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ORIGINAL PAPER

A well-studied parasitoid fly of field crickets uses multiple alternative hosts in its introduced range

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Abstract

Organisms and their natural enemies can have dynamic coevolutionary trajectories, but anthropogenic effects like species introductions interrupt existing coevolutionary relationships. For parasites in particular, if they are introduced to a location without their hosts, they can only persist in the new environment if alternative hosts are (1) present, (2) detectable to parasites, and (3) capable of sustaining parasites. The circumstances surrounding the addition of alternative hosts to a parasite's repertoire are rarely observed. The parasitoid fly *Ormia ochracea* locates its field cricket hosts by orienting acoustically to their conspicuous mating songs. In Hawaii, *O. ochracea* is only known to parasitize one species, *Teleogryllus oceanicus*, but rapid evolution of *T. oceanicus* mating song over the past 20 years has led to several prevalent morphs of the cricket that produce no song or novel songs that the flies cannot detect. Yet flies persist in populations that lack ancestral singing *T. oceanicus*, prompting us to investigate the possibility of alternative hosts in Hawaii. We demonstrate first that three potential alternative hosts (*Gryllodes sigillatus*, *Gryllus bimaculatus*, and *Modicogryllus pacificus*) are present. Second, *O. ochracea* exhibits a positive phonotactic response to all three species' songs in the field and in the lab. And third, *O. ochracea* can successfully develop to pupae and emerge as adults in all three species. Our discovery of alternative hosts for *O. ochracea* in Hawaii infuses the system with intriguing complexity and offers extensive opportunities for future work.

Introduction

Organisms and their natural enemies can have dynamic evolutionary trajectories as each species evolves in response to the other (e.g., Ter Hofstede and Ratcliffe 2016). Parasites and parasitoids tend to be especially tightly linked to their hosts evolutionarily since they are

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dependent on them for survival. Therefore, parasites must respond evolutionarily or plastically to changes in their hosts, including changes in host abundance and host adaptations to avoid parasitism. Coevolution between hosts and parasites becomes further complicated when parasites are able to use multiple suitable host species (hereafter, alternative hosts) within the same geographic area. For instance, parasites may be able to move back and forth between host species (i.e., spillover and spillback), and in such assemblages, individual host species may act as reservoirs or parasite 'amplifiers' to other hosts (Chalkowski et al. 2018). You might expect transmission of multi-host parasites to evolve to favor higher quality hosts (Woolhouse et al. 2001; Gandon 2004), which could lead to diversification (and even cospeciation, Paterson and Gray 1997; Johnson et al. 2003), but in many cases multiple hosts are maintained over evolutionary time (Johnson et al. 2003). Multi-host parasites may encounter hosts more frequently (Hellgren et al. 2009) and be less vulnerable to small and/or dynamic host population sizes (Jaenike and Dombeck 1998). In multi-host parasite assemblages, coevolution is likely 'diffuse', meaning that "selection on traits often reflects the actions of many community members as opposed to pairwise interactions between species" (Strauss et al. 2005 adapted from Janzen 1980). Few studies have measured diffuse coevolution (Strauss et al. 2005). Given that we know less about the dynamics of multi-host systems, there have been recent calls to consider the ecology and evolution of study systems with increased biotic complexity, rather than focusing only on single host-parasite pairs (Betts et al. 2016; Ashby et al. 2019).

Ecological disturbances like species introduction (Torchin et al. 2003; Santiago-Alarcon and Merkel 2018), urbanization (Bradley and Altizer 2007), climate change (Hoberg and Brooks 2008), and other anthropogenic impacts can disrupt existing host-parasite relationships. Introduced species are commonly released from the parasites and pathogens that they experience in their native ranges (Torchin et al. 2003; Santiago-Alarcon and Merkel 2018), but in other instances, parasites are introduced either alone (Kirk 2003; Chapman et al. 2012), or with their hosts (Lymbery et al. 2014). Previously unavailable, but potentially suitable hosts may be present and able to be detected and located by introduced parasites (Bartholomew and Reno 2002; Prenter et al. 2004). *Ormia ochracea* is a parasitoid fly that was introduced from California (Gray et al. 2019) to Hawaii sometime before 1989 (Evenhuis 2003). *Ormia ochracea* parasitizes 17 known field cricket hosts in mainland North America where the fly is native, though it specializes regionally on one or a few cricket host species (Gray et al. 2007, 2019); none of these known host species are present in Hawaii. In Hawaii, the fly began using the Pacific field cricket, *Teleogryllus oceanicus* (Le Guillou), which was also introduced there sometime before 1877 (Kevan 1990). These two species only co-occur in Hawaii (Lehmann 2003), and it is widely accepted that *T. oceanicus* is the only cricket in Hawaii capable of hosting *O. ochracea* (Otte 1994; Zuk et al. 1993, 2018; Heinen-Kay and Zuk 2019), though this has not been tested experimentally. Recent rapid evolution of *T. oceanicus* has prompted us to challenge the idea that Hawaiian *O. ochracea* only parasitize *T. oceanicus*.

