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Maximization of host encounters by parasitoids foraging in the field: females can use a simple rule

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Abstract Searching animals maximizing resource encounters should use reliable foraging cues. *Biosteres juglandis*, a braconid parasitoid of *Rhagoletis juglandis* larvae feeding in fruits of the Arizona walnut, searches for hosts both on walnuts that are on the tree and those that have fallen to the ground. Field and laboratory assays were conducted to determine the cues used by *B. juglandis* to choose ground walnuts on which to alight. After walnuts are infested with fly larvae, they change color from yellow to black. In field studies, wasps preferentially landed on walnuts on the ground that had at least some yellow on them. At one south-eastern Arizona site, yellow fruits were more likely to contain fly larvae than those that were all black. Yellow fruits also contained younger larvae in which wasps had greater oviposition and/or developmental success. At another site, black fruits were more likely than yellow to contain larvae, but wasps were searching yellow walnuts only. A laboratory experiment suggested that visual contrast may be one reason why wasps prefer to land on yellow walnuts in the field.

Key words *Biosteres* · Braconidae · *Diachasmimorpha* · Foraging · Visual cues

Introduction

Foraging theory predicts that animals foraging in a patchy environment should make decisions which maximize the rate at which they encounter resources (Charnov 1976; Iwasa et al. 1981). Parasitoids are ideal organisms for testing optimality theory, because their host-search behavior directly affects the number of offspring produced. Searching parasitoids should maximize the rate at which they encounter appropriate hosts (Hubbard and Cook 1978; Waage 1983), a prediction that has been tested both in the laboratory (e.g., Cook and Hubbard 1977; Hubbard and Cook 1978; Haccou et al. 1991; Hemerik et al. 1993) and in the field (Stamp 1982; Waage 1983; Thompson 1986; Janssen 1989; Rosenheim et al. 1989; Heimpel et al. 1996).

When choosing patches to search, animals should respond to cues which most reliably predict the presence of resources. A recent focus of parasitoid behavioral experiments in the laboratory has been on responses to odors produced by the plant or substrate on which their host feeds (Elzen et al. 1986; Eller et al. 1988; Whitman 1988; Turlings et al. 1990, 1991; Whitman and Eller 1990; Udayagiri and Jones 1992; Steinberg et al. 1993). Female parasitic wasps are innately attracted to some odors of plant origin (Navasero and Elzen 1989; Wiskerke and Vet 1994; Geervliet et al. 1996) and also learn odors associated with oviposition that are either relevant to their normal ecological context (e.g., Kaiser and Cardé 1992; Poolman Simons et al. 1992; Vet et al. 1995), or novel (Lewis and Takasu 1990; De Jong and Kaiser 1991).

Use of both visual and olfactory cues simultaneously should enhance insect foraging success by providing a greater amount and higher precision of information about patch quality (Prokopy 1986; Wäckers 1994; Wäckers and Lewis 1994). Study of the use of visual cues by host-searching parasitic wasps has nonetheless been limited (Arthur 1967; Takahashi and Pimentel 1967; Weseloh 1972, 1986; Sugimoto et al. 1988; Wardle 1990; McAuslane et al. 1991; Wäckers and Lewis 1994). All that is known about cue use by parasitoids foraging in their natural environment has been learned through sticky trap collections (Weseloh 1972, 1986; Vargas et al. 1991) and the release and recapture of laboratory wasps (Papaj and Vet 1990).

Biosteres juglandis is a parasitoid that forages within discrete patches (host-infested fruits), and follows

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theoretical predictions by varying its search intensity depending on the density of hosts in a patch (Henneman 1996). The goal of this study was to determine if *B. juglandis* females foraging in the field use specific cues or cue combinations to locate profitable patches. In order to elucidate the functional value of, and possible mechanism underlying, cue use in this species, I also conducted a series of laboratory experiments.

