Heredity **72** (1994) 228–236
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Received 7 July 1993

Population structure of a predatory beetle: the importance of gene flow for intertrophic level interactions

MOSHE COLL*, LAURA GARCIA DE MENDOZA & GEORGE K. RODERICK†
Department of Entomology, University of Maryland, College Park, MD 20742, U.S.A.

Migration and gene flow of natural enemies play an important role in the stability of predator–prey interactions and community organization in both natural and managed systems. Yet, relative to that of their herbivorous insect prey, the genetic structure of natural enemy populations has been little studied. We present evidence that populations of the predatory coccinellid beetle *Coleomegilla maculata* (Coleoptera: Coccinellidae), are not genetically subdivided and that levels of gene flow among these populations are extremely high. Furthermore, in the same geographical area, gene flow of *C. maculata* was significantly (one order of magnitude) greater than that of an abundant prey species, the Colorado potato beetle *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae). The high mobility of this natural enemy relative to the insect herbivores on which it feeds may contribute to its effectiveness as a biological control agent in agricultural systems.

Keywords: allozyme, biological control, electrophoresis, gene flow, metapopulation, natural enemies.

Introduction

The genetic structure of populations is a function of their spatial arrangement and amount of gene flow among them. The extent of gene flow will determine not only the potential for populations to diverge genetically but will also influence local population dynamics. For predatory species, these effects are also likely to be coupled with the dynamics and movement of their prey. The association between predator and prey is well illustrated, theoretically and experimentally, by predators and parasitoids (collectively termed natural enemies) and the herbivorous insects which they attack. For example, movement of natural enemies may contribute to their aggregative response to sites harbouring varying numbers of prey (Murdoch *et al.*, 1985; Strong, 1988). Under some conditions, such aggregative response by natural enemies may have, at least theoretically, stabilizing effects on populations (Hassell, 1978; Hassell & May, 1988) or metapopulations (Taylor, 1991) of predators and prey.

*Correspondence: USDA, ARS, Insect Biocontrol Laboratory, BARC-East, Bldg. 402, Beltsville, MD 20705, U.S.A.
†Present address: Hawaiian Evolutionary Biology Program, University of Hawaii, 3050 Maile Way Gilmore 310, Honolulu, HI 96822, U.S.A.

Despite the recognized importance of mobility of natural enemies, little is known about their population structure, especially the amount of gene flow (Roderick, 1992) and dispersal (Coll, 1991) among field populations. This lack of information stands in contrast to the studies of the genetic structure of herbivorous insect populations in both natural (Slatkin, 1985a, 1987; McCauley & Eanes, 1987) and managed systems (Loxdale & den Hollander, 1989; Roderick & Caldwell, 1992).

Many studies have examined the role gene flow plays in the development of local adaptation in herbivores, including the evolution of host races (Butlin, 1990; Roderick, 1993) and the development of insecticide resistance in pest species (Comins, 1977; Georghiou & Taylor, 1977; Taylor & Georghiou, 1979; Tabashnik & Croft, 1982; Caprio & Tabashnik, 1992b). Selection pressure from pesticide application will also affect natural enemies (Rosenheim & Hoy, 1986; Rosenheim & Tabashnik, 1991). In general, low levels of gene flow may permit local adaptations such as the evolution of insecticide resistance (Caprio & Tabashnik, 1992b). If natural enemies are indeed more mobile than their hosts or prey (Murdoch *et al.*, 1985) then natural enemies may not develop insecticide resistance as rapidly as their herbivorous prey. In turn, differences in susceptibility to insecticides between herbivores and natural enemies may facilitate pest out-

breaks and resurgence because of the removal of predators and parasites by pesticide applications. It is unclear, however, how differences in gene flow between natural enemies and their herbivorous prey affect their susceptibility to insecticides.

Two approaches are commonly used to estimate gene flow among populations: direct measures, such as release–recapture, and indirect estimates based on patterns of genetic similarity among populations (Slatkin, 1985a, 1987). Although direct measures of dispersal represent actual observations, they may be biased by not reflecting rare gene flow events or non-random contributions to subsequent generations (Ehrlich & Raven, 1969; Endler, 1979; Slatkin, 1987). By contrast, indirect estimates of gene flow, based on F_{ST} (Wright, 1951) or rare alleles (Slatkin & Barton, 1989), reflect variations in allele distribution that were produced over long periods (Slatkin, 1987; McCauley, 1991).

