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Abstract

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Keywords

convergent ladybeetle, allozymes, gene diversity, augmentation, biological control

Disciplines

Entomology | Evolution | Other Ecology and Evolutionary Biology | Population Biology

Comments

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COMPARATIVE STUDIES OF THREE POPULATIONS OF THE LADY BEETLE PREDATOR *HIPPODAMIA CONVERGENS* (COLEOPTERA: COCCINELLIDAE)

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ABSTRACT

Allozyme electrophoresis showed much genetic variation in *Hippodamia convergens*, suggesting the possibility of geographic genetic differentiation. Twenty-two of 31 putative allozyme loci resolved on acrylamide gels from *H. convergens* populations were polymorphic (71%). Heterozygosity (diversity) averaged over all loci was $21.3 \pm 4.2\%$. However, thirteen polymorphic loci examined in F1 Honduran \times Iowa hybrids indicated that all alleles were shared in the two populations. In addition, no significant geographic variation was observed in developmental and reproductive responses of *H. convergens* from Iowa, California, and Honduras to aphid prey densities. All inter-population and backcrosses produced fertile eggs. Adult body size of *H. convergens* from Iowa and Honduras was similar. This study indicates that augmentatively released California *H. convergens* could successfully mate with local *H. convergens* populations in Iowa and Honduras.

Key Words: convergent ladybeetle, allozymes, gene diversity, augmentation, biological control

RESUMEN

Electroforesis de alozima demostró gran variación genética en *Hippodamia convergens*, sugiriendo la posibilidad de diferenciación genética por geografía. Veintidós de 31 lugares de alozimas putativas resueltas en geles de acrilamida de poblaciones de *H. convergens* fueron polimórficos (71%). Heterozigosidad (diversidad) promedio sobre todos los lugares fue $21.3 \pm 4.2\%$. Sin embargo, trece lugares polimórficos examinados en híbridos F1 Hondureño \times Iowa indicaron que todos los alelos fueron compartidos en ambas poblaciones. Adicionalmente, no se observó variación geográfica significativa en respuestas reproductivas y de desarrollo de *H. convergens* de Iowa, California, y Honduras a densidades de presa de áfido. La inter población y cruces de híbridos "backcross" produjeron huevos fértiles. El tamaño del cuerpo adulto de *H. convergens* de Iowa y Honduras fue similar. Este estudio indica que *H. convergens* liberado aumentativamente pudiera aparear satisfactoriamente con poblaciones locales de *H. convergens* en Iowa y Honduras.

Yearly mass collections and augmentative releases of overwintering adult *Hippodamia convergens* from California are made for aphid suppression, even though evidence for effectiveness is limited (Hagen 1962; Majerus 1994; Hodek & Honek 1996; Obrycki & Kring 1998). Dreistadt & Flint (1996) reported a temporary 3-day decline in aphid densities following release of *H. convergens* adults. Release of *H. convergens* from California may have negative effects on local populations of *H. convergens* because of the distribution of pathogens and parasitoids found in adults (Lipa & Steinhaus 1959; Sluss 1968; O'Neil et al. 1998). An additional concern that has been raised for *Danaus plexippus* L., a species that is also distributed widely by humans (Brower et al. 1995), relates to the idea that

unique local populations with favorable co-adapted genotypes may be compromised by releases of foreign genotypes. Characterization of *H. convergens* intra-specific variation is needed to assess the potential effects of releases of California beetles on local *H. convergens* populations.

One trait that has been examined in *H. convergens* populations from Arizona, Cuzco (Peru), New York, and Oregon, is the thermal requirement for development (Butler & Dickerson 1972; Escalante 1972; Obrycki & Tauber 1982; Miller 1992). Consistency in developmental thresholds of *H. convergens* across geographically separated populations in North America has been reported by Miller (1992). However, earlier studies on *H. convergens* reported differences in thermal responses between populations from Arizona and

New York (Butler & Dickerson 1972; Obyrcki & Tauber 1982). A second set of traits that may be used to characterize intra-specific variation are those related to predator responses to prey species, e.g., prey suitability (Tauber et al. 1995).

