Bulletin of Entomological Research (1996) **86**, 355–361

Genetic estimates of dispersal ability in the leucaena psyllid predator *Curinus coeruleus* (Coleoptera: Coccinellidae): implications for biological control

Peter A. Follett and George K. Roderick

Center for Conservation Research and Training, University of Hawaii at Manoa, Honolulu, Hawaii

Abstract

The leucaena psyllid, *Heteropsylla cubana* Crawford, can devastate plantings of *Leucaena leucocephala* (Leguminosae), an economically important tree species in the Pacific Islands, Southeast Asia, Australia, India, Africa, and elsewhere. The predatory beetle, *Curinus coeruleus* Mulsant (Coleoptera: Coccinellidae), has been introduced into many of these areas from Hawaii for biological control of the psyllid. In this study, collections of *C. coeruleus* were made from 11 populations on four islands in the Hawaiian archipelago to determine population structure and estimate levels of gene flow. Over all populations, a measure of population subdivision, θ, was 0.095, and the estimate of $N_e m$, the average migration rate, was 2.4. θ values for the individual islands were 0.02, 0.12, 0.24 and 0.05 for Kauai, Hawaii, Maui, and Oahu, respectively. Estimated levels of gene flow between populations were not correlated with geographic distance, therefore isolation by distance does not appear to be an important process structuring *C. coeruleus* populations. Gene flow estimates can be used to characterize dispersal capabilities in insects or other organisms released for biological control. In this case, the inferior dispersal ability of *C. coeruleus* likely limits its rapid widespread establishment during release programmes.

Introduction

Curinus coeruleus Mulsant (Coleoptera: Coccinellidae) was introduced into Hawaii from Mexico in 1922 for biological control of the coconut mealybug, *Nipaecoccus nipae* (Maskell) (Homoptera: Pseudococcidae) (Swezey, 1923; Funasaki *et al.*, 1988). It became established and persisted in Hawaii, occasionally found in association with *N. nipae*, *Chrysomphalus aonidum* (Linnaeus) (Diaspididae), *Aleurodicus dispersus* Russell (Aleyrodidae) and *Aphis nerii* Boyer de Fonscolombe (Aphididae), but was uncommon and never considered an important predator of these pests. Densities of *C. coeruleus* remained low until the recent accidental introduction to the Hawaiian Islands of the leucaena psyllid, *Heteropsylla cubana* Crawford (Homoptera: Psyllidae) (Beardsley *et al.*, 1989).

Correspondence: P.A. Follett, Department of Entomology, 3050 Maile Way, Gilmore 310, University of Hawaii at Manoa, Honolulu, Hawaii 96822, USA.

H. cubana, a narrowly oligophagous herbivore that feeds on *Leucaena leucocephala* (Leguminosae), is believed to have originated in Mexico, where *L. leucocephala* is native (McClay, 1989). The psyllid was first detected on the island of Oahu in April of 1984 attacking both *Leucaena leucocephala* (hereafter referred to as *Leucaena*) and *Samanea samen* (Leguminosae). Two months later it had been reported from the other five major islands of Hawaii: Hawaii, Kauai, Lanai, Maui, and Molokai (Uchida *et al.*, 1992). Hawaii was a stepping stone for *H. cubana*: By 1987–88 it had spread from Hawaii to many countries in the Pacific Ocean, insular and continental Southeast Asia, northern Australia, and as far west as Sri Lanka, India, and parts of Africa (Mitchell & Waterhouse, 1987; Napompeth, 1989). Soon after the introduction of the psyllid in Hawaii, *C. coeruleus* was observed in high numbers in stands of *Leucaena* heavily infested by the psyllid. Presently, *C. coeruleus* is the most abundant coccinellid in the Hawaiian archipelago (Funasaki *et al.*, 1989).

In Hawaii, *Leucaena* is a rapidly growing leguminous tree found in dry to mesic habitats on all islands at elevations up to 700 m. Approximately 60 years ago, it was deliberately broadcast over lowland habitats as a fodder plant (Smith, 1985), and it is now the dominant plant species in many lowland areas. Although in Hawaii it is considered an undesirable weed, in many parts of the world *L. leucocephala* is highly valued for its many uses (shade tree in vanilla, cocoa, tea, and coffee plantations; reforestation and soil reclamation; forage for cattle; fuelwood; timber for light construction; and food for humans) (Beardsley *et al.*, 1989). Feeding by *H. cubana* can devastate the tree and cause economic losses, and, therefore, *C. coeruleus* from Hawaii have been introduced into many countries for biological control of this psyllid. After only a few years, *C. coeruleus* has become a key component of biocontrol programmes in several areas and shows promise in many others (Wagiman *et al.*, 1989; Showler, 1995).

