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TESTS OF INBREEDING EFFECTS ON HOST-SHIFT POTENTIAL IN THE PHYTOPHAGOUS BEETLE *OPHRAELLA COMMUNA*

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Abstract.—Although inbreeding, on average, decreases additive genetic variance, some inbred populations may show an increase in phenotypic variance for some characters. In those populations with increased phenotypic variance, character changes by peak shifts may occur because of the effects of the higher variance on the adaptive landscape. A population's increased phenotypic variance may place it in the domain of attraction of a new adaptive peak or increase the likelihood of a selection-driven peak shift as the landscape of mean fitness flattens. The focus of this study was to test for increased variance, in inbred populations, in a behavioral character involved in adaptive diversification and probably speciation. We examined the effect of inbreeding on feeding responses of the leaf beetle *Ophraella communa* in a series of inbred lineages across a range of levels of inbreeding (f = 0.25, 0.375, 0.5). We measured the feeding response of inbred lineages of *O. communa* on its normal host, *Ambrosia artemisiifolia,* and on two novel plants, *Chrysopsis villosa* and *Iva frutescens,* that are the hosts of other *Ophraella* species. The results show that feeding responses on the different plants are not correlated, indicating that the feeding responses to the different plants are to some degree genetically independent. Despite apparent genetic variation in lineage feeding responses, we could not statistically demonstrate increases in phenotypic variance within the lineages. Thus, the experimental results do not support the idea that host shifts in this beetle evolved by peak shifts in bottlenecked populations.

Key words.—Chrysomelidae, host shifts, inbreeding, *Ophraella,* phytophagous insects, shifting balance theory, variance-induced peak shifts.

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As a model of adaptive character evolution, Wright's (1932) shifting balance theory is highly controversial (Coyne et al. 1997), as are related models of founder effect speciation (Mayr 1954; Carson and Templeton 1984). Among the criticisms of these models is the argument that phenotypic changes by peak shifts are unlikely because bottlenecks or founder events decrease the amount of genetic variance in a population (Barton and Charlesworth 1984; Charlesworth and Rouhani 1988). However, some other theoretical treatments (Kirkpatrick 1982; Wade 1992; Whitlock 1995) have described conditions under which the probability of peak shifts as a result of population bottlenecks may be greater than simple additive models suggest.

Inbreeding in an initially panmictic population divides the population into inbred genetic lineages, or subpopulations, each with its own variance. Founder events give rise to such subpopulations. The variance among inbred subpopulations increases as the lineage means diverge (Wright 1977). For additively inherited traits, the mean effect of inbreeding on the variance within a lineage, that is, the effect of inbreeding averaged across several lineages, is a decrease in genetic variance (Falconer and MacKay 1996). However, although the additive genetic variance decreases on average, random changes in allele frequencies may increase the genetic variance within some individual subpopulations, at least temporarily. Moreover, genetic drift can increase the additive genetic variance by converting nonadditive genetic variance, owing to dominance or epistasis, into additive genetic variance (Robertson 1952; Goodnight 1987, 1988). Finally, many characters display increased nongenetic (environmental) phenotypic variance in inbred lineages relative to outbred controls, evidently as a consequence of decreased canalization or buffering against developmental noise and environmental perturbations (Lerner 1954; Wright 1977).

Consequently, the effect of inbreeding on the phenotypic variance within individual genetic lineages is highly variable (Avery and Hill 1977; Lynch 1988; Meffert 1995; Pray and Goodnight 1995, 1997; Whitlock and Fowler 1996), with some lineages actually increasing in phenotypic variance relative to outbred controls. Such increases have been attributed both to increased sensitivity to developmental and environmental sources of variation (Wright 1977), and to changes in genetic variance (e.g., Bryant et al. 1986; Bryant and Meffert 1988; Carson and Wisotzkey 1989; López-Fanjul and Villaverde 1989).

