Constraints Imposed by a Natural Landscape Override Offspring Fitness Effects to Shape Oviposition Decisions in Wild Forked Fungus Beetles

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ABSTRACT: Oviposition site decisions often maximize offspring fitness, but costs constraining choice can cause females to oviposit in poor developmental environments. It is unclear whether these constraints cumulatively outweigh offspring fitness to determine oviposition decisions in wild populations. Understanding how constraints shape oviposition in natural landscapes is a critical step toward revealing how maternal behavior influences fundamental phenomena like the evolution of specialization and the use of sink environments. Here, we used a genetic capture-recapture technique to reconstruct the oviposition decisions of individual females in a natural metapopulation of a beetle (*Bolitotherus cornutus*) that oviposits on three fungus species. We measured larval fitness-related traits (mass, development time, survival) on each fungus and compared the oviposition preferences of females in laboratory versus field tests. Larval fitness differed substantially among fungi, and females preferred a high-quality (high larval fitness) fungus in laboratory trials. However, females frequently laid eggs on the lowest-quality fungus in the wild. They preferred high-quality fungi when moving between oviposition sites, but this preference disappeared as the distance between sites increased and was inconsistent between study plots. Our results suggest that constraints on oviposition preferences in natural landscapes are sufficiently large to drive oviposition in poor developmental environments even when offspring fitness consequences are severe.

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Introduction

In species that lack parental care, oviposition site choice is the primary mode through which females influence the developmental environment of their offspring (Bernardo 1996; Resetarits 1996; Awmack and Leather 2002; Warner 2014). The oviposition preference-offspring performance ("preference-performance") hypothesis predicts that females select oviposition sites that maximize the performance of their offspring (Mousseau and Fox 1998; Gripenberg et al. 2010; Refsnider and Janzen 2010). Consistent with this hypothesis, maternal preferences for oviposition sites that positively affect offspring phenotype and fitness have been demonstrated in many taxa (Resetarits and Wilbur 1989; Rudolf and Rödel 2005; Miller and Emlen 2009; Reedy et al. 2012; Mitchell et al. 2013; Warner 2014; Touchon and Worley 2015). However, these preferences are not universally observed (Thompson 1988; Gripenberg et al. 2010; Clark et al. 2011; Potter et al. 2012; Soler et al. 2012). One explanation for oviposition in sites that do not maximize offspring fitness is that costs and constraints in complex environments can cause oviposition to deviate from preferences expressed in simplified laboratory assays (Jaenike 1990; Mavhe 1997; Rudolf and Rödel 2005; Refsnider and Janzen 2010; Cunningham 2012).

Egg-laying decisions that negatively affect offspring fitness occur in many species and are typically attributed to countervailing factors that influence female behavior (reviewed in Gripenberg et al. 2010; Refsnider and Janzen 2010). Elevated mortality risk, energetic costs, or time constraints associated with searching can prevent the expression of female preferences that would enhance offspring fitness (Ghalambor and Martin 2001; Stamps et al. 2005; Rosenheim et al. 2008). Fitness benefits at other life stages can similarly re-

sult in oviposition in poor developmental environments (the "optimal bad motherhood" hypothesis"; Mayhew 2001; Garcia-Robledo and Horvitz 2012). For example, divergent nutritive requirements of adults and juveniles can drive oviposition decisions that reflect female dietary preferences rather than those of their offspring (Courtney 1981; Scheirs et al. 2000). Similarly, the quality of available mates or male harassment can draw females to environments that are suboptimal for juveniles (Refsnider and Janzen 2010; Noriyuki 2015).

Countervailing influences on female behavior could cause oviposition preferences in natural landscapes to deviate from the predictions of the preference-performance hypothesis (i.e., offspring fitness; Warner 2014). Yet these countervailing factors shaping choice are often studied one at a time in artificial laboratory experiments. Does offspring fitness offset the cumulative action of other factors to determine oviposition decisions in natural populations? If costs of choice often outweigh offspring fitness to determine oviposition site use, it may impact fundamental ecological and evolutionary processes (Resetarits and Wilbur 1989). Subordination of offspring fitness to other factors could perpetuate species' associations with sink environments that limit population growth (Pulliam 1988; Dias 1996; Holt 1997; Heinrichs et al. 2015; Furrer and Pasinelli 2016; but see Brown et al. 2017). Furthermore, strong constraints on choice could interfere with the evolution of specialization in heterogeneous landscapes (Kawecki 2008; Anderson and Geber 2010).

In principle, the hypothesis that constraints on oviposition cause a mismatch between oviposition preferences and offspring performance can be tested by comparing preferences in the wild to those in the laboratory, where constraints are absent (Refsnider and Janzen 2010). However, testing this hypothesis is often prohibitively challenging in nonnesting species because it requires reconstructing the oviposition decisions of individual wild females. To date, studies of oviposition in free-living populations are dominated by taxa amenable to visual observations (e.g., reptiles, amphibians, and birds; Warner and Shine 2008; Angilletta et al. 2009; Mitchell et al. 2013).

Genetic capture-recapture, which reconstructs individual movements using tissue samples instead of visual observations, can be used to circumvent this logistical challenge in species in which oviposition is difficult to observe. Insects that feed on multiple host species are one such group. Crucially, host-associated insects—model systems for resource specialization—are underrepresented in the current literature on oviposition site choice in wild populations, although there are a few notable exceptions. Singer and colleagues found support for the preference-performance hypothesis in natural populations of the butterfly *Euphydryas editha* (Singer et al. 1988) but showed that the distribution and relative abundance of host species shaped host use patterns at the population level (Singer 1983, 2015; Singer and Wee 2005). Field tests in crop pests have also found evidence for context-dependent effects on preference under seminatural conditions (Åsman 2002; Greenberg et al. 2002; Mendesil et al. 2016). Nevertheless, in most oviparous species, it remains unclear whether oviposition preferences enhance offspring fitness in free-living populations. Integrating oviposition site choice in natural landscapes into these systems is a key step toward incorporating ecological realism into our understanding of the processes governing (mal)adaptation in heterogeneous environments.

In the present study, we used genetic capture-recapture to reconstruct oviposition decisions in a free-living metapopulation of a mycophagous beetle (*Bolitotherus cornutus*), which lays eggs on three fungus species. We compared the oviposition preferences of wild females to preferences expressed in the laboratory where constraints on oviposition choice were minimized and assayed larval fitness in the three fungus species on which oviposition occurs.

Methods

Study System

The forked fungus beetle (*Bolitotherus cornutus*) lives on three wood-rotting polypore fungi (fig. 1*A*): tinder fungus (*Fomes fomentarius*), artist's conk (*Ganoderma applanatum*), and hemlock varnish shelf (*Ganoderma tsugae*; Liles 1956; Wood et al. 2013). Wild females lay eggs singly on the fruiting bodies ("brackets") throughout the summer. Under laboratory conditions, females lay an egg every few days (Liles 1956). On average, adults live 2–3 months but can live several years (Heatwole and Heatwole 1968; Conner 1988; Whitlock 1992). Adults and larvae feed on fungal tissue (Liles 1956). Larval growth differs among the three fungi (Wood et al. 2014); in the laboratory, larvae grew slowest on *F. fomentarius*.

