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PLANT-MICROBE-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Host selection by an insect herbivore with spatially variable density dependence

William C. Wetzel[1,2] · **Donald R. Strong**[1]

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Abstract Many species of phytophagous insects do not oviposit preferentially on plants that yield high offspring performance. One proposed explanation is that negatively density-dependent offspring performance would select for females that disperse eggs among plants to minimize competition. Recent work showing larval density dependence often varies substantially among plants suggests that ovipositing females should not only respond to the density of competitors but also to traits predictive of the strength of density dependence mediated by plants. In this study, we used field and greenhouse experiments to examine oviposition behavior in an insect herbivore that experiences density-dependent larval performance and variability in the strength of that density dependence among host-plant individuals. We found females moved readily among plants in the field and had strong preferences for plants that mediate weak offspring density dependence. Females, however, did not avoid plants with high densities of competitors, despite the fact that offspring performance declines steeply with density on most plants in natural populations. This means females minimize the effects of density dependence on their offspring by choosing plants that mediate only weak larval density dependence, not by choosing plants with low densities of competitors. Our results suggest that explaining the lack of positive preference-performance correlations in many systems may not be as simple as invoking density dependence. Resource selection behavior may depend not just on the presence or absence of density-dependent offspring performance but also on variation in the strength of offspring density dependence among sites within populations.

Keywords Host-plant preference · Offspring performance · Oviposition behavior · Tephritidae · Plant–insect interaction

Introduction

The preference-performance hypothesis proposes that female phytophagous insects should prefer to place eggs on plants that maximize the performance of their offspring (Levins and MacArthur 1969; Jaenike 1978; Thompson 1988). Although this theory is central to our understanding of plant–insect interactions and appealing in its simplicity, empirical evidence for the theory has been mixed. Of 111 reviewed species, only 55 % showed significant positive correlations between female preference and offspring performance (Mayhew 1997). A recent meta-analysis of 29 species found overall significant support for the preference-performance hypothesis, but both the direction and magnitude of effect sizes were variable (Gripenberg et al. 2010), suggesting that the static view of oviposition behavior as placing eggs on "high-quality" plants may be too simple.

Oviposition theory was developed when it was thought that phytophagous insects rarely experienced intraspecific competition (Jaenike 1990). As evidence that herbivores commonly experience competition accumulated (Denno et al. 1995), Valladares and Lawton (1991) proposed that many species may lack positive preference-performance

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✉ William C. Wetzel
wcwetzel@cornell.edu

[1] Department of Evolution and Ecology, University of California, Davis, CA, USA

[2] Present Address: Department of Entomology, Cornell University, Ithaca, NY, USA

correlations because females—in the face of negatively density-dependent offspring performance—should avoid crowded hosts of high nutritional quality in favor of less crowded hosts of lower nutritional quality. In other words, when herbivore performance declines with herbivore density, host-selection behavior should take into account the density of conspecific competitors on potential hosts (Ellis 2008). This behavior, in the extreme case of perfect information and free movement, would lead to an ideal free distribution, in which consumer density matches host quality such that fitness is equal across the landscape (Fretwell and Lucas 1969). In an ideal free distribution, an observational study of insect performance that ignored density dependence would find no correlation between habitat preference and offspring performance—a potential explanation for the equivocal support for the preference-performance hypothesis.

Despite this intuitive prediction, species that experience density dependence vary in whether or not they have density-dependent oviposition behavior. Taxa including tephritid flies, leaf-mining moths, and sawflies experience strong density dependence but ignore or cannot detect conspecific density (e.g., Auerbach and Simberloff 1989; Craig et al. 2000; Cronin et al. 2001; Digweed 2006). On the other hand, there are classic examples of species that experience density dependence and, as predicted, distribute eggs to minimize conspecific density (Roitberg and Prokopy 1987). For example, some frugivorous tephritid flies and seed-feeding beetles have reduced larval survival when multiple larvae develop in single plant organs, and accordingly females avoid organs with previous ovipositions (e.g., Prokopy 1972; Mitchell 1975).