Materials and methods

Natural History

B. juglandis (Braconidae: Opiinae) (in the process of being reclassified as *Diachasmimorpha juglandis* (Wharton 1988; R.A. Wharton personal communication) is a solitary larval/pupal endoparasitoid of the tephritid flies *Rhagoletis juglandis* and *R. boycei* (Wharton and Marsh 1978). As larvae, these flies feed within the husks surrounding walnuts of the species *Juglans major* (Juglandaceae) in southwestern North America (Boyce 1934; Buckingham 1975).

Walnut fruits turn greenish yellow as they become ripe. Flies oviposit clutches of 10–20 in fruits when fruits are on the tree and ripe (i.e., soft enough for a fly to insert her ovipositor). Several females usually oviposit in a single fruit (Papaj 1994), which generally supports *c.* 30 larvae to pupation (C. Nufio, unpublished work; Henneman 1996), though large fruits may support more than 60 larvae (M.L. Henneman and C. Nufio, unpublished data). The natural rotting process of a fruit is accelerated as larvae develop within, and dark brown patches appear over areas in which larvae have consumed the inner husk material. There are changes in the odor of an infested walnut associated with these changes in appearance (M.L. Henneman, R.A. Raguso, J. Takabayashi, and E.G. Dyreson unpublished work). The fruit then falls from the tree and larval development is completed on the ground. When larvae exit the fruit to pupate in the soil, the entire inner husk has usually been consumed, and the fruit is nearly always completely black. Total development time from oviposition to pupation is *c.* 3 weeks (Buckingham 1975).

B. juglandis oviposits through the walnut husk into the second and third (final two) instars of *R. juglandis* and *R. boycei* larvae, both while fruits are on the tree and after they have fallen to the ground. After the host pupates, the wasp completes its larval development by consuming all the host material inside the puparium (Buckingham 1975). Both flies and wasps diapause until the following summer when walnut fruits are again available (Boyce 1934; Buckingham 1975).

Walnut trees are clumped in discrete areas along washes at the sites in this study, with hundreds of meters between clumps, creating a patchy environment on a large scale. It is unknown whether wasps migrate among clumps, but they may remain in one area for several days (M.L. Henneman, unpublished work).

Field assays

I conducted two field experiments to determine (1) whether wasps foraging on the ground show a preference for fruits of a particular phenological stage (identified by appearance) and (2) how this preference correlates with host distribution among ground (fallen) fruit stages.

Ground fruit preference

I collected data from July to September 1995 and July 1996 at three field sites in southeastern Arizona: Garden Canyon (Huachuca Mountains, Ft. Huachuca, Cochise Co., Arizona), Rucker Canyon (Chiricahua Mountains, Cochise Co., Arizona), and Arcadia campground on Mt. Graham (Pinaleño Mountains, Graham Co., Arizona). *R. juglandis* occurs alone at the first two sites and with *R. boycei* at the latter site.

I arranged fruits collected from the ground underneath a single walnut tree in one array under that tree consisting of six rows of fruits, in seven to ten columns, alternating mostly-black and mostly-yellow fruits that had fallen from the tree. Fruits were placed *c.* 2 cm apart. All remaining fruits under the tree were collected to increase the opportunity for wasps to find array fruits.

When a wasp entered the array, the position and color of each walnut on which it landed during its foraging bout was noted. The number of landings on black and yellow walnuts was tallied for each separate wasp visit, and a Wilcoxon signed-rank test was performed to compare the number of landings each wasp made on yellow versus black walnuts.

Free foraging assay

I conducted this study at two field sites. The first was Garden Canyon (Huachuca Mountains), where I collected data over seven dates between July 22 and August 8, 1996. The second was Wet Canyon in the Pinaleño Mountains, where I collected data on August 16 and 22 1996.