We conducted our study in the southern Appalachian Mountains at Mountain Lake Biological Station (lat. 37.3738 N, long. 80.5351 W) in Giles County, Virginia (fig. A1; figs. A1–A4 are available online). Hereafter, we use "subpopulation" to refer to all the beetles on a single log and "metapopulation" to refer to all subpopulations in our study area (Formica et al. 2011; Wood et al. 2013). We excluded logs colonized by more than one fungus from the present study. The three host fungi grow intermixed in the local landscape (Wood et al. 2013). There is substantial gene flow between *B. cornutus* subpopulations occupying different species of fungi (Wood et al. 2013); approximately 25% of *B. cornutus* migrate to other logs (Whitlock 1992; Ludwig 2008).

We performed all analyses in R, version 3.2.4 (R Core Team 2016). We used deviation coding (contr.sum) for categorical variables, which is appropriate for type III tests on unbalanced

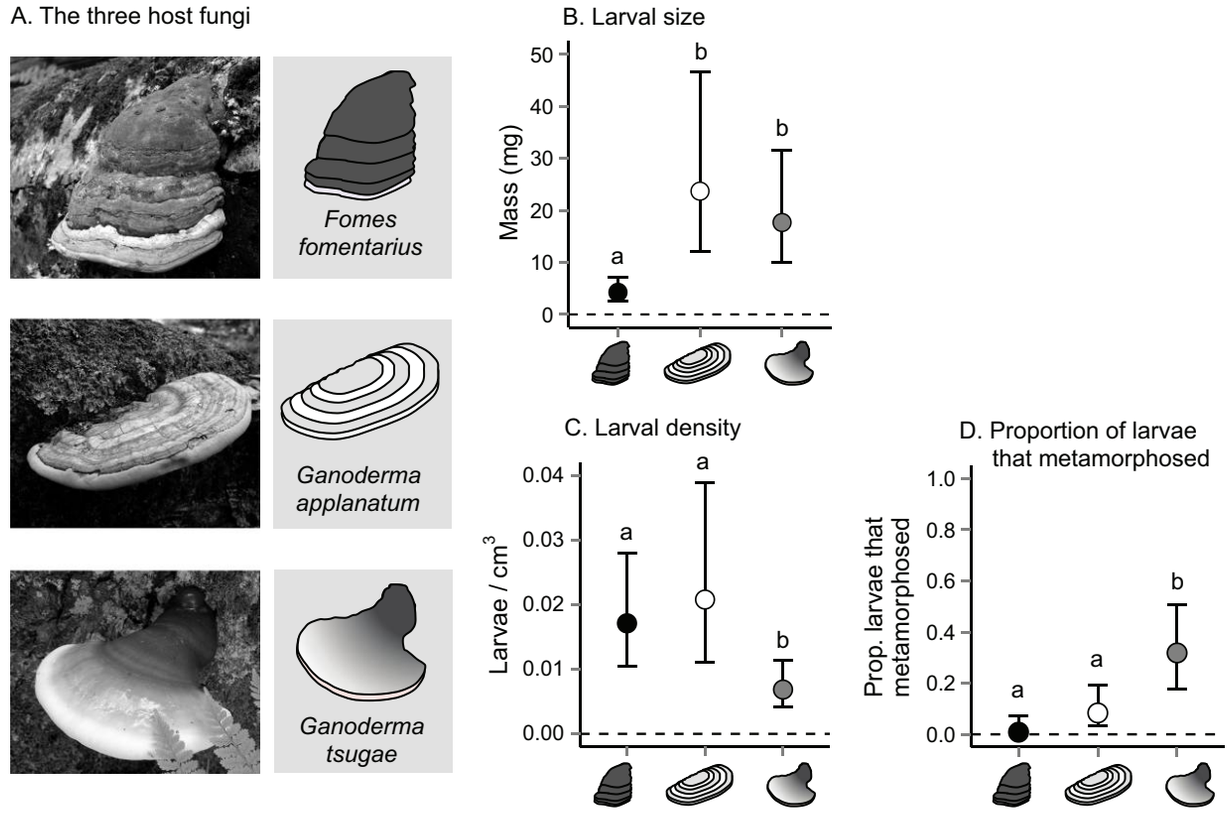

Figure 1: *A*, The three host fungi. *B–D*, Larvae and adults from field-collected fungus brackets. *B*, Larval mass. *C*, Larval density (number of larvae per cm^3 of bracket). *D*, Proportion of larvae that metamorphosed into adults within 3 months of collection. Comparisons with different letters are significantly different according to Tukey's post hoc tests. Values are least squares means and 95% confidence intervals.

data when models include an interaction (Fox and Weisberg 2011). Unless stated otherwise, we ran all models using the lmer function in the lme4 package (Bates et al. 2015) and tested significance with Wald *F*-tests using the Kenward-Roger degrees of freedom approximation and type III sums of squares in the ANOVA function in the car package (Fox and Weisberg 2011). We assessed significance of pairwise differences between performance on different fungi using Tukey's post hoc tests with the glht function in the multcomp package (Hothorn et al. 2008).

Fungus Effects on Offspring Fitness: Mortality

We used a cross-sectional field sample to estimate larval mortality because laboratory estimates can be poor proxies for environmental effects on phenotype (Mayhew 2001; Warner and Shine 2009). We did not sample longitudinally because larvae cannot be extracted from the woody fungus brackets without destroying the brackets. In our cross-sectional sample, size differences between larvae from the three fungi may be partially due to differences in age structure caused by mortality. In the summer of 2013, we collected 65 fungus brackets with signs of beetle presence (i.e., eggs or exit holes) from 25 logs ($N = 28$ *F. fomentarius* brackets, 14 *G. applanatum*, and 23 *G. tsugae*). We dissected the brackets and weighed all *B. cornutus* larvae (AX205 DeltaRange balance, Mettler Toledo, Columbus, OH). Larvae were housed individually on tissue from their original bracket in an incubator (23°C, 16:8 photoperiod) and checked throughout the winter of 2013 until they metamorphosed.

We tested for fungus effects on larval mortality by comparing the size of collected larvae, larval density, and the proportion of larvae that metamorphosed among fungi. We estimated the volume (cm^3) of each bracket by measuring water displacement in a graduated cylinder. To test whether larval size differed among fungi, we ran a linear mixed model with log-transformed larval mass as the dependent variable, fungus as a fixed effect, and bracket and log as random effects. To test whether larval density (larvae per cm^3; log transformed) and the proportion of metamorphs per bracket (binomial error distribution) differed among fungi, we ran similar models without the bracket random effect. For the proportion of metamorphs, we specified a matrix of dependent variables using the syntax "cbind(successes, failures),"

where successes were the number of larvae that metamorphosed and failures were the number that did not.

Finally, we estimated the proportion of adults that emerged from each fungus in our study site by multiplying total bracket volume by larval density (larvae/cm^3) and the probability of metamorphosis. We could not calculate total bracket volume from our cross-sectional sample because we did not sample brackets in proportion to each fungus's representation in our study site. Instead, we measured the radius and height of 363 brackets (215 *F. fomentarius*, 90 *G. applanatum*, and 58 *G. tsugae*), recorded the approximate shape of each bracket (cylinder, half-cylinder, cone, or half-cone), and used these measurements to estimate mean bracket volume for each fungus. We estimated total bracket volume by multiplying mean bracket volume by the mean number of brackets on a log and the total number of infected logs, which we estimated from a field survey of 558 infected logs (Wood et al. 2013).

