A STUDY OF THE CHRYSOPIDS (NEUROPTERA: CHRYSOPIDAE) IN TWO OLD FIELDS IN QUEBEC

by

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Short title

CHRYSOPIDS OF THE OLD FIELD : BIOLOGY, ECOLOGY, GENETICS

ABSTRACT

Faunistic composition and population dynamics of chrysopids were investigated in two old fields in Québec. Nine species were collected; Chrysopa oculata Say and Chrysopa chi Fitch are dominant and resident.

Parasitism due to Chrysopophthorus americanus Mason has little effect on the reproductive potential of C. oculata and C. chi populations. However, embryonic mortality, resulting from autosomal translocations, is a major mortality factor in both species. Their karyotypes are described and developmental studies conducted on them and Chrysopa lineaticornis Fitch are reported.

Inheritance of wing and cephalic characters was investigated in C. oculata. A population genetics study revealed seasonal selection against the allelic gene B (black gradates) and superior fitness of its recessive counterpart b (green gradates). A meiotic drive mechanism also favors the b allele, and the allele A determining "facial band" expression.

Chrysopa chi exhibits obligatory and facultative prepupal diapause. The field population, however, is primarily univoltine. Voltinism is controlled by two independently segregating autosomal genes; the recessive alleles, in the homozygous state, determine obligatory diapause and, consequently, univoltinism. Diapause termination is reported.

RESUME

La composition de la faune et la dynamique des populations des chrysopides furent étudiées dans deux vieux champs au Québec. Neuf especes furent récoltées mais de celles-ci Chrysopa oculata Say et Chrysopa chi Fitch sont les espèces les plus nombreuses et résidentes.

Le parasitisme causé par Chrysopophthorus americanus Mason est d'une importance négligeable au potentiel de la reproduction de C. oculata et C. chi. Cependent, une mortalité chez les embryons, le résultat des translocations des autosomes, est un important facteur de la mortalité. Par surcroît, leurs karyotypes sont décrits et des études de développement, faites sur elles et Chrysopa lineaticornis Fitch sont également signalées.

L'héritage des caractères d'aile et de la tête de C. oculata fut étudié. Une étude de la génétique des populations indique qu'il y a une sélection saisonnière contre le gène B (nervures scalariformes noires) mais sa contrepartie récessive b (nervures scalariformes vertes) montre une adaptation plus grande. Un méchanisme directionnel de la méiose favorise les gènes b, et A qui détermine la manifestation de la bande faciale.

Chrysopa chi manifeste chez la prépupe, la diapause obligatoire et facultative. Néanmois, la population est essentiellement monovoltine. La voltinisme est sous le contrôle

de deux gènes des autosomes, de qui la ségrégation est indépendante; les allèles réccessifs, dans l'état homozygotique, déterminent la diapause obligatoire et, par conséquent, la monovoltinisme. La termination de sa diapause est signalée aussi.

CONTRIBUTIONS TO ORIGINAL KNOWLEDGE

A. The following were investigated for the first time:

1 The chrysopid fauna of a North-American old field habitat;

2 Inheritance of the described wing and cephalic characters in *Chrysopa oculata* Say.

- The "facial spots" phenotype is described for the first time.
- Meiotic drive and segregation distortion are reported for the first time in chrysopids;

3 Population genetics of *Chrysopa oculata* Say - the first such study in chrysopids and, among beneficial insects, it appears to be the only one of its kind;

4 Inheritance of obligatory and facultative prepupal diapause (hence voltinism) in *Chrysopa chi* Fitch - the first such study in chrysopids.

- The possession, by *C. chi*, of both types of prepupal diapause is also reported for the first time;

5 Termination of obligatory diapause in *Chrysopa chi* Fitch.

B. Reported also for the first time are the following:

1 Chromosomal translocations in chrysopids and, also, an associated embryonic mortality. Descriptions of the karyotypes of *Chrysopa oculata* Say and *Chrysopa chi* Fitch are the firsts for North American chrysopids;

2 Reproductive development in *Chrysopa oculata* Say;

3 A description of the hitherto unknown egg of *Chrysopa lineaticornis* Fitch - the species was reared for the first time from the egg to the adult;

4 A gonadal intracellular bacterial organism in chrysopids;

5 Mermithid (Nematoda) parasitism in North American chrysopids;

6 Phoretic associations in chrysopids;

7 New chrysopid host records for the parasites *Helorus anomalipes* (Pauzer), *Dichrogaster crassa* (Prov.), *Isodromus iceryae* Howard and *Chrysopophthorus americanus* Mason;

8 Developmental biology of *Chrysopophthorus americanus* Mason.

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TABLE OF CONTENTS

Page

TITLE PAGE i

ABSTRACT ii

RESUME iii

CONTRIBUTIONS TO ORIGINAL KNOWLEDGE v

ACKNOWLEDGEMENTS vii

LIST OF TABLES xii

LIST OF FIGURES xvi

LIST OF PLATES xvii

INTRODUCTION 1

GENERAL LITERATURE REVIEW 3

Mass-culturing techniques 3

Dietary and other influences affecting fecundity and fertility 4

Artificial larval diets 7

Biological control studies 8

Pesticide toxicity 12

Population dynamics and ecology 14

Responses of adult chrysopids to ultrasound ... 16

The probability of sound production and its role in courtship 17

Diapause and photoperiodic responses 19

Genetic studies on chrysopids 25

Cytogenetics of chrysopids 27

Systematics of the genus Chrysopa s.l. 27

OBJECTIVES 29

MATERIALS AND METHODS 32

Description of the study areas 32

- Collection and treatment of field material 34
- Maintainance of laboratory cultures of *Chrysopa oculata* Say and *Chrysopa chi* Fitch 36
- Description of rearing containers 37
- Developmental and genetic studies 38
- Cytogenetics 40

RESULTS 42

- Faunistic composition and population dynamics 42
- 24-hour oviposition studies 43
- Ecology and parasitism of immature stages 43
- Ectoparasitism and phoretic associations of adult chrysopids 45
- Endoparasitism of adult chrysopids 46
  - Mermithids (Nematoda) and intracellular bacteria 46
  - The incidence of parasitism by the euphorine *Chrysopophthorus americanus* Mason (Hymenoptera: Braconidae) and its effect on the host 47
- Developmental biology of *Chrysopophthorus americanus* Mason (Hymenoptera: Braconidae) 51
- Developmental studies on *Chrysopa oculata* Say and *Chrysopa chi* Fitch 53
- Embryonic mortality in *Chrysopa oculata* Say and *Chrysopa chi* Fitch 55
- Development of *Chrysopa lineaticornis* Fitch 56
- Genetic studies on *Chrysopa oculata* Say 58
  - Inheritance of black pigmentation on the forewing 58
  - Linkage between forewing pigmentation and pigmentation of some cephalic characters 60
  - Inheritance of the interocular, sub-antennal band and its reduced form 60
  - The effect of meiotic drive (or gametic competition) on genotype occurrence 62
- Population genetics of *Chrysopa oculata* Say: frequency of the allelic genes *B* and *b*, and *A* and *a* 64
- Diapause studies on *Chrysopa chi* Fitch 65
  - Termination of obligatory diapause 65
  - Inheritance of obligatory diapause 67
- Cytogenitics of *Chrysopa oculata* Say and *Chrysopa chi* Fitch 69
  - Karyotype and meiotic stages 69

Chromosomal translocations 70

DISCUSSION AND CONCLUSION 72

Faunistic composition and population dynamics 72

Oviposition rhythm, field distribution of eggs and egg parasites 74

Ecology and parasitism of larvae and cocoons 75

Ectoparasitism of adult chrysopids 77

Phoretic associations of adult chrysopids 77

Endoparasitism of adult chrysopids 78

Mermithids (Nematoda) and intracellular bacteria 78

The incidence of parasitism by *Chrysopophthorus americanus* Mason (Hymenoptera: Braconidae: Euphorinae): its effect on the host and on the reproductive potential of the host population .. 79

Developmental biology of *Chrysopophthorus americanus* Mason (Hymenoptera: Braconidae) 83

Developmental studies on *Chrysopa oculata* Say and *Chrysopa chi* Fitch 86

Development of *Chrysopa lineaticornis* Fitch 89

The allelic genes *B* and *b* of *Chrysopa oculata* Say: genetic inheritance, linkage and population genetics 90

The allelic genes *A* and *a* of *Chrysopa oculata* Say: genetic inheritance and population genetics 93

Meiotic drive (or gametic competition) in *Chrysopa oculata* Say: its effect on gene frequency and on genotype occurrence 94

Embryonic mortality and cytogenetics of *Chrysopa oculata* Say and *Chrysopa chi* Fitch 95

Karyotype of *Chrysopa oculata* Say and *Chrysopa chi* Fitch 97

Diapause in *Chrysopa chi* Fitch: inheritance, effect on the field population, and termination under laboratory conditions 98

SUMMARY 102

REFERENCES 113

TABLES 139

FIGURES 183

PLATES 195

LIST OF TABLES

I Chrysopid species and abundance in two old fields in Quebec.

II Chrysopids collected on Ile Perrot, Quebec, in 1977.

III Chrysopids collected on Ile Perrot, Quebec, in 1978.

IV Chrysopids collected on Mt. St. Hilaire, Quebec, in 1977.

V Chrysopids collected on Mt. St. Hilaire, Quebec, in 1978.

VI Chrysopids collected on Mt. St. Hilaire, Quebec, in 1979.

VII Fertility and ovarian development in *Chrysopa oculata* Say on Ile Perrot, Quebec, in 1977.

VIII Fertility and ovarian development in *Chrysopa oculata* Say on Mt. St. Hilaire, Quebec, in 1977.

IX Recovery of chrysopid eggs on Ile Perrot, Quebec.

X Recovery of chrysopid eggs on Mt. St. Hilaire, Quebec.

XI Oviposition rhythm of field-collected *Chrysopa oculata* Say and *Chrysopa chi* Fitch under field conditions: 16-17 July 1978.

XII Oviposition rhythm of field-collected *Chrysopa oculata* Say and *Chrysopa chi* Fitch under field conditions: 21-22 June 1979.

XIII Recovery of chrysopid larvae on Ile Perrot, Quebec.

XIV Recovery of chrysopid larvae on Mt. St. Hilaire, Quebec.

XV Recovery of chrysopid cocoons on Mt. St. Hilaire, Quebec.

XVI The incidence of parasitism by *Chrysopophthorus americanus* Mason, in *Chrysopa oculata* Say, on Ile Perrot, Quebec.

XVII The incidence of parasitism by *Chrysopophthorus americanus* Mason, in *Chrysopa oculata* Say on Mt. St. Hilaire, Quebec.

XVIII Recovery of mature larvae of *Chrysopophthorus americanus* Mason, from males of *Chrysopa oculata* Say, and their subsequent development under long-day conditions.

XIX Recovery of mature larvae of *Chrysopophthorus americanus* Mason, from males of *Chrysopa oculata* Say, and their development under laboratory and outdoor conditions.

XX Incidence of *Forcipomyia eques* (Johannsen) on wings of *Chrysopa oculata* Say on Mt. St. Hilaire and Ile Perrot, Quebec.

XXI Development (days) of *Chrysopa oculata* Say (from Mt. St. Hilaire, Quebec) in two types of larva-rearing cages.

XXII Survival (lx) in laboratory rearings of *Chrysopa oculata* Say from Ile Perrot, Quebec.

XXIII Comparison of male and female development time (days) in *Chrysopa oculata* Say, originating from Ile Perrot, Quebec.

XXIV Comparison of male and female development time (days) in *Chrysopa oculata* Say, originating from Mt. St. Hilaire, Quebec.

XXV Comparison of male and female development time (days) in *Chrysopa chi* Fitch, originating from Mt. St. Hilaire, Quebec.

XXVI Emergence (cumulative per cent of progeny) pattern in *Chrysopa oculata* Say from Ile Perrot, Quebec.

XXVII The occurrence of sperm shift in males of *Chrysopa oculata* Say.

XXVIII Ovarian development in *Chrysopa oculata* Say on a feeding regime of live pea aphids and sucrose solution.

XXIX Embryonic mortality in a laboratory culture of *Chrysopa oculata* Say from Ile Perrot, Quebec.

XXX Embryonic mortality in a laboratory culture of *Chrysopa oculata* Say from Mt. St. Hilaire, Quebec.

XXXI Embryonic mortality in a laboratory culture of *Chrysopa chi* Fitch from Mt. St. Hilaire, Quebec.

XXXII Observed and predicted ratios of phenotypes from matings of *Chrysopa oculata* Say originating from Ile Perrot, Quebec. Inheritance of the allelic genes *B* and *b*, determining black *vs* green gradate crossveins on the forewing.

XXXIII Observed and predicted ratios of phenotypes from matings of *Chrysopa oculata* Say originating from Mt. St. Hilaire, Quebec. Inheritance of the allelic genes *B* and *b*, determining black *vs* green gradate crossveins on the forewing.

XXXIV Observed and predicted ratios of phenotypes from matings of *Chrysopa oculata* Say from Ile Perrot, Quebec. Inheritance of the allelic genes *B* and *b*, determining black *vs* green gradate crossveins on the forewing, and of the allelic genes *A* and *a* determining respectively, presence of the sub-antennal facial band and spots.

XXXV Observed and predicted ratios of phenotypes from matings of *Chrysopa oculata* Say from Ile Perrot, Quebec: segregation distortion.

XXXVI Observed and predicted ratios of phenotypes from matings of *Chrysopa oculata* Say, originating from Ile Perrot, Quebec. Inheritance of the post-antennal spot in the green-gradate phenotype (*bb*).

XXXVII Frequency of characters not usually associated with the green-gradate and black-gradate phenotypes of *Chrysopa oculata* Say.

XXXVIII Frequency of the allelic genes *B* and *b*, determining black *vs* green gradate crossveins in *Chrysopa oculata* Say, on Ile Perrot, Quebec.

XXXIX Frequency of the allelic genes *B* and *b*, determining black *vs* green gradate crossveins in *Chrysopa oculata* Say, on Mt. St. Hilaire, Quebec.

XL Frequency of the allelic genes *A* and *a*, determining respectively, presence of the sub-antennal facial band and spots, in *Chrysopa oculata* Say, on Mt. St. Hilaire, Quebec.

XLI Observed progeny phenotypes from matings of *Chrysopa chi* Fitch from Mt. St. Hilaire, Quebec. Inheritance of obligatory diapause.

XLII Termination of obligatory diapause in *Chrysopa chi* Fitch: regression analysis

XLIII Termination of obligatory diapause in *Chrysopa chi* Fitch: summarised data.

LIST OF FIGURES

1. Population dynamics of *Chrysopa oculata* Say and *Chrysopa chi* Fitch on Ile Perrot, Quebec: 1977 and 1978.

2. Population dynamics of *Chrysopa oculata* Say and *Chrysopa chi* Fitch on Mt. St. Hilaire, Quebec: 1977.

3. Population dynamics of *Chrysopa oculata* Say and *Chrysopa chi* Fitch on Mt. St. Hilaire, Quebec: 1978 and 1979.

4. Oviposition rhythm of field-collected *Chrysopa oculata* Say and *Chrysopa chi* Fitch under field conditions: 16-17 July 1978.

5. Oviposition rhythm of field-collected *Chrysopa oculata* Say and *Chrysopa chi* Fitch under field conditions: 21-22 June 1979.

6. Survival (lx) in laboratory rearings of *Chrysopa oculata* Say from Ile Perrot, Quebec.

7. Emergence pattern in laboratory rearings of *Chrysopa oculata* Say from Ile Perrot, Quebec.

8. Frequency distribution of embryonic mortality in a laboratory culture of *Chrysopa oculata* Say from Ile Perrot, Quebec.

9. Forewing of *Chrysopa oculata* Say.

10. Phenotypes of *Chrysopa oculata* Say.

11. Seasonal change in frequency of the allelic genes *B* and *b*, determining black *vs* green gradate crossveins in *Chrysopa oculata* Say, on Ile Perrot and Mt. St. Hilaire, Quebec.

12. Termination of obligatory diapause in prepupae of *Chrysopa chi* Fitch. The effect of cold exposure on emergence (Fig. 12.1), days to pupation, duration of pupal stage and overall development time (Fig. 12.2).

LIST OF PLATES

1. *Chrysopophthorus americanus* Mason, a parasite of adults of *Chrysopa oculata* Say: host pathology and parasite developmental stages.

2. *Chrysopophthorus americanus* Mason, a parasite of *Chrysopa oculata* Say: developmental stages.

3. Intracellular bacteria (Rickettsia?) in gonads of *Chrysopa chi* Fitch.

4. Chromosomes of *Chrysopa oculata* Say.

5. Chromosomes of *Chrysopa chi* Fitch.

6. Chromosomal translocations in *Chrysopa oculata* Say.

7. Chromosomal translocations in *Chrysopa chi* Fitch.

INTRODUCTION

The concept of using predatory insects to control insect pest species is not new. Chrysopa was one of the insect groups recommended by Linnaeus as early as 1763, for the control of aphids (Usinger 1964), and Chapais (1916) recommended that we "pay it as much respect as it deserves for its usefulness." These early suggestions went largely unheeded, however, with the advent of the botanical and inorganic insecticides, and with the appearance in the 1940's of the organics, which were effective, easily applied and relatively inexpensive. Over the years this led to several undesirable effects, not the least of which is the development of insecticide resistance in insects. Georghiou and Taylor (1976) reported an increase of 62.5 per cent over that of the 1967 survey, of the number of insect and acarine species in which resistant strains developed.

Crop protection now, as in the past, is still heavily dependent on synthetic chemicals for pest control and, in the light of this situation, there is today, a renewed interest in the potential of chrysopids and other beneficial insects in biological and integrated control programs. All chrysopid larvae are predaceous but the adults of many species are not. Chrysopids, or green lacewings, constitute an important component of the predator complex of corn (Chiang and Holdaway 1955; Sparks et al. 1966), sugarcane (Negm and Hensley 1969), alfalfa (Rakickas and Watson 1974; Goodarzy and Davis 1958), apple orchards (MacLellan 1977), cotton (Reed 1965; Orphanides *et al.* 1971; Ehler *et al.* 1973; Irwin *et al.* 1974; Mostafa *et al.* 1976; Bar *et al.* 1979) and other crops.

Until the 1950's chrysopids were little studied save for regional treatments of species. Biological control studies have been conducted almost exclusively on a single species (*Chrysopa carnea* Steph.) and although there are several such studies, very few have placed any emphasis on ecology.

Chrysopids are world-wide in distribution and some species occur in both hemispheres (Adams 1978). Some inhabit fields and meadows (Throne 1971) while others are dendrophilic (Smith 1922; Throne 1971), montane and xerophilic (Adams 1978).

GENERAL LITERATURE REVIEW

MASS-CULTURING TECHNIQUES

3

A major step in the use of chrysopids in biological control was made in the late 1940's with the successful demonstration of natural control of mealybugs on unsprayed pear trees (Doutt 1948) and in field plots artificially colonized by laboratory-reared eggs (Doutt and Hagen 1949). Subsequently, Doutt and Hagen (1950) established the proper timing of releases and the density of eggs per tree.

These achievements were made possible by Finney's mass-culture technique (Finney 1948) for obtaining large numbers of adults and eggs, and the use in adult nutrition of a protein hydrolysate of yeast which significantly increased egg production beyond that obtainable on a diet of honeydew (Finney 1950a, b). Finney's mass-culture technique suffered, however, from a great deal of cannibalism and resulted in about 50 per cent of hatched eggs reaching the adult stage; this was because larvae were held in a common rearing container and were not isolated from each other. The subsequent development of the grid method by Ridgway _et al_. (1970) and its modification by Morrison _et al_. (1975), Barnes (1975a) and Ru _et al_. (1976), simplified and increased the efficiency and productivity of mass-culturing. Hassan (1975) also mass-reared larvae in a manner similar to Finney (1948) and Tulisalo (1978) developed and described a continuous culture method in which all developmental stages are simultaneously present.

In mass-cultures larvae were reared on eggs and mature larvae of the potato tuber moth *Gnorimoschema operculella* (Zeller) (= *Phthorimaea operculella* (Zeller) (Finney 1948, 1950a) and on eggs of the Angoumois grain moth, *Sitotroga cerealella* (Oliver) (Ridgway *et al*. 1970; Morrison *et al*. 1975; Morrison and Ridgway 1976; Barnes 1975a). Tulisalo *et al*. (1977b) used adults of the Angoumois grain moth as the sole source of food while Hassan (1975) substituted eggs in the later instars by larvae of *Plodia interpunctella* and *Barathra brassicae*. Larvae have also been mass-reared on eggs and larvae of the cabbage looper, *Trichoplusia ni* (Hubner) and soybean looper, *Pseudoplusia includens* Walker (Ru *et al*. 1976), and Pasqualini (1975) experimented with eggs and larvae of the pyralid moth *Ephestia kuehniella* (Z.). Mass production and harvesting of eggs were described by Finney (1948, 1950a), Ridgway *et al*. (1970), Barnes (1975a), Ru *et al*. (1976) and Morrison and Ridgway (1976), and conditions for storage were investigated by Kuznetsova (1970) and Hassan (1974).

DIETARY AND OTHER INFLUENCES AFFECTING FECUNDITY AND FERTILITY

Studies of the reproductive potential of chrysopids have indicated that females need a protein meal to stimulate high-level fecundity (Hagen and Tassan 1966a , 1970; Sheldon and MacLeod 1971; Philippe 1972) and that mated females have a much higher oviposition rate than virgin females (Philippe 1971, 1972). Investigations into dietary influences on reproduction, conducted by Tauber and Tauber (1973b, 1974a), disclosed that, in some species, females only or both sexes need to have a protein meal for successful mating and initiation of oviposition, while this was not a requirement in other species. Some aphid species used as prey were found to induce a partial sterility in adults (Canard 1970a,b) and also larval and nymphal mortality (Canard 1970b;Hydorn and Whitcomb 1979). In addition, Hydorn and Whitcomb (1972) found that infertility, as well as development time and reduction in the number of offspring reaching maturity, increased with parental age.

