



Behavioural specialization among populations of the acoustically orienting parasitoid fly *Ormia ochracea* utilizing different cricket species as hosts

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Tightly coupled evolutionary associations between parasites and their hosts are well known. What is less well characterized is the behavioural specialization of parasites that exploit different hosts in different parts of the parasite's geographical range. Here we examine behavioural specialization among populations of a parasitoid fly, *Ormia ochracea*, that exploit different host species of crickets in different parts of the fly's range. We conducted a field experiment to compare phonotactic attraction of flies from Florida, Texas, California and Hawaii (U.S.A.) to the songs of their local host species of cricket versus their attraction to the songs of species of crickets utilized as hosts elsewhere within the flies' range. We found strong behavioural specialization of fly populations, with preferential phonotaxis towards the song of the local host species of cricket. These results suggest strong behavioural specialization of flies, but that specialization does not constrain or preclude the rapid adoption of novel hosts.

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Behavioural specialization among coevolved taxa is often tightly coupled with the evolutionary histories of organisms (Thompson 1994), and such associations between parasites and their hosts, including parasite–host cospeciation, are well known (Page 2002). However, behavioural specialization of parasites that exploit different hosts in different parts of the parasite's geographical range is less well characterized. For example, essentially all of the theoretical and empirical work on local adaptation of parasites and hosts relies on gene-matching coevolutionary arms races of two species that are geographically structured into metapopulations (Kaltz & Shykoff 1998; Thompson 1999; Dybdahl & Storfer 2003). Here we examine behavioural specialization among populations of a parasitoid fly, *Ormia ochracea*, that exploits different

host species of crickets in different parts of its range. Behavioural specialization on cues of their primary local host may enhance host-seeking behaviour of parasitoids, but may trade off against maintenance of more generalized responses that might allow exploitation of novel hosts. Thus, the degree of behaviourally mediated local host specialization of parasitoids is an interesting question, especially because it affects the strength of the coevolutionary coupling of species' histories, as well as possibly reflecting a trade-off between specialization and generalization.

All flies in the family Tachinidae (>8000 named species) are parasitoids, some with very generalist host ranges and others far more specialized (Arnaud 1978; O'Hara & Wood 2004). Several species of tachinid flies are known to be acoustically orienting parasitoids of nocturnal Orthoptera, particularly crickets, mole crickets and katydids (Cade 1975; Burk 1982; Fowler 1987; Allen 1995; Shapiro 1995; Lehmann & Heller, 1998). *Ormia ochracea* is a particularly intriguing tachinid because it appears to be highly

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specialized, while continuing to retain sufficient evolutionary lability to exploit a variety of host species and adapt rapidly to the opportunity for novel host exploitation. The female fly's hearing and sound localization mechanisms are specialized for cricket song, with peak sensitivity of female hearing near the energy peak (5 kHz) of cricket song (Robert et al. 1992, 1994; Mason et al. 2001). Most North American *Gryllus* crickets have a song peak frequency of 4–5 kHz, although the temporal pattern of cricket song is highly variable across species. In the continental United States, *O. ochracea* utilizes *Gryllus rubens* as its primary host in Florida, *G. texensis* in Texas and *G. lineaticeps* in southern California (Cade 1975; Walker & Wineriter 1991; Wagner 1996). In Hawaii, *O. ochracea* has been introduced, where it parasitises the cricket *Teleogryllus oceanicus*, itself introduced (Zuk et al. 1993). The songs of these parasitized cricket species differ greatly in temporal features such as pulse duration, pulse rate, numbers of pulses per unit of song and complexity of song (Fig. 1). Thus in terms of the temporal pattern of

host songs, it might appear that *O. ochracea* is not particularly specialized.

Parasitized cricket species have, however, been the subject of a great deal of research. Components of this research have shown repeatedly that flies do in fact pay close attention to the temporal features of song (Walker 1993; Wagner 1996; Zuk et al. 1998; Gray & Cade 1999; Müller & Robert 2002). Selection operating within local fly populations may be expected to favour flies with precise recognition of the temporal features of their local host species of cricket. Coevolution between crickets and flies might thus be expected to result in geographical variation in fly response to temporal features of cricket song, as suggested by Walker (1993).