Fungus Effects on Offspring Fitness: Development Time

To test for fungus effects on development time, we captured eclosing adults from nine focal logs in our study area (three logs of *F. fomentarius* with 105 brackets total; two logs of *G. applanatum* with 78 brackets total; and four logs of *G tsugae* with 159 brackets total). We enclosed all brackets in aluminum screen cages in March 2013 (before beetles are active; C. Wood, personal observation) to capture adults that emerged from eggs laid during or before the summer of 2012. *Ganoderma applanatum* and *F. fomentarius* produce perennial brackets (Gilbertson and Ryvarden 1986), so they were caged attached to the log. We removed bark surrounding the base of each bracket, stapled screening to the log, and sealed holes with waterproof silicone caulk (GE, Huntersville, NC) to prevent escape or entrance by beetles. *Ganoderma tsugae* produces annual brackets. Because removal would not affect long-term bracket health, we removed *G. tsugae* brackets, sealed them individually into aluminum screen cages, and nailed the cages to the log.

We collected and dissected all *G. tsugae* brackets ($N = 159$) in September–October 2013. Because many *B. cornutus* in the *G. applanatum* and *F. fomentarius* brackets were still larvae, we collected only a small sample of these two species at this time ($N = 9$ and 27, respectively). The remaining brackets of these species were left in the field to complete development under natural conditions. One year later (September–October 2014), we dissected a sample of the remaining caged *G. applanatum* and *F. fomentarius* brackets ($N = 10$ and 18, respectively). We estimated the surface area of each *F. fomentarius* and *G. applanatum* bracket by overlaying it with a 3 × 3-cm grid. We estimated only the area of 87 out of 159 *G. tsugae* brackets because many were in an advanced state of decay.

To test whether development time differed among fungi, we compared the number of *B. cornutus* adults and larvae collected from each species. This analysis assumes that there is little year-to-year variation in host preference, a reasonable assumption given that eggs were laid on all three fungi each year that we worked in the study area (2011–2015; C. Wood, personal observation). We ran a general linear model with log-transformed beetle density (individuals per cm^2 of bracket) as the dependent variable and year, fungus, life stage, and the fungus × life stage interaction as fixed effects. A significant fungus × life stage interaction would indicate that the larva : adult ratio differs among fungi, which we interpret as a difference in development time.

Oviposition Preferences in the Lab

To test for oviposition preferences in a simplified environment with minimal costs or constraints on choice, we performed a three-way choice experiment using females from known developmental environments. These females were collected as late-instar larvae in our cross-sectional larval sample (see "Fungus Effects on Offspring Fitness" above). We assayed oviposition preferences only in females from *G. applanatum* ($N = 17$) and *G. tsugae* ($N = 32$) because only one adult female emerged from *F. fomentarius* (see "Results").

Each female was paired with a *G. tsugae*-reared male and housed in an incubator (23°C, 18 : 6 photoperiod) for 3–4 weeks. We used only *G. tsugae* males because we did not collect enough males from the other two fungi to pair with experimental females. It is unlikely that paternal effects on preferences are sufficiently strong to account for our results. After the majority of pairs mated, we transferred females to choice arenas: round plastic containers 18 cm in diameter, covered in plaster of paris and topped with hardwood mulch. A 5-cm^2 piece of each fungus was imbedded in the plaster equidistant from the other fungi. We checked arenas daily for 15 days, recorded the fungus on which any new eggs were laid, and marked them with a dot of Testors Gloss Enamel (Testors, Vernon Hills, IL). We ran the experiment in two temporal blocks in December 2013 and February–March 2014. The first block included equal numbers of *G. applanatum* and *G. tsugae* females ($N = 12$ and 11, respectively); the second block included all remaining *G. applanatum* females ($N = 5$) and 21 *G. tsugae* females. We excluded females that did not lay eggs (22/49) from analysis.

We used a χ^2 goodness-of-fit test to examine whether the first egg was laid on any fungus more often than expected by chance. We used a generalized linear mixed model (Poisson error) to test whether the number of eggs differed among fungi. This model included temporal block, fungus, female origin (*G. applanatum* or *G. tsugae*), and their interaction as fixed effects. Because this analysis included multiple ob-

servations of each female (one for each of the three fungi), we included female as a random effect. We visualized our results in ternary plots using the ggtern R package (Hamilton 2016).

Oviposition Preferences in the Field

Data Collection. To measure oviposition preferences in a natural *B. cornutus* metapopulation, we genotyped and assigned maternity to all eggs laid on the nine logs used to estimate fungus effects on development time, as well as on 10 nearby logs (8 *F. fomentarius* logs, 3 *G. applanatum*, and 8 *G. tsugae*; fig. A1). Logs were clustered into two study plots 1 km apart (fig. A1). We collected eggs from June to August 2012 to assign maternity; we then allowed eggs to accumulate from August to October before caging the brackets the following spring to estimate development time.

We collected eggs every 2–3 weeks, the average hatching time of *B. cornutus* eggs (Liles 1956), and maintained them in an incubator (23°C, 16 : 8 photoperiod) until they hatched. To assign maternity to eggs and larvae, we captured adults on any fungus-infected logs in the area (within an approximately 50-m radius; $N = 47$ logs total) and nondestructively sampled 0.2–5 μL of hemolymph (Donald et al. 2012). We painted each adult with a unique ID using Testors Gloss Enamel and released it at its log of capture within 72 h (Wood et al. 2013).

We extracted DNA from all egg, larvae, and hemolymph samples using Promega's DNA IQ system (Donald et al. 2012). Due to financial constraints, we genotyped a stratified random sample of 1,880 (of the 2,499 collected) eggs at 28 microsatellite loci (table A1; tables A1–A4 are available online) using Qiagen's Multiplex PCR kit and microsatellite protocol. Fragment analysis was performed at the DNA Analysis Facility at Yale University (New Haven, CT). We scored microsatellite genotypes in GeneMarker (SoftGenetics, State College, PA). We assigned parentage to eggs using full likelihood scores from a single medium-precision run in COLONY (Jones and Wang 2010; Wang 2013), in which we allowed for inbreeding and polygamy in both sexes; included null allele frequencies estimated in MICRO-CHECKER (Van Oosterhout et al. 2004); and disabled sibship scaling (J. Wang, personal communication). This parentage analysis included all individuals genotyped at ≥14 loci (1,407 eggs and larvae, 146 males, and 238 females). We assigned paternity to 689 offspring (49.0%) and maternity to 887 (63.0%) with ≥95% confidence. We assigned an average of 4.8 eggs to each female (range: 1–17).

Data Analysis. We tested for oviposition preferences in the field in three ways. First, we compared egg densities (eggs per cm^2) among fungi in the field. This analysis included all eggs ($N = 2,463$) regardless of whether they were genotyped but excluded 36 eggs (1.4%) laid on the bark. Egg density was severely zero inflated, so we used a generalized linear model (binomial error) to test whether egg presence differed among fungi, including fungus, collection period (June–July or July–August), and their interaction as fixed effects. Using only the brackets with at least one egg, we ran a similar model (Poisson error) to test whether egg densities differed among fungi. We included the number of females captured on a log in these models to control for subpopulation size.