Human dietary supplements (rich in amino acid content) at specific concentrations and supplemented with honey were as effective in stimulating egg production as a diet of honeydew plus honey (Hagen 1950). Although honey by itself resulted in the lowest oviposition, however, when used as a supplement to the diet of honeydew, it resulted in a level of egg production which was significantly greater than that obtained on honeydew alone (Hagen 1950).

Enzymatic protein autolysates and hydrolysates of Brewer's yeast (Saccharomyces cerevisiae) plus a carbohydrate moiety (either honey, fructose or sucrose) also elicited a much greater egg production than non-hydrolysed yeast plus fructose (Hagen and Tassan 1966a,b). Though fructose by itself, like honey, results in very little oviposition (Hagen and Tassan 1966a, 1970), as a supplement to the less expensive autolysate, its effect on egg production was far greater than that of honey, and was as effectively replaced in the diet by sucrose (Hagen and Tassan 1966a).

A very high fecundity, equivalent to that obtained with the autolysate of Brewer's yeast, was also obtained with the relatively inexpensive whey products (Food Wheast(R) and Feed Wheast(R)) which contained intermediately autolysed (17 hours) yeast (Saccharomyces fragilis); they were more effective than non-hydrolysed yeast or yeast autolysed for 36 hours (Hagen and Tassan 1970). Botto and DeCrouzel (1979) also reported that powdered beer yeast and honey in a 1:1 proportion was the best of five artificial diets tested.

Hagen and Tassan (1966b) found that fecundity on a complete chemically defined diet of 19 amino acids was comparable to that on yeast hydrolysate, and was superior to a chemically defined diet of 10 amino acids in that fecundity was greater and mortality lower (Hagen and Tassan 1972). Females fed only chemically defined diets lacking in amino acids, B-vitamins or salts, showed a severely depressed fecundity, indicating that there is some transfer of these metabolites from the larval stage, and that adults, in order to support a high fecundity, must acquire these substances from an extraneous source (Hagen and Tassan 1972). Amino acid elimination and suppression studies showed that elimination of any one of eight essential amino acids would result in a drastic drop in oviposition (Hagen and Tassan 1972) and that the extracellular symbiotic yeast *Torulopsis*, found in the diverticulum of the foregut (Hagen and Tassan 1966a), was a producer of the amino acid valine, and probably also phenyalanine and threonine (Hagen and Tassan 1972). A semi-defined diet described by Sundby (1967) produced a low level fecundity which was stimulated by the addition of flowers to the holding cage, indicating that the diet *per se* was incomplete.

ARTIFICIAL LARVAL DIETS

Semi-defined diets for rearing larvae were described and used by Hagen and Tassan (1965, 1966c), and by Vanderzant (1969, 1973) who reared seven and eighteen generations. Larvae were also reared on a complete chemically defined diet and, by means of amino acid omission studies, 10 amino acids were found to be indispensable to growth (Vanderzant 1973). Bigler *et al.* (1976) reared *C. carnea* and *C. perla* on a modified Vanderzant (1969, 1973) diet and *C. perla* on a modified Ferran (1975a,b) diet, but failed to rear both species on a modified diet of Ponomareva and Begliarov (1973; *vide* Bigler *et al.* 1976). A semi-defined diet based on easily acquired ingredients was also described by Hassan and Hagen (1978); three successive generations were reared but development was longer than when reared on eggs of *S. cerealella*. Larvae were also successfully reared on drone honeybee brood, lyophilized into a powdery form (Okada *et al.* 1974; Matuska *et al.* 1978).

Artificial diets were supplied to larvae in diet-saturated fragments of sponge (Vanderzant 1969, 1973) and dental cotton (Bigler et al. 1976), and in droplets thinly coated with paraffin wax (Hagen and Tassan 1965, 1966c; Hassan and Hagen 1978; Martin et al. 1978). Martin et al. (1978) found mortality only in first instar larvae reared on the encapsulated Vanderzant (1969, 1973) diet, but mortality was greater and weight gain less than in those reared on insect eggs. In addition, the capsules were generally larger than eggs of the grain moth, very few were penetrated by first instar larvae, and their resistance to dehydration was found to be intermediate between that of grain moth eggs and eggs of the tobacco budworm, Heliothis virescens (F.) (Martin et al. 1978).

BIOLOGICAL CONTROL STUDIES

Numerous studies have shown chrysopids to be potentially useful in biological control. Smirnoff (1953) reported that larvae of Chrysopa vulgaris Schneider fed exclusively on the palm diaspidid. Lingren et al. (1968a) showed in laboratory studies on predation that after the coccinellids, the chrysopids were the next major group of predators, and demonstrated in field cage studies, a 96 per cent reduction in the population of budworm eggs (260,000 per acre) by inundative releases of larvae (420,000 per acre). Ridgway and Jones (1968, 1969) demonstrated in field and field-cage experiments that inundative releases of eggs or larvae were also effective in reducing bollworm and tobacco budworm populations on cotton, and found that predation efficiency was not seriously depressed by the presence of alternate prey (Ridgway and Jones 1968). A functional response to predation in the absence of alternate prey was recorded by Ables et al. (1978) while Galecka and Zeleny (1969) and Lopez and Teetes (1976) observed a numerical response.

In other studies on cotton, Van den Bosch et al. (1969) investigated and evaluated each component of the predator complex and reported that *Chrysopa carnea* had a heavy impact on the bollworm population. Tejada (1976) found that *C. carnea* was the most efficient predator of eggs and larvae of *Heliothis* and that second instar larvae were more efficient than the first. Lopez et al. (1976) evaluated predators of the cotton budworm and tobacco budworm and reported that the first instar larva of *C. carnea* was the most effective in destroying first instars of the bollworm and budworm.

Shands et al. (1972b) investigated insect predators on potatoes; they reported that placement of chrysopid eggs in plots gave better control of the green peach aphid than the potato aphid, and attributed the lack of significant differences among predator treatments (in treated and untreated plots) to interplot migration of the predators: evidence of migration in search of food was recorded by Ridgway and Jones (1968). In subsequent studies Shands and Simpson (1972) and Shands et al. (1972c) established rates and schedules of introduction in small fields and in large field cages.

Prey-predator ratios established in field plots and field-cage studies for the control of _Rhopalosiphum padi_ (L.) indicated that 15 to 20 times more eggs than larvae were needed to achieve the same level of control (Rautapaa 1977). Rates of release were also established in greenhouse studies for the control of aphids on chrysanthemums and cucumbers (Scopes 1969) and on green peppers (Tulisalo and Tuovinen 1975) and parsley (Tulisalo _et al_. 1977a). Methods for the field distribution of eggs were described by Shands _et al_. (1972a), Jones and Ridgway (1976) and Ables _et al_. (1979).

Apart from the use of inundative releases to increase predator populations in the field, Schiefelbein and Chiang (1966) demonstrated that chrysopids can be concentrated in an area through the use of sucrose sprays, though there was no significant increase in oviposition. Sucrose _per se_ has no attractive power; it functions as an arrestant (Hagen _et al_. 1971, 1976) but was shown to stimulate a much higher fecundity when added to protein hydrolysate diets (Hagen and Tassan 1966a).

Protein hydrolysate food sprays (Wheast$^{(R)}$+ sucrose + water) used as artificial honeydews were shown to be attractive to chrysopids even though few aphids were present, and elicited an increased as well as premature oviposition, which prevented the build-up of aphids on alfalfa, and bollworms on cotton (Hagen _et al_. 1971). Sprayed cotton-fields also had fewer damaged bolls than unsprayed fields (Hagen _et al_. 1971). In other trials, food spray applications likewise resulted in greater oviposition and fewer aphids in treated fields of bell peppers (Hagen and Hale 1974), and potatoes (Ben Saad and Bishop 1976a). Shands et al. (1972b) found, however, no appreciable effect on the aphid population, or on the number of chrysopid larvae in treated potato fields, and Butler and Ritchie (1971) observed that oviposition did not increase consistently with the increased population of adults in sprayed cotton fields.

Tassan et al. (1979) felt that these contradictions reported in the literature may have been due to seasonal changes in the oviposition rate and in the number of ovipositing females. As a result of field studies conducted over a 17-week period, they found that the oviposition response to nutritionally complete food sprays and naturally-occuring foods changed with time, and concluded that the intensity of the response can be modified by seasonal changes in the quality and quantity of naturally-occuring foods, as well as by the number of adults in the area. They also observed that nutritionally complete food sprays elicited a greater oviposition response than naturally-occuring foods.

Protein hydrolysates are rich in free amino acids and field tests indicated tryptophan to be the most attractive of 10 essential amino acids (Hagen et al. 1976). It was incorporated into food sprays (Hagen et al. 1976; Ben Saad and Bishop 1976a,b) thereby increasing their attractiveness to chrysopids and their efficiency as artificial honeydews.

Laboratory studies on olfaction indicated indole acetaldehyde to be the most attractive breakdown product of tryptophan (Van Emden and Hagen 1976).

Chrysopid adults were also found to be attracted to terpenyl acetate (Caltagirone 1969), methyl eugenol (Suda and Cunningham 1970) and caryophyllene (Flint _et al_. 1979), and Sakan _et al_. (1970) isolated and tested attractants from the plant _Actinidia polygama_ Miq. In addition, kairomones, involved in prey finding and/or acceptance by larvae, were demonstrated on eggs of _Heliothis zea_ (Boddie) (Nordlund _et al_. 1977). A hexane extract obtained from scales of _H. zea_ was shown to increase the predation rate (Lewis _et al_. 1977).

PESTICIDE TOXICITY

Chrysopids, the larvae particularly, are remarkably tolerant to pesticides. Van den Bosch _et al_. (1956) and Wilkinson _et al_. (1975) reported that they were the most tolerant of the predators, and Van Steenwyk _et al_. (1975) found that this predator group was one of the least affected by increased insecticide usage on cotton. Bartlett (1964) tested eggs, larvae and adults against 60 pesticides, several of which showed zero toxicity; various chlorinated hydrocarbons including DDT almost lacked toxicity in contrast to others which were highly toxic, while day-old residues of some organophosphates were not appreciably toxic. Doutt and Hagen (1949) found that DDT was particularly injurious to adults, and Putman (1956) reported that larvae of Chrysopa plorabunda Fitch were more resistant than those of Chrysopa rufilabris Burm. The differential toxicity exhibited by these two species is believed to have effected a reversal in dominance, resulting in C. plorabunda becoming the common species (Putman 1956).

Chrysopid larvae show marked tolerance to nicotine fumigation (Tulisalo and Tuovinen 1975) and to all pyrethroids (Shour and Crowder 1980). They are reported to be almost immune to carbaryl (Brettell 1979) and dimethoate (Eveleens et al. 1973; Eveleens 1974; Vickerman and Sunderland 1977), and show little or no toxicity to pirimicarb (Helgesen and Tauber 1974; McDonald and Harper 1978; Summers et al. 1975) and chlorobenzilate (Lawrence et al. 1973; Lawrence 1974; Bartlett 1964). The growth regulator diflubenzuron did not appear to adversely affect field populations of adults (Ables et al. 1977; Keever et al. 1977) though it did have a serious effect on eggs and larvae (Ables et al. 1977) and was recommended for use in integrated control where it was desirous to conserve adult insects (Wilkinson et al. 1978). Trichlorfon was reported to be the least toxic of five insecticides tested (Lingren and Ridgway 1967; Lingren et al. 1968b) and showed moderate and limited toxicity in different formulations (Dinkins et al. 1971).

Larvae of Chrysopa oculata Say and Chrysopa rufilabris Burm. were virtually immune to feeding on aphids killed by the systemic insecticide Systox(R) (Ahmed et al. 1954) whereas only first instar larvae of Chrysopa vulgaris Schneider showed toxicity to Systox$^{(R)}$and schradan (Ahmed 1955). Greenhouse studies on cotton indicated that soil applications of Temik$^{(R)}$ and stem applications of Azodrin$^{(R)}$did not affect larvae of *Chrysopa* spp (Ridgway *et al*. 1967). Low-level sidedress treatments and in-furrow applications of the systemic insecticide aldicarb also had no detrimental effect on the chrysopid population of cotton (high-level sidedress treatments were detrimental), but sidedress applications followed by foliar applications of monocrotophos, another systemic, greatly affected the total predator complex (Kinzer *et al*. 1977). Monocrotophos was reported to be 13 times as toxic to adults of *Chrysopa zastrowi* Esb.-Pet. as endosulfan (Barnes 1975b). In addition, the nuclear polyhedrosis virus, *Baculovirus* sp., was found to have no effect on eggs, larvae or adults (Hassan and Gröner 1977).

POPULATION DYNAMICS AND ECOLOGY

While chrysopids occur in most habitats and several studies exist on the faunistic composition of regions, there are few, however, which deal with population dynamics and faunistic composition in specific habitats. Zeleny (1965) investigated these aspects in cultural steppe and reviewed similar studies in crop systems in Europe. Canard and Laudeho (1977) did likewise for olive groves in Greece, Judd and Masteller (1977) for vinyards in the United States, and Dinkins *et al.* (1970a,b) for cotton fields, also in the United States.

Like population dynamics, ecology has been a somewhat neglected field. Neumark (1952) made an extensive study of the biology and ecology of C. carnea in Israel. Séméria (1974a) studied the faunistic composition of two biocenoses and calculated Sorensen coefficients of affinity between members of pairs of species, which suggested that real tendencies towards cohabitation between species may be related to the specific type of larval development and competition. In other studies, Séméria (1978,1980a) reported on faunistic composition, sex ratio, cohabitation between species, and parasites and predators.

Blum et al. (1973) identified the repellent fractions in the prothoracic gland secretion of Chrysopa oculata Say and postulated that the non-odoriferous species may be Batesian mimics of it. Like Tjeder (1966), Séméria (1979) observed that the repugnant species all belong in the genus Chrysopa s.s., and further stated that they exhibit convergence in body markings with a tendency towards uniformity, this coloration being also shared by a few species of Anisochrysa. Séméria (1979) recognized a pseudo-batesian mimicry between species of Chrysopa s.s. (odoriferous) and Anisochrysa (non-odoriferous), a situation so termed as the mimics were more numerous than the model. He recognized also within Chrysopa s.s. a Müllerian mimicry, though the condition of cohabitation was flexible (the model and mimic often appeared to exclude each other from a specific biotope), and within Anisochrysa (non-odoriferous and usually unmarked) an Arithmetic mimicry which is based on high density of both species (safety in numbers).

The predatory nature of ants and the facultative helotism of some species with aphids make for direct competition with chrysopid larvae. Bose and Ray (1975) observed that chrysopid larvae were ignored by some aphid-tending ant species but were attacked by *Camponotus compressus* (Fabricius). Larvae of *Chrysopa slossonae* (Banks) were reported to live in, and feed on colonies of the wooly alder aphid, and to escape attack by aphid-tending ants by covering themselves with the waxy secretion of the aphids (Eisner *et al*. 1978). Moreover, denuded larvae deliberately clothe themselves with the waxy secretion, and larvae, starved and denuded, gave as much priority to clothing as to feeding (Eisner *et al*. 1978). In greenhouse-conducted biological control studies, Tulisalo *et al*. (1977a) observed that control by chrysopid larvae was impaired by ants while Sterling *et al*. (1979) found that the imported fire ant, *Solenopsis invicta* Buren, exerted no significant predation on field populations of chrysopids. Rezk *et al*. (1975) observed competition between *Scymnus* and *Chrysopa* when *Coccinella* began to increase in number.

RESPONSES OF ADULT CHRYSOPIDS TO ULTRASOUND

Chrysopid adults respond to ultrasonic pulses by falling to the ground (Roeder 1962), a response which is similar to the evasion of bats by moths (Roeder and Treat 1961). Miller and MacLeod (1966) identified the tympanal organ as the acoustic receptor. This was accomplished by means of histological and electrophysical studies, and also by selective destruction of parts of the insect's body while observing the response of the third axillary sclerite to ultrasound.

A histo-morphological study of the tympanal organ showed that it differs from the typical insect tympanum in that the cavity is primarily fluid-filled and the ventral membrane is rippled and consists of a single tissue layer (hypodermis) and cuticle (Miller 1970). Miller (1970) concluded that the organ functions as a pressure receptor, rather than as a pressure gradient receptor as in other typical insect tympanal organs. The tympanum was also described by Fröhlich (1973) as a new chordotonal organ, though in less detail than Miller (1970). Physiological responses to ultrasound, mediated through the tympanum, were also investigated in wing and flight muscles (Miller 1971; Olesen and Miller 1979), while Miller (1974, 1975) reported on behavioral responses in stationary flight, and Miller and Olesen (1979) on avoidance behavior of free-flying lacewings to both bats and ultrasound.

THE PROBABILITY OF SOUND PRODUCTION AND ITS ROLE IN COURTSHIP

Stridulatory structures on the second abdominal sternum and on the hind femora of males of Meleoma schwarzi (Banks) were described by Adams (1962), who suggested that the sound produced may be involved in courtship, though sound production was never demonstrated. Adams (1962) also suggested that the sound may be received by the alary chordotonal organs or other receptors such as the pedal chordotonal organs and Johnston's organ. Miller and MacLeod (1966) contend, however, that it is improbable that such low frequency sound may be received by the tympanal organ, and favor instead, the pedal chordotonal organs or the trichobothrial setae of the last abdominal segment as the more likely receptors.

Courtship studies on three sympatric _Chrysopa_ species revealed that the temporal pattern of abdominal jerking exhibited by the members of an interacting pair differs from one species to the other (Henry 1978). Though sound production was never demonstrated during the abdomen-jerking behaviour, Henry (1978) postulated that there was an acoustical communication which functioned over short distances to bring about reproductive isolation in morphologically and ecologically similar species.

Further studies in _C_. _carnea_ showed that an interacting pair establishes a duet of precise, reciprocal abdominal jerking, and that the respective patterns exhibited by homosexual and heterosexual pairs, as well as by individuals, are consistent and predicatable (Henry 1979a). Henry (1979a) also observed that opaque barriers did not interfere with the reciprocating pattern of an interacting pair and ruled out an olfactory stimulus since regulated releases of pheromone would become disorganised in transit, thereby affecting the precision of the interaction. Instead, he proposed the existence of a sound-transmitted stimulus which, he postulated, was produced by the interaction between the modified metanotal surface and the patch of microtrichia on the ventral surface of the anal area of the forewing. These structures were described by Henry (1979a), and also by Eichele and Villiger (1974) who likewise postulated their involvement in sound production. However, recent data published by Henry (1980a), indicate substrate-transmission of low frequency acoustic signals produced by abdominal jerking, but no high frequency sound production, and no involvement of the metanotal surface and microtrichia patch of the forewing in courtship.

Oscillographs of abdominal jerking patterns of _C. carnea_ and _Chrysopa downesi_, two closely related species, showed distinctly different patterns which indicate an allopatric speciation of these two species (Henry 1979b). This conclusion is supportive of Hendrickson's (1978) argument that there is no evidence for the claim (Tauber and Tauber 1977a,b) of sympatric speciation of these two species. Oscillographic studies of abdominal jerking were also done for _Chrysopa chi_ Fitch and _Chrysopa rufilabris_ Burm., the latter showing sexual dimorphism of abdominal jerking as well as two distinct patterns in the male (Henry 1980b).

DIAPAUSE AND PHOTOPERIODIC RESPONSES

Studies on diapause and photoperiodic responses have contributed to an understanding of phenology and physiology, as well as population dynamics, reproductive development and reproductive isolation of sympatric species. Diapause has been most intensely investigated in _C_. _carnea_, in which both its reproductive diapause and the associated color phase were shown to be under photoperiodic control (MacLeod 1967; Tauber and Tauber 1969; Tauber _et al_. 1970a). Assumption of the diapause color phase, however, is not an indicator of diapause onset as color change occurs subsequent to diapause onset (Honek 1973a) and, in addition, is temperature dependent-high temperatures decrease the assumption of the diapause color phase (Honek 1973b). Photoperiod also controls seasonality in those species which overwinter as adults (Tauber and Tauber 1973a, 1973d, 1974b, 1976a,b) as well as those which do so in the cocoon stage (Propp _et al_. 1969; Tauber and Tauber 1972c, 1975b).

Reproductive diapause is induced by short photoperiods, and is expressed in new females by non-engagement of the ovaries in oogenesis (MacLeod 1967), and in ovipositing females by a reduction in fecundity (Tauber and Tauber 1969, 1970b). Reproductive diapause was also reported to be one of two distinct components of dormancy (Bowden 1979), each of which is initiated by a different photoperiod, the other component being flight activity which shows an all or none response. In addition, Tauber and Tauber (1972b, 1973a, 1975a) reported a food-mediated summer diapause in the _mohave_ race of _C_. _carnea_, and discussed the regional advantages of the two races with respect to biological control.

All stages of C. carnea are sensitive to photoperiodic induction of reproductive diapause in the adult by short-day conditions, but the third instar larva within the cocoon, the pupal and adult stages are the most sensitive (Tauber and Tauber 1970a). Kowalska (1971) found, however, that only the adults were photosensitive and observed that at photoperiods longer than 14 hours gonads matured and oviposition occurred. Photoperiod was also shown to affect significantly, the maturation rate of females but not of males (Sheldon and MacLeod 1974b). In addition, adults reared under short day were found to have a relatively short diapause but a more enduring diapause is obtained by transfering from long-day to short-day conditions (Tauber and Tauber 1970a; Tauber et al. 1970a). Diapause intensity is subject to geographic variation (Tauber and Tauber 1971a, 1972a), and duration appears to be under polygenic control (Tauber and Tauber 1971a).

Diapausing adults show a quantitative response to day lengths below the critical photoperiod, diapause duration (days to oviposit) being inversely proportional to daylength (Tauber and Tauber 1971a, 1973c). Adults of C. carnea also respond to directional changes in photoperiod which do not encroach on the critical photoperiod; a decrease in daylength above the critical photoperiod induces diapause, while an increase in daylengths less than the critical photoperiod averts it (Tauber and Tauber 1970b). Kowalska (1971) observed diapause termination under diapause inducing photoperiod but this may have been because the photoperiod used represented an increase over that which existed. Critical photoperiod is influenced by temperature (Sheldon and MacLeod 1974a) and, like diapause intensity, it is also subject to geographic variation (Tauber and Tauber 1971a, 1972a).

