, no fruit punctures were necessary, so in 'resident absent' trials we simply placed the focal fly at the center of a fruit. In trials with a naïve or experienced resident, we introduced the focal fly to the side of the resident after she had initiated boring.

RESULTS

In trials with a resident present, the resident and focal flies were within less than fly length in 92.5% of the trials; the flies showed clear interactions in 72% of the trials. Such interactions typically involved head waggling and wing waving, and sometimes also head butting and foreleg kicking. Following such an exchange, focal and resident flies departed the fruit in 10% and 11% of the trials respectively.

The presence of either a naïve or experienced resident fly did not affect the propensity of focal flies to initiate oviposition bouts ($\chi^2 = 1.0$, df = 2, $P > 0.4$, Fig. 1a). The only notable trend was a slightly higher propensity to bore by experienced than naïve focal flies ($\chi^2 = 3.0$, df = 1, $P = 0.08$, Fig.

1a). Similarly, the average latency to bore by focal flies was similar among the 3 resident-type treatments ($F_{2, 87} = 0.09$, $P > 0.5$, Fig. 1b).

EXPERIMENT 3: THE TENDENCY TO ALIGHT ON OCCUPIED FRUITS

In this experiment, we tested whether flies preferred to land on a fruit already occupied by a fly over an unoccupied fruit. The experiment was conducted in a cylindrical nylon-screen field enclosure 4 m wide and 2.5 m high containing 2 large potted coffee plants creating a canopy ca. 1 m wide and ca. 2 m high. At the start of each of the four days of the experiment we released approximately 200 naïve 10-14 day old flies (males and females in approximately equal numbers) inside the enclosure. Using coated wire twists, we hung 2 kumquats matched for size from a thin copper wire stretched between 2 branches. The 2 fruits were 20 cm apart.

Prior to the start of a trial, we punctured 2 holes on opposite sides of each kumquat. We then
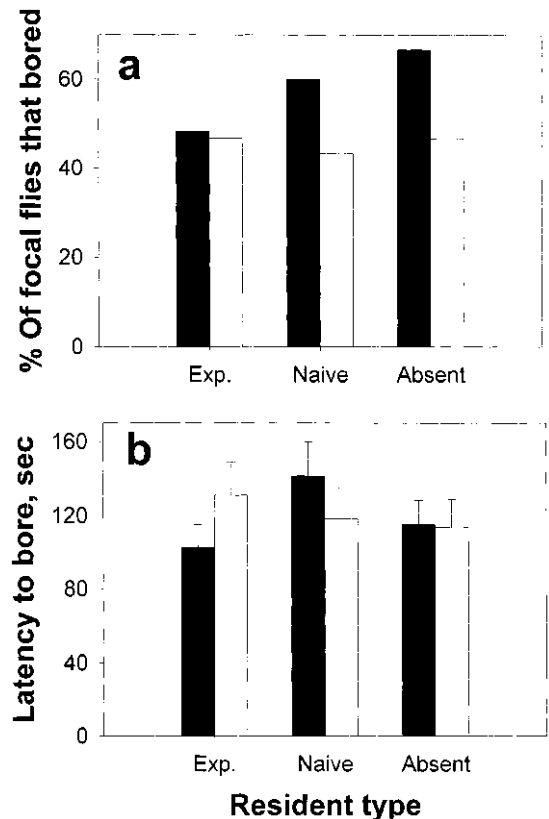

Fig. 1. (a) The proportion of experienced (dark bars) and naïve (clear bars) focal flies that initiated boring in a kumquat occupied by an experienced, naïve or no fly, and (b) the average latency from placement on a fruit to initiation of boring by those focal flies that bored.

placed a resident fly on one of the 2 kumquats and watched for alighting flies. The resident fly typically initiated inspection of the fruit, followed by boring and egg laying. We noted the choice of the first alighting fly and her behavior after landing on a fruit. At the end of each trial, we removed the resident and any alighting fly from the enclosure except for a few occasions where these flies flew off a fruit and could not be located. We conducted a total of 100 trials, while haphazardly alternating the side of the occupied fruit within each block of two successive trials (i.e., the occupied fruit was on the right side in one trial and on the left side in the other trial within a block).

RESULTS

The flies showed no side preference, landing in identical proportions (0.5:0.5) on the left and right fruits. Neither did the flies preferentially land on the fruit occupied by a resident fly, which they chose in only 54% of the trials ($\chi^2 = 0.6$, df = 1, P > 0.5). The proportion of flies that initiated egg laying was similar for flies that landed on fruit with or without a resident, 57% and 60% respectively. Finally, the latency to bore was similar for the 2 fly categories, 95.3 ± 10.8 s for flies landing on the fruit occupied by a resident and 90.3 ± 11.4 s for the flies that landed on an unoccupied fruit ($F_{1, 57} = 0.1$, P > 0.5).