Second, we tested for genetic structure in the eggs using a hierarchical analysis of molecular variance (AMOVA) in GenoDive (Meirmans and Van Tienderen 2004). This model included effects of population (i.e., log) nested within fungus and egg nested within log, and was run on all eggs genotyped at ≥14 of 28 microsatellite loci ($N = 1,407$). Significant genetic differentiation among fungi would indicate individual females laid most eggs on a single fungus type; differentiation among logs would indicate females laid most eggs on a single log.

Third, we used genetic mark-recapture to reconstruct the sequential oviposition decisions of individual females and tested for preferences by determining whether females moved nonrandomly among fungi to lay eggs. We used multistate capture-recapture models to estimate transition probabilities among fungi, using all eggs that were assigned maternity with ≥95% confidence to construct a genetic capture-recapture record for each female. Each recapture is an egg assigned to a female during one sampling occasion ($N = 4$ sampling occasions). We performed our analysis in RMark (Laake 2013), an R interface for program MARK (White and Burnham 1999). We analyzed each study plot separately (fig. A1) and excluded 30 females that were assigned eggs collected from both plots. Our final sample consisted of 140 females (51 from plot A and 89 from plot B).

Genetic capture-recapture methods use genetic analysis of tissue samples in lieu of visual observations as capture data (Lukacs and Burnham 2005). Genetic recaptures introduce two complications not encountered with traditional data. First, they are associated with higher error rates than visual recaptures (Lukacs and Burnham 2005), and maternity assignment may introduce additional error in our study. Identification errors may impact survival and encounter probabilities but are unlikely to bias us toward finding preference (i.e., females moving nonrandomly among fungi). Second, in genetic capture data, a single individual can be observed in multiple locations in one sampling occasion if several tissue samples are collected from different sites (Lukacs and Burnham 2005). These observations cannot all be counted because order matters when estimating transition probabilities, and it is impossible to determine where the animal was first. To minimize the number of transitions we excluded and avoid downward-biasing survival and encounter

probabilities, we did not exclude these females. Instead, we randomly assigned each affected female (25/140 females, or 17.8%) to one of the logs on which she was observed during the problematic occasion. This procedure may downward-bias transition probabilities by eliminating movement events. To evaluate whether this procedure qualitatively affected our results, we ran our candidate model set (described below) on nine additional data sets with different randomly assigned locations for these females. Our results were similar across all data sets (table A2; figs. A2–A4).

Multistate capture-recapture models estimate three types of probabilities: survival, encounter (recapture), and transitions between states (Lebreton et al. 2009). We fixed survival probabilities at 1 because many parameters were unidentifiable when we estimated survival from the data, a common problem when values are near 0 or 1 (Cooch and White 2016). High short-term survival is consistent with visual capture-recapture data in *B. cornutus* (Ludwig 2008). We modeled encounter probabilities as constant across fungi. We modeled transition probabilities as functions of (1) the distance between logs; (2) the distance and the fungus a female moved to; (3) the distance and the fungus moved from; or (4) the distance and the fungus moved to and the fungus moved from. The average distance between fungus-infected logs was similar in both plots (plot A: 38.1 m; plot B: 42.1 m); we report the average pairwise differences in meters between the three fungi in table A4. We evaluated the goodness-of-fit ($\hat{c}$) of our general (i.e., full) model using the parametric bootstrap in Program MARK (White and Burnham 1999). We simulated 500 data sets, tested for overdispersion by comparing the observed deviance to the distribution of simulated deviances, and estimated $\hat{c}$ by dividing the observed deviance by the mean of the simulated deviances. The general model fit well for all 10 replicate data sets for both plots ($P_{\text{overdispersion}} \geq 0.094$; table A3). We obtained qualitatively similar results using median $\hat{c}$ (Cooch and White 2016).

To test for preference, we evaluated whether models in which transition probabilities depended on fungus fit better than models in which transition probabilities were only a function of distance between logs. We compared candidate model fit using the quasi-likelihood Akaike information criteria (QAICc), which is AIC adjusted for overdispersion (Burnham and Anderson 2002). Models with ΔQAICc values ≤2 are plausible models; models with ΔQAICc values much greater than 4 fit poorly (Burnham et al. 2010). We extracted model-averaged estimates of transition probabilities, averaged across the four candidate models, weighted by model support.

Results

We report a qualitative summary of all our results in table 1. Data underlying figures 1–5 are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.r9f11 (Wood et al. 2018).

Table 1: Summary table of the qualitative results across all field and laboratory experiments

	Fomes fomentarius	*Ganoderma applanatum*	*Ganoderma tsugae*
Performance:			
Larval size	4.3 mg	23.7 mg	17.7 mg
Larval density	.017/cm^2	.021/cm^2	.006/cm^2
Survival	1.2%	12.1%	29.7%
Development time	≥2 years	≥2 years	1 year
Preference:			
In the lab	…	…	…
In the field	…	Plot B	Plot A

Fungus Effects on Offspring Fitness: Mortality

We collected 83 larvae from *Fomes fomentarius* brackets, 141 from *Ganoderma applanatum*, and 91 from *Ganoderma tsugae*. Larval densities differed significantly among the three fungi ($F_{2,\,16.977} = 6.746, P = .007$) and were lower on *G. tsugae* than the other two species (fig. 1*C*). It is unlikely that differences in larval density are due to shorter development times in *G. tsugae*. Because *G. tsugae* brackets are produced annually, the brackets were only 1 or 2 months old when we sampled them in early-mid summer, too short a time for larvae to complete development and leave the bracket as adults.

Larvae collected from *F. fomentarius* were smaller than those from the two *Ganoderma* species ($F_{2,\,21.755} = 9.389$, $P = .001$; fig. 1*B*), and significantly fewer larvae collected from *F. fomentarius* metamorphosed into adults within 3 months of collection ($\chi^2 = 14.082$, df = 2, $P < .001$; fig. 1*D*). Our data are consistent with high mortality in *F. fomentarius*. Only 1% of larvae collected from this host metamorphosed into adults (1/83), while 30% of larvae collected from *G. tsugae* (27/91) and 12% of larvae collected from *G. applanatum* (17/141) metamorphosed into adults (fig. 1*D*).

Based on larval density, the probability of metamorphosis, and the total bracket volume of each fungus at our study site, we estimated that only 8% of adults in our focal metapopulation emerge from *F. fomentarius*, even though *F. fomentarius* brackets make up 57% of total bracket volume in our study site. By contrast, we estimated that 25% percent of adults emerge from *G. applanatum* (14% of total bracket volume), and 67% emerge from *G. tsugae* (29% of total bracket volume).