In this study, we first used allozyme electrophoresis to examine the population structure of a predatory beetle, *Coleomegilla maculata* De Geer (Coleoptera: Coccinellidae). Then, we tested the hypothesis that level of gene flow among populations of this predator is greater than that among populations of one of its sympatric abundant prey species, the Colorado potato beetle, *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae).

Methods

Biological material

The predatory beetle *C. maculata* is native to North America and is widely distributed east of the Rocky Mountains (Obrycki & Tauber, 1978). In both natural and managed systems, larvae and adults are important natural enemies of aphids, insect eggs and soft-bodied immatures (Smith, 1960; Atallah & Newsom, 1966; Warren & Tadic, 1967, and references therein). The predator is common in maize, alfalfa, cotton, potato, tobacco, curcubits and cole crop systems (Ewert & Chiang, 1966; Richardson & DeLoach, 1973; Elsey, 1974; Wright & Laing, 1980; Marck & Smilowitz, 1982; Cosper *et al.*, 1983; Groden *et al.*, 1990; Coll & Bottrell, 1991; Hazzard *et al.*, 1991). In potatoes, *C. maculata* can be a major natural enemy of the Colorado potato beetle (Groden *et al.*, 1990; Hazzard & Ferro, 1991; Hazzard *et al.*, 1991).

Six populations of overwintering adult *C. maculata* were sampled in Maryland, U.S.A., between 31 March and 10 April 1992 (Fig. 1). The sampling sites were in the following counties: Washington (39°30′55″N; 77°44′50″W), Frederick (39°16′05″N; 77°28′05″W), Montgomery (39°17′30″N; 77°12′25″W), Howard (39°12′45″N; 76°56′10″W), Prince George