Walnuts on the ground were not manipulated, but scanned for the presence of wasps for 2 h each day between 1330 and 1630 hours. When I found a wasp on a walnut, I marked the walnut with a number. Wasps were observed for 10 min or as long as they stayed on the walnut to determine whether they exhibited search behavior. Searching wasps tap their antennae on the surface and halt their motion every few seconds, presumably locating host larvae by feeling their vibrations beneath the surface (Lawrence 1981; Glas and Vet 1983). I followed landings by wasps on several successive walnuts, when they occurred. Wasps were collected when possible after observation to maximize the number of individuals observed.

Each day at the end of the sampling period, I collected for dissection a subset ($n = 8$–16) of the walnuts on which I had observed wasps. The distribution of host larvae in these was compared with an equal number of ground walnuts that had not been observed with wasps on them. These were collected by walking a transect through the observation area and picking up the appropriate number of walnuts. I noted whether or not each fruit collected had at least some yellow on it, or was completely black.

To test whether wasps were selecting fruits nonrandomly with respect to presence of host larvae, I performed *G*-tests. Data were pooled across all Garden Canyon sampling dates, but I tested the two dates at Wet Canyon separately, as the data from this site were not homogeneous (see Results).

Laboratory assays

Based on field results, I tested two hypotheses in the laboratory concerning fruit choice in the field: (1) wasp perception of visual contrast is a mechanism for fruit choice in the field, because fruits at an earlier stage that are still at least partly yellow are more conspicuous than all-black fruits against the dark leaf litter under trees; and (2) wasps have higher reproductive success in younger hosts associated with yellow fruits than in older, pre-pupal larvae associated with all-black fruits.

Mechanism of fruit choice

Wasps of unknown age and experience were collected in the field from two locations, Wet Canyon and Jerome, Arizona. They were tested in the laboratory to compare their landing behavior on fruits placed against differently colored backgrounds.

On the bottom of a 30-cm cubic screen cage, I arranged a 4×4 array of all-black and mostly yellow walnuts similar to the field arrays described above, on top of either a black cloth or a light green cloth. I released female wasps in the cage, and noted the total number of landings on yellow and black walnuts. In each replicate, both backgrounds were presented for equal periods of time ranging from 30 to 60 min. Individual wasps were not marked, but based on the number observed on fruits at any one time, at least 13 individuals made landings over the course of the experiment.

Two replicates were run with *c*. 30 wasps collected from Wet Canyon, who were presented with the light and then the black background. The next day, the same wasps were presented with the backgrounds in reverse order. A new set of walnuts was used in the array. The same day, *c*. 15 wasps collected in Jerome, Arizona were presented with the same array against the black and then the light background. I dissected walnuts at the end of the experiment to confirm that they were infested.

A *G*-test was used to compare numbers of landings on yellow and black walnuts against each background, for each replicate.

Wasp oviposition/larval success in young last-instar and pre-pupal hosts

To test whether the younger larvae in yellow fruits are more suitable for parasitization than the older prepupal larvae in black fruits, larvae from each fruit type were presented to wasps in artificial fruits for oviposition in the absence of fruit cues. Artificial fruits consisted of a damp sponge ball covered with parafilm, to contain the larvae moving around on the surface of the sponge. I placed two artificial fruits, one with 25 young last-instar host larvae from yellow fruits and the other with 25 prepupal host larvae from black fruits, in a 4-l plastic cage containing 40 wasps for 4 h in one case, and 45 wasps for 8 h in another. Host larvae were removed and maintained on a walnut mash diet for several days, or until pupation, in order to allow any wasp larvae to hatch. I dissected every surviving host larva (n = 72) for wasp larvae, which ranged from first to fourth (final) instars. I used a *G*-test to compare the number of young versus old host larvae with and without developing wasps.

Power analyses for nonsignificant *G*-tests were based on the noncentral χ^2 distribution with the noncentrality parameter equal to the χ^2 value of the test (Patniak 1949; Walsh 1968; Self et al. 1992).