Fungus Effects on Offspring Fitness: Development Time

There was a significant fungus × life stage interaction for beetle density in the caged brackets, indicating that the

Table 2: Results from the general linear model testing for differences in the number of individuals of each life stage (larvae and adults) collected from caged brackets of the three fungi

	F	df	*P*
Fungus	**14.530**	**2, 273**	**<.001**
Life stage	.029	1, 273	.866
Fungus × life stage	**3.924**	**2, 273**	**.021**
Year	.822	1, 273	.365

Note: Boldface indicates significant values ($\alpha = .05$).

larva : adult ratio differed among fungi (table 2). This interaction was driven by shorter larval development time in *G. tsugae* than in *G. applanatum* and *F. fomentarius* (fig. 2; table 2). Most beetles collected from *G. tsugae* 1 year after brackets were caged were already adults (table 2), indicating that development is completed in this host within a year. By contrast, similar numbers of larvae and adults were collected from *G. applanatum* and *F. fomentarius* in both years, indicating that development takes at least 2 years in both perennial species. More individuals (adults and larvae) were collected from *G. applanatum* than the other two fungi (fig. 2; table 2).

Oviposition Preferences in the Lab

Females strongly preferred *G. tsugae* in laboratory choice trials (fig. 3). Most females laid their first egg on *G. tsugae* ($\chi^2 = 14.889$, df $= 2$, $P < .001$). Females laid significantly more eggs on *G. tsugae* than on the other two fungi (fungus main effect: Wald $\chi^2 = 97.068$, df $= 2$, $P < .001$). Females that developed in *G. applanatum* and *G tsugae* did not lay different numbers of eggs (female origin main effect: Wald $\chi^2 = 0.001$, df $= 1$, $P = .975$), and oviposition choice did not depend on a female's origin (i.e., her developmental fungus environment; fungus × female origin interaction: Wald $\chi^2 = 0.574$, df $= 2$, $P = .751$). Both *G. applanatum*- and *G. tsugae*-raised females laid most of their eggs on *G. tsugae* (fig. 3).

Oviposition Preferences in the Field

The proportion of brackets with eggs ("presence") and the density of eggs on brackets differed significantly among fungi in the field (presence: $F_{2, 616} = 7.915$, $P < .001$; density: $F_{2, 375} = 33.589$, $P < .001$; fig. 4). A greater proportion of *G. tsugae* brackets than *G. applanatum* had at least one egg laid on them (post hoc Tukey's test, $P = .005$). There were no significant differences between *F. fomentarius* and the two *Ganoderma* species. The opposite was true for egg densities on brackets with at least one egg, which were significantly lower on *G. tsugae* than the other two fungi (post hoc Tukey's test, *G. tsugae*–*F. fomentarius*: $P < .001$, *G. tsugae*–*G. applanatum*: $P < .001$). The proportion of brackets with eggs and egg density decreased from the first to the second collection periods (presence: $F_{1, 616} = 7.720$, $P = .006$; den-

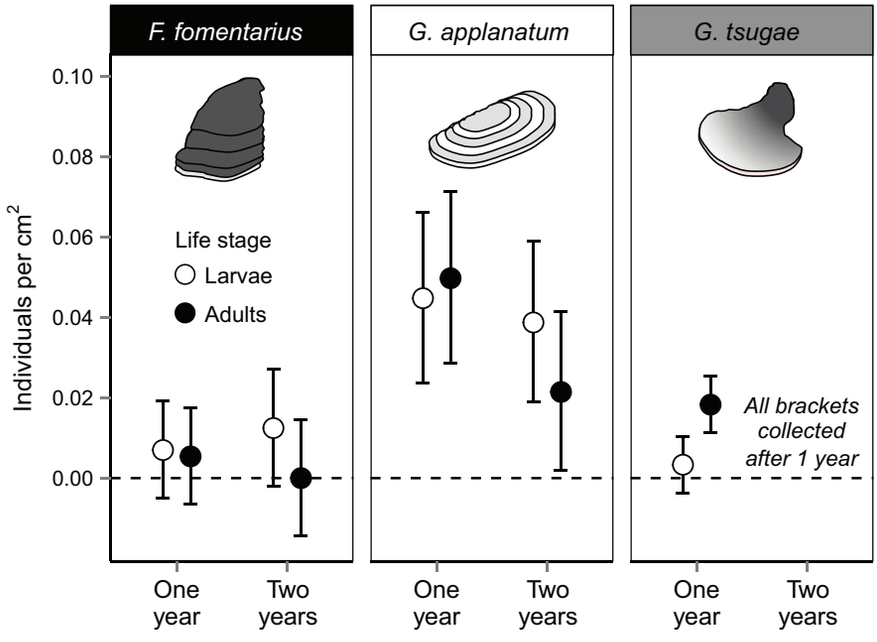

Figure 2: Number of larvae (white) and adults (black) collected from caged brackets 1 and 2 years after the brackets were caged (2013 and 2014, respectively). See table 2 for statistics. Values are least squares means and 95% confidence intervals.

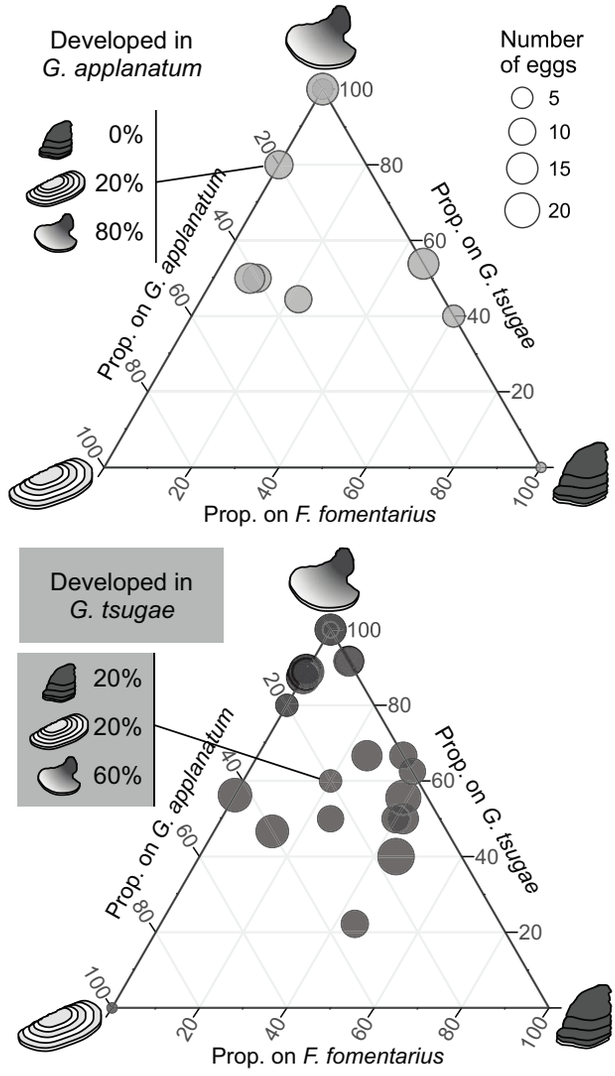

Figure 3: Oviposition preferences in laboratory choice trials. Each point represents eggs laid by a single female, and its location in the ternary plot (triangle) represents the proportion of eggs she laid on each of the three species. The point highlighted in each panel illustrates how to interpret a point's location in the triangle. Moving along any of the three axes toward a vertex represents an increase in the proportion of eggs laid on the fungus species located at the vertex. Points located on any of the three vertices are females that laid 100% of their eggs on that fungus. Points located along an axis represent females that laid eggs on only two of the three fungi, while points inside the triangle are females that laid eggs on all three species. *Top panel*, females that developed as larvae in *Ganoderma applanatum*. *Bottom panel*, females that developed as larvae in *Ganoderma tsugae*. Females from both *G. applanatum* (*top*) and *G. tsugae* (*bottom*) laid a greater proportion of their eggs on *G. tsugae* than on the other two fungi.

sity: $F_{1, 375} = 15.038$, $P < .001$), and this pattern was similar across fungi (fungus × collection, presence: $F_{2, 616} = 0.658$, $P = .518$; density: $F_{2, 375} = 0.157$, $P = .855$). Differences among fungi in egg presence and density remained significant when the number of females collected from each log was included to control for subpopulation size (presence: fungus main effect: $F_{2, 615} = 4.816$, $P = .008$; density: fungus main effect: $F_{2, 374} = 28.997$, $P < .001$).

