Biochemical Preadaptations, Founder Events, and the Evolution of Resistance in Arthropods

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ABSTRACT We conducted literature-based comparative analyses of pesticide resistance evolution to evaluate 2 aspects of microevolutionary response to strong novel selection pressures. First, it has been proposed that herbivorous arthropods are preadapted to evolve resistance by a system of detoxifying enzymes the evolution of which was elaborated in response to plant defensive chemicals. To test this hypothesis, we note that arthropods that feed on plant vascular tissues (phloem and xylem, which are less strongly chemically defended than other tissues) have lower levels of detoxifying enzyme activities than species that chew or feed on cell contents, and might therefore be expected to be less strongly preadapted to pesticides. The record of pesticide resistance evolution in 615 arthropod pests of North American agriculture is consistent with the biochemical preadaptation hypothesis; phloem- and xylem-feeding species have a significantly diminished ability to evolve resistance when compared with either chewing or cell content-feeding species. The same result is obtained in an analysis restricted to species within the order Homoptera. We caution, however, that feeding behavior is confounded with taxonomy in these analyses; thus, strong inferences of a causal relationship between feeding mode and resistance evolution would be premature. Second, conventional theory suggests that population bottlenecks that occur during the initiation of geographically isolated populations can have profound effects on the genetic structure of populations, including particularly the loss of allelic diversity. Arthropods that have been introduced to North America, and thus have undergone founder events, might therefore be expected to be depauperate for key resistance-conferring genetic variants. Our analyses find no support for this founder event hypothesis; native and introduced species do not differ significantly in resistance evolution. We evaluate the importance of possibly confounding variables in the interpretation of these results and emphasize the need to integrate experimental results with these comparative broad-scale results.

KEY WORDS detoxification enzymes, population bottleneck, founder event, colonization, herbivory, pesticide resistance

THE WIDESPREAD INTRODUCTION of synthetic organic insecticides into agricultural production inadvertently has initiated a massive experiment in microevolution. The experiment has been conducted on a global scale, involved thousands of arthropod species, and continued for nearly a half-century. Furthermore, data that document the course of the experiment have been gathered by a community of economic entomologists concerned primarily with the impact of pesticide resistance on pest management and our ability to produce food and fiber (Georghiou and Lagunes-Tejeda 1991).

Only rarely, however, has our knowledge of resistance evolution in arthropods been used to address basic issues in evolutionary ecology (McKenzie and Batterham 1994). Also rare are empirical studies that attempt to derive broad insights that will be useful in predicting the trajectory of resistance evolution ("resistance risk assessment") (Keiding 1986). Here we use a comparative approach to examine the effects of biochemical preadaptations and founder events on the ability of populations to evolve in response to strong selection pressure.

Biochemical Preadaptations. The rapid and pervasive evolution of pesticide resistance in arthropod pests of agriculture led to a search for general explanations of the prodigious capacity of herbivorous arthropods to respond to selection by toxins. A key hypothesis, first proposed by Gordon (1961), is that pesticide resistance in herbivorous insects is based upon modifications of enzyme systems previously used in the metabolic detoxification of plant defensive compounds. Subsequent biochemical studies have shown that the enzyme systems responsible for the metabolism of insecticides and plant defensive compounds are indeed one and the same (Mullin 1985, 1986; Brattsten

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1988; Soderlund and Bloomquist 1990; Mullin and Scott 1992). One dramatic demonstration of this overlap of biochemical function is the observation that enzymes whose activity is induced by feeding on toxic plants may also confer decreased susceptibility to insecticides (Yu 1986, Brattsten 1988). Furthermore, Gould et al. (1982) demonstrated that experimental selection of a spider mite population for survival on a toxic host plant produced elevated baseline tolerance to some insecticides. Thus, insects may have been preadapted to the novel selective pressures exerted by synthetic insecticides by a system of detoxifying enzymes whose evolution was elaborated in response to the biochemical diversity of plant defensive chemicals.