Results

Field assays

Ground fruit preference

I observed at least 15 different wasps over 22 visits to the arrays at the three sites. Wasps landed more often on fruits that were mostly yellow (Wilcoxon signed ranks test; n = 22 wasp visits, T = 0, P < 0.0002; Fig. 1). Half the visits included no landings on black walnuts. Example paths of four individuals are shown in Fig. 2.

Free foraging assay

Throughout the study at Garden Canyon, yellow fruits were more likely to contain fly larvae than were black fruits (Fig. 3). Over the course of the study, the proportion of all-black fruits with fly larvae declined.

Data from all days at Garden Canyon were pooled for this test, because a chi-square test for heterogeneity among the individual sampling days was not significant

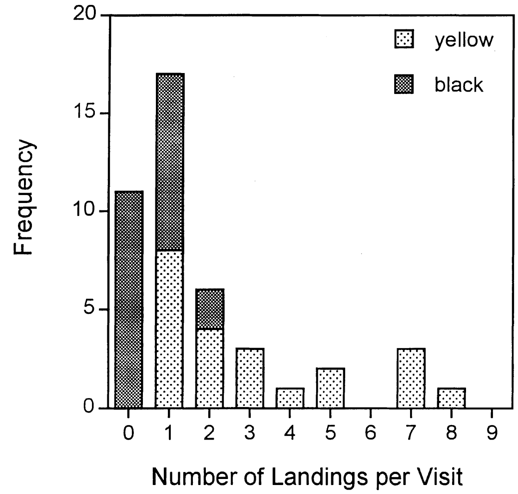

Fig. 1 Frequency histogram of number of landings on each fruit type per visit to the array. Data represent 22 wasp visits. Median landings per visit on yellow fruits = 2; median landings per visit on black fruits = 0.5

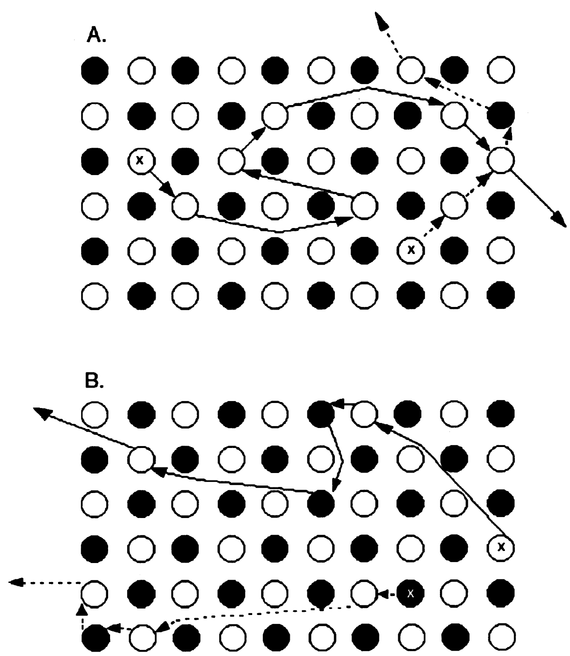

Fig. 2A,B Examples of four visits by wasps to two arrays. *Filled circles* represent mostly-black walnuts, and *open circles* represent mostly-yellow walnuts. *Solid lines* and *dashed lines* represent different individual wasps. The first walnut of each visit is denoted by *x*. **A** Two visits to an array at Rucker Canyon, Chiricahua Mountains, **B** Two visits to an array at Arcadia Campground, Mt. Graham, Pinaleño Mountains

(χ^2 = 3.195, df = 5, P > 0.5). Wasps were present most often on fruits with hosts. Two fruits with wasps versus 31% of fruits overall contained no hosts (G = 14.34, df = 1, P < 0.0002; Fig. 4A). On average there were 27.5 mostly third-instar larvae per infested fruit (n = 125). Wasps were seen only twice on all-black fruits, each time for a few seconds and they exhibited no search behavior.

