Inheritance of seasonal cycles in *Chrysoperla* (Insecta: Neuroptera)

CATHERINE A. TAUBER AND MAURICE J. TAUBER

Department of Entomology, Comstock Hall, Cornell University, Ithaca, N.Y. 14853, USA

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Summary

Two separate, but interacting, genetic systems underlie the variation in seasonal cycles among members of the *Chrysoperla carnea* species-complex. The two systems are expressed as all-or-none reproductive responses to photoperiod and prey (i.e. short-day/long-day requirement for reproduction versus long-day reproduction and prey requirement for reproduction versus reproduction without prey). In each case the alternative to reproduction is reproductive diapause. The photoperiodic responses are determined by alleles at two unlinked autosomal loci. The expression of dominance by the alleles at these loci varies among geographical populations. The genes that determine the photoperiodic responses also act as suppressors of the genes that govern responsiveness to prey. An autosomal, polygenic system, with a threshold for the expression of diapause, determines responsiveness to prey. The two genetic systems are important to seasonal diversification and speciation within the *C. carnea* species-complex.

1. Introduction

Patterns of genetic differences among taxa provide vital clues to past evolutionary events, and they offer insights into the action of evolutionary processes (see Endler, 1977; Arnold, 1981; Lewontin, 1986). In general, information about the types and amount of genetic variation among taxa comes from three major sources: (*a*) evaluation of morphological, behavioural and physiological differences; (*b*) identification of patterns of variability, for example in chromosomal configurations, electrophoretically mobile proteins and DNA sequences; and (*c*) analysis of the inheritance of diversified traits through hybridization studies. Each approach constitutes a powerful tool. Each has strengths and weaknesses, and each gives a different insight into existing genetic variation.

Of the three approaches, hybridization studies with animals are the least prevalent. Many species are not amenable to rearing or study under controlled conditions. Animals with significant ecological and behavioural differences often will not interbreed successfully. Furthermore, in many cases interspecific variation, especially ecological variation, is not sufficiently well known to identify specific, inherited traits for genetic analysis (see Tauber, Tauber & Masaki, 1986).

Some of the above problems have been overcome for the *Chrysoperla carnea* species-complex (Insecta: Neuroptera: Chrysopidae), and it is possible to investigate the genetics of interspecific and interpopulation differences among populations and species. First, production and analysis of interpopulation and interspecific hybrids are possible under laboratory conditions (Tauber & Tauber, 1977; Tauber, Tauber & Nechols, 1977; Henry, 1985). Secondly, geographical populations and sympatric species within this species-complex show great variation in their seasonal and behavioural patterns of reproduction (Tauber & Tauber, 1982*a*, 1986*a*; Henry, 1985). Finally, and perhaps most important, the specific ecophysiological traits that underlie much of the seasonal variation are known for a large number of populations in the Nearctic region (Tauber & Tauber, 1982*a*, 1986*a*). Thus it is possible to go beyond the usual types of genetic analyses of insect seasonal cycles (see references in Tauber, Tauber & Masaki, 1986) by examining the inheritance of specific response patterns that control diapause.

Our study analyses the inheritance of two sets of response patterns (responses to photoperiod and responses to prey) that underlie the diversity of seasonal cycles in the *C. carnea* species-complex. We included in this study two sympatric species whose largely asynchronous seasonal patterns of reproduction preclude reproductive interaction during most of

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the year. Also included were seasonally differentiated populations from three geographical areas of the United States; northeast (Ithaca, New York), northwest (St Ignatius, Montana), and west coast (Strawberry Canyon, California). The differences among these geographical populations represent both interspecific and interpopulation variation. Therefore our findings can shed light on the genetic changes underlying the evolutionary diversification of taxa.

In all we conducted five sets of hybridization experiments with four populations. Each test began with large field-collected samples and required approximately eight months of rearing and observation in the laboratory. Thus, our report represents five years of intensive study, and it constitutes a comprehensive analysis of the inheritance of the responses underlying interspecific and interpopulation differences in the ecological traits of animals.

2. Parental populations

The *C. carnea* species-complex, the common green lacewings, occurs throughout the Holarctic region, where it is typified by ecologically and behaviourally diversified populations (Tauber & Tauber, 1982a, 1986a; Henry, 1985). Females lay their eggs at the end of silken stalks. The larvae are predacious, feeding on a variety of soft-bodied arthropods. Within about 15 days of hatching, larvae undergo three moults; the mature third-instar larva spins a silken cocoon within which the final moult, to the pupa, takes place. With the exception of one strain (the *mohave* strain; see below), adults of the *C. carnea* species-complex are not predacious; they feed on honeydew and pollen. Diapause occurs only in the adult stage, and overwintering and aestivation (when it occurs) are accomplished by adults. Sex determination is XX in females and XY in males.