Those lineages that show increased phenotypic variance as a result of inbreeding may more easily shift to new adaptive peaks, for two reasons. First, the "hillside" leading to an adaptive peak may be embraced only by highly variable populations if the peak is distant (Fig. 1). Kirkpatrick (1982) suggested that this model may explain some "punctuations" in the fossil record. Second, as Whitlock (1995) has noted in his model of variance-induced peak shifts (VIPS), increases in phenotypic variance cause the landscape of mean fitness to flatten, thus enhancing the likelihood of a selection-driven peak shift from one stable state to another. Even if the increase in phenotypic variation is not genetically based, the probability of evolution by VIPS increases, provided there is additive genetic variance for the trait in question (Whitlock 1995). Studies that explicitly consider the distribution of in-

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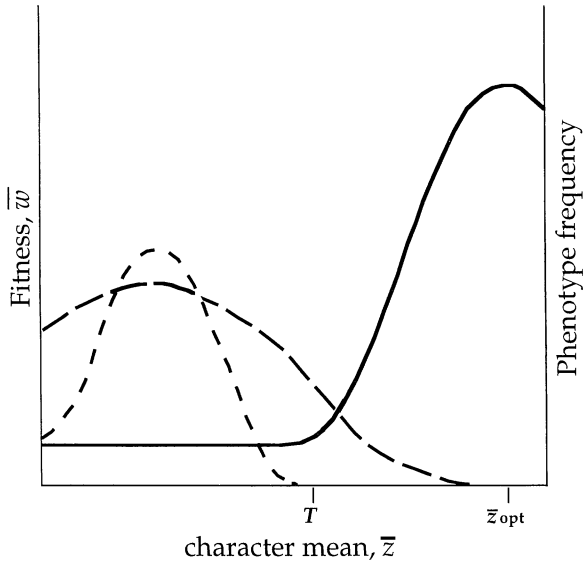

FIG. 1. An adaptive landscape (solid curve) for a quantitative character (z) that affects fitness in a novel environment, such as feeding rate on a novel plant when an insect's normal host is absent. T represents a threshold feeding rate required for positive growth and survival. Evolution to the new adaptive peak ($\bar{z}_{opt}$) is more likely if the phenotypic variance is large, embracing the "adaptive slope," than if it is small (dashed curves).

breeding effects across inbred lineages have shown an increase in the phenotypic variance of some lineages relative to outbred control populations for some traits (reviewed in Fowler and Whitlock 1999). These studies suggest that enhancement of character evolution by founder effects may be more probable than in the traditional shifting balance theory (Whitlock 1995).

In this paper, we test for increased variance in inbred populations in a behavioral character that bears strongly on adaptive diversification and probably on speciation: host preference in a specialized phytophagous insect. Evolutionary shifts to new host plant species are strongly associated with speciation in many groups of such insects (Mitter and Farrell 1991), due in at least some instances to sympatric speciation (Bush 1975; Feder et al. 1993) and, perhaps more generally, to the ecological isolation that may arise between populations that have acquired different host preferences in allopatry. It is plausible to imagine that some host shifts might occur by VIPS because the chemical and other differences between the hosts of some pairs of sister species are so great that almost complete mortality ensues if either insect species is experimentally reared on the host of the other. Often, a low propensity to feed on the sister species' host plant contributes to the failure to develop on it. Thus, one can readily envision that the "adaptive peak" represented by feeding on a novel plant at a high enough rate to sustain growth and survival is so distant from the population mean that selection for feeding on the plant can be effective only if the variance in feeding response is high enough (Fig. 1). Given the evolution of a host shift, the possible role of a VIPS would presumably be greater the more distantly related and phenotypically dissimilar the novel plant is from the insect's previous host.

We have examined the effect of inbreeding on feeding responses of the leaf beetle *Ophraella communa* (Chrysomelidae: Galerucinae) to its normal host, *Ambrosia artemisiifolia,* and to two novel plants, *Chrysopsis villosa* and *Iva frutescens,* that are the hosts of other species of *Ophraella. Ophraella communa* feeds only on common ragweed, *A. artemisiifolia* (Asteraceae, tribe Heliantheae, subtribe Ambrosiinae), in eastern North America and on several other members of the Ambrosiinae in western North America. According to a phylogenetic analysis based on mitochondrial DNA sequence data, the nearest relative of *O. communa* is *O. bilineata,* which is hardly more divergent in sequence from *O. communa* than some *O. communa* sequences are from each other (Funk et al. 1995; Knowles and Futuyma, unpubl. ms.). The phylogeny implies that the association of *O. communa* with Ambrosiinae is ancestral, relative to the derived association of *O. bilineata* with *C. villosa,* which is in the tribe Astereae. Although few data on the chemical properties of *Chrysopsis* are available, its close relatives in the Astereae differ substantially from Ambrosiinae in the profile of many classes of secondary compounds—the kind that influence feeding behavior in other insects. *Iva frutescens,* the host of a more distantly related species (*O. notulata*), is in the Ambrosiinae; it is closely related and chemically quite similar to *Ambrosia* (Futuyma and McCafferty 1990).