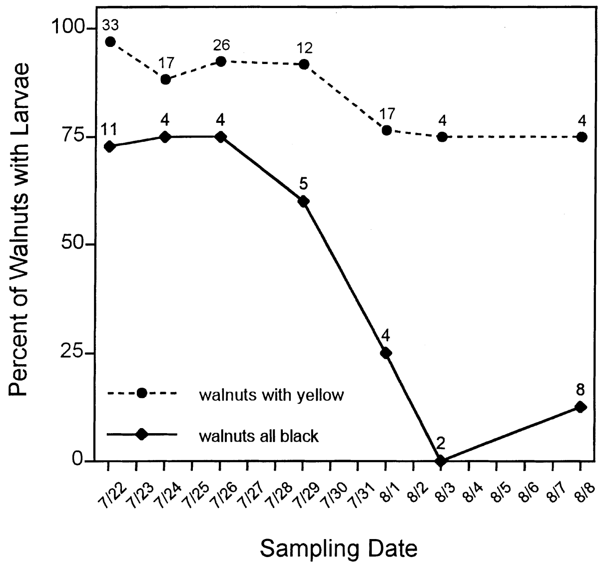

Fig. 3 The percent infested of total walnuts collected over the course of the study at Garden Canyon, categorized as either completely black or having at least some yellow. *Sample sizes* are given for each point

On the first day at Wet Canyon, wasp presence on a fruit was not significantly associated with host presence ($G = 1.90$, $df = 1$, $P > 0.16$; power $= 0.28$; Fig. 4B). All fruits I collected were nearly identical in appearance: mostly yellow, with small dark areas of mostly external physical damage. About 50% of the ground fruits at Wet Canyon were infested with first- to second-instar fly larvae, stages successfully utilized less often than third-instars by *B. juglandis* (Buckingham 1975).

On the second sampling date at Wet Canyon, many fruits had turned black, and 75% overall were infested with larvae. The wasps were found only on yellow fruits, but nearly half of these did not contain hosts ($G = 6.03$, $df = 1$, $P < 0.014$; Fig. 4B). Results from the two days were significantly different in a heterogeneity test ($\chi^2 = 10.309$, $df = 1$, $P < 0.003$). Over both days there were an average of 5.5 ($n = 77$) hosts per infested fruit.

Laboratory assays

Mechanism of fruit choice

Wasps from Jerome were significantly more likely to land on black walnuts when arrays were placed on a light background than when placed on a dark background ($G > 6$, $df = 1$, $P < 0.02$). Wet Canyon wasps behaved similarly in the first replicate ($G = 7.41$, $df = 1$, $P < 0.02$). In the second replicate, wasps did not respond differentially to background ($G = 0.006$, $df = 1$, $P > 0.9$; power $= 0.05$). Regardless of the background, wasps always preferred to land on yellow walnuts (Fig. 5), despite the fact that five of eight yellow walnuts in one of the arrays were not infested, and all of the black walnuts were.