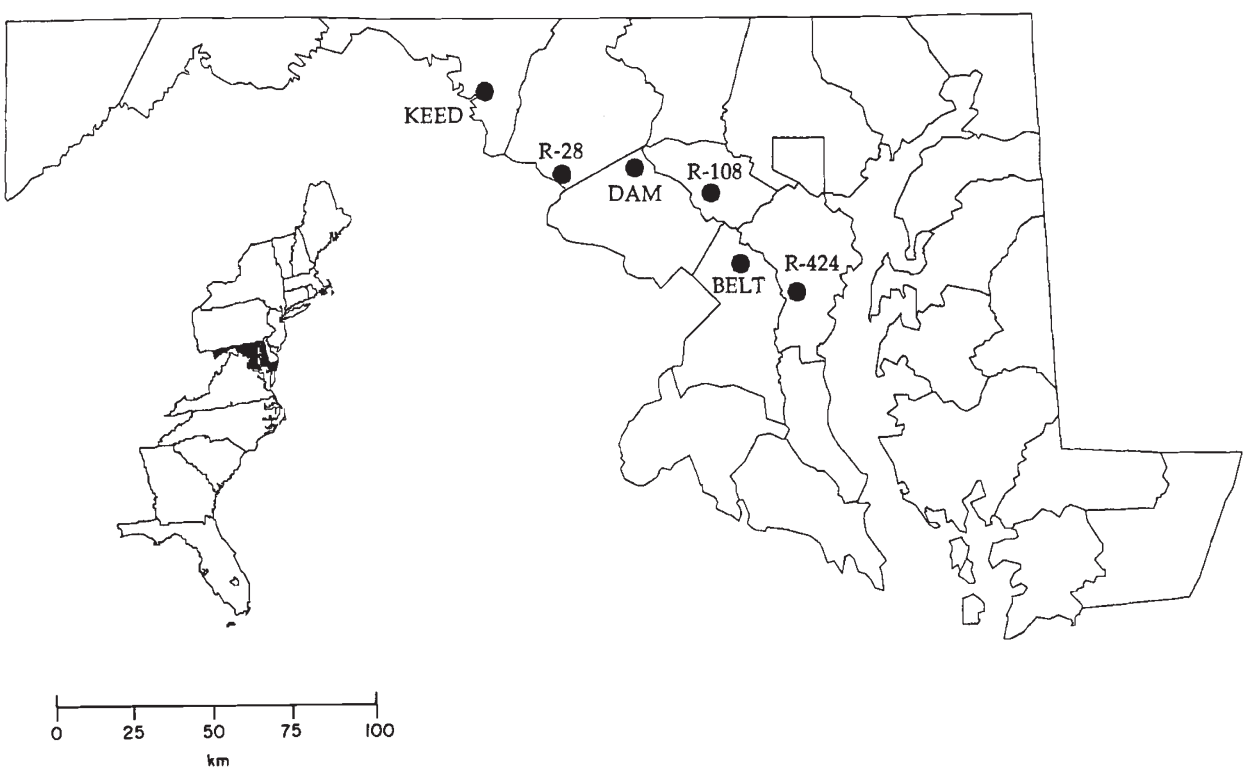

Fig. 1 Collection sites of six *Coleomegilla maculata* overwintering aggregations in Maryland, U.S.A.

(39°00′40″N; 76°49′55″W) and Anne Arrundel (38°55′50″N; 76°37′45″W). The approximate distance between the westernmost and the easternmost populations was 116 km. The beetles were collected from overwintering aggregations at the base of prominent trees at the edge of maize fields. Since *C. maculata* does not exhibit a long distance migratory behaviour to overwintering sites (Hagen, 1962), all beetles collected from the same aggregation are considered to belong to the same population or random breeding unit. The beetles were maintained in the laboratory (25 ± 3°C; 15:9 L:D) until they were no longer in diapause (determined by flight and feeding behaviours) and after any parasitoids (*Dinocampus* (= *Perilitus*) *coccinellae* (Hymenoptera: Braconidae)) had emerged (about 25 April). The beetles were frozen at −80°C until preparation for electrophoresis.

Electrophoresis

Cellulose-acetate gels (Helena Laboratories Inc.) were used for electrophoresis (Richardson *et al.*, 1986; Hebert & Beaton, 1989). Before electrophoresis, beetles were homogenized individually in 50 μl of distilled water and centrifuged for 5 min at 4°C. Resolving gels were maintained at 4°C during electrophoresis. A preliminary survey of 17 enzyme systems revealed nine polymorphic resolvable loci. The following seven enzyme systems encoded by nine presumptive loci were scored in all six populations: fumarate hydratase (*FUM*); isocitrate dehydrogenase (*IDH*, two loci: fast [*f*] and slow [*s*]); malate dehydrogenase (*MDH*, two loci: [*f* and *s*]); peptidase (*PEP*); 6-phosphogluconate dehydrogenase (*6PGDH*); phosphoglucose isomerase (*PGI*) and phosphoglucomutase (*PGM*). The buffer systems found to be most suitable for resolving the above loci are listed in Table 1. Staining techniques for these enzyme systems were adopted from Hebert & Beaton (1989). Electromorphs were labelled alphabetically with 'A' as the fastest running electromorph.

Genetic analysis

The fixation index, F_{ST} is a measure of genetic differentiation among populations and can range between 0 (no genetic differentiation) and 1 (complete differentiation) (Wright, 1951). It has several equivalent interpretations. F_{ST} can be expressed as the absence of heterozygotes in subpopulations relative to what is expected in the total population (i.e. $F_{ST} = (H_T - H_S)/H_T$, where H_S is the average heterozygosity of subpopulations and H_T is the predicted total heterozygosity). F_{ST} also represents the standardized variance in allele frequencies among local populations (Weir, 1990). While these formulations of F_{ST} are for one locus and one allele, similar statistics can be estimated for two alleles at one locus (Wright, 1951) and for more alleles at many loci (as G_{ST}; Nei, 1973, 1977; Birky *et al.*, 1989). An alternative to F_{ST} is the statistic of coancestry, θ, which represents the correlation of genes of different individuals in the same populations (Weir & Cockerham, 1984; Weir, 1990).

For neutral alleles, F_{ST}, G_{ST} or θ, can be used to estimate the number of migrants exchanged by populations per generation (gene flow) ($F_{ST} = 1/(4N_e m + 1)$, where N_e is the effective local population size and m is the average rate of immigration or the proportion of the population that migrate each generation (Wright, 1943)). By estimating $N_e m$ we can compare the magnitude of gene flow without the need for exact estimates of the average effective population size, N_e.