One potential reason for the mixed support for density-dependent oviposition is that density dependence is not a binary phenomenon. It varies in form and strength among species (Sibly et al. 2005) as well as among sites within species. Recent work shows that the parameters of density dependence experienced by insect herbivores can vary substantially among plant individuals within a population because of differences in a variety of nutritive and defensive traits (Agrawal 2004; Underwood 2007; Miller 2007; Wetzel 2014). These findings suggest that ovipositing females should not only respond to the density of competitors but also to traits predictive of the strength of density dependence mediated by plants. There is, however, little empirical evidence suggesting how insect herbivores distribute offspring when offspring performance is density dependent and the strength of that density dependence varies among host-plant individuals within a population. The now strong evidence that herbivore competition is ubiquitous and typically occurs at the scale of plant individuals (Kaplan and Denno 2007) suggests that our understanding of plant-herbivore interactions will be incomplete until we understand how mothers cope with density dependence.

In this study, we used an insect herbivore that experiences variability in the strength of larval density dependence among plant individuals to test the following competing hypotheses about oviposition behavior:

1. Ovipositing females prefer plants with low densities of competitors.
2. Ovipositing females prefer plants that mediate weak larval density dependence.
3. Ovipositing females simultaneously prefer plants with low densities of competitors and weak larval density dependence.

In our study species, *Eutreta diana* (Tephritidae), per capita larval survival declines strongly with increasing female density on the majority of host-plant individuals in a population and weakly on a small minority (Wetzel 2014). We expected females to seek plants with low competitor density because larval density dependence, averaged across the landscape, is strong. In contrast, we expected females to ignore competitor density and to respond mainly to plant traits associated with strength of larval density dependence because competitor density has only a weak effect on fitness on those rare plants with weak density dependence (Wetzel 2014). If oviposition choices were mainly a function of the density of competitors, this would suggest that oviposition behavior were driven by the average plant, which has strong density dependence. If oviposition choices were mainly a function of the strength of density dependence (via traits indicative of this strength), this would suggest that oviposition behavior were driven by the rare plants with weak density dependence. Finally, if oviposition choices were a function of both competitor density and the strength of density dependence, this would suggest that both the mean and extremes of density dependence were important.

First we used a field experiment to test if *E. diana* females move freely among plants in natural populations for oviposition. This was necessary to show that females have the opportunity to exert oviposition choices. Next we used two behavioral assays to test if females avoid plants with high competitor density and if they prefer plants that mediate weak larval density dependence.

Materials and methods

Study system

We studied *Eutreta diana* (Tephritidae) oviposition behavior at the Valentine Eastern Sierra Reserve (VESR), California, USA. The sole host for this population is mountain big sagebrush (*Artemisia tridentata* subsp. *vaseyana*). *E. diana* has one generation each year: females deposit eggs singly in sagebrush vegetative buds in midsummer; first instars overwinter in the bud; buds develop into galls after snowmelt in the spring; larvae feed and develop inside the galls; and adults emerge from galls in early summer (Goeden 1990).

There is high variance in larval (gall) density among individual plants at small scales—i.e., most plants in a population support relatively small numbers of galls, but a few plants have extremely high gall abundances. In 2011, gall abundances on 355 plants at this study site ranged from 0 to >100: about 50 % of plants had from zero to two galls, while less than 5 % of plants had >30 galls (Wetzel 2014). The interplant variation in gall densities is related to variation in the strength of density dependence in larval survival among plants. The many plants with low gall densities have strong density dependence, whereas the rare plants with high *E. diana* densities have weak density dependence. Differences in gall densities among plants are not related to density-independent demographic parameters like the intrinsic rate of increase or fitness at low herbivore density (Wetzel 2014). The relative abundances of galls among plants are highly correlated through time (Pearson's $r = 0.7$–0.8) at least over 4 years, suggesting that density dependence within plants is also consistent through time (Wetzel 2014).