The objectives of this study were to 1) compare allozyme variation and developmental responses of *H. convergens* from two North American (Iowa and California) and one Central American (Honduras) population to aphid prey, and 2) test for reproductive isolation among *H. convergens* populations from Honduras, Iowa, and California.

MATERIALS AND METHODS

Developmental Characteristics

In 1994, *Hippodamia convergens* adults were collected at the Escuela Agrícola Panamericana, Zamorano, Honduras, and in Story and Marion Counties, Iowa. Approximately 50 adult *H. convergens* were sent from Honduras to the USDA-ARS, Beneficial Insects Introduction Research Laboratory, Newark, DE, where they were reared for one generation. First laboratory generation adults were sent to Iowa State University. Six lines, each descended from a different single pair mating, were established from Honduras beetles and 10 lines were established from Iowa beetles; eggs were collected daily. Pairs were kept at 24°C, (L:D) 16:8 and fed pea aphids, *Acyrtosiphon pisum* (Harris), and green peach aphids, *Myzus persicae* (Sulzer) *ad libitum*. Forty larvae from each pair were reared individually on 2-4 *A. pisum* per day at 24°C, (L:D)16:8. Observations on larval survival and developmental stage were made every 24 h.

In 1997, *H. convergens* were collected in Ames, Iowa, and in the Departamento Francisco Morazan, Honduras. Adults from California were provided by Gardens Alive, Lawrenceburg, IN. Five pairs from each population, (California, Iowa, and Honduras) were maintained at 24°C, 16:8 L:D; eggs were collected daily. To examine developmental responses to prey density, 25 first instars from each population were reared on three levels of *A. pisum*: two per day, three per day and >20 per day.

Inter-population Crosses and Reproductive Responses

In 1994, 30 pairs of second laboratory generation individuals were established using virgin females from Honduran and Iowan populations: 3 pairs were Honduras × Honduras crosses, 3 were Iowa × Iowa crosses, 12 were Iowa female × Honduras male, and 12 were Honduras female × Iowa male. Pairs were fed daily *ad libitum* with *A. pisum* and *M. persicae*. Eggs were collected every day for seven days to determine fecundity (number of eggs laid) and fertility (proportion of fertile

eggs). Following eclosion of at least half of the eggs in each egg mass, the egg masses and newly eclosed larvae were frozen to avoid cannibalism. The number of fertile eggs in each egg mass was estimated by adding eclosed larvae and darkened eggs. Eggs were considered infertile if they were pale yellow and slightly shrunken.

Fifteen larvae from each of the thirty mating pairs were reared individually at 24°C, (L:D)16:8. Twelve adults from each cross were used in a backcross experiment. Twelve pairs were backcrossed to Honduras, [(H×IA) × (H×H)], 12 were backcrossed to Iowa [(H×IA) × (IA×IA)], and 12 were Honduras × Iowa reciprocal crosses [(H×IA) × (H×IA)]. The pairs were fed daily with *A. pisum* and *M. persicae*. Eggs were collected every day for 7 days to determine fecundity and fertility. Observations of larval development and survival were made every 24 h on ten larvae from each pair.

In 1997, F1 adults reared from Iowa, California, and Honduras populations were crossed. Thirty pairs were established: 7 pairs were Iowa females × Honduras males, 7 were Iowa males × Honduras females, 3 were Iowa females × California males, 6 were Iowa males × California females, 6 were California females × Honduras males, and 1 pair was California male × Honduras female. The pairs were fed >20 *A. pisum* per day for 15 days. When egg masses were observed, they were placed in glass vials and held to determine fertility. Larvae were removed from the vials daily to prevent cannibalism.

Size of adult *H. convergens* from Honduras and Iowa

To compare morphometric characteristics of *H. convergens* adults from Honduras and Iowa, intercrosses, and reciprocal backcrosses, pronotal and elytral length and width were measured by using NIH image software (Macintosh version 1.57). Before measurements were taken, each adult was pinned through the right elytron at exactly the same distance from the head of the pin. Each beetle was photographed using a color video camera (JVC-TK1070U) mounted on a stereo zoom microscope. The filmed images were digitally captured, amplified and measured in millimeters.

