

Role of colour and shape stimuli in host-enhanced oogenesis in the walnut fly, *Rhagoletis juglandis*

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Abstract. This study aimed to quantify effects of the host plant on oogenesis in the walnut-husk-infesting fly, *Rhagoletis juglandis* Cresson (Diptera: Tephritidae), and to assess the role of physical cues in those effects.

In laboratory assays, the presence of fruit was manipulated independently of the presence of foliage for newly emerged females. After eight days, in each of two trials, females with fruit were found to have significantly higher egg loads than females without fruit. Foliage presence had little effect.

In a second experiment, females held with fruit or a fruit model (plastic yellow sphere of a size similar to fruit) had significantly higher egg loads than females held with neither fruit nor model. Egg loads of females with fruit were not significantly different from those of females with models.

In a third experiment, females were held with spheres of various colours or no sphere at all. Females with yellow or green spheres (similar to the colour of walnut fruit) had significantly higher egg loads than females with black, blue or red spheres of other colours or females without spheres.

In a fourth experiment, females held with spheres had significantly higher egg loads than females held with cubes of equivalent surface area or females held without a model.

Finally, cohorts of newly emerged females held with yellow spheres or without spheres were sampled periodically. In the sphere treatment, mean egg load increased sharply from negligible levels between days 8 and 10. The pattern was similar in the no-sphere treatment, although the increase in egg load appeared to occur a day later.

From these experiments, we conclude that physical host fruit stimuli known to be important in host selection in *Rhagoletis* flies, including colour and shape, also enhance oogenesis in the first egg maturation cycle, and that enhancement of oogenesis via these stimuli requires neither nutritional input from the fruit nor prior egg deposition.

Key words. *Rhagoletis*, tephritid, host selection, oogenesis, sensory stimuli, colour.

Introduction

Ovarian development, like other forms of reproductive development, is regulated by both internal (*endogenous*) and external (*exogenous*) factors. Reproductive physiologists have extensive knowledge of endogenous factors affecting ovarian development in many animals and are fast approaching a

detailed molecular understanding of the basic elements of oogenesis (Raikhel & Dhadialla, 1992; Yin *et al.*, 1993; Hagedorn, 1994; Romans *et al.*, 1995). By comparison, analysis of exogenous factors in ovarian development has been neglected, despite widespread appreciation that reproductive development is a complex process involving physiological, behavioural and environmental elements interacting in a synergistic fashion (Crews, 1992).

The role of resources required by juveniles as an exogenous factor in ovarian development has received particularly scattered attention. This is especially true regarding instances

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in which sensory stimuli associated with such resources act as triggers or promoters of development. In vertebrates, studies of resource-cued reproductive development are relatively numerous and robust (reviewed by Crews, 1992), and would seem to justify increased examination in other animal groups. For example, nest-building behaviour in the pinyon jay, a pinecone specialist, is a function of gonadal development, which is itself triggered by seeing unripe cones (Ligon, 1978). Nest building is consequently delayed in years when pinecones are scarce. An uncommonly well-documented example of a sensory effect on ovarian development in insects is provided in work on burying beetles (*Nicrophorus* spp.). Here, the preparation of the host resource (a small vertebrate carcass) for oviposition initiates oogenesis (Scott & Traniello, 1987). Sensory stimuli received during behavioural assessment of the host carcass generates an abrupt increase in Juvenile Hormone (JH) production which promotes rapid ovarian development (Trumbo *et al.*, 1995). In both the pinyon jay and burying beetle examples, resource-cued development is thought to be adaptive, because the availability of ephemeral resources essential to reproduction cannot be predicted in advance of the appearance of those resources.

The relevant sensory stimuli involved have not been characterized in detail in either system. Generally, analysis of stimuli that trigger or promote reproductive development falls far short of the kind of detailed analysis that has been made of the sensory stimuli involved in reproductive behaviour. The classic work of Hillyer (1965) and Hillyer & Thorsteinson (1969) on fruit flies and diamondback moths, respectively, stand as exceptions. In these studies, it was demonstrated that a single volatile component of the insects' host plants, allyl isothiocyanate, promoted ovarian development to a degree similar to that of the whole plant.