In earlier studies (Futuyma et al. 1993), we determined that larvae of *O. communa* fed rather readily on *I. frutescens* and survived on it fairly well (in one experiment, survival to pupation was 14% compared to 52% on the normal host, *Ambrosia*). Consumption of *Chrysopsis* was much lower, on average, and no larvae survived to pupation. A quantitative genetic analysis, using a half-sib design, provided evidence of genetic variance for larval consumption of both *Iva* and *Chrysopsis.* Nevertheless, the low survival and low mean feeding rate suggest that the shift from *Ambrosia* to *Chrysopsis* that evidently occurred in the evolution of *O. bilineata* from an *O. communa*–like ancestor was a "difficult" one.

METHODS

We examined the effects of inbreeding on phenotypic variation in a series of inbred lineages across a range of levels of inbreeding. Data were collected on 19 lineages of *Ophraella communa* derived from a population near Stony Brook, New York. Beetles were maintained in an environmental chamber at 25°C with a 16:8 h L:D photoperiod and reared on greenhouse-grown *Ambrosia artemisiifolia,* their natural host.

Each lineage was propagated under a full-sib mating design for three generations (f = 0.25, 0.375, 0.5). Each lineage was founded by a single female-male pair randomly selected from the stock population. This stock population came from a laboratory population that had been maintained for nine generations and propagated from at least 60 adults each generation. Within each lineage, five breeding pairs were set up. Data were collected on the progeny of the five breeding pairs, thus providing replicates for the phenotypic variable assayed for each lineage. Subsequent generations were founded from randomly selected full-sib pairs from one of the five replicates for each lineage. Beetles were allowed to mate and oviposit for five days. Each generation was founded by offspring col-

lected in the pupal stage to ensure they had not previously mated.

At each generation, feeding scores of similar-sized second-instar larvae were taken from the progeny of each replicate for each inbred lineage, for an average of five replicates on each of three plant species, *Ambrosia, Chrysopsis,* and *Iva.* Each feeding score consisted of the area of leaf discs of a single plant host (no-choice tests) consumed in 24 h by five larvae. Area of material consumed was measured with an ocular grid using a microscope. Replicates from all 19 lineages were tested at random over a 10-day period on leaf discs collected from multiple leaves of five individuals of each host plant. For each host, leaf discs from the different leaves were mixed thoroughly before being used in feeding trials. Two leaf discs were used per trial to provide adequate feeding material. Feeding trials on *Ambrosia* and *Chrysopsis* were conducted on greenhouse-reared plants. *Iva* foliage was collected in the field from the same plants at the same site for each set of feeding trials each of the three generations and all feeding trials within a generation were completed on a single collection of plant material.

Data from two outbred control populations were analyzed to test for environmental changes during the course of the experiment. The outbred populations were maintained for the duration of the experiment and propagated from the same ancestral stock as the inbred lineages. Each outbred population consisted of 25 breeding pairs, each taken from the progeny of a separate pair and then mated en masse. The same feeding assays as described above were performed on larvae from 10 randomly selected breeding pairs in each control population.

Data were analyzed on JMP (SAS 1995) in a two-way ANOVA with lineage and inbreeding coefficient (f) as main effects; the f and lineage $\times f$ effects were partitioned by means of orthogonal polynomials (Sokal and Rohlf 1995). A natural logarithmic transformation was performed to correct for deviations from normality; however, this did not improve the distribution of the data, nor did it change the results qualitatively. Only results from the untransformed data are presented. For testing equality of within-lineage variances, data were r-transformed (O'Brien 1981) and analyzed in a similar model as mean feeding scores.

Variation in the within-lineage variance was also analyzed with a randomization test. Residuals from the ANOVA with lineage as a main factor were used to avoid effects due to differences in mean feeding scores among the lineages. We ran 10,000 randomizations, in sample sizes equivalent to the sample sizes of the experimental lineages, with each randomization generating a set of within-lineage variances. The variance of the set of values was computed. The distribution of this pseudostatistic assumes that lineages differ in within-lineage variance only due to sampling error. The variance of the experimental within-lineage variances was compared to the distribution of the pseudostatistic to test for a significant increase in the variance of the within-lineage variances.