Here we test whether this predicted among-population phenotypic divergence in host-seeking behaviour has occurred in a manner consistent with the a priori prediction that geographically distinct populations of flies should prefer the songs of their predominant local host species of cricket. Specifically, we test whether there is

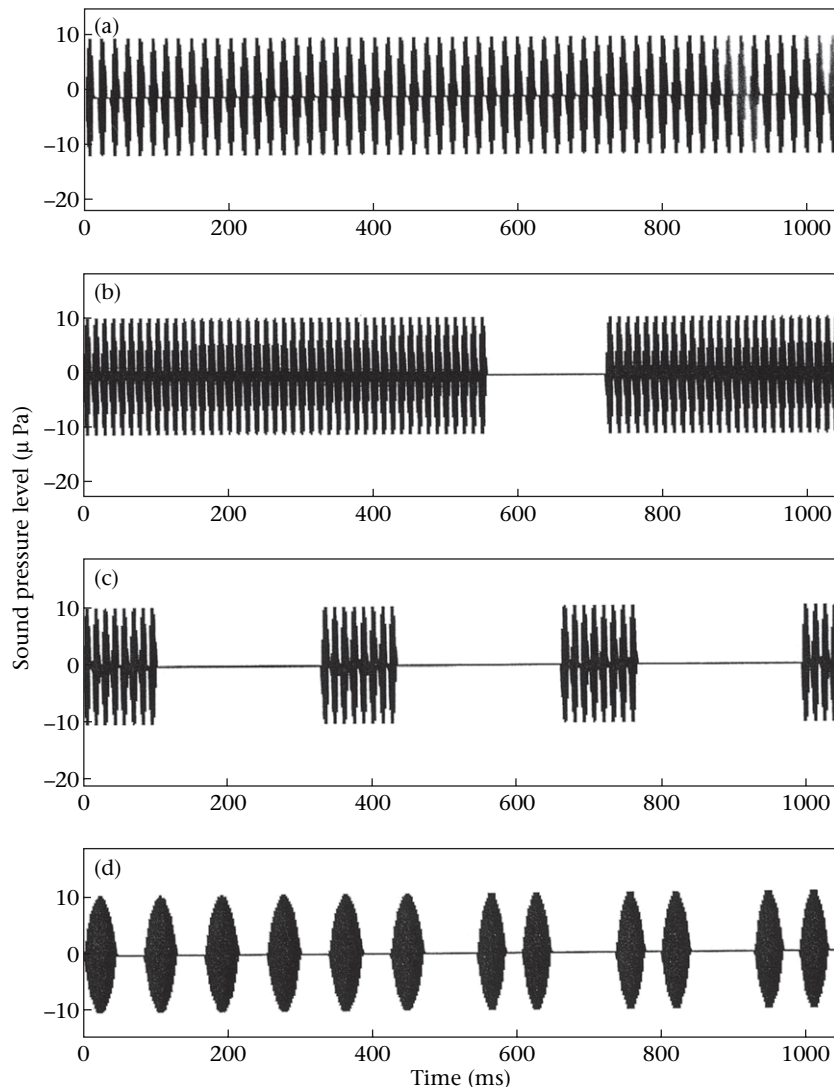


Figure 1. Waveform song diagrams (amplitude versus time, amplitude not calibrated) of (a) *Gryllus rubens* (b) *G. texensis*, (c) *G. lineaticeps* and (d) *Teleogryllus oceanicus* are shown. All songs are at 25°C and are drawn at the same timescale for ease of comparison.

strong geographical covariation among cricket host species and fly song preferences. Our basic approach was to conduct field playbacks of cricket song, and track the numbers of flies attracted to each of the songs. Thus, we conducted field playbacks of the songs of *G. rubens*, *G. texensis*, *G. lineaticeps* and *T. oceanicus* to different fly populations to assess behavioural divergence among fly populations in their acoustic response to local host song.

METHODS

We conducted field phonotaxis experiments using synthetic cricket songs. Songs were constructed using Cool-Edit 2000 (Syntrillium software, Scottsdale, Arizona, U.S.A.). Synthetic songs have the advantage of being precise representations of species-typical stimuli, while avoiding the need to construct multiple exemplars to avoid pseudoreplication (Kroodsma 1989; McGregor et al. 1992). For each of the four cricket species tested, we constructed eight songs, each of which was the species average song for a given temperature (15, 17, 19, 21, 23, 25, 27 and 29°C). Synthetic song parameters were based upon previous work with these species (Maskell 1975; Martin et al. 2000; Walker & Cade 2003; Izzo & Gray 2004). Starting 1 h after sunset, temperature-appropriate songs were broadcast for 4 h at equal peak-amplitude (85 dB, dB re: 20 µPa as measured with a RadioShack 33-2055 and a 5-kHz constant pure tone). Songs were broadcast through speakers placed under traps specifically designed for *Ormia* (Walker 1989). Traps were arranged in a square with 10-m sides. A replicate consisted of 4 nights of playback, not necessarily consecutive, with each song played once from each of the four speaker positions; initial speaker position was determined haphazardly. All attracted flies were collected and immediately preserved in ethanol, thus each fly could be counted once only.