Each of the parental populations we tested has a consistent set of responses to photoperiod (Tauber & Tauber, 1976a, 1981, 1982a, 1986a; Table 1). The Ithaca, New York, population of *Chrysoperla carnea* Stephens (c)* enters reproductive diapause under short-day conditions and undergoes reproduction under constant long-day conditions. We refer to this type of response as *long-day reproduction*. In contrast, adults of *Chrysoperla downesi* Banks from Ithaca,

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* Henry (1983) proposed using the name *Chrysoperla plorabunda* (Fitch) to refer to North American populations of *C. carnea*. Although North American populations may ultimately prove to be differentiated at the species level, we consider this name change to be premature. It was based on a single unsuccessful hybridization test and call differences between only two populations – one from Europe and one from North America. In addition, the controls were insufficiently described. Therefore, we herein resynonymize *C. plorabunda* with *C. carnea* (NEW SYNONYMY). Until a thorough taxonomic study of the entire species-complex considers inter- and intrapopulation variation in a full range of morphological, behavioural and ecological traits, we do not recommend additional name changes; they are highly inconvenient and often confusing for theoretical and applied scientists who work with *C. carnea*.

New York (d) and St Ignatius, Montana (t) enter diapause under all constant photoperiods that we tested; non-diapause reproduction is initiated by an increase in daylength. We refer to this response as *short-day/long-day reproduction*. Most (75–98%) individuals from Strawberry Canyon, California (*C. carnea, mohave* strain, m), have the short-day/long-day requirement for non-diapause reproduction.

Each parental population also has a characteristic pattern of response to prey (Tauber & Tauber, 1973, 1981, 1982a, 1986a; Table 1). Reproduction by *C. carnea*, Ithaca (c) adults is not influenced by prey. In contrast, prey stimulates the initiation of reproduction under constant long-day conditions in most (~ 70%) of the individuals from Strawberry Canyon (*C. carnea, mohave* strain, m). There is a small, but significant, effect of prey on *C. downesi* from St Ignatius (t), but no response in *C. downesi* from Ithaca (d).

The four populations of *Chrysoperla* have distinctly different seasonal patterns of reproduction (Tauber & Tauber, 1976b, 1981, 1982a). The Ithaca population of *C. carnea* (c) is multivoltine (i.e. it produces several generations throughout the summer); the number and timing of the generations is largely determined by photoperiod and temperature, not prey. The two populations of *C. downesi* – from Ithaca (d) and St Ignatius (t) – are univoltine. Reproduction and development are restricted to late spring and early summer; the remainder of the year is spent in reproductive diapause. Prey may play a role in timing the initiation of reproduction in the St Ignatius population (t), but photoperiod is the predominant regulator of reproduction in both populations.

The seasonal cycle of the Strawberry Canyon population of *C. carnea* (m) is unique in several ways. First, the photoperiodic control of reproductive diapause can be modulated by prey. Secondly, the population is polymorphic in its voltinism and variable in the timing of reproduction.

The diverse patterns of reproduction in these four populations are based on variation in two major sets of ecophysiological response: (a) photoperiodic responses – long-day reproduction versus short-day/long-day reproduction, and (b) responses to prey – prey-mediated reproduction versus reproduction without prey (see Table 1). Both sets of traits are expressed in an all-or-none manner; that is, the alternative to reproduction is reproductive diapause.

3. Materials and methods

The origins of the populations, the codes used for describing the hybrids, and the crosses are on Tables 1 and 2. All of the experiments began with first-generation, laboratory-reared offspring of field-collected adults. Rearing procedures are presented by Tauber & Tauber (1976a). All adults received water and a proteinaceous diet (a 1 : 1 : 1 : 1 volumetric mixture of Wheast®, protein hydrolysate of yeast, honey and sugar). In the experiments involving prey, green peach

Table 1. *Parental species and populations of* Chrysoperla

Species	Source	Designation	Requirements for non-diapause reproduction
C. carnea	Ithaca, Tompkins Co., New York	c	Long daylengths, no prey requirement
C. carnea (*mohave* strain)	Strawberry Canyon, Alameda Co., California	m	Polymorphic responses to photoperiod and prey
C. downesi	Ithaca, Tompkins Co., New York	d	Sequence of short days, then long-days, no prey requirement
C. downesi	St Ignatius, Lake Co., Montana	t	Sequence of short days, then long days, minor response to prey

