



Individual consistency, learning and memory in a parasitoid fly, *Ormia ochracea*

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Search images are expected to be important components of predator and parasitoid search strategies as they reduce the search time for prey and hosts. Fixed search images, however, may constrain predators and parasitoids, and render them ineffective at switching to new more abundant prey or hosts. For switching behaviour to be effective, parasitoids need to be able to learn cues associated with abundant hosts, and they need to be able to extinguish preferences for the cues of hosts that are no longer abundant. Here we use the *Gryllus* cricket and *Ormia ochracea* parasitoid fly system to show (1) individual consistency in fly preference for song in the field, (2) learning of host song in the laboratory and (3) that the flies' memory for learned host cues is very short term. These results are interesting and novel in several respects. First, our demonstration that *O. ochracea* satisfies each of the characteristics of an optimally foraging temporary specialist is new. Second, this is only the third demonstration of learning in the Tachinidae, a family of more than 9000 species, all of which are parasitoids. Third, the flexibility inherent in learning and host switching may have been instrumental in allowing expansion of the fly's geographical and host range.

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When predators and/or parasitoids have a range of potential prey/hosts to select among, classical optimal foraging theory predicts that resources should be ranked by criteria that reflect search time, handling time and energetic or nutritional quality (Stephens & Krebs 1987; Hamilton 2010). Improvement in search time or efficiency may be achieved by adoption of search images (Tinbergen 1960); for example, blue jays, *Cyanocitta cristata*, trained to recognize pictures of moths increased their detection of prey when sequentially presented a single type of moth (Pietrewicz & Kamil 1979). Search images are not limited to visual cues, however. For example, the salticid spider *Evarcha culicivora* has recently been shown to be able to use olfactory search images to enhance location of both mates and prey (Cross & Jackson 2010). One key feature of efficient search image use should be the ability to switch search images to favour more abundant prey (Cornell 1976; Ishii & Shimada 2010). Switching behaviour has been studied in several parasitoid insects, especially parasitoid wasps (Cornell & Pimentel 1978; Chow & Mackauer 1991). An essential element of optimal foraging involving switching is the ability to learn host-associated cues. Learning in insects is now widely documented (Dukas 2008). Almost all examples of insect learning

involve foraging; recent taxonomically diverse examples include grasshoppers

(*Schistocerca americana*) showing associative learning for taste, colour and location of food (Dukas & Bernays 2000), antlion larvae learning to associate vibrational cues with prey arrival (Guillette et al. 2009) and larvae of the coccinellid beetle *Coleomegilla maculata* learning to favour high-quality prey (Boivin et al. 2010).

There is also a great deal of evidence that parasitoid insects can learn host-associated cues (Godfray 1994), however, most of this evidence comes from parasitoid wasps (Turlings et al. 1993), with fewer examples of learning in other parasitoid insect groups (Dukas 2008). The most species-rich group of insect parasitoids other than wasps is the fly family Tachinidae, with greater than 9000 described species, all of which are parasitoids (O'Hara & Wood 2004; Stireman et al. 2006; O'Hara 2008). However, within this huge group of flies, only two examples of learning of host-associated cues have been published, and both involved associative learning of artificial cues of no natural ecological relevance. In an early study with captive *Drino bohemica*, the flies learned to associate the insertion of a tray into their cage with the presence of their sawfly host larvae (Montieth 1963). More recently, *Exorista mella*, a generalist tachinid parasitoid mostly of caterpillars, was shown to learn to associate a visual cue (coloured discs) with presence of a caterpillar host (*Grammia geneura*) (Stireman 2002). We are aware of no studies that have demonstrated that a tachinid can learn ecologically relevant host-associated cues.

