# DEFENSE OF OVIPOSITION SITES BY FEMALE ORIENTAL FRUIT FLIES (DIPTERA: TEPHRITIDAE)

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## ABSTRACT

Field observations revealed that females of the oriental fruit fly, *Bactrocera dorsalis* (Hendel), defended oviposition sites on mangos (*Mangifera indica* L.) against conspecific females. In most encounters, females simply lunged at opponents and chased them off the fruit without physical contact. However, head-butting and pushing were observed in about 10% of the contests. Body size was a key determinant of fighting success, with larger females winning 85% of the encounters. In a field experiment, arrivals, oviposition, and aggression of females were compared between intact vs. sliced peaches. Similar numbers of females landed on the two classes of fruits, but a greater proportion of alighting females oviposited on sliced peaches than intact peaches. The adaptive function of female territoriality is discussed in light of these findings.

Key Words: fruit fly, aggression, territory, oviposition, Hawaii

## RESUMEN

Observaciones de campo han indicado que las hembras de la mosca oriental de la fruta, *Bactrocera dorsalis* (Hendel), defienden los sitios de oviposición en mangos (*Mangifera indica* L.) de las hembras de su misma especie. En la mayoría de los encuentros, las hembras simplemente se lanzaron hacia sus oponentes y las espantaron de la fruta sin tener contacto físico directo. Sin embargo, choques de cabeza y empujones fueron observados en el 10% de los encuentros. El tamaño del cuerpo es clave en la determinación del éxito en las luchas; éste se refleja en que las hembras más grandes ganaron en un 85% de los encuentros. En un experimento de campo, llegadas, oviposición, y comportamiento agresivo de las hembras fue comparado entre melocotones intactos y partidos. Un número similar de hembras visitaron las 2 clases de frutas, pero una proporción mayor de las hembras ovipositó en los melocotones partidos en comparación con los intactos. La función adaptativa de la territorialidad de las hembras se discute en base a estos hallazgos.

Territorial behavior has been reported for males of many insect species (Baker 1983, Fitzpatrick & Wellington 1983). In most of these cases, males defend sites containing resources vital to females, thus increasing their mating opportunities. Though less common, territorial behavior has also been reported for females in several insect species, and in these instances site defense is usually related to food resources. For example, female water striders defend particular areas of streams where food resources collect (Vepsalainen 1985, Nummelin 1988), and female aphids defend basal sections of newly developing leaves (Whitham 1979).

In tephritid fruit flies, territorial behavior has been reported frequently for males. Male defense of mating areas has been described for various species of *Rhagoletis* (Boyce 1934, Prokopy & Roitberg 1984), *Anastrepha* (Aluja 1994), and *Bactrocera* (Fletcher 1987) as well as for the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Arita & Kaneshiro 1989). In contrast, there are few reports of female-female aggression in tephritids, and these are typically based on observations made in the laboratory. For example, Biggs (1972) and AliNiazee (1974) described several types of agonistic displays for females of *R. pomonella* (Walsh) and *R. indifferens* (Curran), respectively, caged under high experimental densities. In the wild, however, aggression between *Rhagoletis* females may occur only infrequently (Prokopy & Bush 1973). Similarly, McDonald & McInnis (1985) noted fights between *C. capitata* females at potential oviposition sites, but again these occurred under artificially high densities in the laboratory. An instance of interspecific aggression (between *A. obliqua* (Macquart) and *C. capitata* females) has also been reported in laboratory observations (Camargo et al. 1996).

The apparent low incidence and intensity of female aggression in *Rhagoletis* and *Ceratitis* (as well as *Anastrepha*) may reflect the use of host marking pheromones by ovipositing females in these genera (Fletcher & Prokopy 1991). Following egg-laying, females drag their ovipositor over the fruit surface and deposit a pheromone that tends to deter future oviposition in that fruit by conspecific females (Fletcher & Prokopy 1991). Thus, in these species interference between females may be primarily via chemical signals, with active site defense (involving physical displays or contact) being less important.