We conducted one 4-night replicate in Gainesville, Florida in August 2002 where *G. rubens* is the natural host, probably exclusively (Walker 1986; Walker & Wine-riter 1991), three 4-night replicates in Texas during September 2002 (two in San Antonio, one in Austin) where

G. texensis is the only recorded host (Cade 1975; Gray & Cade 1999), two 4-night replicates in the Santa Monica Mountains, Los Angeles County, California during September and October of 2002–2004 where *G. lineaticeps* is the predominant host, but other occasionally parasitized host species occur at low density (*G. nr. integer* and *G. nr. assimilis*, D. A. Gray, unpublished data), and one 4-night replicate during March 2003 in Hilo, Hawaii where both *O. ochracea* and *Teleogryllus oceanicus* have been introduced (*O. ochracea* by 1989: Preston 1993; Zuk et al. 1993; Evenhuis 2003; *T. oceanicus* by 1877: Kevan 1990). On two occasions, trials in California were stopped earlier than 4 h (after ca. 2.5 and 3 h); this should have no effect upon our results as the majority of flies are attracted within 2–3 h of sunset (Cade et al. 1996).

RESULTS

We caught 768 flies over 28 nights of playbacks. Detailed results by replicate are presented in Table 1. In aggregate, more flies were caught at the song of the primary local host species than at the songs of host species utilized elsewhere; this was true for each of the four host areas (Fig. 2). Our statistical analysis was designed to test, in a global sense, whether the local host song was preferred to the songs of hosts utilized elsewhere. This analysis was thus across all replicates and used an ANOVA on arcsine square-root-transformed proportions of flies caught at the local host song ($N = 7$ replicate samples) versus similarly transformed proportions of flies caught at the songs of hosts utilized elsewhere ($N = 21$ samples). The mean \pm SD untransformed percentage of flies caught at the local host song was $56.7 \pm 18.8\%$ whereas the mean \pm SD untransformed percentage of flies caught at each of the three songs of hosts utilized elsewhere was $14.4 \pm 12.7\%$ (ANOVA: $F_{1,27} = 32.79$, $P < 0.0001$). We also performed a log-linear model test of the hypothesis of no heterogeneity among replicates in the numbers of flies caught by different host species ($\chi^2_{18} = 324.88$, $P < 0.001$). Thus, our global tests unambiguously showed strong behavioural specialization among different

Table 1. Numbers of *Ormia ochracea* caught per 4-night replicate at the songs of four host species utilized in different geographical areas

Locality	Local host*	Flies caught at				P†
		<i>G. rubens</i> song	<i>G. texensis</i> song	<i>G. lineaticeps</i> song	<i>T. oceanicus</i> song	
Gainesville, FL	<i>G. rubens</i>	39	23	9	1	<0.0001
San Antonio, TX (1)	<i>G. texensis</i>	4	18	5	8	0.0007
San Antonio, TX (2)	<i>G. texensis</i>	3	17	5	3	<0.0001
Austin, TX	<i>G. texensis</i>	4	31	17	0	<0.0001
Santa Monica Mtns, CA (1)	<i>G. lineaticeps</i> *	3	3	10	18	0.3360
Santa Monica Mtns, CA (2)	<i>G. lineaticeps</i> *	78	95	262	99	<0.0001
Hilo, HI	<i>T. oceanicus</i>	1	0	0	12	<0.0001

*Local host species is nearly exclusive in Florida (FL), Texas (TX) and Hawaii (HI), however, several hosts are utilized in the western United States. *Gryllus lineaticeps* is the primary local host in our California study areas.

†P values reflect the binomial probability that more flies would be captured at traps broadcasting songs of the local host compared to those broadcasting songs of other hosts.