Wright's formula assumes an 'island model' in which every local population is equally likely to exchange migrants with any other. However, the formula also

Table 1 Presumptive loci scored for *Coleomegilla maculata*

Enzyme	E.C.	Locus†	Buffer‡
Fumarate hydratase	4.2.1.2	*FUM*	Tris-EDTA-Borate 0.13 M, *p*H 8.9
Isocitrate dehydrogenase	1.1.1.42	*IDH-f*	Citrate Phosphate 0.01 M, *p*H 6.4
		IDH-s	Citrate Phosphate 0.01 M, *p*H 6.4
Malate dehydrogenase	1.1.1.37	*MDH-f*	Tris-Maleate-EDTA-$MgCl_2$ 0.05 M, *p*H 7.8
		MDH-s	Tris-Citrate 0.1 M, pH 8.2
Peptidase	3.4.11-13	*PEP*	Tris-Glycine 0.025 M, *p*H 8.5
6-Phosphogluconate dehydrogenase	1.1.1.44	*6PGDH*	Tris-Maleate-EDTA-$MgCl_2$ 0.05 M, *p*H 7.8
Phosphoglucose isomerase	5.3.1.9	*PGI*	Citrate Phosphate 0.01 M, *p*H 6.4
Phosphoglucomutase	2.7.5.1	*PGM*	Tris-Glycine 0.025 M, *p*H 8.5 and Tris-Maleate-EDTA-$MgCl_2$ 0.05 M, *p*H 7.8

†f = fast and s = slow electromorphs.
‡Hebert & Beaton (1989).

approximates gene flow for two-dimensional stepping-stone models (Crow & Aoki, 1984; Crow, 1986; Slatkin, 1987). Indirect methods to estimate gene flow rely on several rarely evaluated assumptions. Four major assumptions must be made (Daly, 1989). (i) Gene flow is random with respect to the genotypes studied. (ii) The rate of gene flow for the studied alleles exceeds the rate of change of allele frequencies due to selection. (iii) The rate of gene flow exceeds a minimum level to offset the effects of genetic drift. (iv) The populations are at genetic equilibrium, such that a balance is achieved between loss of alleles by drift and the gain of alleles from migration. These assumptions are considered in turn below.

The first two assumptions are likely to be met for allozymes that are considered to be either neutral or under weak selection (Kimura, 1983). Also, if many loci give similar results, it would be difficult to argue that all are responding to the same selective pressures (Slatkin, 1987). The last two assumptions are more difficult. For the third assumption, Wright (1931) showed that any gene flow among populations will prevent complete fixation and that genetic drift will only lead to substantial genetic differentiation if gene flow does not exceed a certain minimum level. This condition can be expressed as $m \gg 1/(4N_e)$ or $N_e m \gg 1/4$ (Wright, 1931). Free-living, mobile organisms usually have much higher levels of gene flow. The fourth assumption states that the populations are in genetic equilibrium, such that loss of alleles by genetic drift in any population is balanced by a gain in alleles through migration. At equilibrium this balance will hold over a range of population sizes (Slatkin, 1987). Because *C. maculata* is native to North America, we argue that there has been sufficient time for the effects of migration to balance the effects of genetic drift.

Slatkin & Barton (1989) suggested that estimation of gene flow based on F_{ST} methods (including G_{ST} and θ) is preferable to other methods that use allele frequency data (such as, the private alleles and maximum likelihood methods; Slatkin & Barton, 1989). The use of rare or private alleles (Slatkin, 1985b) is more sensitive to coding errors than methods based on F_{ST} and maximum likelihood methods appear to overestimate gene flow unless a large number of populations (perhaps as many as 40) is sampled (Slatkin & Barton, 1989). For high rates of gene flow, G_{ST} may be a better estimate of gene flow than θ, which appears to overestimate $N_e m$ (Slatkin & Barton, 1989). When the number of sampled populations is small, the relationship between G_{ST} and $N_e m$ may be better estimated by $G_{ST} = 1/(1 + 4N_e m(n/n-1)^2)$ (Takahata, 1983; Takahata & Nei, 1984; Chakraborty & Leimar, 1987). In this study, therefore, we present estimates of θ and corrected G_{ST}.

We used BIOSYS-1 (FORTRAN 77 version, Swofford & Selander, 1981) to analyse gene frequency data. For each locus, as well as over all loci, we estimated G_{ST} and θ as well as F_{IS}, which measures deviation from random mating within subpopulations. We scored 6–11 alleles per locus and could not completely resolve one allele (*PEP*, allele G; Appendix A).

