7-1-2011

Resource Quality or Competition: Why Increase Resource Acceptance in the Presence of Conspecifics?

J. M. Davis
University of Washington Tacoma, jerdavis@uw.edu

C. R. Nufio

D. R. Papaj

Recommended Citation

Davis, J. M.; Nufio, C. R.; and Papaj, D. R., "Resource Quality or Competition: Why Increase Resource Acceptance in the Presence of Conspecifics?" (2011). *SIAS Faculty Publications*. 557.
https://digitalcommons.tacoma.uw.edu/ias_pub/557

Resource quality or competition: Why increase resource acceptance in the presence of conspecifics?

Running Title: Social stimulation of oviposition

Jeremy Davis[1,2], César R. Nufio[1,3] and Daniel R. Papaj[1]

[1]*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona*

[2] *Department of Biology, Vassar College, Poughkeepsie, New York*

[3] *University of Colorado Natural History Museum, Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado*

Corresponding author: jedavis@vassar.edu

Abstract

Some animal species increase resource acceptance rates in the presence of conspecifics. Such responses may be adaptive if the presence of conspecifics is a reliable indicator of resource quality. Similarly, these responses could represent an adaptive reduction in choosiness under high levels of scramble competition. While high resource quality and high levels of scramble competition should both favor increased resource acceptance, the contexts in which the increase occurs should differ. In this paper, we tested the effect of social environment on egg-laying and aggressive behavior in the walnut fly, *Rhagoletis juglandis,* in multiple contexts to determine if increased resource acceptance in the presence of conspecifics was better suited as a response to increased host quality, or increased competition. We found that grouped females oviposit more readily than isolated females when provided small (low quality) artificial hosts, but not when provided large artificial hosts, indicating that conspecific presence reduces choosiness. Increased resource acceptance was observed even when exposure to conspecifics was temporally or spatially separate from exposure to the resource. Finally, we found that individuals showed reduced aggression after being housed in groups, as expected under high levels of scramble competition.   These results indicate that the pattern of resource acceptance in the presence of conspecifics may be better viewed as a response to increased scramble competition rather than as a response to public information about resource quality.

Keywords: Host choice, Social information, Social facilitation, Experience, *Rhagoletis*, Conspecific attraction

Simple models of resource selection, such as ideal free distribution (Fretwell and Lucas, 1969), predict that animals should be less likely to use resources that are being used by potential competitors such as conspecifics. However, in many species, the presence of conspecifics increases an animal's propensity to use a resource (Clayton, 1978; Muller et al., 1997; Onyabe and Roitberg, 1997; Prokopy and Roitberg, 2001; Otis et al., 2006). One explanation for this pattern is that animals use conspecifics as sources of information about the quality of resources (Stamps, 1987; Prokopy et al., 2000; Dall et al., 2005). If individuals are attracted to or arrested by high quality resources, for example, the presence of conspecifics can indicate the presence of a high quality resource.

While conspecifics may be a moderately reliable indicator of resource quality, they should be an even better indicator of competition. The reliability of information about quality depends on the ability of conspecifics to identify quality resources, whereas conspecifics themselves are the sources of competition and should therefore reliably indicate competition (Slaa et al., 2003). Therefore, another possibility – less often considered – is that increased response to resources in the presence of conspecifics reflects an adaptive response to perceived competition. While the potential for competition may decrease the attractiveness of the particular resource item where conspecifics reside, high levels of scramble competition should favor individuals that are less selective and accept a wider range of resource quality more readily as the risk of resource depletion increases (Mitchell, 1990; Van Alphen and Visser, 1990; Visser, 1991; Amita et al., 2010). For example, Plowright and Landry (2000) demonstrated that ~~when~~ solitary~~,~~ pigeons prefer large seeds to small ones but that they more readily accept small seeds ~~when~~ in the presence of a potential competitor.

Information about resource quality and levels of competition will favor different patterns of context-dependent response in foragers. ~~The contexts in which animals alter~~

~~behavior in the presence of conspecifics should depend on what those conspecifics reliably indicate.~~ By testing ~~-~~animals in different contexts, we can determine whether behavioral responses are better suited as a response to information about competition or as a response to information about resource quality. For example, decreased choosiness in response to perceived competition should result in increased acceptance of low quality resources, but little change in acceptance of higher quality resources. Alternatively, if conspecifics indicate increased resource quality, then any resource associated with conspecifics, regardless of intrinsic quality, should be perceived as higher quality than it would without conspecifics and should be accepted more readily.

The location or timing of experience with conspecifics differentially affects the reliability of information about resource quality and competition. Conspecifics observed near a particular resource provide reliable information about that particular resource, but less reliable information about the quality of other resources. Therefore, if individuals are primarily using conspecifics as indicators of resource quality, their response to the presence of conspecifics should be primarily restricted to resources directly associated with conspecifics. Alternatively, when conspecifics are used as indicators of competition, then increased propensity to use resources should be seen at sites away from conspecifics, and due to recent previous encounters with conspecifics.

