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# Seasonal effects on superparasitism by *Rhagoletis completa*

ROBERT G. LALONDE\* and MARC MANGEL

Section of Evolution and Ecology and Center for Population Biology, University of California, Davis,  
CA 95616, USA

## Summary

1. We investigate a host–parasite system in which superparasitism is a more viable strategy than is initial parasitism. Walnut husk flies (*Rhagoletis completa* Cresson) readily use sting holes made by conspecifics as oviposition sites.
2. Superparasitism is probably a viable strategy because husks have sufficient food for more than one fly's offspring and are difficult to parasitize initially due to the toughness of the husks. Flies preferentially attacked nuts with significantly softer husks than those which were unattacked.
3. Furthermore, flies oviposited in nuts with experimental oviposition punctures in preference to unmanipulated controls at the beginning of the season when husks were tough. However, at the end of the season when husks had softened this preference disappeared and flies readily attacked controls.

**Key-words:** superparasitism, oviposition behaviour, walnut husk fly.

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## Introduction

Superparasitism, the phenomenon in which parasitic insects oviposit on hosts that already bear conspecific eggs or larvae, is usually regarded as a behaviour that is expressed when unattacked hosts are relatively rare (Roitberg & Mangel 1988; Papaj, Roitberg & Opp 1989). In this interpretation a female parasite accepts the lower offspring fitness gained by this behaviour, because unattacked hosts are not available in sufficient numbers for all of her eggs (Parker & Courtney 1984; Mangel & Clark 1988). Most described cases of superparasitism have occurred under circumstances supporting this interpretation (Hubbard *et al.* 1987; Bai & Mackauer 1990; Visser, van Alphen & Nell 1990; Speirs, Sherratt & Hubbard 1991; Roitberg *et al.* 1992; Van Alphen, Visser & Nell 1992). An exception to this general rule occurs if an initial oviposition makes a host more available to conspecifics. For example, a host may be more available to subsequent parasites when oviposition breaches some physical barrier, such as a thick host cuticle. In this case, unattacked hosts need not be rare, as long as fitness expected from exploiting already-parasitized hosts is still relatively high. Thus, for example, Mediterranean fruit flies (*Ceratitis capitata*) (Wiedemann)

superparasitize thick-skinned hosts such as citrus fruits in apparent preference to unexploited hosts (Papaj, Katsoyannos & Hendrichs 1989; Papaj *et al.* 1992). Similarly, *Ooencyrtus nezarae* Ishii females prefer hosts (heteropteran eggs with thick cuticles) which have already been parasitized over unattacked hosts when it is unlikely that they are superparasitizing their own offspring (Takasu & Hirose 1988).

Walnut husk flies (*Rhagoletis suavis* group) are parasites of husks of native black walnuts (*Juglans* spp.) in North America (Bush 1966). In Central California, *R. completa* attacks *Juglanshindsii* Jeps (Boyce 1934). Flies lay eggs under the epidermis after first excavating a cavity with their ovipositors. *Rhagoletis completa* flies readily superparasitize hosts already occupied by offspring of conspecifics, often employing the same oviposition puncture (Boyce 1934; our unpublished data). This behaviour is also reported for other walnut husk fly species (Papaj 1993). Female flies apparently prefer superparasitism to oviposition in unattacked hosts. Most parasitized nuts in the field bear far larger clutches of eggs than could be produced by a single fly. Although nut husks contain relatively large amounts of resources, larval survivorship and pupal mass is reduced in hosts supporting large numbers of competing larvae (unpublished data). Male flies commonly guard recent sting holes, attract females and solicit copulations prior to allowing females to oviposit (our observation, Papaj 1993).

\*Present address: Department of Biology, Okanagan University College, Kelowna, B.C., Canada, V1V 1V7.

Unattacked hosts are presumably not limiting because this can occur when most nuts (approximately 95%) are not yet attacked (our observation). Overcoming host defences is not likely to be driving this behaviour, since there is no increase in either larval survivorship or pupal mass with respect to clutch size (our unpublished data).