We found significant genetic differentiation among eggs collected from different logs (AMOVA; $F_{ST} = 0.023$, $P < .001$) but no genetic differentiation between eggs collected from different fungi ($F_{CT} = -0.004$, $P = .906$).

In the capture-recapture analysis, we found that fungus influenced female movement among oviposition sites. In both study plots, models in which transition probabilities were only a function of the distance between oviposition sites were rejected (ΔQAICc ≥ 12; fig. 5*A*, 5*C*; table 3). In the best model, transition probabilities were a function of distance and the fungus to which the female moved (fig. 5*A*, 5*C*; table 3). When a female moved, the destination fungus was the best predictor of where she went, but that predictor was less important at longer distances. There was some support in one of the two plots for models that included the fungus the female moved from, indicating that the fungus the female moved from may have influenced movement as well (ΔQAICc < 2; table 3). The encounter probability was similar in both study plots (plot A: 0.359 ± 0.042 SE; plot B: 0.355 ± 0.031).

Model-averaged transition probabilities indicated movement patterns that differed between study plots. In plot A, females were more likely to move to *G. tsugae* than the other two fungi (fig. 5*B*) and were slightly more likely to move away from *F. fomentarius* (fig. A2). This preference weakened rapidly as the distance between oviposition sites (logs) increased. In plot B, females were more likely to move to *G. applanatum* than the other two fungi, a pattern unaffected by the distance between oviposition sites (fig. 5*D*). There was no effect of fungus on a female's probability of leaving a log (fig. A3).

Females were more likely to remain on a log than move to a new one; our models consistently estimated a 50%–75% probability of remaining on the same log between sampling occasions (fig. A4), in agreement with previously published estimates derived from visual recaptures (Whitlock 1992; Ludwig 2008). The probability of remaining on a log did not depend on fungus in either study plot (fig. A4) and was lower in plot A (range: 0.48 [± 0.15 SE] to 0.74 [± 0.08]) than in plot B (range: 0.76 [± 0.06] to 0.79 [± 0.06]).

Discussion

Although in laboratory trials, females of the mycophagous beetle *Bolitotherus cornutus* preferentially laid eggs on a high-quality fungus, they frequently oviposited on a fungus yielding nearly 100% larval mortality in the wild. Our results show that the costs associated with oviposition choice in natural landscapes can interfere with the expression of putatively

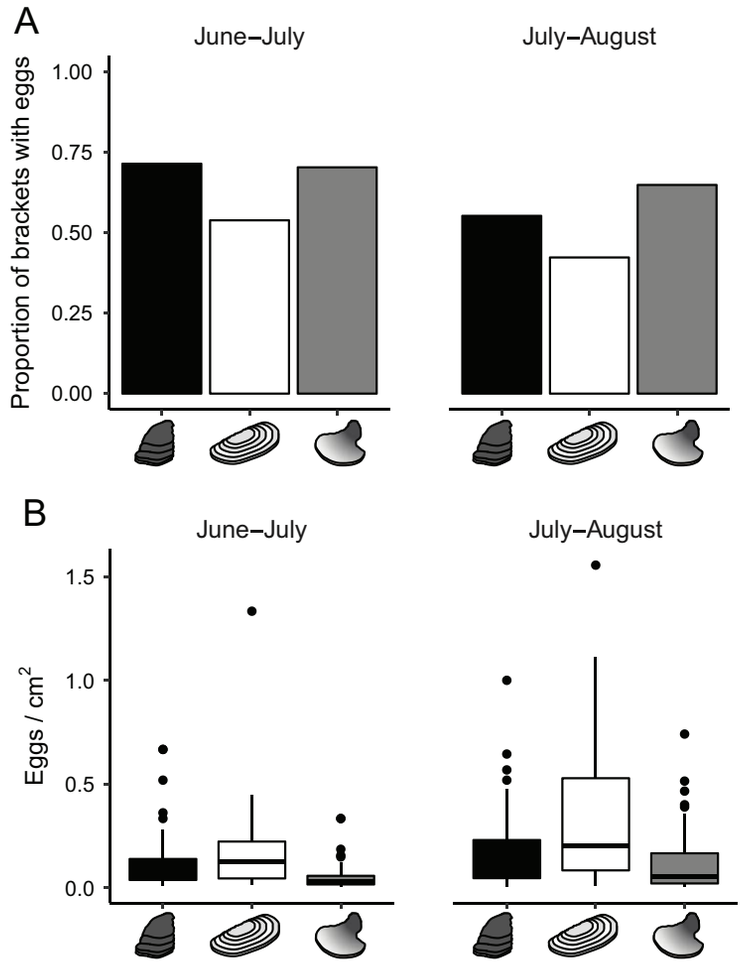

Figure 4: Oviposition in the field. *A*, Proportion of brackets with at least one egg. *B*, Egg density (eggs per cm^2) on brackets with at least one egg.

adaptive preferences even in the face of extremely steep fitness costs to offspring. Our findings suggest that trade-offs imposed by natural landscapes may be substantially stronger than suggested by the laboratory-based work that dominates the literature on habitat choice.

The Three Fungi Differ Substantially in Quality as Developmental Environments

There is substantial variation in larval performance on the three fungus hosts. The two *Ganoderma* species appear to be good hosts, while *Fomes fomentarius* is extremely poor, producing small larvae and few adults (fig. 1*B*, 1*D*). In conjunction with large differences among fungi in larval size in a laboratory-based longitudinal study (Wood et al. 2014), these results suggest that larval mortality is high in *F. fomentarius*. It is unlikely that differences among fungi in larval mass reflect genetic differentiation, as there is no genetic subdivision at the egg stage or the adult metapopulation (Wood et al. 2013). Larval development time also differs considerably between fungi. While development was completed within a year in the annual host *Ganoderma tsugae*, in the two perennial hosts—*F. fomentarius* and *Ganoderma applanatum*—development lasts for at least 2 years (fig. 2), contrary to a previously published estimate of 100 days (Liles 1956).