Resource quality and competition should also differentially affect aggressive behavior. Animals should be more willing to invest in any territorial behavior required to monopolize resources of particularly high quality, but less willing if levels of scramble competition are high (and the resource will be visited by multiple potential competitors)(Dubois et al., 2003). Therefore, ~~being reared~~previous experience with conspecifics should increase aggressive behavior if those conspecifics indicate resource quality, but decrease aggressive behavior~~,~~ if those conspecifics indicate high levels of scramble competition.

In this paper, we test the context-dependent effects of conspecifics on oviposition decisions in the tephritid fruit fly, *Rhagoletis juglandis,* a species in which this phenomenon has not previously been studied. Tephritid fruit flies are a useful system to study the relative importance of conspecifics as potential competitors and as indicators of resource quality. Many species in this family lay their eggs in ripening fruit, providing a situation in which the presence of flies on a fruit indicate the quality of that fruit and/or the risk of host depletion in a tree. In several species, females have been shown to lay eggs more readily when housed in groups (e.g., Prokopy and Bush, 1973a; Robertson et al., 1995; Rull et al., 2003). However, these experiments are typically conducted in contexts in which an increased response is predicted regardless of what information conspecifics provide. Using *R. juglandis*, we tested for the effect of conspecifics on resource acceptance and aggressive behavior in different contexts, (i.e. on different quality hosts, and when conspecifics are spatially or temporally separated from hosts) to determine whether context-dependent patterns of the effect are better viewed as a response to information about competition or about quality.

METHODS

Natural History

In southern Arizona, *Rhagoletis juglandis* uses Arizona walnut, *Juglans major,* as its host. There is a single generation per year. Adult flies emerge between July and September, depending on elevation, from puparia in the soil beneath their natal tree. Females begin ovipositing in fruit one or two weeks after emergence. After oviposition, females deposit a host-marking pheromone (HMP) which deters oviposition (Nufio and Papaj, 2004a). Nonetheless, females show a strong propensity to lay eggs within previously-established oviposition cavities (Papaj, 1993 (Papaj, 1993; Lalonde and Mangel, 1994; Papaj, 1994), 1994; Lalonde and Mangel, 1994). Eggs hatch within four days, and larvae develop over the course of two weeks. Survival is higher and final size larger when larvae develop in larger walnuts (Nufio and Papaj, 2001). Development is usually completed after the fruit fall to the ground, with larvae then leaving the fruit to form puparia in the soil beneath the natal tree. Puparia enter an obligate diapause until the following year.

General Methods

All flies were collected as larvae inhabiting fruit that had fallen from *J. major* trees in southern Arizona. After pupation, flies were kept at 4°C for at least 9 months and warmed to room temperature 4-6 weeks prior to each experiment. As adult flies began to emerge, pupae were transferred to 3.8 L plastic containers (emergence containers), held at 28° C on a 14:10 light:dark cycle, and provided sugar cubes, powdered hydrolyzed yeast, and distilled water (delivered in a cotton wick) *ad libitum*. No hosts were provided at this time.

Experiments 1, 2 and 4 were conducted in 473 mL clear plastic cups (SOLO brand) topped with 10 cm petri dishes (experimental cups). Flies in all experimental cups were provided with water and a strip of paper dipped in a solution of hydrolyzed yeast and sugar. All cups were surrounded by white cardboard barriers to minimize extraneous visual stimuli. Mortality was relatively low (< 10%) and not obviously biased towards particular treatments or collection locations.

Oviposition behavior was assayed in experiments 1 through 3 using 25 and 37 mm diameter artificial hosts wrapped in Parafilm® as artificial walnut hosts. Spheres were prepared using a ratio by weight of 1:2:40 agar to sucrose to water. Two drops of yellow and 1 drop of green food coloring (Kroger brand) were added for every 200 mL of water. The solution was heated until boiling and poured into silicone molds (Chicago School of Mold-Making, Chicago, IL). Spheres were hardened at 4°C and wrapped individually in Parafilm® (2.5 or 4.0 cm^2 pieces stretched over each sphere and twisted into a 'stem').

Experiment 1: Do conspecifics affect oviposition decisions?

Flies used in this experiment were collected from the town square of Patagonia, AZ (31°32'24"N 110°45'14" W). Female flies that had emerged 2 to 3 weeks earlier were removed from emergence cages and placed into experimental cups in one of two treatments: 1) held individually, or 2) held in groups of 3. Flies were allowed to acclimate for 24 hours, after which 25 mm diameter artificial hosts were suspended from the top of each cup. Artificial hosts and flies were removed after 48 hours. Flies were frozen at -10°C. The number of clutches and eggs laid in each artificial host were counted (eggs within clutches laid at the same site occurred in distinct groups, entering the sphere at different angles).

Flies were dissected under stereoscopy and digital images of wings and dissected ovaries were captured with a Canon EOS 20D camera. We counted all fully-yolked and chorionated oocytes (Stage E of egg maturation in Lachmann and Papaj 2001). Furthermore, because body size and oocyte number are known to be positively correlated, we used ImageJ (NIH) software to measure the length of the discal medial cell of the wing. This wing measure was used as an estimate of female size because previous laboratory investigations demonstrated that it was strongly correlated with other indicators of female size such as thorax and head width and femur length (H. Alonso-Pimentel, unpubl. data).