To test the assumption of Wright's (1951) island model (i.e. that a migrant from a population is equally likely to move to any other population), we correlated a measure of genetic distance between pairs of populations (Roger's Modified Distance; Wright, 1978) against the geographical distance between these populations. We used a resampling procedure (Mantel's test; Mantel, 1967; Crowley, 1992) to correct for lack of independency between data points.

Finally, we tested whether the θ estimate (unbiased regardless of sample size: Chakraborty & Leimar, 1987) for *C. maculata* is lower than that for *L. decemlineata* (G. K. Roderick *et al.* and M. L. Azeredo-Espin *et al.*, both unpublished data). Both sets of estimates were obtained over the same geographical area in Maryland. We used nine loci for *C. maculata* and six for *L. decemlineata*. Because sampling distributions of gene diversity components are not known, we used the Mann–Whitney *U*-test (SAS Institute, 1985) to compare the two estimates of θ.

Results

Electromorph frequency data are presented in Appendix A. Data indicate that *C. maculata* has an extremely high number of alleles per locus (9.44 ± 0.73). Similarly, Steiner & Grasela (1993) found twice as many alleles per locus in *C. maculata* than in other beetle species. In our study, allozyme frequencies did not deviate significantly from Hardy–Weinberg expectations (χ^2 goodness-of-fit test with a Sidak adjusted P value; Sokal & Rohlf, 1981). Thus, within the six studied populations, there is no evidence of significant deviations from random mating for any of the loci (also suggested by the relatively low F_{IS} value; Table 3).

Contingency chi-square analysis revealed that there were no significant differences in allele frequencies at each locus across populations ($\chi^2 = 80.67$, d.f. $= 75$, $0.1 < P < 0.5$). Mean rate of heterozygosity (H) over all six populations was 0.250 ± 0.021 (range 0.212–0.273). This level of heterozygosity is one of the highest found in beetles (Steiner & Grasela, 1993). In our study, no longitudinal or latitudinal cline effects were found in allele frequency data. Recently, a cline in heterozygosity in *C. maculata* was found to be associated with latitude and host crop (Steiner & Grasela, 1993). We did not find such cline effects in our study, probably because all beetles were collected near maize

fields and the latitudinal distance was about 12 times smaller than in Steiner & Grasela's study.

Roger's genetic distances between beetle populations averaged 0.059 ± 0.009 (Table 2). The lack of a relationship between genetic distance and geographic distance (Mantel statistic = −0.256, 95 per cent confidence limits = −0.51 and 0.50) provides no evidence with which to reject the island model.

The low estimates of θ and G_{ST} (Table 3) indicate little genetic differentiation among populations. The negative θ's indicate values close to zero because θ is not defined for negative values (Weir, 1990). The θ- and G_{ST}-based estimated numbers of beetles exchanged between populations per generation (N_em) were 166.4 and 15.6, respectively.

In the same geographical region of the present study, θ for the Colorado potato beetle was 0.0157($\pm$0.0044 S.E.), suggesting a level of migration (N_em) of 15.67. This value of θ is significantly smaller than the value estimated for *C. maculata* (Mann–Whitney *U*-test, $P = 0.016$).

Table 2 Genetic distance between pairs of six populations of *Coleomegilla maculata*†

Populations	KEED	R-28	DAM	R-108	BELT	R-424
KEED	—					
R-28	0.058	—				
DAM	0.077	0.071	—			
R-108	0.067	0.056	0.058	—		
BELT	0.060	0.058	0.065	0.051	—	
R-424	0.052	0.044	0.056	0.048	0.060	—

†Modified Roger's genetic distance (Wright, 1978).

Table 3 Statistics summary from six populations of *Coleomegilla maculata*

Locus	F_{IS}	θ†	G_{ST}‡
FUM	−0.031	−0.0055	0.005
IDH-f	0.119	0.0042	0.015
IDH-s	0.038	0.0006	0.011
MDH-f	0.098	0.0030	0.013
MDH-s	−0.023	−0.0021	0.008
PEP	0.056	−0.0003	0.010
6PGDH	0.011	−0.0037	0.007
PGI	0.031	0.0047	0.014
PGM	0.007	0.0010	0.011
Mean	0.033	0.0015§	0.011
S.E.	0.017	0.0006§	0.001

†Weir & Cockerham (1984); Weir (1990).
‡Nei (1977).
§Corrected values (negative θs were entered as 0s). Uncorrected mean and S.E. are 0.0002 and 0.0012, respectively).