DISCUSSION

Social Facilitation?

A focal fly placed on a fruit with a boring fly was not more likely to initiate egg laying than a focal fly placed alone (Experiments 1 and 2; Fig. 1). Moreover, in Experiment 3, we found that flies were not more likely to land on a kumquat occupied by another fly than on a fruit with no fly. These findings are in contrast to findings of social facilitation of alighting and post-alighting behavior of medfly females reported by Prokopy et al. (2000) and Prokopy and Duan (1998).

With respect to social facilitation of alighting behavior, it is relevant to recognize that Prokopy et al. (2000) used artificial fruit-mimicking spheres or hemispheres each occupied by at least four conspecific females (held in place by sticky adhesive), whereas we used punctured kumquats each occupied by just a single conspecific resident female. In our study, the value of odor from punctures in real fruit may have outweighed the value of the presence of a single resident female as information signaling a fruit as a potentially quality resource to a focal female. In the study by Prokopy et al. (2000), the presence of multiple resident females may have overridden the value of other information emanating from artificial fruit. In our judgment, therefore, the propensity of a medfly female to alight on a fruit occupied by one or more conspecific resident females may be influenced by a variety of fruit chemical or visual stimuli whose informational value may or may not exceed that of a resident.

With respect to social facilitation of post-alighting behavior, it is possible that the results reported by Prokopy and Duan (1998) were unique to a set of biotic and abiotic conditions different from the ones in our experiments. Alternatively, some details of experimental protocol may explain the positive results obtained by Prokopy and Duan (1998). First, in the experiment of Prokopy and Duan (1998), as in our experiment 1, 2 punctures were provided per fruit occupied by a resident and only 1 puncture was available in "resident absent" trials. It is possible that under the specific conditions existing during their test, this confounding factor resulted in higher boring propensity in two-than single-punctured fruit. Neither they nor we could find such a positive effect of an additional puncture in separate experiments, but a few other studies have documented positive effects of punctures on oviposition in medflies (Papaj et al. 1989, 1992; Papaj & Messing 1996). The methods we employed in experiments 2 and 3 resolved this possible confound. In experiment 2, we used artificial fruit, which does not require punctures, and in experiment 3, we provided 2 punctures each per occupied and unoccupied fruit. Second, Prokopy and Duan (1998) worked in a relatively exposed location under highly variable weather conditions typical of east coasts of the Hawaiian islands. For example, on a typical morning, there were a few brief showers, a few cloudy and windy periods, and breaks of intense sunshine. Medflies are highly sensitive to such weather fluctuations, with a strong preference to oviposit during calm and sunny times. A "resident absent" trial can be conducted at any moment even if the weather is "bad". In contrast, a precondition for performing a 'resident present' trial is that the weather is above a critical threshold allowing a resident fly to initiate boring. That is, while the weather has to be "good" for all 'resident present' trials, this condition does not necessarily have to be met for "resident absent" trials. An inherent bias of this sort could have led to a finding of apparent social facilitation by Prokopy and Duan (1998). Our experiment 3 addressed this issue because we employed a choice test, simultaneously presenting a 'resident present' and "resident absent" fruit. However, in our experiment 3, there were relatively favorable conditions for boring (60% of focal females on fruit lacking a resident female bored), so it is still possible that social facilitation occurs under less favorable conditions for boring.

These inconsistent results for social facilitation of oviposition-associated behavior in medflies are troubling and strongly suggest that positive re-

sults must be taken with extra caution until repeatedly replicated in meticulously conducted experiments. Moreover, because some of the inconsistencies may be artifacts of laboratory rearing conditions and experimental protocols, we suggest that, in this unusual case, social facilitation ought to be studied in 'natural' field settings. Ultimately, to make a case for the ecological significance of social facilitation in egg-laying behavior, one must demonstrate that females in the field commonly encounter each other on host fruit and that such encounters consistently and significantly increase the tendency for females to lay eggs. Such future demonstration must control for potential confounding factors such as fruit location and damage (see Papaj et al. 1989; Papaj 1994).