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In addition to learning host-associated cues, effective switching behaviour also requires the ability to 'forget' the cues of hosts no longer abundant within the environment. Work on insect memory has lagged behind work on insect learning. Nevertheless, a number of examples of the persistence of learning have appeared in the literature, again primarily but not exclusively with parasitoid wasps. Among parasitoid wasps, chemical cue memory in *Aphidius ervi* lasted at least 3 days (Du et al. 1997); odour cue memory in *Microplitis croceipes* lasted about 24 h (Takasu & Lewis 2003); in *Cotesia kariyai* that had learned to associate plant volatile chemical odours with host infestation, memory declined after 2 days (Fukushima et al. 2001); host-associated fruit odour memory lasted 1–2 days in *Leptopilina boulardi* (Kaiser et al. 2009). Longer-term memory in parasitoid wasps has also been documented (e.g. host oviposition preference memory lasted about 5 days in *Trichogramma nr. brassicae*: Bjorksten & Hoffmann 1998; memory for a learned odour cue associated with hosts of *Lariophagus distinguendus* persisted for more than 144 h: Müller et al. 2006). In taxa other than parasitoid wasps, the tachinid *D. bohemicus*'s learned association of an artificial tray with sawfly host larvae, mentioned above, persisted from a few hours to a few days (Montieth 1963); in the larval coccinellid beetle, also mentioned above, the memory of learned prey characteristics persisted about 48 h (Boivin et al. 2010). These and other examples of limited memory in parasitoids have prompted two recent general treatments attempting to relate persistence of parasitoid memory to neurobiology and the ecological persistence of available hosts (Brassil 2007; Hoedjes et al. 2011). Temporally stable host dynamics should favour longer-term memory of host-associated cues, whereas temporally unstable host dynamics should favour short-term memory and high potential for rapid host switching (Brassil 2007).

Here we examine individual parasitoid consistency, learning and memory in the host–parasitoid system consisting of the tachinid parasitoid fly *Ormia ochracea* and its *Gryllus* field cricket hosts. One special feature of this parasitoid–host relationship is that gravid females of the fly locate their cricket hosts acoustically by using the male cricket calling song as a cue (Cade 1975). Female *O. ochracea* have a specialized ear on the prosternum that is tuned to the 5 kHz song typical of *Gryllus* species (Robert et al. 1992; Robert et al. 1994); male *O. ochracea* have less sensitive hearing and are not attracted to cricket song. *Ormia ochracea* is thus specialized on *Gryllus* field cricket hosts. However, there are a number of different *Gryllus* species with different song structures that are naturally parasitized (reviewed in Sakaguchi & Gray 2011). One striking feature of *O. ochracea* is that different populations of flies show preferences for different songs of suitable known hosts, preferring their locally most abundant host species of cricket, but mtDNA genetic evidence suggests that these populations are not cryptic host races. Flies show song preferences both among host species' songs (Walker & Wineriter 1991; Gray et al. 2007; Sakaguchi & Gray 2011) and for specific song variants within the natural range of host song (Wagner 1996; Gray & Cade 1999; Wagner & Basolo 2007; Sakaguchi & Gray 2011). Gray & Cade (1999) and Sakaguchi & Gray (2011) suggested that fly song preferences may increase the efficiency of fly host location by preferentially focusing on abundant song types. This suggests an acoustic search image, but one that is sufficiently flexible so as not to constrain geographical and host range expansion.

In this context, we studied a coastal southern California population of *O. ochracea* both in the field and the laboratory to examine (1) individual consistency of fly song preference in the field, and (2) learning of host song and (3) host song memory in the laboratory. Individual consistency of song preference was tested in the field using the mark–recapture technique with wild flies

attracted to two alternate song stimuli, *Gryllus lineaticeps* song or *Gryllus integer* song. Learning and memory effects were tested in the laboratory using a laboratory-propagated population of flies previously exposed to either *G. lineaticeps* or *G. integer* song prior to free-walking phonotaxis trials (Mason et al. 2005). To test memory effects, the prior exposure was either daily exposure to song for at least 5 consecutive days before testing (learning protocol), or the same daily song exposure, but with no song exposure the day before testing (memory protocol).

METHODS

Study Site and General Methods

Fly capture and marking was carried out every night during 24–30 September 2008 in an abandoned agricultural field at the King Gillette Ranch near Malibu Creek State Park in the Santa Monica Mountains, Los Angeles County, California (34.104°N, 118.706°W). Two different host songs were broadcast from slit traps designed for acoustic trapping of *Ormia* (Walker 1989). Traps were placed 30 m apart, approximately 5 m outside the canopy of two oak trees on dirt. Each trap was placed over a portable speaker connected to a CD player (Radio Shack, model 40-1441; Emerson, HD8197) broadcasting one of two synthesized cricket songs created with CoolEdit 2000 (Syntrillium Software, Scottsdale, AZ, U.S.A.). Synthetic songs were species-average songs for a given temperature (see Gray et al. 2007), and their use avoids the pseudoreplication associated with recordings of individual males' songs (Kroodsma 1989; Kroodsma et al. 2001). The speaker assigned to play either song was determined randomly. Song playback began at sunset and continued for 2 h, after which captured flies were left in silence for 5–10 min to reduce activity for ease of capture with small plastic vials. Vials were then set in crushed ice for 10–20 min to anaesthetize the flies. Cooled flies were marked on one or both wings with a broad tipped Sharpie® permanent marker. Flies that had responded to *G. lineaticeps* song were marked black, and those that had responded to *G. integer* song were marked red. A pilot experiment in the laboratory indicated that Sharpie® markings on the wings did not appear to impair fly mobility or laboratory survivorship, and that the marks remained visible for 2–3 days. Marked flies were put in an open box for recovery; over the course of the study, all 1060 marked flies flew away on their own. As we did not release marked flies until the end of each night's playbacks, all recaptured flies had been marked at least 24 h previously. All recaptured flies were removed from the wild and used to propagate a laboratory population (i.e. no flies were recaptured more than once).

