

The Role of Males in Host-Fruit Selection by Females of a Walnut Infesting Tephritid (Diptera) *Rhagoletis zoqui*

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Abstract *Rhagoletis zoqui* Bush flies have a mating system in which males guard and defend walnut fruit-hosts from other males and mate, apparently without courtship, with females as they arrive to oviposit. Hypothetically, female selection of a particular fruit may be due to the quality of fruit for larval development (previously determined by guarding males), the quality of the male upon the fruit as a mate, or both, but this is not clear. We performed an experiment to determine if *R. zoqui* females or males select the fruit to oviposit or guard based on its quality for larval development (i.e., size, sugar-content [brix] or hardness), or following male-mediated cues such as chemical residues, related to prior fruit occupation by the male during guarding. Fruit choice by *R. zoqui* females and males were examined under semi-natural conditions on caged branches of English walnut trees, *Juglans regia* L., growing in the highlands of south-central Mexico. A single male or female was allowed to select a fruit and was then removed. An individual of the opposite sex was then introduced to the same branch and presented with the opportunity to choose among the same array of hosts. The pattern of fruit choice was consistent, with female choice on the basis of male presence, suggesting that males left a chemical cue that persisted in their absence. No fruit quality differences were detected between selected and non-selected fruit. Fruit features selected by females and males matched almost exactly, although males rarely select the same fruit as females. We conclude that females preferentially selected fruit previously occupied by males although additional studies are required to determine the cues used by *R. zoqui* for oviposition resource selection by both females and resource guarding males.

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Introduction

Mating systems are hypothesized to have evolved, in part, on the basis of the availability of resources, including females, in time and space (Emlen and Oring 1977; Parker 1979, Prokopy and Papaj 2000; Alcock and Thornhill 2014). Various intra- and inter-sexual selection pressures can result from differences in the variability and distribution of oviposition substrates, food and other resources. For instance, when females are predictably encountered at relatively rare resource-sites, then males could profitably search these sites for potential mates. When such sites are sufficiently discrete, then males have an opportunity to defend these sites from other males and wait for females to exploit their guarded resources (Prokopy and Papaj 2000). A proposed consequence of male rare-resource guarding is that females may find it energetically expensive to resist mating with a defending male or leave a resource site in search of another undefended site. If so, she may benefit by mating with the guarding male that is under little intersexual selection to evolve a courtship that advertises his suitability as a mate (Burk 1981). Nevertheless, the ability to defend and hold a resource site, such as a fruit, could be indicative of “male quality” (Andersson 1994).

Rare-resource-guarding has been predicted as defining the mating system of *Rhagoletis* fruit flies (Tephritidae) (Prokopy 1980; Burk 1981). However, key assumptions of this hypothesis have never been tested, specifically: 1) fruit vary in quality for larvae, 2) high quality oviposition sites are relatively rare, 3) males are able to recognize high quality hosts preferred by females, and 4) males are able to intercept and mate females when they arrive to oviposit. In addition, the possibilities of female fruit choice based on the quality of the guarding male as a mate, and courtship-signals that advertise quality, have not been considered.

Rhagoletis zoqui Bush infests various walnut species including English walnut, *Juglans pyriformis* Liebm. and *Juglans regia* L. (Aluja et al. 2000; Rull et al. 2013). Males defend fruit from other males and await the arrival of a female to initiate mating (Guillén 2008). Such behavior is consistent with that of all known species of *Rhagoletis* (Prokopy and Papaj 2000). Females of several species have been found to respond to specific volatiles and visual cues stemming from the host (Katsoyannos 1989; Bierbaum and Bush 1990; Messina 1990; Alonso-Pimentel et al. 1998; Henneman and Papaj 1999; Linn et al. 2012; Cha et al. 2012), and to combinations of fruit cues and male-derived volatiles (Prokopy and Bush 1972; Prokopy et al. 1973; Prokopy 1975; Katsoyannos 1976; Katsoyannos et al. 1980; Papaj et al. 1996).