Table 2. *Reciprocal crosses to analyse the inheritance of diapause-controlling responses in four* Chrysoperla *populations*

	Fertile pairs			Fertile pairs	
Cross	(%)	(no.)	Cross	(%)	(no.)
c × d	87·5	(42)	c × c	96·0	(25)
c × t	85·7	(6)	t × t	85·7	(6)
d × t	100·0	(4)	d × d	86·3	(44)
d × m	77·8	(18)	m × m	80·0	(15)
c × m	84·6	(13)			

aphids, *Myzus persicae* Sulzer, on cabbage leaves, were provided daily from the time of adult emergence to the end of the experiment. All rearings and tests were conducted at 24 ± 1 °C, under photoperiodic conditions indicated in the tables.

In the interspecific and interpopulation crosses the lengths of the pre-oviposition period (time from adult emergence to oviposition) and the incidence of fertile oviposition were similar to those for intrapopulation pairs (Table 2). Also, there were high rates of hatching and survival among the offspring of all pairings. Thus our studies did not encounter any pre-mating behavioural or post-mating barriers to hybridization (cf. Henry, 1982, 1985; see also Tauber & Tauber, 1982c).

Reproductive diapause was diagnosed by (a) the lack of reproduction, (b) no observed courtship behaviour, (c) the development of a plump, waxy appearance and (d) in most cases a colour change from green to reddish or yellowish brown (see Tauber & Tauber, 1976a, 1986b).

Each time we made a cross, we also tested the responses of the parental stock to determine that no selection, drift or physiological change occurred between generations. In all cases the responses of the parental pairs bred true for the laboratory-reared generations. Thus the results from the various generations were combined for the parental lines on the tables. Similarly, unless otherwise noted, there was no significant difference in the responses of the offspring from reciprocal crosses. Therefore we pooled these data for the tables.

Each testcross also included tests to demonstrate that the progeny did indeed respond to the factor being tested. In the tests of the photoperiodic responses a set of animals of each genotype experienced an increase in daylength from LD 10 : 14 to LD 16 : 8 on the day of cocoon spinning. This resulted in very high incidences of non-diapause reproduction in the hybrid, backcross and intercross progeny from all crosses (Tables 2, 3, 4, 5 and 7). In the tests involving responses to prey, adults of each genotype were maintained without prey. A large percentage of these progeny entered diapause (Tables 6 and 7a). The few insects that did not conform may have resulted from the recombination of modifier genes or from unknown physiological factors.

We tested the results from the various crosses against simple, one- and two-locus Mendelian ratios (G test; Sokal & Rohlf, 1981). Conformance of all-or-none characters to such ratios can also result from polygenic systems involving a threshold (Manning & Hirsch, 1971). Ideally, this possibility is tested using second backcrosses – tests that were not possible in our study. However, where appropriate, we considered this possibility graphically for the parental, F_1 hybrid, backcross and F_2 intercross progeny. Assuming the characters are normally distributed (see Falconer, 1981), we plotted the frequencies of reproductive diapause and non-diapause reproduction for each cross, and we positioned the plots on a linear scale around a threshold that differentiates short-day/long-day reproduction from long-day reproduction. Monomorphic parental populations were positioned by assuming that hybrids fall halfway between the parental populations. For uniformity, the position of the *C. carnea* (c) population was held constant in all cases. The positioning of the plots for the various genotypes was assessed visually.

4. Analysis of interspecific and interpopulation crosses

(i) *C. carnea* (*Ithaca, New York*) × *C. downesi* (*Ithaca, New York*) (c × d)

This section represents a brief re-analysis of data from Tauber, Tauber & Nechols (1977). The data are

Table 3. *Inheritance of short-day/long-day requirement for non-diapause reproduction in* Chrysoperla carnea, *Ithaca (c) and* Chrysoperla downesi, *Ithaca (d), LD 16 :8**

| Population or generation | Percentage Reproductive diapause | Number | | Ratio tested | G_T | d.f. | P |
		With short-day/ long-day requirement	Without short-day/ long-day requirement				
Parental c	0	0	86	—	—	—	—
Parental d	100	76	0	—	—	—	—
F_1	0	0	129	—	—	—	—
Backcross to d†	24·9	50	151	1:3	6·19	4	> 0·1
F_2	6·6	11	155	1:15	0·77	2	> 0·5

* Individuals that experienced an increase in daylength underwent 100% (first generation) and 92·3–100% (second generation) non-diapause reproduction.
† There were no significant differences in the responses of the four types of backcross progeny (G_H = 6·19, d.f. = 3, P > 0·1) or between the two types of F_2 progeny (G_H = 0·73, d.f. = 1, P > 0·1).