Learning and Memory

A laboratory colony of *O. ochracea* was established from wild-caught gravid flies, using house crickets, *Acheta domesticus*, as hosts. Crickets were parasitized by hand using larvae freshly dissected from gravid female flies; crickets were then housed individually in 500 ml polyurethane tubs and provided with water, monkey chow and a section of egg carton for substrate. Tubers were kept in a dark room at 22–24 °C. Upon emergence from hosts, pupae were cleaned of debris and divided haphazardly into two groups. Each group was placed on damp cotton and moved into one of two identical Plexiglas fly cages, each housed within one of two identical incubators (Convion 125-litre incubator, Winnipeg, MB, Canada). Both incubators were programmed for a 16:8 h light:dark cycle and 25:23 °C temperature schedule. Upon adult emergence, flies lived in their Plexiglas cage. The cages measured 100 × 38 × 50 cm and had two mesh-sleeved armholes for access.

Wet kiln bricks and kitchen sponges provided a water source and maintained some level of humidity. Flies were provided with amino acid fortified nectar (Birds Choice Butterfly Nectar, Arbico Organics, Oro Valley, AZ, U.S.A.) in petri dishes with cotton. Flies were maintained at high density to stimulate mating. The density in the experiment varied, but was approximately 100 flies/m³.

A temperature-appropriate song of either *G. integer* or *G. lineaticeps* was played daily to captive flies for 80 min from a portable CD player and portable speakers (Emerson, HD8197; Radio Shack, model 40-1441) placed on the floor inside the Plexiglas cage. Cricket song was played daily for at least 5 consecutive days prior to testing and either included the day prior to testing (learning protocol), or did not include the day prior to testing (memory protocol). Only visibly gravid females were used in playback experiments; however, not all visibly gravid females are responsive to song. To collect responsive females for testing, we played back the cricket song in the females' cage very briefly (<2 min) and captured responding females in a vial. We collected responsive females 0–3 h into the dark phase of the photoperiod, and kept them briefly (<10 min) in a separate quiet dark room until their testing time.

The test arena consisted of a rectangular, collapsible nylon mesh tent (60 × 60 × 180 cm, model 1466D, BioQuip, Rancho Dominguez, CA, U.S.A.). One face of the tent had a zippered opening and another face was clear plastic. The inside of both ends were covered with identical black cotton fabric. Small speakers (Coby, model CSMP23) that plugged directly into a CD player were used in testing. CD player set-ups were placed 50 cm apart on the floor of the tent. Song arrangement (left or right) was randomly determined. The testing room was soundproof, quiet and light tight; all trials took place under dim red light between 22 and 24 °C with the testing songs calibrated for 23 °C. Song volume was 75 dB at 1 m (Radio Shack Sound Level Meter, model 33-2055). Song playback was started before the fly was brought into the room to ensure simultaneous stimulation by both songs. A fly was placed in the centre of the tent, 50 cm from either speaker in an equilateral triangle set-up. The fly was observed until it either touched a speaker or 5 min had passed with no activity. Almost all flies responded within 30 s; no flies failed to respond. After testing, all flies were moved into a separate fly cage to be used for propagation of the laboratory populations. No flies were tested more than once.