One of the desirable attributes of a biological control agent is a high capacity for dispersal. Ideally, a predator would spread under its own power over the entire range of its host after only one or a few localized introductions (Coppel & Mertins, 1977). The dispersal behaviour of *C. coeruleus* has not been carefully studied. The beetle is common throughout the major Hawaiian Islands wherever *Leucaena* is found, a distribution that suggests *C. coeruleus* has a high dispersal ability like many other entomophagous coccinellids (Hagen, 1962; Ewert & Chiang, 1966; Krasfur *et al.*, 1992; Coll *et al.*, 1994). However, recent observations suggest dispersal by *C. coeruleus* might be limited. Wagiman *et al.* (1989) observed that beetles had moved only 5 km three years after its introduction and population increase c a coffee plantation in central Java; likewise, in tea plantatior in West Java, *C. coeruleus* reproduced well but moved litt (Soehardjan, 1989).

A straightforward means to estimate the dispers capacity of this beetle is to monitor spread of the predat in areas where it has recently been released for biologic control. In Hawaii, where *C. coeruleus* is already establishe throughout the islands, the best means to determine dispers rates directly is by recapture of marked beetles. Drawbacl to this direct approach are that: (i) it is usually not feasib to conduct mark-recapture studies for more than one or few generations, so rare but significant dispersal episod may be missed; and (ii) the long distance dispersers may b underestimated because of the limited area over which mark-recapture study can be conducted (Slatkin, 1987, 199 Roderick, 1996). An alternative method that does not sha these limitations is to infer levels of movement indirectl from the geographic structure of genetic variation (Slatki 1987). In this study, we examined genetic similarity amon *C. coeruleus* populations from the Hawaiian archipelag We tested whether beetles within and between islanc are genetically similar, which would be evidence for hig dispersal and gene flow, or whether significant populatic subdivision exists, suggesting limited dispersal.

Materials and methods

We collected adult *Curinus coeruleus* from 11 differer localities on the islands of Maui (3), Oahu (3) and Hawaii (3 between 7–14 June 1993, and on the island of Kauai (2) o

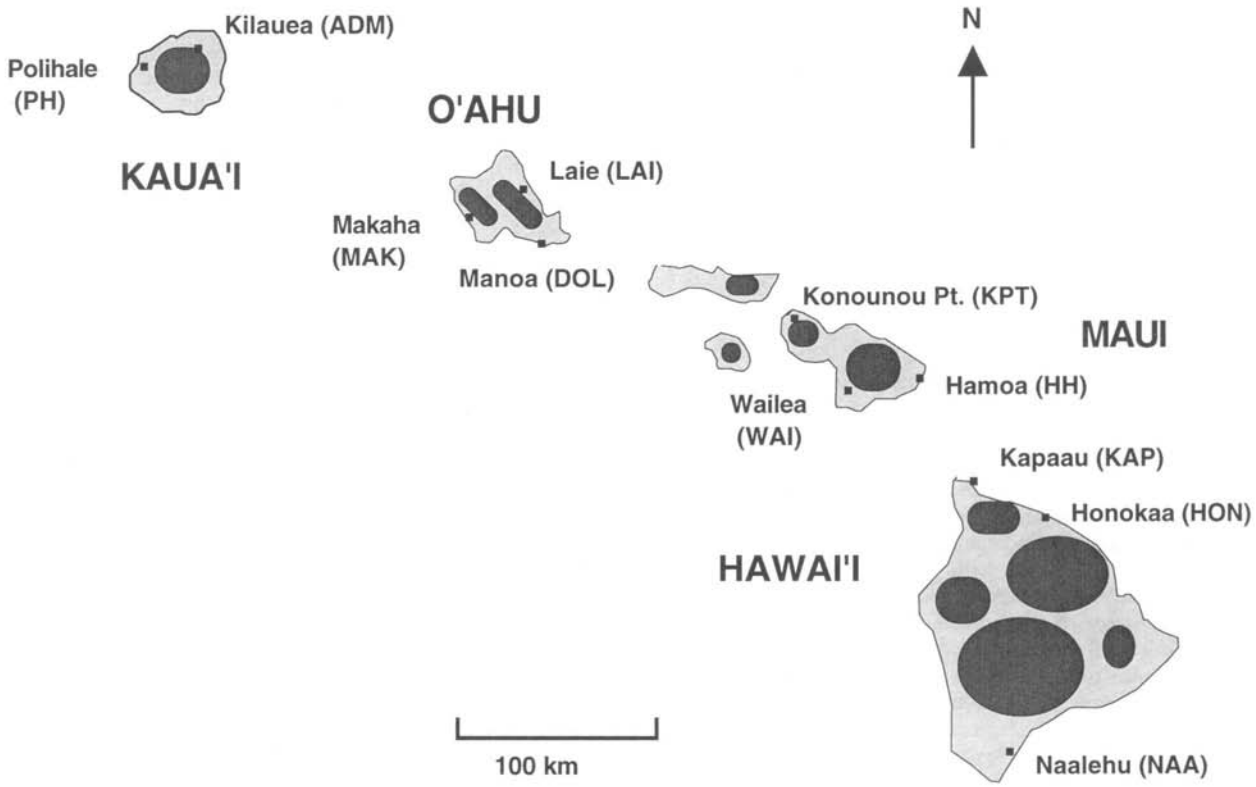

Fig. 1. Collections sites in the Hawaiian Islands of 11 *Curinus coeruleus* populations.