There is only a weak relationship between plant size and gall abundances, suggesting that the strength of density dependence is more a function of plant nutritive or defensive traits than it is a function of plant size (Wetzel 2014). In addition, there is no correlation between gall abundances and mortality due to predators and parasitoids, suggesting that these sources of mortality are density independent at the inter-plant scale. Also, galling rates are not altered by *E. diana* attack in previous years (Emlen 1992; W. C. Wetzel, unpublished data). *E. diana*, unlike some Tephritidae species, does not have aggregative mating behavior, which influences oviposition behavior in other systems (Headrick and Goeden 1999; W. C. Wetzel, personal observation). The following studies focus on the consequences of variation in density dependence among plants, not on the mechanisms underlying the density dependence, which are currently unknown. In addition, we avoid using the term "plant quality" because it implies static differences in expected herbivore performance among plants, which is not true when herbivore performance depends on herbivore density. Instead we focus on the relationships between herbivore choice and the strength of density dependence mediated by plants or the density of herbivores on those plants.

Movement field study

We used a gall-removal experiment in the field to test if ovipositing females move among plants and have the opportunity to exert oviposition choices. In June 2010, we randomly located a 20 m^2 study plot at VESR, mapped the location of all 114 sagebrush individuals in the plot, and counted the number of *E. diana* galls on each plant. We randomly assigned the 71 plants that had galls to either a control group or a gall-removal treatment group. Shortly before adult eclosion, which occurs within galls, we removed all galls (and thus pupae) from the 36 plants in the gall-removal group. In June 2011, we again counted galls on all 114 plants. The gall-removal treatment was unlikely to damage plants because gall tissue senesces when larvae cease feeding and pupate.

If *E. diana* females mostly remain after eclosing to reproduce on their natal plants, movement between plants would be infrequent. Such behavior would produce a strong relationship between gall numbers in 2010 and 2011 on control plants [as has been shown in natural populations in which no galls were removed (Goeden 1990; Wetzel 2014)] and a weaker relationship between those numbers on removal plants because no adults would have emerged and reproduced on the removal treatment plants. Conversely, if *E. diana* females move among plants frequently, then gall removal would have little to no effect on the distribution of galls among plants. In this case, control and removal plants would have the same relationship between gall numbers in 2010 and 2011. We distinguished between these hypotheses using mixed models in the R package glmmADMB (Fournier et al. 2012; Skaug et al. 2013; R Core Team 2014). The response variable was the number of galls on plants in 2011. The predictor variables were treatment (removal vs. control) and number of galls in 2010. We used a likelihood ratio test (Bolker et al. 2009) to test the significance of the interaction between treatment and 2010 gall numbers. A significant interaction would indicate that the number of galls on plants in 2011 depended on whether adults emerged on those plants or not. We used negative binomial models to account for overdispersion, which is inherent in the spatial distributions of most insect herbivores (Ver Hoef and Boveng 2007).

We also examined the hypothesis that females make small movements just among neighboring plants. If this were true, plants in the removal treatment group would be more likely to be recolonized if their neighbors supported many flies. We tested this hypothesis by using a likelihood ratio test to test the significance of local gall density as a predictor of the gall abundances on removal plants. We calculated local density for each plant using the inverse distance weighted sum of gall abundances on all control plants. We excluded removal plants within 2 m of the edge of the study area to reduce edge effects (Fortin and Dale 2005).

Plant choice and larval density-dependence study

We used a laboratory behavioral assay to test the hypothesis that *E. diana* females prefer plants that mediate weak larval density dependence over plants that mediate strong larval density dependence. In July and August 2011, we collected cuttings (20 cm long) from naturally growing pairs of plants (within 5 m of each other) at VESR that differed in the number of galls they supported, which has been shown to be negatively correlated with the strength of larval density dependence (Wetzel 2014). One plant of each pair had four or fewer galls (strong density dependence) and the other had more than ten galls (weak density dependence). From each plant (all approximately 80 cm in diameter) we took two cuttings that had no galls. We put the four cuttings (two from each plant) into upright water picks in a randomly assigned corner of a rectangular flight cage (35 × 35 × 60 cm). Then we placed four lab-reared and lab-mated *E. diana* females into the center of the cage. After an acclimation period of 60 min, we recorded the location of the flies within the cage every 30 min for at least 3 h. We repeated this procedure on 14 pairs of low and high density plants, never using the same plant more than once, and always using cuttings within 24 h of when they were collected.