Apart from inducing diapause, short photoperiods were shown to maintain diapause for a limited time (66 ± 22 days), a resumption of oviposition indicating diapause termination (Tauber _et al_. 1970b). This spontaneous termination suggests that short days of autumn may induce and maintain diapause, and that subsequent to diapause termination at short day, factors other than photoperiod determine the restoration of reproductive activity. In a subsequent study, Tauber and Tauber (1973c) transferred outdoor-diapausing samples into natural (greenhouse) as well as stationary photoperiods, at, before and after the winter solstice, and observed that natural daylengths after the winter solstice had no effect on diapause termination. Tauber and Tauber (1973d) also reported that low temperatures appear to slow diapause development, particularly after the winter solstice, but Hodek and Honek (1976) demonstrated that adults of _C_. _carnea_ perceive short days at cold and that short days promote diapause development under cold conditions. Cold exposure, _per se_, is not a prerequisite for termination of reproductive diapause as activation can be achieved at any time by a return to long-day conditions (Honek and Hodek 1973; Tauber and Tauber 1969; Tauber _et al_. 1970b).

Chrysopa harrisii Fitch, a member of the *carnea* group (Tauber 1974), is similar to *C. carnea* in that reproductive diapause is induced and maintained for a limited time by short day, and is terminated by long-day conditions in the laboratory but not by cold exposure (Tauber and Tauber 1974b). Unlike *C. carnea* which exhibits an inverse relationship between diapause development and daylength (Tauber and Tauber 1973c), in *C. harrisii*, however, neither long days, nor increasing daylength terminate diapause, for diapause ends at or about the winter solstice (Tauber and Tauber 1974b) much earlier than in *C. carnea* (Tauber and Tauber 1973c). Furthermore, based on its non-diapause threshold of development, it probably also has a high temperature threshold for post-diapause development which would thus correlate with its more northerly distribution and ensure that reproduction is not activated in unusually warm winter spells (Tauber and Tauber 1974b). In addition, adults of *C. harrisii* were found to be much more sensitive to diapause-inducing stimuli than those of *C. carnea* (Tauber and Tauber 1974b).

Like the closely related polyvoltine *C. carnea*, univoltine and sympatric *Chrysopa downesi* Banks overwinters in the adult stage; it exhibits a quantitative response (in diapause termination) to daylength, diapause maintainance after the winter solstice is related to short day, and the rate of diapause development (diapause termination) increases with the lengthening of late winter days (Tauber and Tauber 1975b, 1976a). *C. downesi* adults, however, need a series of short days prior to long days for reproduction to occur; that is, it responds to two critical photoperiods in addition to the difference between short and long day, thereby limiting reproduction to spring (Tauber and Tauber 1976b). The photosensitive stages were shown to be the third instar, the prepupa and pupa, but diapause can also be induced by rearing under either constant short day or long day (Tauber and Tauber 1976b).

The two sympatric species, C. carnea and C. downesi, are temporarily separated by the asynchrony of their reproductive cycles, arising from the later-ending diapause of C. downesi - mating begins about a month later than in C. carnea (Tauber and Tauber 1976a, also 1973c, 1975b) - and its higher thermal threshold of development (Tauber and Tauber 1976a, 1973d). These result in the sensitive stages encountering long-day conditions, thereby ensuring that emerging adults enter into reproductive diapause (Tauber and Tauber 1975b, 1976a).

Seasonality is also under photoperiodic control in those chrysopid species which overwinter in the cocoon stage and not as adults. Short day was shown to induce diapause in Chrysopa oculata Say (Propp et al. 1969), Chrysopa nigricornis Burm. (Tauber and Tauber 1972c) and Chrysopa perla (L.) (Canard 1976), for which critical photoperiods as well as sensitive stages were determined. The second and third instars of C. oculata and all three instars of C. nigricornis are photosensitive (Propp et al. 1969; Tauber and Tauber 1972c), and in C. perla, photosensitivity in a facultatively diapausing strain was found to increase progressively from the egg to the third instar larva which was the most sensitive (Canard 1976).

Whereas in C. carnea and C. downesi the adults show a quantitative response to photoperiod (Tauber and Tauber 1973c, 1976a), larvae of C. oculata, C. nigricornis, Meleoma signoretti Fitch and C. perla perceive day or night as being either short or long, and give an "all or none" response to photoperiod (Propp et al. 1969; Tauber and Tauber 1972c, 1975b; Canard 1976). Furthermore, in C. oculata and C. nigricornis, diapause development proceeds very slowly under short day, and termination is spontaneous at the end of a long period (it is also accelerated by long-day exposure within the first four weeks of diapause), indicating that diapause is maintained by short day (Propp et al. 1969; Tauber and Tauber 1972c). On the other hand, in C. perla, diapause termination does not occur spontaneously at 20°C and 25°C; termination is dependent on cold exposure but not photoperiod, and a quantitative relationship exists between per cent termination and duration of cold exposure (Canard 1976).

GENETIC STUDIES ON CHRYSOPIDS

A few chrysopid species have been the objects of genetic studies. Bickley (1952) investigated the inheritance of some varietal characters (black post-antennal markings) in C. oculata and concluded that they were under the control of more than one gene. The study also led to new synonymy and the dropping of all varietal names. Also in C. oculata, Tauber et al. (1976)

described a yellow-body mutation in adults, which was under the control of a sex-linked recessive gene.

In C. carnea, MacLeod and Sheldon (1972) reported on a green-eyed mutation which was inherited as a dominant (wild type is gold-eyed), and Tauber and Tauber (1971b) found that an autosomal recessive gene was responsible for the bluish coloration in mutants of non-diapausing adults (wild type color is green). Reported to be apparently under polygenic control are the distinguishing biological traits of C. carnea and C. mohave (Tauber and Tauber 1975a) and diapause duration in C. carnea (Tauber and Tauber 1971a).

Two pairs of unlinked autosomal genes were reported by Tauber et al. (1977) to control seasonal isolation (they control the photoperiodic response) in the sibling species C. carnea and C. downesi, the carnea genotype being dominant over that of downesi. Tauber and Tauber (1977a) found that the dark-green color of C. downesi is controlled by a semi-dominant gene, whose recessive allele in the homozygous state determines the green color of C. carnea. Furthermore, Tauber and Tauber (1977a,b) proposed a sympatric mode of speciation for these two sibling species and hypothesised that speciation had to be preceded by a single gene difference as the basis for differential habitat association, such association being due to color change in the parental stock, rather than a change in habitat choice.

CYTOGENETICS OF CHRYSOPIDS

Cytogenetic investigations have so far been conducted only on old-world species. Naville and de Beaumont (1932, 1933, 1936) described the chromosomes of thirteen European species and Kichijo (1934) did likewise for five species in Japan. In all cases there was precocious segregation of the sex chromosomes. The haploid chromosome number is generally six, except in *Chrysopa septempunctata* Wesmael with *n* = 5, and *Chrysopa flava* Scop. (= *Nineta flava* (Scop.)) with *n* = 7

More recently, the chromosomes of *C. carnea* which were first described by Naville and de Beaumont (1933) under the synonym, *Chrysopa vulgaris* Schneider, were again investigated. Korobko and Romanchenko (1976) karyotyped the species and presented an idiogram, while Kiauta *et al*. (1977), under the synonym *Anisochrysa carnea* (Steph.), described the meiotic stages. Kiauta *et al*. (1977) also presented an annotated list of cytologically studied species, arranged in an up-dated (though not up to date) scheme of classification.

SYSTEMATICS OF THE GENUS *CHRYSOPA* S.L.

The systematics of the genus *Chrysopa* s.l. is at present undergoing change. Banks (1950) separated the Nearctic species into two subgenera, based largely on the shape of the costal cells of the wings. Steinmann (1964) described several new subgenera, based primarily on color, and Tjeder (1966), working from genitalic studies, recognized some of Steinmann's (1964) designations and, at the same time, described new subgenera. Hölzel (1970) later elevated some of Tjeder's (1966) subgenera to full generic status and also described new subgenera and a new genus. Subsequently, Adams (1975) relegated the genus <u>Anisochrysa</u> Nakahara to the synonymy under <u>Mallada</u> Navas, and Séméria (1977) elevated the subgenus <u>Chrysoperla</u> Steinmann to full generic status.

OBJECTIVES

Chrysopids have received but scant attention in Canada. Noteworthy is the early contribution by Chapais (1916) who briefly investigated biology and commented on the potential for biological control. Biology was also briefly investigated by Briand (1931) and Putman (1932, 1937) who looked at control of the Oriental fruit moth and reported on parasites. Putman (1956) also reported on the relative susceptibility of two chrysopid species to DDT, and recently Bucher and Bracken (1976) concluded that, larvae of _C_. _carnea_ could have accounted for the reduction of the Bertha armyworm population in Manitoba. With respect to systematics, Smith's (1932) paper, though inadequate, is still in use.

Whereas the species which occur in Canada are fairly well-known, the same cannot be said for ecology, population dynamics and faunistic composition of any particular habitat. This study was designed to investigate these aspects in the old-field habitat, especially since the faunistic composition would be indicative of those species likely to be encountered in an agricultural ecosystem in this area. A knowledge of these is a prerequisite to an integrated control program.

Preliminary investigations had indicated that _Chrysopa oculata_ Say and _Chrysopa chi_ Fitch are the two most frequently encountered species in Quebec, and not _C_. _carnea_ which has been used almost exclusively world-wide, in biological control programs. Besides, an examination of the Canadian National Collection in Ottawa revealed that these two species, *C. oculata* and *C. chi*, are widely distributed from coast to coast across Canada. Field and laboratory studies were conducted on them in so far as they were relevant to some aspect of ecology or population dynamics.

1. A study of the oviposition rhythm was undertaken with the view to understanding the observed disjunct field distribution of eggs.

2. The developmental studies were designed to elucidate the observed protandry in the field population and in laboratory rearings, and at the same time to develop an efficient technique and rearing cages for maintaining a small research culture.

3. *Chrysopa oculata* is polymorphic in body markings with some forms more common than others. Genetic studies were undertaken to investigate the inheritance of green *vs* black pigmentation of the gradate crossveins of the forewing, to determine subsequently the gene frequency in the field populations and whether any forms were subject to seasonal variation. Also investigated are inheritance of the black subantennal facial band and the relationship of the basicardo and occipital spots (post-antennal) to pigmentation of the gradate crossveins.

4. *Chrysopa chi* has essentially one generation, in spring, and exhibits an obligatory as well as facultative prepupal diapause. Genetic studies were conducted to determine the

mode of inheritance and to elucidate its effect on the population dynamics of the species.

5. Cytogenetic investigations served to elucidate an egg mortality factor in the two dominant species. The chromosome complement was also investigated, particularly in _C_. _oculata_, in view of the fact that one of the genetic characters investigated is characteristic of some Palearctic species, one with a nonusual chromosome number.

6. An attempt was also made to rear _Chrysopa_ _lineaticornis_ Fitch from eggs. The eggs of this species had not been observed or described before now.

Finally, in view of the unsettled nature of the systematics, the generic designation _Chrysopa_ is used in its wide sense.

MATERIALS AND METHODS

DESCRIPTION OF THE STUDY AREAS

The field studies were conducted in two old fields in Quebec, one on Mt. St. Hilaire (Old Orchard, Gault Estate of McGill University), the other on Don Quichotte Road, Ile Perrot, approximately 4 km from the junction of Don Quichotte and St. Joseph Boulevard. Mt. St. Hilaire is one of the Monteregnian Hills, a series of hills in the lowlands of the St. Lawrence River Valley, characterised by geology different from that of the surrounding area, and by vegetation reflecting altitudinal changes and past geological history (Maycock 1961). Maycock (1961) refers to them as "stranded forests oases" and, in a floristic survey of the mountain (Mt. St. Hilaire), he noted that it has remained relatively undisturbed and that some parts are still in the primeval state. Ile Perrot, on the other hand, is essentially flat. It is also part of the lowlands of the St. Lawrence River Valley but has been extensively denuded and cultivated.

The old orchard habitat on Mt. St. Hilaire is now a field which has been fallow since 1973. It stands at an elevation of approximately 700 feet (213.36m). It is approximately four hectares in area and is otherwise little disturbed save for visitors in spring and summer who occasionally wander off the beaten paths. The habitat is characterised by a primary cover of different grass species with an admixture of vetch (Vicia cracca L.), the most common grasses being Poa pratensis L., Desclampsia flexuosa (L.) Trin., Muhlenbergia mexicana (L.) Trin. and Agrostis alba L. There are also extensive stands of shrubs, particularly Solidago spp (golden rod), Asclepias syriaca L. (Milkweed), Rubus spp (blackberry and raspberry), Apocynum androsaemifolium L. and Scrophularia lanceolata Pursh., and few large trees except for a stand of sumac (Rhus typhina L.) and a small stand of deciduous saplings (paper birch and poplar).

By contrast, the Ile Perrot field is approximately two hectares in area and is bordered on each side by a field of similar size. These fields have also been fallow since at least 1973. Like the Mt. St. Hilaire habitat, this old-field habitat is characterised by a primary cover of grasses with an admixture of vetch. The most common grasses are P. pratensis and Agropyron repens (L.) Beauv. The habitat is also characterised by a lack of trees and the presence of stands of golden rod, raspberry, and the grass Phalaris arundinacea L. Also commonly found are milkweed, the asters (Aster spp), the thistle (Cirsium arvense (L.) Scop.), the garden heliotrope (Valeriana officinalis (L.) and timothy grass (Phleum pratense L.).

Potential insect prey species were numerous in both study areas at most times of the growing season. These comprised aphids in the herbaceous layer, as well as other Homoptera and small insect species in the gramineous layer.

The most visible aphids were those on vetch, namely *Aphis craccae* L. and less frequently *Acyrthosiphon pisum* (Harris), and those on golden rod, namely *Dactynotus pieloui* Rich. and the less common *Dactynotus caligatus* Rich. On Mt. St. Hilaire, *Aphis nasturtii* Klalt. is also highly visible and abundant in the extensive stands of *A. androsaemifolium*, and *Euceraphis punctipennis* (Zett.) is common on birch trees. The aphid *Judenkoa lonicerae* (Sieb.) is abundant in late summer on Ile Perrot, in stands of *P. arundinacea* which are frequented by adult chrysopids.

COLLECTION AND TREATMENT OF FIELD MATERIAL

Adult collections were made at weekly intervals in each study area during the course of an hour, while traversing a path which took in the major microhabitats, netting free-flying individuals and gently beating the vegetation to flush out others. This procedure was consistently followed throughout the study and was the more feasible approach to sampling than sweep-netting. Sweep-netting was not practical because of entanglement of the net in prickly vegetation and because the chrysopids respond to violent disturbance by plummeting to the ground where they become invisible. This sampling approach is somewhat similar to the Direct Observation method used by Mayse *et al*. (1978) which they found superior to sweep-netting in numbers caught.

The weekly collections were identified and the two dominant species (*C. oculata* and *C. chi*) were dissected in isotonic NaCl - Ringer solution. They were examined for ovarian development and the presence of sperm in the seminal vesicle, as indicators of recent emergence, particularly that of the F_1 (summer) generation. In addition, the weekly collections of adults of *C. oculata* were scored for color forms, for an eventual determination of gene frequency in the population.

Dissected adults were also examined for parasitism. Those which appeared to be obviously parasitised by the Euphorine wasp, *Chrysopophthorus americanus* Mason, were isolated in mating-oviposition plastic vials (135cc; 80 X 52mm) provided with moist soil and bits of rotted wood. Adults were also maintained over a period of time, in a controlled environment chamber (LD 16:8; 23.0 ± 0.5°C; 60-70% R.H.) and observed for parasitism. They were held in lots of 5 or more, in paper-cup, mating-oviposition containers, or in a battery jar similarly provided with soil and bits of wood. They were fed live pea aphids, *Acyrthosiphon pisum* (Harris), and 10 per cent sucrose solution from a piece of saturated cotton.

Searches were also conducted in the study area for immature stages. Eggs were sought for on plants, particularly on the underside of leaves, and on grasses. Plants, particularly those infested with aphids, were examined for larvae, and cocoons were sought for in the ground litter and around the bases of trees in the border area.

Eggs collected in the field were identified by rearing or, if not practical, by comparison with those of known species in the habitat. Cocoons were similarly identified by rearing, or, if already emerged or parasitized, they were gently boiled in 10 per cent KOH, the larval remains extracted and the integumental pattern of the head capsule compared with that of reared material.

Field-collected females of *C. oculata* and *C. chi* were individually caged in paper-cup, mating-oviposition cages for 24-hour oviposition studies, under natural outdoor conditions. They were supplied with live pea aphids and a cotton pledget soaked in 10 per cent sucrose solution. Temperature and Relative Humidity were monitored on a thermohygrograph. Females were transferred to new cages at the end of every 2-hour interval and the amount of oviposition determined. A red light was used during the scotophase while transferring females.

MAINTAINANCE OF LABORATORY CULTURES OF *CHRYSOPA OCULATA* SAY AND *CHRYSOPA CHI* FITCH

Cultures of *C. oculata* and *C. chi* were started from field-collected material originating from Ile Perrot and Mt. St. Hilaire, Quebec. They were maintained under LD 16:8 at 23·0 ± 0.5°C and 60-70 per cent R.H. Adults and larvae were generally fed live pea aphids, *Acyrthosiphon pisum* (Harris), which were maintained on pea plants grown from untreated seeds. In addition, adults were provided with free moisture from a cotton pledget soaked in 10 per cent sucrose solution. This was placed on the screened lid and was moistened each subsequent day with distilled water.

The culture of C. oculata was also maintained by supplemental feeding on occasions when the pea aphid culture was very low. Late second and third instar larvae readily accepted live larvae of Tribolium confusum Duv. and Trogoderma parabile Beal, but the spiculose exuviae of T. parabile clung tenaciously onto the equally spiculose body of the chrysopid larva, locking its appendages into unnatural positions. The chrysopid larvae also readily accepted frozen pea aphids (stored at - 20°C) and mosquitoes (Aedes spp) immobilized by having their thorax pinched. In the case of the frozen aphids the rearing cages had to be cleaned out daily to avoid decomposition.

Cocoon spinning and emergence in C. oculata was never good when supplemental feeding was heavily relied upon for the nutrition of late second and third instar larvae. On the other hand C. chi was successfully reared on a mixed diet of Aphis fabae Scopoli, Rhopalosiphon maidis (Fitch) (cereal aphid), Euceraphis punctipennis (Zett.) (birch tree aphid), the pea aphid and immobilized mosquitoes (Aedes spp), following completion of its first instar on live pea aphids.

DESCRIPTION OF REARING CONTAINERS

Mating-oviposition cages were constructed from large paper cups (760cc) fitted with snap-on plastic lids. These were modified in a manner which permitted a more ready view of the interior; a large portion of the base was excised and a plastic Petri dish (13 X 90mm) was installed on the inside. The central area of the snap-on lid was similarly excised and replaced by nylon mesh (34 squares per cm.) bonded to its surface. *C. chi* was also paired in large plastic vials (135cc; 80 X 52mm) whose snap-on lids were similarly modified to that of the paper cups. Food, as well as adults were introduced into both types of cages through a side hole secured by a No 2 cork stopper.

Plastic vials (28cc; 51 X 30mm) with snap-on lids were used for rearing larvae following lid modification as in the mating-oviposition cages. A similarly stoppered hole on its side, 1cm above its base, served for the introduction of food to adults. Developmental data pertinent to each larva were recorded on a strip of masking tape along the length of the vial. Another larva-rearing unit consisted of a shell vial (3cc; 35 X 12mm) fitted with a centrally bored (4mm diameter) No 3 cork stopper, the inner surface of which was screened with nylon mesh, glued in position, to prevent the escape of larvae.

DEVELOPMENTAL AND GENETIC STUDIES

In developmental and genetic studies involving *C. oculata* and *C. chi*, eggs were harvested after 3 to 4 days of oviposition and were individually isolated in clean, cotton-stoppered, rimless bacteriological tubes (50 X 6 mm and 25 X 6 mm).

These also facilitated the scoring of fertility and embryonic mortality. First instars were easily shaken out into the larva-rearing cages. Larvae were fed during the photophase at 10.00 hours and were given an excess of live pea aphids. Instar I and early instar II were fed on alternate days - the aphids survived a little longer than a day - and larger larvae were fed daily. The cages were also checked at that time for the occurrence of moulting, pupation and adult emergence.

Larval instars of both species are distinguishable by characters other than size. Instar I larvae have but few setae on the lateral tubercles of the thorax while, in instar II, the number of those setae increase considerably and the tubercles themselves become elaborated. In the third instar the integumental pattern of the head capsule breaks up onto three discrete areas and the setae of the lateral tubercles increase even more in number. Completion of the cocoon by the late third-instar larva was taken as denoting the onset of the prepupal stage. The initiation of the pupal stage was indicated by the presence of the characteristic round black area at one pole of the cocoon.

The developmental studies were conducted on eleventh and first generation C. oculata from the Ile Perrot and Mt. St. Hilaire cultures, respectively, and on first generation C. chi from Mt. St. Hilaire. The data on comparative development of the sexes are based on rearings in plastic vials. Development was also compared in the two types of larva-rearing units, based on a single batch of eggs from a female of

C. oculata, divided for this purpose. Hence the comparison is based on identical stock - same genotype or range of genotypes - originating from a single locality (Mt. St. Hilaire).

CYTOGENETICS

Newly emerged adults, females particularly, were fed pea aphids on the first two days, following which they were allowed to imbibe, over a 10 to 12 hour period, a 0.1 per cent colchine in sucrose solution from soaked cotton pledgets. The colchine solution was prepared from 0.2 per cent stock, by mixing in a 1:1 ratio with 10 per cent sucrose solution. Gonads were dissected in isotonic NaCl-Ringer solution and immediately fixed in acetic-alcohol (33 mls glacial acetic acid: 100 mls 70 per cent ethyl alcohol) for a minimum period of 24 hours. Ovaries, however, were usually teased apart prior to fixation to separate the follicles and remove tracheae.