Table 4. *Inheritance of short-day/long-day requirement for non-diapause reproduction in* Chrysoperla carnea, *Ithaca (c) and* Chrysoperla downesi, *St Ignatius (t), LD 16 :8**

| Population or generation | Percentage Reproductive diapause | Number | | Ratio tested | G_T | d.f. | P |
		Reproductive diapause	Non-diapause reproduction				
Parental c	0	0	58	—	—	—	—
Parental t	100	48	0	—	—	—	—
F_1	0	0	66	—	—	—	—
Backcross to t†	52·6	139	125	1:1	9·34	4	0·05
F_2 (tc–tc)	24·0	23	73	1:3	0·06	1	> 0·5

* Individuals that experienced an increase in daylength underwent 100% (first generation) and 85·0–100% (second generation) non-diapause reproduction.
† The proportions of reproductive diapause are not uniform among the progeny of all four backcrosses (G_H = 8·59, d.f. = 3, P < 0·05). However, the heterogeneity is such that when the data are pooled, the crosses tend to compensate for their respective deviations (cf. Sokal & Rohlf, 1981, p. 725).

presented so that comparisons of all our crosses are readily made.

We emphasize that the Ithaca populations of *C. carnea* and *C. downesi* (c and d) are reproductively isolated. The primary, but not the sole, barrier to interbreeding by these two species is asynchrony in their seasonal cycles (Tauber & Tauber, 1976*a*, *b*, 1982*b*, *c*; cf. Henry, 1982, 1985). *C. downesi* is in reproductive diapause during most of the summer when *C. carnea* is reproductively active. *C. downesi*, whose adult colouration is dark green and which is largely associated with an evergreen habitat, is univoltine. In contrast, the grass-green *C. carnea* usually occurs in meadows and deciduous trees and is multivoltine. Therefore the genetic variability that we examined represents *interspecific* variability, and it involves traits that are of major importance to reproductive isolation between the two sympatric species.

The asynchrony in the seasonal cycles of the two species largely results from different responses to photoperiod. *C. carnea* reproduces under constant long-day conditions, whereas *C. downesi* requires a sequence of short days followed by long days for non-diapause reproduction. Thus we analysed the inheritance of the short-day/long-day requirement for reproduction.

The F_1 hybrids (males and females) from both of the reciprocal crosses underwent non-diapause reproduction under constant long-day conditions (Table 3). Therefore the short-day/long-day requirement for non-diapause reproduction is recessive, or a relatively high threshold is involved in the expression of the trait. The trait is not sex-linked.

Under constant LD 16:8, the incidence of reproductive diapause in progeny from the four reciprocal hybrid × *C. downesi* backcrosses was 24·9%, and in the F_2 it was 6·6% (Table 3). The simplest Mendelian model to account for these results involves two autosomal, unlinked loci with complete dominance. Individuals with the short-day/long-day requirement for non-diapause reproduction are those that are homozygous for the recessive allele at both loci. The ratios expected under this model are 1:3 (25%

diapause) in the backcross and 1 : 15 (6·25% diapause) in the F_2. The observed numbers agree very well with this expectation (Table 3).

The frequencies of diapause in the F_1 hybrid and backcross progeny were consistent with a polygenic system with a threshold, but in the F_2 progeny they were higher than the very low frequencies expected from a polygenic system.

We conclude that the interspecific differences in photoperiodic responses between the Ithaca populations of *C. carnea* (c) and *C. downesi* (d) result from two unlinked, autosomal loci; the genotypes are c (long-day reproduction) = AABB and d (short-day/long-day reproduction) = aabb.

(ii) *C. carnea* (*Ithaca, New York*) × *C. downesi* (*St Ignatius, Montana*) (c × t)

C. downesi from St Ignatius, Montana (t) shares many characteristics with *C. downesi* from Ithaca (d). Both primarily inhabit evergreen trees, both are dark green in the adult stage, and both have univoltine seasonal cycles resulting from the short-day/long-day requirement for reproduction. Like the previous set of crosses, this one examines the inheritance of the short-day/long-day requirement for non-diapause reproduction.

Above, we showed that the differences in photoperiodic responses between the Ithaca populations of *C. carnea* and *C. downesi* (c and d) segregated in Mendelian ratios typical of a two-locus system (Section 4(i) above). Therefore we expected the progeny from the crosses of *C. carnea*, Ithaca × *C. downesi*, St Ignatius (c × t), to segregate in similar Mendelian ratios.