RESULTS

Individual Song Preference Consistency in the Wild

A total of 1060 flies were caught, marked and released. For first captures, there was a 65% bias towards the *G. integer* song (versus a null hypothesis of 50% at each trap: $G_1^2 = 94.426$, $P < 0.0001$). To be statistically conservative with our recapture test, we used a ratio of 65% *G. integer* to 35% *G. lineaticeps* (rather than 50/50) as the intrinsic null hypothesis in our subsequent analyses of the recapture data. Of the 1060 marked flies, we recaptured 69; those flies that were recaptured showed significant host song fidelity (Fig. 1). Of the 69 flies, 48 were recaptured at the same song, and 21 were recaptured at the other song ($G_1^2 = 6.886$, $N = 69$, $P = 0.0087$). This result also held for each song tested separately: flies marked at the *G. integer* song trap were more likely than expected to return to the *G. integer* trap (observed = 83%; expected under null = 65%; $G_1^2 = 6.114$, $N = 36$, $P = 0.013$), and flies initially marked at the *G. lineaticeps* trap were more likely than expected to be recaptured at the *G. lineaticeps* trap (observed = 55%; expected under null = 35%; $G_1^2 = 5.136$, $N = 33$, $P = 0.023$).

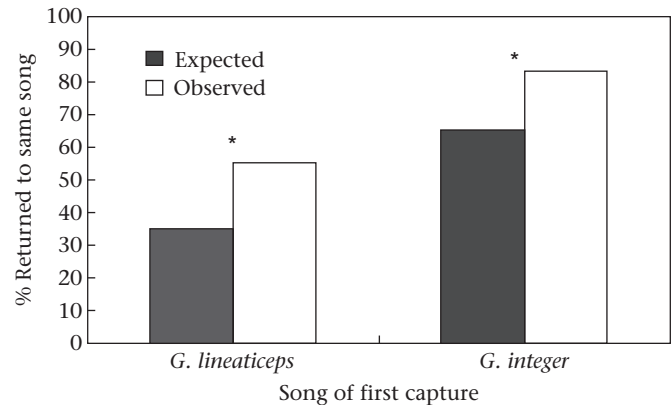


Figure 1. Mark–recapture data for 69 recaptured parasitoid flies, *Ormia ochracea*, caught at traps broadcasting a *G. lineaticeps* or *G. integer* song type. * $P < 0.05$.

Learning

Daily exposure to cricket song until the day prior to testing dramatically affected subsequent song preference of flies (Fig. 2). Of flies familiar with *G. lineaticeps* song, 17 of 23 (73.9%) chose *G. lineaticeps* song over *G. integer* song (exact sign test: $N = 23$, $P = 0.035$), whereas 15 of 19 (78.9%) of flies familiar with *G. integer* song chose *G. integer* song (exact sign test: $N = 19$, $P = 0.019$). Both song treatments were equally effective at altering subsequent preference; that is, strength of preference did not differ between treatments ($G_1^2 = 0.146$, $N = 42$, $P = 0.702$).

Memory

There was no significant host song preference when adult flies experienced no cricket song the day prior to testing (Fig. 2). Of the flies in the *G. lineaticeps* song treatment group, 4 of 10 (40%) chose their treatment song (exact sign test: $N = 10$, $P = 0.75$); of flies in the *G. integer* treatment group, 6 of 14 (42.8%) chose their treatment song (exact sign test: $N = 14$, $P = 0.79$). The loss of preference did not differ between treatments ($G_1^2 = 0.0196$, $N = 24$, $P = 0.889$). We assessed the statistical power of the memory test data using an estimate of the effect size from the learning protocol: in the learning protocol, 73.9% and 78.9% of flies went to the song that

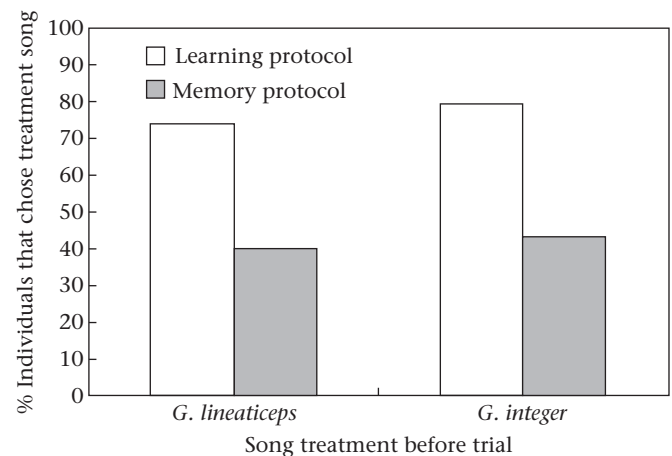


Figure 2. Laboratory results showing the percentage of females that chose their treatment song when later given a choice of two songs. The 'learning' protocol consisted of the treatment song played daily for at least 5 days prior to the choice trial; the 'memory' protocol consisted of the treatment song played daily for at least 5 days prior to the choice trial, but with no song played the day before the trial.