The aims of the present study were two-fold: to quantify the effects of the host plant on oogenesis in a walnut fly, *Rhagoletis juglandis* Cresson (Diptera: Tephritidae) and to assess the role of physical cues involved in those effects. We predicted *a priori* a connection between cues involved in reproductive behaviour and those involved in reproductive physiology. Specifically, we anticipated that host fruit cues influencing oogenesis would be similar in kind to cues used in selection of host fruit for egg-laying. Flies in the family Tephritidae are excellent organisms with which to test such a prediction. There is at least preliminary evidence that host fruit influences ovarian development in members of the family (Fletcher *et al.*, 1978; Fletcher & Kapatos, 1983; Girolami *et al.*, 1987; Koveos & Tzanakakis, 1990, 1993) and thus incentive for examining the issue in our study species. Moreover, host selection behaviour in tephritid flies is particularly well-characterized (reviewed by Prokopy & Roitberg, 1984; Reissig *et al.*, 1985; reviewed by Katsoyannos, 1989; Papaj *et al.*, 1989a,b; reviewed by Fletcher & Prokopy, 1991; Aluja & Prokopy, 1992; Aluja *et al.*, 1993; Papaj, 1993; McPherson & Steck, 1996). Flies are known to use visual, olfactory and tactile cues to locate and accept host fruit for oviposition. At close range (< 1 m), colour and shape cues are especially important for both attraction to fruit and acceptance of fruit for egg-laying (Prokopy, 1977; Owens, 1982;

Katsoyannos, 1989; Vargas *et al.*, 1991; Prokopy *et al.*, 1993; McPherson & Steck, 1996). Experiments were, therefore, designed to determine whether these cues in particular would influence oogenesis in *Rhagoletis juglandis*.

Materials and Methods

Natural history

Rhagoletis juglandis is a member of the *Rhagoletis suavis* group (Bush, 1966; McPherson & Han, 1997). Like other members of this group, *R. juglandis* females lay eggs in the husks of walnuts and larvae develop exclusively within those husks (Boyce, 1934). In southern Arizona, this species uses the Arizona walnut, *Juglans major*, which is found in montane canyons from between 1200 and 2700 m in elevation. As in other *Rhagoletis* species, the mating system of *R. juglandis* is characterized by resource defence, in which males establish territories on fruit and contest those fruit with intruder males. Males mate with females that arrive on fruit in search of egg-laying sites. Egg deposition is typical of other *Rhagoletis* species in the *suavis* group: females drill through the surface of the walnut husk with their ovipositor and deposit a clutch of up to twenty eggs in the puncture. In all *Rhagoletis* species that have been studied, females deposit a marking pheromone on the fruit after egg-laying and avoid laying eggs in such marked fruit. Despite engaging in a genus-typical pattern of marking behaviour, however, *R. juglandis* females (like other members of the *suavis* group) actively re-use oviposition punctures on marked fruit (Papaj, 1993, 1994; Papaj & Alonso-Pimentel, 1997). Males guard these punctures and increase mating success as a consequence (Papaj, 1994). Larvae complete development in the fruit within 2 weeks, after which they exit the husk and pupate in the soil beneath the natal tree. Pupae enter an obligate diapause and emerge the following summer as adults.

General protocol

Unless otherwise noted, all experiments below adopted the following general protocol. Flies were collected the previous year as larvae in fruit from lower Garden Canyon in Cochise County or from the town square of Patagonia in Santa Cruz County in southern Arizona. Pupae were stored at 5–10°C in total darkness for at least 4 months to break diapause. Upon warming to room temperature, flies typically emerge as adults within 5 weeks. Adult flies were placed in 473-ml clear plastic cups assigned to one of various treatments in the experiments described below, and were given *ad libitum* water and food in the form of free sugar and a slip of enzymatic yeast hydrolysate/sugar mixture. Flies in different cups were visually isolated from one another using opaque white partitions. Cups were surrounded from behind, below and from each side by a white background. Daylight-mimicking fluorescent light provided light from above. Unless otherwise indicated, flies were left in cups for 8 days at $\approx 27^\circ\text{C}$, after which they were removed

and dissected. The number of fully mature oocytes present in the abdomen of each fly (referred to hereafter as 'egg load') was recorded. Fully mature oocytes are readily distinguished from earlier stages by the complete absence of nurse cells and the occurrence of a distinct chorion. Occasionally, fully yolked but unchorionated eggs were noted and included in our counts; however, such eggs were relatively uncommon.