This experiment was performed in three blocks (72 hour periods) across several weeks. No block or block*treatment effects were seen, so data were pooled across blocks. Binomial tests (see Results) were conducted on the presence or absence of eggs in each artificial host. For those cases where eggs were present, the number of eggs or clutches were analyzed with ANOVA (Type III) ~~(on square root transformed values where needed to fit variance and normality assumptions)~~. Egg load data were also analyzed with an ANOVA. All egg data required square root transformation to fit variance and normality assumptions (tested with Levene's and Shapiro-Wilk tests, respectively). All statistical tests~~s~~ were conducted with SPSS 17.0 (SPSS, Inc.). All continuous data is report with standard errors of the mean.

Experiment 2: Does the effect of conspecifics depend on host quality?

To test for changes in choosiness~~This experiment was designed to determine whether the effect of conspecifics depended on the quality of the host presented to females~~ in response to the presence of conspecifics, we conducted a pair of no-choice tests ~~. -~~Flies used in this experiment were collected from the town square of Patagonia, AZ~~the same Patagonia, AZ site~~. The experiment was set up similarly to experiment 1, but with a crossed design in which both host size and social condition were manipulated. Flies were housed alone or in groups of three. Half of the cups in each social treatment received artificial hosts (25mm diameter) identical to those in experiment 1, and half received larger artificial hosts (37 mm diameter). This experiment was performed in three blocks across several weeks. No block or block*treatment effects were seen, so data were pooled across blocks. Statistical analysis was conducted as described for experiment 1.

Experiment 3: Is the effect of conspecifics restricted to the resource item on which conspecifics reside?

This experiment was designed to determine whether the presence of conspecifics resulted in a general increase in the propensity to oviposit, or whether increased oviposition was specifically directed at fruit near conspecifics. All females used in the experiment were collected from Canelo Hills Cienega Reserve (31°33’40”N 110°31’46”W). Fly behavior was tested in 3.8 L plastic arenas. On either side of the arena, we placed a 297 mL clear plastic beverage cup (Solo brand) which would hold test stimuli to which a focal female released into arena could respond. A vial of water, and a yeast/sugar strip was placed in the middle of the arena and in each cup. A couplet of 25 mm artificial hosts attached with gardening wire was placed over the edge of each cup, such that one host was outside of cup and the other was inside the cup. ~~and t~~The top of each cup was covered with square of cloth mesh to allow olfactory cues to escape into the arena (Figure 1a).

During the first trial of this experiment, in half of the arenas neither cup received females (n=10), while in the other half of the arenas, 12 female flies were placed in one of the two cups (n=10). In the second trial, conducted in two blocks, one of the two cups contained 12 females in all arenas (n=40). To control for position effects, in each block, an equal number of arenas were set up with fly-containing cups placed on either side of the arena. Focal flies that had eclosed 2-3 weeks prior to the experiment were held singly outside of the arenas in 473 mL cups for 48 hours prior to being introduced to arenas at 1100 on the first day of each trial. Arenas were scanned hourly from 1100-1800 for 2 days (number of scans per arena = 15). During these scans we noted the side of the arena on which females were located and whether or not they were on one of the walnut models. 72 hours after focal females were placed in arena, walnut models were removed and the eggs laid in each model were counted.

Experiment 4: Does previous experience with conspecifics increase oviposition response?

In this experiment, we used a crossed design to determine the roles of previous and current experience with conspecifics on the propensity of a female to oviposit. Flies used in this experiment were collected from a variety of sites in southern Arizona. We placed females within two days of eclosion into experimental cups. Half of the females were placed alone in a cup, the other half were held 10 to a cup (single vs. group rearing treatment). Flies were tested for their propensity to oviposit when they were 12 to 21 days old.

A test began by suspending a ripe *J. major* fruit by wire from the ceiling of a 17.2cm x 17.2cm x 17.2cm plexiglass-frame screen cage. Fruit were 26-38mm in diameter, and had been previously punctured once with a 00 insect pin. Females are attracted to these pin pricks and oviposit in them, as they typically do with naturally-formed oviposition punctures (Papaj, 1994).

In half of the tests, we next placed a ‘resident female’ gently on the test fruit; in the other half, the fruit was left unoccupied (resident vs. no resident treatment). The resident was a female of the same or similar population origin as the focal female. When placed on the fruit, the resident almost always began ovipositing into the artificial puncture. If the resident attempted to oviposit in other areas of the fruit, she was gently nudged towards the artificial puncture with a probe. Residents that did not oviposit within 5 minutes were removed.

A focal female from either the isolated or the grouped treatment was placed gently on a test fruit. If a resident was present, we placed the focal female on the fruit out of sight from the resident. We noted any oviposition attempts made by the focal female, as well as successful egg deposition. An oviposition attempt is a conspicuous behavior in which a female turns the tip of her abdomen down towards the fruit surface, extending her needle-like ovipositor, and bores into the fruit with the ovipositor. Oviposition, or egg deposition, begins when the ovipositor-boring female becomes virtually motionless. If a resident was present on the fruit, we also noted the occurrence and form of any aggressive interactions by the focal female. Aggressive interactions included lunges, chases, head butting, and foreleg-kicking.