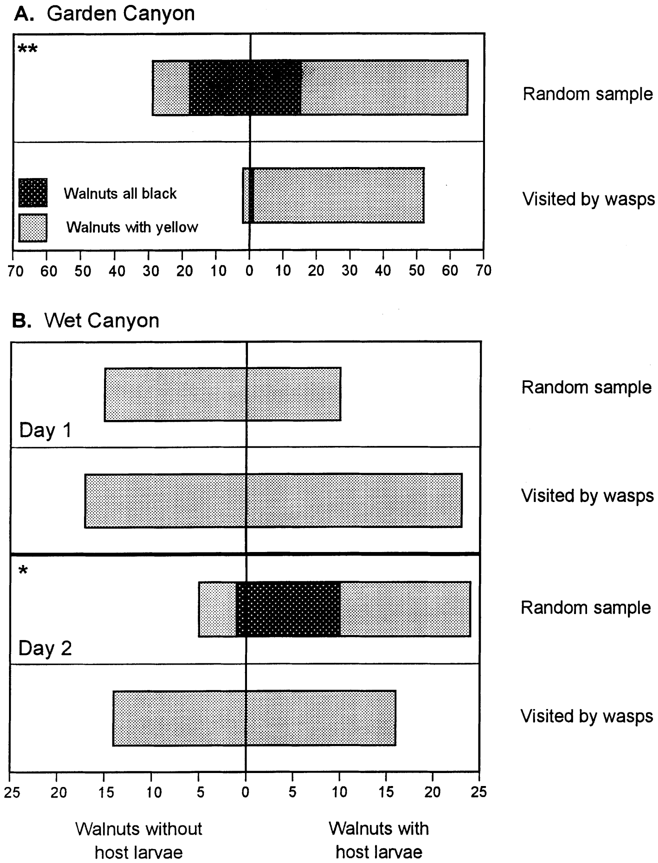

Fig. 4A,B Numbers of infested and uninfested fruits, all-black and partly yellow, randomly collected compared with those chosen by wasps, plotted by site. **A** Garden Canyon, **B** Wet Canyon day 1, and Wet Canyon day 2. Contingency *G*-tests were conducted on fruits with host larvae for each site. (Garden Canyon data are pooled across all sampling dates.) *$P < 0.014$, **$P < 0.0002$

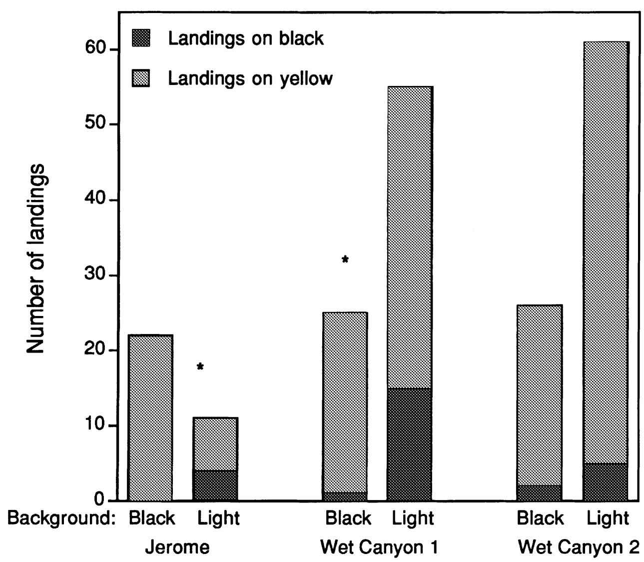

Fig. 5 Numbers of landings on all-black walnuts and walnuts with at least some yellow on different backgrounds. Jerome wasps: ($n \geq 5$), with the black background presented first. Wet Canyon wasps trial 1: ($n \geq 8$), light background presented first. Wet Canyon wasps trial 2: ($n \geq 7$), black background presented first. *$P < 0.02$

Wasp oviposition/larval success in young last-instar and pre-pupal hosts

Wasps larvae were able to develop successfully in both old and young hosts. However, 41.7% of old hosts versus 5.5% of young hosts contained no developing wasps ($n_{old} = n_{young} = 36$; $G = 14.35$, $df = 1$, $P < 0.0002$). Oviposition scars present on many of the unparasitized older hosts indicated that a wasp's ovipositor had penetrated the cuticle and either the wasp rejected the host, or the egg did not survive.

Discussion

Use of fruit cues for host location and successful parasitization by *B. juglandis*

In the first part of the study I found that wasps in the field preferred to land on walnuts that had yellow on them over walnuts that were all-black, even when black walnuts were more likely to contain host larvae (Fig. 4). In general, yellow walnuts are more likely than black walnuts to contain host larvae (Fig. 3), and the younger fly larvae relatively more common in younger fruits are more conducive to wasp oviposition and/or larval development. Two out of three contrast replicates suggest that perception of visual contrast is a mechanism that makes black walnuts less apparent than those with yellow against leaf litter on the ground (Fig. 5), causing wasps to overlook them.