We tested the hypothesis that females would spend more time on the cuttings from weak larval density-dependence plants using binomial generalized linear mixed models in the lme4 package in R (Bates et al. 2014; R Core Team 2014). We examined how female preference scaled with difference in strength of larval density dependence by regressing fly location (weak or strong density-dependence plant) on the difference in the number of galls on the two plant types. We calculated generalized R^2 and tested the significance of the difference in number of galls as a predictor of the strength of female preference using a likelihood ratio test (Cox and Snell 1989; Bolker et al. 2009).

Plant choice and competitor density study

We used a laboratory behavioral assay to test the hypothesis that *E. diana* avoids plants with a high density of previous ovipositions and prefers hosts free of previous ovipositions. In the assay, females could chose between two genetically identical potted sagebrush clone twins: one of the twins had received many previous *E. diana* ovipositions while the other twin had never been exposed to *E. diana*. The use of clones grown in pots under identical conditions removed the effects of any intrinsic differences between plants, including strength of larval density dependence. We started the clones in July 2012 by cutting vegetative buds from randomly selected mature plants at VESR. We dipped the cut ends into 1 % indole-3-butyric acid to encourage root growth, planted them in trays of clay profile, and kept them on a mist bench until root growth, when we transferred them to individual pots (Alvarez-Cordero and McKell 1979; Karban et al. 2013). In July 2013, we selected 26 clones that had grown to have canopies of approximately 18 cm in diameter and placed them in individual flight cages. We randomly assigned one twin of each clone to a control group or an oviposition treatment group. We placed three lab-reared, lab-mated pairs of *E. diana* females and males into the cages of clone twins in the oviposition treatment group. The clone twins assigned to the control treatment were kept free of flies. We left clones in these individual cages for 9 days, during which time we replaced any flies that died with fresh ones. We observed many ovipositions on clone twins in the oviposition treatment. Ovipositions are obvious because females insert their abdomen deep into vegetative buds. Three females on plants of this size for 9 days are sufficient to bring the plants to a high density of *E. diana* eggs. *E. diana* females carry approximately 15–25 eggs at any one time (W.C. Wetzel, personal observation), and most species of non-frugivorous tephritids, like *E. diana*, can produce 50–150 eggs in a lifetime (Headrick and Goeden 1998).

After the 9-day oviposition treatment, we put each pair of clone twins together into a fresh flight cage (35 × 35 × 60 cm) and introduced three fresh lab-reared, lab-mated females. We let the flies acclimate for 30 min and then recorded their locations every 30 min for at least 6 h. We tested the hypothesis that females would be observed significantly more frequently on the control clone twin than on the twin with previous ovipositions using binomial generalized linear mixed models in the lme4 package in R (Bates et al. 2014; R Core Team 2014). We report the mean and 95 % confidence interval (CI) of the probability that females would be found on the clone without previous ovipositions instead of the clone with ovipositions. Finally, we confirmed that oviposition effort was related to time spent on plants by using logistic regression to test the significance of the relationship between the number of times we observed females on a plant not ovipositing and the probability that we observed at least one oviposition on that plant.

Results

Movement field study

All but two of the 36 plants from which we experimentally removed *E. diana* galls (and pupae inside)

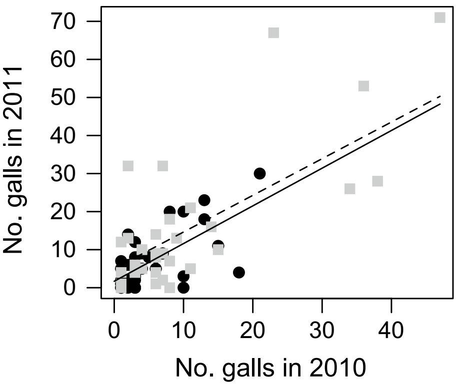

Fig. 1 The relationship between the number of galls on plants in 2010 and 2011 did not differ significantly between control plants (*circles, solid line*) and plants in the gall-removal treatment (*squares, dashed line*) (slope for control plants = 0.99 ± 0.33 SE, gall-removal interaction term = −0.027 ± 0.46 SE, $X_1^2 = 4.64$, $P = 0.098$). The five plants with the highest 2010 gall abundances are all in the gall-removal treatment because each one happened to be assigned to that treatment by random chance