Effect of fruit vs. foliage

This experiment was designed to assess the effects of the presence of the walnut fruit and foliage on oogenesis. Fruit and foliage of *Juglans major* were freshly picked and stored under refrigeration for up to a week before treatment. Four treatments were prepared: cups containing either a single fruit, a bouquet of several leaves, both fruit and foliage, or neither. The fruit was suspended from the top of the cup. Foliage stems were trimmed and cut ends of the stem were immersed in water in small glass vials. Four cups of each treatment were prepared, each cup containing four females. The experiment was run twice. Fruit was replaced once during the course of each trial.

Effect of fruit vs. fruit model

This experiment aimed to determine if a fruit model affected oogenesis to an extent similar to that of real fruit. Three treatments were prepared. In one treatment, a slightly unripe walnut fruit was present in the cup. In another, a yellow plastic sphere (actually, a fluorescent yellow table tennis ball, Franklin Sports, Inc., Stoughton, MA) about the size of the fruit (3.7 cm in diameter) was present. In the third, neither fruit nor fruit model was present. Four cups of each treatment were prepared, each cup containing six females. The experiment was run twice, once using an unidentified *Juglans* species planted in Reid Park in Tucson as host fruit and once using *Juglans major* fruit.

Effect of model colour

This experiment was designed to assess the effect of model colour while keeping model shape constant. Plastic spheres were painted either black, blue, green, red or yellow. Fluorescent tempera paint (Pro Art, Beaverton, OR; Fluoro Blue, Fluoro Green, Fluoro Yellow, Fluoro Red) was used, except in the case of black spheres which were treated with regular tempera paint (Pro Art brand, Black). Each treatment cup received one of the painted models, except for a control in which no model was placed. Four cups of each treatment were prepared, each cup containing six females.

Effect of model shape

This experiment was designed to assess the effect of model shape while keeping model colour constant. Wooden spheres

3.81 cm in diameter (surface area = 60.80 cm²) and wooden cubes 3.18 cm in diameter (surface area = 60.48 cm²) were painted yellow using fluorescent tempera paint (Pro Art brand, Fluoro Yellow). Each cup received one model, except for the control in which no model was present. Five cups of each treatment were prepared, each cup containing six females.

Time course of sensory effects

Day-old virgin females were randomly placed either into a 2-l clear plastic container with two 3.7-cm diameter yellow plastic spheres suspended by wire from the top of the container, or into a similar container lacking spheres. Both containers also contained sugar, two slips of protein hydrolysate and water. Three replicates of each treatment were established over consecutive days. The first two replicates consisted of roughly eighty flies in each treatment. Owing to limits in fly availability, the third replicate consisted of just fifty flies in each treatment.

Once replicates were established, four flies were haphazardly removed every other day from replicates 1 and 2 of both treatments. Two flies were haphazardly removed every other day from replicate 3. Flies were placed into glass vials and stored in the freezer until they were dissected and eggs counted.

Statistical analysis

For univariate analyses, we employed a nested ANOVA with cup cage nested within treatment. Contrasts were performed using the Tukey method (Sokal & Rohlf, 1995). In none of these univariate analyses was there a significant effect of the nesting factor, cup. Therefore, in our lone factorial analysis (where analysis of nesting effects is problematic), we felt justified in pooling data over cups within a treatment.

Results

Effect of host fruit vs. foliage

In the first trial, mean egg load was significantly higher for flies held with host fruit than for flies held without fruit, regardless of the presence of host foliage (Fig. 1a; two-way ANOVA, Fruit effect, $F_{1,51} = 9.04$, $P = 0.004$). In contrast, host foliage had no significant effect on mean egg load (Fig. 1a; two-way ANOVA, Foliage effect, $F_{1,51} = 1.09$, NS). There was no significant interaction between the two factors (Fig. 1a; two-way ANOVA, Fruit \times Foliage effect, $F_{1,51} = 0.01$, NS).