An observation ended when either the focal female had initiated oviposition or the focal female had left the fruit for at least 5 minutes. As soon as the observation ended, the focal female was frozen at -10ºC and measurements of body size and egg load were made under stereoscopy. Oviposition behavior was analyzed with a logit loglinear model (SPSS 17.0). The improvement in model fit provided by each factor was assessed with chi-square tests.

RESULTS

Experiment 1: Do conspecifics affect oviposition decisions?

Group housing increased the probability that flies oviposited in small artificial hosts. When held alone, 7 of 39 females laid eggs in the artificial host provided to them. Given this percentage of oviposition in isolation (= 18%), if there were no effect of social treatment, eggs should have been laid in only 45% of the cups holding 3 females (1-probability that none of 3 females in a cup lay eggs = $(1-[1-0.18]^3=0.45)$). In fact, eggs were laid in 81% (29 of 36) of the cups holding 3 females (exact b~~B~~inomial ~~test~~probability <~~,~~ 0~~p <0~~.0001| expected = 45%).

Using the percentage of groups in which no female laid eggs (= 19%), the probability (f) that a given female laid eggs when in the presence of 2 other females is: f = P(1 grouped female lays eggs) = $1 - \sqrt[3]{\mathrm{P(3\ females\ not\ laying\ eggs)}} = (1 - \sqrt[3]{0.19})$ = 0.42. Thus, we estimate that the probability that a female lays any eggs in a small artificial host increases from 0.18 to 0.42 when she is housed with conspecifics.

While social environment affected the probability of ovipositing, it did not affect the number or size of clutches laid per female. We estimated an average 1.56 females oviposited in grouped treatments where eggs were found (see Appendix). Given this estimate, each ovipositing female in grouped treatments (N=29 cups) laid an average of 15.69 (± 1.80~~ SE~~) eggs and an average of 4.1 (±0.50~~ SE~~) clutches. Isolated females that laid eggs (N=7) laid an average of 11.00 (± 3.22) eggs and an average of 2.86 (±0.86~~ SE~~) clutches. These differences between ovipositing isolated and grouped females were not statistically significant ($t_{\mathrm{sqrt(eggs)}}$=1.39, df=34, p=0.17; $t_{\mathrm{sqrt(clutches)}}$=1.20, df=34, p=0.24). Furthermore, the size of individual clutches did not differ between treatments (Grouped: 5.85 ± 0.50 eggs per clutch; Isolated: 4.28 ± 0.79 eggs per clutch; t_{eggs}=1.42, df=34, p=0.16).

Post-test dissections revealed that females housed in groups and females housed in isolation had similar egg loads at the end of the assay (Isolated: average # of mature oocytes= 24.7±2.4~~ s.e.~~; Grouped: avg. # of mature oocytes per female: 24.6±1.3; ANOVA:

$F_{1,69}$~~=~~≤0.~~00~~01, p=0.89). ~~In order to estimate overall per capita egg production, we added the number of eggs laid and the number of eggs in female ovaries. There was a trend for females housed in groups to have overall higher per capita egg production, (Single= 26.7±2.53; grouped = 31.1±1.89). However, this difference was not statistically significant (ANOVA:~~ ~~$F_{1,69}$=2.56, p=0.12).~~

Experiment 2: Does the effect of conspecifics depend on host quality?

The effect of social treatment was detected when small agar spheres were offered to females, but not when they were offered large agar spheres. Controlling for social treatment, large spheres were more likely to contain eggs (85% contained eggs) than small spheres (52% contained eggs) (Mantel-Haenszel χ^2 =26.2, df=1, p<0.0001). As in experiment 1, only a small proportion of females held alone laid eggs in small spheres (11 of 45 = 0.24); the proportion of cups of grouped females in which eggs were laid into small fruit was greater than expected, based on oviposition by isolated females (expected proportion of spheres with eggs = $1\text{-}[1\text{-}0.24]^3$ =0.56; observed: 0.81 [33 of 41]; (exact binomial probability = 0.0009| expected = 56%)~~Binomial test: p=0.001~~). As in experiment 1, females housed in groups with small spheres had an estimated probability of laying eggs of $f = 1 - \sqrt[3]{0.19} = 0.42$.

When females were held in isolation with large spheres, a majority of females laid eggs (32 of 44 = 0.73). Given this high rate of acceptance, almost all large agar spheres housed with 3 females would be expected to contain eggs (expected prob.= $1\text{-}[1\text{-}0.73]^3$ = 0.98) regardless of any effect of conspecifics. This expectation was met (observed: 98% (41 of 42); Binomial test p=0.8). Females housed in groups with large spheres had an estimated probability $f = 1-\sqrt[3]{0.02} = 0.71$ of laying eggs.

