

# A Meta-Analysis of Adaptive Deme Formation in Phytophagous Insect Populations

Peter A. Van Zandt\* and Susan Mopper

Department of Biology, University of Southwestern Louisiana, Lafayette, Louisiana 70504-2451

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**ABSTRACT:** The adaptive deme formation (ADF) hypothesis predicts that herbivorous insects become locally adapted to their host plants over time. Since its inception, approximately 17 independent studies have tested ADF, and they are divided in support and rejection of the hypothesis. This field of insect evolutionary ecology has a contentious history, and the contradictory studies obscure our understanding of the general evolutionary importance of adaptive deme formation in phytophagous insects. We conducted a meta-analysis in an attempt to clarify this issue. Meta-analysis is a statistical method for quantitatively comparing and synthesizing the results of different studies in a way that is more objective than a traditional literature review. Our analysis indicates that local adaptation is an important phenomenon in diverse insect systems. Contrary to predictions of the original hypothesis, there was no evidence that insect dispersal ability, and ostensibly gene flow, was associated with local adaptive differentiation. There was some indication that breeding (parthenogenetic, haplodiploid, diplodiploid) and feeding (exophagous, endophagous) modes may influence the evolution of locally adapted demes. Our analysis supports the theory of adaptive deme formation and provides guidance for future research directions.

*Keywords:* evolutionary ecology, local adaptation, statistical power.

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Individual plants are highly heterogeneous resources for the insects that feed on them (Denno and McClure 1983; Mopper et al. 1991; Michalakis et al. 1993; Sork et al. 1993). Because of their phenotypic variation, long-lived host plants can represent discrete and unique resource patches to which specialist insects with limited dispersal may become locally adapted. This hypothesis, known as adaptive deme formation (ADF), was first formulated for phytophagous insects by Edmunds and Alstad (1978),

\* E-mail: pvz@usl.edu.

who proposed that sedentary, specialist insect herbivores should form localized demes adapted to individual trees. The ADF hypothesis makes several predictions that have been tested in the literature to different degrees (Boecklen and Mopper 1998), including: insects that become adapted to their natal host plants become maladapted to novel host plants; sessile insects are more likely to become locally adapted than are dispersive insects; and haplodiploid insects are more likely to become locally adapted than are diplodiploid species.

Since its inception, the predictions of the ADF hypothesis have been examined in approximately 17 independent studies. Recent reviews of these studies (Mopper 1996; Boecklen and Mopper 1998; Strauss and Karban 1998) conclude that they are about evenly divided in support and rejection of the ADF hypothesis. Additionally, Alstad (1998) recently retracted the experimental results and deme formation hypothesis proposed in the original study by Edmunds and Alstad (1978). This field of insect evolutionary ecology has been somewhat contentious, and combined with the inconsistent results of the experimental field studies, a clear picture of the biological role of adaptive deme formation in the evolution of phytophagous insect populations has been impossible to obtain using traditional literature reviews.

Meta-analysis offers a solution to this dilemma because it is a statistical method for comparing and synthesizing the results of independent studies testing the same hypothesis (Hedges and Olkin 1985; Gurevitch et al. 1992; Gurevitch and Hedges 1993; Cooper and Hedges 1994). It has been used extensively in the medical and social science fields within the last 10–15 yr and is now becoming recognized in the fields of ecology and evolution (Gurevitch and Hedges 1993). Meta-analysis is powerful because it can reveal the existence and importance of a purported biological phenomenon by quantifying the magnitude of the treatment effect from each study included in the analysis, then assessing the overall significance of the average effect over all studies examined (Hedges and Olkin 1985; Cohen 1988).

One problem plaguing many ADF studies is experi-

mental power, or the lack of it. Because of the difficulty of manipulating natural insect populations in the field, several experiments suffer from “underreplication,” and their power to detect a statistically significant difference is low (Horton et al. 1991; Arnqvist and Wooster 1995a; Boecklen and Mopper 1998). Unlike the more traditional “vote-counting” methods, which become inconclusive when treatment effects diminish and studies disagree (Gurevitch et al. 1992), meta-analysis is especially useful for summarizing experiments with low sample sizes and weak treatment effects because it serves as a powerful method of controlling Type II errors (Arnqvist and Wooster 1995a).