Two general, non mutually-exclusive, hypotheses can explain this behaviour. First, excavating a sting hole may be an inherently costly activity. For example making a sting hole is time-consuming and could expose females to predation or cause ovipositor damage. In either case superparasitizing flies trade off reduced offspring success against increased reproductive opportunity. Secondly, nuts may vary in hardness. If softness does not correlate with any visual or olfactory stimuli, finding nuts with soft husks may be very time-consuming. In this case, the best indicator that a host is suitable for oviposition may be the presence of a conspecific's puncture.

Walnut husks can be expected to soften over the season as they ripen. Thus, we should expect to see a change in preference for existing sting holes as nut husks get softer and the cost of making an initial puncture diminishes. In this paper, we investigate whether (i) flies preferentially parasitize nuts with existing punctures; (ii) whether flies preferentially select soft nuts for initial colonization; (iii) whether nut husks soften as the season progresses; and (iv) whether any preference for existing sting holes will reduce as nuts become softer.

## Materials and methods

### SEASON SAMPLES

Six trees on the campus of the University of California Davis were selected for sampling. Sampled nuts were identified prior to the appearance of flies and randomly assigned a sample week, using a coloured flagging tape. When the first sting-holes appeared, nuts were collected on a weekly basis. On the day of sampling, nuts were measured across the widest and narrowest points with a pair of vernier calipers. A measure of husk toughness is the force required to penetrate the epidermis of the husk. A spring penetrometer, calibrated in grams, was used to measure this force. To increase the sensitivity we modified the tip so that a blunted probe (approximately a 1-mm<sup>2</sup> surface), penetrated the husk, rather than the much blunter standard tip. We averaged two measures of husk toughness for each nut for purposes of analysis. If a nut was attacked these measures were taken at least 3 cm from the sting hole. Furthermore, if any eggs had hatched by the time of sampling, no measure of nut toughness was taken. If the nut bore a recent sting hole, any eggs were dissected out and counted. For purposes of analysis of this dataset and the exper-

iments described below, we log-transformed values obtained for numbers of eggs per host.

### STING HOLE PREFERENCE EXPERIMENT

Unparasitized nuts were tagged and systematically assigned to either the stung or unstung treatment groups. We probed nuts in the first treatment group with a No. 00 insect pin to simulate a fly's sting. In order to facilitate discrimination of our sting from any fly stings upon later sampling, we drew a 3-cm diameter circle around our puncture with an indelible black felt marker. The second treatment group was a control and consisted of unmanipulated nuts. Whenever possible, we paired our treatments; nuts frequently occurred on twigs in clusters of two nuts, one of which was assigned to each treatment group. Nuts were left for 3 days after manipulation; then all nuts were collected and processed. This protocol was executed early in the season (4 August), part-way through (12 August) and towards the end of the season when most nuts were parasitized (7 September). We bagged unattacked nuts 2 weeks prior to the final trial (7 September), in order to ensure that enough unattacked nuts would be available for our experiment.

## Results

### SEASONAL EFFECTS

Nut toughness declined significantly during the season. Nuts parasitized by the flies were consistently softer than those that were not parasitized (Fig. 1). Flies did not select nuts that were different in size from unattacked nuts (Fig. 2). The number of eggs in attacked nuts remained high throughout the season. Until the last sampling date, attacked nuts bore over

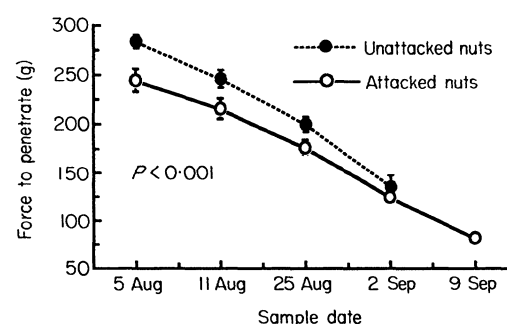
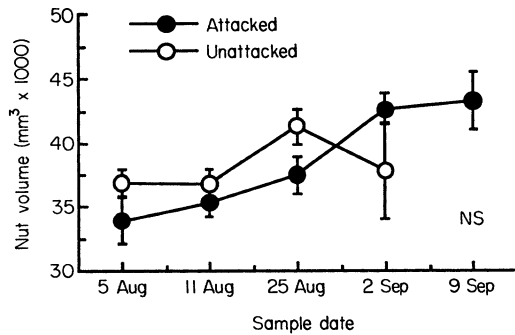