We estimated that in cups of grouped females where eggs were laid, an average of 1.56 and 2.19 females per cup laid eggs in small and large spheres, respectively. The number of eggs laid per ovipositing female (square root transformed) was influenced by a marginally significant interaction between the size of the sphere and the social treatment ($F_{(size)1,113}=4.87$, p=0.03, $F_{(social)1,113}=4.20$, p=0.04, $F_{(social*size)1,113}=3.50$, p=0.06). Grouped females laid significantly more eggs in small spheres per ovipositing female than isolated females (t=2.07, df=42, p=0.04), while grouped and isolated females laid a similar number of eggs in large agar spheres (t=0.18, df=71, p=0.86; Figure 2a). We found no significant effects of sphere size or social treatment on the number of clutches laid per ovipositing female ($F_{(size)1,113}=0.88$, p=0.35 $F_{(social)1,113}=2.91$, p=0.09, $F_{(social*size)1,113}=2.04$, p=0.16; Figure 2b). There was a trend for larger clutches to be found in large agar spheres, Clutch size in the different social treatments did not differ significantly ($F_{(size)1,113}=2.17$, p=0.14, $F_{(social)1,113}=0.02$, p=0.89, $F_{(social*size)1,118}=0.08$, p=0.78; Figure 2c).

In summary, the effect of conspecifics on oviposition was not independent of sphere size; the effect was only detectable when flies were provided with small spheres. This may indicate that the presence of conspecifics decreased choosiness, but we are faced with the possibility that the lack of an observed effect in the large sphere treatment was due to a ceiling effect. However, if grouped females were more likely to lay eggs than isolated females in the large sphere treatment (i.e. f > 0.73), then our estimate of the number of females ovipositing per cup (2.19) would be an underestimate. We would expect in turn that our estimate for the number of eggs per ovipositing female would be higher in groups than for isolated flies. This was not the case. In fact, our measures of eggs and clutches laid in large spheres per ovipositing female were nearly exactly identical in isolated and grouped conditions (Figure 2a + b). Therefore, it seems unlikely that the lack of an observed effect of social treatment on propensity to oviposit was due to a ceiling effect.

Experiment 3: Is the effect of conspecifics restricted to the resource item on which conspecifics reside?

The results of experiment 3 indicated the facilitating effect of conspecifics was not restricted to artificial hosts near those conspecifics. The first trial of this experiment indicated that the presence of females in one cup influenced the oviposition behavior of focal females in the arena. Only 2 of 10 females in arenas without conspecifics present laid any eggs. In contrast, 6 of 10 females in arenas with conspecifics present laid eggs. The difference is marginally significant (Fisher's exact test, p=0.08). The presence of females in one of the cups resulted in an increase in the percentage of scans during which the focal female was seen on either sphere (with~~/~~ flies: 2.37 (± 0.74~~ SE~~) of scans; without~~/o~~ flies: 0.97 (± 0.31~~ SE~~) scans; Mann-Whitney U test: U = 22, $N_1 = N_2 = 10$, P < 0.02). Given that only 2 isolated females laid eggs, we cannot statistically compare the clutch number or size, however, there was a trend for females in arenas with conspecifics to lay more and larger clutches (mean # of clutches$_{\text{isolated}}$=3.5; mean # of clutches$_{\text{with }\cancel{/}\text{conspecifics}}$=8.17; mean clutch size$_{\text{isolated}}$=1.8, mean clutch size$_{\text{with }\cancel{/}\text{conspecifics}}$=3.4). Amongst the 10 pairs of cups that contained flies in one of the cups, no strong bias was observed towards or away from the cup containing the female cues. Data from these 10 pairs of cups were analyzed along with data from the two blocks of the

2nd trial of this experiment to increase our statistical power to detect any bias towards or away from cup containing conspecifics.

Fifty females across 3 blocks were tested for a tendency to spend time and/or lay their eggs near conspecifics. There was a significant trend for females to be seen more often on the sphere set away from conspecifics (t=2.309, df=49, p=0.025). However, in general, focal females demonstrated no strong bias towards or away from conspecifics (Figure 1b). Females did not spend more or less time on the side of the cage with containing conspecifics (t=0.122, df=49, p>0.91). Similarly, there was no difference in the number of clutches laid in either sphere (t=.379, df=49, p=0.76), or in the size of clutches laid on either side (t=0.715, df=12, p=0.49; Figure 1b).

Experiment 4: Does previous experience with conspecifics increase oviposition response?

Rearing flies in groups increased their propensity to lay eggs and decreased their aggressive behaviors. The probability that females attempted oviposition was higher for those reared with other females ($\chi^2 = 5.28$, df=1, p<0.025). Similarly, the presence of a resident female on the host during testing, increased the probability that a female attempted oviposition ($\chi^2 = 5.28$, df=1, p<0.025) (Figure 3). There were marginally significant trends in same direction when analyzing the proportion of females that successfully oviposited (rearing treatment: $\chi^2 = 3.52$, df=1, p<0.06; resident presence: ($\chi^2 = 3.52$, df=1, p<0.06) (Figure 3). There was no significant interaction between treatment factors on either attempted or successful ovipositions. While nearly all of the successful ovipositions were in the puncture provided (20 of 21 ovipositions when no conspecific was present; 31 of 33 when conspecific was present), oviposition attempts were not more frequent on the side of the fruit containing the puncture (pooled across treatments, proportion of attempts on puncture side = 0.51, $t_{one\text{-}sample}=0.373$, df=80, p=0.78).