Overall effects of inbreeding on both the phenotypic variance and mean were tested with respect to f and lineage main effects. The lineage main effects were used to test whether the variance and mean feeding scores differ among lineages (i.e., test whether lineages are homogeneous with respect to feeding behavior). Significance of the f main effect was used to test for overall inbreeding depression. Linear contrasts of f were used to test if changes in the variance or mean feeding scores were significantly different than zero; a positive slope would indicate an overall increase in phenotypic variance or mean as a result of inbreeding. The lineage $\times f$ interaction term was used to test whether the response to inbreeding differed among lineages.

TABLE 1. Analysis of variance of the effects of inbreeding on lineage mean larval feeding score on each of three host plants. The linear components refer to the partitioning of the f effect and interaction term by means of orthogonal polynomials.

Source	df	MS	F-ratio	P-value
Feeding on *Ambrosia*				
f	2	1203.99	3.7327	0.0336
f_{linear}	1	3111.39	9.6461	0.0037
Lineage	18	250.94	0.7798	0.7229
Lineage $\times f$	36	322.55	1.0024	0.4717
Lineage $\times f_{\text{linear}}$	18	313.34	0.9737	0.4910
Error	226	321.78		
Feeding on *Chrysopsis*				
f	2	52.19	6.4841	0.0046
f_{linear}	1	48.77	6.0594	0.0198
Lineage	15	27.80	4.2074	0.0000
Lineage $\times f$	30	8.05	1.2180	0.2132
Lineage $\times f_{\text{linear}}$	15	6.12	0.9261	0.5360
Error	199	6.61		
Feeding on *Iva*				
f	2	1397.83	10.7430	0.0002
f_{linear}	1	2738.54	21.0471	0.0001
Lineage	18	117.68	2.1345	0.0057
Lineage $\times f$	36	130.12	2.3600	0.0001
Lineage $\times f_{\text{linear}}$	18	178.96	3.2460	< 0.0001
Error	230	55.13		

RESULTS

No significant environmental changes were detected during the course of the experiment, based on nonsignificant f effects in both control populations (tested with one-way ANOVAs). Therefore, data from the control populations were not incorporated into the analyses of inbred lineages.

There was an overall effect of inbreeding depression, that is, decreased mean feeding scores, across all host species (significant f_{linear} effects; Table 1; Fig. 2). Inbreeding depression was quite severe on novel hosts, with a 54% and 86% drop in mean feeding on *Chrysopsis* and *Iva,* respectively, versus a 15.7% drop on the natural host *Ambrosia.* There was also, on average, a decline in the within-lineage variance of feeding scores on potential hosts (*Iva, Chrysopsis*) as well as the native host *Ambrosia* (significant f_{linear} effects; Table 2).

Although the slopes of individual lineages appear to differ (Fig. 3), statistically significant differences in the effects of inbreeding on the variance within lineages were not detected (non-significant lineage $\times f_{\text{linear}}$ effects; Table 2). There was significant variation among lineages in mean feeding scores on both potential hosts, presumably due to genetic variation in the base population (significant lineage effect, Table 1).