30 June 1994 (fig. 1). Shaded areas in the figure represent mountain ranges or volcanoes. Accordingly, on each island, sampling sites were chosen around the perimeter to maximize the spatial separation/isolation of populations. At each site, beetles were sampled from as many different *Leucaena* plants as was practical to reduce the probability of collecting siblings. Once back in the laboratory, live beetles were frozen at −75°C until preparation for electrophoresis.

Cellulose-acetate gels (Helena Laboratories Inc., Beaumont, Texas) were used for allozyme electrophoresis (Richardson *et al.*, 1986; Herbert & Beaton, 1989). Before electrophoresis, whole beetles were homogenized individually in 40 µl of distilled water (in 1.5 ml microcentrifuge tubes) and centrifuged at 6000 rpm for 5 min at 4°C. Gels were run in Zip-zone electrophoresis chambers (Helena Laboratories) maintained at 4°C. A preliminary survey of 20 enzymes and eight buffer systems revealed five polymorphic loci that could be clearly resolved: aldehyde oxidase (AO; E.C. 1.2.3.1); isocitrate dehydrogenase (IDH; two loci: fast [f], slow [s]; E.C. 1.1.1.42); 6-phosphogluconate dehydrogenase (6PGDH; E.C. 1.1.1.44); and phosphoglucomutase (PGM; E.C. 2.7.5.1). A single buffer system, Tris-citrate (0.1 M, pH 8.2) (Richardson *et al.*, 1986), resolved all five loci well. Electrophoretic gels were run at 175 v for either 45 min (AO, IDH, 6PGDH) or 2 h (PGM). Staining techniques were unmodified from Herbert & Beaton (1989). Genotypes were determined for 36 adult beetles from each collection site, except Polihale (PH; island of Kauai) where 24 beetles were used.

Wright (1951) introduced *Fst*, a measure of population subdivision for a two-allele one locus system. *Fst* ranges from 0, indicating no genetic differentiation, to 1, showing complete differentiation. One formulation of *Fst* is $Fst = (1-(Hs/Ht))$, where *Hs* is the average heterozygosity within subpopulations and *Ht* is the predicted total heterozygosity. Similar statistics, such as Nei's *Gst*, can be estimated for many alleles at many loci (Nei, 1973; 1977; Birky *et al.*, 1989; Chakraborty & Leimar, 1987). A related measure of population subdivision is θ, which equals the between-population component of variance (Weir & Cockerham, 1984; Weir, 1990). *Fst*, *Gst* and θ all estimate the same population parameter. Wright (1951) showed that for neutral alleles, $Fst = 1/(1+4N_em)$, where N_e is the effective population size and m is the average rate of migration in an island model of population structure. Rearranging the equation gives $N_em = 1/4(1/Fst - 1)$, which is an estimate of gene flow, the average number of migrants between populations each generation (Slatkin, 1987). Especially for moderate ($N_em = 5$) and high ($N_em = 10$) levels of gene flow, θ is more accurate in its estimate of N_em than *Gst* (Slatkin, 1994).

Gst and θ were calculated using electrophoretic data for individuals from the 11 different collection sites (unpublished computer program adapted from Weir (1990)). Biosys-1 (Swofford & Selander, 1981) was used to analyse gene frequenty data. χ^2 was used to test for deviation from Hardy-Weinberg proportions at each collection site and to test for differences in allele frequencies among populations, within populations, and overall.

Stepping stone, lattice, and island are all models that describe the pattern of movement between subpopulations (Slatkin, 1985, 1987). The stepping stone model assumes migrants move to the nearest neighbouring populations at a higher rate than to more distant subpopulations. The lattice model is a two-dimensional version of the stepping-stone model. Wright's island model assumes that a migrant from one population is equally likely to move to any of the other populations. To test for isolation by distance, we estimated gene flow (using N_em) for all pairs of populations and regressed it with straight line geographic distance (log-plots, Slatkin, 1994). To test the significance of the relationship we used the Mantel test (Mantel, 1967; Crowley, 1992) to correct for lack of independency between data points (GKR, unpublished computer program). A significant negative slope is evidence for isolation by distance which supports the stepping stone or lattice models. Also, because *Leucaena* is distributed primarily around the island edges, circumferential distances between populations within islands might be a better description of dispersal routes than straight line distances; circumferential distances were regressed against N_em to test for isolation by distance, as well.