they had experienced previously. We averaged these two values (76.4%), then used an online statistical power calculator (<http://udel.edu/~mcdonald/statexactbin.html#power>) to determine the statistical power. With a sample size of 24, the power to detect a unidirectional (i.e. one-tailed) departure from a 50% null, given this effect size, was about 78%. The results of this 24 h memory protocol ($N = 24$) were strongly and significantly different from the results of the daily protocol ($N = 42$): 32 of 42 flies in the daily protocol subsequently chose the song that they had been exposed to daily, whereas only 10 of 24 flies in the 24 h memory protocol subsequently chose the song that they had been exposed to daily except for during the previous 24 h ($G_1^2 = 7.817$, $N = 66$, $P = 0.0052$).

DISCUSSION

These results are dramatic confirmation of (1) individual consistency of fly behaviour in the wild, (2) learning of an ecologically relevant host-associated cue by a tachinid fly and (3) the very short-term persistence of that learning. These are important results that support the idea of flexible and reversible search images that would facilitate adaptive host switching. Learning coupled with short-term persistence of memory would increase host encounter rate, particularly in a species that utilizes multiple hosts (Brassil 2007). These results are also quite novel: this is to our knowledge the first study to demonstrate a learned acoustic search image in a species other than bats (Page & Ryan 2006), only the third demonstration of learning in a tachinid, and the only demonstration of tachinid learning that involves an ecologically relevant host-associated cue.

The individual consistency results from the field are interesting, especially because of how they relate to our laboratory findings. First, it was a surprise to us that 65% of flies had their first capture at the *G. integer* song rather than the *G. lineaticeps* song. This is because within our study area *G. lineaticeps* is the primary local host species, and is two to three orders of magnitude more abundant than *G. integer*, although *G. integer* does occur in the area and is a known host. However, *G. lineaticeps* has its peak abundance in mid to late summer, and then the population of calling males crashes in late summer and autumn (Paur & Gray 2011). In fact, during the time of our playbacks (24–30 September), no calling males had been heard in our study area for about 2 weeks (since 12 September), despite regular and systematic acoustic surveys (Paur & Gray 2011). If a learned response bias expires within 1 day, as our laboratory memory results suggest, then all of our responding flies in the field were essentially acoustically naïve responders. As our playbacks were the only ‘cricket’ sounds in the area at that time, flies caught at our playbacks on one night may have become primed to respond more to that song type on the following night(s). Thus, our laboratory learning and memory results help explain both the absence of an overwhelming preference for *G. lineaticeps* song at the first capture and the recapture of flies preferentially at the same song where they were first captured. Nevertheless, our laboratory results do not explain the preference of flies for *G. integer* song in the field at a time when no field crickets were calling. It is entirely possible that these flies have both an innate song template and the ability to modify that template in the light of recent experience; this would be an excellent area for future research.

One feature of our study that differs from many of the studies of insect learning is that our study cannot be considered a case of associative learning. Most studies of learning in parasitoids and other insects have paired an ecologically irrelevant cue, such as vanilla odour (Matsumoto & Mizunami 2000; Takasu & Lewis 2003) or coloured discs (Stireman 2002) with a particular reward (food, hosts). In our study, we provided prior experience with a normal

ecologically relevant host cue, but we did not pair that cue with any reward (i.e. female flies that responded to our broadcast cricket song encountered a speaker, rather than a usable host). It is possible that host song fidelity (in the field) and learning effects (in the laboratory) might have been enhanced if females had encountered suitable hosts rather than speakers. This feature of our experiment applies to both our field and laboratory tests, and suggests that the type of learning was more akin to sensitization than associative learning. Sensitization has been described in several other insect systems (Papaj & Prokopy 1989; Walters et al. 2001; Stelinski et al. 2003). This has very important implications for biological control of insect pests using tachinids. The ability of a tachinid to learn natural, ecologically relevant host-associated cues could be used to help target parasitoids to particular pests. In contrast, associative learning of irrelevant cues, such as vanilla odour or coloured discs, may be of limited utility for pest managers since agricultural pests do not provide such cues. Although other studies have not used ecologically relevant cues, it is reasonable to expect that the ability of many parasitoids to learn arbitrary cues exists only because the parasitoids do in fact learn ecologically relevant cues in the wild.