The variance within some lineages appears to increase at

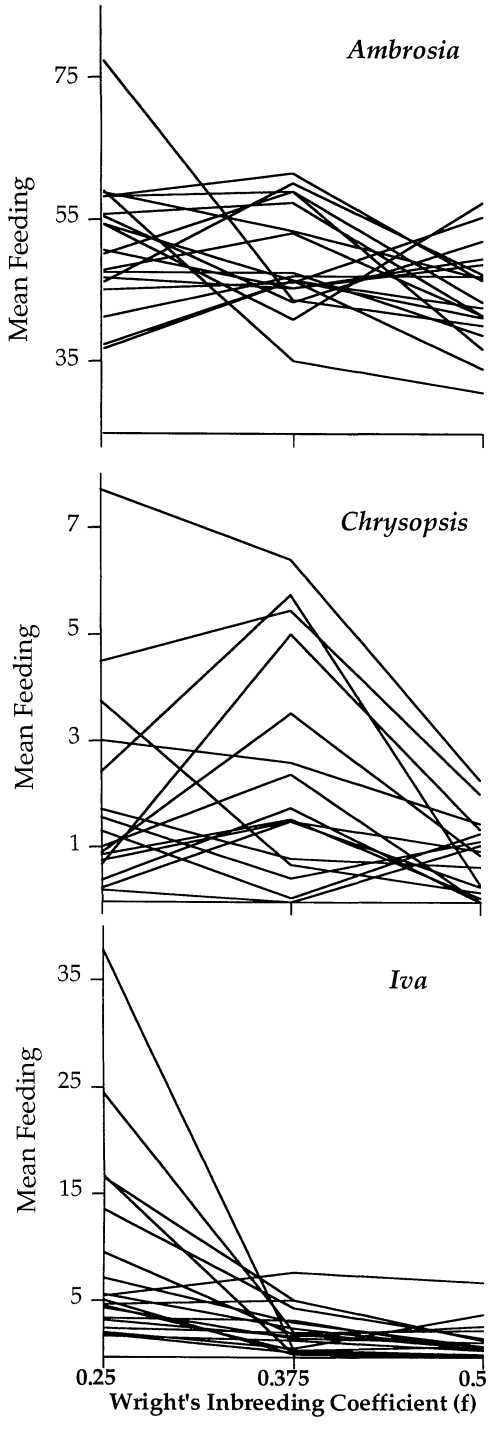

FIG. 2. Changes in mean feeding score on normal and potential hosts across levels of Wright's inbreeding coefficient (f).

lower levels of inbreeding ($f = 0.25$, Fig. 3). The inbreeding coefficient at the third generation of inbreeding ($f = 0.5$) tends to be higher than those in which VIPS might apply (Whitlock and Fowler 1996). Therefore, a randomization test was used to test for differences among lineages in within-lineage variance at $f = 0.25$. If the variance within some lineages significantly increased, the among-lineage variance component would be inflated relative to the simulated distribution, reflecting an increase in the tail of the distribution of within-lineage variances.

TABLE 2. Analysis of variance of the effects of inbreeding on the within-lineage variance in larval feeding score on each of three host plants. The linear components refer to the partitioning of the f effect and interaction term by means of orthogonal polynomials.

Source	df	MS	F-ratio	P-value
Feeding on *Ambrosia*				
f	2	1590342	2.6172	0.0869
f_{linear}	1	4182209	6.8826	0.0127
Lineage	18	480842	0.5510	0.9304
Lineage × f	36	607654	0.6963	0.9032
Lineage × f_{linear}	18	709178	0.8126	0.6846
Error	226	872729		
Feeding on *Chrysopsis*				
f	2	2213.40	7.7660	0.0019
f_{linear}	1	569.07	1.9967	0.1679
Lineage	15	507.37	1.7133	0.0507
Lineage × f	30	285.01	0.9624	0.5275
Lineage × f_{linear}	15	108.54	0.3665	0.9857
Error	199	296.14		
Feeding on *Iva*				
f	2	623376	3.6786	0.0352
f_{linear}	1	1149045	6.7807	0.0133
Lineage	18	156322	1.2251	0.2419
Lineage × f	36	169459	1.3280	0.1119
Lineage × f_{linear}	18	231234	1.8121	0.0249
Error	230	127604		

Some inbred lineages appear out in the tail of the distribution of phenotypic variance (Fig. 4). These apparent outliers were not the same lineages across the different host plants, based on nonsignificant correlation coefficients (Table 3). However, the distribution of phenotypic variances within experimental lineages does not appear to differ from a random expectation, given that the among-lineage variance was not significantly different from the random distribution of among-lineage variances.

DISCUSSION

The characters we measured are indices of the rate of feeding of a specialized phytophagous insect on its normal host and two novel plants, both of which are hosts of congeneric insects. Host-specific insects will starve rather than eat most plants other than their normal hosts and some closely related plants, so a feeding response is a necessary, although not sufficient, condition for the evolution of new host associations. Both previous work on *Ophraella communa* (Futuyma et al. 1993) and the among-lineage variance reported in this study indicate that genetic variation exists in feeding response to all three plants. Moreover, the lack of significant among-lineage correlations in the responses to the several plants suggests that the variation is not simply in a generalized variable such as "vigor" or feeding rate as such, but rather that the feeding responses to the different plants are to some degree genetically independent; that is, we have measured three characters rather than one. This conclusion is also suggested by evidence that inbreeding depression was more pronounced in feeding rates on the novel plants than on the normal host. The inbreeding depression suggests, inciden-