Fixed material was transfered by pipette into a Syracuse watch glass (No 9790 N 12; Thomas Scientific, Philadelphia, PA) for staining. Excess fixative was pipetted off and the material was then passed through a lacto-acetic acid (1 part 85 per cent lactic acid + 1 part glacial acetic acid) rinse prior to staining. Testes so treated, pricked with a micro-dissecting needle and allowed to stand for a few minutes (depending on the duration of fixation) in the lacto-acetic acid solution, become swollen and turgid, and the testicular envelope ruptures. The envelope can then be teased away with the needles, thereby permitting a better spreading of the cells after staining. Removal of the testicular envelope is more difficult in long-preserved material.

Prepared tissue was then covered with a few drops of 2 per cent lacto-aceto-orcein (2 gms Gurr's natural orcein + 50 mls 85 per cent lactic acid + 50 mls glacial acetic acid) and allowed to stain at room temperature for an hour and a half, and longer if necessary. Stained material was pipetted onto a clean microscope slide, covered with a coverslip and squashed between folds of paper towelling. With ovarian material, however, the terminal and subterminal oocytes were dissected away on the slide, and the remaining portion of the follicles were then arranged prior to squashing.

Squash preparations were cleaned and then ringed with Permount, followed when dry, by an application of nail varnish to protect the Permount from Immersion oil. These semi-permanent mounts are enduring. The preparations were examined under a Nikon compound microscope fitted with Nikon phase contrast optics (LKe condenser and DLL objectives). Photographs of meiotic stages were taken with the attached Nikon Automatic Microflex (Model AFM) on Ilford Pan F or Kodak Panatomic X film, and developed in Acu 1 (Acufine, Inc., Chicago, Illinois).

RESULTS

FAUNISTIC COMPOSITION AND POPULATION DYNAMICS

A total of 9 chrysopid species were collected over a three-year period (1977, 1978, 1979) on Mt. St. Hilaire, but only three were obtained for the years 1977 and 1978 on Ile Perrot (Table I). In each year and in each locality, *C. oculata* was clearly the dominant species, followed next by *C. chi*; the other species were taken but infrequently (Tables II-VI).

There was no difference between the two study areas in the number of generations of *C. oculata* and *C. chi*, and in the time of their occurrence. Figs 1-3 indicate that there are two generations of *C. oculata*, the first emerging in spring and ending in mid-summer, the second (F_1) beginning in mid-summer and lasting into early Fall. The F_1 is generally the larger population, but is shorter-lived and declines very rapidly. The presence of an F_1 generation was indicated also by the occurrence of fresh males without sperm in the seminal vesicles (See Table XXVII) and of females with weakly sclerotised and empty spermathecae and ovaries not yet engaged in oogenesis (See Table XXVIII). The F_1 appears to start in the last week of July (Figs 1-3). In *C. chi* there tends to be but one generation, occurring simultaneously with the spring generation of *C. oculata*, and occasionally an extremely weak F_1 presence (Figs 1-3) which was likewise confirmed by dissection. In the two study areas the sex ratio was approximately 1:1 in both generations of C. oculata. It also approached a 1:1 ratio in C. chi, except in the 1977 data for Mt. St. Hilarie which showed a bias towards females.

24-HOUR OVIPOSITION STUDIES

The 24-hour oviposition studies conducted in 1978 and 1979, indicated that the rhythm was essentially unimodal in C. oculata and C. chi (Tables XI, XII; Figs 4,5). Maximum oviposition in C. chi occurred approximately between two in the afternoon and twelve midnight, and peaked at or about sunset. In C. oculata, it occurred approximately between four in the afternoon and two in the morning, also peaking a little before or after sunset, and with a small second peak of activity being apparent before noon. The oviposition rhythm was not influenced by the rise and fall of temperature and relative humidity.

Mean oviposition rate per day in both studies was higher in C. oculata than in C. chi. The values for C. chi were about the same in each year (Mean approximating 25; combined range of 13-37). In C. oculata the values were higher in 1978 (Mean 41.08; Range 9-73) than in 1979 (Mean 32.6; Range 18-46).

ECOLOGY AND PARASITISM OF IMMATURE STAGES

Searches carried out in the herbaceous layer throughout 1977, and sporadically during 1978, failed to turn up large numbers of eggs. Eggs of C. oculata were found sporadically on and below leaves in both habitats (Tables IX and X) but the findings appear contradictory since gravid females were to be found at most times (Tables VII and VIII). This suggested that the oviposition recorded was either only incidental while feeding, or that females broadcast their eggs in the environment. Subsequent to the 1978 24-hour oviposition study (Table XI; Fig 4) searches in the gramineous layer led to the recovery of numerous eggs in close association, and not isolated as those in the herbaceous layer. Eggs taken in both the herbaceous and gramineous layers on Mt. St. Hilaire were parasitised by the scelionid wasp Telenomus chrysopae Ashmead (Table X). Eggs of C. chi were also found infrequently in both habitats and its oviposition site may be similar to that of C. oculata. In addition, an egg of Meleoma signoretti Fitch was found in the Mt. St. Hilaire habitat, but its occurrence in the herbaceous layer is in all probability not a true oviposition site of the species.

As in the case of eggs, larvae were infrequently encountered during visual searches of the herbaceous layer in 1977 (Tables XIII and XIV). Two species, C. oculata and C. lineaticornis were found in both localities. A third instar larva of C. oculata was found to be parasitised by the wasp, Helorus anomalipes (Pauzer) (= Helorus paradoxus (Prov.,)). The larva cocooned normally and the parasite emerged subsequently. Larvae of C. oculata were also observed feeding on vetch (V. cracca) and Solidago aphids (Aphis craccae L. and Dactynotus pieloui Rich. respectively), and one on nectar of Solidago flowers (Tables XIII and XIV). Several larvae of C. lineaticornis were encountered on Ile Perrot, scurrying over inflorescences of Solidago.

Cocoons were equally difficult to locate in searches of different microhabitats, carried out in 1977 and 1978, in both localities. Both the litter and ground surface were examined. Searches in 1979, mounted in early spring along a transect on Mt. St. Hilaire, yielded within the old-field habitat overwintered cocoons of C. oculata and C. chi (oculata in an area of grass and Apocynum androsaemifolium ; chi in a stand of Solidago), and in the border area in the soil around the bases of birch trees (Betula papyrifera Marsh.), cocoons of M. signoretti (Table XV). One cocoon of C. oculata was parasitised by the ichneumonid wasp Dichrogaster crassa (Prov.), and encyrtid wasps, Isodromus iceryae How, were reared from a cocoon of M. signoretti. The location of cocoons of M. signoretti at the base of birch trees appears to be a specific cocooning site of this species as cocoons are readily found there.

ECTOPARASITISM AND PHORETIC ASSOCIATIONS OF ADULT CHRYSOPIDS

Adults of C. oculata were sometimes parasitised by females of the ceratopogonid, Forcipomyia eques (Johannsen), which feed on hemolymph from wing veins. As indicated in Table XX, the parasite occurred frequently on Mt. St. Hilaire, in spring and early summer, but not all beyond June.

Parasitism tends to be limited to males (one record of a female) and ranged as high as 42.86 per cent of that sex. The number of parasites per chrysopid host was usually one, rarely two. On Ile Perrot, however, it appears to be much less frequent; it was not collected in 1977 and was found only once in 1978 (July 3).

An accidental parasitism (or possibly phoresy) appears to be the case of first instar larvae of Perilampus chrysopae Crawford (Hymenoptera: Perilampidae) which were found attached to adults of C. oculata from Ile Perrot (Aug 7, 1978) and Mt. St. Hilaire (2 and 17 Aug. 1979). Larvae of Rhipiphorus sp. (Coleoptera: Rhipiphoridae) occurred also on the head of an adult of C. oculata from Ile Perrot (July 17, 1978) and represent only a phoretic association.

ENDOPARASITISM OF ADULT CHRYSOPIDS

Mermithids (Nematoda) and intracellular bacteria

Larval mermithids were recovered on two occasions (July 30, August 17, 1979) from males of C. oculata on Mt. St. Hilaire. The parasitism occurred within the F_1 generation and amounted to 1.9 per cent of males or 1.2 per cent of the population. All adults of the overwintered and F_1 generations were dissected.

Gonads of C. chi (both sexes) were often observed during examination of aceto-orcein squash preparations, to harbour rod-shaped, intracellular organisms (Plate III a-d), similar to small gram negative bacteria. The organisms stained dark red and had an average size of 1.6 X 0.6 micrometers. It appears to be widespread. On Mt. St. Hilaire (1978), one out of five specimens, and on Ile Perrot four out of eight specimens collected in the years 1977 (1/3), 1978 (1/4) and 1980 (2/4) were positive. Six out of eleven specimens from Ste Anne de Bellevue were also positive. Gonads of C. oculata, however, were always negative.

The incidence of parasitism by the euphorine Chrysopophthorus americanus Mason (Hymenoptera: Braconidae) and its effect on the host

Adult chrysopids in both study areas were parasitised by endoparasitic larvae of Chrysopophthorus americanus Mason (Hymenoptera: Braconidae: Euphorinae). Parasitism was restricted almost entirely to males of C. oculata, rarely the females (Table XVI, XVII), and only once was it observed in C. chi (a female) (Table XVII, footnote).

The level of parasitism observed on Mt. St. Hilaire in 1977 (based on observation of males and dissection of females) and 1978 (based only on observation of males) ranged from 14.29 to 25.0 per cent of males (Table XVII). In 1979, however, the course of parasitism was followed over two consecutive generations, through dissections of both sexes as well as by observation of suspects. Parasitism occurred as early as June 20 (egg) and as late as September 7 (the mature larva emerged from the host a week later). Most cases of active parasitism occurred at the end of June and in the month of July, attaining levels within that period which ranged as high as 30.0 per cent of males. The elevated level observed in September is probably an artifact, due to the small size of the sample. Noteworthy, also, are the egg recovery on June 20, the second on July 26 (36 days later) and the caudate first instar larva on August 17 (58 days after recovery of the first egg) from an apparent F_1 male (wings bright-green, pliable and undamaged). There was no parasitism of females as in the two preceding years.

On Ile Perrot (Table XVI) the level of parasitism in males of C. oculata ranged over the period 1977-1979 (parasitism determined as on Mt. St. Hilaire, the first year as in 1977, the second and third as in 1978), from less than 6.0 per cent in 1979 to levels of 60.0 and 100.0 per cent in 1978. The latter values are probably distorted because of the small sample sizes involved. Only two parasitised females were observed within that period, one in 1977, the other in 1978. In 1980, the level of parasitism in males (determined by holding them for a very long period) ranged from 26.67 to 33.33 per cent. The values are greater than those obtained with equally large samples within the same period of the previous year (reflecting no doubt the method of determination), and were similar to the levels observed during the period of greatest activity (end of June to end of July) on Mt. St. Hilaire in 1979.

Generally, there was one parasite larva per host, but a case of double parasitism occurred in 1978 on Mt. St. Hilaire (Table XVII) - a mature larva and a dead first instar larva were recovered from the same host. Another case was observed in 1978 (July 15, Ste Anne de Bellevue) in which the host, a male of C. oculata, bore a live larva (probably the penultimate instar) and also showed the characteristic signs of an earlier and successful, and probably simultaneous parasitism. Adults which were successfully parasitised show a characteristic black wound on the abdomen (Plate 1a) and, in the male, the head capsule of the first instar larva (Plate 1c) can usually be located near the accessory glands. Attached internally to the exit would is the exuvia of the penultimate larva (vide Principi 1948) which extends anteriorly, as a tube, into the second abdominal segment. The exit would in C. oculata is usually located laterally in the intersegmental membrane between abdominal segments six and seven; in the single case observed in C. chi it was located between the tergum and sternum of abdominal segment seven.

Actively parasitised males, in the final stages of parasitism, have large and ponderous abdomen which bulge medially, and at first glance they may appear to be gravid females. Parasitism did not damage the reproductive organs. However, the fat bodies, the site of protein synthesis and storage (also glycogen storage), were usually atrophied and amorphous, testes were sometimes colorless, but sperm remained motile and viable in the seminal vesicles. In one specimen the parasite's exit wound was observed to be sealed off by a testis. Hosts were observed to be in a debilitated condition after the exit of the parasitic larva, and survival was variable in the presence of food (aphids and 10 per cent sucrose solution). Males surviving parasitism mated successfully with virgin females which subsequently produced fertile eggs. In the field population, surviving males may live for an indefinite period of time, as evidenced by the capture of such individuals which are actively feeding and vigorous.

Parasitism likewise did not damage the reproductive organs of females. Parasitised females of C. oculata (one current and one past) had no mature eggs. Most follicles showed little yolk incorporation in the terminal oocytes and none in the subterminal ones. The terminal oocytes appeared degenerate; they were larger than those of newly emerged, non-fed females. Some showed traces of green yolk within them, others were yellowish, or contained a small mass of conspicuous yellow matter. A yellow-orange mass was also present in the oviduct immediately posterior to some terminal oocytes. The fat bodies were not visibly amorphous as in most parasitised males. Sperm were motile in the spermatheca and, in the case of a successfully parasitised female of C. chi (confirmed by dissection), fertile and viable eggs were oviposited.

Adults which were actively parasitised had trophamnion cells (Plate 1b) in the hemolymph. The trophamnion is a sheath which surrounds the embryo and is derived from fusion and subsequent amitotic division of the two polar bodies

(Wigglesworth 1967); its cells absorb nutrients from the hemolymph to provide nutrition to the embryo. Subsequent to eclosion, the trophamnion disintegrates, the cells continue to absorb nutrients and later serve as a source of nutrition to the developing larva (Tobias 1965; Loan 1967). The trophamnion cells were observed to be single and free of each other. Those cells associated with first instar larva were round and had a diameter of 62 ± 7 micrometers (Mean ± 1 Std. Dev.; n = 50), while those associated with the penultimate larva measured 201 ± 30 x 219 ± 33 micrometers (Mean ± 1 Std. Dev.; n = 60). Specimens which were previously parasitised usually had no trophamnion cells in the abdominal cavity or occasionally only a few.

DEVELOPMENTAL BIOLOGY OF *CHRYSOPOPHTHORUS AMERICANUS* MASON (*HYMENOPTERA: BRACONIDAE*)

The egg of *Ch. americanus* (Plate Id) is transparent, more or less uniformly wide, elongate, curved medially and with a short stalk at one end. The two eggs measured (in micrometers) 917 x 308 and 632 x 173 (length x width), and their stalks were respectively 55 and 69 micrometers in length. The first instar larva is caudate (Plate IIa,b) and its large head capsule is distinctive. A head capsule (Plate Ic) measured 243 x 257 micrometers (greatest length x width) and had a mid-width length of 215 micrometers. The other larval instars are vermiform (Plate IIc). The cocoon and adult are shown on Plate IId and e respectively.

It appears that there are five larval instars. Exuviae of early instars were found attached to the anterior end of the tube-like penultimate exuvia, after it was stained in Chlorazol Black E (Bram and Bickley 1963) and teased apart. There are definitely two such earlier exuviae (head structures present) and also a third, the smallest, lacking in head structures. This, the smallest, may in fact be that of the first instar whose head capsule is usually located, free, near the accessory glands.

Larvae which emerged from the host did not pupate unless they had access to a loose substrate (small fragments of rotted wood or vermiculite) into which they readily burrowed. They appear to need a thigmotactile stimulus to initiate cocooning. The data in Table XVIII indicate that, following cocoon-spinning, larvae enter into a state of obligatory diapause which terminates spontaneously under favourable laboratory conditions after a variable period of time (42-88 days). The data also indicate that the duration of larval development within the host is at least 19 days long.

Earlier data on diapause termination (Table XIX) indicated that in two outdoor diapausing cocoons (cocoons in cages buried flush with soil surface and covered with litter), days to emerge did not differ greatly (11 and 12 days; Mean 11.5) following their return to laboratory conditions at different times. This suggests that diapause development had terminated on or before the earlier date of return to the laboratory (Jan 4), and that days to emergence represent the post-diapause development. The table also indicates diapause termination in a single specimen after exposure at 5°C. However, as diapause terminates spontaneously (See Table XVIII), a considerable portion of its diapause development must have taken place during its 22 days under laboratory conditions prior to cold treatment. The data presented in this table are obviously inadequate, however, to determine the earliest termination of diapause development in the field and the effect of cold exposure, if any, on diapause development.

DEVELOPMENTAL STUDIES ON *CHRYSOPA OCULATA* SAY AND *CHRSOPA CHI* FITCH

Larval development of *C. oculata* was statistically, significantly faster in plastic vials (28cc; 51 X 30mm) than in shell vials (3cc; 35 X 12mm) (Table XXI). This was true in both sexes, of all developmental stages except the pupa which was insensitive to cage-type. Larvae reared in plastic vials also had more success (95 per cent plus) in spinning perfect cocoons than did those reared in shell vials (41 per cent). Survival in plastic vials (n = 30 rearings) was quite high for all developmental stages (Table XXII; Fig. 6) and resulted in a mean rearing success rate of 87 per cent; the greatest mortality occurred in larvae of instar I. A similarly high rearing success rate with the same vials was also obtained for *C. chi*.

Males of both species developed faster than females (Tables XXIII - XXV) and, as shown in the case of *C. oculata*

(Table XXVI; Fig 7), this was reflected in a protandrous emergence. The developmental difference between the sexes was statistically significant in the prepupal and pupal stages and total developmental time. Development of the male sex was also significantly faster in the third instar of the Ile Perrot strain of C. oculata. Total development time was shorter in C. chi (F_1; Table XXV) than in the two strains of C. oculata (F_1 and F_{11} from Mt. St. Hilaire and Ile Perrot respectively) which themselves differed widely (Tables XXIII, XXIV).

Sperm shift (the migration of sperm into the seminal vesicles) occurs in approximately 50 per cent of C. oculata males on the second day after emergence (Table XXVII) and is independent of aphid-feeding. It was at a maximum on the third day (93.3 and 100 per cent), but was less on the fifth (84.6 and 80.0 per cent).

Oogenesis was initiated in females of C. oculata after one day on a feeding regime of live pea aphids and 10 per cent sucrose solution (Table XXVIII). Newly emerged females and those which had not yet completed a day of aphid-feeding showed no yolk incorporation. The first subterminal oocytes are engaged after completion of two days on the regime, the second subterminal after the third day when terminal oocytes then begin to mature, and eggs are present in the oviduct after the fourth day. The data suggest that newly emerged females, up to three days old, are identifiable on the basis of ovarian development, size and color of oocytes.

In addition, newly emerged females can be recognised by the lightly sclerotised spermatheca and its lack of sperm.

EMBRYONIC MORTALITY IN *CHRYSOPA OCULATA* SAY AND *CHRYSOPA CHI* FITCH

An egg mortality factor persisted in the Ile Perrot culture of *C. oculata.* It was evident at the outset of colonization, and manifested itself in mortality of the late embryo prior to eclosion, and often also at eclosion which showed the larva to be partially trapped within the embryonic moult. Mortality among fertile eggs ranged from 40.8 to 78.1 per cent with a mean of almost 60 per cent (Table XXIX also Tables XXXII, XXXIV, XXXVI). The frequency distribution of this mortality is shown in Table XXIX and Fig. 8.

A similar mortality factor occurred in the Mt. St. Hilaire culture of *C. oculata*. It persisted through four generations descended from a set of field-collected eggs in which it was also present (Series A and C of Table XXX). The mortality factor was apparently not universal in the lot of field-collected eggs, judging by the selection of a line displaying mortalities ranging from very low and probably normal, to zero (Series B of Table XXX).

An embryonic mortality, similar to that of *C. oculata*, occurred also in eggs of *C. chi* from Mt. St. Hilaire (Table XXXI and XLI). It was present in the F_1 progenies descended from eggs of four wild-caught females. Mortality in a few progenies ranged from zero (two progenies) to fairly low (6.5, 13.0 and

13.3 per cent). In the majority, however, it ranged from 20.0 to 82.8 per cent.

The embryonic mortality observed in the cultures of both species was independent of the allelic genes investigated (Tables XXXII-XXXIV, XXXVI, XLI; See Section on Genetics) and may have been caused by the presence of chromosomal translocations (See Section on Cytogenetics).

DEVELOPMENT OF CHRYSOPA LINEATICORNIS FITCH

A total of 45 eggs were oviposited over a two-day period by a field-collected female (Ile Perrot, 14 July 1979). It did not accept aphids, and there was no subsequent oviposition during the period of its captivity. The eggs are smaller than those of other chrysopids; they are a pale lemon-green, with coarse hexagonal sculpturing on the chorion (clearly visible at 25 times magnification), and measured 0.85 ± 0.04 x 0.42 ± 0.00mm (Mean ± Std. Error, n = 45). Stalk length was highly variable as in other chrysopid species. By contrast, eggs of C. oculata and C. chi are green and the mean value of their measurements approximate 1.10 X 0.45mm.

Eggs hatched in six days, beginning on the sixth day after the first day of oviposition, and was completed by the seventh. The first two instars were fed pea aphids (A. pisum) and Solidago aphids (D. pieloui). The third instar was maintained on immobilized mosquitoes (Aedes spp), the birch aphid (E. punctpennis) and the corn aphid (R. maidis). Larvae were reared in plastic vials, some indoors (LD 16:8; 23.0 ± $0.5^{o}C$; 60-70% R.H.) and some outdoors as indicated in the following table. They did not cover themselves with debris as occurs in nature.

	Laboratory	Outdoors
Mean ± Std. Error (I-III)*	32.25 ± 0.98	32.07 ± 0.59
n	16	14
Range*	28 - 40	30 - 38
No entering prepupal stage	16	14
No completed cocoons	4	2

* development duration (days).

Mean development times under laboratory and outdoor conditions were similar, indeed almost identical, though the range in the former was greater. Generally, cocoon completion was poor. In the laboratory-reared material there were four completed cocoons, one of which continued to develop without a diapause. It had an overall development time of 51 days with a cocoon stage (prepupa plus pupa) duration of 23 days. The other three cocoons showed no further development 25, 29 and 34 days after cocooning. They were then placed under cold conditions ($5^{o}C$) for almost a year (September 24 to August 15) but failed to develop on return to laboratory-rearing conditions. One had died in the pupal stage and the other two as prepupae.