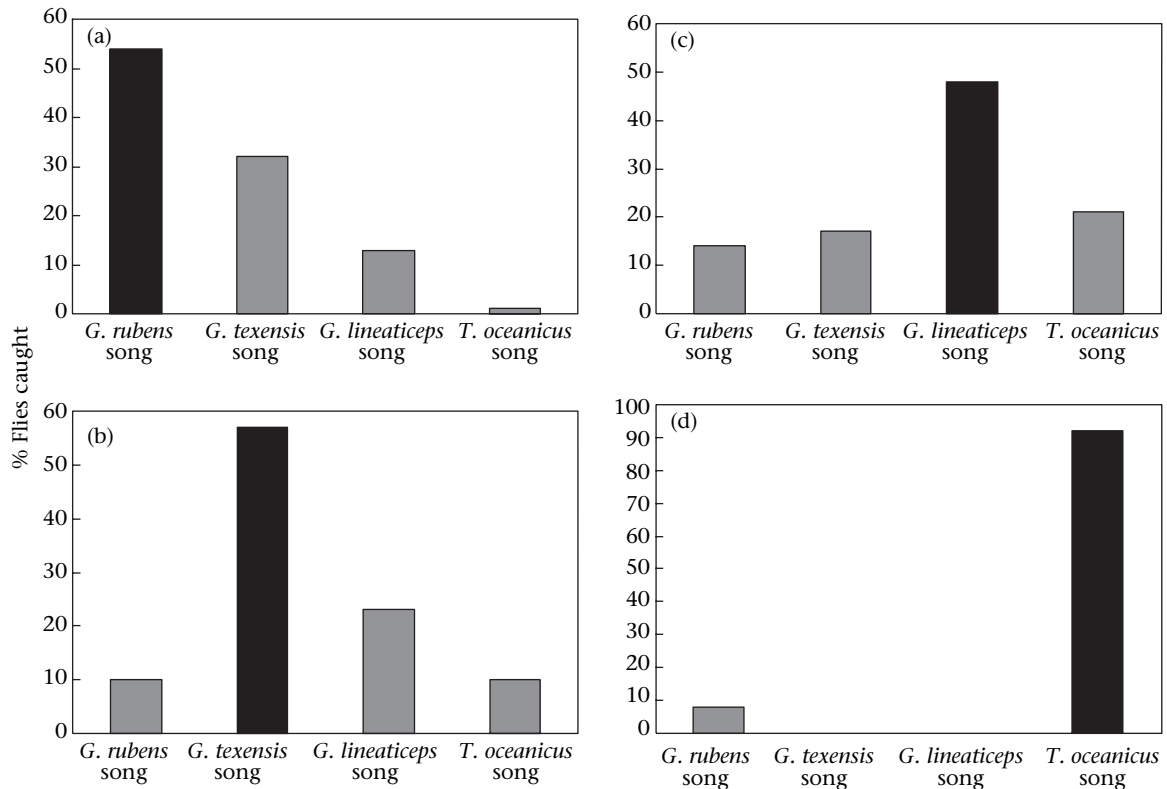


Figure 2. Percentages of flies caught at each of the four cricket songs tested in (a) Florida ($N = 72$ flies, one 4-night replicate), (b) Texas ($N = 115$ flies, three 4-night replicates), (c) California ($N = 568$ flies, two 4-night replicates) and (d) Hawaii ($N = 13$ flies, one 4-night replicate).

populations of flies. In fact, in six of the seven replicates treated individually, the local host song outperformed all other songs (all $P < 0.001$, binomial tests of the numbers of flies caught at the local host song versus at the songs of hosts utilized elsewhere, with prior probabilities of 0.25 for local host and 0.75 for hosts utilized elsewhere, all comparisons remained significant after application of Bonferroni correction for multiple comparisons); the one exception was one of the California replicates in which the local host song attracted the second-highest number of flies, rather than the highest.

DISCUSSION

Our results show that *O. ochracea* local populations show strong behavioural preferences for the songs of their primary local host. The phenotypic divergence among fly populations could be due to a variety of sources, and whether or not the behavioural divergence reflects genetic adaptation is unknown. Other than direct genetic effects, one interesting possibility is suggested by West-Eberhard (2003): phenotypic plasticity in host-finding behaviour could both allow the expression of adaptive behavioural phenotypes and subsequently drive the evolution of genetic adaptation. For *Ormia* song preferences this possibility remains speculative, but is the subject of ongoing experiments. An interesting and related question is the degree of genetic isolation among fly populations. If fly

populations are genetically homogenous throughout their range, then this would appear to increase the likelihood of plasticity-driven origins of the behavioural divergence among fly populations. Alternatively, fly populations may experience very limited gene flow, thereby increasing the likelihood of genetic differentiation among populations. Genetic relatedness among fly populations is currently an active area of our research. Despite our interest in fly population genetics, we note that the gene-for-gene model of local adaptation in host–parasite systems (Kaltz & Shykoff 1998) is clearly unlikely to apply because the different hosts are distinct species, rather than a broadly distributed metapopulation.