Discussion

Little genetic differentiation exists among *C. maculata* populations in Maryland. Given the long history of these populations, these data suggest relatively high rates of gene flow among populations. Through simulations, Slatkin & Barton (1989) demonstrated that for high levels of gene flow, G_{ST} underestimates N_em, especially when a small number of populations is sampled (Chakraborty & Leimar, 1987). The same pattern appears in our study, i.e. G_{ST}-based N_em is about seven times smaller than the θ-based estimate.

The mean value for θ in this study (0.0015) is an order of magnitude smaller than the value estimated in another predatory coccinellid beetle, *Coccinella septempunctata*, in North America ($\theta = 0.0148$; Krafsur *et al.*, 1992). Krafsur *et al.* (1992) suggested that the low θ value for *C. septempunctata* is the result of its recent introduction into North America (Angalet *et al.*, 1979). *C. maculata*, however, is native to North America and its populations are likely to have reached genetic equilibrium. Furthermore, genetic differentiation among native populations of *C. septempunctata* (i.e. in Eurasia) was even lower (0.003; Krafsur *et al.*, 1992) and more similar to our estimates for *C. maculata*. Recently, a low level of genetic differentiation ($F_{ST} = 0.14$) was also reported in *C. maculata* in the midwest region of the U.S.A. (Steiner & Grasela, 1993).

Low levels of genetic differentiation may result from aggregative behaviour exhibited by many coccinellid beetles at overwintering sites (Hagen, 1962; Hodek, 1973). However, unlike other coccinellids (e.g. *Coccinella septempunctata*, *Hippodemia convergens*), *C. maculata* does not exhibit such long distance seasonal migratory behaviour. Instead, adult *C. maculata* aggregate at the base of prominent objects near open areas, such as fields (Hagen, 1962). Alternatively, low F_{ST}'s and the associated high N_em values in coccinellid species may reflect generally high mobility of these efficient predators.

However, predator–prey interactions will be influenced not so much by the absolute movement rate of predators but rather by the relative mobility of predators and their prey. *C. maculata* is a generalist predator that consumes primarily aphids, insect eggs and immatures (Groden *et al.*, 1990; Hazzard *et al.*, 1991). It was therefore of interest to compare the genetic differentiation among populations of *C. maculata* in our study with genetic differentiation among populations of its prey. In Maryland, and elsewhere in the eastern U.S.A., *C. maculata* is an important predator of

Colorado potato beetle eggs and young larvae (Groden *et al.*, 1990; Hazzard & Ferro, 1991; Hazzard *et al.*, 1991). Over the same geographical area, estimates of genetic differentiation for the Colorado potato beetle were significantly greater than for *C. maculata* and therefore the estimated level of migration was significantly lower than that for *C. maculata*.

Greater levels of population differentiation, relative to *C. maculata*, were also evidenced in other prey species. For several North American lepidopteran pests fed on by *C. maculata*, F_{ST} ranged from 0.021 to 0.084 (Pashley *et al.*, 1985) and for surface-dwelling coleopteran prey (excluding predatory and cave-dwelling species) F_{ST} values ranged from 0.011 to 0.154 (McCauley & Eanes, 1987; Hsiao, 1989). By contrast, small genetic differentiation of *C. maculata*, suggests that its movement may be one or even two orders of magnitude greater than that of its prey. This difference in mobilities may help to explain the remarkable efficiency of *C. maculata*, even in the face of a yearly habitat destruction as found in annual cropping systems.

Differential mobility of predators and their prey is also likely to be important in the evolution of pesticide resistance. Often, pest species are more resistant to pesticides than natural enemies (Croft & Brown, 1975; Tabashnik, 1986). Two hypotheses have been advanced to explain this phenomenon; preadaptation (Gordon, 1961) and food limitation (Huffaker, 1971; Georghiou, 1972). Our results suggest yet another mechanism: the higher mobility of natural enemies relative to their prey may slow the evolution of pesticide resistance: (1) because natural enemies may move more readily out of treated areas (in response to prey scarcity) and thus be less exposed to pesticide selection pressure and/or (2) because more susceptible individuals may immigrate into treated fields to dilute the selective effect of pesticides. These effects, however, may be confounded by a greater exposure of the more mobile natural enemies to pesticide residues in treated areas.