The fly locates its field cricket hosts acoustically by eavesdropping on their conspicuous mating songs (Cade 1975; Robert et al. 1992), and in the past 20 years *T. oceanicus* has evolved a silent morph protected from flies (Zuk et al. 2006; Tanner et al. 2019) and at least two novel songs (purring and rattling) that still attract female crickets but are nearly undetectable by flies (Tinghitella et al. 2018, 2021; Gallagher et al. 2022). From the fly's perspective, the evolution of these novel undetectable songs is equivalent to a host cricket extinction event since flies can no longer locate *T. oceanicus* where the ancestral male type (typical males who produce loud, tonal songs) is not present; in other words, evolution has mimicked a dramatic reduction in host frequency even though *T. oceanicus* density may not have actually changed (Ashby et al. 2019). Indeed, the ancestral morph has been absent for at least five years in several populations that are now primarily composed of the purring morph (Tinghitella et al. 2021; Gallagher et al. 2022), and other populations have been dominated by silent morphs for even longer (Zuk et al. 2006; Pascoal et al. 2014; Zuk et al. 2018; Rayner et al. 2019). Additionally, in November 2021, we documented the complete absence of *T. oceanicus* at one site on the island of Molokai (see results for more details about cricket presence). Yet, in all of these populations, *O. ochracea* is still abundant. We, therefore, hypothesized that *O. ochracea* in Hawaii were using alternative host species (in addition to *T. oceanicus*) that they switched to (host switching, Murdoch 1969) upon colonizing Hawaii or more recently (associated with inconspicuous novel morphs and loss of *T. oceanicus*). If Hawaiian *O. ochracea* are using multiple alternative hosts, this complex and dynamic system would provide an opportunity to test the ecological and evolutionary conditions facilitating the establishment and maintenance of multi-host parasite systems as well as how eco-evo feedbacks shape future evolutionary trajectories.

We used two historically studied Hawaiian populations of *T. oceanicus* that contain *O. ochracea* but now lack the ancestral morph of *T. oceanicus* (the only known host in HI) to explore the possibility that flies are using alternative hosts. We hypothesized that alternative hosts are (1) present, (2) detectable to parasitoids, and (3) capable of sustaining parasitoids. We sampled for the presence of other field cricket species in each population, used phonotaxis experiments to ask if flies were attracted to and could locate alternative cricket species' songs, and conducted an infestation experiment to ask if flies could develop in these other potential hosts.

Methods

Searching for T. oceanicus and alternative cricket hosts

As part of a larger study, we sampled adult *T. oceanicus* once every six months from 2017 to 2021 (pandemic permitting) across Hawaii including the Wailua and Kalaupapa populations studied here (22.067346157810245, -159.3961179153435 and 21.18858739081132, -156.9821734027572). Both the Wailua and Kalaupapa populations have contained only the purring morph and the silent morph for the past six years (Tinghitella et al. 2021; Gallagher et al. 2022). We documented the presence of potential alternative hosts anytime we observed them during these regular sampling trips. We considered potential alternative hosts for *O. ochracea* to be any crickets that were present in fields or that we could locate by sound where we collected *T. oceanicus*. For example, *Gryllodes sigillatus* (Walker) was often under rocks or wood on the periphery of our fields rather than in the grass, but we could easily locate them by following their loud calling songs (Fig. 1). We identified *G. sigillatus* and *Gryllus bimaculatus* (De Geer) using species descriptions and song comparisons (http://orthoptera.speciesfile.org, https://orthoptera.org.uk). We also collected a cricket unfamiliar to us in Wailua in 2019 as well as at a separate site on Oahu in 2020 and identified the species as *Modicogryllus pacificus* (Otte) using complementary molecular and phenotypic approaches (see supplemental methods for details). Briefly, we first sequenced the mitochondrial 16 S gene for 5 samples and built a maximum likelihood tree using 900 Grylloidea reference sequences from GenBank (Supplemental Fig. 1). We then confirmed the species identification through phenotyping. We compared recordings of male song, photographs of adult males and females, and dissections of male genitalia to published descriptions (Supplemental Fig. 2), and sought expert confirmation from Daniel Otte, who first identified and described *Modicogryllus pacificus* (Otte 1994). We also verified that all three potential alternative host species are known to be present in Hawaii (Otte 1994).

Fly phonotaxis to alternative species

Next, we conducted field phonotaxis and laboratory phonotaxis experiments in Kalaupapa and Wailua to determine whether *O. ochracea* is attracted to the songs of the potential hosts present in each location. For field phonotaxis, we played long-distance calling songs from the singing crickets in the population. Kalaupapa had three stimuli (*G. sigillatus, G. bimaculatus*, and purring *T. oceanicus*) and Wailua had four stimuli since there is an additional potential alternative host that is absent in Kalaupapa (*M. pacificus*). We broadcasted stimuli in competition from funnel-shaped sound traps fashioned from 2 L plastic bottles (following Walker 1989) at biologically realistic volumes based on our recordings and the literature. Amplitude of the calling song for *G. bimaculatus* (Simmons 1988), *G. sigillatus* (Sakaluk and Belwood 1984; Sakaluk 1987), and ancestral *T. oceanicus* (Broder et al. 2021; Gallagher et al. 2022) are very similar and overlapping, so we chose to hold amplitude standard for these stimuli (65 dBa at one meter for the field phonotaxis and 70 dBa at 1 m for the laboratory phonotaxis). We played purring *T. oceanicus* at a lower amplitude (53 dBA) because they naturally produce a much quieter song (Broder et al. 2021; Gallagher et al. 2022). We used a VL6708 Digital Sound Level Meter (VLike) to measure mean dBA at 1 m using the fast setting. Note that in Kalaupapa we originally included a fourth trap in each replicate broadcasting *G. bimaculatus* courtship song, but chose to only compare fly responses to calling song among species in analyses, so we excluded these data for this paper. Sound traps were 10 m apart from one another in a square (location of each determined using a random number generator), and we broadcast songs from AGPTEK A02 MP3 players (a small mobile speaker producing a relatively flat spectral output) for approximately two hours each evening when flies are most active (beginning approximately 30 min before sunset; Cade et al. 1996). At the end of the playback, we counted the number of flies in each funnel trap (dependent variable = flies per trap per night). Though typical ancestral *T. oceanicus* are not present in either location, we also determined whether flies were attracted to and could locate the ancestral host in Hawaii. So on separate nights, we broadcast ancestral *T. oceanicus* song at 70 dBA from the same fly traps described above using the same stimulus song as in previous work (e.g., Tinghitella et al. 2021).