Few studies have identified host cues that guide males or females to a specific fruit resource and that serve as selection criteria once a fruit has been examined. *Rhagoletis cerasi* L. and *R. pomonella* males are attracted to fruit by pheromones deposited by females after oviposition, thereby enhancing the probability of encountering a mate in the vicinity (Prokopy and Bush 1972; Katsoyannos 1975). Males of *Rhagoletis juglandis* Cresson and *Rhagoletis boycei* Cresson guard superficially-damaged fruit to improve their probability of mating with females arriving to oviposit into existing fruit cavities as these superficial cavities reduce both the time required by females for oviposition and the risks of predation (Papaj 1993, 1994; Papaj and Alonso-Pimentel

1997). Females of different species of walnut infesting *Rhagoletis* prefer to oviposit in larger fruit, in which their offspring may gain improved fitness-related traits compared to conspecifics that develop in smaller fruit (Guillén et al. 2011). Sugar content and fruit firmness are also important in host selection by females of other species of *Rhagoletis* (Prokopy and Papaj 2000). For example, *Rhagoletis indifferens* Curran prefers to oviposit in softer fruit with higher concentrations of sugars (Messina et al. 1991). Several species of walnut infesting *Rhagoletis*, including *R. zoqui*, have been hypothesized to overcome fruit chemical defenses by reusing oviposition punctures and so benefit by fruit-superparasitism (Prokopy and Papaj 2000; Guillén 2008). Additionally, *R. zoqui* males have been observed dabbing the tip of their abdomen on to the surface of guarded fruit, a behavior that could be indicative of the deposition of a chemical mark (Guillén 2008).

From the perspective of a frugivorous insect such as *R. zoqui*, oviposition preference should accurately reflect host quality for the development of progeny, i.e., fruit with the quantity and quality of nutrients for optimal larval development (Balagawi et al. 2005). As such, oviposition site selection may be influenced not only by the size of the fruit, but also by the presence and sex of conspecifics, or chemical cues that provide information on the history of the oviposition resource such as ODPs (oviposition deterring pheromone), physical oviposition damage, or evidence of male defense of the resource (Jaenike 1990; Mayhew 1997; Roitberg and Mangel 1998; Aluja and Mangan 2008).

To determine the roles of these putative cues, host choice was observed within large conical muslin bags placed over fruiting walnut branches in the field. A male or female was allowed to occupy a fruit, that fly was removed and an individual of the opposite sex was provided an opportunity to choose among host fruits of the same branch. Features of walnut fruit likely related to resource quality, both for larval development and as sheltered sites for oviposition, were measured, including size, firmness, and sugar concentration. We predicted that female fruit choice for oviposition would be influenced by fruit guarding choices made by previous male occupants of each cage, which in turn would be indicative of fruit quality for larval development, and that male fruit choice for guarding would be influenced by particular fruit features.

Materials and Methods

Study Site

Foraging studies were carried out on *J. regia* (English walnut) trees in Cuapiaxtla, Tlaxcala, Mexico (19°17'79" N: 97°46'16" W, at an altitude of 2440 masl). The study site was a small village surrounded by agricultural fields with a mean annual precipitation of 612 mm and an average temperature of 13.4 °C. During July, the month when adult flies were active in the field, the average minimum temperature was 6.8 °C and the maximum 21.6 °C.

In March 2010, 4 fruiting branches of 6 *J. regia* trees were caged with white chiffon fabric bags (1 × 0.80 m) to protect fruit from *R. zoqui* natural infestation. Each branch bore different numbers of walnut clusters (*J. regia* trees produce clusters of two or three fruit, each cluster comprising fruit of a uniform size and developmental stage). Fruit

within each cluster were highly uniform with little if any visible variation when examined by a human observer. The total number of fruit per branch varied between 6 and 32.

Source and Use of Adult Flies

Rhagoletis zoqui flies used in foraging studies emerged from *J. regia* fruit collected in Cuapixtla, Tlaxcala in the previous year, at the end of July 2009. Infested fruit were placed in plastic baskets over trays containing vermiculite and checked every three days to recover pupae. Pupae were placed in a 250 ml plastic cup with a 2.5 cm layer of damp vermiculite at the bottom and sealed with a chiffon cloth and perforated plastic lid that allowed ventilation. Containers were kept in a room at ambient environmental conditions and sprayed with a 2 % sodium benzoate-water solution, to prevent fungal growth, every 15 days until emergence of adult flies.