Three corollary hypotheses, each of which could potentially serve as the basis for a comparative test, can be erected from Gordon's (1961) original preadaptation hypothesis. First, Croft and Morse (1979) and Croft and Strickler (1983) proposed that insect predators and parasitoids, which experience reduced direct exposure to plant toxins, should have lower levels of enzyme activity and as a result less capacity to evolve pesticide resistance. The development and evaluation of this hypothesis has been reviewed by Croft (1990) and Tabashnik and Johnson (1996). Comparative biochemical studies have documented some apparently general differences between herbivores and natural enemies (Mullin and Croft 1984, Mullin 1985), and natural enemies do have a less extensive documented record of resistance evolution. Nevertheless, it is difficult to infer strong support for the preadaptation hypothesis from these observations. There are other compelling reasons why natural enemies might not evolve resistance as readily as herbivores (Tabashnik and Johnson 1996). In particular, reproduction by natural enemies is dependent on host–prey populations that may be eliminated by pesticide applications, thereby reducing the advantages normally associated with a pesticide-resistant genotype. There is also probably a bias in the documentation of cases of resistance evolution: resistance in natural enemies may often be inconspicuous and fail to be detected, whereas resistance in herbivores often causes control failures, with the potential for attendant crop losses that attract the attention of researchers. Thus, a comparison of natural enemies and herbivores does not provide a strong test of the importance of biochemical preadaptation.

A second corollary of the preadaptation hypothesis is that generalist herbivores, which may have greater enzyme activities than specialists (Krieger et al. 1971, Mullin and Croft 1984, Mullin 1985), may have greater abilities to evolve pesticide resistance. We are unaware of any attempts to assess this idea.

We propose a third corollary of the preadaptation hypothesis. Our hypothesis is built on the comparative biochemical work of Mullin (1985, 1986), who has shown that herbivores with chew-

ing mouthparts or herbivores that use sucking mouthparts to feed successively on the contents of different plant cells have greater activities of some detoxifying enzymes (cytochrome P-450-dependent mixed-function oxidase, trans-epoxide hydrolase) than do herbivores that suck on plant phloem. This difference is presumably caused by the greater exposure of chewing or cell-content feeding herbivores to secondary plant compounds. Work on the within-plant distribution of plant defensive compounds has shown that, although some classes of defensive compounds, including alkaloids, phenolics, and cardenolides, may be present in phloem and xylem, they are generally found at concentrations lower than those found in other defended tissues (Raven 1983, Mullin 1986). Many other plant toxins are absent from vascular tissues because of low solubility or the potential for autotoxicity (McKey 1979, Raven 1983, Mullin 1986, Berenbaum 1991). Digestibility-reducing defensive compounds also are largely absent from vascular tissues because nutrients in the phloem and xylem do not require substantial digestion (Raven 1983). The primary storage site for defensive chemicals are intracytoplasmic vacuoles, which are often found in epidermal or parenchyma cells (McKey 1979, Wiermann 1981, Seigler 1991) and which are absent from the phloem and xylem (Raven 1983). Furthermore, the piercing mouthparts of insects that feed on vascular tissue do not generally produce sufficient mechanical damage in plant tissues to release spatially sequestered enzymes that activate defensive chemicals by releasing them from chemical complexes (Raven 1983, Seigler 1991). Thus, vascular tissues should not be considered completely free of defense, but they do appear to be less substantially defended chemically. We therefore propose that arthropods feeding on plant vascular tissues (phloem, xylem) should, under the preadaptation hypothesis, exhibit reduced capacities to evolve pesticide resistance.

We tested the preadaptation hypothesis by assessing whether phloem- and xylem-feeding insects have reduced abilities to evolve pesticide resistance in comparison with species that chew or feed on cell contents. This comparison is more direct than the comparison of herbivores with natural enemies discussed above, because we are comparing species with similar ecology (all herbivores) and with similar capabilities of being pests and thus attracting the attention of researchers who document resistance evolution. The comparison is far from ideal, however, and in the discussion section we address other factors that may confound the comparison of herbivores with different feeding modes.

Founder Events. Evolution at the population level is a 2-stage process. First, genetic variation is produced by mutation and recombination; second, the relative frequencies of different genetic forms change under the influence of drift, migration, and natural selection. Although there is general accep-

tance of this 2-stage model, a spectrum of opinion exists regarding the relative importance of the 2 stages in determining the overall rate of evolution. The boundaries of this spectrum of opinion are represented by the extreme neutralist view that the rate of mutation is the sole determinant of the rate of evolution, and by the extreme neo-Darwinian view that it is instead natural selection operating on unlimited genetic variation that is the sole determinant of the rate of evolution (Endler 1986, Nei 1987).

Resolving the importance of genetic constraints to evolution is of considerable academic and practical significance to the nascent field of insecticide resistance management. Although some verbal models of resistance evolution recognize the role of mutation in generating resistance genotypes (Comins 1977, 1979; Sutherst and Comins 1979; Whitten and McKenzie 1982; Brattsten et al. 1986), nearly all quantitative models of resistance evolution assume that resistance alleles are present in arthropod populations at some low equilibrium frequency before the advent of pesticide selection (reviewed by Tabashnik 1990). The strong influence of these models has resulted in widespread acceptance of the extreme neo-Darwinian viewpoint of unlimited genetic variation (but see Caprio and Tabashnik 1992, Raymond et al. 1992, Raymond and Marquine 1994). Resistance development has therefore generally been viewed as a deterministic process, with the resulting expectation that resistance development can be predicted and that these predictions can be used to allocate resistance management efforts (Dover and Croft 1986, Keiding 1986).