Results

Each of the five loci tested exhibited only two electromorphs; allele frequencies for each population are given in table 1. In our study, allozyme frequencies for each population generally did not deviate significantly from Hardy-Weinberg expectations. Of the 55 possible chi-square tests for Hardy-Weinberg frequencies (11 populations × 5 loci), 45 tests were performed, the other ten being omitted because a locus for a particular population was monomorphic (table 1). When the p-value criteria were adjusted for multiple contrasts (by lowering α to $\alpha' = 1-[1-\alpha]^{1/k}$, where $\alpha = 0.05$, $k = 55$; Sokal & Rohlf, 1981) none of the tests allowed rejection of the null hypothesis that allele frequencies were those expected by Hardy-Weinberg.

The overall estimates of *Gst* and θ in our study were 0.098 and 0.095, respectively (table 2). Bootstrapping over loci, the 95% confidence intervals around θ were 0.037–0.15, indicating significant population structure ($\theta > 0$). Negative θ's for three loci indicate values that can not be considered different from 0 (θ is not defined for negative values; Weir, 1990). Estimates of θ for the individual islands were 0.017 (95% conf. limits 0.005–0.031) for Kauai, 0.122 (95% conf. limits 0.055–0.187) for Hawaii, 0.238 (95% conf. limits 0.05–0.35) for Maui, and 0.05 (95% conf. limits 0.00–0.104) for Oahu. The relatively high estimates for *Gst* and θ indicate that there was significant genetic differention among populations both within islands and over all islands (table 2), which suggests limited gene flow among populations at both geographic scales.

χ^2 analysis of gene frequencies confirmed that significant population structure exists between populations within islands. For the islands of Hawaii, Maui, and Oahu, three or four of the five loci showed significantly different allele frequencies for the three populations within the island (table 2). Over all islands, χ^2 analysis of gene frequencies showed highly significant differences for all loci, and the estimate of gene flow, N_em, derived from θ, was 2.4 migrants per generation (95% confidence limits 1.4–6.6) (table 2). There was no significant relationship between N_em and the straight-line geographic distance between populations (Mantel statistic −0.006, 95% confidence limits = −0.27–0.25 (fig. 2). There was also no significant relationship between N_em and circumferential distances, where distances between

Table 1. Allozyme frequencies of 11 populations *Curinus coeruleus* (see fig. 1 for localities).

Locus	Population										
	KPT	WAI	HH	DOL	MAK	LAI	PH	ADM	KAP	HON	KAA
AO											
(N)	36	36	36	36	36	36	24	36	36	34	36
A	0.00	0.03	0.00	0.04	0.06	0.00	0.04	0.13	0.08	0.00	0.14
B	1.00	0.97	1.00	0.96	0.94	1.00	0.96	0.88	0.92	1.00	0.86
IDH-*s*											
(N)	35	36	36	36	36	34	24	35	35	35	36
A	0.56	0.90	0.89	0.61	0.85	0.72	0.77	0.66	0.63	0.91	0.97
B	0.44	0.01	0.11	0.39	0.15	0.28	0.23	0.34	0.37	0.09	0.03
IDH-*f*											
(N)	36	36	36	36	36	36	24	36	36	35	36
A	0.00	0.06	0.17	0.14	0.14	0.17	0.06	0.11	0.26	0.14	0.04
B	1.00	0.94	0.83	0.86	0.86	0.83	0.94	0.89	0.74	0.86	0.96
6PGDH											
(N)	36	36	36	36	36	36	24	36	35	36	35
A	1.00	0.97	0.97	0.93	0.99	1.00	0.83	0.94	0.93	1.00	0.96
B	0.00	0.03	0.03	0.07	0.01	0.00	0.17	0.06	0.07	0.00	0.04
PGM											
(N)	36	33	23	35	36	36	24	36	35	35	36
A	0.42	0.00	0.00	0.26	0.03	0.06	0.02	0.06	0.01	0.03	0.19
B	0.58	1.00	1.00	0.74	0.97	0.94	0.98	0.94	0.99	0.97	0.81

Table 2. *F* statistics and χ^2 analysis for 11 Hawaiian Island populations of *C. coeruleus* at five polymorphic loci.

Locus	Island				All islands
	Hawaii	Kauai	Maui	Oahu	
Populations	3	2	3	3	11
θ					
AO	0.054	0.026	0.014	0.013	0.044
IDH-*s*	0.220	0.013	0.198	0.054	0.105
IDH-*f*	0.077	−0.002	0.089	−0.015	0.036
6PGDH	0.019	0.042	0.000	0.027	0.358
PGM	0.121	−0.002	0.390	0.139	0.189
θ (all loci)	0.122	0.017	0.238	0.050	0.095
G_{st} (all loci)	0.094	0.018	0.180	0.044	0.098
Estimated N_em (from θ)	1.8	14.4	0.8	4.7	2.4
χ^2					
AO	9.8**	2.4	4.0	3.8	40.2**
IDH-*s*	35.5**	1.7	32.1**	10.1**	82.5**
IDH-*f*	14.0**	0.8	15.1**	0.3	36.6**
6PGDH	5.1	4.0*	2.0	7.2*	35.4**
PGM	19.4**	0.9	55.8**	22.2**	134.4**
Total	83.7**	9.8	109.0**	43.7**	329.0**

*P value < 0.05, **P value < 0.01.

populations within islands were measured around the island perimeter (Mantel statistic −0.02, 95% confidence limits= −0.29–0.30).