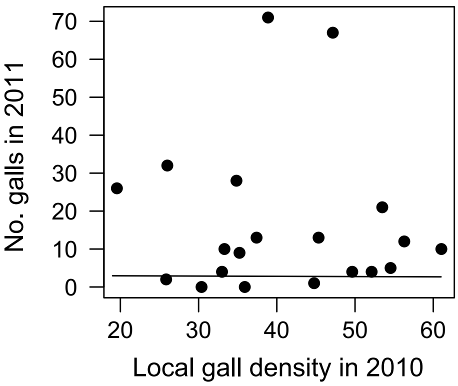

Fig. 2 The local density of galls in 2010 had no influence on the recolonization of plants in the gall-removal treatment (slope = −0.0067 ± 0.025, $X_1^2 = 0.071$, $P = 0.79$, generalized $R^2 = 0.004$). Local gall density is the sum of galls on all control plants weighted by the inverse distances between those plants and the focal plant. For example, plants with low local gall density were spatially isolated and/or had neighboring plants that supported few galls. Removal plants within 2 m of the plot boundary are excluded to remove edge effects

were recolonized within one generation of removal. The slope of the relationship between galls on plants in 2010 and 2011 was not significantly different between control plants and gall-removal plants (slope for control plants = 0.99 ± 0.33 SE, gall-removal interaction term = −0.027 ± 0.46 SE, $X_1^2 = 4.64$, $P = 0.098$, Fig. 1). In other words, gall abundances on plants were correlated from 2010 to 2011 whether or not adult *E. diana* actually emerged from galls on those plants in the 2010 generation. This indicates that females do move among plants during oviposition and that the number of galls plants support is consistent between fly generations. The inverse distance weighted sum of galls on neighboring plants in 2010 did not influence the number of galls on removal plants in 2011 (slope = −0.0067 ± 0.025 SE, $X_1^2 = 0.071$, $P = 0.79$, generalized $R^2 = 0.004$; Fig. 2). That is, the recolonization of plants in the removal treatment was independent of the local neighborhood density of *E. diana*, suggesting female movement is not limited to neighboring plants. Moreover, flies were able to recolonize even the most isolated plants in the experiment, indicating they can move distances of at least 4.0 m in search of hosts during oviposition.

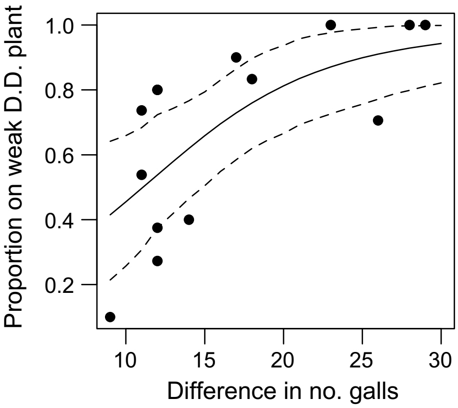

Fig. 3 The proportion of times *Eutreta diana* females were observed on cuttings from weak larval density-dependence (*D.D.*) plants (more than ten galls) versus strong larval density-dependence plants (four or less galls) increased as a function of the difference in the number of galls on the plants (difference in strength of larval density dependence). Three females were tested in each pairwise choice assay. The *solid line* shows the mean and the *dashed lines* the 95 % confidence interval from a binomial generalized linear mixed model ($X_1^2 = 8.7$, $P = 0.003$, generalized $R^2 = 0.46$)

Plant choice and larval density-dependence study

E. diana females displayed strong preferences for the cuttings from plants with more than ten galls (weak larval density dependence) over cuttings from plants with four or fewer galls (strong larval density dependence). The probability of observing a fly on a cutting from a weak density-dependence plant was 0.69, which was significantly greater than 0.5 or no preference (95 % CI 0.53–0.84, $z = 2.1$, $P = 0.035$). This means that flies were observed on weak density-dependence cuttings about 2.2 times as often as they were on strong density-dependence cuttings.