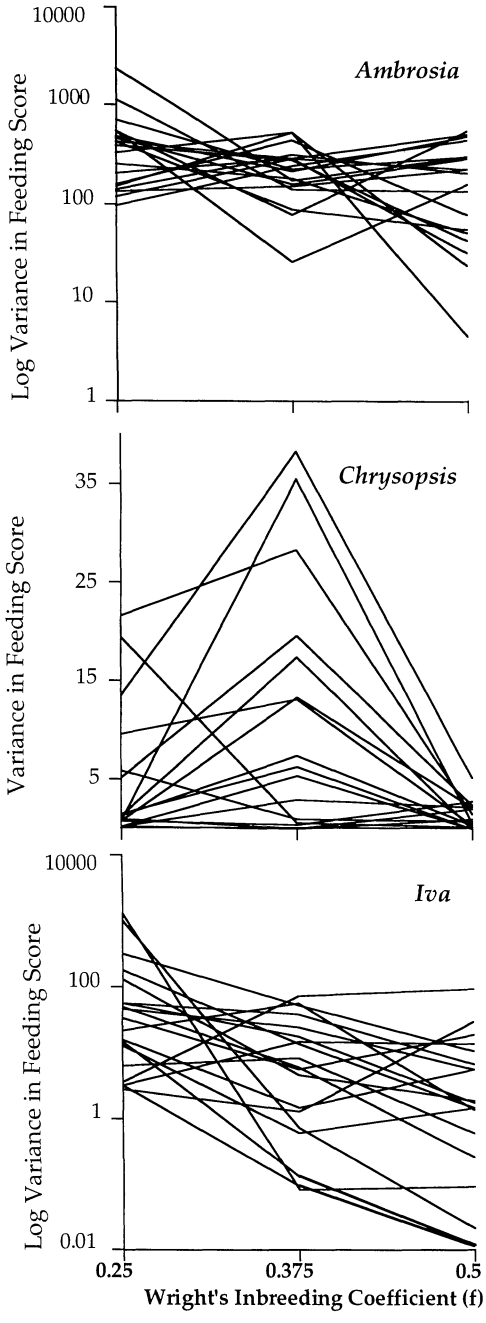

FIG. 3. Changes in within-lineage variance in feeding score on normal and potential hosts across levels of Wright's inbreeding coefficient (f).

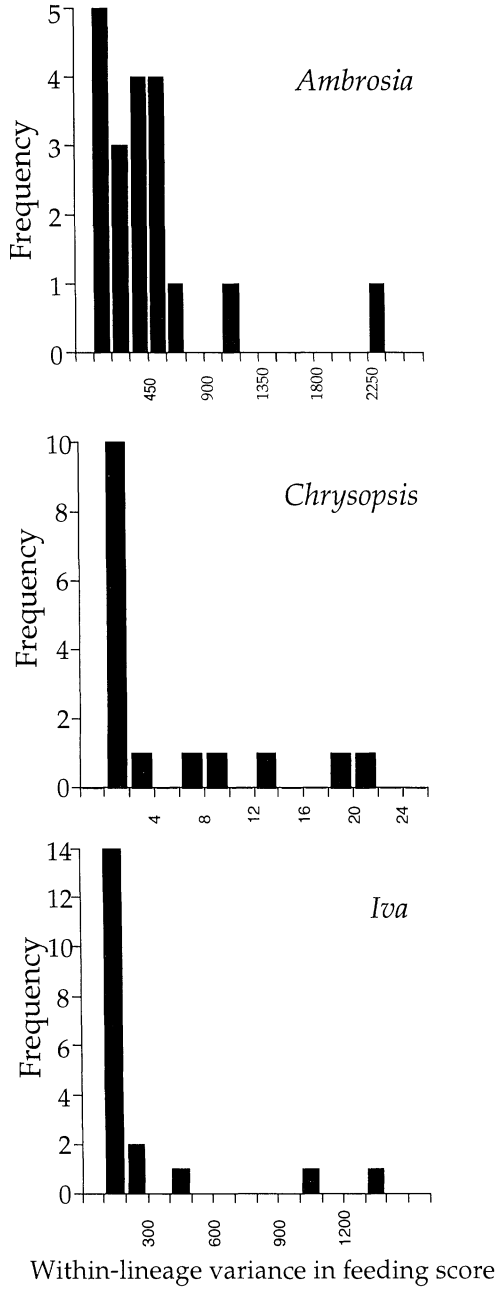

FIG. 4. Frequency distribution of within-lineage variance in feeding scores on normal and potential hosts at $f = 0.25$.

tally, that partially or completely recessive alleles contribute substantially to the genetic variance.