In the first trial, mortality for females in fruit treatments was higher than that of females in no-fruit treatments, making it conceivable that an inadvertent selection process generated the apparent effect of fruit on egg load. In the second trial, there was no such difference in mortality, yet patterns were essentially identical to those of the first trial (Fig. 1b). Mean egg load was significantly higher for flies held with host fruit than for flies held without fruit, regardless of the presence of host foliage (Fig. 1b; two-way ANOVA, Fruit effect, $F_{1,53} = 52.48$, $P =$

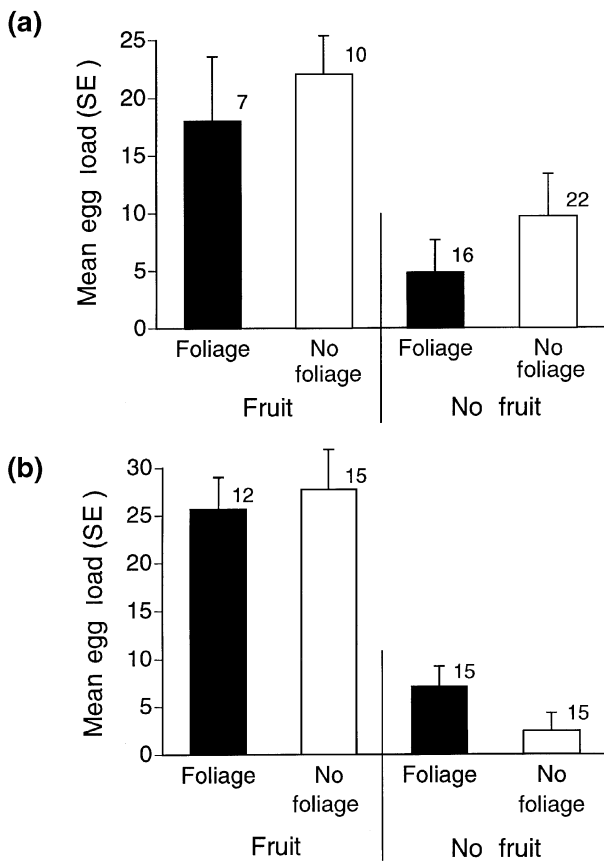


Fig. 1. Effect of host fruit and host foliage on mean egg load (\pm SE) in *R. juglandis*. (a) Trial 1, (b) Trial 2. Sample sizes reflect number of replicate cages. Overall sample size was fifty-five flies for Trial 1 and fifty-seven flies for Trial 2.

0.0001). By contrast, host foliage had no significant effect on mean egg load (Fig. 1b; two-way ANOVA, Foliage effect, $F_{1,53} = 0.17$, NS). There was no significant interaction between the two factors (Fig. 1b; two-way ANOVA, Fruit \times Foliage effect, $F_{1,53} = 1.21$, NS). In each trial, a small but undetermined number of eggs were laid in fruit.

Effect of host fruit vs. fruit model

In the first trial, where an unidentified *Juglans* spp. of fruit was used, the mean egg load was significantly different among the three treatments (Fig. 2a; nested ANOVA, $F_{2,20} = 11.90$, $P = 0.001$). The nesting effect was not significant ($F_{20,55} = 1.48$, $P = 0.13$). Mean egg load was significantly higher for flies held with *Juglans* fruit than for control flies held without fruit or model (Fig. 2a; Tukey method, $P = 0.001$) and significantly higher for flies held with the surrogate fruit model than for control flies (Fig. 2a; Tukey method, $P = 0.001$). The difference in mean egg load between the fruit and fruit model treatments was not statistically significant (Fig. 2a; Tukey method, $P = 0.68$).