The strength of female preference was even more apparent when we took into account the difference in the numbers of galls on the plants. When the weak density-dependence cuttings came from a plant with just ten more galls than on the strong density-dependence plant, females had about a 0.5 chance (0.26–0.66, 95 % CI) of being observed on cuttings from the weak density-dependence plant, indicating no preferences (Fig. 3). But as the difference in gall abundances increased to the point where the weak density-dependence plant had 25 more galls than the strong density-dependence plant, females had a 0.90 chance (0.76–0.99, 95 % CI) of being observed on cuttings from the weak density-dependence plant. Indeed the difference in gall abundances was a strong predictor of the strength of preference for the high-abundance plant ($X_1^2 = 8.7$, $P = 0.003$, generalized $R^2 = 0.46$). These results indicate that ovipositing *E. diana* females discriminate among plants with weak and strong density dependence in the field, and that the strength of their discrimination scales with the difference in the strength of density dependence.

Plant choice and competitor density study

E. diana females displayed no avoidance of clones that had previously been exposed to ovipositing females. Females had a 0.57 chance of being observed on oviposition-free clones, with a CI that generously overlapped 0.5 (0.39–0.74, 95 % CI). A power simulation suggested that this result was not due to lack of statistical power (Bolker 2008): the test had a 0.8 or higher probability of correctly rejecting the null hypothesis of no preference given the true sample size and a preference for control plants of 0.6 or higher. In addition, despite extensive observation of many ovipositions during this experiment, we did not once observe a female exhibit the obvious marking behavior characteristic of other species that mark oviposition sites with pheromones to deter subsequent ovipositions, reducing larval competition. In this behavior a female drags her ovipositor along the plant surface for as long as 30 s in some species (Prokopy 1972). These results suggest that *E. diana* females do not avoid hosts with a high density of previous ovipositions. Finally, the probability of observing at least one oviposition on a plant increased significantly with the number of times we observed females on that plant not ovipositing ($X_1^2 = 14.0$, $P < 0.001$, generalized $R^2 = 0.59$). This result indicates that the number of times we observed a fly on a plant is indicative of oviposition preference.

Discussion

Our results show that *E. diana* females move among plants during oviposition and have strong preferences for the few plants in the population that mediate weakly density-dependent larval survival. Yet, despite the fact that most plants mediate strong density dependence and despite the apparently strong ability of females to discern among plants that differ in strength of larval density dependence, *E. diana* females do not avoid plants with a high density of conspecific ovipositions, even when plants with and without conspecific ovipositions are genetically identical. In other words, females minimize the effects of density dependence on their offspring by choosing plants that mediate only weak larval density dependence, not by choosing plants with low densities of competitors.

When Valladares and Lawton (1991) proposed that density dependence could be the explanation for why many species lack positive female preference-offspring performance relationships, they assumed that species facing negatively density-dependent larval performance would display negatively density-dependent oviposition behavior by avoiding plants with high competitor densities. Since that time, however, a number of species across a range of taxa have been reported to have density-independent oviposition despite having density-dependent larval performance. For example, *Eurosta solidaginis*, a tephritid gall former on goldenrod (*Solidago* spp.), rarely succeeds in forming more than one gall per plant ramet, but females do not respond to conspecific density and will continue to oviposit on already occupied ramets even when unoccupied ramets are nearby (Craig et al. 2000; Cronin et al. 2001). At least one species of leaf-mining moth (*Lithocolletis quercus*) experiences increased larval mortality due to interference competition and premature leaf abscission at high mine density, but females of this species nonetheless oviposit in an extremely aggregated distribution and make no apparent effort to reduce competition by dispersing offspring among leaves (Auerbach and Simberloff 1989). These systems and others, e.g., Blaustein and Kotler (1993), Digweed (2006), suggest that density-dependent oviposition may not be the only strategy that mothers use to cope with density-dependent offspring performance. However, not enough was known about the details of density dependence in these systems to look for more nuanced relationships between the strength of density dependence and female oviposition choices, as we have in the *E. diana* system.