Newly emerged adults were sorted by sex and placed in 30 × 30 × 30 cm Plexiglas cages. Flies were fed ad libitum with a mixture of three parts of granulated sugar-one part of hydrolyzed protein (Greif Bros. Corp., Delaware, Ohio, US). Water was continuously available through a cotton wick inserted into the lid of a 20 ml plastic bottle. Cages were placed in a laboratory under a 12:12 h light:dark cycle, at a temperature of 27 ± 1 °C and 80 % RH. Males and females of *R. zoqui* mate multiple times and females oviposit after each mating in the presence or absence of males (Guillén 2008). Therefore, recently mated flies of both sexes were used to ensure that females were suitable to select a host for oviposition or guard a fruit resource in the case of males. For this, 12 h prior the onset of experimental observations, sets of 5 pairs of virgin females and males aged 10–20 d old were placed together in a Plexiglas cage (20 × 20 × 20 cm) and allowed to mate (mating was observed from approximately 8:00 am onwards each day). Each time that a mating pair was observed, the pair was carefully covered with a glass vial, taking care not to disturb it. When copulation ended, the female and male were transferred to different cages to avoid re-mating.

Bioassay

Fruit choice bioassays were performed in July and August, 2010. Each day, before observations, branches with fruit were prepared as follows. Chiffon bags protecting the branches were replaced by organza muslin bags (0.70 m long × 0.35 m of diameter) that allowed direct observation of insect activities inside each bag. Additionally, some leaves were removed to improve the visibility of fruit clusters and flies during observations.

To observe male and female resource choice decisions, first (step 1), 3 recently mated males or females were released onto a branch. The time that elapsed for the first female or male to select a fruit for oviposition or guarding, respectively, and the fruit that was selected by each insect were recorded. In the case of females, a fruit was considered selected when a female first attempted to oviposit; at which moment she was immediately removed to prevent fruit infestation. A fruit was considered selected by a male if the male walked over the surface of the fruit and remained on it for at least 3 min. The first fly that selected a fruit was captured and isolated in a 2 L plastic container cage-type with water and food. The remaining two flies were removed and

discarded. In the second step (step 2), 3 recently mated individuals of the opposite sex were released on to the same branch. The time for the first fly to select a fruit for oviposition (females) or guarding (males) and the fruit selected were recorded as described in step 1.

Observations were performed between 09:00 and 15:30 h. Each sequence of introduction (female released first or male released first) was performed ten times. At the end of the experiment, selected and unselected fruit were removed, immediately transported to the laboratory, and their sugar content, firmness and size were measured as follows. Each fruit was weighed using a semi-analytical balance (Ohaus Precisión Plus TP4KD), fruit length was measured to an accuracy of 1 mm using a vernier caliper and firmness was measured using an Accuforce III, penetrometer (Ametek, Mansfield & Green Division, Mod. TCD200 with a 1 mm diameter \times 10 mm long needle). Finally, sugar content (brix) was measured using a digital refractometer (Atago[®], Pocket Pal-1).

Statistical Analyses

To preserve, as much as possible, the natural state of the fruiting branches, we neither removed nor added fruit. Thus, the number of fruit per branch varied. The likelihoods of flies choosing the same fruit as the previous individual were calculated through a Fisher exact test.

To compare fruit features (i.e., weight, long, wide, G-brix and firmness) of selected and non-selected fruit, a nested design generalized linear model (GLM) was employed. To determine if prior occupancy of hosts by the opposite sex affected host-selection decisions by subsequent foragers, the times to find and select fruit before and after opposite sex visits were compared by t-test. It was assumed that if the second fly was influenced by previously visited fruit this would be reflected in the time taken to choose a host.

Analyses were performed using the Statistica 7.0 program (StatSoft Inc. 2004).