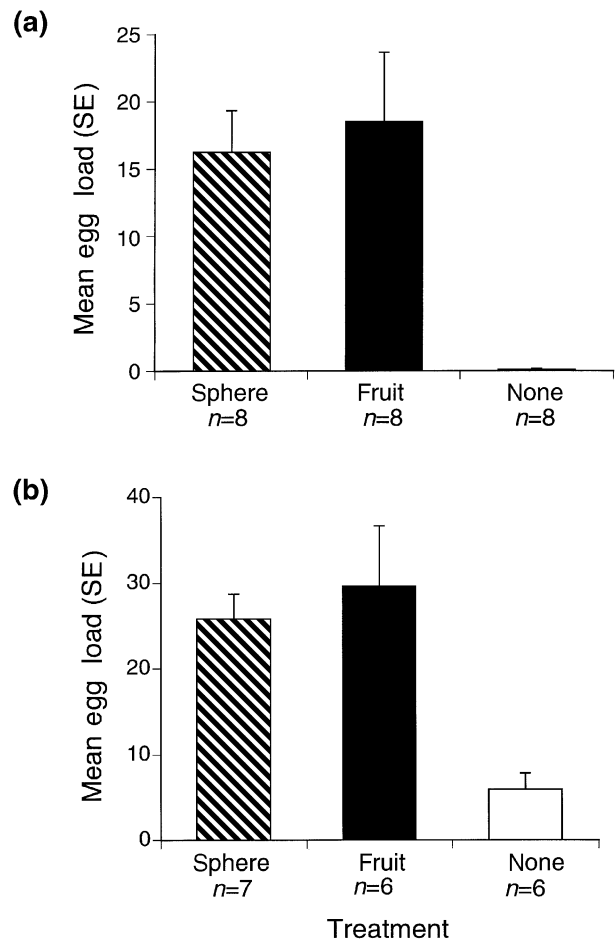


Fig. 2. Effect of fruit vs. surrogate fruit model sphere on mean egg load (\pm SE). (a) Trial with *Juglans* spp. fruit, (b) Trial with *Juglans major* fruit. Means reflect averages of mean values computed for each replicate cup. Sample sizes reflect number of replicate cages. Total sample size per treatment was seventy-eight flies for Trial 1 and forty-six flies for Trial 2.

In the second trial, where *Juglans major* fruit was used, patterns were essentially identical. Mean egg load was significantly different among the three treatments (Fig. 2b; nested ANOVA, $F_{2,16} = 8.06$, $P = 0.004$). Again, the nesting effect was not significant ($F_{9,35} = 0.66$, $P = 0.74$). Mean egg load was significantly higher for flies held with fruit than for control flies held without fruit or model (Fig. 2b; Tukey method, $P = 0.005$) and significantly higher for flies held with the surrogate fruit model than for control flies (Fig. 2b; Tukey method, $P = 0.01$). The difference in mean egg load between the fruit and fruit model treatments was not statistically significant (Fig. 2b; Tukey method, $P = 0.81$).

Effect of model colour

Mean egg load depended highly significantly on sphere colour (Fig. 3; nested ANOVA, $F_{5,108} = 7.27$, $P < 0.0001$). The nesting effect was again not significant ($F_{18,108} = 1.25$, $P =$

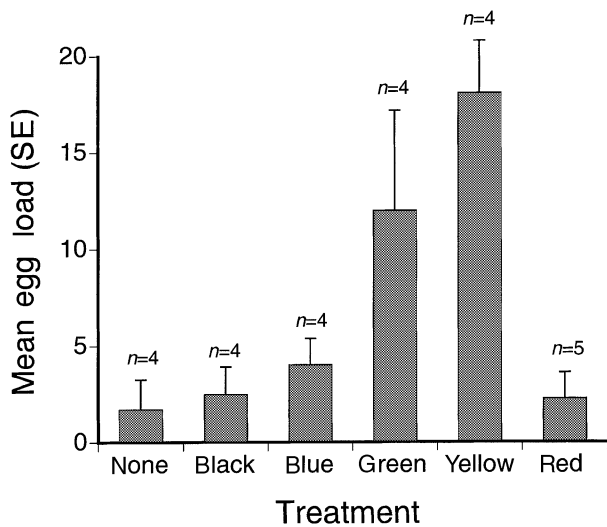


Fig. 3. Effect of sphere colour on mean egg load (\pm SE). Means reflect averages of mean values computed for each replicate cup. Sample sizes reflect number of replicate cages. Total sample size was 131 flies.