The results from the F_1 progeny were not inconsistent with this hypothesis, but those from the backcross and F_2 progeny were inconsistent with it.

Male and female F_1 hybrids from both of the reciprocal crosses exhibited long-day reproduction (Table 4). Thus, as in Section 4(i) above, the short-day/long-day requirement for non-diapause reproduction is recessive, or a relatively high threshold is involved in the expression of the trait. The trait is not sex-linked.

Under LD 16:8, the incidence of diapause in the backcross progeny was 52·6%, and in the F_2 it was 24% (Table 4). The simplest Mendelian model to account for these results involves a single autosomal locus with complete dominance. The short-day/long-day requirement is the recessive trait. The ratios expected under this model are 1 : 1 (50% diapause) in the backcross and 1 : 3 (25% diapause) in the F_2. The observed numbers agree very well with the expected (Table 4).

When we examined the results against a polygenic model with a threshold for the expression of diapause, we found that the frequencies of diapause in the F_1 hybrid and backcross progeny were consistent with

the model. However, the frequency of diapause in the F_2 progeny was higher than expected from a polygenic system.

We conclude that the interspecific differences in photoperiodic responses between *C. carnea* from Ithaca and *C. downesi* from St Ignatius (c and t) result from allelic differences at a single autosomal locus. To acknowledge the difference in inheritance of the short-day/long-day requirement in the c × d and c × t crosses, we tentatively designate the genotype of t (short-day/long-day reproduction) as a^1a^1bb (see Discussion).

(iii) *C. downesi* (*Ithaca, New York*) × *C. downesi* (*St Ignatius, Montana*) (d × t)

These two populations share the short-day/long-day requirement for reproduction but, as shown above, the mode of inheritance differs between the two populations. Hybridization tests were therefore designed to determine if the photoperiodic requirements for reproduction are homologous (i.e. determined by the same genes) in the two populations.

The F_1 hybrids from the reciprocal crosses between d and t uniformly had the short-day/long-day requirement for reproduction. Similarly, 100% of the F_2 progeny from the t–d × t–d cross also had the short-day/long-day response. The reciprocal cross (d–t × d–t) was not tested.

Had the short-day/long-day requirement been controlled by genes at different loci in the two populations, the trait would have segregated in the F_2 offspring. It did not, and we conclude that the short-day/long-day requirement for reproduction is based on homologous, rather than analogous genetic systems in the Ithaca and St Ignatius populations of *C. downesi*. Thus the designations of the genotypes of the two populations remain: d = aabb and t = a^1a^1bb.

(iv) *C. downesi* (*Ithaca, New York*) × *C. carnea mohave* strain (*Strawberry Canyon, California*) (d × m)

These populations differ in many respects (adult coloration, habitat association, seasonal cycle, responsiveness to prey), but they are similar in that a high proportion of individuals in both populations has a short-day/long-day requirement for reproduction. The *C. downesi*, Ithaca (d) population is monomorphic, whereas *C. carnea* from Strawberry Canyon (m) is polymorphic (75–98%) for this trait.

We used this cross to examine two sets of responses. First, we considered whether the similarities in the photoperiodic responses of the two species are homologous, i.e. based on the same genetic mechanisms. Secondly, we analysed the nature of the genetic variation underlying the differential responses of the two species to prey. The crosses involved unselected, first-generation offspring of field-collected adults. Our experience has shown that laboratory cultures of the

Table 5. *Homology of the short-day/long-day requirement for non-diapause reproduction in* Chrysoperla downesi, *St Ignatius, MT* (d) *and* Chrysoperla carnea, *Strawberry Canyon, CA* (m), *LD 16:8**

Population or generation	Reproductive diapause	
	Percentage	Number
Parental (d)	100	73
Parental (m)	93·3	105
F_1	95·7	138
Pooled backcross to (d)	98·7	220
Pooled backcross to (m)	95·9	219
F_2	95·9	122

* Individuals that experienced an increase in daylength underwent 87–100% (no. = 15–34) non-diapause reproduction. The variation in response was unrelated to genotype.