Much like herbivores, individuals of *C. maculata* show resistance to insecticides in heavily-treated areas (Head *et al.*, 1977; Graves *et al.*, 1978). Models have demonstrated that high levels of gene flow (more than 10 per cent) between treated and untreated fields can retard the evolution of resistance in treated fields, on the one hand, and increase the frequency of resistance alleles in untreated fields, on the other (Caprio & Tabashnik, 1992b). Assuming that population density of *C. maculata* in maize is similar across our sampling region, population sizes in fields adjacent to the sampled aggregations (based on densities in our western collecting site; Coll & Bottrell, 1991) are estimated at approximately 100,000 adults. Because the effective population size may be smaller by as much as 90 per cent (Wright, 1978), an upper limit of the average migration rate, m, is 0.02 ($N_e m = 166.4$; $N_e = 10{,}000$). Gene flow at this level is too low to retard significantly the development of resistance in *C. maculata* by high immigration of susceptible beetles from untreated fields and yet is too high to slow the spread of initially rare, resistant alleles (Caprio & Tabashnik, 1992a,b).

The mobility of predators and parasites in both natural and managed systems is clearly important in determining the stability of predator–prey interactions and in insect pest control. Yet, few previous studies have examined the population structures of both predator and prey in the same system (Taylor, 1991). Such studies are likely to be rewarding not only for what they will reveal about the organisms themselves but also for what they will contribute to our understanding of population dynamics and community organization.

Acknowledgements

We thank C. Smith for assistance, C. Mitter and M. M. Yang for advice and R. Gillespie, A. Hilbeck, M. Johnson and an anonymous reviewer for helpful comments on drafts of the manuscript. This work was funded by grants from the USDA (to G.K.R.), the Maryland Agricultural Experiment Station Competitive Grants Program (to G.K.R. and M.C.), the General Research Board of the University of Maryland (to G.K.R.), and NIH Biomedical Research Funds (to G.K.R.). The Department of Entomology, University of Maryland and the Hawaiian Evolutionary Biology Program, University of Hawaii, provided additional support. This is scientific article A6414, contribution 8607, of the Maryland Agricultural Experiment Station.

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Appendix A

Electromorph frequencies and sample size (N) for six populations of *Coleomegilla maculata*. See Table 1 and Fig. 1 for abbreviations of loci and populations, respectively