The two completed cocoons in the outdoor-reared material (instars I-III developing from July 22 to August 24) appeared to be in diapause, for pupation did not occur up to 31 and 34 days after cocooning. These were cold-treated, identical to and simultaneous with the indoor-reared material. Emergence occurred in 20 and 21 days on return to laboratory-rearing conditions.

GENETIC STUDIES ON CHRYSOPA OCULATA SAY

Inheritance of black pigmentation on the forewing

Chrysopa oculata is a polychromatic species which exist in two principal forms, one in which the veins of the forewings are almost entirely green, and the other in which they are extensively marked with black. The green-winged form is always black on the humeral, second medial and first cubital crossveins, and also basally on the cubitus posterior (Fig. 9). It may also be lightly tinged on parts of the anal veins, on the first medial crossvein, and on the ends of some costal and radial crossveins where the latter abut the radius.

The predominantly black-winged form is marked similarly to the green-winged form, but the inner and outer gradate crossveins are always black medially. Furthermore, the costal and radial crossveins, and the basal and distal portions of the radial sector branches, numbers four to ten, may, in extent, be variably yet distinctly marked on both ends. The two forms can thus be consistently separated on the basis of pigmentation of the gradate crossveins of the forewing. The hindwing, however, shows little or no phenotypic difference.

The data presented in Tables XXXII-XXXIV are consistent with the hypothesis of a two-allele autosomal gene, in which the allele determining green gradates (b) is recessive to the allele determining black pigmentation (B). This is seen in crosses of green x green phenotypes (Table XXXIV, Crosses 1-7) which all produced green (bb) phenotypes, in crosses of black x black phenotypes (Table XXXII, Crosses 1-3; Table XXXIII, Cross 6; Table XXXIV, Crosses 8-14) which produced black (BB and Bb) and green (bb) progeny in conformity with a 3:1 ratio (probabilities ranging from 0.1 to 1.0), and in backcrosses (black x green) which produced black (Bb) and green (bb) progeny in a proportion which fitted a 1:1 model (Table XXXII, Crosses 4-6 and Table XXXIII, Crosses 1-5; probabilities ranging from 0.2 to 1.0). The data also indicate that the embryonic mortality (Tables XXXII-XXXIV) was independent of any specific genotype.

The alleles were maintained in the two cultures (Ile Perrot and Mt. St. Hilaire) by a crossing scheme of black (Bb) x green (bb) which provided the phenotypes used in most of the crosses. The viability of the homozygous dominant (BB) was confirmed in Crosses 15 and 16 of Table XXXIV. It appears to be more intensely pigmented than the heterozygote but is often difficult to distinguish. Probabilities were generally high in spite of the high embryonic mortality and the sexes usually approximated a 1:1 ratio.

Linkage between forewing pigmentation and pigmentation of some cephalic characters

Associated with the green-wing phenotype was the usual presence of a single pair of post-antennal black spots (Fig. 10a) and the absence of black pigmentation on the basicardo. On the other hand, two pairs of post-antennal spots (Fig. 10c) and black on the basicardo (Fig. 10b) were always associated with the black-wing (BB and Bb) phenotype. The data presented in Table XXXVI indicate that in the greenwing phenotype the presence of the post-antennal spot is controlled by a two-allele, autosomal gene, with the allele determining absence being recessive to the one determining presence. Field-collected data (Table XXXVII) showed, however, the occurrence of black-phenotype-associated characters in green phenotypes and vice versa but the frequencies, based within phenotype, are quite small. The field data suggest that these associated characters (basicardo and post-antennal spots) are under independent genetic control and that the genes controlling them are probably closely linked to those determining pigmentation in the forewing.

Inheritance of the interocular subantennal band and its reduced form

Chrysopa oculata is characterised by an interocular black facial band which borders the antennal sockets ventrally (Fig. 10a, c). A deviation in this character became apparent in progeny resulting from black (*Bb*) x green (*bb*) matings -

the crossing scheme which always produced Bb and bb genotypes - in which a considerable number of the black phenotypes had the facial band reduced to three well defined spots, one interantennal and the other two subantennal (Fig. 10d). The parental types possessed the normal interocular facial band except that it was not solidly black medially (Fig. 10e). Repeated crosses and reciprocal matings of these two parental types all produced the same three phenotypes (Table XXXIV Crosses 17-25).

The facial-spot, black-gradate (Bb) phenotype crossed with one another (Table XXXIV Crosses 8-14) produced black and green progeny in a proportion which fitted a ratio of 3:1. Only one cross was rejected at the 0.05 level of probability while in the others it ranged from a low between 0.2 and 0.1 to a high of 1.0. The black-gradate phenotype carried the parental pattern of clearly defined spots (Fig. 10d) but in the green-gradate, the genotype (bb) exerted an epistatic effect on the expression of the subantennal spots - they bordered the antennal socket and appeared as two narrow, nonconnected subantennal bands (Fig. 10f).

The data (Table XXXIV) suggest that "facial spots" is a homozygous recessive condition, determined by the recessive allele (a) of an autosomal gene whose dominant allele (A) determines presence of the interocular subantennal band. This is demonstrated in matings between facial-spot phenotypes (Crosses 8-14, parental types as in Fig. 10d) which resulted in only spot phenotypes, between facial-band phenotypes (restricted to the bb genotype) which resulted in only band phenotypes (Crosses 1-3, parental types as in Fig. 10a; Cross 4, parental types as in Figs 10a,e), and in the case of Crosses 5 and 6 (parental types as in Fig. 10e) by band and spot progeny, in a ratio which fitted a 3:1 model (probabilities of 1.0 and 0.5 - 0.7). A backcross (Cross 7) of facial spots x facial band (as in Figs 10a,f) gave the expected 100 per cent band phenotype (Fig. 10e), and the dihybrid backcross (Cross 26) produced the expected four classes of progeny which conformed to a 1:1:1:1 model (probability 0.1 - 0.2). Crosses 15 and 16 demonstrate viability of the BBaa genotype. These data also indicate independence of the mortality factor of any specific genotype.

The effect of meiotic drive (or gametic competition) on genotype occurrence

Although the green-gradate, facial-spots (bbaa) phenotype was shown to be viable (Table XXXIV Crosses 5,6, 8-14, 26), it did not occur as expected in the progeny of several crosses (Table XXXIV Crosses 17-25, 27-31). If the ba male gamete were eliminated in Crosses 17-21, then this would preclude the possibility of having both black and green-gradate progeny with facial spots (Bbaa and bbaa respectively), leaving only two phenotypic classes, black gradates with facial band (BbAA, BbAa) and green gradates with facial band (bbAA and bbAa). On the other hand, elimination of the ba gamete from the double heterozygous female parent (BbAa) would result in the loss of only one phenotypic class, green gradates with facial spots (bbaa), as observed in the case of Crosses 17-21. Similarly, in the reciprocal Crosses 22-25, the loss of the bbaa genotype (the phenotypic class of green gradates with facial spots) could only be achieved by elimination of the ba gamete of the double heterozygous male parent.

Elimination of the ba male gamete in Cross 29 would preclude the possibility of having the phenotype classes of green gradates with facial spots (bbaa) and green gradates with facial band (bbAa), leaving two phenotypic classes, black gradates with facial band (BBAa, BbAa) and black gradates with facial spots (BBaa, Bbaa). On the other hand, elimination of the ba gamete from the double heterozygous female parent (BbAa) would result in the loss of only one phenotypic class, green gradates with facial spots (bbaa) as observed in this cross. Likewise in Crosses 27 and 28 (reciprocal to each other) in which one parent was a double homozygous recessive (bbaa), selective elimination of the bbaa genotype could only be achieved by elimination of the ba gamete of the double heterozygote. By way of contrast, in those crosses where the bbaa genotype (green gradates with facial spots) was obtained, only two kinds of gametes were possible from either sex - the ba gamete in conjunction with either bA or Ba. The ba gamete does not occur in conjunction with BA as the only other meiotic product - the genome does not exist.

It would appear that there is a meiotic drive mechanism or probably gametic competition which works to the complete detriment of the ba gamete, male or female, when it is one of four possible meiotic products of the double heterozygote (BbAa). Either the BA gamete, by itself, or its presence simultaneously with Ba and bA is responsible for this phenomenon. Furthermore, as seen in Table XXXV (an abbreviation of Table XXXIV) even with elimination of the ba gamete from the contributing pool of the double heterozygous parent, there is segregation distortion of the progeny away from the new expected ratio, very much in favour of the "green gradate - facial band" phenotype (bbAA and bbAa). Thus, the bA gamete is the most competitive in the milieu of the four meiotic products.

POPULATION GENETICS OF *CHRYSOPA OCULATA* SAY: FREQUENCY OF THE ALLELIC GENES B AND b, AND A AND a

The overwintered and F_1 generations of *C. oculata* were scored for frequency of the green gradate (bb) phenotype. The data presented in Tables XXXVIII and XXXIX indicate that in both study areas, frequency of the b allele was higher in both the overwintered and F_1 generations; frequency of the b allele was also generally higher on Ile Perrot (0.66 - 0.83) than on Mt. St. Hilaire (0.54 - 0.76). In both areas, frequency of the B allele was lower in the overwintered generation than in the F_1 while the reverse was true for the b allele (Fig. 11), which suggested that the B allele is being selected against during winter.

The generations were also scored for the "facial-spots" (aa) phenotype (Figs 10d,f). Although the allelic genes a and A were first recognised in the culture originating from Ile Perrot, the homozygous recessive (aa) was never collected in that area, though forms similar to the laboratory-reared heterozygotes (Aa) were observed. On Mt. St. Hilaire, however, the homozygous recessive was collected each year and frequency of the a allele ranged from 0.08 to 0.12 with a mean of 0.10 (Table XL).

DIAPAUSE STUDIES ON CHRYSOPA CHI FITCH

Termination of obligatory diapause

An obligatory prepupal diapause was present in the joint progeny of four field-collected (Mt. St. Hilaire)females and in the ensuing generations (Table XLI). Chrysopa chi also has a facultative, photoperiod-dependent diapause as indicated in the following table. The four lots of eggs were from a single laboratory-reared female, and all rearings were at 20.0 ± 0.5°C and 60-70% R.H.

Lot no	L:D	No larvae	No diapausing	Per cent diapause
1 + 2	16:8	64	16*	25
3	13:11	41	41**	100
4	12:12	32	32**	100

* obligatory
** obligatory + facultative

Prepupae in obligatory diapause were held as long as 39 days before being subjected to variable cold treatments ($5^{o}C$), and the following observations were made on their return to long-day conditions (L:D 16:8; 20.0 ± $0.5^{o}C$; 60-70% R.H.) : per cent emergence, days to pupation, duration of pupal stage and total days to emergence (overall development time). The data were subjected to regression analysis and all correlation coefficients were significant (Table XLII). The data are presented also in summarised form in Table XLIII and in Fig. 12.

There was a quantitative response in emergence to the length of cold treatment (Table XLIII, Fig. 12.1). Emergence increased from 12.5 per cent (1/8) at 16 weeks to 100 per cent (9/9) at 26 weeks. Non-emerged material was alive and remained in the diapause state. The emergence pattern and particularly the emergence rate at 16 weeks, suggest the existence of a critical threshold period of cold exposure for the stimulation of development. The critical period may be close to 16 weeks.

Whereas 100 per cent emergence was obtained at 26 weeks, Fig. 12.1 indicates that the cold exposure requirement for 100 per cent emergence, may indeed be fulfilled, at the latest, at the end of 24.5 weeks. Days to pupation, duration of the pupal stage and total days to emergence also showed a quantitative but inverse response to the length of cold treatment (Fig. 12.2). The response rate was greater in total days to emergence ($m = -1.2898$) than in days to pupation ($m = -1.1125$), implying that the low response shown in duration of the pupal stage ($m = -0.2030$) was nevertheless real and significant.

Inheritance of obligatory diapause

Sibling crosses of non-diapausing F_0 progeny (Table XLI, Crosses 1-6) produced non-diapausing and diapausing phenotypes which fell within acceptable probabilities (0.05 to 1.0) of having been produced in a 3:1 ratio. While this suggests that diapause may be under the control of a single recessive gene, sibling crosses of diapausing F_0 phenotypes (Crosses 10-12) also produced both phenotypes, indicating that, at the very least, a second gene pair may be involved. The phenotypes are not sex-linked since both sexes were obtained from each phenotypic class.

In a postulated system of two independently segregating gene pairs where the alleles determining non-diapause are dominant ($\underline{D_1}$, $\underline{D_2}$), and those determining diapause are recessive ($\underline{d_1}$, $\underline{d_2}$), the individuals of the non-diapausing phenotype will be expected to be of the genotypes shown in the following table. The possible crosses between them will produce the phenotypic ratios as indicated.

Genotype code	Non-diapausing genotype
f	$D_1D_1\ D_2D_2$
g	$D_1D_1\ D_2d_2$
h	$D_1d_1\ D_2d_2$
i	$D_1d_1\ D_2D_2$
Crosses	**Non-diapause : Diapause**
fxf, fxg, fxh, fxi, gxi	100 per cent
gxg, ixi, gxh, hxi	3 : 1
hxh	9 : 7

The non-diapause x non-diapause crosses agree with this postulate. Crosses 1-6 are within acceptable probabilities (0.05 to 1.0) of having been produced in a 3:1 ratio, and Cross 9, though the numbers are small, agrees with a 9:7 expectation ($p = 1.0$). Cross 7 did not agree with a 3:1 expectation (nor 9:7) and may be considered to have met the expectation of 100 per cent non-diapausing phenotype as in Cross 8.

Likewise, the diapausing phenotype will have any one of the genotypes shown in the following table and the possible crosses between them will produce the phenotypic ratios as shown.

Genotype code	Diapausing genotype
a	$d_1d_1\ D_2D_2$
b	$d_1d_1\ d_2D_2$
c	$d_1d_1\ d_2d_2$
d	$D_1d_1\ d_2d_2$
e	$D_1D_1\ d_2d_2$
Crosses	**Non-diapause : Diapause**
axa, bxb, cxc, dxd, exe, axb, axc, bxc, cxd, cxe, dxe.	100 per cent
bxd	1 : 3
axd, bxe	1 : 1
axe	100 per cent

The results of Crosses 10-12 also tend to agree with this postulate, though the numbers reared in this series are small; embryonic mortality was very high and the rearing success rate was poor. Nevertheless, Crosses 10 and 12 are within acceptable probabilities (0.95 - 1.0 and 0.1 - 0.2) of having been produced in a 1:3 ratio and Cross 11 shows a greater probability of having been produced in a 1:1 ratio ($p = 0.5$) than in a 1:3 ratio ($p = 0.1 - 0.2$).

The backcross (Cross 13) also tends to support the hypothesis of two independently segregating gene pairs. The observed phenotypic ratio shows best agreement with a 3:1 ratio ($p = 0.7 - 0.9$). This proportion of diapausing progeny could only have been obtained if the parent of the diapausing phenotype were heterozygous in the second gene pair ($\underline{d_1d_1\ d_2D_2}$) and if such heterozygosity were also present only in the homologous gene pair of the other parent of the non-diapausing phenotype ($\underline{D_1D_1\ d_2D_2}$).

CYTOGENETICS OF *CHRYSOPA OCULATA* SAY AND *CHRYSOPA CHI* FITCH

Karyotype and meiotic stages

Chrysopa oculata and *C. chi* both exhibit an XY sex-determining mechanism and a diploid number of $2n = 12$ (Plate IV a-d; Plate V a-d). In *C. oculata* the chromosome complement consists of one large submetacentric pair (the largest) and five pairs of acrocentrics of progressively decreasing size (Plate IVb,d). The sex chromosome pair is clearly the smallest and the Y is about one half the size of the X (Plate IVb,e). Sex-bivalent formation (Plate IVi) as well as unpaired elements (Plate IVh,g) were observed, respectively, in late and early diakinesis. However, sex-bivalent formation could not be determined with certainty in the more frequently encountered early diakinesis stage because of the despiralized nature of the chromosomes. Nevertheless, the sex chromosomes always segregated precociously at first metaphase (Plate IVe). The second metaphase stage is shown in Plate IVf.

The chromosome complement of C. chi consists, however, of only acrocentrics (Plate V a-d). The sex chromosome pair is only slightly smaller than the smallest autosome pair and the Y is almost subequal in size to the X (Plate Vb,e). The sex chromosomes also pair in diakinesis (Plate Vh,i) and segregate precociously at first metaphase (Plate Ve). The second metaphase stage is shown in Plate Vf and a pachytene stage in Plate Vg.

Chromosomal translocations

Chromosomal anomalies which appear to be the result of translocations were found in the cultures of C. oculata originating from Mt. St. Hilaire and Ile Perrot; in both cultures an embryonic mortality persisted (Tables XXIX, XXX, XXXII, XXXIV, XXXVI). The anomalies, which were usually observed at first metaphase, took the form of stickiness between some autosomes;

distinct chromatin bridges were evident. Translocations were generally not observable in other gonial metaphases probably because the chromosomes involved are all acrocentrics of gradually decreasing size.

In the Mt. St. Hilaire culture, chromatin bridges were observed in 45.5 per cent of males examined, between pairs of chromosomes (Plate VId,e) as well as between triplets (Plate VI a–c). Plate VIc shows the complete segregation of a triplet into two unbroken triads. Chromatin bridges were also observed in the Ile Perrot culture (60 per cent of males examined), between triplets (Plate VI f,i), in addition to chain formation in first metaphase (Plate VIg) and an apparent double translocation in premetaphase I (Plate VIh). In both cultures the second and third, and either the fourth or fifth autosomes appear to be the ones involved.

Similar translocations were seen in C. chi (50 per cent of males examined) originating from Mt. St. Hilaire (diapause inheritance study). Chromatin bridges were present between pairs of metaphase I chromosomes (Plate VII a-d), and appeared to involve the medium-sized autosomes (possibly the third and fourth). An embryonic mortality was also present in this laboratory-reared material (Tables XXXI and XLI). Field-collected material from Ile Perrot also showed the presence of translocations, involving pairs of metaphase I chromosomes, triplets and quadruplets (Plate VII e-g).

DISCUSSION AND CONCLUSION

FAUNISTIC COMPOSITION AND POPULATION DYNAMICS

The occurrence of more species on Mt. St. Hilaire was not altogether unexpected, taking into account the history of the mountain (*vide* Maycock 1961) and the proximity of the study area to extensive forested areas. Only two species, *C. oculata* and *C. chi* appear to be true inhabitants of the old-field habitat. They were frequently encountered in both study areas and often, also, their developmental stages. Throne (1971) also observed *C. oculata* to be an inhabitant of open fields, roadsides and gardens, and Smith (1922) reported it to have the greatest range of any American species.

Chrysopa chi, the less common of the two species, never realises a large population although it appears about a week earlier in spring than *C. oculata* (Figs 1-3) and, in comparison, has a fairly high, though lower, oviposition rate (Tables XI, XII). Availability of food does not appear to be a limiting factor, and the disproportionate representation of these two species, both of which are in the genus *Chrysopa* s.s. and have the same type of larval development, may be due to competition, as Séméria (1974a)suggested. A contributory factor may be the essentially univoltine nature of *C. chi*, whose obligatorily diapausing prepupae are susceptible to environmental hazards over a longer period of time, than would be the case if the species were primarily multivoltine, and diapause facultatively induced by the shorter photoperiods of the advanced season.

The other species encountered in the old-field habitat are accidentals, even though as in the case of *C. lineaticornis*, a dendrophilic species (Throne 1971; Smith 1922), larvae were encountered in both study areas. The larvae of *C. lineaticornis* are extremely active and may have migrated from wooded areas. Smith (1922) recorded them on honeysuckle and underbrush.

The occurrence of six more accidental species, only in the Mt. St. Hilaire habitat, is undoubtedly due to the encirclement of the study area by deciduous forest. *C. nigricornis*, *C. rufilabris* and the two species of *Meleoma* are basically tree inhabiting species (Throne 1971; Smith 1922). Adults of *C. nigricornis* and *M. signoretti* occurred in the border of the woods, and the presence of cocoons of the latter, at the base of birch trees in that area, strongly suggest that it is an ecotone species. Interestingly, *C. carnea* falls into the category of accidentals as only one specimen was taken. Throne (1971) observes that, in Wisconsin, it may be found in fields and gardens, along roads, in open woodlands and to some extent in broad-leaf forests. The sixth accidental species, *Chrysopa* sp. (*Chrysopa* s.s.), of which only one specimen was taken, is apparently also dendrophilic

OVIPOSITION RHYTHM, FIELD DISTRIBUTION OF EGGS AND EGG PARASITES

The oviposition rhythm was unimodal in *C. chi* and bimodal in *C. oculata*. In both species the period of maximum oviposition extended from the afternoon to the evening and, in the case of *C. oculata*, even into the early hours of the morning. Oviposition, in both species, continued for the remainder of the night and day, though at a diminished rate. By contrast, maximum oviposition in *C. carnea* occurs virtually at night (8.00 pm - 1.00 am), with a second peak of activity discernible between two and three in the morning, and practically no oviposition taking place during the remaining hours of the night and daylight hours (Jones *et al*. 1977).

The oviposition rhythm of *C. oculata* and *C. chi* indicated that a fair amount of oviposition might occur in overnight resting sites, since flight activity of chrysopids reaches a maximum about an hour after sunset and then declines (Banks 1952). Smith (1922) also observed increased flight activity until nine or ten in the evening. It is probable, therefore, that the aggregations of eggs of *C. oculata* such as were later found in the gramineous layer, and the oviposition in clusters which Banks (1903) mentions, might indeed be due to oviposition in overnight resting sites. Also, the sparse oviposition in the herbaceous layer (Tables IX, X) is probably incidental to feeding during the daylight hours of the morning and early afternoon when the oviposition rate is diminished.