A common failing of literature reviews is that nonsignificant studies are less likely to be published than are those that find significant results (Cooper and Hedges 1994). This is known as the “file drawer problem” (Arnqvist and Wooster 1995a). Although meta-analysis is no more immune to this than other methods of synthesis, it enables one to estimate the number of unreported studies that would produce a nonsignificant effect (Arnqvist and Wooster 1995a). We chose not to employ this method in our analysis because of the unique history of the studies investigating adaptive deme formation in natural insect populations. The original experiments by Edmunds and Alstad (1978) have been strongly criticized (e.g., Unruh and Luck 1987; Cobb and Whitham 1993; Alstad 1998), and the notion of adaptive deme formation was, and is, somewhat controversial. Studies refuting the ADF hypothesis were probably as likely to be published as studies supporting it, resulting in a relatively balanced literature. The number of published studies reporting positive and negative results are roughly equal, further evidence that little publication bias exists for this hypothesis.

### Contrasts of Interest

In this meta-analysis, we determine the generality of insect adaptive deme formation and also investigate several factors associated with this phenomenon. We ask the following questions.

*What is the direction and magnitude of the difference in performance between natal and novel lines of insects in studies examining the ADF hypothesis?* The most frequently tested prediction of the ADF hypothesis is that insect populations specialize on their natal host at the cost of decreased performance on novel hosts. This prediction is usually addressed by comparing the performance of insects reciprocally transferred between natal and novel hosts. In these studies, performance is measured as survival, growth, or fecundity of the herbivores. Although there is no clear trend in the literature regard-

ing performance differences (Mopper 1996; Boecklen and Mopper 1998), meta-analysis can reveal if this results from low experimental power owing to low sample sizes or large variances.

*Is local adaptation more apparent in sedentary than dispersive organisms?* Edmunds and Alstad (1978) originally formulated the ADF hypothesis for sessile insects with extremely low dispersal and, presumably, gene flow. Subsequent tests examined insects with limited dispersal abilities, whereas more recent experiments have expanded their scope to include dispersive insect species. This enabled us to use meta-analysis to ascertain the influence of dispersal behavior on local adaptation. We categorized insect dispersal ability according to the authors' assessments.

*Is local adaptation associated with insect feeding mode?* It has been proposed that endophagous insects should be more likely to become locally adapted than exophagous insects because endophagy brings the insect into close and continuous contact with plant chemical, mechanical, or phenological traits (Mopper 1996; Stiling and Rossi 1998). We used meta-analysis to determine if feeding mode was associated with patterns of adaptive differentiation.

*Does insect breeding system influence the level of adaptive differentiation?* The original ADF hypothesis suggested that insects with a haplodiploid breeding system would exhibit deme formation more readily than a diplodiploid breeding system (Edmunds and Alstad 1978, 1981). Similarly, parthenogenetic organisms may become locally adapted most readily because adapted gene complexes are less likely to be disrupted by recombination (Williams 1975; Maynard Smith 1978). Insect breeding system was categorized either by the author of the study or, where this information was absent, by researching the organism in the primary literature.

### Methods

#### *Literature Search*

We compiled studies for this meta-analysis by assembling the references reported in several recent literature reviews of the ADF hypothesis (Mopper 1996; Boecklen and Mopper 1998; Stiling and Rossi 1998; Strauss and Karban 1998). We also performed a literature search for the keywords “local” and “adaptation” using the Colorado Alliance of Research Libraries (CARL) corporation's Uncover library searching program. From these papers, we selected only those studies that met the criteria that follow.

*The study conducted reciprocal transfer field experiments of insects to compare their performance on natal and novel host plants.* The single exception to this criterion was the study by Stiling and Rossi (1998), in which plants rather

than insects were reciprocally transferred among different islands, because this design allowed comparisons of insect performance between natal and novel hosts. We restricted our analysis to reciprocal transfer experiments because this design is the most rigorous test of the ADF hypothesis and is also the most commonly employed.

The study estimated performance of the insects as density, survival, mortality, or fitness (table 1). A basic assumption of meta-analysis is that the dependent variables must be “linearly equatable” (Hedges and Olkin 1985; Gurevitch and Hedges 1993; Rosenberg et al. 1997). It is possible to include qualitatively different dependent variables in a single meta-analysis, but the resulting conclusions must necessarily be more general (Rosenberg et al. 1997). For this analysis, we felt justified in equating measures such as density, survival, mortality, and fitness. We omitted one study that measured the synchronization of insect oviposition to host phenology (Komatsu and Akimoto 1995). We also omitted a study in which the volume of gall was used to estimate indirectly insect density (Ozaki and Itahana 1997) because of potentially confounding plant genotypic effects on gall size. Typically, experiments were performed over a period of one to three insect generations.