The recent emergence of controversy about Wright's (1932) shifting balance theory and theories of speciation based on founder events has focused interest on the dynamics of genetic and phenotypic variance within bottlenecked or inbred populations (Wade 1992; Whitlock et al. 1995). The early literature of quantitative genetics provides many instances in which the environmental variance (V_E) of characters is greater in inbred lines than in outbred, heterozygous genotypes,

TABLE 3. Product-moment correlations of lineage means and within-lineage variances in feeding scores between hosts at each level of inbreeding (df = 11, $P > 0.13$ for each test). *Amb, Ambrosia*; *Chr, Chrysopsis*.

	Means			Variances		
	$f = 0.25$	$f = 0.375$	$f = 0.5$	$f = 0.25$	$f = 0.375$	$f = 0.5$
Chr/Amb	0.35	−0.09	−0.05	0.29	0.12	0.26
Iva/Amb	0.06	0.00	−0.36	−0.13	−0.44	0.22
Iva/Chr	−0.11	−0.09	0.18	−0.17	−0.29	−0.10

such as the F_1 offspring of crosses between inbred lines (Wright 1977). Fowler and Whitlock (1999) have reviewed much of this literature and found that this effect is more pronounced for life-history traits, in general, than for morphological characters. In recent experiments designed explicitly to document the effect of inbreeding on within-line phenotypic variance, several authors have reported increases in additive genetic variance in bottlenecked populations, in morphological, behavioral, and life-history characters (Bryant et al. 1986; Fernández et al. 1995; Meffert 1995; Bryant and Meffert 1996; Wade et al. 1996), and others have described increases in phenotypic variance without having determined the genetic component (Pray and Goodnight 1997). In contrast, the genetic variance for some characters decreases with inbreeding in conformity with the additive model (e.g., Brakefield and Saccheri 1994; Wade et al. 1996; Whitlock and Fowler, unpubl. ms.).

Although the phenotypic variance within a few of our experimental lineages appeared to increase at moderate levels of inbreeding, we could not demonstrate any increase statistically even though the replication within lines equaled and the number of lines exceeded that in some experiments in which such increases have been discerned (Pray and Goodnight 1997). Although the error variance of behavioral traits tends to be large (Meffert 1995) and interaction terms carry higher standard errors than main effects (Wade 1992), a power analysis indicated that the probability of detecting a lineage $\times f$ effect at the $\alpha = 0.05$ level ranged from 0.71 (for *Ambrosia*) to 0.98 (for *Iva*).

Thus, at least in this experiment, the three characters (feeding rates) we measured seem not to be among those that might evolve by peak shifts in bottlenecked populations. This conclusion conforms with our current understanding of the actual history of evolutionary change in these features. As described above, one of the novel plants in this experiment, *Chrysopsis villosa,* is the host of a close relative (*Ophraella bilineata*) of our experimental organism (*O. communa*), and phylogenetic evidence strongly implies that *O. communa* retains the plesiomorphic host association. The evolutionary shift to *Chrysopsis*-feeding in *O. bilineata* appears not to have been associated with a substantial reduction in population size because sequence variation in the mitochondrial DNA of *O. bilineata* provides no indication of a bottleneck in this species' history (Knowles and Futuyma, unpubl. ms.). Evidence from both population history and the experiment reported here provides no reason to reject the hypothesis that the behavioral response to a novel potential host plant has a largely additive genetic basis, and thus would respond to selection faster in large than in small populations.

Much of the literature on the effects of inbreeding is concerned with inbreeding depression. As such, it is largely focused on life-history traits and other characters (e.g., size) that are generally considered correlates of fitness. In natural populations, fitness is often strongly dependent on particular morphological, physiological, or behavioral characters such as photoperiod responses or, in this instance, the feeding responses of host-specific insects. For only a few such characters, such as the critical photoperiod for diapause in mosquitoes (Hard et al. 1993), do we know enough about the genetic architecture to evaluate the role that epistasis and population structure may play in their evolution (Moreno 1994; Whitlock et al. 1995). Our conclusion that feeding responses in this population of this species of leaf beetle are unlikely to evolve by peak shifts cannot yet be generalized to other species or to other ecologically important characters. Only a diversity of studies will provide a general conclusion on the importance of peak shifts.

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