Only one egg parasite, _Telenomus chrysopae_ Ashmead (Hymenoptera: Scelionidae) was found. It parasitised eggs of _C. oculata_ taken from both the gramineous and herbaceous layers on Mt. St. Hilaire, and is the only North American _Telenomus_ known to be parasitic in Neuroptera. Krombein _et al_. (1979) record as host _Chrysopa_ spp and _Lomamyia flavicornis_ (Wlkr.). Eggs of _C. oculata_ have also been reported to be parasitised by _Trichogramma_ (Krombein _et al_. 1979).

ECOLOGY AND PARASITISM OF LARVAE AND COCOONS

The infrequency of finding larvae, particularly those of _C. oculata_ and _C. chi_ which are inhabitants of the old-field habitat, may be due to the approach used. Larvae were sought for visually on plants, particularly aphid-infested ones, of which there was no lack. The poor yield of this approach (only a few larvae of _C. oculata_ found) may possibly be attributed to searching during the inactive phase of a diel activity cycle. Perhaps more fruitful results could have been achieved by beating vegetation, or better yet by collecting samples of the gramineous and litter layer and processing them in the laboratory. The presence of larvae of _C. lineaticornis_ in the old-field habitat is most likely due to migration. The species is dendrophilic (Throne 1971; Smith 1922) and the larvae are fast-moving.

Searches were also conducted in the field, for cocoons, in the hope of identifying specific cocooning sites of

C. oculata and C. chi, and to determine also the extent of parasitism. This approach yielded very few cocoons and the basic objectives of this exercise remain largely unfulfilled. However, intensive sampling of the soil and litter layer for subsequent examination might have been a more successful approach.
C. oculata was reported to pupate in the soil (Burke and Martin 1956) and was also observed to do so in the laboratory. By contrast, cocoons of M. signoretti were regularly found at the base of birch trees in the border area but not beyond; the bases of other tree species were negative.

Helorus anomalipes (Pauzer) (= H. paradoxus (Prov.) (Hymenoptera: Heloridae) was reared from a cocoon of C. oculata which, prior to spinning,was collected as a third instar larva. The parasite is Holarctic in distribution. Killington (1936) reports it from Chrysopa spp in England and, in North America, it was reported from Chrysopa spp and C. majuscula Banks (= C. nigricornis Burm.) (Krombein et al. 1979). Clancy (1946) also observed that it is a larval parasite which emerges subsequent to spinning of the host cocoon.

The ichneumonid Dichrogaster crassa (Prov.) (Hymenoptera: Ichneumonidae), was reared from a cocoon of C. oculata. The parasite is wide-spread in North America and was reported from Hemerobius sp. and several species of Chrysopa (Krombein et al. 1979). D. crassa probably also parasitises resting larvae and cocoons (prepupae and pupae) as in the closely related Chrysopoctonus patruelis Cushman (now Dichrogaster chrysopae patruelis (Cushman)) reported by Clancy (1946).

Encyrtid wasps, Isodromus iceryae Howard (Hymenoptera: Encyrtidae), were reared from an overwintered cocoon of Meleoma signoretti Fitch. The parasite is cosmopolitan and, in North America, was reported from two species of Sympherobius and three species of Chrysopa (Krombein et al. 1979). This is the first report of parasitism in cocoons of Meleoma and constitutes also a new host record of the parasite. Clancy (1946) reported on the biology of the parasite.

ECTOPARASITISM OF ADULT CHRYSOPIDS

The ceratopogonid Forcipomyia eques (Johannsen), the only known dipterous parasite of chrysopids, has been reported from several North American species (Smith 1922; Clancy 1946). In the two study areas, parasitism was limited almost entirely to males of C. oculata, rarely females, and the parasites were always of the female sex. Parasitism ranged as high as 42.86 per cent of males of C. oculata. Smith (1922) also observed that only females were found on the wings of hosts. He recorded an average parasitism of 9.5 per cent of all C. oculata adults collected, but did not indicate whether any sex was preferentially parasitised.

PHORETIC ASSOCIATIONS OF ADULT CHRYSOPIDS

The first instar or planidium larva of Perilampus chrysopae Crawford is ectoparasitic on chrysopid larave, but the adult parasite does not actively engage in parasitising the host (Clancy 1946). Clancy (1946) reported that eggs are oviposited on vegetation and, on hatching, the planidium larva attaches itself to the substrate by its anal sucker, to await the passing of its natural hosts which are chrysopid larvae. The planidium larva is non-feeding and long-lived, and feeding and development only occurs after host pupation. It will also attach to other insects (on which it will not develop) but will detach to await a potential host if its carrier dies. The occurrence of planidium larvae on adults of _C_. _oculata_ can thus be regarded as a type of phoresy.

Also to be regarded as a phoretic association, though leading to nowhere, is the presence of triungulin larvae of _Rhipiphorus_ sp. (Coleoptera: Rhipiphoridae) on adult chrysopids. The triungulin larva of _Rhipiphorus_ is parasitic on bees but the adult parasite oviposits on flowers (Linsley and MacSwain 1951). The mode of host infestation is unknown but it is believed that either the eggs or the triungulin larvae are transported to host nests on the bodies of flower-visiting bees (Imms 1970).

ENDOPARASITISM OF ADULT CHRYSOPIDS

Mermithids (Nematoda) and intracellular bacteria

Mermithid parasitism has not been previously reported in North American chrysopids. Two larval forms were obtained from adults of _C_. _oculata_ on Mt. St. Hilaire, and amounted to 1.2 per cent of the F_1 generation. The low rate of infection and the rarity of the event suggest that mermithid parasitism is an insignificant mortality factor. Elsewhere, the only case reported is by Mehra _et al_. (1968) who obtained _Hexameris_ sp. from _Chrysopa_ _madestes_ Banks, in India.

The intracellular organism found in the gonads of C. chi (both sexes) is not obligate and occurs widely. The identity of this organism and whether it is a pathogen, commensal or mutualistic symbiont are at present unknown. However, its length, at least, falls within the range of Rickettsia (vide Krieg 1963 and Poinar and Thomas 1978). Neither intracellular bacteria nor bacterial pathogens have been reported in chrysopids.

The incidence of parasitism by Chrysopophthorus americanus Mason (Hymenoptera: Braconidae: Euphorinae): its effect on the host and on the reproductive potential of the host population

The euphorine parasite Chrysopophthorus americanus Mason is widely distributed in the United States, and Chrysopa carnea (now Chrysoperla carnea) is reported to be a host (Krombein et al. 1979). Ch. americanus has not been documented in Canada before now. It was found to parasitise adults of C. oculata and C. chi which are new host records, and its occurrence in Quebec thus extends the species range. Biology and ecology were not previously reported.

Chrysopophthorus americanus is one of seven species in the cosmopolitan genus Chrysopophthorus Goidanich, and is closely related to the Palearctic Chrysopophthorus hungaricus (Zilahi-Kiss) (= Ch. chrysopimaginis Goidanich: Mason 1964),[1]

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[1] For the sake of simplicity and to avoid confusion, the current name Chrysopophthorus hungaricus (Zilahi-Kiss) will be used subsequently, although authors cited may have used Chrysopophthorus chrysopimaginis Goidanich.

the only other species to be investigated (Principi 1948; Séméria 1976a). Ch. hungaricus parasitises several Palearctic chrysopids including the cosmopolitan C. carnea (= Chrysoperla carnea) (Principi 1948; Séméria 1976a).

Parasitism by Ch. americanus was limited almost exclusively to males of C. oculata and contrasts sharply with that of Ch. hungaricus which parasitises both sexes of six chrysopid species in France (Séméria 1976a). Furthermore, as Séméria (1976a, 1980a) indicated, the species parasitised by Ch. hungaricus all belong in the genera Anisochysa and Chrysoperla, while members of the genus Chrysopa s.s. which are contemporaneous in emergence and activity are never parasitised. By contrast, Ch. americanus is now known to parasitise two chrysopid genera, Chrysopa s.s. and Chrysoperla, if the host reported in Krombein et al. (1979) is indeed valid.

The activity of Ch. americanus in the male population of C. oculata (Mt. St. Hilaire 1979) was similar in time of onset, period of peak activity but not termination, to that of Ch. hungaricus, reported by Séméria (1976a) in a chrysopid population (ten species and two subspecies) in France. Termination was earlier (mid-September) in Ch. americanus and parallelled the demise of the host population. Parasitism observed during the period of peak activity (end of June to end of July) attained levels (30.0 and 33.33 per cent of males - Mt. St. Hilaire 1979 and Ile Perrot 1980) which were more than double that reported by Séméria (1976a) for the parasitic activity of *Ch. hungaricus*, in France.

Females of *C. oculata* were almost never parasitised and the rate of parasitism in *C. chi* was extremely low (only one female observed). This situation is enigmatical since females of *C. oculata* occur as frequently as do males, and *C. chi* occurs simultaneously with *C. oculata* in the old-field habitat (Figs 1-3). The population of *C. chi* is very small, however, which would increase the odds against such an event taking place. This phenomenon in *C. oculata* is probably achieved by a differential response of the parasite to biochemical, ecological and behavioral differences between the sexes. These host-parasite relationships may also be at work in *C. chi*, and are probably responsible for the lack of parasitism reported by Séméria (1976a) in *Chrysopa* s.s., which he attributes to the architecture of the cocoon (Séméria 1980a),thereby also implying that the cocoon is the stage susceptible to parasitism. On the contrary, the selective parasitism of males of *C. oculata*, and the recovery of eggs from them well after the beginning of spring emergence, indicate that the adult is the susceptible stage.

Parasitism did not lead to damage of the reproductive organs in females of *C. oculata*. Sperm were maintained in a viable state in the spermatheca and, in the case of *C. chi*, parasitism did not impair the insect's ability to subsequently oviposit fertile eggs. Séméria (1976a) also observed no damage to the reproductive organs of *Anisochrysa flavifrons* Br., and reported oviposition of fertile eggs by previously parasitised females, as well as by a female in the final stage of parasitism. In _C_. _oculata_, the condition of the ovaries indicates that parasitism causes degeneration of maturing oocytes and drastically inhibits oogenesis, effecting in reality a sterility which to all appearances is temporary. Euphorine parasitism was also reported to cause termination of oviposition in Coleoptera (Weiss and Williams 1980; Loan and Holdaway 1961) and similar degenerative effects in the ovaries (Loan and Holdaway 1961).

Parasitism in males likewise did not result in damage to the reproductive organs or other organ-systems, but there was atrophying of the fat bodies and decoloration of the testicular envelope as Principi (1948) reported in _Chrysopa_ _ventralis_ Curtis. A similar physiological condition of the fat bodies occurs also in euphorine-parasitised Coleoptera (Timberlake 1916; Loan and Holdaway 1961) and, in males, potency was reported to be maintained (Loan and Holdaway 1961). Males of _C_. _oculata_ also remained potent. Sperm were viable in the seminal vesicles during the course of the parasitism and, upon its termination, a resumption of sexual activity was indeed possible. Actively parasitised males of _C_. _oculata_ are thus not temporarily sterilized as in the case of females but, because of their ungainly size during the penultimate stage of the larva, they may be incapable of going through the mechanics of mating. Some males do survive parasitism under field conditions.

In spite of the high levels of parasitism observed in C. oculata, the deletion effect of parasitism on the reproductive potential of the population is probably low; females are almost never parasitised (and even then they may be capable of ovipositing fertile eggs subsequently) and males, if they survive, can resume sexual activity. Furthermore, the loss of parasitised males will have little or no effect on the reproductive population for their reproductive effort can be executed by other males.

DEVELOPMENTAL BIOLOGY OF CHRYSOPOPHTHORUS AMERICANUS MASON (HYMENOPTERA: BRACONIDAE)

The egg of Ch. americanus is described; it was recovered on two occasions from males of C. oculata, and is the first observation and description for the genus. The eggs differed in size, but the discrepancy is a result of functioning of the trophamnion and the development of the embryo (vide Tobias 1965). There are five larval instars, the first is caudate and typically euphorine, the others vermiform. The fifth instar escapes from the host to pupate. Larval stages have also been described in Ch. hungaricus (Principi 1948), whose first instar is known only from its head capsule. The duration of larval development in Ch. americanus was observed to be at least 19 days (difference between host collection date and the parasitic larva's exit date; Table XVIII).

The high frequency of single parasitism (one parasite larva per host) indicates that larvae of Ch. americanus are solitary endoparasites. Two cases of double parasitism were observed, however, one in which a developing first instar larva had died, the other in which the host (male caught on July 15) bore the tell-tale exit wound with attached penultimate exuvia, a live penultimate larva and two first instar head capsules in the abdomen. It is possible that in this second case parasitism may have been sequential, considering that parasite activity is evident around mid-June, and that larval development takes at least 19 days. It is also quite likely that parasitism may have been simultaneous at some point in time and, similar to Leiophron pallipes Curtis (Loan 1965), the second parasite may have remained alive, undergoing minimal development in the presence of the first.

As the parasitic larva develops, trophamnion cells in the hemolymph of the host also increase in size as Loan (1965) reported for the euphorine, L. pallipes. The cells were observed to be numerous during the penultimate stage, but were practically non-existent in those whose parasitism had terminated. Trophamnion cells are nutritive in function to the developing larva (Tobias 1965) and, as Loan (1965) suggests, they are probably crushed and consumed by the penultimate larva prior to its moulting and exit from the host.

Unlike the larva of Ch. hungaricus which apparently cocooned without difficulty at the bottom of a glass tube (Principi 1948; Séméria 1976a), mature larvae of Ch. americanus did not do so unless they had a loose substrate into which to burrow. They appeared to need a thigomotactile stimulus and, on cocooning, they entered into a state of obligatory diapause which terminated spontaneously between 42 and 88 days (Table XVIII). In Ch. hungaricus, Séméria (1976a) observed a variable duration of 16 to 32 days (three cocoons) and Principi (1948) a duration of 19 days (one cocoon).

Variability in duration of the cocoon stage (Table XVIII) is an expression of diapause intensity, and appears to be under polygenic control since host-experienced photoperiod does not appear to be a likely factor. The sunrise to sunset daylength on the earliest approximate date of parasitism (June 29; obtained by extrapolating 19 days from the exit date of larvae) and the latest host capture date (July 16) were essentially long (15 hr. 45 min and 15 hr. 25 min. respectively). Furthermore, addition of the twilight zones to the sunrise to sunset daylength would give effective photoperiods at, or in excess of LD 16:8.

Pupation occurs in the field mainly in the months of July and August, as indicated by the presence of individuals showing signs of prior parasitism. Laboratory studies showed that larvae enter into a state of obligatory diapause on cocooning and, in two outdoor diapausing cocoons in which larvae had pupated on July 29 and August 1 (Table XIX), diapause development was completed on or before January 4. Therefore winter conditions might serve to delay post-diapause development and subsequently to synchronize parasite emergence in spring. Parasite activity is first evident in mid-June. On Mt. St. Hilaire, the first egg was recovered on June 20, a second 36 days later, and a caudate first instar larva (Aug 17) 58 days after recovery of the first egg. Since observed larval development is at least 19 days and emergence can occur 42 days after pupation (or even sooner as it is variable), the possibility exists that a few of the very early pupae could emerge and initiate a small second generation parasitism. The occurrence of a caudate larva on August 17 indicates that two generations of the parasite are indeed a distinct possibility.

DEVELOPMENTAL STUDIES ON *CHRYSOPA OCULATA* SAY AND *CHRYSOPA CHI* FITCH

Developmental studies on *C. oculata* reared in plastic and shell vials showed the former to be more suitable; development was significantly faster, cocooning was more successful and rearing success greater. Larvae reared in the shell vials may have been stressed by inadequate gaseous exchange through the ventilated stopper, as well as by excessive humidity within its confines, produced by the aphids and arising also from liquid excretions of the larva. As a consequence, vials had to be cleaned out regularly to avoid decomposition of dead aphids. Indeed, in *Chrysopa perla* (L.), Canard and Prudent (1978) found that a dry and loose substrate was ideally suited for cocooning, whereas excessive humidity and free water prolonged the prespinning, searching phase of the third instar and, in addition, led to imperfect cocooning.

The shell vials offer an economy in space but are clearly not suitable for use in developmental and genetic studies. They may be used, nevertheless, in rearing developmental stages for morphological studies. However, better results may possibly be obtained with them if the capacity for air exchange were improved. By contrast, the plastic vials were more easily manipulated, they were always dry and only needed to be cleaned out after cocoon construction. Although their usage in the individual-rearing of larvae is still labour-intensive, it appears to be a less cumbersome approach than Barnes' (1975a) stopper method, and may offer more convenience than those employed in previous developmental and genetic studies (*vide* Bickley 1952, Sheldon and MacLeod 1974b, Ru *et al*. 1975). The units are easily constructed and maintained, developmental data may be recorded on them (on masking tape), and developmental stages may easily be grouped or removed.

Developmental data on *C. oculata* and *C. chi* indicated that overall development time was significantly faster in males and led to a protandrous emergence; the developmental difference was also consistently and significantly expressed in both the prepupal and pupal stages. A similar development was demonstrated in *C. perla* in which the duration of the cocoon stage (prepupa and pupa) was shown to be shorter in males (Canard 1973), and in *Chrysopa flavifrons* Brauer where it was significantly so (Principi *et al*. 1975). A shorter development time was also reported in males of *C. carnea* (Sheldon and MacLeod 1974b).

Protandry was evident also in the field populations of *C. oculata* when collections were made on consecutive days very early in spring (Table II), and often also at the start of the F_1 generation (Tables IV,VI). It appears to be a regular feature of the Chrysopinae and stems largely from the shorter development time of the prepupal and pupal stages. Canard (1973) also reported a protandrous emergence of *C. perla* in spring, and Zeleny's (1965) population dynamics study indicates protandry in the summer generations of *C. carnea*, and in the spring population of the univoltine *Chrysopa phyllochroma* Wesmael.

The independence of *C. oculata* on aphid-feeding, for the maturation and migration of sperm to the seminal vesicles, is in accord with an earlier report that they are capable of fertile matings on a diet of sugar and water (Tauber and Tauber 1973b). On the other hand, *Chrysopa nigricornis* Burmeister is reported to require a protein meal (Tauber and Tauber 1974a) and, in *C. perla*, a glucidic diet (honey) was found to impair sperm maturation and migration to the seminal vesicles and also spermatophore development (Philippe 1972). Sperm shift in *C. oculata* occurred on the second day after emergence, hence fertile matings may be possible at that time (pairing in the laboratory was usually done on the third day when its incidence was greatest). By contrast, sperm shift occurred on the third day in *C. perla* (Philippe 1972), and in little less than a day in *C. carnea* (Sheldon and MacLeod 1974b).

One objective of the reproductive development studies was to identify certain criteria by which new field emergence, and hence the start of a new generation, may be recognised. The data show that, for males, sperm shift as an indicator was reliable for individuals up to one day old. With females, however, ovarian development (assuming normal feeding and prey availability) was reliable for individuals up to three days old, in addition to which, the spermatheca of such females may be devoid of sperm and may not yet be heavily sclerotised.

DEVELOPMENT OF *CHRYSOPA LINEATICORNIS* FITCH

The trash-carrying larva of *C. lineaticornis* was described and reared by Smith (1922) but the egg stage has remained, until now, unknown and undescribed. Eggs were obtained as a result of oviposition of a field-collected female. They appear distinctive in color, size and chorionic sculpturing. Oviposition occurred over a two-day period but not subsequently, and the female did not accept pea aphids; it may thus be a pollen and honey dew feeder. Smith (1922) reported no success in obtaining oviposition from captured females.

The packet of debris is a constant characteristic of all the instars (Smith 1922) but, for reasons unknown, all larvae consistently failed to cover themselves with debris (dead aphids and aphid exuviae) from the rearing cages. There was, in addition, a low yield in completed cocoons which may be the result of inadequate larval nutrition as Andresen (1974) suggested in the case of Chrysopa chrysops (L.) Larvae were fed several species of aphids and mosquitoes, and may not have been receiving their natural prey. In a field observation (Morgan Arboretum, St. Anne de Bellevue), a third instar larva was seen to attack and feed on an egg of Meleoma.

The development of instars I to III was not very different under the two rearing conditions. Under laboratory long-day conditions, development was continuous in one specimen (two other cocoons failed, one each in the prepupal and pupal stages), but diapause existed in the two cocoons obtained under outdoor-rearing conditions. The data are too few to draw any definite conclusions, but it may be that univoltine C. lineaticornis has a facultative diapause which may be induced by short or decreasing daylength. Smith (1922) also reported having had limited success in carrying pupae on to the adult state but the rearing conditions are unknown.

THE ALLELIC GENES B AND b OF CHRYSOPA OCULATA SAY: GENETIC INHERITANCE, LINKAGE AND POPULATION GENETICS

The inheritance of pigmentation in the gradate cross-veins of the forewing is of interest not only from a viewpoint of ecological and population genetics of field populations, but also because the character occurs widely among chrysopids and has been used, in conjunction with others, in the separation of species and subspecies (Tauber 1969; Séméria 1976b).

The data support the hypothesis of a two-allele autosomal gene in which black pigmentation is determined by the dominant allele (B), and the lack of it (green veins) by the recessive allele (b) in the homozygous state. These results are similar to studies in Lepidoptera which show melanism to be determined by a dominant gene (Lorimer 1979; Vakkari 1980), and follow the pattern of other studies in *C. oculata* in which body pigmentation, albeit aberrant, is determined by a single gene (Tauber and Tauber 1971b; Tauber *et al*. 1976).

Pigmentation of the gradate crossveins is also linked to pigmentation of other wing veins, such that the veins of the green-gradate phenotype appear to be almost entirely green, and those of the black-gradate phenotype to be predominantly black and variable. The genetic control of pigmentation in these other veins was not investigated. In addition, the green phenotype in the laboratory stock was always associated with the lack of black pigmentation on the basicardo, and the usual presence, on the vertex, of a single pair of post-antennal spots (Fig. 10a), whose absence is determined by a single recessive autosomal allele in the homozygous state. On the other hand, the basicardo was always black-pigmented in the black phenotype, and the vertex always carried an additional pair of spots (Fig. 10 c). In field specimens, however, the phenotype-associated cephalic characters were sometimes lacking, or were present in the alternate phenotype. This indicated that each was under independent genetic control and that the genes controlling them are probably very closely linked to the gene determining gradate pigmentation. Thus, in contrast with the green phenotype, the black phenotype is at most times a distinctly pigmented insect.