0.24). The mean egg load of flies held with green or yellow spheres was highly significantly higher than mean egg load of flies held without spheres (Tukey method, $P = 0.007$ and $P = 0.002$, respectively). The difference in mean egg load between yellow sphere and green sphere treatments was not statistically significant (Tukey method, $P = 0.66$). The mean egg load of flies held with blue, black or red spheres was not significantly higher than mean egg loads of flies held without spheres (Fig. 3; Tukey method, $P = 0.91$, $P = 0.19$ and $P = 0.76$, respectively). The failure of black spheres against white background to generate significant egg production suggests that intensity contrast of dark sphere against light background was not a factor in promoting oogenesis.

Effect of model shape

Mean egg load depended highly significantly on model shape (Fig. 4; nested ANOVA, $F_{2,54} = 5.76$, $P < 0.005$). The nesting effect was not significant ($F_{12,54} = 1.25$, $P = 0.28$). Mean egg load of flies held with a yellow sphere was significantly greater than that of flies held with a yellow cube (Fig. 4; Tukey method, $P < 0.014$) or control flies held without a sphere (Fig. 4; Tukey method, $P < 0.016$). By contrast, mean egg load of flies held with a yellow cube was not significantly different than that of flies held without a model (Fig. 4; Tukey method, $P = 0.99$).

Time course of sensory effects

Dissection of cohorts sampled over time indicated that, independent of the presence of a yellow sphere, mature eggs were not produced until at least day 6 (Fig. 5). Mature eggs were few in number in the sphere treatment until day 10, by

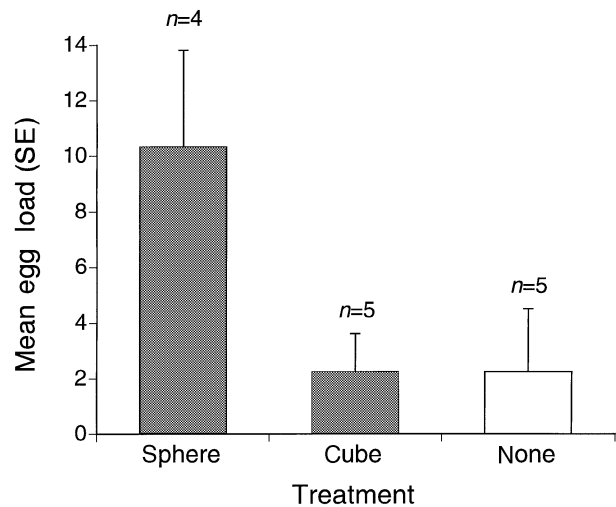


Fig. 4. Effect of model shape on mean egg load (\pm SE). Means reflect averages of mean values computed for each replicate cup. Sample sizes reflect number of replicate cages. Total sample size was sixty-eight flies.

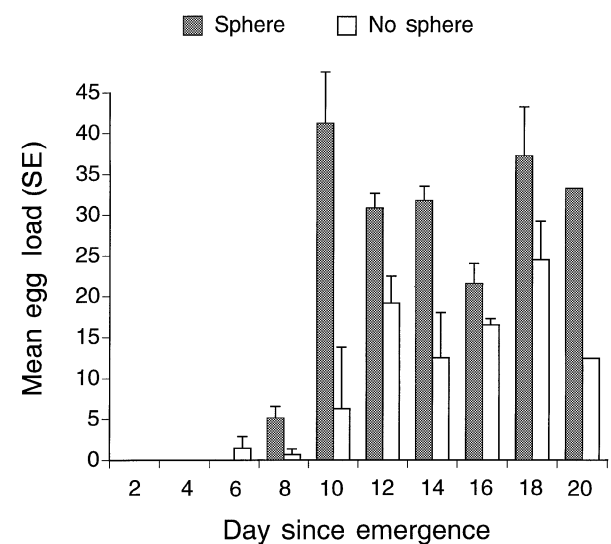


Fig. 5. Mean egg loads for cohorts of *R. juglandis* females sampled at progressively later times after emergence. Means reflect averages of mean values computed for each replicate cage, except for day 20, where data are from a single replicate with surviving flies.

which time mean egg load had risen sharply above zero levels; for flies in the no-sphere treatment, by contrast, mean egg load rose sharply later on, between days 10 and 12 (Fig. 5). On day 10 and thereafter, mean egg load in the sphere treatment was consistently higher than that in the control treatment (Fig. 5).