The response data were reported such that means, standard deviations, and sample sizes could be determined. Variance estimates were not required for the response ratio analysis (see “Meta-Analysis Calculations” below).

The experiment was free from design problems. The original study by Edmunds and Alstad (1978) has been criticized by several authors (Kareiva 1982; Unruh and Luck 1987; Hanks and Denno 1993), and the results were recently retracted by Alstad (1998). Therefore, it was not included in this analysis.

#### Data Extraction

We used several methods to extract data from the original literature. In many cases, insect survival data were presented in tabular form for each experimental unit (usually the whole plant). From these values, we calculated means and standard deviations for the control and experimental groups. When data were presented as figures with error bars, we scanned them to produce a digital copy, then estimated the values for means and standard errors using the UTHSCSA ImageTool program (University of Texas Health Science Center 1996). The accuracy of this method was within 0.8% of the true value, based on our tests with spreadsheet-generated figures.

In some cases, mean values were reported without variance estimates. If the output of an ANOVA table was presented, the standard deviation ( $s$ ) was estimated using

$$s = \sqrt{\frac{\text{MSE}}{\text{df}}}, \quad (1)$$

where MSE was the within-group mean square term, and df was the degrees of freedom term for the error (Gurevitch et al. 1992). If the standard error was reported, standard deviation was calculated as:

$$s = \text{SE} \sqrt{p}, \quad (2)$$

where  $p$  is the number of plots (Gurevitch et al. 1992).

Data from two studies were provided by authors (Cobb and Whitham 1993; Mopper et al. 1995), and the value used for the Stiling and Rossi (1998) response ratio calculation was extracted from a review article (Strauss and Karban 1998). The data from all other studies used in this meta-analysis were taken from the original published papers (table 1).

Studies that reported several sets of results were entered as separate values only if the data presented were obtained from independent experiments. When several host plants were used in one experiment (e.g., Alstad 1998) or when the same measure was taken at two different time periods (e.g., Karban 1989), the data were not considered independent. In the first case, all the results were grouped by generating overall means for the control and experimental groups. For studies where data are recorded as a time series as in the second case, we used the final measurement only, as suggested by Rosenberg et al. (1997). When studies measured dependent variables for different life stages (e.g., Wainhouse and Howell 1983), only one survival estimate was used in the meta-analysis (that of the most advanced life stage). In studies where data from separate, independent experiments were reported in the same paper or where results were reported for males and females separately (e.g., Hanks and Denno 1994), the data were considered independent and each experiment was entered separately in the meta-analysis result set (see table 1).

#### Meta-Analysis Calculations

Currently, the most commonly used metric in meta-analysis studies is the effect size, measured as Hedge’s  $d$  (Hedges and Olkin 1985):

$$d = \frac{\bar{Y}_c - \bar{Y}_e}{s} J(m), \quad (3)$$

where  $\bar{Y}_c$  is the mean of the control group (insects transferred back to their natal host) and  $\bar{Y}_e$  is the mean experimental group (insects transferred to a novel host). Therefore,  $d$  is the difference between the experimental group and the control group means in terms of standard deviation units. For this analysis, a positive value of  $d$  in-

Table 1: Summary statistics from the studies used in this meta-analysis

Study	Breeding			Data source	Result	Dependent	d	RR
	Feeding	mode	Mobility					
Rice 1983	Ex	Hap	Sessile	Figure 1	0	Survival	NA	-.310/-.203
Wainhouse and Howell 1983	Ex	Parth	Sessile	Tables 1 and 3	+	Survival	.697/.525	-.300/-.674
Unruh and Luck 1987	Ex	Hap	Sessile	Table 2	0	Survival	-.566	.040
Karban 1989	Ex	Parth	Sessile	Table 2	+	Density	2.230	-.697
Hanks and Denno 1994	Ex	Hap	Sessile	Figure 2	+	Survival	*	†
Memmott et al. 1995	Ex	Hap	Mobile	Figure 5	0	Survival	NA	.045
Mopper et al. 1995	End	Dip	Mobile	Author supplied	+	Mortality	1.793	-.562
Kimberling and Price 1996	End	Parth	Sessile	Figure 3	0	Survival	NA	-.345
Strauss 1997	Ex	Dip	Mobile	Text	0	Survival	-.044	.009
Alstad 1998	Ex	Hap	Sessile	Table 1.1	0	Survival	-.077	.029
Cobb and Whitham 1998	Ex	Hap	Sessile	Text and author supplied	0	Mortality	-.029	.0143
Stiling and Rossi 1998	End	Hap	Mobile	Strauss and Karban 1998	+	Fitness	NA	-.673