When residents were present, the frequency of attacks by a focal female on a resident, measured in terms of lunges, head butts and foreleg kicks, depended on social history treatment, as well as whether or not females attempted oviposition (Figure 4). In both rearing treatments, females that attempted oviposition engaged in more attacks than females that did not attempt oviposition (reared alone: Mann-Whitney U = 172.0, $N_{attempt}=22$, $N_{no\ attempt}=31$, p=0.001; reared socially: Mann-Whitney U = 279.0, $N_{attempt}=32$, $N_{no\ attempt}=24$, p=0.042). Among females that attempted oviposition, those reared alone engaged in a markedly greater number of attacks on the residents than females reared in groups (Mann-Whitney U = 240.0, $N_{social}=32$, $N_{isolated}=24$, p=0.038) (Figure 4).

The effect of social history on egg-laying and aggression was not due to an effect of rearing conditions on egg maturation. Among individuals used in the analysis (i.e., individuals with egg load > 0), females held alone carried 27.62 (±1.57 ~~s.e.~~) mature oocytes on average (N=75), while females held in groups carried 25.19 (±1.49 ~~s.e.~~) mature oocytes on average (N=83). As in experiment 1, the difference in egg load is not statistically significant ($t_{156}=1.12$, p=0.26). Females in social history treatments also did not differ significantly either in age or in wing vein length, a proxy for body size (t-tests, p>0.26).

DISCUSSION

Our experiments demonstrate that the presence of conspecific females increases the probability that individual *R. juglandis* will lay eggs. Several species in the family Tephritidae show the same basic pattern, indicating that the social environment plays an important facilitating role in the oviposition decisions of this group (Prokopy and Bush, 1973b; Robertson et al., 1995; Prokopy and Duan, 1998; Prokopy et al., 1999; Díaz-Fleischer and Aluja, 2003; Rull et al., 2003). This is particularly interesting since larval density has a negative effect on both size and survivorship in tephritid flies (Nufio and Papaj, 2004b; Burrack et al., 2009), and many species, including *R. juglandis,* use host marking pheromones after oviposition that inhibit superparasitism by conspecifics (Nufio and Papaj, 2001).

The context-dependent responses observed in experiments 2 and 4 are well suited as a response to high levels of scramble competition (host depletion or larval competition). In experiment 2, oviposition in large spheres (which represent superior resources (Nufio and Papaj, 2004a)) was not influenced by social treatment, while oviposition in small spheres was seen more often in group housed females. This quality-dependent response to conspecifics indicates that flies in groups are less choosy than flies held alone, a predicted response to higher levels of scramble competition, but not to high levels of resource quality.

Commented [VU1]:

The pattern of female aggressive encounters observed in experiment 4 also supports the hypothesis that females use the presence of conspecifics as an indicator of high competitor density. Females were more aggressive towards another female on a fruit when they attempted oviposition. The association between oviposition and aggression suggests that aggression functions to monopolize resources for a female's offspring (see also Papaj and Messing, 1998). If prior experience with conspecifics indicates the presence of high quality hosts, females should engage in more aggressive encounters when they are reared with conspecifics. Instead, females were much less aggressive when they were reared with conspecifics. This pattern in aggression makes more sense if previous experience with conspecifics indicates high competitor density. At high densities, fighting with the resident may have relatively little value because the fruit will likely be visited later and exploited often by other females (Nufio and Papaj, 2004b). In fact, fighting with the resident under these conductions may incur an opportunity cost related to finding and utilizing other fruit. On the other hand, at low to intermediate competitor densities there is a relatively high payoff to a female that fights with a resident female, if such fighting expels the resident from the fruit before her clutch is completed (Dubois et al., 2003).

The patterns of oviposition observed in experiments 3 and 4 do not support the hypothesis that females use the presence of females as indicators of the quality of particular fruit. In experiment 3, when given a choice between hosts near or away from conspecifics, females did not oviposit more near conspecifics, and in fact alighted more often away from conspecifics (Figure 1b). A similar pattern has been observed in *Anastrepha ludens* (Díaz-Fleischer and Aluja, 2003). Similarly, in experiment 4, the resident female could have provided inadvertent social information about the location of an area on the fruit that was especially appropriate for oviposition. However, females did not appear to use such information as they did not obviously position their oviposition attempts near the resident females. Finally.in experiment 4, previous encounters with conspecifics, which should have provided little information about the quality of the resource provided during the test, affected oviposition efforts (Figure 3).

In summary, the pattern of social stimulation of oviposition (and concurrent inhibition of aggression) observed in *R. juglandis* seems best viewed as a response to increased competition in the local environment. Thus, social stimulation of oviposition in tephritid flies may represent a case in which animals increase acceptance of a resource in the presence of conspecifics, even if conspecifics provide no information about the quality of that resource.