Table 6. *Inheritance of responsiveness to prey in relation to reproductive diapause in* Chrysoperla carnea, *Strawberry Canyon* (m) *and* Chrysoperla downesi, *Ithaca* (d), *LD 16:8, prey provided**

Population or generation	Reproductive diapause†	
	Percentage	Number
Parental (m)	36·5	148
Pooled backcross to (m)	59·8	214
F_1	66·2	77
F_2	72·2	115
Pooled backcross to (d)	86·5	215
Parental (d)	94·9	78

* Individuals that did not receive prey underwent 94·4–100% reproductive diapause; under these conditions, the incidence of diapause is independent of genotype (95% confidence limits, Sokal & Rohlf, 1981).
† The incidence of diapause when prey are provided is linearly related to genotype; i.e. as the expected proportion of (d) genes increases, the incidence of diapause increases (regression analysis of unpooled, arcsine transformed data; $\ominus = \arcsin \sqrt{P/100}$ (Sokal & Rohlf, 1981); $y = 0.672 (\pm 0.072) + 0.007 (\pm 0.001)x$; $r^2 = 0.703$; $P < 0.0001$).

C. carnea species-complex begin to decline after three or four generations; this phenomenon precluded us from selecting homogeneous lines of the polymorphic *C. carnea*, Strawberry Canyon (m) for testing.

(A) *Response to photoperiod.* Under conditions of LD 16:8, almost all F_1, F_2 and backcross progeny entered reproductive diapause (Table 5). Similarly, when the progeny from the various crosses experienced an increase in daylength, most underwent non-diapause reproduction. These findings indicate that the genetic systems controlling the short-day/long-day requirement for reproduction are homologous in (m) and (d).

The observed frequencies of diapause and non-diapause reproduction by the hybrid progeny fell between those of the intrapopulation controls (Table 5; 95% confidence limits (Rohlf & Sokal, 1981)). Therefore the Strawberry Canyon population (m), probably contains a very low frequency of genes for long-day reproduction.

(B) *Response to prey.* Because responsiveness to prey is only expressed in individuals with a short-day/long-day requirement for reproduction, the (d × m) crosses provided the opportunity to examine the genetic basis for this trait. Individuals from the (m) population respond to prey, i.e. when adults have access to prey, the incidence of diapause under constant LD 16:8 is much lower (about 35%) than when prey are absent (about 75–98%). In contrast (d) individuals enter diapause under long-days whether or not prey are present.

When hybrid adults received prey, the incidence of diapause was linearly related to the expected fraction of parental genes in the genome; i.e. as the expected proportion of *C. downesi* genes increased, the incidence of diapause increased (Table 6). This linear relationship suggests polygenic control of responsiveness to prey. The genes governing this trait are additive, and a threshold is probably involved in the expression of diapause.

In summary, the data from the crosses between *C. downesi*, Ithaca, and *C. carnea*, Strawberry Canyon (d × m) are consistent with the following conclusions. The Strawberry Canyon population largely contains genes for the short-day/long-day requirement for reproduction; however, it also contains a low frequency of genes that produce long-day reproduction. By contrast, the *C. downesi* population is largely homozygous for the short-day/long-day requirement. The short-day/long-day requirement for reproduction is determined by homologous genes in the two species.

The Strawberry Canyon population (m) is also heterogeneous for the genes controlling responsiveness to prey; about 60% of the individuals are responsive. In contrast, the *C. downesi*, Ithaca (d) population is homozygous for unresponsiveness to prey. Responsiveness to prey is determined by an autosomal polygenic system. These genes appear to be additive, and their expression involves a developmental threshold.

(v) *C. carnea, mohave strain, Strawberry Canyon, California × C. carnea, Ithaca, New York* (m × c)

Data from this set of crosses present some difficulties in interpretation. First, the differences between the two populations involve responses to both photoperiod and prey. Secondly, the traits interact in their expressivity (Tauber & Tauber, 1986b), and thirdly, the Strawberry Canyon population is polymorphic for the traits under study (see Section 4(iv) above). The results show the following.

(A) *Response to photoperiod.* The F_1 hybrids from both reciprocal crosses underwent non-diapause

Table 7(*a*). *Inheritance of short-day/long-day requirement for non-diapause reproduction in* Chrysoperla carnea, Ithaca (*c*) *and* Chrysoperla carnea, *Strawberry Canyon* (*m*), *LD 16 :8, no prey**

| Population or generation | Percentage Reproductive diapause | Number | | Ratio tested | G_T | d.f. | *P* |
		Reproductive diapause	Non-diapause reproduction				
Parental (c)	0	0	128				
Parental (m)	90·3	131	14				
F_1	0	0	131				
Backcross to (m)†	32·4	94	196	0·375:0·625	7·58	4	> 0·1

Table 7(*b*). *Inheritance of responsiveness to prey in relation to diapause, LD 16 :8, prey provided*

Parental (c)	0	0	68
Parental (m)	26·1	17	48
F_1	0	0	80
Backcross to (m)	5·3	6	108

* Insects that experienced an increase in daylength underwent 92·3–100% nondiapause reproduction.