Interestingly, host marking pheromones are apparently absent in *Bactrocera* females (Fletcher & Prokopy 1991), and, based on one study at least, inter-female aggression may correspondingly be more frequent and intense in these species. In his study of *B. tryoni* (Froggatt), Pritchard (1969) reported that females on fruit, even those already engaged in egg-laying, were easily disturbed by intruders and made threat displays that occasionally escalated to head-butting and pushing. Nearly 20% of females observed ovipositing in the wild interrupted egg-laying to drive off conspecific females. Despite female aggression, Pritchard (1969) found that eggs were not uniformly spaced, as might be expected, but were highly aggregated both among and within fruits.

The present paper supplies information on female defense of oviposition sites in the oriental fruit fly, *Bactrocera dorsalis* (Hendel). Field observations provided data on the incidence and intensity of female aggression on host fruits, and a field experiment was performed to examine the influence of fruit wounds on the occurrence of oviposition and female-female fighting. The function of female territoriality in this species is discussed in light of the present findings.

## MATERIALS AND METHODS

### Field Observations

Behavioral observations were made at a single mango tree (*Mangifera indica* L.) in a vacant lot in Honolulu, Hawaii, during June 1993. The tree (approximately 10 m high) bore a large crop but had already dropped many ripe fruits. Female *B. dorsalis* were abundant on the fallen mangos, and all observations were made on these fruits. Data were gathered by 1-3 observers between 1200-1400 hours on 5 sunny days with air temperatures ranging between 28 and 31°C.

Individual females were observed continuously or until lost from view. Observations were recorded on tape for later transcription, and the following information was noted: total observation time, number of different mangos visited, time spent on a given mango (underestimates in many cases, because females were already on fruits for unknown time intervals when observations commenced), number and duration of oviposition bouts (operationally, oviposition was equated with ovipositor-boring into a fruit), number of different oviposition sites on a given fruit, presence of a conspicuous hole or gash (in fruit surface) at the oviposition sites, number and outcome of aggressive interactions with conspecific females. I also classified fruit departures and oviposition stoppages either as unprovoked (without apparent cause) or as resulting from aggression.

To determine whether fighting ability was size-dependent, agonistic encounters between *B. dorsalis* females were observed on 6 additional dates at the same site, and the participants were collected for body size measurements. As an index of overall size, the length of the posterior edge of the discal cell was measured to the nearest 0.1 mm using a dissecting microscope equipped with a disc micrometer. The female remaining on the fruit after aggression was identified as the winner, and the departing female was considered the loser. Females were also classified as resident (individual initially seen on fruit) or intruder.

### Field Experiment

Work was conducted in July 1993 at the University of Hawaii Agricultural Experiment Station in Waimanalo, Oahu, Hawaii. Experimental fruits were placed on the ground beneath a row of large mango trees. Many ripe mangos were on the ground, and female *B. dorsalis* were seen ovipositing on these fruits. Males were not observed on these fruits. Data were gathered by 1-3 observers between 1100-1300 hours on 5 sunny days with air temperatures ranging from 30 to 33°C.

Studies on *C. capitata* (Papaj et. 1989) and *B. tryoni* (Oi & Mau 1989) have demonstrated that ovipositing females prefer fruits with wounds or holes over intact fruit, presumably to facilitate egg-laying. Accordingly, the field study compared female arrivals, oviposition, and aggression on intact vs. sliced groups of peaches (*Prunus persica* L.). Peaches were placed on the ground at 1100 hours and observed continuously over the next 2 h. Store-bought California peaches were used to avoid any prior infestation and to insure size uniformity. The fruits were washed and dried prior to use. Peaches in the intact group were not modified in any way, while those in the sliced group received a single cut (4-5 cm long; 1-2 cm deep) immediately before observations. A single observer monitored 4-6 fruits simultaneously (placed 0.6-0.75 m apart in the shade) and recorded the following information on tape for later transcription: number of female arrivals, duration of female residency, total duration of oviposition activity, site of oviposition (cut vs. smooth surface in sliced fruits), and the number and outcome of aggressive encounters. As before, departures from fruit and termination of egg-laying were categorized as unprovoked or as a consequence of aggression.