We conducted laboratory phonotaxis experiments in Kalaupapa in January 2022 and in Wailua in July 2022 following (Tinghitella et al. 2021; Broder et al. 2022). Again, we played songs of potential host crickets that were present in each location, plus controls. For both populations we played ancestral *T. oceanicus* (70 dBA at 1 m), purring *T. oceanicus* (53 dBA at 1 m), *G. bimaculatus* (70 dBA at 1 m), *G. sigillatus* (70 dBA at 1 m), a negative silent control, and we added *M. pacificus* (70 dBA at 1 m), which is not present in Kalaupapa, for the experiment in Wailua. There was a slight difference in the purring stimulus: we played a single purring stimulus in Wailua (a loop of randomly selected individuals following (Tinghitella et al. 2018), but in Kalaupapa we played eight different purring exemplars following (Broder et al. 2022) and pooled all responses resulting in a higher sample size for the purring stimulus compared to the other four stimuli. The flies used in these experiments were collected at fly traps broadcasting songs of the species identified as potential alternative hosts on each island as well as ancestral *T. oceanicus.* Upon collection, we housed flies in mesh butterfly containers (40 × 40 × 60 cm, Transfit brand) with fruit juice, water, and shelter for 24 h in silence before using them in phonotaxis experiments. We kept flies indoors at ambient temperatures (no climate control) in partial shade where they experienced natural sunlight to maintain photoperiod. We began conducting trials 30 min before sunset and conducted trials while flies were active. We ran trials indoors at ambient temperatures and used red light to illuminate the experimental cage (ambient light from outside also illuminated the room). To begin each trial, an individual gravid female fly was placed in an empty butterfly mesh cage (40 × 40 × 60 cm) and gently directed to the top of the cage. Underneath the bottom of the mesh cage, we placed a speaker (AOMAIS Sport II, which also has a relatively flat spectral output) in one of four corners (speaker location randomized for each song stimulus). For each song played, we measured the vertical distance the fly traveled toward the speaker (max distance to the speaker = 58 cm) and whether the fly contacted the speaker (yes or no). Between playbacks we gently directed flies back to the top of the cage. After the experiments, all flies were immediately released at their capture site.

Infestation experiments

Lastly, we conducted a series of experiments to determine whether *O. ochracea* can infest *G. sigillatus, G. bimaculatus*, and *M. pacificus.* First, in Wailua we artificially infested *G. sigillatus, M. pacificus*, and *T. oceanicus* (control) to see if planidia can mature in those hosts. A detailed artificial infestation study has already demonstrated that *G. bimaculatus* can host *O. ochracea* (Adamo et al. 1995). Second, in a small exploratory experiment in Kalaupapa we asked if gravid *O. ochracea* would spray planidia on *G. sigillatus* and *G. bimaculatus* and if those larvae could enter inside the body cavity of the live cricket. Third, we collected adult *M. pacificus* in Wailua and held them for two weeks to see if they had been parasitized in the wild.

For the artificial infestation experiment in Wailua in January 2022, we collected adult *G. sigillatus, M. pacificus*, and *T. oceanicus* (n = 10 per species). We measured the pronotum of each cricket and placed them in an individual container (0.5 L deli cup with rabbit food, moist cotton, and egg carton). We infested them with live planidia following (Vincent and Bertram 2010). Briefly, we dissected several live gravid *O. ochracea* females and gently transferred 1–2 planidia to the exposed muscle of the cricket between the head and pronotum. We cleaned containers every three days and noted the presence of pupae and/or flies daily for three weeks.

Next, in a small exploratory experiment in Kalaupapa (November 2021) we asked if live gravid *O. ochracea* would spray planidia on field-collected *G. sigillatus* and *G. bimaculatus* (collected in Kalaupapa in the area that previously contained purring *T. oceanicus* (Tinghitella et al. 2018, 2021); *T. oceanicus* were absent in this location when we conducted this experiment). We first placed three gravid *O. ochracea* in a mesh butterfly cage with three male and two female adult *G. sigillatus.* We observed the male crickets calling and courting females nearly continuously for approximately one hour; courtship song and calling song are very similar in *G. sigillatus*. After two hours, we dissected the three male crickets to determine whether planidia were present inside the body cavities. Next, we used the same mesh cage and tested three different gravid *O. ochracea* with a tethered live male *G. bimaculatus*. Courtship song of *G. bimaculatus* has very different acoustic properties from calling song (much higher frequency, much lower amplitude; Libersat et al. 1994; Miyashita et al. 2016) and may thus be unlikely to elicit a response from flies. Because we were unable to prompt males to produce calling song, we tethered a live *G. bimaculatus* male to a speaker broadcasting *G. bimaculatus* calling song (same as stimulus used in phonotaxis experiments above). We placed white filter paper under the tethered male and recorded whether planidia were present on the filter paper after the experiment.