It is worth discussing our laboratory phonotaxis methodology in more detail for two reasons: (1) getting flies to respond to playback in the laboratory was problematic, and we attempted several playback designs before settling on the one described here; our experiences may be useful to future researchers, and (2) our use of females that had responded to a brief pretrial playback in their cage could have potentially biased our results (but we argue that it did not; see below). We settled on walking phonotaxis trials using females that had responded to a short pretrial playback of cricket song; we attempted several other designs for testing free-flying phonotaxis, but females’ responses to playbacks were not consistent. Many dozens of females were used in these alternate protocols, the majority of which ignored our playbacks (single stimulus as well as dual stimuli). These females, of course, could not be retested as their acoustic experience was altered by the attempted test. Our rearing methodology is labour intensive, as crickets were parasitized by hand, so wasting large numbers of female flies in nonresponsive tests was not productive. The walking phonotaxis methodology we describe here, using only females that had responded to a pretrial playback of their treatment song, resulted in 100% of flies responding in the subsequent choice tests. However, use of the treatment song as the pretrial test also has the potential to confound the results, and could result in the appearance of learning when there was in fact none. Imagine two scenarios, one in which flies learn song preferences and one in which flies have fixed song preferences. First, imagine that flies do in fact learn songs (either entire songs or songs modified from an innate template based on recent experience), then those flies that had learned their treatment song would be the flies that pass the pretrial test, and then also choose their treatment song in the subsequent choice test. As researchers, we would conclude that the flies showed learning, and we would be correct. Imagine instead that all flies have fixed innate song templates, not modifiable by experience, but that some are *G. lineaticeps* song templates and some are *G. integer* song templates. Then, one could imagine that only the genetic *lineaticeps*-song flies would respond to the *lineaticeps* pretrial song, and when subsequently given a choice between *lineaticeps* and *integer* song, they would, of course, choose the *lineaticeps* song, and so give the false appearance of having learned that song. If this were the case, then the pretrial song protocol would have clearly biased the results, and our conclusion that flies learn would be wrong. However, if the fixed innate song template scenario (that would produce biased results in the learning protocol) were true, then there would be no difference in the results between our ‘learning’ and our ‘memory’ protocols; the same bias would apply equally to

both. The results of these two protocols are strikingly different, and this can only be accounted for by a true learning effect in the 'learning' protocol. Thus, we think that, despite the potential for bias, our results were not biased by the use of the pretrial treatment song. We conclude that recent acoustic experience does in fact modify song preference in *O. ochracea*; however, alternative pretrial designs might be explored in future work (e.g. using a third distinct song for the pretrial stimulus would be good, as would experiments attempting to serially switch song preferences reversibly in the same individuals based on experience).

Our results fit well with what we know about the ecology and host relations of this fly. Across its known geographical range, *O. ochracea* utilizes at least nine species of *Gryllus* hosts (Gray et al. 2007; Sakaguchi & Gray 2011) and has recently adopted *Teleogryllus oceanicus* as a host in Hawaii, where both the cricket and the fly have been introduced (Otte 1994; Evenhuis 2003). The Hawaiian cricket–fly interaction is a fascinating story of rapid evolution of the new cricket host (Zuk et al. 2006) that was probably facilitated by pre-existing behavioural flexibility in cricket mating behaviour (Tinghitella & Zuk 2009). It is also a dramatic illustration of how rapidly the fly can adopt a novel host having a song structure very different from that of its ancestral hosts. When wild Hawaiian *O. ochracea* were given a choice between the song of their new Hawaiian host, *T. oceanicus*, versus the songs of three species of *Gryllus* utilized as hosts in continental North America, 11 of 12 captured flies were caught at the *T. oceanicus* song (Gray et al. 2007). The rapid development of such a strong behavioural song preference suggests some predisposing factor in the fly's host-finding behaviour. Our results presented here suggest that learning and transient memory for acoustic host-associated cues may have been a key element of the fly's pre-existing behavioural flexibility that facilitated its rapid adoption of *T. oceanicus* as a host.

In summary, our results make an important contribution to studies of learning and memory in insects. Ours is among the first to combine ecologically relevant host cues with both field and laboratory study in parasitoids, particularly tachinids. Furthermore, our results suggest that adaptive host-switching behaviour is facilitated by both learning and forgetting. That is, we often are inclined to view 'poor' memory as a failure, or at least a limitation of insect neural capacity. Instead, rapid decay of learned host-associated cues is likely to be adaptive, as it may promote fitness via increased exploitation efficiency of transiently abundant hosts.

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