Fig. 1. Nut toughness, measured as the average of two measures of the force required to push a probe through the epidermis, throughout the season. Open circles are mean nut toughness of unattacked nuts at each sample date; closed circles are mean nut toughness of attacked nuts. Flies consistently attacked softer nuts on average throughout the sampling period ( $P < 0.001$ , two-way ANOVA).



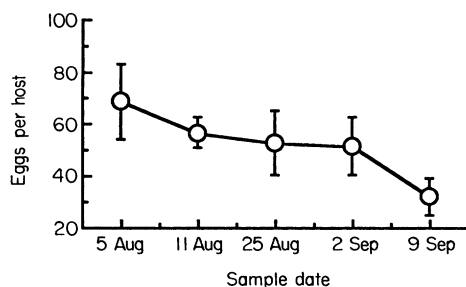
**Fig. 2.** Size of attacked (closed circles) and unattacked (open circles) nuts throughout the sampling period. There was no significant difference between attacked and unattacked nuts with respect to their size (two-way ANOVA,  $P > 0.05$ ). Bars represent 1 SE.

50 eggs on average (Fig. 3). Eggs were almost always located within the same sting hole.

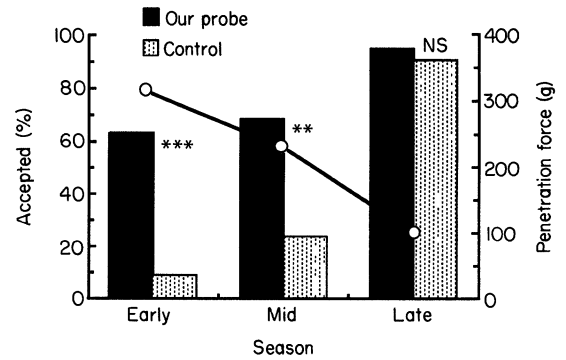
#### PREFERENCE FOR STING HOLES

Our manipulations had a significant effect on host selection, which interacted with time of season. Nuts that were artificially stung early or midway through the season were attacked by flies significantly more frequently than were controls ( $G$ -test; early  $P < 0.001$ , midway  $P < 0.01$ , Fig. 4). In contrast, there was no significant difference between the proportion of stung nuts and control nuts that were attacked in the late-season trial [ $G$ -test;  $P = 0.5782$ , power = 92.5% (Zar 1984), Fig. 4]. Over this same experimental period average husk toughness declined significantly (ANOVA;  $P < 0.001$ , Fig. 4). Flies increasingly selected untreated nuts as the season progressed, and were more likely to lay eggs in their own sting holes on nuts where sting holes were already available (Kruskal-Wallis;  $P = 0.0037$ , Fig. 5).

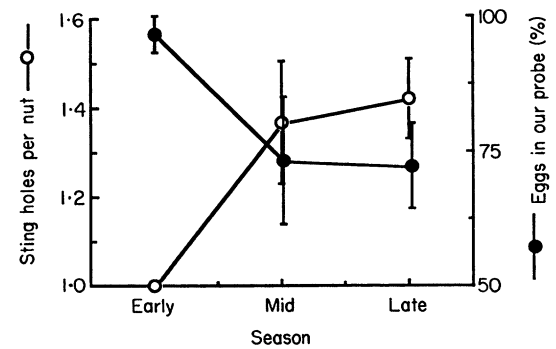
Nuts that did not have an artificial sting hole, but were parasitized during the 3 days of exposure to the fly population differed from artificially-stung nuts in that they contained significantly more eggs (ANOVA;  $P = 0.0129$ , Fig. 6). Such parasitized control nuts



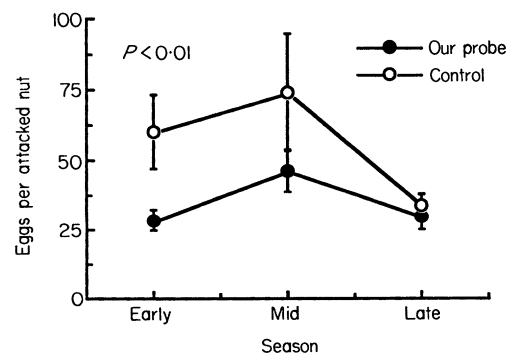
**Fig. 3.** Eggs per attacked nut throughout the sampling period. Bars represent 1 SE.