Experimental investigations of genetic constraints to resistance evolution have not been conducted and would be limited by the ability to detect extremely low-frequency alleles. Here we attempt to provide an insight into the occurrence of genetic constraints by comparing 2 groups of arthropod pests differing in their likelihood to exhibit such constraints. We compare species native to North America with those introduced to North America from another biogeographic region.

The initiation of geographically isolated populations by a small number of individuals can have profound effects on the genetic structure of populations. Initial theoretical analyses showed that genetic drift operating during founder events depresses allelic diversity, average heterozygosity, and additive genetic variance (James 1971, Nei et al. 1975, Lande 1980, Maruyama and Fuerst 1985). These theories were supported by electrophoretic studies of protein polymorphism which, with few exceptions, revealed decreased variability in founder populations compared with their source populations (Schwaegerle and Schaal 1979, Tabachnick and Powell 1979, Heuttel et al. 1980, Bryant et al. 1981, Harrison et al. 1983, Berlocher 1984, Baker and Moeed 1987, McPheron et al. 1988, Sheppard 1988, St. Louis and Barlow 1988, McPheron 1990).

The influence of a founder event on average heterozygosity and additive genetic variance is dependent on the severity and duration of the associated population bottleneck (Nei et al. 1975, Lande 1980), which are generally not known for introductions of pest arthropods. However, population bottlenecks of widely varying severity are expected to remove very low frequency alleles from founder populations, including potential resistance-conferring alleles in populations not previously exposed to pesticides. We therefore propose to test the null hypothesis of no difference between the ability of native and introduced species to evolve resistance, and suggest the alternate hypothesis that introduced species have decreased abilities to develop resistance because of the increased incidence of genetic constraints.

Materials and Methods

Data Base Construction. We analyzed a data base (available from J.A.R.) that combines biological information with the history of pesticide resistance evolution for 685 arthropod pests of agriculture in North America. For each species, the data base has fields for (1) scientific and common name, (2) status as native versus introduced to North America, (3) the number of generations per year, (4) an index of documentation effort, (5) taxonomic order, (6) feeding mode, and (7) an index of pesticide resistance evolution. We now explain each of these data fields.

A list of 671 major insect and mite pests of agriculture in the United States and Canada was obtained from Davidson and Lyon (1987). This list was supplemented with 14 additional pests of agriculture reported to have evolved resistance by Georghiou (1981) and Georghiou and Lagunes-Tejeda (1991). Pests of ornamental shrubs, rangelands, and forest trees were included only if they were described by Davidson and Lyon (1987) as being subject to pesticide control.

Species were categorized as native or introduced according to the following 5 sources: (1) the primary reference was NAIAD, the North American Introduced Arthropod Database, an unpublished data base compiled by R. I. Sailer and the United States Department of Agriculture (see Sailer [1983], Knutson et al. [1990], and Whitehead and Wheeler [1990] for a full description of NAIAD); (2) BIOCAT, an unpublished data base compiled by the Commonwealth Agricultural Bureau International; (3) Clausen (1978); (4) Furniss and Carolin (1977); and (5) Davidson and Lyon (1987). Eight species introduced after 1945, when the use of synthetic organic pesticides began in North America, were excluded from the analysis.

Species with intermediate numbers of generations per year exhibit the greatest ability to evolve resistance (Rosenheim and Tabashnik 1990, 1991, 1993); we therefore included the number of generations per year in the data base to control statis-

tically for its influence. Many literature sources contributed estimates of generations per year; complete citations are available from J.A.R. When a range of values associated with latitude was cited, the mean was used. We estimated the number of generations per year for 58 species for which no references were available by taking the mean value reported for congeners. This approximation was not applied to genera demonstrating large heterogeneity in generations per year. For 20 species in 2 families for which estimates were particularly difficult to obtain (Aphididae and Tetranychidae), we used average values for confamilial species whenever values for congener were not available. This left 51 species (7.7% of the taxonomically defined species present in North America by 1945) for which no estimate of generations per year were available, and which were therefore excluded from the analysis.