Theory predicts that the information value of a cue such as the presence of conspecifics depends on how reliably that cue is associated with the environmental factor of interest and how uncertain that factor is when the cue is unavailable (Stephens, 1989; McLinn and Stephens, 2006). As such, it is unsurprising that walnut flies behave as though conspecifics provide them information about competition that is more valuable than information they provide about the quality of resources. First, it is reasonable to assume that the presence of conspecifics is reliably correlated with level of competition present in the environment because conspecifics are the source of that competition. Any correlation between conspecific presence and resource quality is probably weaker than the correlation between conspecific presence and the level of competition because it relies on the conspecifics ability to identify high quality larval resources. Furthermore, it seems likely that in the absence of conspecific cues, individuals will not be able to estimate the level of competition they will encounter. Conversely, individuals can use size and perhaps chemical cues to determine the quality of walnuts.

IMPLICATIONS

Recently, the idea that conspecifics provide ‘public information’ about resource quality has gained increasing attention (Danchin et al., 2004; Dall et al., 2005). Discussion of the use of public information often implicitly assumes animals are choosing among several available resources (using a “best-of-n” search strategy), where the relative fitness gain of accepting one of the sampled resources is the major factor in adaptive choice. When this is the case, if two resources are of equal intrinsic quality then individuals are expected to choose the resource where competition will be lower (typically, the resource without conspecifics).

Therefore, in those cases where animals choose resources that contain conspecifics, it is concluded that the conspecifics must be providing information about intrinsic resource quality.

While there seems little doubt that animals use the presence and behavior of conspecifics as indicators of resource quality, when considering animals that sequentially search for resources it is important to consider that adaptive decision making is based not only on the quality of a given resource but also on the distribution of quality in the local environment. Individuals using sequential search can use the presence of conspecifics on a resource not only as an indicator of quality and the level of competition for~~of~~ that resource, but also of the quality and level of competition in the local environment. Our results indicate that using conspecifics as indicators of local levels of competition can affect decision making in ways that are superficially similar to using conspecifics as sources of information about resource quality.

Appendix:

We estimated the number of females that were responsible for the eggs found in spheres in order to obtain a ‘per ovipositing female’ estimate of clutch number in cups containing 3 females. The mean number of females laying eggs in spheres where eggs were found (x) was estimated as:

$$x = \sum_{k=1}^{3} k \frac{\binom{3}{k} f^{k} q^{3-k}}{1 - q^{3}}$$

where f is the probability of ovipositing and q= (1-f). In experiment 1, given each group-housed female has a probability, f=0.42, of laying eggs, an estimated mean x= 1.56 females held in groups contributed to the total number of eggs laid by the group.

Acknowledgements: We thank R.J. Prokopy for helpful discussions on experimental design and S. Duffy, J. Hoyos, K. Hobaica for technical assistance. This work was supported by the United States Department of Agriculture [NRI Grant 9702562 to RJP]; National Institutes of Health [Grant GM00708 to the Center for Insect Science, University of Arizona].

REFERENCES

Amita H, Kawamori A, Matsushima T, 2010. Social influences of competition on impulsive choices in domestic chicks. Biology Letters 6:183-186.

Burrack HJ, Fornell AM, Connell JH, O'Connell NV, Phillips PA, Vossen PM, Zalom FG, 2009. Intraspecific larval competition in the olive fruit fly (Diptera: Tephritidae). Environmental Entomology 38:1400-1410.

Clayton DA, 1978. Socially facilitated behavior. Quarterly Review of Biology 53:373-392.

Dall SRX, Giraldeau LA, Olsson O, McNamara JM, Stephens DW, 2005. Information and its use by animals in evolutionary ecology. Trends in Ecology & Evolution 20:187-193.

Danchin E, Giraldeau LA, Valone TJ, Wagner RH, 2004. Public information: From nosy neighbors to cultural evolution. Science 305:487-491.

Díaz-Fleischer F, Aluja M, 2003. Influence of conspecific presence, experience, and host quality on oviposition behavior and clutch size determination in *Anastrepha ludens* (Diptera: Tephritidae). Journal of Insect Behavior 16:537-554.

Dubois F, Giraldeau LA, Grant JWA, 2003. Resource defense in a group-foraging context. Behavioral Ecology 14:2-9.

Fretwell SD, Lucas HLJ, 1969. On territorial behavior and other factors influencing habitat distribution in birds part 1, theoretical development. Acta Biotheoretica 19:16-36.

Lalonde RG, Mangel M, 1994. Seasonal Effects on Superparasitism by Rhagoletis completa. Journal of Animal Ecology 63:583-588.

McLinn CM, Stephens DW, 2006. What makes information valuable: signal reliability and environmental uncertainty. Anim Behav 71:1119-1129.

Mitchell WA, 1990. An optimal control theory of diet selection - The effects of resource depletion and exploitative competition. Oikos 58:16-24.

Muller KL, Stamps JA, Krishnan VV, Willits NH, 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). American Naturalist 150:650-661.

Nufio CR, Papaj DR, 2001. Host marking behavior in phytophagous insects and parasitoids. Entomologia Experimentalis et Applicata 99:273-293.

Nufio CR, Papaj DR, 2004a. Host-marking behaviour as a quantitative signal of competition in the walnut fly *Rhagoletis juglandis*. Ecological Entomology 29:336-344.

Nufio CR, Papaj DR, 2004b. Superparasitism of larval hosts by the walnut fly, *Rhagoletis juglandis*, and its implications for female and offspring performance. Oecologia 141:460-467.