† There is no significant difference in the responses of the four types of backcross progeny (7*a*: $G_H = 4·3$, d.f. = 3, $P < 0·1$; 7*b*: $G_H = 4·7$; d.f. = 3, $P > 0·1$).

reproduction under constant LD 16:8 (Table 7*a*). Therefore, long-day reproduction is dominant and not sex-linked.

Under LD 16:8 and in the absence of prey, the incidence of diapause in the progeny from the four (hybrid × m) backcrosses was 32% (Table 7*a*). This figure falls between the 1:1 and 3:1 (non-diapause: diapause) ratios that typify the segregation of one and two autosomal loci with dominance. However, it does fit the expected situation if a pair of alleles at a single autosomal locus is responsible for the variation and if one of the parental populations is polymorphic at this locus (expected gene frequencies: p = 0·87, q = 0·13). In this case the expected non-diapause :diapause ratio is 0·625:0·375; our observations agree well with this figure (Table 7*a*). Therefore, the (m × c) cross is consistent with previous crosses (e.g. t × c and m × d), and the pattern of inheritance of the long-day/short-day requirement for non-diapause reproduction in the (m × c) cross does not contradict that expected from a single autosomal locus with complete dominance.

Individuals with long-day reproduction, e.g. the F_1 hybrids, averted diapause regardless of the presence or absence of prey. Thus the genes that control the photoperiodic responses also control the expressivity of the genes that determine responsiveness to prey.

(B) *Response to prey*. Among the backcross progeny, the average incidence of diapause was reduced from 32% to 5% when adults received prey (Table 7*a*, *b*). Considering that these percentages represent only those individuals that have the

short-day/long-day requirement for reproduction, the level of responsiveness to prey by the progeny from the (m) backcrosses is consistent with that of the (d × m) backcross progeny (Table 6). Therefore the results do not contradict the proposal that responsiveness to prey is determined by a polygenic, threshold mechanism.

A summary of our conclusion from the two crosses with the Strawberry Canyon population (m) is as follows. Diapause-regulating responses in the Strawberry Canyon population are controlled by two polymorphic genetic systems. The primary system, which determines the photoperiodic requirements for reproduction (long-day reproduction versus the short-day/long-day requirement for reproduction), consists of a single autosomal locus with complete dominance. The short-day/long-day requirement is recessive.

In addition to determining the photoperiod responses, the primary genetic system also controls the expressivity of the secondary system, such that all individuals with dominance in the primary unit avert diapause, regardless of the genetic composition of the secondary system. The propensity for diapause in recessive individuals (those with the short-day/long-day requirement for reproduction) is determined by the genetic composition of the secondary system.

The secondary genetic system determines the prey requirement for reproduction (prey-mediated reproduction versus reproduction without prey). This system probably consists of two or more autosomal loci. The genes comprising this polygenic system act in an additive manner, and their expression involves a developmental threshold.

5. Discussion

The five crosses with the diverse populations of the North American *C. carnea* species-complex showed some clear patterns, and they also pose some intriguing questions. First, the data indicate that genetic, rather than environmental or maternal factors, determine the considerable phenotypic variation in seasonal response patterns. Secondly, there is genetic variation among geographical populations of the same species and between sympatric populations

of the two species, *C. carnea* and *C. downesi*. This variation involves two sets of phenotypic traits (responsiveness to photoperiod and responsiveness to prey) and two separate genetic systems.

(i) *Responses to photoperiod*

Photoperiod is the primary controller of reproduction in all members of the *C. carnea* species-complex (Tauber & Tauber, 1982*a*, 1986*a*). Interspecific and interpopulation variability in photoperiodic responses is large, and it involves differences in the frequencies of two sets of all-or-none responses. Within all crosses, the patterns of inheritance of the photoperiodic responses are consistent with a simple Mendelian system, and the genetic units governing the photoperiodic responses are homologous among all populations tested. However, comparisons between crosses show geographical variation in the mode of inheritance of the responses.

In one case (the cross between *C. carnea*, Ithaca, and *C. downesi*, Ithaca – c × d), the inheritance of the photoperiodic requirements for reproduction is clearly consistent with a model of two unlinked autosomal loci, but in two other cases (the crosses between *C. carnea*, Ithaca and both *C. downesi*, St Ignatius, and *C. carnea*, Strawberry Canyon; c × t and c × m), the pattern of inheritance corresponds to a single autosomal locus.