Lastly, we investigated natural parasitism rates in *M. pacificus* in Wailua in March 2022. We collected 7 adult males and 26 adult females in Wailua and held them under standard laboratory conditions until death by natural causes (maximum 14 days). We monitored individuals and recorded whether pupae emerged (yes/no) daily.

Statistics

In all of our models except for one (distance traveled towards a speaker), we encountered cases of complete separation among predictor variables, where one group had responses of all ‘0’s or all ‘1’s (e.g., zero flies contacted speakers during silent control playbacks and pupae emerged from all infested *T. oceanicus*). This necessitated a multi pronged approach where we first performed likelihood ratio tests of generalized linear models (GLM) which included all levels of predictor variables. These omnibus models allowed us to test the null hypothesis that there is no effect of our predictors (e.g. song stimuli or host species) on responses. However, because standard errors, and therefore p-values, are inflated in contrasts that include cases of complete separation, post-hoc comparison required additional tests. We did this in two ways: where possible, we conducted Firth’s bias-reduced penalized-likelihood logistic regression that allows for inclusion of variables with complete separation (package *logistf;* Heinze et al. 2022). Alternatively, we ran generalized linear models (GLM) that excluded levels of predictors with complete separation, followed by post-hoc comparisons to examine pairwise differences among variables that did not perfectly predict responses (package *emmeans*; Lenth et al. 2019).

For the field fly trapping experiments, song type was the predictor variable and flies caught per trap per night was the response variable. Small sample sizes (Kalaupapa: n = 7; Wailua: n = 9) prevented the Firth’s bias-reduced penalized-likelihood logistic regression model from converging. We therefore conducted Poisson-distributed generalized linear models (GLM) for each population (one for Wailua and one for Kalaupapa) with all predictor variable levels included, and then we repeated the models excluding levels of predictors with complete separation and conducted post-hoc comparisons (*emmeans*).

For the lab phonotaxis experiments, our dependent variables were whether the fly contacted the speaker broadcasting song (binomial) and the distance traveled toward the speaker in cm (Gaussian), and we again modeled each population separately. For contact, for each population we performed a likelihood ratio test of generalized linear models (binomial GLM) and then a Firth’s bias-reduced penalized-likelihood logistic regression with all stimuli included. Because no flies contacted the silent control, we performed binomial GLMs with the silent stimuli removed followed by post-hoc pairwise comparisons (*emmeans*). For distance traveled, for each population we conducted a Gaussian-distributed GLM with song type as our predictor variable and distance traveled (in cm) as the predictor variable followed by post-hoc pairwise comparisons (*emmeans*).

For the artificial infestation experiment, we used the same modeling approach for both dependent variables (whether pupae emerged from infested crickets (binomial) and whether adult flies emerged from pupae (binomial)); the predictor variable was host species (*G. sigillatus*, *M. pacificus*, and *T. oceanicus*). The Firth's penalized-likelihood logistic regression allowed us to compare the predictor variable (host species) with complete separation to the other levels. We then excluded the species with complete separation and conducted a binomial GLM to compare the remaining two species. All statistics were conducted in R (version 4.0.2).

Results

Evidence of available alternative hosts

In Wailua (Kaua'i), we collected *G. bimaculatus* in November 2021 and *G. sigillatus* in January 2022. We also collected and identified *M. pacificus* in January 2022 (Fig. 1a). We first noted the presence of *M. pacificus* in Wailua in 2019, but they are not unique to Kaua'i; we also collected these crickets in Laie (O'ahu) in 2020 and 2021.

In Kalaupapa, we first noted the presence of *G. sigillatus and G. bimaculatus* in 2019 (Fig. 1a). We heard dozens of singing *G. sigillatus* in June 2019 and November 2021, and we exhaustively sampled for *G. bimaculatus* in November 2021, collecting 19 animals in 21 search hours. Importantly, we also observed the absence of the only known host species, *T. oceanicus*, in November 2021. We discovered purring *T. oceanicus* in Kalaupapa in summer 2017 (Tinghitella et al. 2018), and they were present during regular visits through June 2019; *T. oceanicus* was absent in November 2021 (Supplemental Fig. 3).

Evidence flies can locate alternative hosts

To estimate fly attraction to various crickets' songs in the wild, we used fly traps deployed in the field, playing the songs that exist in each population in competition (choice test). In both populations, the playback stimuli broadcast from traps influenced the number of flies captured (all stimuli included in models, Wailua: GLM $LR\ X^2 = 31.36$, df = 3, $p < 0.001$; Kalaupapa: GLM $LR\ X^2 = 22.27$, df = 2, $p < 0.001$; Fig. 1b). In Wailua, we caught zero flies to purring *T. oceanicus* song, and we caught approximately equal numbers of flies per trap to the three alternative host songs: *G. sigillatus, G. bimaculatus*, and *M. pacificus* (Fig. 1b; GLM with purring excluded: $LR\ X^2 = 2.6$, $p = 0.27$). In Kalaupapa, we also caught zero flies to purring *T. oceanicus*. We caught the most flies to the two alternative host songs with a trend of more flies caught at *G. sigillatus* than *G. bimaculatus* (Fig. 1b; GLM with purring excluded: $LR\ X^2 = 3.62$, $p = 0.057$). When we played ancestral *T. oceanicus* song alone (not in competition), we caught 0.625+/-0.74 flies per trap per night in Wailua (n = 8) while we caught zero flies to ancestral *T. oceanicus* in Kalaupapa (n = 24 traps).