Phenological plasticity is common in heterogeneous environments (Wilbur 1997; Galloway 2005; van Asch et al. 2010; Kasumovic et al. 2012; Burghardt et al. 2015). Differences in *B. cornutus* development times reflect the life histories of the three fungus hosts, consistent with adaptive plasticity in response to reliable cues of future conditions (Simons 2014) rather than bet hedging (Slatkin 1974; Simons 2014). However, we cannot infer the fitness consequences of developmental plasticity from our data. Rapid development can be beneficial when it allows fast developers to escape predators (Eck et al. 2015) and ephemeral environments (Pfennig 1990) or to preempt rivals in resource

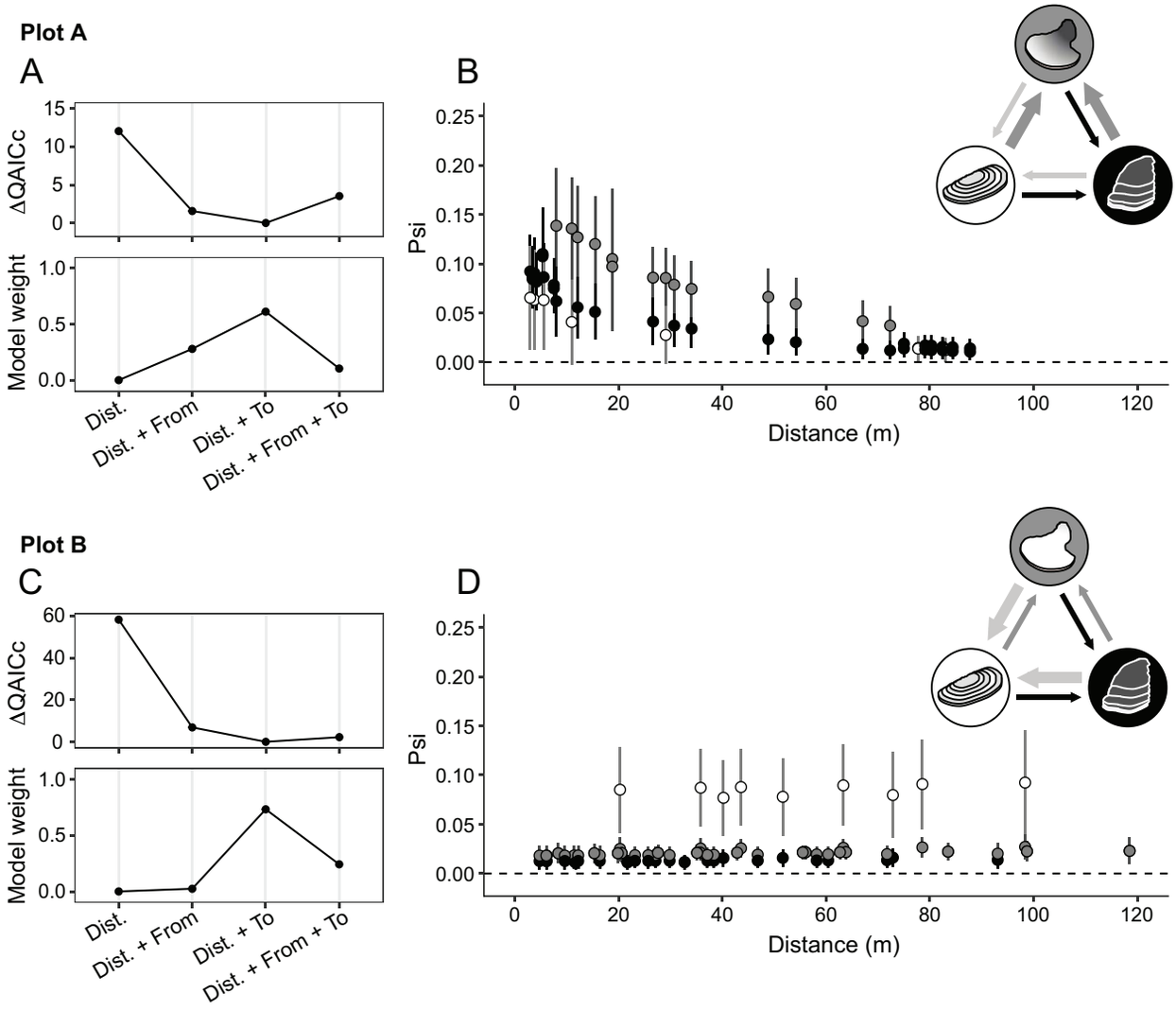

Figure 5: Results of the capture-recapture analysis for the two study plots. *A*, *C*, Changes to the quasi-likelihood Akaike information criteria (ΔQAICc) and model weights for the four candidate models. The *X*-axis indicates how transition probabilities were modeled ("Dist." = distance; "To" = fungus moved to; "From" = fungus moved from). In all models, survival probability was fixed at 1 and recapture probabilities were constant across fungi. *B*, *D*, Model-averaged transition probabilities between logs (± SE). Each point is the transition probability between two logs, colored according to the fungus moved to. In plot A, females that moved between oviposition sites were more likely to move to *Ganoderma tsugae*; in plot B, females were more likely to move to *Ganoderma applanatum*.

or mate competition (Kasumovic and Andrade 2006). On the other hand, slow developers often attain larger adult size and higher fitness (Kasumovic and Andrade 2006; Kingsolver and Huey 2008).

Oviposition Patterns in a Natural Metapopulation Deviate from Laboratory Preferences

In laboratory trials that minimized the costs of preference, *B. cornutus* females preferred *G. tsugae* regardless of the fungus they developed in (fig. 3). The preference for *G. tsugae* is consistent with the preference-performance hypothesis, as mortality is low in this host. Given that there was no detectable effect of the maternal developmental environment on preference, we think it is unlikely that the paternal developmental environment (i.e., the fact that all females were mated to *G. tsugae* males) is solely responsible for the strong preference for *G. tsugae* we observed in the lab. Why females discriminated between the two *Ganoderma* species is not clear, although one possibility is that elevated larval competition deters oviposition in *G. applanatum* (Wood et al. 2014). Free-ranging females in the wild, however, frequently laid eggs on the host associated with poor offspring performance (fig. 4). Although females were significantly more likely to

Table 3: Model quasi-likelihood Akaike information criteria (QAICs), ΔQAICs, weights, and Qdeviances for the four candidate models in each study plot

Plot, transition probability (Ψ)	No. parameters	QAICc	ΔQAICc	Weight	Qdeviance
Plot A:[a]					
Dist + to	5	274.875	.000	.613	160.657
Dist + from	5	276.439	1.564	.280	162.221
Dist + from + to	7	278.398	3.523	.105	159.537
Dist	2	286.915	12.040	.001	179.267
Plot B:[b]					
Dist + to	5	468.702	.000	.734	230.817
Dist + from + to	7	470.916	2.215	.242	228.660
Dist + from	5	475.548	6.847	.024	237.664
Dist	2	526.888	58.187	.000	295.339

[a] $\hat{c}_{\text{general model}} = 1.110$.
[b] $\hat{c}_{\text{general model}} = 1.095$.

move to the higher-quality hosts, the difference in transition probabilities between fungi was small in absolute terms (fig. 5*B*, 5*D*). Moreover, the preferred *Ganoderma* species differed between plots, and in one plot, preference was undetectable for females that moved more than 50 m, the median dispersal distance in *B. cornutus* (Ludwig 2008; fig. 5*B*).