Locus	Allele	Population					
		KEED	R-28	DAM	R-108	BELT	R-424
FUM	(N)	45	45	46	46	35	45
	A	0.000	0.000	0.011	0.000	0.000	0.000
	B	0.000	0.011	0.000	0.000	0.000	0.000
	C	0.000	0.011	0.000	0.000	0.000	0.000
	D	0.000	0.000	0.000	0.011	0.000	0.000
	E	0.011	0.011	0.000	0.011	0.000	0.011
	F	0.956	0.944	0.967	0.946	0.971	0.944
	G	0.011	0.000	0.011	0.011	0.000	0.000
	H	0.000	0.000	0.000	0.000	0.014	0.011
	I	0.000	0.000	0.000	0.011	0.000	0.011
	J	0.011	0.000	0.000	0.000	0.000	0.000
	K	0.011	0.022	0.000	0.000	0.014	0.011
	L	0.000	0.000	0.011	0.011	0.000	0.000
	M	0.000	0.000	0.000	0.000	0.000	0.011
IDH-f	(N)	45	44	46	46	35	45
	A	0.000	0.000	0.000	0.000	0.014	0.000
	B	0.011	0.000	0.000	0.000	0.000	0.000
	C	0.011	0.000	0.011	0.000	0.000	0.000
	D	0.000	0.023	0.033	0.000	0.014	0.000
	E	0.000	0.000	0.000	0.000	0.014	0.000
	F	0.967	0.909	0.946	0.957	0.886	0.978
	G	0.011	0.034	0.011	0.043	0.029	0.022
	H	0.000	0.011	0.000	0.000	0.000	0.000
	I	0.000	0.000	0.000	0.000	0.014	0.000
	J	0.000	0.023	0.000	0.000	0.000	0.000
	K	0.000	0.000	0.000	0.000	0.029	0.000
IDH-s	(N)	45	43	46	46	35	46
	A	0.000	0.012	0.022	0.000	0.000	0.000
	B	0.000	0.000	0.000	0.000	0.000	0.022
	C	0.011	0.012	0.000	0.000	0.000	0.000
	D	0.000	0.012	0.011	0.011	0.014	0.033
	E	0.956	0.953	0.935	0.967	0.986	0.913
	F	0.000	0.012	0.000	0.000	0.000	0.000
	G	0.022	0.000	0.022	0.000	0.000	0.000
	H	0.000	0.000	0.000	0.011	0.000	0.011
	I	0.011	0.000	0.000	0.011	0.000	0.022
	J	0.000	0.000	0.011	0.000	0.000	0.000
MDH-f	(N)	45	45	46	46	35	46
	A	0.000	0.000	0.000	0.000	0.014	0.000
	B	0.000	0.000	0.000	0.011	0.014	0.000
	C	0.000	0.000	0.000	0.011	0.014	0.000
	D	0.978	1.000	0.978	0.935	0.957	0.978
	E	0.000	0.000	0.000	0.022	0.000	0.022
	F	0.022	0.000	0.011	0.022	0.000	0.000
	G	0.000	0.000	0.011	0.000	0.000	0.000
MDH-s	(N)	45	45	46	46	35	45
	A	0.011	0.000	0.000	0.011	0.000	0.000
	B	0.000	0.000	0.011	0.011	0.000	0.000
	C	0.000	0.000	0.000	0.011	0.000	0.000
	D	0.989	0.978	0.978	0.946	0.986	0.978
	E	0.000	0.022	0.000	0.011	0.000	0.011
	F	0.000	0.000	0.011	0.011	0.014	0.011
PEP	(N)	45	44	46	46	34	44
	A	0.000	0.000	0.011	0.033	0.000	0.023
	B	0.056	0.057	0.098	0.065	0.059	0.045
	C	0.000	0.057	0.000	0.011	0.015	0.034
	D	0.278	0.205	0.304	0.207	0.294	0.250
	E	0.011	0.000	0.000	0.000	0.029	0.000
	F	0.533	0.625	0.467	0.587	0.559	0.580
	G[1]	0.100	0.023	0.109	0.087	0.044	0.068
	H	0.011	0.011	0.000	0.000	0.000	0.000
	I	0.011	0.000	0.011	0.000	0.000	0.000
	J	0.000	0.000	0.000	0.011	0.000	0.000
	K	0.000	0.023	0.000	0.000	0.000	0.000
6PGDH	(N)	43	44	46	46	35	45
	A	0.000	0.023	0.011	0.000	0.000	0.000
	B	0.000	0.000	0.011	0.011	0.000	0.000
	C	0.000	0.000	0.000	0.022	0.000	0.011
	D	0.000	0.023	0.022	0.000	0.000	0.011
	E	0.000	0.000	0.000	0.000	0.014	0.000
	F	0.965	0.909	0.913	0.924	0.943	0.956
	G	0.023	0.011	0.011	0.011	0.014	0.000
	H	0.012	0.034	0.033	0.033	0.029	0.022
PGI	(N)	45	44	44	46	35	44
	A	0.000	0.011	0.023	0.011	0.000	0.000
	B	0.022	0.000	0.011	0.000	0.014	0.011
	C	0.111	0.136	0.216	0.185	0.143	0.205
	D	0.689	0.580	0.477	0.554	0.643	0.557
	E	0.000	0.023	0.000	0.033	0.000	0.023
	F	0.122	0.159	0.170	0.087	0.114	0.170
	G	0.022	0.000	0.000	0.054	0.000	0.000
	H	0.033	0.091	0.068	0.065	0.071	0.023
	I	0.000	0.000	0.011	0.000	0.014	0.011
	J	0.000	0.000	0.023	0.011	0.000	0.000
PGM	(N)	45	39	44	46	34	45
	A	0.000	0.000	0.000	0.000	0.015	0.000
	B	0.011	0.013	0.000	0.011	0.044	0.000
	C	0.067	0.051	0.034	0.033	0.059	0.044
	D	0.322	0.359	0.398	0.424	0.441	0.367
	E	0.000	0.000	0.000	0.022	0.000	0.011
	F	0.567	0.538	0.432	0.435	0.412	0.533
	G	0.000	0.026	0.057	0.000	0.000	0.000
	H	0.033	0.013	0.068	0.076	0.029	0.044
	I	0.000	0.000	0.011	0.000	0.000	0.000

[1]Allele could not be completely resolved. It consists of several electromorphs with a continuous range of mobilities.