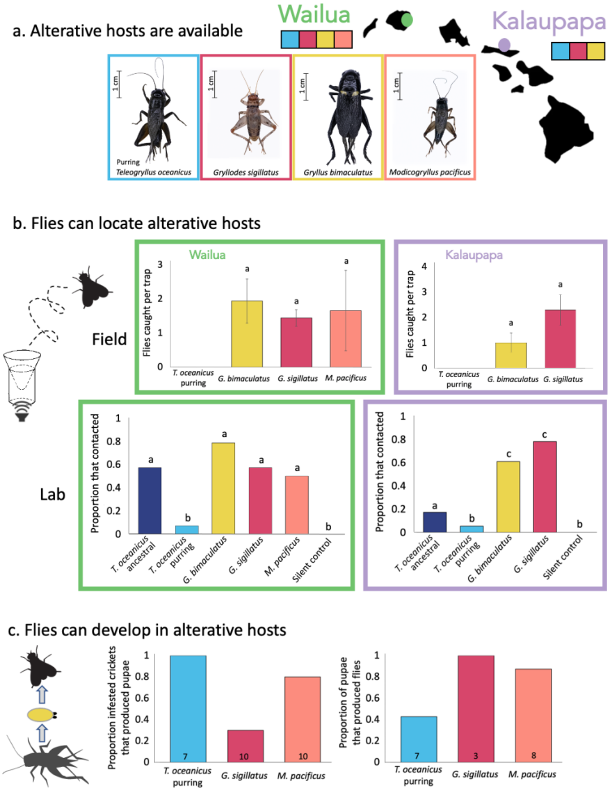

Fig. 1 All three components of alternative host use are met in two populations of *Ormia ochracea* in Hawaii. **(a)** Potential alternative hosts are available. Photos to scale of male crickets representing available host species: *T. oceanicus, G. sigillatus, G. bimaculatus*, and *M. pacificus.* The map shows the two populations studied. The colored blocks next to population names indicate which species are present in each location. Both populations only contain purring (light blue) and silent *T. oceanicus.* Photos by GTW **(b)** Flies can locate alternative hosts. We show (top row) the total number of flies caught per trap per night in field-based fly phonotaxis experiments in Wailua (n=9 replicates) and Kalaupapa (n=7 replicates). Error bars show standard error. In the lab (bottom row) the proportion of flies that contacted a speaker broadcasting each stimulus for Wailua (green, n=28 trials) and Kalaupapa (purple, n=23 trials). Error bars show standard error. Letters above each bar indicate statistical significance from post hoc tests. **(c)** Flies can develop in alternative hosts. Proportion of infested adult crickets from which a pupae emerged (left), and proportion of pupae from which adult flies emerged (right). Sample sizes are written on bars. See results for statistical significance.

In the laboratory phonotaxis experiments with wild caught flies, we also played songs of the potential hosts that exist in each population. Song stimuli strongly predicted whether or not flies contacted the playback speaker in both populations (all stimuli included in models, Wailua: GLM $LR\ X^2=69.4$, df=5, $p<0.001$; Kalaupapa: GLM $LR\ X^2=94.89$, df=4, $p<0.001$; Fig. 1b). In Wailua, flies contacted all alternative host songs more than silence (all pairwise comparisons $p<0.001$ from Firth's penalized *LR*) but contacted purring and silence equally (pairwise $X^2=1.53$, $p=0.22$ from Firth's penalized *LR*). When we removed silence, pairwise contrasts between stimuli were qualitatively identical to the model that included silence; Wailua flies contacted all alternative host songs more than purring (Tukey's contrasts of estimated marginal means from GLM: all pairs $p<0.01$), and there was no difference in

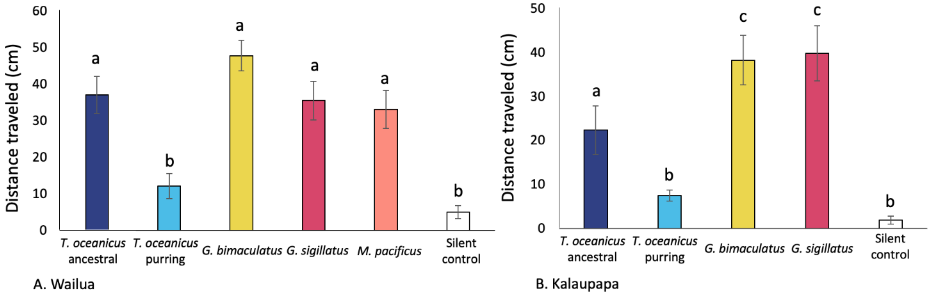

Fig. 2 Laboratory fly phonotaxis experiments in two locations (A. Wailua, n = 23; B Kalaupapa, n = 28). Distance traveled (cm) to different stimuli. Error bars show standard error. The letters above each bar indicate statistical significance from post hoc tests