Note: "Feeding" signifies either endophagous (End) or exophagous (Ex) herbivores. Hap, Parth, and Dip are haplodiploidy, parthenogenesis, and diplodiploidy, respectively. For study conclusion ("Result"), 0 indicates no significance, while + indicates that the original study detected significant differences between novel and natal insect populations.  $d$  = Hedge's  $d$ , which is calculated as  $d = [(\bar{Y}_e - \bar{Y}_c)/s]J(m)$ , and the response ratio (RR) is calculated as  $RR = \ln(\bar{Y}_e/\bar{Y}_c)$ , where  $\bar{Y}_e$  is the mean of the treatment populations (insects transplanted to a novel host),  $\bar{Y}_c$  is the mean of the control populations,  $s$  is the pooled standard deviation, and  $J(m)$  is a correction factor for small sample sizes. Positive values of  $d$  and negative values of RR signify increased performance of herbivores on their natal host relative to a novel host. For the Hanks and Denno study, four independent values were reported corresponding to male survival on near trees, female survival on near trees, male survival on distant trees, and female survival on distant trees.

\* The corresponding  $d$  values are -0.475, 0.315, 2.001, and 1.328.

† The corresponding RR values are 0.182, -0.105, -0.531, and -0.406.

indicates that the performance of insects was greater on their natal host plant than on a novel host plant. The pooled standard deviation ( $s$ ) in equation (1) is estimated as

$$s = \sqrt{\frac{(N_e - 1)(s_e)^2 + (N_c - 1)(s_c)^2}{N_e + N_c - 2}}, \quad (4)$$

where  $N_e$  and  $N_c$  are the total sample sizes of the experimental and control groups, respectively, and  $s_e$  and  $s_c$  are the standard deviations of the experimental and control groups, respectively. The effect size calculated as  $d$  is subject to small sample size bias, which is corrected by multiplying by the correction term  $J$ , approximated at each integer ( $m$ ) as:

$$J(m) = 1 - \frac{3}{4m - 1} \quad (5)$$

(Hedges and Olkin 1985);  $J(m)$  approaches 1 as the sample size increases.

A newly developed metric for assessing the effect size of experimental results is known as the response ratio (RR; Rosenberg et al. 1997), which is calculated as

$$RR = \ln\left(\frac{\bar{Y}_e}{\bar{Y}_c}\right). \quad (6)$$

The response ratio has the advantage that only the means and sample sizes are required from published studies; however, resampling techniques are necessary (Adams et al. 1997; Rosenberg et al. 1997). In this analysis, a negative RR indicates that insects exhibit superior performance on their natal host plant compared with their performance on a novel host plant.

Both  $d$  and RR effect sizes were calculated for each experiment, where data were available. Weighted average effect sizes ( $d_{++}$  and  $RR_{++}$ ) were then calculated for performance differences across all studies. Confidence intervals for both  $d_{++}$  and  $RR_{++}$  were calculated using non-parametric (resampling) techniques. All calculations and analyses were carried out using the MetaWin program, version 1.0 (Rosenberg et al. 1997). The overall effect sizes were tested for significant differences from 0 using  $\alpha = 0.05$ .

The tests were performed with a recently developed mixed-model meta-analysis (Raudenbush 1994). Usually, meta-analyses are performed using a fixed-effects model

(similar to a fixed-effects ANOVA model), which assumes that the studies being compared share a common true effect size: an unlikely assumption in ecological studies (Rosenberg et al. 1997). A mixed-effects model still assumes that studies share a common mean effect but differs from a fixed-effects model in that it incorporates an additional error component introduced through the combined effects of random variation and sampling variation (Raudenbush 1994; Rosenberg et al. 1997), similar to mixed-model ANOVAs (Rosenberg et al. 1997).