Our results indicate that when density dependence varies among host-plant individuals, as has recently been shown to happen in a number of systems (Agrawal 2004; Underwood 2007; Miller 2007) including *E. diana* (Wetzel 2014), female oviposition behavior may be focused on finding plants that mediate weak density dependence, rather than finding plants with low densities of competitors. This means that resource selection behavior may depend not just on the presence or absence of density-dependent offspring performance but also on the details of how offspring density dependence varies in strength among sites within populations. In *E. diana*, oviposition behavior appears to be driven not by the strong larval density dependence on the average plant but instead by the rare plants with weak larval density dependence. This indicates that a detailed understanding of density dependence is needed for making predictions about preference-performance relationships.

There are several reasons why a behavioral strategy that seeks for plants that mediate weak density dependence may be more successful even than a strategy that responds to both competitor density and the strength of density dependence mediated by plants. First, the larval carrying capacities on plants that mediate strong density dependence are extremely low (Wetzel 2014), which means that to achieve high lifetime fitness using strong density-dependence plants, a female would have to oviposit on many plants. This strategy could be costly if moving among plants required significant time, energy, or exposure to predators. If so, this would likely decrease selection for females to use strong density-dependence plants with low *E. diana* density even after weak density-dependence plants reach high *E. diana* oviposition densities. The gall-removal experiment indicates that females move among plants, but it unfortunately does not reveal the costs of movement. Second, informational constraints could also combine with the inter-plant heterogeneity in density dependence to reinforce selection for females to have density-independent oviposition behavior. Even if females could accurately assess the current density of ovipositions on individual plants, uncertainty about the number of future ovipositions could mean that assessments of current density are not predictive of competition intensity. Third, there may be no selection for females to mark oviposition sites with oviposition-deterring pheromones, as do other species with density-dependent oviposition, if competition were asymmetrical in time such that early larvae negatively influenced the performance of later larvae but not vice versa. Temporally asymmetrical competition has been shown in many systems with delayed induced plant responses to herbivory (Fordyce 2003; Kaplan and Denno 2007), though it is unknown if it occurs in this system.

E. diana oviposition behavior likely contributes to the high spatial and low temporal variation that occurs in natural *E. diana* populations. Previous work suggests this abundance pattern is established by the density-dependent larval survival, which would stabilize dynamics in time, and the spatial heterogeneity in the strength of that larval density dependence, which would lead to variability in space (Wetzel 2014). The present work suggests that strong female preference for plants with weak density dependence reinforces that spatial variability because females favor the same plants repeatedly. Finally, the lack of avoidance of conspecific density both reinforces spatial aggregation because females do not seek plants of low conspecific density and reinforces temporal stability because the aggregation increases the realized strength of density dependence on weak density-dependence plants. Although, it is also possible that preference itself is the driver that establishes this pattern. Temporally stable and spatially variable abundance patterns are pervasive among specialist phytophagous herbivores with so-called latent population dynamics (Price et al. 1990; Karban and Agrawal 2002). We suggest that the syndrome of behavior exemplified by *E. diana* could be a common contributor to this pattern of population dynamics. Latent herbivores are believed to have strong host-plant preferences, as does *E. diana*, but our work suggests an additional contributor to this pattern of dynamics could be a lack of behavioral avoidance of potential competitors despite density-dependent larval performance.

In conclusion, our work indicates that the relationship between oviposition behavior and offspring density dependence is more nuanced than previously appreciated. Density-dependent oviposition, seen in other systems, is but one strategy for reducing larval competition. Another strategy, seen in *E. diana*, is finding and ovipositing on plants that mediate weak density dependence. The complexity of the relationship between female oviposition behavior and larval density dependence suggests that we should not be surprised by the diversity of female preference-offspring performance relationships observed in nature.

Author contribution statement W. C. W. conceived the project. W. C. W. and D. R. S. designed and performed the experiments. W. C. W. analyzed the data. W. C. W. and D. R. S. wrote the manuscript.

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Conflict of interest The authors declare that they have no conflict of interest.

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