Discussion

Barriers to gene flow

Our evidence for moderate levels of genetic differentiation among populations on each island coupled with the widespread abundance of food on the islands where collections were made, indicates that *C. coeruleus* does not disperse readily. Many possible barriers to gene flow exist. In species with low mobility, gene flow may be restricted by physical barriers such as bodies of water, mountain ranges, or areas without suitable host plants (Roderick, 1996). Ocean is an obvious barrier between the islands in the Hawaiian archipelago and the mountainous relief and deeply carved valleys typical of the volcanic islands form potential barriers to direct gene flow among populations within each island (Simon *et al.*, 1984). A number of ecological factors also can influence the success of migrants in a new habitat, such as asynchrony of migration events with food availability or the reproductive season of the new habitat, assortative mating for resident genotypes, and territoriality in residents (Roderick, 1992). Although *Leucaena* and the psyllid are now abundant over much of the dry and mesic lowland areas ringing the Hawaiian Islands and host plant/prey are

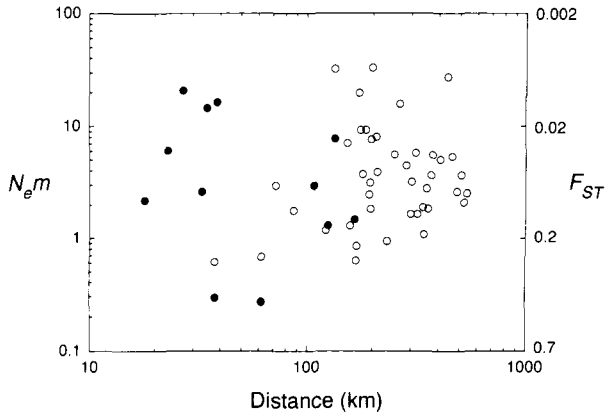

Fig. 2. Plot of gene flow (N_em) against geographical distance for all pairs of the 11 populations. Solid dots (•) are for pairs of populations within islands and open dots (○) are for pairs of populations from different islands. Estimates of N_em were obtained using Weir and Cockerham's θ. Levels of gene flow between populations were not correlated with geographic distance.

abundant, before the introduction of *H. cubana* in 1984 the habitat of *C. coeruleus* was probably patchier and population densities much lower. In addition, the host psyllid populations may show temporal patchiness: populations appear to thrive much of the year and disappear for several months in winter coinciding with population fluctuations in *H. cubana* (two years, personal observation). Small population size and local extinctions are factors that could have influenced the genetic structure we observed in *C. coeruleus* (McCauley, 1991).

Genetic assumptions

The use of electrophoretic or other genetic information to determine population structure makes the important assumption that genetic structure is largely the consequence of gene flow among populations (Daly, 1989). For this to be valid several assumptions must be met: (i) gene flow must be random with respect to the genotypes studied; (ii) the rate of gene flow must exceed the effects of selection; (iii) the rate of gene flow must exceed a minimum level to offset the effects of genetic drift; and (iv) the population must be at genetic equilibrium, a balance between the forces of gene flow and genetic drift (Daly, 1989). Assumptions (i) and (ii) are likely to be met for allozymes that are considered to be neutral or under very weak selection. Also, if many loci give the same results it is unlikely that all are responding similarly to the same selective force. For assumption (iii), Wright (1951) showed that even one migrant every other generation is sufficient to prevent substantial genetic differentiation due to genetic drift.