Meta-analyses assume that observations in the control and experimental groups of each study are normally distributed. This assumption is justified if the number of samples in the control and experimental groups exceeds 10 (Adams et al. 1997), but ecological studies frequently have fewer than 10 samples per treatment. It is unknown how robust parametric meta-analytic calculations are to violations of this assumption (Adams et al. 1997). Because they generate their own distributions, methods such as bootstrapping are free from the assumptions of normality and are often more powerful than standard parametric techniques (Adams et al. 1997; Manly 1997). Meta-analysis confidence limits obtained through randomization techniques are considered to be more conservative than parametric methods for meta-analysis (Adams et al. 1997). For this analysis, nonparametric tests were performed using bias-corrected confidence limits calculated by bootstrapping over 20,000 trials using MetaWin (Rosenberg et al. 1997). Following the recommendation of Efron (1987), only bias-corrected 95% confidence intervals were used in the interpretation of results because so many of the studies in this analysis had small (<10) sample sizes.

Besides the estimate of overall effect size ( $d_{++}$  and  $RR_{++}$ ), additional comparisons can be made in a meta-analysis by contrasting studies of different groupings to determine if the effect of these groups is different between studies (such as the influence of insect mobility on the likelihood of local adaptation). This process is similar to testing main effect terms for significance in an ANOVA. To perform the contrasts of interest, we calculated  $Q_b$ , the between-class heterogeneity statistic (Hedges and Olkin 1985) and compared all studies for the second through fourth questions outlined above. Nonparametric mixed model tests were performed for  $Q_b$ , with the bias-corrected percentile bootstrap confidence limits calculated as previously described. A significant  $Q_b$  indicates that the effect size is significantly different for the levels of group under examination. For example, a significant value of  $Q_b$  for a comparison of sessile versus mobile insects is evidence that local adaptation is more likely in one group than the other. A non-significant  $Q_b$  indicates that no difference in response be-

tween groups could be detected. Significant effect sizes indicated that there was a difference from 0 for the effect size of interest: a significant group effect size ( $d_+$ ,  $RR_+$ ) indicated that the group in question differed from 0, while an overall group effect size ( $d_{++}$ ,  $RR_{++}$ ) indicated that local adaptation across all groups and all studies was detected.

For the analysis using Hedge's  $d$ , there were eight studies that provided enough information to be included (table 1). Two of these presented more than one independent data set, so the total number of separate experiments was 12. For the response ratio (RR) analysis, 12 studies presented sufficient data, resulting in a total of 17 independent result sets (table 1). Because of the limited number of studies in each category for the  $d$  analysis, only the contrasts for herbivore dispersal ability and reproductive mode could be examined. There were two mobile groups in the  $d$  dispersal contrast, and only two diploid studies in the  $d$  and RR breeding system contrasts, thus the inferential power of these comparisons was potentially low or sensitive to influential studies. Currently, there is no method of estimating the power of a meta-analysis (Arnqvist and Wooster 1995b), so the magnitude of Type II errors due to low power could not be determined.

Because there were relatively few studies in this meta-analysis, we were concerned that the results might be influenced by one or two studies with large effect sizes. Consequently, we reran all analyses after removing Karban's (1989) study, which had the largest effect size. Although this changed the numerical estimates of overall effect sizes ( $d_{++}$  and  $RR_{++}$ ) and their 95% confidence intervals, both remained significant at the  $\alpha = 0.05$  level, indicating that the results are robust to influential studies. The effects of removing this study on the rest of the contrast statements are noted in the results.

## Results

*What is the direction and magnitude of the difference in performance between natal and novel insect lines in studies examining the ADF hypothesis?* Both Hedge's  $d$  and the response ratio (RR) analyses produced a significant effect size and provided evidence that insects become locally adapted to their natal hosts. In the  $d$  analysis, the total effect size ( $d_{++}$ ) across all studies ranged from 0.495 to 0.501. This range results from how the mixed model is calculated and is expected as each comparison in a mixed model is weighted differently by the groups being compared (Rosenberg et al. 1997). The bootstrapped, bias-corrected 95% confidence intervals were 0.075–1.018 for the smallest  $d_{++}$  and 0.075–1.033 for the largest  $d_{++}$ . When using RR as the measure of effect size, the pro-