The weak oviposition preferences expressed in our focal metapopulation are striking given the disparity in offspring performance on the three fungi and the strong preferences in laboratory trials. The costs associated with oviposition decisions in a natural environment must be substantial to drive oviposition on *F. fomentarius*, a host in which larval mortality is extremely high. What caused oviposition in the wild to deviate from the putatively adaptive pattern we documented in the laboratory?

It is important to note that discrepancies between preferences in the laboratory and field are not necessarily surprising. Laboratory choice assays, in which all options are tested simultaneously, tend to overestimate preference relative to no-choice tests that present one option at a time (Withers and Mansfield 2005; Dougherty and Shuker 2015). Qualitative observations of *B cornutus* in the laboratory confirm that the less preferred host is acceptable under no-choice conditions: beetles lay eggs on any of the three fungi when only one is available, although we have not quantified oviposition under these conditions. Our field data demonstrate that the nonpreferred host is accepted in the field. What makes the discrepancy between the preferences of laboratory and wild females in our system remarkable are the extreme larval fitness differences between hosts. Our data demonstrate that although they are able to discriminate between hosts, wild females frequently oviposit on a host associated with nearly 100% larval mortality. Even though *F. fomentarius* comprises 57% of total bracket volume in our study site, we estimate that it contributes only 8% of adults to our metapopulation.

Although our study was not designed to pinpoint the underlying factors that interfere with the alignment of oviposition preference with offspring performance in the wild, we can address a few competing hypotheses. In some systems, oviposition in a poor habitat can persist if some females are competitively excluded from high-quality habitats (the ideal despotic distribution; Fretwell 1972). However, competition for oviposition sites is unlikely in *B. cornutus*, given that egg densities were lowest on the preferred fungus in the field. Nor is there conflict between the nutritional requirements of larvae and adults, as adults prefer to feed on *G. tsugae* (Heatwole and Heatwole 1968).

Alternatively, landscape ecology may significantly shape oviposition behavior. The fact that oviposition preferences appeared to differ between our two study plots (fig. 5*B*, 5*D*) is consistent with the hypothesis that the structure of the local landscape influences oviposition behavior in natural populations. The use of low-quality resources persists when high-quality resources are temporally unpredictable or rare (Jaenike 1990) because avoiding poor oviposition sites is time intensive, energetically expensive, and incurs a high mortality risk (Doak et al. 2006). Our study site seems to fit these characteristics. The poorest host, *F. fomentarius*, accounts for 70% of the infected logs (Wood et al. 2013). The preferred host, *G. tsugae*, may have been even rarer in the recent past. The hemlock woolly adelgid, a sap-sucking insect responsible for widespread hemlock death in eastern North America, invaded our study site in the 1990s (Fitzpatrick et al. 2012). By increasing the abundance of dead hemlocks, the adelgid invasion may have increased the local frequency of *G. tsugae*—a hemlock specialist—in as little as 20 years.

Landscape ecology is an important factor influencing patterns of host use in other oviparous species. The consequences of host species spatial distribution have been extensively explored in checkerspot and Glanville fritillary

butterflies, which oviposit on multiple host plants in fragmented landscapes. In these species, the connectivity of plant patches and the proximity of the two host types determined the relative use of alternative host plants (Kuussaari et al. 2000; Singer and Wee 2005; Singer 2015). Field cage tests in agricultural systems arrived at similar conclusions, demonstrating that oviposition rates on focal crop species depended on the presence of nontarget (trap) crops (Åsman 2002; Greenberg et al. 2002). A rigorous test of the landscape ecology hypothesis in our system, however, would require manipulative experiments to evaluate whether host abundance influences oviposition preferences.

Differences in host life history can also drive a seasonal shift in patterns of oviposition in natural metapopulations (Widenfalk et al. 2012). In our system, the preferred host (*G. tsugae*) is functionally absent early in the summer before its annual brackets mature (C. Wood, personal observation). A seasonal shift in the host community could explain why the total number of eggs laid on the three hosts was similar (fig. 4) despite the fact that movement was biased toward the two *Ganoderma* species (fig. 5). Females may lay few eggs on *G. tsugae* early in the summer, but biased movement toward this host eventually spreads eggs evenly across hosts.

Alternatively, foraging *B. cornutus* females may deposit eggs on unfavorable hosts as a by-product of increasing their own diet diversity, laying eggs opportunistically as they move among resources. Feeding on a mixture of food sources is associated with better performance in many taxa, from herbivorous insects to parasitic plants (Marvier 1998; Kelly and Horning 1999; Randolph and Cameron 2001). Improved performance on mixed diets has been attributed to a variety of mechanisms, including nutrient balance and the dilution of toxic secondary compounds found in a primary food source (Hagele and Rowell-Rahier 1999).

Regardless of the mechanism driving their use, marginal habitats like *F. fomentarius* can have profound demographic and evolutionary consequences (Kawecki 2008). Marginal habitats (known as sinks) depend on immigration from source habitats (Pulliam 1988; Holt 1997; Forister and Wilson 2013; Furrer and Pasinelli 2016) but can facilitate population persistence when high-quality resources are temporally variable or rare (Holt 1997; Hanski 1999; Frouz and Kindlmann 2015; Heinrichs et al. 2015). *Fomes fomentarius* may perform a similar demographic role in our focal metapopulation; if so, source-sink metapopulation dynamics may contribute to the lack of resource specialization in polyphagous species like *B. cornutus* (Wood et al. 2013). Immigration into sink habitats dilutes locally adapted alleles and prevents adaptation to these marginal environments (Holt 1996; Kawecki 2004). If landscape-imposed constraints on oviposition preferences are common, they may frequently interfere with the evolution of resource specialization.

Evaluating whether the oviposition choices of wild females are truly maladaptive at the population level is challenging. It ultimately requires integrating fitness estimates across life stages to demonstrate that population persistence is threatened by oviposition in a host associated with poor offspring performance. If, for example, the pattern of adult mortality is opposite that of offspring performance, oviposition in poor developmental environments may be adaptive (Scheirs et al. 2000; Garcia-Robledo and Horvitz 2012). Consistent with this possibility, Brown and colleagues showed that population growth rates in checkerspot butterflies were similar on alternative host plants despite differences in performance on the hosts at some life stages (Brown et al. 2017). Comparing population growth on different hosts is crucial to link individual habitat choice to population-level source-sink dynamics.

Nevertheless, our results suggest that constraints on oviposition behavior imposed by complex natural landscapes can be strong enough to counterbalance near-total larval mortality in a marginal developmental environment. Building on laboratory studies of choice, future work should evaluate the relative importance of the suite of constraints hypothesized to shape oviposition behavior in natural populations. The alternative mechanisms that we proposed above are testable in the laboratory and under seminatural conditions (e.g., field cages), facilitating comparison of their relative impact on habitat use in the wild. Future research should also explore the demographic and evolutionary ramifications of such strong constraints on oviposition site choice. Host-associated insects, ecological model systems in studies of local adaptation, are excellent species in which to investigate these questions. To these ends, the genetic capture-recapture method we used to reconstruct the oviposition decisions of individual females in the wild should be applied more broadly to complement population-level data (i.e., egg counts) when egg laying is difficult to observe. Integrating the study of oviposition preferences—a form of habitat choice—with local adaptation in these taxa is a key step toward understanding the constraints on specialization in natural landscapes.

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