Assumption (iv), that populations are in genetic equilibrium, is the most difficult to satisfy: several factors will influence the rate of approach to equilibrium including migration rate, population size, the genetic make-up of the individuals founding the populations, and extinction events. The time in generations for *Gst* to go half way to equilibrium is approximately $(ln\ 2)/(2m+1/2N_e)$ (Crow & Aoki, 1984). Solving this equation requires an estimate of m, the migration rate, and N_e, the effective population size. From our own data N_em for *C. coeruleus* is estimated as 2.4 migrants per generation; this level of gene flow is comparable to several other beetle species (Daly, 1989), but lower than estimates for two other cocinellid species (Krafsur *et al.*, 1992; Steiner & Grasela, 1993; Coll *et al.*, 1994). If we estimate the average local population size, N_e, at 1000 (prior to the introduction of *H. cubana*; effective population size is probably much higher since 1984), our estimate of m is 0.0025 and the 1/2 time to genetic equilibrium will be 126 generations. If *C. coeruleus* can complete four generations per year in Hawaii as it does elsewhere (Napompeth & Maneeratana, 1989), approximately 280 generations would have elapsed between the time the beetle was first introduced (1922) and the time when we made our collections (1993–94). Given these conditions, our populations would be close to genetic equilibrium, as required by the model. However, whether the 11 populations that were sampled became established and persisted since shortly after the introduction of *C. coeruleus* 70 years ago is uncertain. Prior to the introduction of *H. cubana*, *C. coeruleus* is reported to have been established on all the major Hawaiian Islands (Funasaki *et al.*, 1989). Historical records of releases of *C. coeruleus* are limited to the initial releases of beetles from Mexico made on the islands of Oahu (1391 beetles) and Maui (50 beetles) in 1922 by the Hawaii State Department of Agriculture, and releases of beetles from Trinidad, West Indies made on Oahu in 1953–54 (316 beetles). More beetles were brought into Hawaii from Guatemala in 1962 but there is no record of a release. There is insufficient information to determine whether *C. coeruleus* was carried to other islands after the initial releases. Without this information it is impossible to speculate whether the present distribution of *C. coeruleus* in the islands is the result of natural dispersal from the initial release sites or human-facilitated dispersal.

Population structure in other coccinellids

Estimates of population subdivision have been made for two other predatory coccinellids: in *Coleomegilla maculata* DeGeer, θ was estimated as 0.0015 ($N_em=166.4$) (Coll *et al.*, 1994) and *Fst* was estimated as 0.14 ($N_em=1.5$) (Steiner & Grasela, 1993); and in *Coccinella septempunctata* Linnaeus the estimate of θ was 0.0148 ($N_em=16.6$)) (Krafsur *et al.*, 1992). Krafsur *et al.* (1992) suggested that the low θ value for *C. septempunctata* populations in North America was a reflection of their recent ancestry rather than extensive gene flow: numerous releases of *C. septempunctata* from Europe were made in the US between 1957 and 1978, but the first detection of self-sustaining populations and the rapid spread of its geographic distribution did not occur until the 1980s (the *C. septempunctata* populations that were detected at this time may actually have been accidental introductions) (Krafsur *et al.*, 1992). *Coleomegilla maculata* on the other hand is native to North America and populations are likely to have reached genetic equilibrium. Krafsur *et al.* (1992) also estimated θ for three populations of *C. septempunctata* from Europe, within the native range of *C. septempunctata*, and found levels of gene flow ($\theta=0.003$; $N_em=83.1$) similar to *C. maculata* from Maryland (Coll *et al.*, 1994). The disparity in estimates of N_em between the two *C. maculata* studies (166.4 vs. 1.5) may be a reflection of the scale and design of the two studies: populations collected by Coll *et al.* (1994) were all from corn fields in Maryland (USA) and the maximum distance between populations was about 120 km, whereas the populations examined by Steiner & Grasela

(1993) were from multiple crop types across a five state region in the midwestern United States, with a latitudinal distance between the furthest populations that was 12 times that of the Maryland study. The level of population subdivision in Hawaiian *Curinus coeruleus* is comparable to the estimate for *C. maculata* in the midwestern United States (Steiner & Grasela, 1993); the maximum distance between populations was approximately 500 km for *Curinus coeruleus* and 1000 km for *C. maculata*.

A relatively large number of *C. coeruleus* (n=1400) were initially introduced to the Hawaiian Islands. The pattern of genetic differentiation between populations within islands and over all islands may indicate that different parts of the islands were founded by small numbers of individuals. Since 1984, the leucaena psyllid has provided *C. coeruleus* with a more abundant source of prey and population sizes are now large. Due to the availability of prey, *C. coeruleus* probably has expanded its distribution within individual islands. Our data, however, indicates that local populations are still distinct and therefore populations have not mixed extensively.

Implications for biological control

Dispersal characteristics of *C. coeruleus* may limit its rapid widespread establishment during release programmes. A system based on mass rearing was developed in Indonesia to overcome this limitation and should serve as a model for other release programmes for this predator. The emphasis in Indonesia was placed on training personnel from government agencies and private industry; these trainees learned to mass-rear *C. coeruleus* and then returned to the provinces to train small land holders and crop protection staff in these techniques. Within a year, over 4000 people were trained and they produced a total of 350,000 beetles for local releases (Soehardjan, 1989). In 1989, the predator was being mass produced in 14 provinces and 88 smaller substations throughout the country. In addition, farmers were encouraged to collect *C. coeruleus* from areas where they were thriving and disseminate them to additional fields, a practice that took hold nationwide (Soehardjan, 1989).