**Fig. 4.** Percentage of artificially stung (with a No. 00 insect pin; solid bars) and control nuts (open bars) that were subsequently attacked by *R. completa* females at three periods in the season. Open circles represent husk toughness (measured as force required to penetrate) of all experimental nuts for each date. (\*\*\*)  $P < 0.001$ , (\*\*)  $P < 0.01$ , (NS)  $P > 0.05$ ;  $G$ -test of independence).



**Fig. 5.** Allocation of eggs among sting holes within a nut. Dark circles represent percentage of eggs in the provided sting hole in treated nuts. Open circles represent average number of sting holes on all nuts over the three experiments. Bars represent 1 SE.



**Fig. 6.** Eggs per attacked nut for hosts where we experimentally provided a puncture (solid circles) and for unprobed controls (open circles). On the first two experimental dates flies allocated significantly more eggs to attacked controls (ANOVA,  $P < 0.01$ ). Bars represent 1 SE.

were significantly larger than unparasitized controls (ANOVA;  $P = 0.0073$ , Fig. 7a), but did not differ measurably in husk toughness (ANOVA;  $P = 0.7344$ , power = 40%, Fig. 7b).

## Discussion

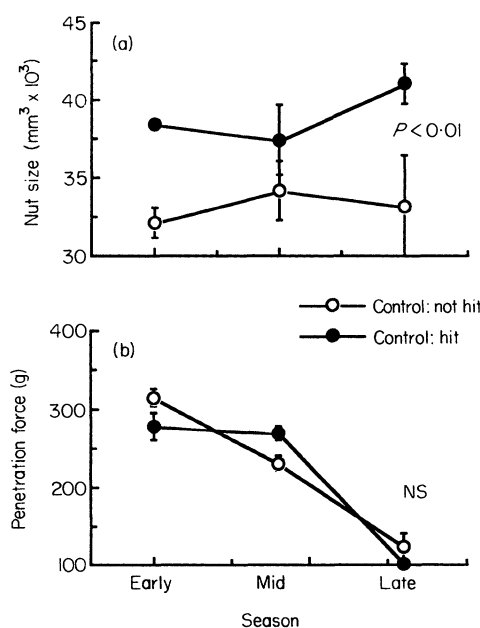
Although superparasitism is usually regarded as a strategy for coping with situations of low host availability, walnut husk flies evidently prefer to express this behaviour, even when hosts are abundant. Walnut husk flies clearly prefer to parasitize nut husks with existing stings and we presume this behaviour is preferred over initial parasitism because of the cost of making an initial sting hole. Exploitation of existing sting holes in preference to nuts without sting holes occurred at the beginning of the season, when husks are hard, but not at the end, when they are soft, suggesting that ease of penetration is the critical factor. Flies also have a much lower life expectancy at the end of the season, a factor that can also affect host selection, independently of host quality (Mangel & Clark 1988). However, parasites that have a lower expectation of life generally express an increase, rather than a reduction in their tendency to superparasitize (Roitberg *et al.* 1992).

Apple maggot flies preferentially attack trees with riper (and presumably softer) host fruit under field conditions (Averill & Prokopy 1989; Murphy, Wilson

& Dówell 1991), but once in the tree may not discriminate among hosts on the basis of ripeness (Prokopy & Papaj 1989). Significantly, our flies selected softer nuts among season samples, but apparently did not prefer softer control nuts in the sting hole experiment (Fig. 7b). Flies may select trees or regions of the tree where hosts are more suitable than average, but may not discriminate beyond a particular threshold once in that region.