**Table 2:** Effects of local adaptation for studies with effect size calculated as  $d_+$ 

<i>Comparison and grouping contrast</i>	N	$d_+$	95% CI	$Q_b$	$P_{Q_b}$	<i>df</i>
Mobility of insect				.050	.833	1
Sessile	10	.47	.007 to 1.051			
Mobile	2	.61	-.044 to 1.793			
Breeding mode of insect				1.476	.544	2
Parthenogenetic	3	1.05	.525 to 2.230			
Haplodiploid	7	.26	-.215 to .970			
Diplodiploid	2	.60	-.044 to 1.793			

Note:  $N$  is the number of experiments used in each contrast;  $d_+$  values  $>0$  indicate evidence for local adaptation;  $Q_b$  is the between-groups heterogeneity statistic. Bias-corrected 95% confidence intervals and  $P_{Q_b}$  are the result of bootstrapping over 20,000 replicates.

gram defaulted to a fixed-model analysis because the variation in effect size among studies was not large enough to warrant a mixed model. Therefore, all estimates of effect size ( $RR_{++}$ ) were equal at  $-0.264$  (bias-corrected 95% CI =  $-0.401$  to  $-0.131$ ). Both analyses showed a consistently significant effect of local adaptation.

*Is local adaptation more common in sedentary than dispersive organisms?* When insect mobility was contrasted in the analysis using  $d$ , only sessile groups had an effect size ( $d_+$ ) significantly different from 0 (table 2). However, between-group heterogeneity ( $Q_b$ ) was not significant (table 2), indicating that sessile insects were no more likely to form locally adapted demes than mobile insects. When this analysis was performed without the Karban (1989) study of sessile thrips insects, neither the sessile nor the dispersive groups produced effects significantly different from 0 (sessile  $d_+ = 0.328$ , 95% CI  $-0.077$  to  $0.838$ ; mobile  $d_+ = 0.568$ , 95% CI  $-0.044$  to  $1.793$ ).

In the RR analysis, only the sessile group had a significant effect size (table 3). As in the  $d$  analysis,  $Q_b$  was

not significant (table 3), indicating that local adaptation was not more common in sessile than dispersive insects. The high degree of overlap in the 95% confidence intervals for sessile and dispersive insects suggests that lack of significance was not produced by low experimental power. These results were not substantially changed by removing the Karban (1989) study.

*Is local adaptation associated with insect feeding mode?* There were too few studies available to examine this question in the  $d$  analysis. In the RR analysis, both exophagous and endophagous insects had effect sizes significantly different from 0 (table 3), and the two groups did not differ significantly from each other (table 3). However, the endophagous group effect size was larger than the exophagous group, and the overlap in the 95% confidence intervals was very small (0.012). Because the endophagous group was only represented by three experiments, the failure to detect a difference between internally and externally feeding insects could be a result of low power in this analysis. Without the Karban (1989) study of exophagous thrips, both groups remained sig-

**Table 3:** Effects of local adaptation for studies with effect size calculated as  $RR_+$ 

<i>Comparison and grouping contrast</i>	N	$RR_+$	95% CI	$Q_b$	$P_{Q_b}$	<i>df</i>
Mobility of insect				.005	.806	1
Sessile	13	-.25	-.404 to -.111			
Mobile	4	-.29	-.618 to .027			
Level of intimacy				.252	.084	1
Exophagous	14	-.21	-.357 to -.071			
Endophagous	3	-.53	-.673 to -.345			
Breeding mode of insect				.488	.046	2
Parthenogenetic	4	-.50	-.685 to -.323			
Haplodiploid	10	-.12	-.270 to .001			
Diplodiploid	3	-.41	-.673 to .009			

Note:  $N$  is the number of experiments used in each contrast;  $RR_+$  values  $<0$  indicate evidence for local adaptation;  $Q_b$  is the between-groups heterogeneity statistic. Bias-corrected 95% confidence intervals and  $P_{Q_b}$  are the result of bootstrapping over 20,000 replicates.

nificantly different from 0 (exophagous  $RR_+ = -0.170$ , 95% CI =  $-0.316$  to  $-0.045$ ; endophagous  $RR_+ = -0.527$ , 95% CI =  $-0.6733$  to  $-0.345$ ), but the difference between the two was now significant ( $P_{Q_b} = .042$ ), with the endophagous group showing a stronger effect.