Genetic Diversity Estimates

To estimate gene diversity, beetles from Honduras and Iowa were killed by freezing and stored at -80°C. Reciprocal crosses of Honduras and Iowa beetles provided hybrid progeny; 46 of which were frozen for genetic analysis. Procedures for preparing ladybeetle homogenates for allozyme electrophoresis, histochemical demonstration of putative loci, and statistical methods were those already published (Krafsur et al. 1996a, b).

Voucher specimens of *H. convergens* are deposited in the Iowa State University Insect Collection.

Data Analysis

In 1994, data obtained from rearing and adult body measurements were summarized by mating pair and means were calculated. Five variables were compared among the populations, crosses and backcrosses, using analysis of variance (PROC GLM, SAS Institute 1985): developmental time, survivorship, fecundity, fertility and adult body size. Means were separated by using a least significance difference test (LSD). Percentage survival and fertility were arcsine transformed [$\arcsin(\sqrt{\text{proportion}})$] before analysis. In 1997, two-way ANOVA was used to compare the effects of aphid prey and population of *H. convergens* on development and survival.

A preliminary analysis revealed that the adult body measurements were correlated to each other. Thus, adult size was compared among groups using an average of the four standardized body measurements. The standardization was done by subtracting the measurement mean among groups from each measurement, and then dividing by the standard deviation among groups.

RESULTS

Developmental Responses

Individuals from Honduras required approximately 3-4 more days to complete preimaginal development than individuals from Iowa, Honduras \times Iowa crosses, and the backcrosses to Honduras and Iowa (Table 1). Similarly, in 1997, Honduran beetles reared on *A. pisum* per day required 27.3 ± 3.2 days to complete development, approximately 2-5 days longer than the Iowa and California beetles (Table 2). Developmental time varied with population ($F = 98.63$; $df = 2, 101$; $P = 0.001$), sex ($F = 7.89$; $df = 1, 101$; $P = 0.048$), diet ($F = 514.6$; $df = 2, 101$; $P = 0.001$) and the interaction

between population and diet ($F = 14.3$; $df = 4, 101$; $P = 0.012$).

Preimaginal survival of *H. convergens* from Honduras and Iowa and the Honduras - Iowa crosses ranged from 78 to 89% (Table 3). In 1997, survivorship of Iowa, California, and Honduras beetles on three levels of aphid prey was similar; no effect of population ($F = 5.81$; $df = 2, 4$; $P = 0.066$) or diet ($F = 1.88$; $df = 2, 4$; $P = 0.265$) was observed (Table 2). For Iowa and Honduran *H. convergens*, survivorship increased with higher levels of *A. pisum* per day, but this was not observed for the California beetles (Table 2).

Reproductive Responses

No differences were observed among groups in fertility and fecundity, however, large variation within groups was observed in both fecundity and fertility (Table 4). Fertility ranged from 70-76% and 79-94% for the Honduran and Iowan populations, respectively. Fertility ranged from 4-93% for the Honduras \times Iowa crosses, 66-96% for the backcrosses to Honduras, and 34-97% for backcrosses to Iowa. In 1997, all 30 crosses among California, Iowa, and Honduras *H. convergens* produced similar numbers of fertile eggs (Gomez 1998).

Size of Adult *Hippodamia convergens*

The average pronotal width and length of Honduras and Iowa *H. convergens* was 2.68 and 1.27 mm, respectively (Table 5). The average elytral width and length among these groups was 2.16 and 4.98 mm, respectively (Table 5). Significant differences were observed among original populations, crosses and backcrosses in the standardized female body size ($F = 7.96$; $df = 4, 51$; $P = 0.001$) but not in the standardized male body size ($F = 0.42$; $df = 4, 45$; $P = 0.79$).

TABLE 1. DEVELOPMENTAL TIME (DAYS; $X \pm SE$) OF *HIPPODAMIA CONVERGENS* FROM HONDURAS, HONDURAS \times IOWA CROSSES AND RECIPROCAL BACKCROSSES; REARED ON 2-3 APHIDS PER DAY, 24°C, L:D 16:8.