Our index of the ability of a species to evolve resistance was based on cases of resistance reported in the literature (see below). Such a literature-based index is likely to be influenced both by the actual history of resistance development of a pest and by the degree to which resistance has been formally documented by researchers. We therefore generated an index to measure the intensity of general research effort devoted to each pest species. This index of documentation effort, which is likely to reflect the overall severity of each pest species, was calculated by summing the number of times each species was cited in the Review of Applied Entomology, 1950–1953 (Hall, 1950–1953). Only field studies of North American populations or laboratory studies published in North American journals were tallied. We used a time period (1950–1953) before the major onset of resistance to minimize the degree to which a species' ability to evolve resistance would influence its documentation effort score. Eighteen species not clearly defined taxonomically as of 1950 were excluded.

Taxonomic order and feeding mode (chewing, sucking on cell contents, sucking on phloem or xylem sap) were coded following Borror et al. (1989), Carver et al. (1991), and Sorensen et al. (1995). All Homoptera were classified as phloem or xylem feeders except for the typhlocybine Cicadellidae, which feed primarily on parenchyma (Carver et al. 1991, Sorensen et al. 1995). This broad categorization undoubtedly includes some inaccuracies; for example, some aphids feed in part on mesophyll tissues (Raven 1983). However, the detailed histological and behavioral studies that would be necessary to provide a more finely dissected index of feeding mode are not available for most species in the data base.

Finally, an index of the ability of each species to evolve resistance was measured as the number of synthetic organic insecticide–acaricide classes to which some North American populations had been reported as resistant. Pesticides were grouped into the following 6 classes: (1) DDT and analogues,

(2) benzene hexachloride and cyclodienes, (3) organophosphates, (4) carbamates, (5) pyrethroids, and (6) miscellaneous compounds, including nitrophenols, chlordimeform, propargite, and so on, following Georghiou and Lagunes-Tejeda (1991). Our analysis does not require that resistances to different classes of pesticides be caused by independent mechanisms; observations of cross-resistances that extend between pesticide classes (Soderlund & Bloomquist 1990) suggest that our resistance score may be a nonlinear measure of the number of different resistance mechanisms. Thus, in all statistical analyses, resistance score was treated as an ordinal variable.

Statistical Analysis. Data were analyzed with logistic regression for an ordinal response variable, implemented under JMP (SAS Institute, 1994) and BMDP (Dixon 1990). This analysis allowed us to include, within a single statistical model, independent variables that were nominal, ordinal, and continuous without the assumptions of normality and homoscedasticity required for linear regression models. Both stepwise addition of variables and the model-building strategy advocated by Hosmer and Lemeshow (1989) yielded the same final model.

We treated each pest species as an independent datum because, unlike most or all traits previously studied using the comparative approach, pesticide resistance is of recent historical origin. Therefore, the presence of resistance in related taxa could not result from inheritance from a common ancestor. Closely related arthropod pest species often inhabit different environments (that is, crops) and experience different pesticide selection regimes. Even different populations of a single pest species may commonly evolve resistance to a given pesticide via different biochemical mechanisms (Wood and Bishop 1981). However, correlations among the independent variables tested, and potential correlations between independent variables and other, unmeasured variables, make determinations of causality difficult in some cases, as we discuss below.

To graphically display the effects of key variables while statistically controlling for the effects of all other significant variables, we present mean residual values. Residuals were obtained as the difference between the observed resistance index score and that predicted by the logistic model containing all of the statistically significant independent variables except for the variable of interest.

Results

Summary statistics from the data base show that the arthropod groups whose ability to evolve resistance we wished to compare differ in terms of the important covariates (Table 1). Specifically, introduced species have higher scores for mean documentation effort than native species, and phloem and xylem feeders have higher mean numbers of

Table 1. Mean documentation effort index and number of generations per year for arthropod pest species grouped by independent variables examined in the main analysis