A simple rule

Wasps attacking endophytic hosts must rely on plant cues to find them, choosing the cues that best predict host presence (Vet et al. 1991), although there is usually not a perfect correlation between host and plant cue. The eulophid *Sympiesis sericeicornis*, which attacks leaf miners, is attracted to mines regardless of whether or not a host is present (Casas 1989). It seems probable that *B. juglandis* uses both visual and olfactory cues to locate infested walnuts, as suggested by other laboratory experiments, and the fact that there are odor changes correlated with visual changes in decaying fruits (M.L. Henneman, R.A. Raguso, J. Takabayashi, and E.G. Dyreson unpublished work). Simultaneous use of several cues should enhance foraging success.

At Garden Canyon color was a reliable cue because all the fruits on a tree became infested, and dropped from the tree over a period of two weeks when they were still mostly yellow. The proportion of infested black fruits decreased markedly over the days sampled as fly larvae exited to pupate, while the proportion of infested yellow fruits started higher and dropped less over the same period (Fig. 3). Thus, throughout the study at Garden Canyon, any yellow fruit on the ground was more likely than any black fruit to have fly larvae. Given this result alone, it would be a useful rule for wasps to avoid all-black fruits and land on fruits that are yellow, assuming wasps are time- or energy-limited to any degree. If wasps are egg-limited, they should choose yellow walnuts because they contain higher quality hosts.

A rule to search yellow fruits is functional only if most fruits in the vicinity of a wasp's search contain host larvae. In the unusual case where the infestation level is low, the proportion of yellow fruits with larvae on the ground can actually be lower than the percentage of black fruits with larvae, because larval feeding causes the fruits to blacken. At Wet Canyon, wasps continued to land on yellow fruits, and thus were not likely to find hosts. High infestation is typical, however. In addition to personal observations of high infestation rates at sites in three mountain ranges over five years, specific data from 1996 showed that over a large sampling area, 85% of fruits surveyed became infested with larvae ($n = 188$ fruits from 23 trees at 10 sites in 5 mountain ranges across southeastern Arizona; one tree had zero infestation) (Henneman 1997). In 1994, of 57 fruits removed from a different tree at Garden Canyon, 81% contained fly larvae, and 14% contained fly eggs (Henneman 1997; unpublished work). Finally, in 1993, 90% of 61 dissected ground fruits from Arcadia Campground (*c.* 5 km from Wet Canyon) in the Pinaleño Mountains contained fly larvae (unpublished data).

At Wet Canyon in 1996, there not only low numbers of infested fruits, but low numbers of hosts per fruit. On the first sampling date, although 51% of walnuts sampled were infested, only 15% had fly larvae large enough to be successfully attacked by wasps (Buckingham 1975). Six days later, 75% of fruits were infested with larvae suitable for attack (probably due to larvae hatching in fruits that had previously contained only eggs, and/or an influx of infested walnuts from the tree). However, the average number of larvae per infested fruit over both sampling dates was only 5.5 compared to 27.5 at Garden Canyon. In 1994 there were 21.3 larvae per infested fruit at different Garden Canyon tree clump ($n = 46$) and in 1995 in Rucker Canyon (Chiricahua Mountains), infested fruits from two trees had an average of 47.1 larvae ($n = 51$) (M.L. Henneman, unpublished work).