By virtue of its location in the middle of the Pacific, Hawaii has been invaded by many immigrant insect species from east and west; more biological control introductions against immigrant species have been initiated in Hawaii than anywhere else in the world (Funasaki *et al.*, 1988). This reservoir of introduced organisms (predatory insects and mites, parasitic insects and fungi, phytophagous insects, dung beetles, predatory snails and amphibians, etc.) could be used to improve the success of biological introductions elsewhere. Most biological control releases are made for the first time without prior knowledge of the dispersal characteristics of the released organism. Natural history information about the organism can reveal limits to the range and distribution of the organism in its native environment, but the actual extent of movement of individuals within the range may be poorly understood. Hawaii provides a unique natural laboratory to examine dispersal. Where accurate records of releases of a biological control organism have been kept, present patterns of distribution in the islands can give clues to the vagility of the organism. If sufficient genetic variability can be detected, allozyme electrophoretic or DNA sequence data can be used to determine population structure and estimate migration rates (Roderick, 1996). This information could be used to develop release strategies for biological control programmes in other areas using the species studied or a related species. In addition, studies of population structure can be used to establish baseline genetic data for evaluating the importance of genetic variation in classical biological control programmes (see Roderick, 1992).

Acknowledgements

We are grateful to Rosemary Gillespie for her critique of an earlier draft of this paper. Support for this research was provided by the Center for Conservation Research and Training at the Pacific Biomedical Research Center, University of Hawaii at Manoa. Laboratory support is provided by grants from USDA, CDFA, IRRI, and the Rockefeller Foundation. The Hawaii State Department of Agriculture kindly provided historical records of biological control releases.

References

Beardsley, J.W., Mitchell, W.C. & Uchida, G.K. (1989) The leuceana psyllid: a case history of an epidemic agroforestry pest. ADAP Crop Protection Conference.

Birky, C.W., Fuerst, P. & Maruyama, T. (1989) Organelle gene diversity under migration, mutation, and drift: equilibrium expectations, approach to equilibrium, effects of heteroplasmic cells, and comparison of nuclear genes. *Genetics* **121**, 613–627.

Chakraborty, R. & Leimar, O. (1987) Genetic variation within a subdivided population. pp. 89–120 *in* Ryman, N. & Utter, F. (*Eds*) *Population genetics and fisheries management*. Seattle, Washington, University of Washington Press.

Coll, M., Garcia de Mendoza, L. & Roderick, G.K. (1994) Population structure of a predatory beetle: the importance of gene flow for tritrophic level interactions. *Heredity* **72**, 228–236.

Coppel, H.C. & Mertins, J.W. (1977) *Biological insect pest suppression*. New York, Springer Verlag.

Crow, J.F. & Aoki, K. (1984) Group selection for a polygenic behavioral trait: estimating the degree of population subdivision. *Proceedings of the National Academy of Sciences (USA)* **81**, 6073–6077.

Crowley, P.H. (1992) Resampling methods for computation-intensive data analysis in ecology and evolution. *Annual Review of Ecology and Systematics* **23**, 405–447.

Daly, J.C. (1989) The use of electrophoretic data in a study of gene flow in the pest species *Heliothis armigera* (Hubner) and *H. punctigera* Wallengren (Lepidoptera: Noctuidae). *in* Loxdale, H.D. & Den Hollander, J. (*Eds*) *Electrophoretic Studies on Agricultural Pests*. New York, Oxford University Press.

Ewert, M.A. & Chiang, H.C. (1966) Dispersal of three species of coccinellids in corn fields. *Canadian Entomologist* **98**, 999–1003.

Funasaki, G.Y., Jai, P.Y., Nakahara, L.M., Beardsley, J.W. & Ota, A.K. (1988) A review of biological control introductions in Hawaii: 1890 to 1985. *Proceedings of the Hawaiian Entomological Society* **28**, 105–160.

Funasaki, G.Y., Lai, P-Y. & Nakahara, L.M. (1989) Status of natural enemies of *Heteropsylla cubana* Crawford (Homoptera: Psyllidae) in Hawaii. pp. 153–158 in *Leuceana psyllid: problems and management*. Proceedings of an International Workshop held January 16–21, Bogor, Indonesia.

Hagen, K. (1962) Predaceous Coccinellidae. *Annual Review of Entomology* **7**, 289–326.

Herbert, P. & Beaton, M. (1989) *Methodology for allozyme electrophoresis using cellulose acetate.* Beaumont, Texas, Helena Laboratories.

Krafsur, E.S., Obrycki, J.J. & Flanders, R.V. (1992) Gene flow in populations of the seven-spotted lady beetle, *Coccinella septempunctata. Journal of Heredity* **83**, 440–444.

Mantel, N. (1967) The detection of disease clustering and a generalized regression approach. *Cancer Research* **27** (2), 209–220.

McCauley, D.E. (1991) Genetic consequences of local population extinction and recolonization. *Trends in Ecology and Evolution* **6**, 5–8.

McClay, A.S. (1989) Distribution of leucaena psyllid and its nautral enemies in Mexico: implications for biological control. pp. 139–143 in *Leuceana psyllid: problems and management.* Proceedings of an International Workshop held January 16–21, Bogor, Indonesia.