*Does insect breeding system influence local adaptation?* The Hedge's  $d$  statistic was significant for parthenogenetic insects (table 2), but not for the other breeding systems. However, a nonsignificant  $Q_b$  for this comparison indicated that the three breeding modes did not differ significantly from each other in influencing the overall effect size. These results were not qualitatively changed by excluding the Karban (1989) study.

In the RR analysis, parthenogenetic insects were again the only group to have a significant effect size, although diploidiploid insects had a very similar response and were nearly significantly different from 0 at the  $\alpha = 0.05$  level (table 3). Haplodiploid insects were also nearly significant, but their effect size was not as large as the other two groups (table 3). Contrary to the  $d$  analysis,  $Q_b$  was significant in the RR analysis (table 3), suggesting that parthenogenetic and diploidiploid insects may be more likely to demonstrate local adaptation than haplodiploid insects. Parthenogenetic insects were still significant in the reanalysis without the Karban (1989) study, but  $P_{Q_b}$  increased to .114, meaning that the three groups were statistically indistinguishable at  $\alpha = 0.05$ .

### Discussion

The adaptive deme formation (ADF) hypothesis predicts microevolutionary fine tuning of insects to their host plants over time. Because of the difficulties associated with reciprocally transferring insects in natural populations, experiments testing local adaptation theory usually have low replication and high variances. This limits their ability to detect differences in performance between insects on natal and novel hosts; that is, they have low experimental power (Horton et al. 1991; Boecklen and Mopper 1998). In traditional "vote-counting" literature reviews, studies are weighted equally, regardless of the statistical power of the design (Hedges and Olkin 1985; Cooper and Hedges 1994). Meta-analysis weights each study by its variance and sample size, thereby accounting for the power of a study to detect differences between treatments (Hedges and Olkin 1985; Rosenberg et al. 1997). As such, meta-analysis provides a powerful, quantitative method for determining general patterns of biological phenomena that would be impossible in a narrative review (Arnqvist and Wooster 1995a).

We addressed four specific questions in this meta-analysis. The first concerned the overall strength of local adaptation when all studies were examined. We also ex-

amined three factors that might facilitate the process of local adaptation: insect dispersal, mode of feeding, and breeding system. One caveat with this contrast procedure is the potential lack of independence among different categories. For example, dispersal ability could be confounded with breeding mode. Although not prominent in the local adaptation data set, meta-analyses with relatively few studies are vulnerable to this problem.

The overall local adaptation effect size measured as Hedge's  $d$  for this analysis was approximately 0.50. Based on Cohen's (1988) recommended interpretations of effect sizes, this is considered a "moderate" effect size. By way of comparison to previous meta-analyses, Gurevitch et al. (1992) found a "strong" ( $d = 0.80$ ) effect of plant competition on biomass and Wooster (1994) and Dahl and Greenberg (1996) found "weak to moderate" effects ( $d = 0.13$ – $0.51$ ) of stream predators on the density of prey.

In the RR analysis of this study, the effect size was also consistently significantly different from 0. As yet, there are no rules of thumb for interpreting meta-analyses using RR as the effect size, and to our knowledge ours is the first application of this approach to empirical studies. Taken together, the implication of our meta-analysis using both  $d$  and RR estimates is that local adaptation of phytophagous insects to individual host plants is a significant biological phenomenon when the results of all possible studies analyzing this question are combined. That significance was detected despite approximately half of the studies reporting negative results suggests that the failure of some studies to detect local adaptation may have resulted from low statistical power.

The remaining comparisons that we addressed attempted to determine which factors make local adaptation of insect herbivores to their host plants more likely. First, we assessed the influence of insect dispersal ability on local adaptation. Edmunds and Alstad (1978) posed the original ADF hypothesis specifically for sessile herbivores, but several recent studies have tested the ADF question using mobile insects. Contrary to the original hypothesis, we found no evidence that insect mobility constrained local adaptation. That is, for studies that have tested the ADF hypothesis so far, there is no indication that sessile insects are more likely to form locally adapted demes than mobile insects. Although only the sessile group exhibited an effect significantly different from 0, the two groups had similar effect sizes in both analyses (tables 2 and 3).