	N ^c	Days \pm SE ^{a, b}						
		Egg	Instar I	Instar II	Instar III	Instar IV	Pupa	Egg-Adult
Honduras	89 (6)	3.9 \pm 0.2	3.7 \pm 0.5	2.6 \pm 0.3	2.9 \pm 0.5	6.9 \pm 0.5 a	7.0 \pm 0.8 a	26.9 \pm 1.4 a
Iowa	236 (8)	3.5 \pm 0.2	3.2 \pm 0.1	2.1 \pm 0.1	2.5 \pm 0.1	6.8 \pm 0.3 a	5.3 \pm 0.1 b	23.1 \pm 0.6 b
Hon \times IA	424 (36)	3.6 \pm 0.1	3.2 \pm 0.1	2.4 \pm 0.1	2.6 \pm 0.1	5.9 \pm 0.1 b	5.6 \pm 0.1 b	23.4 \pm 0.2 b
F1 \times Hon	160 (12)	3.5 \pm 0.2	3.6 \pm 0.3	2.6 \pm 0.2	2.8 \pm 0.1	6.2 \pm 0.2 ab	5.6 \pm 0.3 b	24.3 \pm 0.4 b
F1 \times IA	87 (9)	3.7 \pm 0.1	3.4 \pm 0.3	2.3 \pm 0.2	2.9 \pm 0.2	6.1 \pm 0.3 b	5.4 \pm 0.1 b	23.7 \pm 0.4 b
	(F; df)	(1.2; 4, 64)	(1.4; 4, 64)	(1.1; 4, 64)	(1.5; 4, 64)	(3.9; 4, 64)	(3.8; 4, 64)	(6.9; 4, 64)
	(P)	(0.304)	(0.246)	(0.344)	(0.210)	(0.007)	(0.008)	(0.001)

^aValues represent means of mating pairs.

^bMeans followed by the same letter in a column are not statistically different ($P > 0.05$).

^cNumber of individuals (number of pairs).

TABLE 2. DEVELOPMENTAL TIME, SURVIVAL, AND ADULT CHARACTERISTICS OF THREE POPULATIONS OF *HIPPODAMIA CONVERGENS* REARED ON THREE LEVELS OF *ACYRTHOSIPHON PISUM*; 24°C; 16:8 L:D; 1997.

Population	<i>A. pisum</i> /day	Dev. time Days; X ± SD	Survival* %	Sex ratio F: M	Female weight (mg)	Male weight (mg)
Honduras	2	27.3 ± 3.2	52 [13]	5:8	8.7 ± 2.3	8.0 ± 0.4
	3	23.4 ± 2.0	56 [14]	8:6	8.5 ± 1.6	8.9 ± 0.9
	>20	16.8 ± 1.0	84 [21]	15:6	24.8 ± 3.6	19.3 ± 2.6
Iowa	2	24.6 ± 1.2	48 [12]	3:9	8.2 ± 0.7	6.9 ± 0.4
	3	21.4 ± 2.2	56 [14]	5:9	10.1 ± 0.6	8.3 ± 0.6
	>20	16.9 ± 0.6	72 [18]	11:7	21.7 ± 2.5	17.9 ± 1.5
California	2	21.7 ± 1.1	28 [7]	3:4	8.4 ± 1.5	8.3 ± 0.8
	3	19.5 ± 1.1	44 [11]	6:5	10.7 ± 1.3	9.1 ± 1.1
	>20	15.7 ± 1.0	28 [7]	5:2	25.6 ± 3.0	21.4 ± 4.0

*Numbers in square parentheses = number of *H. convergens* that completed development; 25 first instars started on each aphid diet.

In 1997, sex ($F = 23$; $df = 1,101$; $P = 0.009$), levels of aphid prey provided to the larvae ($F = 412.3$; $df = 2,101$; $P = 0.001$) and the interaction between diet and sex ($F = 7.83$; $df = 3,101$; $P = 0.001$) affected weight of adult *H. convergens*, but no differences among populations were observed ($F = 4.89$; $df = 2,101$; $P = 0.084$) (Table 2). A positive correlation was observed between levels of *A. pisum* provided to larvae and adult weight of Iowa ($R^2 = 0.91$), California ($R^2 = 0.92$) and Honduras ($R^2 = 0.87$) *H. convergens*.