In general, *Rhagoletis* flies lay single-egg clutches and ordinarily avoid parasitizing hosts already exploited by conspecifics. Larvae are usually cannibalistic and destroy smaller conspecifics (Averill & Prokopy 1987); this behaviour presumably reinforces selection for single-egg clutches (Godfray 1986; Rosenheim 1993). *Rhagoletis completa* larvae are non-cannibalistic. This allows adults to allocate large clutches to hosts without facing the increased offspring mortality imposed by cannibalism. Thus, non-cannibalistic larvae, large quantities of food present in each host, and relatively high costs associated with parasitizing unattacked hosts evidently make superparasitism a tactic that is at least equally viable as initial parasitism. Phylogeny is frequently invoked as a historical constraint on the evolution of novel adaptations (Gould & Lewontin 1979). Indeed, *Rhagoletis pomonella* (Walsh), a congener of *R. completa* normally parasitizes the small fruits of hawthorns (*Crataegus* spp.). Within the previous century, however, some populations have adopted a much larger host, domestic apple [*Pyrus malus* (L.)] (Bush 1966). On apples, *R. pomonella* retains the habit of laying single-egg clutches and host-marking (Prokopy 1977). However, flies often allocate more than one egg per host, but spread eggs in single-egg clutches over the surface of the apple (Illingworth 1912). As noted above, apple maggot larvae are cannibalistic and may be thus constrained from adopting a true clutch-laying habit, even when attacking substantial hosts.

With the walnut husk fly, however, both initial parasites and superparasites evidently allocate large numbers of eggs at each oviposition. It seems that the strongest determinant of the final clutch size in each host is the number of times that a nut is located by ovipositing flies. Not surprisingly, this leads to a large degree of variation in degree of exploitation. Studies of other tephritids such as the Mediterranean fruit fly (*Ceratitis capitata*) and the apple maggot (*R. pomonella*), indicate that these flies provide information to conspecifics about the degree of prior parasitism by depositing a water-soluble marking pheromone after oviposition, which is discerned by tarsal contact (Prokopy 1975, 1977; Prokopy, Malavasi & Morgante 1982; Prokopy & Roitberg 1984). Thus, for example, whereas *C. capitata* flies parasitizing kumquats prefer to oviposit into existing sting holes, accumulation of pheromone reduces this preference (Papaj *et al.* 1992). We have observed many ovipositions both in the field and in the laboratory, and



**Fig. 7.** Characteristics of attacked and unattacked controls. (a) Nut volume. Attacked control nuts were significantly larger than unattacked controls (two-way ANOVA,  $P < 0.01$ ). (b) Nut toughness (force required to penetrate). There was no significant difference in the force required to penetrate either attacked or unattacked nuts (two-way ANOVA,  $P > 0.05$ ). Bars represent 1 SE.

only once saw a female dragging her ovipositor in a manner similar to other *Rhagoletis* flies that are known to deposit host marks. Therefore, we suggest that if flies use such a pheromone, they do not necessarily use it all the time, for the following reasons. Deposition of a mark is thought to benefit the initial parasite in two ways. First, it prevents a fly searching locally within an area from superparasitizing her own offspring. Secondly, it provides information to other parasites that an older, competitively superior offspring is already present in that host (Roitberg & Mangel 1988). Marked hosts are thus devalued for superparasitism if larvae are cannibalistic, and food and space in the host are limited. Because the initial larva does not always win in competition (Averill & Prokopy 1987), deposition of a mark enhances offspring success for the initial parasite. In the *J. hindsi*/*R. completa* system, initial parasites probably deposit all available eggs in one host; the danger that the same female will superparasitize her own clutch is thus very small. Finally, use of a marking pheromone may actually be a disadvantageous behaviour as it could enhance location of sting holes. Presumably, *R. completa* flies could deposit and respond to a host mark when husks are more easily penetrated at the end of the season. Unattacked hosts are rare on our site by that time, however. Flies are presumably so host-limited then that they will readily superparasitize in any case. Thus, it may be that there is little or no selection for *R. completa* flies to ever express host-marking behaviour.

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