### Statistical Analysis

Means were compared using the nonparametric Mann-Whitney test to avoid assumptions of normality, though variation about means was described using the standard deviation (SD). Contingency tests were performed using the G test (log likelihood ratio test) with Yates' correction for continuity. The normal approximation to the binomial test was used to test for resident advantage in aggression. Computational procedures followed Zar (1974).

## RESULTS

### Field Observations

Over the entire study, 137 observations were made ranging from 0.2 to 33.3 min in length and totalling approximately 14 h. Females usually (119/137) remained on a single fruit during observations, but in some cases they visited 2-5 fruits. Thus, the total number of fruits visited (n = 164 over all females) exceeded the number of observations made (n = 137). Females were seen ovipositing during nearly 1/3 (39/137) of the observations.

The length of female residency on a fruit was dependent on her oviposition activity. On average, females that did not oviposit on a given fruit stayed for 136 s (SD = 159, n = 125). By comparison, females that laid eggs on a given fruit remained for an average of 732 s (SD = 452, n = 39; $P < 0.001$; Mann Whitney test). Females that oviposited did so for an average of 35% (SD = 23, n = 39) of their time on a given fruit. In most cases (25/39), females oviposited, not in a single episode, but during multiple bouts on the same fruit. Females often interrupted oviposition temporarily, walked around the fruit, and then returned to the original area for further egg-laying. On average, females seen ovipositing did so over 2.5 bouts (SD = 2.0, n = 39), and each bout lasted 1.65 min (SD = 1.4, n = 99). In almost all cases (34/39), eggs were laid at only one site on a given fruit, and most of these sites (27/39) had either a visible hole or gash in the fruit surface.

The incidence of aggression was related to the oviposition activity of females. During visits in which no oviposition occurred, females rarely engaged in aggression with other females (14/125). In contrast, females that oviposited on a given fruit interacted aggressively with conspecific females in 1/2 of the instances (19/39; $P < 0.001$; G test). At first glance, this difference appears to have been directly related to residency time on a fruit: visits with oviposition were, on average, about 5.5 times longer than those without oviposition (732 s vs. 136 s, respectively) and were about 4.5 times as likely to be accompanied by agonistic encounters as those without oviposition (49 vs. 11%, respectively). However, data regarding the rate of fighting reveal that, independent of residency duration, aggressive encounters occurred far more frequently on fruits on which oviposition was observed. On average, the number of aggressive encounters occurring per minute was nearly 5 times greater during visits with oviposition ($x=0.19$/min, n = 39) than those without oviposition ($x = 0.04$/min; n = 125; $P < 0.001$; Mann Whitney test). Resident females detected most intruders, and only 10% (10/101) and

15% (2/13) of intruding females went unnoticed by ovipositing and non-ovipositing females, respectively ($P > 0.05$; G test). Intruders in these cases usually stayed less than 20 s and departed on their own volition.

Consistent with these data, losing an agonistic encounter was a more likely cause of female departure from fruits where the female oviposited than from fruits where she did not. In 1/3 (13/39) of the visits during which oviposition occurred, the resident female left the fruit immediately after fighting with an intruding female (who invariably remained on the fruit). In contrast, in visits without oviposition female departures were usually unprovoked and only infrequently (14/125) followed aggression ($P<0.001$; G test). In addition, female-female aggression also limited the duration of individual oviposition bouts: 37% (37/99) of egg-laying bouts ended when the resident female detected and subsequently fought with an intruding female.

