

AGGRESSION BETWEEN WILD AND LABORATORY-REARED
STERILE MALES OF THE MEDITERRANEAN FRUIT FLY
IN A NATURAL HABITAT (DIPTERA: TEPHRITIDAE)

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Mediterranean fruit flies, *Ceratitis capitata* (Wiedemann), exhibit a lek mating system. Males settle nonrandomly on particular host or non-host trees (Shelly et al. 1994) and defend individual leaves as mating territories (Arita & Kaneshiro 1989; Hendrichs & Hendrichs 1990). While on their territory, males emit a pheromone attractive to females and, following female arrival, perform a brief courtship display involving wing and head movements and then mount the female (Feron 1962; Arita & Kaneshiro 1989). Females may decamp during courtship or mounting attempts, or they may remain stationary and copulate.

The importance of male-male aggression in the mating system remains unclear. In a field study, Whittier et al. (1992) reported that, although most matings occurred on only a small subset of all the trees available, they occurred on many different leaves within these trees. This study also showed that intruders were more likely to win aggressive interactions than were resident males. Together, these results indicate that territory position within a given tree and hence fighting success may have little effect on male mating success. On the other hand, Ramos (1991) observed wild Costa Rican medflies in a field cage and reported that residents won over 80% of the aggressive encounters. This suggests that residents increased their level of aggressiveness in order to maintain possession of their territory and that control of particular leaves conferred reproductive benefits (e.g., increased encounters with females) over others.

The purpose of this note is to present data describing the outcome of aggression between wild and sterile males of *C. capitata* in a naturally occurring population. In particular, I report the fighting success of wild and sterile males both as residents (original territory occupants) and intruders (arrivals to an already occupied territory). The data reported here were gathered during prior studies (Shelly et al. 1994, Shelly & Whittier 1996) on the mating competitiveness of sterile males released in a natural population occurring in a fruit orchard on Maui, Hawaii. These studies involved systematic censuses of the orchard to record the distribution of both wild and sterile *C. capitata* among host trees, the incidence of male calling and male-male aggression, and the identities (wild or sterile) of mating individuals. A total of eight releases was made during these studies, and 3,400-7,400 sterile males were used per release (ratios of sterile: wild males on the day of release varied from 61:1 to 198:1). Two or three observers made censuses over 3-8 days immediately after the release of marked, sterile males.

Sterile males were obtained from a long-established colony (>40 years) maintained by the Hawaii Fruit Fly Rearing Facility in Waimanalo, Oahu, HI. Pupae that had been exposed in air to 15 krad of gamma radiation from a ¹³⁷Cs source were obtained 2 days before eclosion. Adults were separated by sex the day of eclosion, cooled and marked on the thorax with enamel paint, and then transported and released at the study site on Maui. Mortality during transportation was minimal (Shelly et al. 1994, Shelly & Whittier 1996). Sterile males were 6-8 days old upon release.

I considered aggression to have occurred when, during temporary occupation of the same leaf, one male oriented to and approached the other and then displayed wing-waving motions and/or lunged. Males were never observed to "share" leaves, and aggressive interactions invariably occurred within seconds of the arrival of an intruder. When wing-waving, males held their wings perpendicular to the long axis of the body and moved them up-and-down repeatedly, often while moving from side-to-side in front of the other male (a behavior that differs greatly from the wing movements exhibited during courtship; Feron 1962, Arita & Kaneshiro 1989). Lunges, or rapid forward movements of the entire body, sometimes followed wing-waving motions but were also initiated in the absence of any other prior display. In addition, lunges may or may not have been accompanied by rapid wing flicks toward the other male. Although systematic data were not collected, lunges clearly did not always result in physical contact between males, and when occurring, contact involved head butts or wing strikes or both (males may have used their forelegs as well, but I was unable to detect this). Although prolonged (>5 min) instances of head pushing have been reported (Arita & Kaneshiro 1989), no such interactions were observed during this study. I considered males that remained on the leaf the "winner" of the contest and the males that left the "loser".

Wild and sterile males had equivalent success in aggressive encounters (Table 1). In cases where the resident was a wild male, the resident won 58% of the encounters

TABLE 1. OUTCOME OF AGGRESSIVE INTERACTIONS BETWEEN WILD AND STERILE MALES OF *C. CAPITATA*.

	Intruder	Resident	
		Win	Lose
A. Wild resident	Wild	15	11
	Sterile	17	19
B. Sterile resident	Wild	16	15
	Sterile	9	13

against wild intruders and 47% against sterile intruders ($\chi^2 = 0.7$; $P > 0.05$). Similarly, in cases where the resident was a sterile male, the resident won 52% of encounters against wild intruders and 41% against sterile intruders ($\chi^2 = 0.6$; $P > 0.05$). Wild and sterile resident males won similar proportions of all encounters ($\chi^2 = 0.2$; $P > 0.05$). Independent of resident-intruder status, wild males won 48% (32/67) and sterile males 52% (35/67) of their interactions against heterotypic males, proportions not significantly different from 50% as expected by chance alone ($Z = 0.4$; $P > 0.05$; normal approximation to binomial distribution here and below).

As these results suggest, no resident advantage was evident in the observed interactions. In encounters involving wild resident males, the resident won only 52% of all interactions, a proportion not significantly different from 50% ($Z = 0.25$; $P > 0.05$). Likewise, sterile resident males won only 47% of all interactions ($Z = 0.4$; $P > 0.05$). Independent of wild vs. sterile status, residents won 50% (57/115) of all interactions ($Z = 0.1$; $P > 0.05$).

Previous studies (Shelly et al. 1994, Shelly & Whittier 1996) demonstrated that sterile *C. capitata* males from this same 40-year old laboratory strain successfully located and joined natural leks, signaled (pheromone-called) as frequently as wild males, and produced a pheromonal signal as attractive to females as that produced by wild males. Despite these similarities, however, sterile males had low mating success with wild females. The present findings indicate that this poor mating performance did not result from a lowered success in agonistic encounters, since sterile males were as likely to win aggressive encounters as wild males. This conclusion does not rule out the possibility that selection pressures in the laboratory (or the irradiation procedure per se) produced some qualitative or quantitative changes in the aggressive behavior of the sterile males. However, it does suggest that such changes, if occurring, did not have a large effect on male aggression in the present study. This situation contrasts with that of Briceno et al. (1998), who observed flies in a field-caged host tree and found that wild males won most encounters against sterile males (from a 4.5 year-old strain). These differing results suggest that mass-reared strains may vary in their aggressiveness. The prevalence and magnitude of such inter-strain variation as well as the impact of such variation on sterile insect release programs involving *C. capitata* are presently unknown.

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SUMMARY

The outcome of aggressive interactions between wild and lab-reared, sterile males of the Mediterranean fruit fly, *Ceratitis capitata*, was recorded under natural conditions in a fruit orchard on Maui, Hawaii. Success in aggression was independent of either male type (wild vs. sterile) or territorial status (resident vs. intruder).

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