It is possible that insect mobility per se does not adequately characterize the frequency of gene exchange among populations. Unfortunately, however, few local adaptation studies explicitly quantified gene flow. In a recent literature review on life history and genetic structure

of herbivorous insects (Peterson and Denno 1998), gene flow was generally higher in vagile species than sessile species. However, this is not always the case (Liebherr 1988), and using observations of the movements of individuals to estimate the magnitude of gene flow has many limitations (Slatkin 1987; Roderick 1996). The magnitude of local selection pressures must also be considered because strong selection can overcome substantial gene flow (Slatkin 1987), as observed in a recent study of gene flow and local adaptation in an oak leafminer population (Mopper et al. 1995, 1999).

The next question investigated the relationship between feeding behavior and adaptive differentiation. Some authors have proposed that insects that spend the majority of their life cycle inside of the host plant may be more likely to exhibit local adaptation than insects that feed externally because endophagy brings the insect into greater contact with the host's chemical, mechanical, and phenological defensive characteristics (Mopper 1996; Stiling and Rossi 1998). Only three studies have examined local adaptation in endophagous insects, so our ability to determine a significant effect was limited, and there is currently no method for estimating the power of a meta-analysis (Arnqvist and Wooster 1995*b*). Additionally, we could only examine this contrast using the RR effect metric, which did not indicate a significant difference between external and internal insects at the  $\alpha = 0.05$  level (table 3). However, endophagous insects showed a larger effect size (a more negative RR<sub>+</sub>) and a slight overlap in 95% confidence intervals with the exophagous group (table 3). Excluding the Karban (1989) study of exophagous thrips insects resulted in a significantly larger effect for endophagous insects ( $P_{Q_b} = .042$ ). These results lend tentative support for the notion that feeding mode could facilitate or constrain local adaptive evolution.

Our final question concerned the relationship between breeding mode and local adaptive differentiation, and we compared three types of breeding systems: parthenogenesis, haplodiploidy, and diplodiploidy. In the *d* analysis, there was no significant difference between these three groups. In contrast, the RR analysis indicated a significant difference between the three groups at the .05 level (table 3), with parthenogenetic insects showing the strongest effect size and the haplodiploid insects showing the weakest effect size. Although this difference was not significant without the Karban (1989) study ( $P_{Q_b} = .114$ ), parthenogenetic insects still had the highest magnitude of effect size and haplodiploid insects the lowest. These results indicate that a revision of the "haploid handicap" corollary of the ADF hypothesis (Boecklen and Mopper 1998) might be necessary, but this finding could also be driven by the strong effect size in one of the two studies that examined diplodiploid insects (Mop-

per et al. 1995). Strauss and Karban (1994) found that the performance of locally adapted thrips (Karbon 1989) differed depending on whether the thrips lines were produced parthenogenetically or sexually. Clearly, the importance of insect breeding system to rapid adaptive evolution is an important direction for further theoretical and experimental work.

We would be remiss if we failed to present some alternative explanations for patterns of local adaptation, such as maternal body size (Cowley et al. 1989), maternal age (Bridges and Heppell 1996), or maternal behavior (Roosenburg 1996). For example, mothers on certain host plants could impart antimicrobial plant compounds to their offspring (e.g., Dussourd et al. 1988) that would only be advantageous on the natal host plant. In this case, the superior performance of insects on natal hosts would result from a nongenetic acclimation and would not represent local adaptation of populations over successive generations (Mousseau and Fox 1998; Rossiter 1998).

Two studies suggest that maternal effects are not the cause of increased performance of natal populations. Karban (1989) found evidence for local adaptation in an experiment where maternal effects were controlled for by conditioning insects on nonnatal hosts for several generations prior to their transfer to natal and novel plants. Also, in the oak leafminers examined in another study (Mopper et al. 1995), only larvae feed on host plants, making transmission of maternally derived plant material from mothers to eggs less likely. Future studies examining the ADF hypothesis should be designed to account for the influence of nongenetic effects.

In conclusion, although published studies are divided between support and rejection of the ADF hypothesis, this meta-analysis provides convincing evidence that local adaptation of insect herbivores to their host plants is a real biological phenomenon that occurs in diverse systems. Clearly, more empirical studies are needed to identify the life-history traits and selection pressures associated with local adaptation, and this meta-analysis provides clues about the mechanisms that make local adaptation of insect herbivores to their host plants more likely.

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