Three mechanisms may account for this variability. First, there may be geographical differences in the alleles at one of the loci controlling the trait. Thus the c population = AABB, the d population = aabb, and the t population = a^1a^1bb. If the a^1 allele has a very large effect so that a^1a^1 alone (without the b locus) is sufficient to produce the short-day/long-day requirement for non-diapause reproduction, the ratios we observed would occur.

The second possibility is that variation in the genetic background of individuals from different populations results in geographical differences in the expression of dominance. A somewhat similar type of geographical variability in the expression of dominance occurs in British populations of the moth, *Triphaena comes* (Ford, 1975).

The third possible explanation for geographical variation in the expression of genes involves differences in crossover suppression, if the two loci that control the photoperiodic responses are distantly linked. However, the close correspondence between observed frequencies and the ratios expected from the segregation of two independent loci in the crosses between *C. carnea*, Ithaca, and *C. downesi*, Ithaca, does not argue in favour of this suggestion.

Distinguishing between the three possible genetic mechanisms controlling the photoperiodic responses of the *C. carnea* species-complex is of considerable interest. For example, dominance modifiers and linkage between fitness traits may have quite different

evolutionary roles. Endler (1977) emphasized the significance of these mechanisms in the diversification and speciation of parapatric and sympatric populations.

(ii) *Responses to prey*

Our results show that the responses to photoperiod and prey are both phenotypically and genetically hierarchical in their expression. Only individuals with the short-day/long-day requirement for reproduction can respond to prey. Those with long-day reproduction may reproduce whether prey are present or absent.

The pattern of phenotypic expression is consistent with our analysis of genetic variation. For example, only a proportion of backcross individuals (c × m and d × m crosses) expresses responsiveness to prey, and they do so roughly in the frequencies expected for short-day/long-day individuals. Thus, the genes controlling the photoperiodic responses also act as suppressors that control the expressivity of the genes controlling responsiveness to prey.

The evolution of a secondary genetic system that regulates responsiveness to prey has considerable ecological significance. In environments where the seasonal occurrence of prey is variable and unpredictable, it allows the otherwise rigid photoperiodic determination of diapause to be modulated when prey are abundant. The Strawberry Canyon population, and numerous other populations from across western North America, appear to incorporate this genetically based flexibility into their seasonal patterns of reproduction (Tauber & Tauber, 1986*a*).

Genetic systems, such as those examined in our study, do not operate in isolation. On the one hand, they are subject to modification by other genetic systems. For example, the critical photoperiod for diapause induction in populations with long-day reproduction is geographically variable and polygenically controlled (Tauber & Tauber, 1972). On the other hand, it is also likely that the genes regulating the major responses to photoperiod and prey have effects other than those we reported here. For example, we have shown that the ability to use prey as a diapause-controlling cue is always associated with a long, non-diapause pre-oviposition period – a trait that may significantly constrain the evolution of prey-mediated diapause (Tauber & Tauber, 1986*a*). The covariance of these traits is dealt with elsewhere (Tauber & Tauber, in preparation).

(iii) *Implications to speciation*

These findings have important implications for the hypothesis that sympatric diversification is important in the *C. carnea* species-complex (Tauber & Tauber, 1977). Recent theoretical analyses suggest that reproductive isolation can evolve sympatrically if certain conditions are fulfilled (e.g. Kondrashov &

Mina, 1986). These conditions include two that pertain to the genetics of ecological traits. First, the initial population must contain sufficient genetic heterogeneity in traits that determine patterns of resource utilization. Secondly, differences in several (up to 10) loci must be sufficient to adapt the evolving species to different niches and to establish reproductive isolation.

Results, both here and elsewhere, suggest that these conditions hold true for parts of the *C. carnea* species-complex. First, the group expresses considerable interpopulation and intrapopulation variation in ecophysiological response patterns that determine seasonal cycles of reproduction and development (Tauber & Tauber, 1986*a*, *b*). The variation in these response patterns underlies important ecological differences and, in some situations, reproductive isolating mechanisms. Secondly, differences in very few Mendelian units account for the ecologically divergent and reproductively isolated populations (see also Henry, 1985).

In the *C. carnea* species-complex, the traits that underlie reproductive isolation between sympatric species are homologous with those that exist within genetically polymorphic, allopatric populations. Thus it is now possible to examine the evolution of homologous traits that contribute to diversification and speciation in this group of insects.

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