Wasps would benefit from searching yellow fruits at any of those sites and years, but they would not at Wet Canyon in 1996. There are several possible reasons why wasps at Wet Canyon preferred yellow walnuts over black even when they contained fewer hosts. First, the foraging experience of the wasps to that date may have included only yellow walnuts, and there was a lag time after which wasps would learn that black fruits were more profitable. Second, given the wasps' experience it could be beneficial to specialize on yellow fruits over the course of their lifetime, even if doing so were unprofitable in the short term (Smithson and MacNair 1996). Third, the wasps were fixed in their behavior and could not learn to search fruits of another color. Unfortunately, floods swept away the walnuts at the Wet Canyon site shortly after the second sampling date, so a follow-up study could not be done to distinguish among these possibilities.

Parasitoid larvae are more successful in younger hosts

In addition to finding more hosts overall, wasps are likely to produce more offspring when they attack hosts in younger fruits. Black fruits tend to contain prepupal hosts, older than those in yellow fruits. Wasps may choose yellow fruits because they are more likely to contain larvae in which (1) adults can successfully oviposit, and/or (2) wasp larvae can develop successfully. Older larvae may have a tougher cuticle that is more difficult to penetrate (van Lenteren 1976; Vet et al. 1994), and they can be stronger and better able to fight back or escape (Kouame and Mackaver 1991). Some older fly larvae without developing wasps had scars from oviposition attempts, indicating rejection by females or death of offspring. Buckingham (1975) confirmed only one instance of encapsulation of wasp eggs by fly larvae in this system. However, Wong et al. (1990) found that larval mortality of *Diachasmimorpha tryoni*, a congener of *B. juglandis*, was 71.7% in late third instars of its host, the tephritid *Ceratitis capitata*. *D. longicaudata* has a similar developmental dependence on host age (Lawrence et al. 1976). High levels of ecdysone combined with low levels of juvenile hormone seem to be necessary for wasp eggs to hatch, and for larvae to molt properly and complete development (Lawrence 1982). Similar relationships between parasitoid developmental success and host age have been found in other systems (Cals-Usciati 1969; Smilowitz 1974).

Younger hosts may be less likely to have been previously parasitized by other females, but it is unclear whether larval competition is significant enough to affect selection of yellow fruits. The parasitization rate of *R. juglandis* in the field by *B. juglandis* is generally not more than 10% (Buckingham 1975), so encounters with previously parasitized hosts are probably low. In congeners of this species, there is also evidence that when two wasp eggs are laid in a single host, the second one (if laid within 2–3 days) is more likely to kill the first and complete development (Pemberton and Willard 1918), suggesting that foraging females should not necessarily avoid parasitized hosts.

Perception of visual contrast as a mechanism for fruit choice

Rhagoletis pomonella (apple maggot flies) prefer darker colored fruit models which contrast highly with a light sky (Owens and Prokopy 1984). *R. pomonella* are also attracted to red models in tree foliage, but not green, in the absence of odor, which could be an effect of color contrast of the models against the foliage (Aluja and Prokopy 1993). Contrast may similarly be useful to *B. juglandis* because while still on the tree, walnut fruits darkened with feeding damage are more attractive than undamaged fruits (M.L. Henneman, unpublished work.). At the same time, fruits that have some visible yellow provide higher contrast against dark leaf litter on the ground than do the black ones. In each case, the higher contrast choice is the functional one.

Although the laboratory background was more uniform than the leaf litter beneath a tree, wasps foraging in the cage with the black background behaved in a similar manner to wasps observed in the field, suggesting that the color or contrast played a role. Wasps also preferred yellow fruits on the light background (Fig. 5), so while contrast may affect fruit choice, it is apparently not of primary importance. Because attraction to yellow is commonly found in parasitic Hymenoptera (Weseloh 1986), innate color preference probably affects fruit choice in *B. juglandis*.

Conclusions

While foraging on the ground, *B. juglandis* females apparently assess the distribution of their hosts in the field by using a simple cue: the presence of yellow (and/or associated odor) on a walnut. There is not a perfect correlation between fruit color and infestation level, but by exclusively using yellow fruits, females are more likely to find hosts suitable for wasp larval development where they land, because usually, nearly all fruits on a tree eventually become infested.

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