Genetic Diversity

Of 31 putative allozyme loci resolved on acrylamide gels, 22 were polymorphic (71%). Heterozygosity (diversity) averaged over all loci was $21.3 \pm 4.2\%$; an average 2.9 ± 0.3 alleles per locus was observed (Table 6). The heterozygosity of only polymorphic loci was $30 \pm 4.8\%$ with 3.6 ± 1.3 alleles. The distribution of single locus heterozygosities (Fig. 1) shows high levels of diversity and is

consistent with the neutral theory of mutations (Nei et al. 1976). Examination of F1 Honduran × Iowa hybrids at 13 polymorphic loci showed no alleles not detected in North American beetles.

DISCUSSION

Response to aphid prey levels was similar among populations, even though *A. pisum* has not been reported from Honduras and therefore may not be a common prey species there (Castro 1993). Total developmental time was inversely correlated with the number of aphid prey provided to *H. convergens* larvae. A reduction of more than 4 days in the total developmental time was observed when aphid prey was increased from 3 to > 20 *A. pisum* per day. Similarly, a reduction in total developmental time was observed for the hemipteran predator *Podisus maculiventris* (Say) when fed greater quantities of Mexican bean beetle larvae, *Epilachna varivestis* Mulsant (Legaspi and O'Neil 1994).

TABLE 3. PERCENTAGE SURVIVAL (X ± SE) FOR LIFE STAGES OF *HIPPODAMIA CONVERGENS* FROM HONDURAS, IOWA, HONDURAS × IOWA CROSSES AND RECIPROCAL BACKCROSSES.

	Survival (% ± SE) ^a					
	Instar I	Instar II	Instar III	Instar IV	Pupa	Preimaginal
Honduras	90.0 ± 4.5 ab	97.0 ± 1.6	96.2 ± 3.3	97.2 ± 2.3	95.0 ± 5.0	78.1 ± 8.1
Iowa	98.6 ± 0.7 b	96.9 ± 1.6	98.4 ± 0.9	97.9 ± 0.9	96.6 ± 1.3	88.9 ± 2.1
Hon × IA	95.1 ± 1.4 b	97.1 ± 0.9	99.5 ± 0.4	97.3 ± 1.0	98.9 ± 0.6	88.3 ± 1.7
F1 × Hon	87.7 ± 3.9 a	94.4 ± 3.1	98.3 ± 1.7	97.6 ± 2.4	94.8 ± 2.8	76.7 ± 6.4
F1 × IA	92.2 ± 2.8 ab	98.8 ± 1.1	96.5 ± 2.4	99.1 ± 0.9	98.6 ± 1.4	85.7 ± 2.3
(F; df)	(2.54; 4, 64)	(0.47; 4, 64)	(1.30; 4, 64)	(0.36; 4, 64)	(1.43; 4, 64)	(1.32; 4, 64)
(P)	(0.04)	(0.75)	(0.28)	(0.83)	(0.23)	(0.27)

^aMeans followed by the same letter in a column are not statistically different ($P > 0.05$).

TABLE 4. MEAN FECUNDITY AND PERCENTAGE FERTILITY OF *HIPPODAMIA CONVERGENS* EGGS FROM HONDURAS AND IOWA, THEIR OFFSPRING (HONDURAS × IOWA) AND RECIPROCAL BACKCROSSES.

Group	N ^a	Fecundity			Fertility (%)		
		(X ± SE)	min.	max.	(X ± SE)	min.	max
Honduras	6	119.0 ± 32.8	59	172	73.7 ± 1.5	70.1	76.3
Iowa	8	120.7 ± 56.0	24	218	84.7 ± 4.7	79.2	94.0
Hon × IA	35	111.8 ± 8.8	7	225	72.0 ± 3.3	4.4	93.5
F1 × Hon	12	119.8 ± 10.8	23	208	84.8 ± 0.2	66.1	95.5
F1 × IA	12	104.8 ± 10.0	31	188	76.0 ± 3.6	34.0	97.2
(F; df; P)		(0.11; 4, 55; 0.97)			(1.58; 4, 55; 0.24)		

^aNumber of females.