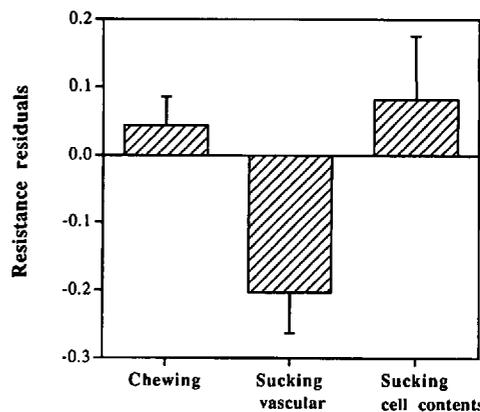| Species group	No. species	Documentation effort	No. generations/yr
Source			
Native	468	2.12 ± 0.29	3.84 ± 0.30
Introduced	140	5.29 ± 0.85	4.81 ± 0.55
Mode of feeding			
Chewing	392	2.42 ± 0.35	1.92 ± 0.08
Sucking (vascular)	126	3.52 ± 0.64	9.83 ± 1.01
Sucking (cell contents)	97	3.49 ± 0.95	5.44 ± 0.52
Order			
Orthoptera	26	1.96 ± 0.76	1.12 ± 0.08
Dermaptera	1	3.00	1.50
Thysanoptera	12	2.92 ± 1.36	7.42 ± 0.81
Hemiptera	31	2.13 ± 0.68	2.63 ± 0.31
Homoptera	150	3.15 ± 0.55	8.64 ± 0.88
Coleoptera	161	1.96 ± 0.50	1.46 ± 0.11
Lepidoptera	144	3.56 ± 0.76	2.34 ± 0.12
Diptera	40	1.48 ± 0.33	2.92 ± 0.42
Hymenoptera	20	0.45 ± 0.26	1.63 ± 0.23
Acarina	30	6.97 ± 2.84	10.00 ± 1.16

Fig. 1. Mean ± SE resistance score residual for arthropods with different modes of feeding. Residuals were calculated as difference between observed resistance score and that predicted by the logistic regression model, including terms for generations per year (generations per year)^2, and documentation effort score.

generations per year than do species that feed by chewing or by sucking on cell contents. Thus, to test the hypotheses that resistance evolution is influenced by biochemical preadaptations and founder events, we need to build a multivariate statistical model that allows us to assess the roles of these independent variables while statistically controlling for the influences of documentation effort and generation number.

A logistic regression model fitted to the data set indicates that both covariates (generations per year, documentation effort) are highly significant (Table 2), with a curvilinear effect for generations per year, as previously reported (Rosenheim and Tabashnik 1990, 1991, 1993). After controlling for the influences of these covariates, species feeding mode is highly significant; species feeding on phloem or xylem have a substantially smaller historical record of pesticide resistance evolution than do species that feed either by chewing or by sucking

on cell contents (Fig. 1). Chewers and cell content feeders have very similar mean residual values (Fig. 1). None of the possible 2-way interaction terms involving feeding mode were significant ($P > 0.4$). These results are as predicted by the biochemical preadaptation hypothesis; those species with less exposure over evolutionary time to defensive compounds of plants appear to have a reduced ability to evolve pesticide resistance compared with species feeding on more highly chemically defended plant structures.

What appears to be the same effect is also evident in the significant effect of taxonomic order (Table 2). All sap-feeding insects are found in the order Homoptera, which contains 84% (126/150) sap feeders and 16% (24/150) cell content feeders. Taxonomic order is too highly correlated with feeding mode for both variables to be considered within the same statistical model, but an inspection of mean residuals for each taxonomic order reveals that the Homoptera has a lower mean residual val-

Table 2. Polychotomous logistic regression of factors influencing evolution of pesticide resistance

Variable	Coefficient, mean ± SE	χ^2	df	P
Terms in model				
Generations per year	0.32 ± 0.06	26.6	1	<0.0001
(Generations per year)^2	−0.010 ± 0.002	22.1	1	<0.0001
Documentation effort	0.081 ± 0.012	51.2	1	<0.0001
Feeding mode		99.7	2	<0.0001
Chewing	(0.41)^a	—	—	—
Vascular	−0.87 ± 0.25	—	1	—
Cell content	0.46 ± 0.19	—	1	—
Term not in model				
Introduced vs native	—	2.1	1	0.14

Model structure and coefficients were very similar when the variable "taxonomic order" was substituted for "feeding mode"; the effect of taxonomic order was significant ($\chi^2 = 112.0$, df = 9, $P < 0.0001$).

^{a} Two dummy variables are used to code the 3 feeding mode categories; the analysis generates coefficients for the 2 dummy variables only (here, vascular feeders and cell content feeders). Included is the mean value of the coefficient for chewing species (the 3rd category) for descriptive purposes only.
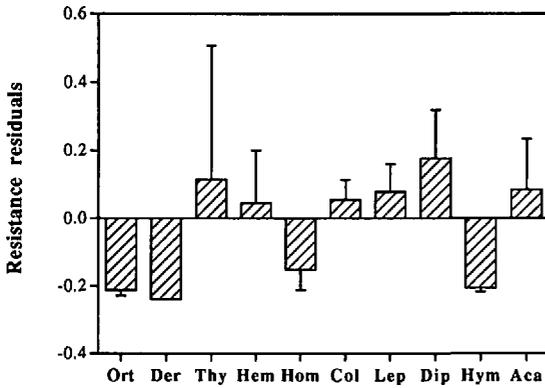
Fig. 2. Mean ± SE resistance score residual for arthropods in different taxonomic orders. Ort, Orthoptera; Der, Dermaptera, Thy, Thysanoptera; Hem, Hemiptera; Hom, Homoptera; Col, Coleoptera; Lep, Lepidoptera; Dip, Diptera; Hym, Hymenoptera; Aca, Acarina. Residuals were calculated as difference between observed resistance score and that predicted by the logistic regression model, including terms for generations per year (generations per year)^2, and documentation effort score.