Results

Males did not prefer to visit fruit previously occupied by a female. In 90 % of the fruit choice events, males selected a fruit that differed from that previously selected by a female (Fig. 1). However, females were significantly more likely to visit fruit previously occupied by a male, even when they had many fruit among which select. (Fig. 1, Fisher's exact $p = 0.0286$).

There were no significant differences between chosen and non-chosen fruit by females and males in terms of mean weight ($F_{10, 229} = 0.35$; $p = 0.96$), length ($F_{10, 229} = 0.78$; $p = .96$), width ($F_{10, 229} = 1.03$; $p = 0.36$), sugar concentration ($F_{10, 229} = 0.45$; $p = 0.92$) or hardness ($F_{10, 229} = 0.95$; $p = 0.48$). The mean values for fruit weight, fruit length, fruit width, sugar content and hardness for fruit selected by females and males were almost identical in all cases (Table 1).

There were no significant differences in the mean time that females took to select a fruit that had been visited or not by a male fly ($t_{18} = 1.53$; $p = 0.18$). However, after a male visit to the branch, females took almost the half of the time to select a fruit (Fig. 2).

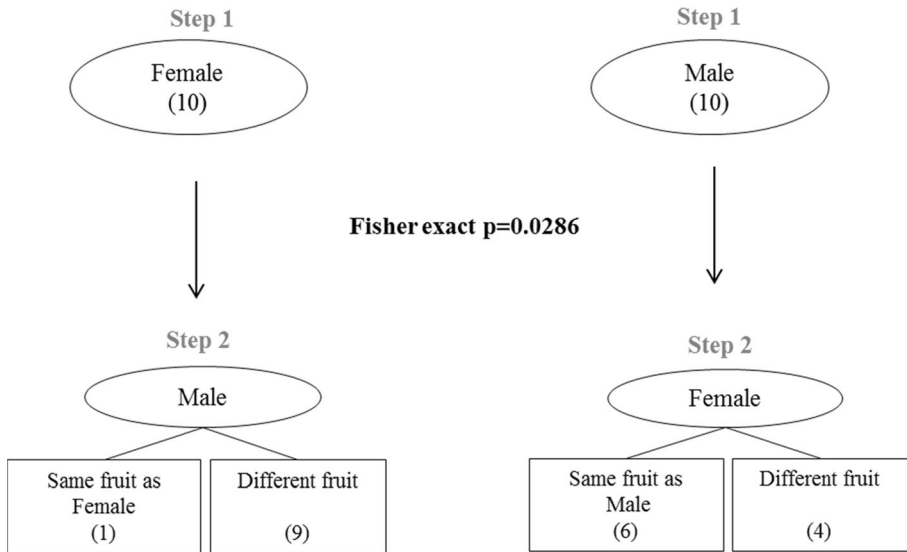


Fig. 1 The patterns of host-fruit choice by male and female *Rhagoletis zoqui*. Step 1, indicates the sex of fly initially introduced into the cage containing a walnut branch to select a fruit. Step 2, indicates the sex of fly introduced subsequently. The number between in parentheses indicates the frequencies of selected fruit

Similarly, males took a similar mean time to select a fruit whether or not it had been previously visited by a female fly ($t_{18} = 1.14$; $p = 0.25$). Although males did not tend to select the same fruit as females, when they selected a fruit after a female had occupied the branch, they required approximately 10 min less time to select a fruit, although this was not significant (Fig. 3).

Discussion

Previous male occupancy played a significant role in *R. zoqui* female fruit choice. Females were likely to visit the same fruit a male had guarded, but males were not more likely to guard fruit in which females had previously attempted to oviposit. Such a result supports the hypothesis that females selected fruit, at least when males are in the vicinity, on the basis of male fruit occupancy or guarding; possibly in response to a

Table 1 Features of selected and non-selected fruit by *R. zoqui* females and males

Fruit features	Fruit selected by		Non-selected (mean \pm SE)
	Females (mean \pm SE)	Males (mean \pm SE)	
Weight (g)	37.52 \pm 1.86	37.51 \pm 1.86	39.88 \pm 0.58
Length (cm)	4.11 \pm 0.06	4.08 \pm 0.06	4.23 \pm 0.02
Width (cm)	3.75 \pm 0.07	3.74 \pm 0.07	3.82 \pm 0.02
Hardness (N)	5.41 \pm 0.30	5.11 \pm 0.30	5.12 \pm 0.09
Sugar content ($^{\circ}$ brix)	7.20 \pm 0.18	7.28 \pm 0.18	7.02 \pm 0.06