Bickley (1952) investigated the inheritance of the post-antennal markings on the vertex of two varieties of *C. oculata*. He concluded that the *oculata* variety (four spots on vertex; *vide* Fig. 10c) as opposed to the *illepida* (two longitudinal bands on vertex), is determined by two or more genes, any one of which in the recessive state produces the *oculata* phenotype. The findings of this present study indicate, however, that the *oculata* condition is determined by probably no more than two independently acting genes and, as far as one pair of spots is concerned, it is the expression of the dominant allele.

Frequency of the recessive allele (*b*) was greater than that of the dominant (*B*), in both the overwintered and F_1 generations on Mt. St. Hilaire, as well as on Ile Perrot (Fig. 11). The *b*-allele frequency was itself much greater on Ile Perrot, the alleles thus demonstrating a spatial variation in gene frequency which has been observed in other insect species (Cockley *et al*. 1977; Farish and Scudder 1967) and mammals (Glover *et al*. 1977; Selander *et al*. 1971). In both localities, the frequency of the dominant allele (*B*) was lower in the overwintered generation than in the F_1, indicating selection against it during winter. This is not unlike the seasonal and altitudinal changes in chromosome frequency in Drosophila pseudoobscura, which Dobzhansky (1948, 1956) reported to result from natural selection. Selection against a genotype may lead to a loss of genetic equilibrium in a population. This, however, could not be ascertained in the two generations as the heterozygote and homozygous dominant could not be separated with absolute certainty.

THE ALLELIC GENES A AND a OF CHRYSOPA OCULATA SAY: GENETIC INHERITANCE AND POPULATION GENETICS

A reduced form of the interocular subantennal band, the "facial spots" configuration, occurred in the laboratory culture originating from Ile Perrot (Fig. 10d). The results of an inheritance study support the hypothesis of a two-allele autosomal gene whose dominant allele (A) determines "facial band" expression, and whose recessive allele (a) in the homozygous state determines the expression of "facial spots". It was found also that the bb genotype (green gradate crossveins) exerts an epistatic effect on "facial spots" expression (Fig. 10f), such that the subantennal spots were elongate and band-like, but nevertheless remained discrete. Although the "facial spots" character was first recognized on Ile Perrot, the phenotype was field-collected only on Mt. St. Hilaire, but rarely. Gene frequency was quite low and indicated a low fitness of the a-allele.

The "facial spots" character is present in the North American species Chrysopa assimilis Banks, and is characteristic also of some Palearctic species (vide Séméria 1974b,1980b) which are congeneric (Chrysopa s.s.) with C. oculata. In addition, "facial band" is itself possessed by the congeneric North American species, Chrysopa pleuralis Banks and Chrysopa incompleta Banks. However, until such time as there is information on the biogeography of Chrysopa s.s. (vide Kevan 1979) and the taxonomic relationships of its members, it would be premature to speculate as to whether "facial spots" in C. oculata might be genetically homologous with the apparently identical character in C. assimilis and some Palearctic species, and whether or not "facial band" might be a recently derived character.

MEIOTIC DRIVE (OR GAMETIC COMPETITION) IN CHRYSOPA OCULATA SAY: ITS EFFECT ON GENE FREQUENCY AND ON GENOTYPE OCCURRENCE

A meiotic drive mechanism appears to be a contributory factor to the depression of the a-allele frequency. The double homozygous recessive (bbaa) genome was shown to be viable, yet it was selectively eliminated in some crosses. This was shown to occur only when the ba gamete was one of four possible meiotic products of the double heterozygous parent (BbAa), irrespective of its sex. The bbaa genome was realised when the parents were heterozygous in only one gene, for the alleles A and a. The ba gamete can thus occur with either Ba or bA, but never with BA, as the only other meiotic product. Elimination of the ba gamete from the double heterozygote thus appears to be linked with the presence of the BA gamete, by itself, or in concert with Ba and bA, probably very early in gametogenesis. Furthermore, in such crosses, there is distortion of the new expected progeny ratio which favours the bA gamete, and ultimately the alleles b and A.

Mechanisms of meiotic drive were reviewed by Zimmering *et al*. (1970), and Hartl (1975) distinguished it from gametic selection which is independent of parental zygosity but depends on the genetic constitution of the gamete. The circumstances of the abnormal segregation pattern do not appear to fit any of the mechanisms of meiotic drive described in *Drosophila* and other insect species (*vide* Zimmering *et al*. 1970). While the cytological basis for the distortion is unknown, the fact remains that it occurs in the presence of the BA gamete. A case for gametic selection might be made, however, if the concept of genotype environment affecting fitness (Hartl 1975) were applied at gametogenesis in the double heterozygote.

EMBRYONIC MORTALITY AND CYTOGENETICS OF *CHRYSOPA OCULATA* SAY AND *CHRYSOPA CHI* FITCH

The persistent embryonic mortality in the Ile Perrot and Mt. St. Hilaire-derived cultures of *C. oculata* (evident at the outset of colonization) was not related to any of the genotypes under study,for they were all shown to be viable. Furthermore, its magnitude and range were not suggestive of a balanced lethal system, and certainly not of a single recessive lethal gene. A similar mortality occurring in the Mt. St. Hilaire-derived culture of *C. chi* likewise bore no relationship to the phenotypic classes (diapause and non-diapause) under investigation.

A cytogenetic investigation of the cultures revealed, however, aberrant chromosomal associations (extreme stickiness and chromatin bridges) indicative of translocations, which could have accounted for the mortality (*vide* Knipling and Klassen 1976) as in the case of the german cockroach (Ross and Cochran 1976). Translocations were also observed in field-collected *C. chi* from Ile Perrot and, as in the cultures, it did not involve the sex chromosomes.

The occurrence of translocations in two widely separated populations of both *C. oculata* and *C. chi* raises the question whether this is mere coincidence, the translocations being spontaneous, or whether they could have been induced by agents such as pesticides (insecticides, herbicides, and fungicides), some of which are known to cause meiotic and mitotic problems in plants (Amer 1965; Amer and Ali 1968; *vide* Review by Grant 1978). Some of these agents also cause chromosomal abnormalities in mammalian cells (*vide* Table 2 in Grant 1978) and, in the grasshopper, Klassen *et al*. (1969) reported aberrations in the meiotic chromosomes of the testes following apholate treatment. It is quite probable, therefore, that the chromosomal abnormalities of *C. oculata* and *C. chi* could have been induced by pesticides for, being field and meadow species, they are the ones which would more frequently encounter these agents in the environment. In Neuroptera, translocations have been reported in one hemerobiid species

(Naville and de Beaumont 1933) and in the mantispid Plega signata (Hagen) in which it resulted in a neo-XY system (Hughes-Schrader 1979).

KARYOTYPE OF CHRYSOPA OCULATA SAY AND CHRYSOPA CHI FITCH

Chrysopa oculata and C. chi have a haploid chromosome number of n = 6, which is typical of most chrysopid species, the exceptions being three species of Chrysopa s.s. with n = 5 and Nineta flava (Scop.) with n = 7 (vide Kiauta et al. 1977). As in all species which have been karyotyped, C. oculata and C. chi have an XY sex-determining mechanism in which the male is the heterogametic sex, the sex chromosomes constitute the smallest pair and the Y is smaller than the X (vide Kiauta et al. 1977). The cytological observations thus confirm earlier genetic evidence of male heterogameity in C. oculata (Tauber et al. 1976).

Cytologically, C. oculata differs from C. chi in that it possesses a submetacentric which is the largest chromosome, all others being acrocentrics, and in the relative size of the Y which is approximately one half that of the X. In C. chi, however, the elements are all acrocentrics and the Y is subequal in size to the X. Chrysopa chi is thus cytologically similar to Chrysopa intima MacLachlan (Kichijo 1934), and therefore supports the synonymy (C. chi is a senior subjective synonym of C. intima) established by Adams (1978).

The sex chromosomes of C. oculata and C. chi were observed to be tangentially joined in diakinesis as Kiauta et al. (1977) reported in Anisochrysa carnea (Steph.) (= Chrysoperla carnea (Steph.)). However, conjunction did not persist into first metaphase, and does not appear to occur always in diakinesis. Hughes-Schrader (1969) had earlier reported no contact pairing or evidence of chromosome-specific terminal connections between the elements. In other neuropteran groups (mantispids and sisyrids), Hughes-Schrader (1975a, 1979) reported the presence of both distance segregation (no diakinesis sex bivalents) and sex-bivalent formation with or without precocious segregation. Sex bivalent formation with precocious segregation was also reported in Raphidioptera (Achtelig and Kristensen 1973) but Hughes-Schrader (1975b) found conjunction infrequent, to be of a fibrillar nature and only transient at best.

DIAPAUSE IN CHRYSOPA CHI FITCH: INHERITANCE, EFFECT ON THE FIELD POPULATION, AND TERMINATION UNDER LABORATORY CONDITIONS

Larvae of C. chi are polymorphic with respect to diapause. Some individuals exhibit an obligatory prepupal diapause under diapause-averting conditions, leading to univoltinism, and others a facultative diapause which is dependent on short photoperiods. Inheritance of univoltinism in C. chi is therefore equivalent to that of its obligatory prepupal diapause. The results of 13 crosses on diapause inheritance, though lacking in more back-crosses and in larger numbers of progeny, nevertheless support the hypothesis of two independently segregating gene pairs, the recessive alleles of which, in the homozygous state, determine obligatory diapause, and the dominant alleles continuous development (non-diapause). In the field, however, C. chi is essentially univoltine, which suggests that the diapause-determining recessive alleles must occur in very high frequency.

Similar diapause characteristics were reported in Chrysopa perla L.[1] (Canard 1973) which also overwinters in the prepupal stage. Canard (1973) reported that there was a tendency towards univoltinism in the spring and early summer generations (a large portion of the progeny automatically diapaused), whereas in the third generation, in August, there was a near total induction of diapause. Canard (1973) attributed the diapause of the third generation to shorter photoperiods, and also to the fairly long critical photoperiod of C. perla (Canard 1976). However, in the case of the spring and early summer generations, particularly that of spring which had a greater portion of diapausing progeny, the diapause was attributed to malnutrition and the probable existence of a two-year cycle (Canard 1973). No mention was made, however, of a possible genetic determination. In other chrysopid species, Tauber and Tauber (1975a) reported that the facultative reproductive diapause of the mohave race of C. carnea was under polygenic control. Alrouechdi and Canard (1979) reported on a

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[1] C. perla is reported to be closely related to Chrysopa intima MacLachlan (Dorokhova 1979; Okamoto 1919) which is now a subjective synonym of Chrysopa chi Fitch (Adams 1978).

biotype of *Chrysoperla carnea* (= *C. carnea*) with no diapause whatsoever, but the genetic basis of this was not investigated.

Univoltinism in insects stems from an obligate or facultative suppression of development at a specific stage in the life cycle. Under natural conditions, it was shown to be determined by photoperiod (Tauber and Tauber 1976a), microclimate (Shapiro 1975), and nutritional factors modifying gene expression (Brown *et al*. 1979). It was also correlated with temperature (Lakovaara *et al*. 1972). Univoltinism in *C. chi* stems from its obligatory prepupal diapause and follows a pattern of simple autosomal Mendelian inheritance, in contrast with the silkworm moth where voltinism is determined by three sex-linked alleles and three autosomal genes (Tanaka 1953), and with the pattern of polygenic inheritance reported in blowflies (Ring 1971; Vinogradova and Tsutskova 1978), *Drosophila* (Lakovaara *et al*. 1972) and the spruce budworm (Harvey 1957). Furthermore, the recessive nature of univoltinism in *C. chi* is similar to that reported in the European cornborer (Arbuthnot 1944), in *Papilio* (Oliver 1969) and in *Drosophila ovivororum* (Lakovaara *et al*. 1972: nec *littoralis*, Lumme *et al*. 1975). In *D. littoralis*, however, the reverse appears to be true (Lumme *et al.* 1975).

Prepupae of *C. chi* in obligatory diapause were not held for a sufficiently long period under laboratory rearing conditions (actually held for 39 days and less) to determine whether diapause does not terminate spontaneously as reported in a facultatively diapausing strain of *C. perla* (Canard 1976), or whether termination is spontaneous as in *C. oculata* (Propp *et al.* 1969) and *C. nigricornis* (Tauber and Tauber 1972c), and as shown earlier on in the euphorine parasite, *Chrysopophthorus americanus*. However, in response to variable cold treatments, obligatorily diapausing prepupae of *C. chi* showed a quantitative response in adult emergence and development time, similar to that shown by *C. perla* (Canard 1976). A quantitative response was also seen in days to pupation and duration of the pupal stage.

SUMMARY

The chrysopid fauna has not been investigated previously in the North American old-field ecosystem. Such a fauna is likely to be represented in agricultural ecosystems and, as such, it is of importance in terms of biological and integrated control. A total of nine species were encountered in two old-fields in Quebec but, of these, only two species, *C. oculata* and *C. chi* can be considered inhabitants; they were, in addition, the most frequently encountered species. The seven other species occurred infrequently and are accidentals, mostly dendrophilic species which strayed in from neighbouring woods. *Chrysopa oculata*, the dominant species, is the most widely distributed of the American species (Smith 1922) and also occurs right across Canada. In Quebec, it realises two generations per year, whereas *C. chi* is essentially univoltine and occurs mainly in spring. Immature stages (eggs, larvae and cocoons) were not located in sufficiently large numbers to determine the extent of parasitism. This was undoubtedly due to the limiting approach of *in situ* searching which was designed to disturb the habitat as little as possible, and to identify, if possible, stage-specific microhabitats.

The paucity of eggs in the herbaceous layer was certainly not in keeping with the abundance of gravid females. Twenty-four hour oviposition studies indicated the pattern to be bimodal in *C. oculata* and unimodal in *C. chi* but, more importantly, the studies indicated that a fair amount of oviposition might occur in overnight resting sites. Aggregations of eggs of C. oculata were subsequently found in the gramineous layer. The studies also suggested that the poor herbaceous oviposition might be accounted for by the diminished oviposition of the morning and early afternoon, and which is probably incidental to feeding.

Eggs of C. oculata in the gramineous and herbaceous layers were parasitised by the scelionid wasp, Telenomus chrysopae Ashmead. A larva of C. oculata was found to be parasitised by the helorid wasp, Helorus anomalipes (Pauzer), and the ichneumonid wasp Dichrogaster crassa (Prov.) was reared from a cocoon, also of C. oculata, and is a new host record of the parasite. Encyrtid wasps, Isodromus iceryae Howard, were reared from a cocoon of Meleoma signoretti, an accidental species in the old-field habitat, and represents also a new host record. M. signoretti appears to be an ecotone species; its cocoons are found regularly at the base of birch trees in the border area.

The planidium larva of Perilampus chrysopae Crawford (Hymenoptera: Perilampidae), a parasite of chrysopid larvae, and the triungulin larva of Rhipiphorus sp. (Coleoptera: Rhipiphoridae), a parasite of bees, were found on the bodies of adult chrysopids. These, however, are only accidental phoretic associations. On the other hand, the ceratopogonid Forcipomyia eques (Johannsen), is an ectoparasite of adult chrysopids and was found on C. oculata. It preferentially parasitised the male sex (females rarely parasitised), and fed on hemolymph from wing veins. Parasitism was observed only in the month of June.

Mermithid parasitism is recorded for the first time in North American chrysopids. Larval forms were recovered on two occasions from *C. oculata*, but infection is rare, its rate is low, and it thus appears to be an insignificant mortality factor. *Chrysopa chi* was often the host of an intracellular, non-obligate bacterial organism which occurred in the gonads of both sexes. *C. oculata*, however, was never affected. The organism is widespread; its identity and function, whether as a pathogen, commensal or mutualistic symbiont remain unknown. There is no prior report of any such organism in chrysopids.

Adults of *C. oculata* and *C. chi* were also parasitised by the euphorine *Chrysopophthorus americanus* Mason (Hymenoptera: Braconidae). This is the first report of the parasite in Canada and also constitutes new host records. Males of *C. oculata* were preferentially parasitised, rarely the females, and only once was parasitism observed in *C. chi*, a female. The predominance of male parasitism and the egg recoveries from them well after the start of the chrysopid spring emergence indicate that it is the adult stage which is susceptible to parasitism. The predominance of male parasitism is probably a result of a differential response of the parasite to biochemical, ecological or behavioral differences between the sexes. While these factors may also be operative in the population of *C. chi*, the small size of its population may, however, be the major limiting factor in the incidence of its parasitism.

Parasitism did not result in damage to internal organs but fat bodies were atrophied as a result of depletion of their stores. The testicular envelope, in males, was usually decolorised, and females were termporarily sterilized as a result of inhibition of oogenesis and yolk resorption. Sperm, however, were maintained in a viable state in the spermatheca of females, and in the seminal vesicles of males. Survival of parasitism was variable, and both sexes were capable of subsequently resuming their reproductive functions. The parasite thus exhibits a very advanced level of association with its host. Furthermore, since parasitism in C. oculata is restricted almost entirely to males, its effect on the reproductive potential of the population is undoubtedly low.

Chrysopophthorus americanus is a solitary endoparasite but double parasitism may occur occasionally, with consequences which may or may not be disastrous to the other. The observation and description of the egg are a first for the genus. There are five larval instars, the first is caudate and possesses the typical large euphorine head capsule; the others are vermiform. Duration of larval development is at least 19 days, probably not very much more. The fifth instar escapes from the host to pupate.

Mature larvae need a thigmotactile stimulus to initiate cocooning, whereupon they enter into a state of obligatory diapause which terminates spontaneously in 42 to 88 days under long-day conditions. Intensity of the diapause does not appear to bear any relationship to field photoperiods experienced by the parasitised host; they were essentially long and similar. Diapause intensity may thus be under polygenic control. Outdoor diapausing cocoons completed development on or before January 4, therefore winter conditions serve to retard post-diapause development and subsequently to synchronise emergence in spring. Parasite activity is first evident in mid-June and, in Quebec, a second generation of the parasite is a distinct possibility.

Cages were constructed for the individual-rearing of chrysopid larvae in developmental and genetic studies. Those constructed from plastic vials were superior to the smaller glass vials in permitting a significantly shorter development time, a rate of successful cocooning which approached 100 per cent, and a rearing success rate which was also much greater. In addition, the plastic vials were more easily manipulated and required little or no house-cleaning during the course of a rearing. They were also amenable to the recording of developmental data.

Males of _C_. _oculata_ and _C_. _chi_ developed significantly faster than females. The source of the protandry stems from the highly significant shorter development time of the prepupa and pupa. Protandry is also evident in the field when collections are initiated on a daily basis at the start of the emergence period.

Reproductive development studies on C. oculata showed that recent emergence can be recognised up to one day in males and three days in females. This, in males, is based on sperm shift which occurs on the second day independently of aphid-feeding and, in females on an aphid regime, by the progressive, step-wise engagement of positional oocytes in vitellogenesis, as well as by their progression in size and color. This development was used to confirm recent field emergence, particularly the start of a new generation.

The fortuitous capture of a gravid female of C. lineaticornis which subsequently oviposited, provided an opportunity to describe the egg which had hitherto not been observed, and to rear the larval stages. It did not accept aphids and may thus be a pollen and honeydew feeder. The eggs are much smaller than those of C. oculata and C. chi, and are distinctive in size, color and chorionic sculpturing. Larvae were reared without mortality but they did not cover themselves with debris as occurs normally in nature. Cocooning, however, was very poor, probably because of an inadequate diet. Development was continuous in long-day conditions (one specimen) while diapause existed under short-day. It may be that univoltine C. lineaticornis has a facultative diapause which is induced by short day, or decreasing day length.

An embryonic mortality was present at the outset of colonization of C. oculata (from Ile Perrot and Mt. St. Hilaire) and C. chi (Mt. St. Hilaire). It was also present in the lot of field-collected eggs from which the Mt. St. Hilaire culture of *C. oculata* originated. The mortality manifested itself in the late embryo prior to eclosion, and often at eclosion when larvae remained trapped within the embryonic moult. The mortality was not related to any of the genotypes or phenotypic classes under investigation, but appears to stem from chromosomal translocations which involved the autosomes. Aberrant chromosomal associations (extreme stickiness and chromatin bridges), indicative of such, were present in all three cultures, and also in field-collected *C. chi* from Ile Perrot.

Chrysopa oculata and *C. chi* have a haploid chromosome number of $\underline{n} = 6$, and an XY sex-determining mechanism in which the male is the heterogametic sex. The two species differ in the composition of their chromosomal complement which, in *C. chi*, is composed entirely of acrocentrics, and likewise in *C. oculata* except for the largest element which is submetacentric. They also differ in the relative size of the sex chromosomes. The karyotype of *C. chi* is also similar to that of *Chrysopa intima* MacLachlan, thereby supporting the synonymy which places *C. chi* as a senior subjective synonym. Although conjunction of the sex chromosomes was observed at diakinesis in *C. oculata* and *C. chi*, it did not always appear to take place. Nevertheless, the sex chromosomes always segregated precociously.

Pigmentation of the gradate crossveins of the forewing of _C_. _oculata_ is controlled by a two-allele autosomal gene whose dominant allele _B_ determines black pigmentation, and the recessive allele _b_, in the homozygous state, green pigmentation. Pigmentation of the gradate crossveins is also linked to pigmentation of other wing veins such that in the green-gradate phenotype the veins are almost entirely green, in addition to which the phenotype is unmarked on the basicardo and usually bears one pair of black post-antennal spots on the vertex. The absence of this spot is determined by a recessive autosomal allele in the homozygous state. By contrast, in the black-gradate phenotype, most of the veins are predominantly black, the basicardo is black, and there is an additional pair of black post-antennal spots. The black-gradate phenotype, unlike the green, is therefore a distinctly pigmented insect. However, in the field population, these phenotype-associated cephalic characters (basicardo and post-antennal pigmentation) were found to be sometimes lacking or were present in the alternate phenotype. This indicated that they are under independent genetic control and that the genes controlling them are probably closely linked to the gene determining gradate pigmentation.