the number of contacts among alternative host songs (Tukey's contrasts of estimated marginal means from GLM: all $p > 0.1$). In Kalaupapa, flies contacted *G. sigillatus* ($X^2 = 33.75$, $p < 0.0001$), *G. bimaculatus* ($X^2 = 22.54$, $p < 0.0001$), and ancestral *T. oceanicus* ($X^2 = 4.05$, $p = 0.04$) more than silence, but silence did not differ from purring *T. oceanicus* ($X^2 = 0.69$, $p = 0.41$, all pairwise comparisons from Firth's penalized *LR)*. When we removed the silent control, pairwise comparisons were qualitatively the same, but also revealed additional differences between alternative host songs and *T. oceanicus* songs. Specifically, flies were more likely to contact *G. sigillatus* than either ancestral *T. oceanicus* (z=-3.8, $p < 0.001$) or purring *T. oceanicus* (z=-6.88, $p < 0.0001$), and they were more likely to contact *G. bimaculatus* than either ancestral *T. oceanicus* (z=-2.87, $p = 0.02$) or purring *T. oceanicus* ($z = 6.14$, $p < 0.0001$). There was no difference between *G. sigillatus* and *G. bimaculatus* (z=-1.27, $p = 0.58$) or between ancestral and purring *T. oceanicus* ($z = 2.03$, $p = 0.18$).

The distance flies traveled to the stimuli showed the same pattern as the results for speaker contact. In both populations, the playback stimuli broadcast from traps strongly influenced the distance traveled (Wailua: $F_{5,162} = 14.1$, df = 5, $p < 0.0001$; Kalaupapa: $F_{4,271} = 31.19$, $p < 0.0001$). Wailua flies traveled furthest to *G. bimaculatus*, *M. pacificus*, ancestral *T. oceanicus*, and *G. sigillatus* (all pairwise $p > 0.05$), and distance traveled to purring *T. oceanicus* did not differ from silence (Fig. 2a; pairwise purring-silence: t=-1.17, $p = 0.85$). In Kalaupapa, flies traveled further to *G. sigillatus* and *G. bimaculatus* than to ancestral *T. oceanicus* (t=-3.66, $p = 0.003$; t=-2.82, $p = 0.041$ pairwise respectively) or to purring *T. oceanicus* (t=-8.4, $p < 0.0001$, $t = 7.28$, $p < 0.0001$ pairwise respectively); distance traveled to purring *T. oceanicus* did not differ from silence (t=-1.31, $p = 0.69$ pairwise) and *G. sigillatus* did not differ from *G. bimaculatus* (t=-0.84, $p = 0.92$; Fig. 2b).

Evidence flies can parasitize alternative hosts

We conducted an artificial infestation experiment in Wailua to determine whether *O. ochracea* could develop inside adult *G. sigillatus* (n = 10), *M. pacificus* (n = 10), and *T. oceanicus* (control, n = 7). Note that it has already been established that *O. ochracea* can develop inside *G. bimaculatus* (Adamo et al. 1995). All three species produced pupae and adult flies indicating that all can serve as hosts (Figs. 1c and 3). Host species affected the likelihood of pupal emergence (all levels included in model, Firth's penalized *LR* $X^2 = 9.55$, df = 2, $p = 0.008$). *Teleogryllus oceanicus* and *M. pacificus* were equally likely to produce

Fig. 3 Pictures of alternative cricket hosts from the artificial infestation experiment immediately after pupae have emerged from *Modicogryllus pacificus* (left) and *Gryllodes sigillatus* (center) as well as a dissected *G. sigillatus* with a live larvae inside (right)

pupae (pairwise *LR* $X^2=1.04$, $p=0.31$ from Firth's penalized *LR*), and *T. oceanicus* was more likely than *G. sigillatus* to produce pupae (pairwise $X^2=8.36$, $p=0.004$ from Firth's penalized *LR*). After removing *T. oceanicus* from the model due to complete separation, *M. pacificus* and *G. sigillatus* were equally likely to produce pupae (GLM *LR* $X^2=2.36$, df = 1, $p=0.12$). We also recorded the proportion of pupae that developed into flies. Host species did not affect the likelihood of adult flies emerging from pupae (all levels included in model, Firth's penalized *LR* $X^2=3.9$, df = 2, $p=0.14$; Fig. 1c). The average pronotum size (mean +/- SD) for the adults from this infestation experiment are as follows: *T. oceanicus* (5.47 +/- 0.14 mm), *G. sigillatus* (3.35 +/- 0.21), and *M. pacificus.* (3.55 +/- 0.19).

Next, we conducted an exploratory experiment using live flies and *G. bimaculatus* and *G. sigillatus.* We found that *O. ochracea* deposited live planidia on and around both potential hosts. For *G. sigillatus*, we found live planidia (> 10 per male) inside each dissected male after the one hour experiment where three gravid *O. ochracea* interacted with live singing *G. sigillatus.* For *G. bimaculatus*, following the experiment where we broadcast *G. bimaculatus* calling song under a live tethered *G. bimaculatus* male, we identified the presence of live planidia (> 20) on the filter paper underneath the cricket.

Finally, we investigated natural parasitism rates in *M. pacificus* by collecting adults from the wild in Wailua. Larvae emerged and developed into pupae from one of the seven males, a parasitism rate of 14% for males and 0% for females.