Discussion

Effects of oviposition

Host resources have been shown to affect egg production in four major orders of insects (Diptera, Lepidoptera, Homoptera

and Coleoptera) in work dating back to the 1940s. Numerous studies of herbivorous insects in particular have addressed the influence of hosts on egg production to varying degrees (Voukassovitch, 1949; Labeyrie, 1960; Cadeilhan, 1965; Hillyer, 1965; Hillyer & Thorsteinson, 1969; Leroi, 1975; Deseo, 1976; Fletcher *et al.*, 1978; Pouzat, 1978; Fletcher & Kapatos, 1983; Girolami *et al.*, 1987; Scott & Traniello, 1987; Weston & Miller, 1987; Koveos & Tzanakakis, 1990, 1993; Weston *et al.*, 1992; Kostal, 1993; Horton *et al.*, 1994; Trumbo *et al.*, 1995; Hopkins & Ekblom, 1996). This large database notwithstanding, most previous studies were not designed to evaluate direct sensory effects of the host on ovarian development, and their experimental design precluded that evaluation. For example, investigators often counted eggs laid in hosts or host models, rather than dissecting ovaries or, if ovaries were dissected, performed dissections only after eggs were laid. Such methodology cannot distinguish between a direct enhancing effect of host stimuli on ovarian development and an effect of host stimuli on egg deposition which then stimulates production of more eggs (Koveos & Tzanakakis, 1990). In cabbage root flies, for example, exposure to cabbage stimulates oogenesis, but only after some eggs are laid (Kostal, 1993). Such an effect, although important to recognize, is not particularly surprising: the facilitatory effect of oviposition on future egg production is well documented in insects (Adams *et al.*, 1968; Benz, 1969; Clift, 1971).

Only by using periods of host exposure too brief to permit egg-laying (Labeyrie, 1960), or by otherwise preventing oviposition, can facilitatory effects of oviposition be ruled out as a basis for host enhancement of ovarian development. In our study, females deposited eggs into fruit in initial experiments and, although numbers laid were usually small, egg deposition could have accounted in part for the effect of fruit on mean egg load. Females could not oviposit into the plastic surrogate fruit spheres in subsequent experiments and yet these spheres enhanced oogenesis to a degree similar to real fruit. In short, host fruit stimuli clearly enhance oogenesis independent of egg deposition in *R. juglandis*.

The magnitude of fruit stimuli effects was variable. In separate experiments, 8-day old females in yellow sphere treatments had mean egg loads of 16, 26, 18 and 6. The source of this variability is not known. However, egg load is highly sensitive to fly size and it is possible that fly size varied from one experiment to another. Also, day 8 is a 'flash point' at which egg loads escalate rapidly; had data been collected at day 10, variability among experiments might have been less extreme.

Nutritional effects of the host

Even where effects of oviposition were ruled out, previous studies have often failed to distinguish unambiguously between sensory and nutritional effects of the host on ovarian development. For example, work on the olive fly, *Dacus oleae* (the only tephritid fly species studied extensively with respect to sensory effects on ovarian development), indicated that host olives enhanced ovarian development (Fletcher *et al.*, 1978;

Fletcher & Kapatos, 1983). However, authors attributed the enhancement effect to increased protein intake due to adult feeding on olive juice. Girolami *et al.* (1987) showed that wax domes (a kind of surrogate fruit model) enhanced egg production in olive flies, implying that nutritional input alone did not account for host enhancement. As noted by Koveos & Tzanakakis (1990), however, the work of Girolami *et al.* depended exclusively on oviposition counts into domes and therefore confounded direct sensory effects on oogenesis with indirect effects of oviposition. Although the experimental design of Koveos & Tzanakakis (1990) avoided this confounding effect, their results were mixed. In three assays, wax domes had a significant effect (though substantially weaker than that of real fruit), but in four other similar assays, there was no effect at all. In all assays, by contrast, real olives strongly promoted ovarian development. Koveos & Tzanakakis (1993) hypothesized that females imbibe bacteria living on the olive fruit surface and that ovarian development is stimulated by nutrients liberated by the action of the bacteria in the gut. The same authors acknowledged that, without further study, 'the question of [sensory] contact vs. nutritional effect of the olive fruit on ovarian maturation would remain unanswered.'