Table 3. Polychotomous logistic regression of factors influencing the evolution of pesticide resistance: order Homoptera only (mean ± SE)

Terms in model	Coefficient	χ^2	df	P
Generations per year	0.32 ± 0.13	6.3	1	0.012
(Generations per year)^2	−0.011 ± 0.005	6.7	1	0.010
Documentation effort	0.087 ± 0.028	7.4	1	0.007
Feeding mode	−0.72 ± 0.34	4.3	1	0.039

ue than the major orders of cell content feeders (Hemiptera and Acarina) or the major orders of chewing species (Coleoptera and Lepidoptera) (Fig. 2). Large mean negative residuals for other taxonomic orders may not be biologically meaningful because these orders are represented by small sample sizes (Dermaptera) or comprise primarily species with low documentation effort scores (Hymenoptera; Table 1). The mean negative residual for the Orthoptera may simply reflect the inclusion of many species of rangeland grasshoppers (19 of 26 species = 73.1%), which may experience less selection pressure from insecticides than do most pests of cultivated crops.
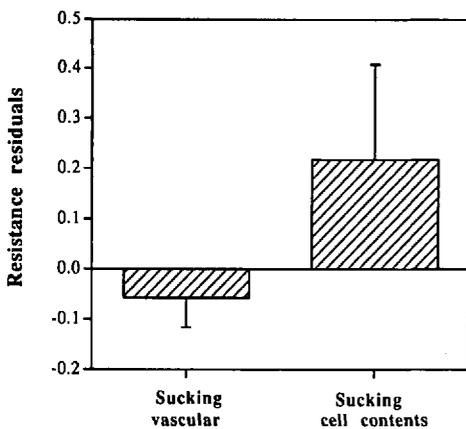
Feeding mode is seriously confounded with taxonomy in our primary analysis; all of the phloem and xylem feeders are in the order Homoptera. Thus, our observation of a highly significant effect for the "feeding mode" variable could reflect essentially any characteristic of the order Homoptera, and not just biochemical differences associated with their sap-feeding habit. We therefore conducted a secondary analysis of resistance evolution among only the members of the Homoptera to compare sap feeders with cell content feeders (the typhlocybine Homoptera). Despite the reduced sample sizes, the coefficients of the statistical model are very similar to those observed in the full data base analysis, and the same significant variables are identified (Table 3). In particular, vascular tissue feeders are still associated with a significantly reduced ability to evolve resistance compared with cell content feeders (Fig. 3). This secondary analysis decreases the severity of the taxonomic confound by demonstrating that the difference between feeding modes is consistent even within a more narrowly defined taxon. The typhlocybine Homoptera share many traits with the remaining Homoptera; thus, differences between these groups of homopteran species are perhaps less likely to reflect differences unrelated to feed-
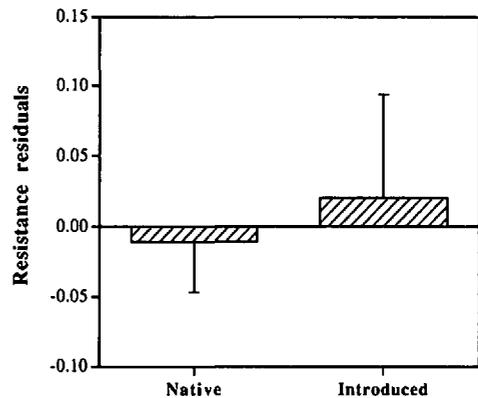

Fig. 3. Mean ± SE resistance score residual for Homoptera that feed on vascular tissues versus those that feed on cell contents. Residuals were calculated as difference between observed resistance score and that predicted by the logistic regression model, including terms for generations per year (generations per year)^2, and documentation effort score.