Mitchell, W.C. & Waterhouse, D.F. (1987) Spread of the *Leucaena* psyllid, *Heteropsylla cubana*, in the Pacific. *Leucaena Research Reports* **7** (1), 6–8.

Napompeth, B. (1989) Leucaena psyllid problems in Asia and the Pacific. pp. 1–7 in *Leuceana psyllid: problems and management.* Proceedings of an International Workshop held January 16–21, Bogor, Indonesia.

Napompeth, B. & Maneeratana, T. (1989) Biological and partial ecological life tables of *Heteropsylla cubana* Crawford and its predator, *Curinus coeruleus* Mulsant, in Thailand. pp. 130–138 in *Leuceana psyllid: problems and management.* Proceedings of an International Workshop held January 16–21, Bogor, Indonesia.

Nei, M. (1973) Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences (USA)* **70**, 3321–3323.

Nei, M. (1977) F-statistics and analysis of gene diversity in subdivided populations. *Annals of Human Genetics* **41**, 225–233.

Richardson, B.J., Baverstock, P.R. & Adams, M. (1986) *Allozyme electrophoresis.* New York, Academic Press.

Roderick, G.K. (1992) Post-colonization evolution of natural enemies. pp. 71–86 *in* Kauffman, W.C. & Nechols, J.E. (*Eds*) *Selection criteria and ecological consequences of importing natural enemies.* Thomas Say Publications in Entomology: Proceedings.

Roderick, G.K. (1996) Geographic structure of insect populations: gene flow, phylogeography, and their uses. *Annual Review of Entomology* **41**, 263–290.

Showler, A.T. (1995) Leucaena psyllid, *Heteropsylla cubana* (Homoptera: Psyllidae), in Asia. *American Entomologist* **41**, 49–54.

Simon, C.M., Gagne, W.C., Howarth, F.G. & Radovsky, F.J. (1984) Hawaii: a natural entomology laboratory. *Bulletin of the Entomological Society of America* **30** (3), 8–17.

Slatkin, M. (1985) Gene flow in natural populations. *Annual Review of Ecology and Systematics* **16**, 393–430.

Slatkin, M. (1987) Gene flow and the geographic structure of natural populations. *Science* **236**, 787–792.

Slatkin, M. (1994) Gene flow and population structure. pp. 3–17 *in* Real, L.A. (*Ed.*) *Ecological Genetics.* Princeton University Press, Princeton, New Jersey.

Smith, C.W. (1985) Impact of alien plants on Hawaii's native biota. pp. 180–250, *in* Stone, C.P. & Scott, J.M. (*Eds*) *Hawaii's terrestrial ecosystems preservation and management.* Cooperative National Park Resources Studies Unit, University of Hawaii, Honolulu.

Soehardjan, M. (1989) Transfer of technology in the utilization of *Curinus coeruleus* Mulsant. pp. 181–183 in *Leuceana psyllid: problems and management.* Proceedings of an International Workshop held January 16–21, Bogor, Indonesia.

Sokal, R.R. & Rohlf, F.J. (1981) *Biometry.* W.H. Freeman & Company, San Francisco.

Steiner, W.W.M. & Grasela, J.J. (1993) Population genetics and gene variation in the predator, *Coleomegilla maculata* (DeGeer) (Coleoptera: Chyrsomelidae). *Annals of the Entomological Society of America* **86**, 309–321.

Swezey, O.H. (1923) Records of introduction of beneficial insects into the Hawaiian Islands. *Proceedings of the Hawaiian Entomological Society* **5**, 299–304.

Swofford, S.L. & Selander, R.B. (1981) Biosys-1: a Fortran program for the comprehensive analysis of electrophoretic data in population genetics and systematics. *Journal of Heredity* **72**, 281–283.

Uchida, G.K., Beardsley, J.W., Reimer, N.J., & Wheeler, R.A. (1992) Comparison of populations of *Heteropsylla cubana* Crawford (Homoptera: Psyllidae) and its parasitoids on seven accessions of *Leucaena* (Leguminose: Minosoideae) in Hawaii. *Proceedings of the Hawaiian Entomological Society* **31**, 97–107.

Wagiman, F.X., Mangoendihardjo, S. & Mahrub, E. (1989) Performance of *Curinus coeruleus* Mulsant as a predator against leucaena psyllid. pp. 163–165 in *Leuceana psyllid: problems and management.* Proceedings of an International Workshop held January 16–21, Bogor, Indonesia.

Weir, B.S. (1990) Intraspecific differentiation. *in* Hillis, D.M. & Moritz, C. (*Eds*) *Molecular systematics,* Sunderland, Massachusetts, Sinauer Associates.

Weir, B.S. & Cockerham, C.C. (1984) Estimating F-statistics for the analysis of population structure. *Evolution* **38**, 1358–1370.

Wright, S. (1951) The genetical structure of populations. *Annals of Eugenics* **15**, 323–354.

(Accepted 22 December 1995)