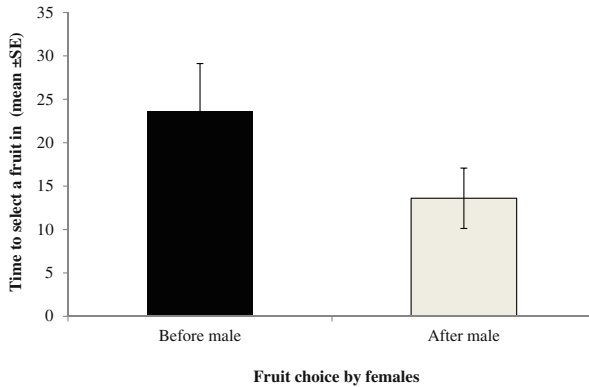


Fig. 2 Mean time spent by *Rhagoletis zoqui* females to select a fruit before and after of the fruit-choice by male

male-produced chemical compound deposited on the fruit surface. These results are equally inconsistent with the hypothesis that males attempt to place themselves in the vicinity of females based on evidence of prior selection of fruits by ovipositing female flies. Certainly sizes, sugar content and hardness of chosen and non-chosen fruit failed to show any physically attractive quality in the chosen fruit. This finding is inconsistent with the possibility that chosen fruit were particularly suited for larval development and so represented unusually high quality fruits, at least for the features measured in this study. Qualitative differences among fruit on a branch could be masked by tree-specific variation in factors such as different nutritional status, or age, etc. The information obtained from the fruit parameters we measured indicated that these differences were too small to detect using the methods we employed, although small physical or chemical variation may be highly apparent to searching tephritids. For example, *R. zoqui* males were observed walking around the circumference of a fruit several times before the initiation of fruit guarding, a behavior that was not observed in females and which may be important in the process of fruit quality evaluation by the male fly (Guillén 2008). Previous tree-wide samples of fruit in the same walnuts trees used in the present study failed to find any significant relationship between *R. zoqui* infestation

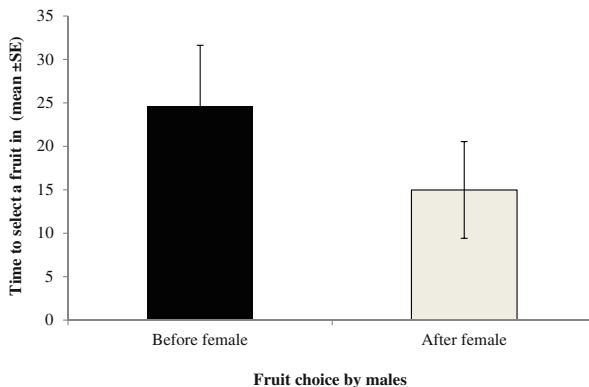


Fig. 3 Mean time spent by *Rhagoletis zoqui* males to select a fruit before and after of the fruit-choice by female

levels and fruit hardness or sugar content, although a significant but weak positive effect of size was detected ($r^2 = 0.05$; Guillén 2008).

If females take male-association into account when choosing a fruit, what cues do they use and why would inseminated females place themselves in the position of re-mating? The first question may be answered by the female preference for male-occupied fruit in the absence of males. Since male-related visual and auditory cues were not present (Sivinski et al. 1984; Sivinski et al. 2004) during female fruit selection, it was likely that males left a chemical cue, perhaps a pheromone deposited during the previously mentioned abdominal dabbing behavior (Guillén 2008). As noted earlier, male-derived volatiles in combination with fruit volatiles have been implicated in female *Rhagoletis* attraction to fruit (Prokopy and Bush 1972; Prokopy et al. 1973; Katsoyannos 1976; Katsoyannos et al. 1980; Papaj et al. 1996).