Because plastic spheres presumably offered nothing to our flies by way of nutritional input, host enhancement of oogenesis in *R. juglandis* appears not to require nutritional input from the host. However, the possibility remains that host stimuli promote non-host-based nutrient uptake. As in other tephritids, protein consumption is critical to egg production in *Rhagoletis* flies (Webster & Stoffolano, 1978; Webster *et al.*, 1979; Tsitsipis, 1989). In the blowfly *Phormia regina*, a protein meal activates the neuroendocrine cascade leading to oogenesis (Yin *et al.*, 1993), a cascade which in Diptera involves production of Juvenile Hormone (JH) and 20-hydroxyecdysone (20-HE) by the corpora allata (Koeppel *et al.*, 1985; Okuda & Chinzei, 1988; Raikhel & Dhadialla, 1992).

That host enhancement of oogenesis might involve similar neuroendocrine events has been proposed in work on burying beetles. In such beetles, exposure to the oviposition resource is accompanied by an increase in JH (Trumbo *et al.*, 1995). It is thus reasonable to suppose that host stimuli affect egg production in *R. juglandis* in either of two ways; first, by stimulating the corpora allata directly through neural pathways or, second, by stimulating a higher rate of protein intake which in turn increases corpora allata activity. Current results do not permit us to distinguish between these two mechanisms.

Sensory links between behaviour and physiology

Our results are consistent with a basic pattern in the literature on host stimuli and egg production, namely that the kinds of stimuli used by females in finding and accepting hosts for oviposition are important in enhancement of oogenesis. In this regard, we suspect that, in addition to the physical cues demonstrated to be important in the colour and shape experiments above, both fruit odour and contact chemical cues will also be important factors in enhancement of oogenesis. Both fruit odour and contact chemical stimuli are known to be

involved in host selection behaviour in tephritid flies (Aluja & Prokopy, 1992; Aluja *et al.*, 1993; McPherson & Steck, 1996).

The greater impact of a sphere relative to a cube could reflect an effect of tactile input, visual input or both. The colour effect, by contrast, is visually based. While our results suggest that the characteristic green-yellow colour of walnut husks is important in enhancing oogenesis, our experimental design did not exclude the possibility that differences in intensity (i.e. the brightness of a surface) rather than differences in hue (i.e. the predominant wavelength reflected from a surface) account for the observed effect of colour. Discrimination based on hue (and not on intensity) is commonly invoked as a criterion for colour vision (Prokopy & Owens, 1983). Both hue discrimination and intensity discrimination are factors in host selection by fruit flies (Katsoyannos, 1989). The failure of a black sphere against a white background to enhance oogenesis suggests that intensity contrast, which is important in host selection in some tephritid species (Katsoyannos, 1989), is not a factor in host-enhanced oogenesis in this species.

Functional aspects

If a walnut fly increases its fitness by waiting to mature eggs until hosts are available, it follows that there must be a cost or costs associated with producing and/or maintaining a full egg load in the absence of host fruit. The increase in weight associated with egg load may hamper flies when moving. Berrigan (1991) found that sarcophagid flies with well-developed ovaries suffered a 40% loss in net lift during take off. Forestalling egg production until host fruit are available may thus increase the metabolic efficiency of flight associated with food-foraging, mate seeking, and predator avoidance. The same advantage of delaying egg production may be realized in terms of movement from one host tree to another. Casual observations suggest that flies emerging under non-bearing trees may need to disperse up to several kilometres in order to find walnut trees with suitable fruit (D. R. Papaj, H. Alonso-Pimentel and C. Nufio, personal observation).

Finally, there may be a basic physiological cost of maintaining a full egg load. Although the nature of this cost is unknown, phenomena such as oosorption and dumping of unfertilized eggs (which have been observed in other insects; Bell & Bohm, 1975) provide indirect evidence that there are physiological costs of maintaining a full egg load. If a female does not produce eggs, she may thus have more energy and material resources to invest in flight or other activities.

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