The Nature and Adaptive Significance of Fly Interactions on Fruit

In our study, the interactions between resident and focal flies varied between experiments. The frequency of interaction between the resident and focal fly was just 20% in Experiment 1 but 72% in Experiment 2. In Experiment 1, resident females frequently proceeded to oviposit, rather than engage in interactions with the focal female. In Experiment 2, by contrast, interactions were the norm. The difference in frequency of interactions may reflect a difference between the experiments in the acceptability of oviposition substrates. In Experiment 1, we used kumquats, which are highly acceptable fruits in terms of oviposition. In Experiment 2, we used artificial fruits, which are considerably less acceptable for oviposition than kumquats. In contrast to resident flies on kumquats (Experiment 1), resident flies on the less acceptable agar spheres (Experiment 2) were evidently more likely to abort boring, thus providing opportunity to interact with focal flies. A pattern in which ovipositing resident medflies ignored intruders, as in Experiment 1, was noted by Prokopy and Duan (1998) and Papaj and Messing (1998), again on real fruit. Two possible explanations for this behavior are, first, that a female engaged in egg laying does not attend to her surrounding (see Dukas 1998), and second, that the ovipositing female notices the intruder but prefers to continue oviposition rather than confront the intruder, because of the higher expected fitness benefits from the former.

The exact motivation for and effects of interactions between resident and focal females are not fully clear to us. However, many interactions seemed to be aggressive in nature. Indeed, aggressive interactions by female medflies on coffee berries have been described by Papaj and Messing (1998) and female-female aggression has been documented in other tephritids as well (e.g., Prichard 1969; Fitt 1989; Prokopy et al. 1999). At the ultimate level, it is probably easier to understand causes underlying aggression than social facilitation. In small fruits, which are the preferred fruit size by medflies (Katsoyannos 1989), a second egg clutch per fruit may reduce fitness due to larval competition for resources. Such competition reduces survival and growth rate (Debouzie 1989). Results of larval competition experiments in kumquats about 30% smaller than those used in our experiments (R. Dukas, R. J. Prokopy and J. J. Duan, in press) indeed suggest that laying a second clutch per small fruit reduces fitness. Hence a resident fly's attempt to chase away an intruding fly from a small fruit can potentially increase the resident's fitness.

It is not obvious, however, how an intruding fly should respond to either an aggressive or a nonresponding ovipositing resident. First, our observations of fly-fly interactions on fruit revealed that rather than escalating into fighting, aggressive interactions quickly ended either with one fly leaving the fruit, or the two flies staying and ovipositing (see also Papaj and Messing 1998). This suggests that an intruding fly does not risk injury or other costs if she decides to stay. Second, one can imagine some proximate mechanism, such as a stimulating odor emitted by the ovipositing resident, that increases a focal fly's laying propensity under certain conditions. Such odor may simply be fresh fruit volatiles emitted during the boring activity of the resident. The ultimate explanation for a stimulating effect of fruit odor is that punctures usually allow faster oviposition (Papaj 1994).

We believe that a suite of environmental and physiological factors such as fly density, age, nutrition, egg load, fruit size and ripeness, existence of punctures, and even weather should guide a fly's egg laying decisions. An ultimate approach, which seeks to define female fitness in the context of such factors, has been successful in explaining other oviposition decisions in medflies (e.g., Prokopy et al. 1989, 1994; Papaj et al. 1990; Papaj and Messing 1996). In our experiments, focal flies (except for the "experienced" ones in Experiment 2) had no prior experience with fruit, but they had encountered numerous conspecifics in their cage. The perception of high fly density during caging should diminish a fly's tendency to avoid fruits occupied by ovipositing flies, egg infested fruits, and fruits of low quality, because unoccupied, uninfested fruits of high quality are less likely to be found at high fly density. Indeed, several insect studies have documented a higher egg laying propensity per individual under social than solitary conditions (e.g., Prokopy and Bush 1973; Chess et al. 1990; Prokopy and Reynolds 1998). However, these studies, and the body of theory motivating them, do not lead us to predict that a focal fly would *prefer* a fruit occupied by an ovipositing fly over an uninfested fruit of similar quality, as long as laying a second clutch in a fruit is costly in terms of larval competition.

Probably the best explanation for numerous reports on social facilitation in various taxa including nest site selection in birds (Alatalo et al. 1982) and mate choice in fish (Dugatkin 1992) involves issues of information: the focal individual, which is inexperienced, mimics another individual (the model) on the assumption that the model has made an informed choice. By copying the model, the focal individual presumably avoids paying a cost associated with gathering information. Applied to our protocol, this argument implies that a focal fly may be more likely to oviposit after watching a resident ovipositing than when alone because the savings in terms of information-gathering raise the relative value of that fruit to the focal fly. However, the occurrence of such savings is not itself sufficient to favor social facilitation. Rather, the benefit of copying in terms of information-gathering must exceed the cost of competition that a fly's larvae would suffer if deposited into a fruit that is being exploited by another fly. Whether the benefit of copying exceeds this cost is, at present, unclear.

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