Why inseminated females seek out males is a more difficult question to answer. Polyandry research has recently undergone a renaissance (Pizzari and Wedell 2013), and several meta-analyses have indicated that multiple-mates generally have a positive effect on female fitness (Arnqvist and Nilsson 2000; Slayter et al. 2011). This increased fitness can derive from a range of benefits including obtaining additional paternal investment, diluting the effects of selfish genetic elements, increasing genetic variability in broods and encouraging competition among sperm whose phenotypes reflect their genetic qualities (Simmons 2005). Which, if any, of these might select for polyandry in *R. zozui* is unknown, but the range of copulatory frequencies among frugivorous tephritids in general could be the subject of revealing comparative studies.

Female tephritids differ widely in their propensity to re-mate and this variability can be both inter- (Aluja et al. 2009) and intra-specific (Sivinski and Heath 1988; Perez-Staples et al. 2008). As an example of congeneric differences, most female *Anastrepha obliqua* (Maquart) copulate once whereas *Anastrepha ludens* (Loew) is more likely to engage in multiple mating (Aluja et al. 2009). At the generic level, numbers of mates tend to be much higher in *Rhagoletis* spp. than in *Anastrepha* spp. Female *Rhagoletis pomonella* mated an average of 15.5 times over a period of 14 days and some copulated up to 8 times in a single day (Opp and Prokopy 2000), whereas only ~15 % of *A. ludens* mate 4 times or more (Aluja et al. 2009). In the case of *R. zozui*, females can re-mate up to five times in a single day (Aluja et al. 2001).

Frequent mating has been postulated to be a consequence of a male resource-defense mating system (Burk 1981), in which females are forced copulate with host-guarding males in order to gain access to host fruit. However, female *R. zozui* attraction to males and male cues, particularly those on fruit they would not otherwise choose to use for oviposition, is inconsistent with this argument. A factor that could explain this behavior is the host superparasitism phenomenon reported in walnut husk flies (*Rhagoletis suavis* group) (Papaj 1993). In this group, females prefer superparasitized over unused/clean hosts because they get direct benefits (Nufio et al. 2000). For example, infested fruit are softer and as a result easier to penetrate reducing aculeus wear (Papaj 1993; Lalonde and Mangel 1994; Nufio et al. 2000). In addition, reusing existing sting holes saves time and lowers predation risks (Papaj and Alonso-Pimentel 1997). In conjunction with this female behavior, it has been shown that males guard oviposition sites on fruit to increase their mating success (Papaj 1994). So, and in agreement with our results, male or male cues on the fruit could be a critical signal for females aiding them in optimal host selection (Lalonde and Mangel 1994; Papaj and Alonso-Pimentel 1997).

In herbivorous insects, one of the most robust theories explaining patterns of host preference is the “preference-performance hypothesis” (Jaenike 1978; Thompson 1988) which states that female oviposition preference corresponds to patterns of host suitability that in turn optimize larval performance. Nevertheless, this phenomenon is not universal (Balagawi et al. 2013). For example, in *R. juglandis*, another species of the same *suavis* group, it has been found that oviposition preference is negatively correlated with offspring performance (Nufio and Papaj 2004). In the case of this species, females prefer to oviposit in larger fruit and superparasitize them. As a result, high larval densities are created that reduce their survival and pupal weight (Nufio and Papaj 1994). Considering that the “preference-performance hypothesis” does not match the walnut-husk-fly-system (Nufio and Papaj 2004) as apparently females privilege their fitness over the one of their offspring, we postulate here that yet to be determined male and female cues may be at play as critical signals in male/female interactions and female oviposition decisions. Further studies on this are therefore needed.

Single factors are unlikely to be solely responsible for the evolution of a mating system (Ridley 1990). Our study underlines the complexities of both host selection and mate choice and their interactions in insect mating systems. Future research into possible chemical attractants derived from both fruit and adult fruit flies could provide a tool for the development of attractants and/or baits for gravid female flies with applications in the management of *R. zoqui* populations in commercial walnuts. In addition, an improved understanding of the roles of chemical cues involved in host and mate selection could provide insights into the evolution of mating systems in *Rhagoletis* fruit flies.

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