In most of the aggressive encounters observed (90/102), there was no physical contact between the participants. Females extended their legs, thus elevating their body, and held their wings perpendicular to their body. In most of these cases (70/90), one female simply lunged at the other and chased it away. In the remaining observations, the combatants moved back and forth in front of each other for several seconds prior to a chase. When aggression escalated to physical contact (12 cases, all on fruits where oviposition was observed), females ran directly toward one another and butted heads from 1 to 10 consecutive times in interactions lasting 1-63 s. In the longer contests, head butting occurred while the antagonists circled closely about one another, with each trying to push the other off the fruit. Actual wrestling was observed in 3 instances, and in each case the females fell to the ground where they continued grappling for 2-5 s.

Body size was a key determinant of fighting success. Body size measurements were obtained for 41 chases (physical contact absent), and larger females won 85% of the interactions (32/37; combatants were the same size in 4 cases; $P < 0.001$; binomial test). Residency appeared to be unimportant in determining the outcome of agonistic encounters: the proportion of contests won by residents (23/41) did not differ significantly from 50% ($P > 0.05$; binomial test).

### Field Experiment

On average, similar numbers of females landed on intact ($\bar{x} = 3.4$, SD = 3.0) and sliced peaches ($\bar{x} = 3.5$, SD = 3.3, $n = 52$ for both groups; $P > 0.05$; Mann Whitney test). However, the proportion of females that subsequently oviposited was greater for sliced (65/184) than intact (21/174) fruits ($P < 0.001$; G test). As these data suggest, females deposited eggs in a greater proportion of sliced peaches (38/52) than intact ones (16/52; $P < 0.001$; G test).

As before, residency time was related to the incidence of egg-laying. On the sliced peaches, females that oviposited spent an average of 894 s (SD = 778, $n = 65$) on a given fruit compared to only 141 s (SD = 100, $n = 119$) for non-ovipositing females ($P<0.001$; Mann Whitney test). Similarly, on the intact peaches, females that oviposited spent an average of 828 s (SD = 699, $n = 21$) compared to only 129 s (SD = 116, $n=153$) for non-ovipositing females ($P < 0.001$; Mann Whitney test). Also, consistent with the behavioral observations described above, aggression on both sliced and intact fruits usually involved females seen to oviposit. On sliced peaches, agonistic encounters were observed during about 50% of the visits involving ovipositing females (31/65) compared to only 5% (6/119) for non-ovipositing females ($P < 0.001$; G test). On intact peaches, aggression was noted in approximately 25% (5/21) of the visits made by females that oviposited compared to only 3% (4/153) of those visits in which females did not oviposit ($P < 0.001$; G test).

Among females that oviposited, mean residency time did not differ significantly between the two types of fruit ($n_1 = 65$, $n_2=21$; $P > 0.05$; Mann Whitney test). However, females on sliced peaches spent, on average, more time engaged in egg-laying than did those on intact peaches (366 vs. 192 s, $n_1 = 65$, $n_2 = 21$; $P < 0.01$; Mann Whitney test). The incidence and frequency of aggression also differed between females ovipositing on the two fruit types. Despite similar residency periods, females ovipositing on sliced peaches were more likely to have an agonistic interaction than those ovipositing on intact ones (31/65 vs. 5/21, respectively; $P < 0.001$; G test). In addition, fights occurred more frequently on sliced peaches ($x = 0.07$/min, SD = 0.04, $n = 65$) than on intact ones ($x = 0.03$/min, SD = 0.02, $n=21$; $P < 0.001$; Mann Whitney test). As before, resident females nearly always detected intruders, and only 7% (6/59) and 10% (1/10) of intruders arrived (and subsequently departed) unnoticed on sliced and intact peaches, respectively ($P > 0.05$; G test).