Total developmental times of *H. convergens* from Iowa, California, and Honduras fed > 20 *A. pisum* per day were approximately 3 days shorter than *H. convergens* from Arizona, Oregon and New York (20 days) reared at similar temperatures (Miller 1992, Obrycki & Tauber 1982). Hagen and Sluss (1966) showed that developmental time and life span of *H. convergens* from California were influenced by prey species. Thus, these observed differences might be due to the use of different aphid species among studies. Butler and Dickerson (1972) reared *H. convergens* on the cotton aphid, *Aphis gossypii* Glover, and *A. pisum*, whereas Miller (1992) used the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), and the oat-bird cherry aphid, *Rhopalosiphum padi* (L). Differences in developmental time between beetles fed > 20 *A. pisum* per day in our study and those reared by Obrycki & Tauber (1982) on *A. pisum* may be due to geographical variation.

The size of *H. convergens* crosses and backcrosses are within the ranges described by Gordon

(1985). Weight of adult *H. convergens* was highly correlated to levels of *A. pisum* provided to larvae. When the prey provided was increased from 3 to >20 *A. pisum* per day, adult weights doubled.

Hippodamia convergens from Iowa, Honduras, and California mated and exhibited similar fecundity and fertility. The number of eggs produced per day by *H. convergens* inter-population crosses (14 to 17 eggs per day) was slightly lower than that observed by Hagen & Sluss (1966) for California *H. convergens* (20 eggs per day). The fecundity of *H. convergens* was higher in our study than that observed by Wipperfurth et al. (1987), who fed beetles fewer aphids than they could consume on a daily basis.

High levels of gene diversity have been detected in several species of ladybirds (Krafsur & Obrycki 1996; Krafsur et al. 1992, 1995, 1996a, b, 1997). Of the 11 coccinellid species examined, only one, *Coleomegilla maculata* Degeer, shows evidence of being a species complex (Munyanza & Obrycki 1998; Krafsur & Obrycki 2000). The

TABLE 5. SIZE OF PRONOTUM AND ELYTRA OF ADULT *HIPPODAMIA CONVERGENS* FROM HONDURAS AND IOWA, THEIR OFFSPRING (HONDURAS × IOWA) AND RECIPROCAL BACKCROSSES.

Group	Sex (N)	Pronotum (mm; X ± SD)		Elytra (mm; X ± SD)	
		Width	Length	Width	Length
Honduras	F (5)	2.88 ± 0.12	1.42 ± 0.06	2.46 ± 0.18	5.30 ± 0.18
	M (4)	2.72 ± 0.12	1.28 ± 0.05	2.22 ± 0.12	4.95 ± 0.30
Iowa	F (5)	2.65 ± 0.20	1.34 ± 0.11	2.26 ± 0.17	5.01 ± 0.27
	M (5)	2.79 ± 0.12	1.33 ± 0.03	2.34 ± 0.02	4.79 ± 0.21
Hon × IA	F (29)	2.68 ± 0.22	1.26 ± 0.10	2.13 ± 0.15	5.01 ± 0.45
	M (30)	2.63 ± 0.25	1.26 ± 0.13	2.08 ± 0.26	4.91 ± 0.47
F1 × Hon	F (11)	2.64 ± 0.10	1.29 ± 0.10	2.12 ± 0.16	4.89 ± 0.37
	M (9)	2.90 ± 0.12	1.31 ± 0.11	2.38 ± 0.16	5.27 ± 0.27
F1 × IA	F (9)	2.49 ± 0.06	1.15 ± 0.11	2.04 ± 0.10	4.76 ± 0.14
	M (5)	2.74 ± 0.09	1.21 ± 0.08	2.23 ± 0.10	5.06 ± 0.11

TABLE 6. GENE DIVERSITY H_e AT PUTATIVE ALLOZYME LOCI IN *HIPPODAMIA CONVERGENS*.