Discussion

We have been puzzled by the abundant numbers of *O. ochracea* in populations of *T. oceanicus* that lack ancestral males, especially since discovering that *O. ochracea* are not attracted to novel *T. oceanicus* songs (Tinghitella et al. 2021; Broder et al. 2022; Gallagher et al. 2022). Here we offer an explanation for this mystery by presenting several pieces of evidence that, taken together, indicate that *O. ochracea* are using alternative host species in Hawaii. First, other potential, alternative hosts are present in both of the populations that we sampled, and in one population (Kalaupapa) the only known host for *O. ochracea* in Hawaii (*T. oceanicus*) appears to now be locally absent–flies in this population must be using alternative hosts. Second, flies are positively phonotactic to calling songs produced by alternative hosts in both the field and in the lab. Finally, flies can infest all three alternative hosts discussed in this paper; we showed that flies spray planida on *G. sigillatus* and *G. bimaculatus* and that flies can develop to pupae and emerge as adults from both *M. pacificus* and *G. sigillatus*. It has already been established that *O. ochracea* can develop inside *G. bimaculatus* (Adamo et al. 1995).

We identify three previously unknown alternative hosts for *O. ochracea* besides *T. oceanicus* that are present in Hawaii (Fig. 1 A). What do we know about the presence of each species in Hawaii? First, *G. bimaculatus*, also known as the Mediterranean field cricket, is a large cricket native to Europe that arrived in Lihue, HI in 1985, according to (Otte 1994), and quickly spread across Hawaii. It is used as a feeder cricket for pets and may have spread to Hawaii in this manner. *Gryllodes sigillatus* is a tropical house cricket native to Asia that was first documented in the U.S. (Florida) in 1904 (Rehn and Hebard 1905). The first record of *G. sigillatus* in Hawaii is on the island of Lanai in 1927 (Illingworth 1927), and Otte (1994) noted that it was present on all Hawaiian islands by 1994. This species is the most widely distributed cricket in the world and is also used in the pet trade (Otte 1994), though we have only noted the presence of *G. sigillatus* at our field sites in the past six years (they inhabit buildings and lava; Otte 1994). Finally, much less is known about *Modicogryllus pacificus.* It was first described by Otte in 1977, and the holotype was collected in Kona, HI (Otte 1994). It is present on all Hawaiian islands and restricted to Hawaii (Otte 1994). While some hold that *M. pacificus* is a unique species (Otte personal communication), others suggest that there may be synonyms (same species by different name; e.g., Ingrisch 1998).

Flies were positively phonotactic to calling songs from all three alternative host cricket species (Fig. 1b). In fact, flies were even more attracted to the alternative species' song than they were to ancestral *T. oceanicus* song in Kalaupapa and equally attracted in Wailua (Fig. 1b lab); we actually caught zero flies to ancestral *T. oceanicus* song in Kalaupapa in our field experiment conducted in 2022, but this could have been due to other factors like wind as we have caught flies to this stimulus on all other field trips from 2017 to 2019. The lack of preference for *T. oceanicus* may be explained by the fact that neither of these populations has contained ancestral *T. oceanicus* during sampling trips over the past five (Kalaupapa) to ten (Wailua) years (Zuk et al. 2018; Tinghitella et al. 2018; Rayner et al. 2019; Tinghitella et al. 2021; Gallagher et al. 2022). Coupled with the fact that *O. ochracea* rarely locate purring *T. oceanicus* males in the wild (Tinghitella et al. 2021; Broder et al. 2022) and never did in this study (Fig. 1b field), this strongly suggests that flies have been using these alternative hosts for at least the past 5–10 years.

Recall that *O. ochracea* specializes on one or a few hosts regionally (Gray et al. 2019), so upon first arriving in the Hawaiian islands, how did the flies switch to using *T. oceanicus* as well as at least three previously unknown hosts? One way that this may be facilitated is if the novel hosts have songs that are similar to existing hosts. *Gryllus bimaculatus* calling songs have a dominant frequency of 4.7 kHz (Montealegre-Z et al. 2009; Kostarakos et al. 2009; Lankheet et al. 2017), which is similar to the dominant frequencies of ancestral hosts on the mainland (3.6–5.2 kHz; Gray et al. 2019) and nearly the same as ancestral *T. oceanicus* (4.7–4.9 kHz; Tinghitella et al. 2018; Broder et al. 2021; Gallagher et al. 2022). However, *G. sigillatus* (6.2 kHz; http://orthoptera.speciesfile.org) and *M. pacificus* (6.9 kHz based on analysis of our recording; a complete song analysis of this species has yet to be conducted) have dominant frequencies that are much higher, outside the range of all other known hosts (3.6–5.2 kHz; Gray et al. 2019). Ancestral fly populations have peak auditory sensitivity that ranges from 4 to 6 kHz (Robert et al. 1992), suggesting that Hawaiian populations of *O. ochracea* may have been pre-adapted to detect the songs of *G. sigillatus* and *M. pacificus*. It is also possible that neural detection thresholds have evolved in Hawiian populations of

O. ochracea, and future work should investigate this. A second, non-exclusive, possibility is that plasticity or learning allows *O. ochracea* to detect and locate novel host songs. Paur and Gray (2011) showed that *O. ochracea* are capable of learning new songs and remembering them for a very short period of time, and learning has been shown to play a role in adoption of novel hosts in wasps (König et al. 2015). Future work should investigate the potential role of plasticity and learning in the ability of Hawaiian flies to utilize novel hosts. Interestingly, despite studying only two populations, we may be seeing the beginnings of behavioral specialization for specific hosts (Gray et al. 2007): Kalaupapa flies preferred *G. sigillatus* and *G. bimaculatus* song while Wailua flies tended to respond most readily to *G. bimaculatus* (although this difference was not significant; Fig. 1B); future work should investigate this possibility.