The behavioural specialization that we demonstrate here is consistent with Walker's (1993) results and his prediction of behavioural divergence among fly populations. Walker's (1986, 1989, 1993) work in Florida addressed several aspects of fly phonotaxis to cricket song, but primarily focused on species-level and temperature effects, rather than within-population selection on song conspicuousness. Prior work in Texas, California and Hawaii has been more focused on within-population selection on cricket song conspicuousness, including the amount of time spent calling and the time at which it occurs (Cade 1984, 1991; Cade et al. 1996; Kolluru 1999; Bertram 2002; Bertram et al. 2004), as well as identifying cricket song components such as numbers of pulses per unit of song (Zuk et al. 1993, 1998; Wagner 1996; Gray & Cade 1999), or the repetition rate of

song units that affect rates of fly attraction (Wagner 1996, personal communication). The results presented in this study in no way contradict the results of these prior studies: directional, but not open-ended preference functions (see Wagner 1998) may cause directional selection within populations without precluding a species-recognition function. In fact, our results highlight the conceptual distinctness of within-population selection parameters and among-population recognition features of song. Considering numbers of pulses per unit of song (chirps or trills), pulse rate, pulse duration and complexity of song, it is apparent that the songs of the four cricket species tested here represent a very broad range of total cricket song space (Fig. 1). Thus, with the exception of a dominant frequency of 4–5 kHz, we consider it unlikely that single-parameter components of cricket song are universally important to *O. ochracea*'s recognition of cricket song. Rather, we consider it likely that *O. ochracea* has a malleable template of song recognition, with the specific features of song that are most important differing among populations in a manner that reflects their evolutionary association with local host species of crickets. While we consider research into the specific song features most attractive to a particular population of *O. ochracea* interesting, our results tend to suggest that these specific song features will not be universal across different *O. ochracea* populations.

In this study we focused on the most abundant and most commonly utilized local host species of cricket within each of our study areas. These four species are not the only possible hosts of *O. ochracea*. They are however by far the most commonly utilized host species within our study areas. In our Florida study area, *G. firmus* is also an abundant field cricket, a known natural host species (Walker & Wineriter 1991), and one that is capable of rearing *O. ochracea* larvae when experimentally infested (Wineriter & Walker 1990). Despite high abundance of *G. firmus* in the Florida study area, Walker (1993) demonstrated that broadcasts of *G. firmus* song attracted only 3% as many flies as broadcasts of *G. rubens* song. In our Texas study area, no natural hosts other than *G. texensis* have been documented. In our southern California study area, *G. lineaticeps* is estimated to be 100 times more abundant in the autumn (peak season of *O. ochracea* abundance) than either of the next most abundant species of field crickets (*G. nr. integer* and *G. nr. assimilis*), both of which are known natural hosts of *O. ochracea* (D. A. Gray, unpublished data). In Hawaii, the only other *Gryllus* species capable of sustaining *O. ochracea* larvae is *G. bimaculatus* (Otte 1994). Like *Teleogryllus oceanicus*, *G. bimaculatus* is an introduced species of cricket, but it has not reached comparable density: in ca. 12 years of fieldwork in Hawaii by M. Zuk and collaborators, fewer than a dozen *G. bimaculatus* have been encountered.

In summary, we have shown high levels of population specialization consistent with adaptation (*sensu lato*) of parasitoid fly populations to the temporal features of the songs of their primary local host. Our data strongly support Walker's (1993) prediction of regional host specialization. These data do not distinguish the cause of the specialization, phenotypic or genetic, but nevertheless

suggest regional coupling of both *Gryllus* and *Teleogryllus* crickets with *O. ochracea*. The specialization among *O. ochracea* populations, especially the recent adoption of *T. oceanicus* as a host in Hawaii, suggests that behavioural specialization does not necessarily preclude dramatic host shifts, even to species with radically different song structures.

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