Fig. 4. Mean ± SE resistance score residual for arthropods native and introduced to North America. Residuals were calculated as difference between observed resistance score and that predicted by the logistic regression model, including terms for generations per year (generations per year)^2, documentation effort score, and taxonomic order. Similar mean residuals were obtained when the logistic model included the variable for feeding mode instead of taxonomic order.

ing mode than are differences between the Homoptera and the other insect orders. However, as discussed below, this secondary analysis does not fully eliminate the confounding effect of taxonomy (the cell content feeders within the Homoptera are still found within a single taxonomically distinct group); thus, taxonomic correlates of feeding mode must still be considered when formulating possible interpretations of these results.

Contrary to the founder effect hypothesis, native and introduced species do not differ significantly in their history of resistance evolution (Table 2). The mean residuals show that the nonsignificant trend in the data is actually for introduced species to have higher resistance scores rather than the depressed scores that would be expected were these species depauperate for the key genetic variation needed to evolve resistance (Fig. 4).

Discussion

Our comparative analysis of the history of pesticide resistance evolution in arthropod pests of North American agriculture has revealed patterns that are consistent with the predictions of the biochemical preadaptation hypothesis (phloem and xylem sap feeders have depressed resistance scores), but inconsistent with the founder event hypothesis (introduced species do not differ from native species). Here we discuss possible bases for these results and evaluate the potential for confounding effects. We emphasize that, as is true for correlative comparative analyses in general, caution must be exercised when attempting to infer causal relationships.

Biochemical Preadaptations. The biochemical preadaptation hypothesis states that species with an evolutionary history of feeding on heavily chemically defended plant structures should have elevated levels of enzymes that detoxify defensive chemicals, and therefore an enhanced ability to evolve resistance to synthetic toxins. Our finding of apparently diminished ability to evolve resistance among herbivores that feed on poorly defended phloem or xylem sap is thus consistent with this hypothesis. The approximate equivalence of resistance evolution among herbivores that feed by chewing versus by sucking on cell contents is also as expected under the preadaptation hypothesis; both chewers and cell content feeders encounter defensive chemicals in their most important storage location (intracellular vacuoles). Furthermore, comparative biochemical data suggest that leaf chewers and cell content feeders have similar ranges of detoxification enzyme activities (Mullin 1985).

Why might species with initially low detoxifying enzyme activities be less able to evolve resistance? The answer to this question may appear to be obvious at first, but in fact may be somewhat more complicated. Initial activity levels of detoxifying enzymes may influence the initial median toler-

ance to pesticides. As noted by Tabashnik and Johnson (1996), if resistance is defined as any heritable increase in the ability of a population to survive an exposure to a toxin, then the initial tolerance may have little influence on subsequent resistance evolution. However, our data base reflects the published results of insecticide bioassays performed by agricultural entomologists; many if not most of these studies were motivated by control failures in the field. This means that it is not just any level of resistance, but rather only resistance levels sufficient to produce high levels of survival under field conditions that are likely to be represented in our data base. If our data base records primarily those species that have attained a tolerance level greater than field dosages, then species with initially high levels of tolerance may be expected to be represented more often than species with initially low levels of tolerance. Species with initially high tolerance levels may be able to reach the resistance criterion through modest changes in target site sensitivity, pesticide detoxification, or any other physiological change. Species with initially low levels of tolerance are expected to require more dramatic changes, which are presumably produced by only a subset of the genetic modifications that generate field survival for species with higher initial tolerances.

The explanation of why our resistance documentation scores should be higher for species with higher initial tolerances rests on the assumption that field application rates of pesticides are not adjusted to provide a constant "margin" between field rates and the initial tolerance level of the pest population. We think that this is a reasonable assumption. Pesticide application rates are usually determined by a combination of economics and the tolerances of a few key pests in each agroecosystem. All the other arthropods present in the agroecosystem (which represent the vast majority of the species in our data base) will experience the same pesticide application rate, regardless of their initial tolerances.

Feeding mode is unavoidably confounded with taxonomy in our analyses. This raises the possibility that what we are interpreting as an effect of feeding behavior is actually caused by some other difference between the vascular tissue feeders in the Homoptera and other taxa. The difference between species that feed on sap and those that feed on cell contents is still observed within the order Homoptera, making it less likely (but not impossible) that other unmeasured variables associated with the sap-feeding taxa are in fact responsible for the impoverished history of resistance evolution.

It is also important to note that even if the reduced resistance scores associated with sap-feeding species are indeed caused by their feeding mode, this cannot be definitively linked to biochemical specializations. Sap feeders are likely to experience different levels of exposure to systemic

versus nonsystemic pesticides when compared with other arthropods. Furthermore, the sap-feeding habit may tend to evolve in association with other behavioral or physiological traits—for instance, the level of mobility while feeding on the plant, microhabitat selection (and therefore exposure to pesticides), or nutritional ecology. Feeding mode may influence many aspects of the biology of a species in addition to simply the characteristic levels of detoxifying enzyme activities!