We showed that both *M. pacificus* and *G. sigillatus* can host planidia, resulting in pupae and adult flies. It has already been established that *G. bimaculatus* can host *O. ochracea*, and developmental success of infested *G. bimaculatus* actually matches success in the fly's main ancestral hosts in North America: *Gryllus integer* (Cade 1975) and *Gryllus rubens* (Walker 1986; Adamo et al. 1995). Because *G. sigillatus* is much smaller than *T. oceanicus* (Fig. 1) they have previously been considered too small to host *O. ochracea* (e.g., Otte 1994; Heinen-Kay and Zuk 2019). Additionally, parasitoids must adapt to specific host conditions and overcome host defenses in order to successfully develop inside them (Carton et al. 2005). However, *O. ochracea* can develop in diverse orthopteran hosts including juvenile *T. oceanicus* (Vincent & Bertram, 2009) and species not naturally used as hosts (Adamo, Robert, & Hoy, 1995; Thomson, Vincent, & Bertram, 2012) including *Acheta domesticus* (Paur & Gray, 2011a, 2011b; Wineriter & Walker, 1990). Ormiines are likely able to co-opt the cricket immune encapsulation response of numerous hosts because the response is so well-conserved evolutionarily (Gray et al. 2019; Vinson, 1990; Adamo et al. 1995). Considering this flexibility of *O. ochracea* to develop in diverse hosts, it should perhaps not be surprising that *O. ochracea* can develop in the three alternative hosts we identified in Hawaii. Interestingly, though the known cricket host (*T. oceanicus*) had the highest success from infestation to pupae (100%), the other species had higher success rates of flies emerging from pupae (*M. pacificus* 87%, *G. sigillatus* 100%; Fig. 1c). These differences will be important to explore in future work as they may shed light on the length of time that *O. ochracea* has been using each species as a host–we might expect to have lower success in hosts that have time to evolve defenses. One limitation of this study was that because of the difficulty in gaining access to Kalaupapa, we were only able to conduct the artificial infestation experiment with flies from the Wailua population. Considering the strong phonotactic response of Kalaupapa flies to *G. sigillatus* and the abundance of this species in that location, we may have found very different results had we used flies from Kalaupapa, and this should be explored in future work. Finally, though the experiment was small and used only one species (*M. pacificus*), we documented a case of natural parasitism; this provides incontrovertible evidence that *O. ochracea* are using *M. pacificus* as a host species in Wailua.

This study is the first to investigate potential alternative hosts for Hawaiian *O. ochracea*, a species that began using *T. oceanicus* upon introduction to Hawaii and quickly drove the rapid evolution of sexual signals in *T. oceanicus* to be less detectable to flies (e.g., silent males (Zuk et al. 2006) and quiet purring males (Tinghitella et al. 2021)). This work revealed three alternative hosts in two populations, but there could be more hosts that we have not yet discovered. We know that flies are using ancestral *T. oceanicus* in other locations in Hawaii as we regularly collect parasitized males in other locations. Interestingly, additional novel *T. oceanicus* morphs with attenuated song exist in other Hawaiian locations that overlap with the fly's range (e.g., small-wing and curly-wing, Rayner et al. 2019; rattling, Gallagher et al. 2022); future work should investigate what hosts are used in locations where these morphs are present. The degree to which individual flies and even populations of flies are specializing on particular host species or shifting flexibly among hosts remains unknown, though it has important evolutionary implications and should be explored through systematic sampling of all potential orthopteran hosts across Hawaii to measure natural parasitism rates. Importantly, despite knowing approximately when *G. bimaculatus*, *G. sigillatus*, and *M. pacificus* arrived in Hawaii, we cannot identify when *O. ochracea* began using these species as hosts; it could have been immediately upon arrival when they began parasitizing *T. oceanicus* (all three alternative hosts present in HI in 1989 when *O. ochracea* was first documented), or it could be that flies have shifted to include more host species recently in response to the rapid evolution of *T. oceanicus* song (flies are unable to locate silent, purring, and rattling *T. oceanicus* males, which dominate some sites; Tinghitella et al. 2021; Broder et al. 2022; Gallagher and Zonana et al. 2022). Regardless, our current discovery of new hosts in Hawaii changes the way we think about this textbook system thought to reflect tight coevolution between a single eavesdropper and its only local host. There are vast opportunities for future work. For example, we might expect coevolution between these cricket species and *O. ochracea;* hosts may shift the time that they sing to avoid peak fly activity, or flies may evolve to be able to develop inside smaller hosts and perhaps be able to hyperparasitise larger hosts.

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Data availability Data can be found in Dryad: https://doi.org/10.5061/dryad.8gtht76sx. All sequences were deposited in NCBI GenBank (OP942437-OP942441).

Code availability: RMarkdown file can be found in Dryad: https://doi.org/10.5061/dryad.8gtht76sx.

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