Enzyme	Locus	E.C. number system	Buffer	Expected heterozygosity ^a h_e
Acid phosphatase	<i>Acp</i>	EC 3.1.3.2	NAM	0.539
Aconitase	<i>Aco</i>	EC 4.2.1.3	OD	0.502
Aldehyde oxidase	<i>Aox</i>	EC 2.6.1.1.	NAM	0.623
Adenylate kinase	<i>Adk-1</i>	EC 2.7.4.3.	NAM	0.454
	<i>Adk-2</i>			0
Arginine kinase	<i>Argk</i>	EC 2.7.3.3.	NAM	0
Diaphorase	<i>Dia-1</i>	EC 1.6.2.2.	NAM	0
	<i>Dia-2</i>			0
Esterase	<i>Est</i>	EC 3.1.1.-	NAM	
Fructose biphosphatase	<i>Fbp</i>	EC 3.1.3.11.	NAM	0.237
Fumarate hydratase	<i>Fum</i>	EC 4.2.1.2.	OD	0
Glucose-6-phosphate dehydrogenase	<i>G6pd</i>	EC 1.1.1.49	NAM	0.418
Glyceraldehyde-3-phosphate dehydrogenase	<i>G3pd</i>	EC 1.2.1.12	NAM	0.036
Glycerophosphate dehydrogenase	<i>Gpd</i>	EC 1.1.1.8.	TBE	0
Hexokinase	<i>Hk</i>	EC 2.7.1.1.	TBE	0.530
Hydroxy acid dehydrogenase	<i>Had-1</i>	EC 1.1.1.30	NAM, OD	0.311
	<i>Had-2</i>			0.234
Isocitrate dehydrogenase-1	<i>Idh-1</i>	EC 1.1.1.42	NAM	0.036
Isocitrate dehydrogenase-2	<i>Idh-2</i>		NAM	0.053
Malate dehydrogenase	<i>Mdh-1</i>	EC 1.1.1.37	NAM, OD	0.102
	<i>Mdh-2</i>			0
Malic enzyme	<i>Me-1</i>	EC 1.1.1.40	OD	0
Mannose-6-P-dehydrogenase	<i>Mpi</i>	EC 5.3.1.8	NAM	0.114
Phosphoglucosomerase	<i>Pgi</i>	EC 5.3.1.9	OD	0
Phosphoglucomutase	<i>Pgm</i>	EC 5.4.2.2	NAM, OD	0.201
6-Phosphogluconate dehydrogenase	<i>6pgd</i>	EC 1.1.1.44	NAM	0.297
Sorbitol dehydrogenase	<i>Sdh</i>	EC 1.1.1.14	NAM	0.610
Superoxide dismutase	<i>Sod-1</i>	EC 1.15.1.1	OD	0.018
	<i>Sod-2</i>			0.036
Trehalase	<i>Tre</i>	EC 3.2.1.28	NAM	0.683
Triose-phosphate isomerase	<i>Tpi</i>	EC 5.3.1.1	NAM	0.086

Mean of polymorphic loci: $H_e = 0.301$; SD = 0.048

Mean of all loci ($n = 31$): $H_e = 0.213$; SD = 0.042

^aExpected proportions heterozygous when mating is random.

high levels of variation characteristic of ladybirds is indicative of large population sizes and high rates of gene flow, inferences supported by ecological and genetic studies. High rates of gene flow in *H. convergens* argue against the notion that disruption of co-adapted gene complexes (supergenes) will cause local populations to decline dramatically (see discussion in Dobzhansky & Pavlovsky 1960). It remains to be determined if supergenes exist in ladybirds, and if alternative gene arrangements are lethal, or if a lower frequency of supergene carriers somehow causes populations to decline. Colonizing species such as ladybirds must naturally accommodate alternative intervals of local inbreeding and invasion by foreign genotypes throughout much of their evolutionary history. Environmental influences, rather than genetic, most likely explain the failure of deliberate ladybird introductions to become established.