Thus, although our observations are consistent with our prior hypothesis constructed from considerations of comparative insect biochemistry, our results should not be considered definitive. As with most comparative tests, our results will be most valuable when combined with other forms of experimental and observational evidence.

Founder Events. The founder event hypothesis states that introduced arthropod species may lose genetic variation during the population bottleneck that occurs with colonization, and should therefore be less able to evolve resistance. Our analysis has produced no support for this hypothesis. Introduced species do not display a diminished record of resistance evolution.

How can we explain the apparent equivalence of native and introduced species? There are a number of possibilities. First, our test may be methodologically flawed because of the presence of important confounding variables. We may not have treated successfully those confounding variables that were identified (generations per year, documentation effort), or we may have failed to identify other important variables. Specifically, we cannot exclude the possibility that introduced species differ from native species in some way that augments their ability to evolve resistance, thereby offsetting the putative handicap imposed by the loss of important genetic variation. Although it is tempting to suggest that introduced or "invading" species differ from "noninvading" species in many respects, attempts to find traits that characterize invading arthropod species have largely failed (Lawton and Brown 1986, Simberloff 1989). (While perhaps surprising to some readers, this result is mirrored by the failure of extensive research efforts to find traits that characterize invasive plants [Gray 1986].) One trait that might be associated with invasive species is a high intrinsic rate of population increase (Crawley 1986; but see also Lawton and Brown 1986). Our inclusion of generations per year as a covariate in the analyses provided at least partial control for this trait.

It may also be that our test is fundamentally valid, and that we must look to population genetics to understand why native and introduced species are indistinguishable in our analysis. We can identify 2 classes of explanations. First, resistance evolution may not be limited primarily by the availability of key genetic variants but rather by the rate with which resistance-conferring alleles increase in frequency (that is, the extreme neo-Darwinian

viewpoint). Although few studies bear directly on this issue, worldwide resistance evolution in the mosquito *Culex pipiens* L. from a single gene amplification event followed by dispersal across several continents suggests that resistance in this species was constrained by the absence of a key genetic variant (Raymond et al. 1992).

Second, native and introduced species might still have similar abilities to evolve resistance even if genetic variation is a key constraint. Native and introduced species might be less dissimilar than might be expected from the simplest, short-term effects of a population bottleneck. First, some theoretical studies and laboratory experiments (reviewed by Carson 1990, but see also Lynch 1988) suggest that population bottlenecks associated with founder events may actually increase additive genetic variance by converting nonadditive forms of genetic variance (dominance and epistatic variance) into additive variance upon which natural selection may act. Second, because introduced arthropod pest populations often reach extremely large population sizes after the founder event, it may be that rare allelic variants are regenerated rapidly through mutation. Third, it may be that native arthropod pest populations are themselves unable to retain many rare alleles because of population bottlenecks experienced during upper Pleistocene glaciations (e.g., Martin and Simon 1990) or because of their population structure. Gilpin (1991) has shown that metapopulations, comprising a series of subpopulations linked by modest migration rates and subject to extinction and recolonization from neighboring subpopulations, may have genetic effective population sizes that are 10–100 times lower than their census population sizes. Many arthropod pests of agricultural crops may exhibit metapopulation structures. Populations within individual fields may represent subpopulations, which suffer extinctions either as a result of normal farming practices (e.g., yearly crop destruction for annual agroecosystems, or less frequent but still periodic replantings for perennial systems), or as a direct result of pesticide-induced mortality. Although electrophoretic studies of agricultural pests do not reveal the extremely low levels of mean heterozygosity predicted by the strict metapopulation model (Loxdale and den Hollander 1989), it may still be the case that many low-frequency alleles are lost during the cycles of extinction and recolonization. Thus, perhaps both introduced and native species are subject to the rare-gene purging action of colonization events.

The suggestion that introduced arthropods may display relatively "normal" levels of evolutionary flexibility is relevant to conservation biology and the problem of minimum viable population size (Soulé 1987, Lande 1988). One of the primary concerns of conservation biologists working with small populations (especially animals in captive breeding programs) is that the loss of genetic variation may decrease the subsequent ability to evolve

in response to novel selection pressures (Pimm and Gilpin 1989, Hedrick and Miller 1992). At least for introduced arthropod pests, which differ from many endangered species in that their population sizes increased tremendously after the bottleneck, we find no evidence of evolutionary rigidity.

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