## Discussion

The aggressive behavior of *B. dorsalis* females appears very similar to that described for females of *B. tryoni* (Pritchard 1969). Females of both species responded quickly to the presence of intruders and interrupted egg-laying to confront intraspecific females. Though no data were presented, Pritchard (1969) noted that in *B. tryoni* visual displays were “usually effective in causing intruders to leave”, and likewise contests between *B. dorsalis* females rarely (10% of interactions) involved bodily contact. Escalation in both species involved episodes of repeated head butting, and, if this was unsuccessful, prolonged pushing resulted.

As noted in *B. tryoni* (Pritchard 1969; Eisemann & Rice 1985) and *C. capitata* (Papaj et al. 1989), females of *B. dorsalis* preferentially oviposited in existing holes or cuts in the fruit surface (see also Oi & Mau 1989). Evidence for this preference derived from the field experiment where alighting females were found to be approximately 3 times more likely to oviposit on sliced peaches than intact ones. In addition, the great majority of natural oviposition occurred in fruit wounds. Choosing existing holes for oviposition presumably facilitates the physical actions associated with egg-laying and enhances egg and larval survival (Papaj et al. 1989).

Based again on the field experiment, both the incidence and frequency of female defense were higher on sliced fruits than on intact fruits. This trend resulted directly from the higher numbers of intruders alighting on the sliced peaches: intruders arrived twice as frequently on sliced peaches as intact ones. Interestingly, although more intruders arrived at sliced peaches, there was no difference in the numbers of females alighting on unoccupied sliced and intact peaches (see Prokopy et al. [1990] for contrary results). Thus, the combination of alighted female plus surface cut was apparently more attractive to searching females than either a surface cut (on an unoccupied fruit) or a female (on an intact fruit). The difference in aggression levels between fruit types did not result from variation in female vigilance: residents of both sliced and intact peaches detected and interacted with nearly all intruders. Thus, there was no evidence to suggest that females defended sliced peaches more readily than intact ones.

The field observations are consistent with the findings of the field experiment. At the mango tree, oviposition usually occurred in existing holes or cuts in the surface of the fruits. Whether or not the distribution of oviposition among mangos reflected the distribution of suitable holes or wounds is unknown but appears likely. The incidence and mean arrival rate of intruders was also greater during visits where oviposition was observed than visits where oviposition was absent. The propensity of females to oviposit in fruit wounds suggests again that searching females are highly attracted by the co-occurrence of a female and a surface cut.

The adaptive function of female territoriality in *Bactrocera* is presumably related to its effects on larval competition. By defending fruits (even temporarily), females may provide their larvae with a "head start" in growth over unrelated larvae and hence a competitive advantage for host fruit resources. Interestingly, ovipositing *B. dorsalis* females are apparently unable to detect unhatched, conspecific eggs within host fruit and do not discriminate against egg-laden fruits in selecting oviposition sites (Prokopy et al. 1989). This same study showed, however, that females discriminated against fruit containing conspecific (or heterospecific) larvae. Thus, by limiting the opportunity for larval food competition and facilitating growth of its own larvae, aggressive behavior may also serve to deter oviposition (via larval detection) by other females well after the original territorial female has departed.

Female preference for existing holes and their inability to detect and avoid egg-laden fruit may collectively limit the potential advantages of territoriality. Defense of an already infested (i.e., egg-laden) fruit or a fruit soon likely to receive additional eggs (i.e., prior to the hatching of a female's own eggs) would probably not confer significant benefits, since larval competition would not be much reduced. Females do not have perfect information about potential oviposition sites, and this uncertainty jeopardizes the value of their aggressive actions. Still, the potential benefits to larval growth may outweigh the actual costs of site defense, which appear trivial in terms of both time and energy expenditure and risk of injury. In short, territorial behavior most likely has probabilistic benefits; it may confer a fitness advantage, but it does not guarantee one. Therefore, identifying the environmental influences (e.g., population density, host fruit) on the benefits conferred by territoriality is a key step toward elucidating the adaptive value of this behavior.

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