All inter-population *H. convergens* crosses in our studies produced fertile eggs. Thus, no intrinsic reproductive barriers exist among Iowa, Honduras, and California populations. If *H. convergens* from California are augmentatively released in Honduras or Iowa, individuals or their progeny may interbreed. Our results indicate that if *H. convergens* from California do cross with local populations, no detrimental effects in F1 developmental and reproductive parameters in response to one species of aphid prey (*A. pisum*) may occur. Predation of other prey species of local importance may need to be examined (Bogran & Obrycki 1998). However, this does not mean that the F1 *H. convergens* crosses would be well suited to local conditions. For example, photoperiodic responses for diapause induction may be different among California and local populations of *H. convergens*, and this parameter could be altered in the F1 crosses (see Tauber et al. 1997). The observed interbreed-

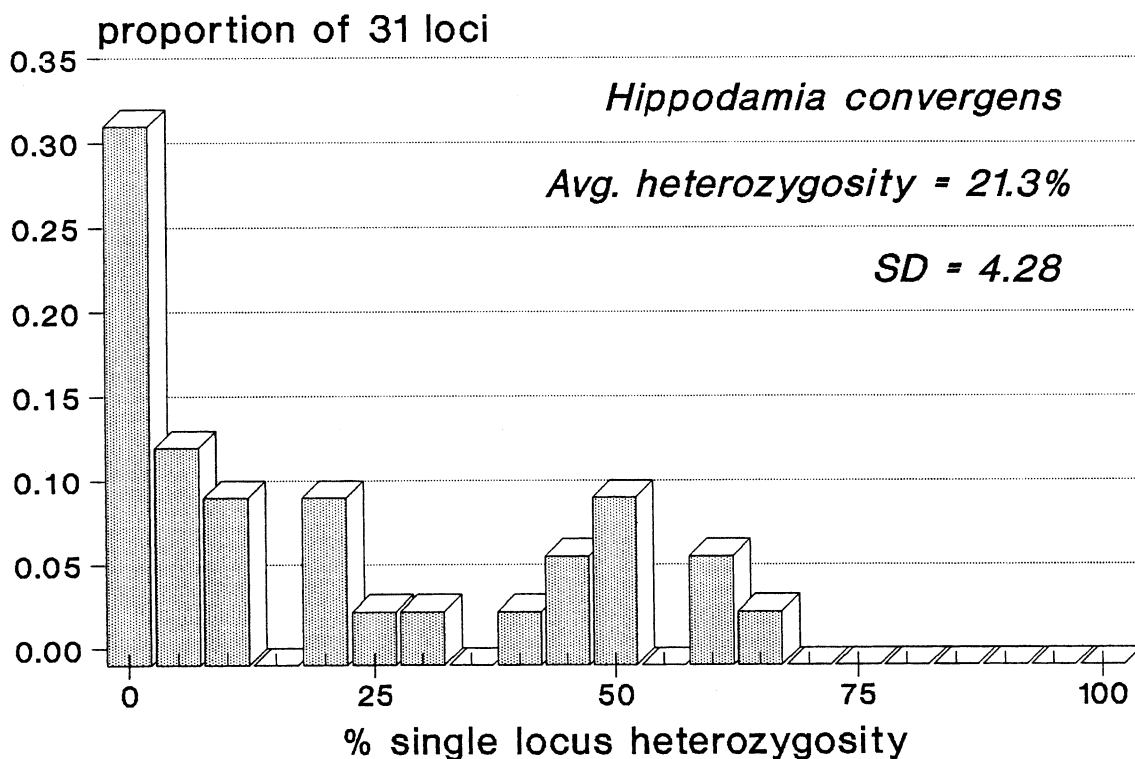


Fig. 1. Single locus heterozygosity (h_e) in *Hippodamia convergens*.

ing among California, Honduras, and Iowa beetles, in addition to the presence of parasitoids and pathogens in California adults, combined with the lack of substantial evidence of effectiveness, suggest that the practice of augmentative releases of field collected *H. convergens* needs to be carefully examined for non-target effects.

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