Onyabe DY, Roitberg BD, 1997. The effect of conspecifics on oviposition site selection and oviposition behaviour in *Aedes togoi* (Theobold) (Diptera: Culicidae). Canadian Entomologist 129:1173-1176.

Otis GW, Locke B, McKenzie NG, Cheung D, MacLeod E, Careless P, Kwoon A, 2006. Local enhancement in mud-puddling swallowtail butterflies (*Battus philenor* and *Papilio glaucus*). Journal of Insect Behavior 19:685-698.

Papaj DR, 1993. Use and avoidance of occupied hosts as a dynamic process in tephritid fruit flies. In: Bernays EA, editor. Insect Plant Interactions Boca Raton, FL: CRC. p. 25-46.

Papaj DR, 1994. Oviposition site guarding by male walnut flies and its possible consequences for mating success. Behavioral Ecology & Sociobiology 34:187-195.

Papaj DR, Messing RH, 1998. Asymmetries in physiological state as a possible cause of resident advantage in contests. Behaviour 135:1013-1030.

Plowright CMS, Landry F, 2000. A direct effect of competition on food choice by pigeons. Behavioural Processes 50:59-64.

Prokopy RJ, Bush GL, 1973a. Oviposition by grouped and isolated apple maggot flies. Ann Entomol Soc Am 66:1197-1200.

Prokopy RJ, Bush GL, 1973b. Ovipositional responses to different sizes of artificial fruit by flies of *Rhagoletis pomonella* species group. Ann Entomol Soc Am 66:927-929.

Prokopy RJ, Duan JJ, 1998. Socially facilitated egglaying behavior in Mediterranean fruit flies. Behavioral Ecology and Sociobiology 42:117-122.

Prokopy RJ, Miller NW, Duan JJ, Vargas RI, 2000. Local enhancement of arrivals of *Ceratitis capitata* females on fruit mimics. Entomologia Experimentalis et Applicata 97:211-217.

Prokopy RJ, Roitberg BD, 2001. Joining and avoidance behavior in nonsocial insects. Annual Review of Entomology 46:631-665.

Prokopy RJ, Romig MC, Drew AI, 1999. Facilitation of ovipositional behavior of *Bactrocera tryoni* flies. Journal of Insect Behavior 12:815-832.

Robertson IC, Roitberg BD, Williamson I, Senger SE, 1995. Contextual ecology. American Entomologist 41:237-240.

Rull J, Prokopy RJ, Vargas RI, 2003. Effects of conspecific presence on arrival and use of hosts in *Ceratitis capitata* flies. Journal of Insect Behavior 16:329-346.

Slaa EJ, Wassenberg J, Biesmeijer JC, 2003. The use of fieldbased social information in eusocial foragers: local enhancement among nestmates and heterospecifics in stingless bees. Ecological Entomology 28:369-379.

Stamps JA, 1987. Conspecifics as cues to territory quality: A preference of juvenile lizards (*Anolis aeneus*) for previously used territories. The American Naturalist 129:629-642.

Stephens DW, 1989. Variance and the value of information. American Naturalist 134:128-140.

Van Alphen JJM, Visser ME, 1990. Superparasitism as an adaptive strategy for insect parasitoids. Annual Review of Entomology 35:59-79.

Visser ME, 1991. Prey selection by predators depleting a patch - an ESS model. Netherlands Journal of Zoology 41:63-80.

Figure 1. Design and results of experiment on spatial scale of conspecific effects. (a) Set-up for all arenas in part 2 of experiment 3. 3.8 L box containing two 297 mL cups, one containing 12 female flies and each with two model walnuts, one inside the cup and one outside. Cups were topped with cloth mesh and furnished with vials of water. (b) Number of observations/flies/eggs on either side of the cage. Significant difference (two-tailed paired t-test, $\alpha=0.05$) indicated with asterisk.

Figure 2. The effect of social environment and host size on oviposition behavior (experiment 2). Number of ovipositing females estimated as described in text. (a) Mean (+ SEM) number of eggs per ovipositing female. Shared letters indicate non-significant differences (t-test, $\alpha=0.05$; interaction marginally significant: $F_{(social*size)1,113}=3.50$, $p=0.06$). (b) Mean (+SEM) number of clutches per ovipositing female (No significant differences), (c) Mean (+SEM) clutch size (no significant differences).

Figure 3. Effect of previous and current social environment on egg-laying decisions (experiment 4). Bars represent proportion of flies in each rearing treatment that attempted to oviposit when presented with a fruit with or without a resident female. Lines represent proportion of females that successfully oviposited. Proportion attempting oviposition was affected by previous ($\chi^2=5.28$, df=1, $p<0.025$) and concurrent exposure ($\chi^2=5.28$, df=1, $p<0.025$) to conspecifics.

Figure 4. Mean (+SEM) number of aggressive encounters (lunges, head butts and foreleg kicks) in flies differing in social rearing condition. Shared letters indicate non-significant differences (Mann-whitney U test, $\alpha=0.05$). Numbers within bars are sample sizes.

Formatted: Space After: 0 pt, Line spacing: single