Frequency of the recessive allele _b_ was greater than that of the dominant (_B_) in both the overwintered and F_1 generations, in both localities. Frequency of the _b_ allele was also greater on Ile Perrot than on Mt. St. Hilaire. The dominant allele (_B_) showed, however, a decrease in frequency in the overwintered generation of both localities, indicating seasonal selection against it and, accordingly, lesser fitness.

Chrysopa oculata is also characterised by a black, subantennal facial band. This band is the expression of the dominant autosomal allele, *A*, whose recessive counterpart (*a*), in the homozygous state, determines its reduced form, the "facial spots" configuration. The *a* allele occurs in very low frequency on Mt. St. Hilaire. The phenotype was collected in only that locality, although it was first recognised in the culture originating from Ile Perrot.

A meiotic drive mechanism, probably gametic selection, causes the selective elimination of the *ba* gamete only when it is one of the four meiotic products of the double heterozygote *BbAa*, irrespective of its sex. In crosses involving it, this results in the loss of the *bbaa* genome from the progeny, even though the genome is viable, as seen in those crosses where the parents were heterozygous in but one gene, for the alleles *A* and *a*. The selective elimination of the *ba* gamete is therefore linked to the presence of the *BA* gamete, by itself, or in concert with *Ba* and *bA*. Furthermore, there is segregation distortion of the new progeny ratio (based on three classes of gametes from the double heterozygous parent) which favors the *bA* gamete and ultimately the alleles *b* and *A*. The dominance of the *b* allele thus stems from its greater fitness, and also from the meiotic drive mechanism and segregation distortion which favor it.

Chrysopa chi displays both an obligatory and facultative prepupal diapause. Under long-day conditions a portion of the progeny automatically diapauses, but short-day induces 100 per cent diapause. Obligatory diapause is determined by the recessive alleles of two independently segregating autosomal gene pairs, whose dominant alleles determine continuous development and, consequently, multivoltinism. Obligatory diapause therefore leads to univoltinism. In the field, however, C. chi is essentially univoltine which indicates that the diapause-determining recessive alleles must occur in high frequency.

Prepupae in obligatory diapause showed a quantitative response to cold treatment, in adult emergence, overall development time, as well as days to pupation.They also showed a slight response in duration of the pupal stage. Prepupae, however, were not held for a sufficiently long period under long-day conditions to determine whether or not diapause terminates spontaneously.

In conclusion, this study shows that C. oculata followed by C. chi, are the major inhabitants of the old-field habitat. Chrysopa oculata realises two generations per year. The impact of parasitism on the immature stages remains unknown. Whereas parasitism of adults by Ch. americanus is high, males are selectively parasitised and often survived ; as a result, there is little or no effect on the reproductive potential of the population. Mermithid parasitism of the adult population was found to be negligible. However, the embryonic mortality demonstrated in the two areas must be considered a major mortality factor; it appears to stem from chromosomal translocations involving the autosomes. The seasonal selection against the *B* allele can also be considered a mortality factor. This, however, is probably compensated for by the greater fitness of the *b* allele (it occurs in higher frequency at all times), and by the meiotic drive mechanism and segregation distortion which favor it and the *A* allele. These findings suggest, therefore, that if *C. oculata* were to be considered for biological or integrated control, the genotype colonized should therefore be one with favored genes, or genes expressing superior fitness.

Chrysopa chi is essentially univoltine and occurs mainly in spring. Its univoltinism is genetically determined. The impact of parasitism on the immature stages likewise remains unknown and the adult stage is hardly ever parasitised by *Ch. americanus*. Adults (both sexes), however, often carried in their gonads, a non-obligate intracellular bacterial organism, the identity of which and effect on the host remain unknown. Like *C. oculata*, the embryonic mortality must be considered a major mortality factor; it also appears to be due to chromosomal translocations which involve the autosomes.

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TABLE I. *Chrysopid species and abundance in two old fields in Quebec*

	Chrysopa oculata Say	*Chrysopa chi* Fitch	*Chrysopa nigricornis* Burm.	*Chrysopa* sp.	*Chrysopa carnea* (Steph.)	*Chrysopa rufilabris* Burm.	*Chrysopa lineaticornis* Fitch	*Meleoma signoretti* Fitch	*Meleoma emuncta* Fitch
1977, Ile Perrot	193	13					2		
1978, Ile Perrot	112	10							
1977, Mt. St. Hilaire	251	33		1	2	1	1	5	1
1978, Mt. St. Hilaire	177	22			1			1	
1979, Mt. St. Hilaire	249	23	1						

TABLE II. *Chrysopids collected on Ile Perrot, Quebec, in 1977*

Collection dates		*Chrysopa oculata*[1] Say		*Chrysopa chi* Fitch		*Chrysopa lineaticornis* Fitch	
		No	m:f	No	m:f	No	m:f
May	30	6	5:1				
	31	15	7:8				
June	1	20	15:5	1	0:1		
	6	16	12:4	3	1:2		
	13	26	10:16	3	1:2		
	20	8	5:3	1	0:1		
	27	13	4:9	3	0:3	1	0:1
July	4	7	3:4				
	11	11	5:6				
	18	6	4:2	1	0:1	1	0:1
	25	4	2:2				
Aug.	1	5	1:4				
	8	13	9:4	1	0:1		
	15	19	9:10				
	29	19	9:10				
Sept.	6	5	1:4				
Total		193	102:92	13	2:11	2	0:2

[1] overwintering generation (May 30- July 18), sex ratio 70:58
F_1 (July 25- Sept. 6), sex ratio 31:34.

TABLE III. Chrysopids collected on Ile Perrot, Quebec, in 1978

Collection dates	*Chrysopa oculata* Say[1] No	m:f	*Chrysopa chi* Fitch No	m:f
May 23	0		1	1:0
29	1	1:0		
June 5	0			
19	14	6:8		
26	12	10:2	1	1:0
July 3	10	4:6	4	0:4
11	7	5:2	1	0:1
17	10	2:8	3	1:2
24	10	3:7		
31	0			
Aug. 7	8	1:7		
14	12	5:7		
21	20	10:10		
30	7	4:3		
Sept. 13	1	1:0		
Total	112	52:60	10	3:7

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[1] overwintering generation (May 23 - July 24), sex ratio 31:33

F_1 (July 31 - Sept. 13), sex ratio 21:27

TABLE IV. Chrysopids collected on Mt. St. Hilaire, Quebec, in 1977.

Collection dates	*Chrysopa oculata*[1] Say		*Chrysopa chi* Fitch		*Chrysopa* sp.		*Chrysopa carnea* Steph.		*Chrysopa rufilabris* Burm.		*Chrysopa lineaticornis* Fitch		*Meleoma emuncta* (Fitch)		*Meleoma signoretti* Fitch	
	No	m:f	No	m:f	No	m:f	No	m:f	No	m:f	No	m:f	No	m:f	No	m:f
June, 10	27	12:15	8	3:5									1	1:0		
23	41	22:19	14	4:10											1	1:0
July, 1	4	3:1	3	0:3												
8	6	4:2	1	0:1												
15	8	7:1	5	0:5			1	1:0			1	1:0			1	0:1
22	0														1	1:0
29	13	12:1													1	0:1
Aug, 5	2	1:1														
12	58	35:23			1	1:0										
19	31	12:19	1	1:0					1	0:1					1	0:1
26	39	10:29	1	1:0												
Sept, 2	21	16:5					1	0:1								
9	1	0:1														
Total	251	134:117	33	9:24	1	1:0	2	1:1	1	0:1	1	1:0	1	1:0	5	2:3

[1] overwintering generation (June 10-July 22), sex ratio 48:38.
F_1 (July 29-Sept. 9), sex ratio 86:79.

TABLE V. *Chrysopids collected on Mt. St. Hilaire, Quebec, in 1978*

Collection dates		*Chrysopa oculata* Say No	m:f	*Chrysopa chi* Fitch No	m:f	*Chrysopa carnea* Steph. No	m:f	*Meleoma signoretti* Fitch No	m:f
May	26	0		5	2:3				
June	2	7	7:0	1	1:0				
	16	7	3:4	4	2:2				
	23	9	5:4	2	0:2				
	30	12	7:5	3	1:2			1	0:1
July	7	17	13:4	3	1:2				
	14	12	5:7						
	21	8	3:5	3	1:2				
	28	2	0:2			1	0:1		
Aug.	4	3	1:2						
	11	16	7:9						
	18	36	21:15	1	1:0				
	25	22	7:15						
Sept.	1	17	10:7						
	8	8	6:2						
	14	1	0:1						
Total		177	95:82	22	9:13	1	0:1	1	0:1

[1] overwintering generation (May 26 - July 21), sex ratio 43:29

F_1 (July 28 - Sept.14), sex ratio 52:53

TABLE VI. Chrysopids collected on Mt. St. Hilaire, Quebec, in 1979

Collection dates	*Chrysopa oculata* Say		*Chrysopa chi* Fitch		*Chrysopa nigricornis* Burm.	
	No	m:f	No	m:f	No	m:f
June 4	5	3:2	7	2:5		
15	7	1:6	4	4:0		
20	16	11:5	4	0:4		
29	13	10:3	3	1:2		
July 5	1	0:1	1	1:0		
12	16	11:5	2	1:1		
16	16	11:5	1	0:1		
19	8	6:2	1	0:1		
26	11	6:5				
30	16	11:5				
Aug 2	24	19:5			1	1:0
9	18	12:6				
17	33	17:16				
24	26	14:12				
30	33	22:11				
Sept 7	4	4:0				
13	2	1:1				
Total	249	159:90	23	9:14	1	1:0

[1] overwintering generation (June 4 - July 19), sex ratio 53:29

F_1 (July 26 - Sept 13), sex ratio 106:61

TABLE VII. Fertility and ovarian development in *Chrysopa oculata* Say on Ile Perrot, Quebec, in 1977

Collection dates		No	PERCENTAGE fertile females	PERCENTAGE females with mature eggs
May	30	1	0.0	0.0
	31	8	25.0	25.0
June	1	5	0.0	0.0
	6	4	0.0	0.0
	13	16	43.75	37.5
	20	3	100.0	100.0
	27	9	66.67	66.67
July	4	4	100.0	100.0
	11	6	50.0	50.0
	18	2	100.0	100.0
	25	2	100.0	50.0
Aug	1	4	75.0	75.0
	8	4	100.0	100.0
	15	10	50.0	40.0

TABLE VIII. Fertility and ovarian development in *Chrysopa oculata* Say on Mt. St. Hilaire, Quebec, in 1977

Collection date		No	PERCENTAGE fertile females	PERCENTAGE females with mature eggs
June	10	15	53.33	40.0
	23	19	66.67	66.67
July	1	1	100.0	100.0
	8	2	100.0	100.0
	15	1	100.0	100.0
	22	0		
	29	1	100.0	100.0
Aug.	5	1	100.0	100.0
	12	23	56.52	52.17

TABLE IX. Recovery of chrysopid eggs on Ile Perrot, Quebec

Collection date	No	Species	Notes
13 June 1977	2	*C. chi*	Under leaves of *Solidago*
27 June	7	*C. chi*	Under leaves of *Solidago* and Sumac (*Rhus typhina* L.)
	1	*C. oculata*	Under leaf of *Solidago*
11 July	9	*C. oculata*	On and below leaves of *Solidago*
18 July	1	*C. oculata*	Under leaf of *Solidago*
8 Aug.	1	*C. oculata*	Under leaf of *Solidago*
21 Aug. 1978	1	*C. oculata*	On grass (*Phalaris arundinacea* L.)

TABLE X. Recovery of chrysopid eggs on Mt. St. Hilaire, Quebec

Collection dates	No	Species	Notes
23 June 1977	2	*C. oculata*	On and below leaves of *Solidago* 1 *Telenomus chrysopae* Ashmead reared
8 July 1977	7	*C. oculata*	On and below leaves of *Solidago* and *Apocynum androsaemifolium* L. 5 *T. chrysopae* reared
	1	*C. chi*	On leaf of *A. androsaemifolium*
	1	*M. signoretti*	Under leaf of *Scrophularia lanceolata* Pursh.
15 July 1977	4	*C. oculata*	Under leaf of *Solidago*
30 June 1978	1	*C. oculata*	Under leaf of *Solidago*
8 Sept 1978	25	*C. oculata*	On blades of grass 4 *T. chrysopae* reared
26 July 1979	1	*C. oculata*	On leaf of *Solidago*

TABLE XI. Oviposition rhythm of field-collected *Chrysopa oculata* Say and *Chrysopa chi* Fitch under field conditions: 16-17 July 1978[1]

	OVIPOSITION INTERVALS												
	PM						AM						
	12 -2	2 -4	4 -6	6 -8	8 -10	10 -12	12 -2	2 -4	4 -6	6 -8	8 10	10 -12	24-hour ovi-position[2]
Chrysopa oculata Say													
Total no eggs (n = 13 females)	2	24	70	157	94	91	42	17	11	8	7	11	534
Mean	0.15	1.85	5.38	12.08	7.23	7.0	3.23	1.31	0.85	0.62	0.54	0.85	41.08
S.E.	0.15	0.95	1.53	3.06	1.62	1.63	0.91	0.57	0.54	0.24	0.24	0.34	4.18
Range	0-2	0-10	0-16	1-33	0-17	0-18	0-12	0-7	0-7	0-3	0-3	0-3	9-73
Chrysopa chi Fitch													
Total no eggs (n = 6 females)	15	25	17	19	24	6	7	11	2	9	8	8	151
Mean	2.5	4.17	2.83	3.17	4.0	1.0	1.17	1.83	0.33	1.5	1.33	1.33	25.17
S.E	1.31	0.79	0.48	1.14	1.13	0.52	0.48	0.79	0.21	0.72	0.42	0.33	1.90
Range	0-7	2-7	1-4	0-8	2-8	0-3	0-3	0-5	0-1	0-5	0-3	0-2	19-33
Per cent R.H.	53	50	55	62	76	85	80	73	75	72	59	51	
Temperature (°F)	77	79	79	73	72	70	69	67	64	67	73	78	
" (°C)	25.0	26.11	26.11	22.78	22.22	21.11	20.56	19.44	17.78	19.44	22.78	25.56	

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[1] sunrise 5.21 am; sunset 8.39 pm

[2] compiled from 24-hour oviposition of individual females

TABLE XII. Oviposition rhythm of field-collected *Chrysopa oculata* Say and *Chrysopa chi* Fitch under field conditions: 21-22 June 1979 [1]

OVIPOSITION INTERVALS

	PM						AM						
	12 -2	2 -4	4 -6	6 -8	8 -10	10 -12	12 -2	2 -4	4 -6	6 -8	8 -10	10 -12	24-hour oviposition[2]
Chrysopa oculata Say													
Total no eggs (n = 5 females)	6	10	24	40	51	13	1	2	0	2	14	0	163
Mean	1.2	2.0	4.8	8.0	10.2	2.6	0.2	0.4	0	0.4	2.8	0	32.6
S.E.	0.73	0.84	1.46	1.22	2.76	1.12	0.20	0.24	0	0.40	1.02	0	4.51
Range	0-3	0-4	0-8	0-12	0-19	0-5	0-1	0-1	0	0-2	0-6	0	18-46
Chrysopa chi Fitch													
Total no eggs (n = 4 females)	16	7	15	12	37	4	5	1	0	0	2	2	101
Mean	4.0	1.75	3.75	3.0	9.25	1.0	1.25	0.25	0	0	0.50	0.50	25.25
S.E.	1.0	0.63	0.95	1.47	3.42	0.58	0.95	0.25	0	0	0.50	0.28	6.01
Range	1-5	0-3	1-5	0-7	3-17	0-2	0-4	0-1	0	0	0-2	0-1	13-37
Per cent R.H.	60	72	78	50	72	85	89	92	72	52	75	59	
Temperature (°F)	73	71	67	74	69	67	64	61	66	71	69	72	
" (°C)	22.78	21.67	19.44	23.33	20.56	19.44	17.78	16.11	18.89	21.67	20.56	22.22	

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[1] sunrise 5.06 am; sunset 8.47 pm

[2] compiled from 24-hour oviposition of individual females

TABLE XIII. Recovery of chrysopid larvae on Ile Perrot, Quebec

Collection date	No	Species	Notes
8 Aug. 1977	4	*C. oculata*	Two instar III - feeding on aphids on vetch (*V. cracca*) and on *Solidago* One instar III - feeding on nectar of *Solidago* One instar III - parasitised by *Helorus anomalipes* (Pauzer) (= H. *paradoxus* (Prov.))
	1	*C. lineaticornis*	Instar III
15 Aug. 1977	13	*C. lineaticornis*	Instar III. On inflorescences of *Solidago*
6 Sept. 1977	1	*C. lineaticornis*	Instar III. On milkweed (*Asclepias syriaca* L.)
7 Aug. 1978	1	*C. oculata*	Instar III. Feeding on aphids on *Solidago*
27 July 1979	5	*C. oculata*	Instar III. On vetch (*V. cracca*) and on grass
29 Aug. 1979	2	*C. oculata*	Instar III. On vetch

TABLE XIV. Recovery of chrysopid larvae on Mt. St. Hilaire, Quebec

Collection date	No	Species	Notes
1 July 1977	2	*C. oculata*	Instar III
15 July 1977	1	*C. oculata*	Instar III - feeding on aphids on vetch (*V. cracca*)
22 July 1977	3	*C. oculata*	Instar III - feeding on aphids on *Solidago*
29 July 1977	1	*C. oculata*	Instar III on *Solidago*
5 Aug. 1977	3	*C. oculata*	Instar III - feeding on aphids on vetch
	1	*C. lineaticornis*	Instar III
18 Aug. 1978	1	*C. oculata*	Instar III
26 July 1979	3	*C. oculata*	Instar III - feeding on aphids on *Solidago*

TABLE XV. Recovery of chrysopid cocoons on Mt. St. Hilaire, Quebec

Collection date	Species	Notes
3 May 1979	*C. oculata*	Cocoon on soil surface in area of grass and *Apocynum androsaemifolium* L. Reared from cocoon: *Dichrogaster crassa* (Prov.)
"	*C. oculata*	Cocoon in same microhabitat as above
"	*C. chi*	Female reared. Cocoon on soil surface in stand of *Solidago*
"	*M. signoretti*	Male reared. Cocoon in soil at base of birch tree (*Betula papyrifera* Marsh.) in periphery of old field
11 May 1979	*M. signoretti*	Cocoon in soil at base of birch tree Reared from cocoon: *Isodromus iceryae* How.
"	*M. signoretti*	Cocoon in soil at base of birch tree
"	*M. signoretti*	Female reared. Cocoon in soil at base of birch tree.

TABLE XVI. The incidence of parasitism[1] by *Chrysopophthorus americanus* Mason, in *Chrysopa oculata* Say, on Ile Perrot, Quebec

Collection date	Sample size males	Sample size females	No parasitised and sex	Parasite stages[2] recovered	Per cent parasitism males only	Per cent parasitism total sample
13 June 1977	10	16	m	L	10.0	3.85
18 July	4	2	m f	L (ex fem.) D	25.0	33.33
3 July 1978	4	6	f	D	0.0	10.0
11	5	2	3m	2L D	60.0	42.86
7 Aug	1	7	m	D	100.0	12.5
13 July 1979	18	30	m	L	5.6	2.1
14	22	25	m	D	4.5	2.1
7 July 1980	6	0	2m	2L	33.33	
14	15	0	4m	L 3D	26.67	
16	24	0	8m	6L 2D	33.33	

[1] determined in 1977 by observation of males and dissection of females; in 1978 and 1979, by observation of males and females; in 1980, by holding males several weeks for observation

[2] L = larva other than the caudate first instar
D = evidence of prior parasitism: exit wound, penultimate larval exuvia and first instar head capsule

TABLE XVII. The incidence of parasitism[1] by *Chrysopophthorus americanus* Mason, in *Chrysopa oculata* Say, on Mt. St. Hilaire, Quebec

Collection date	Sample size males	Sample size females	No parasitised and sex	Parasite stages[2] recovered	Per cent parasitism males only	Per cent parasitism total sample
15 July 1977	7	1	m	L	14.29	12.5
29	12	1	3m	3D	25.0	23.08
30 June 1978	7	5	m	$L+L_1$*	14.29	8.33
21 July **				D**		
11 Aug	7	9	m	D	14.29	6.25
4 June 1979	3	2			0.00	0.00
15	1	6			0.00	0.00
20	11	5	m	Egg	9.09	6.25
29	10	3	3m	3L	30.0	23.08
5 July	0	1			0.00	0.00
12	11	5			0.00	0.00
16	11	5	2m	2L	18.18	12.5
19	6	2			0.00	0.00
26	6	5	m	Egg	16.67	9.09
30	11	5			0.00	0.00
2 Aug	19	5	m	D	5.26	4.17
9	12	6	m	D	8.33	5.56
17	17	16	m	L_1	5.88	3.03
24	14	12			0.00	0.00
30	22	11			0.00	0.00
7 Sept	4	0	m	L	25.0	25.0
13	1	1			0.00	0.00

[1] determined in 1977 by observation of males and dissection of females; in 1978, by observation of males; in 1979, dissection of both sexes and observation of suspects

[2] L_1 = caudate first instar larva
L = larva other than the caudate first instar
D = evidence of prior parasitism: exit wound, penultimate larval exuvia and first instar head capsule

* double parasitism

** *Chrysopa chi* Fitch (female) showing evidence of prior parasitism

TABLE XVIII. Recovery of mature larvae of *Chrysopophthorus americanus* Mason, from males of *Chrysopa oculata* Say, and their subsequent development under long-day conditions[1]

Host[2] collection date	LARVAL EMERGENCE		Adult emerged	Duration (days) cocoon stage
	date ex host	days after host capture		
2 July 80	July 80		5 Sept 80	36 +*
7 July 80	26 July 80	19	6 Sept 80	42
"	26 July 80	19		cocoon failed
14 July 80	24 July 80	10	7 Sept 80	45
16 July 80	July 80		21 Sept 80	52 +*
"	18 July 80	2	24 Sept 80	68
"	24 July 80	8		62 +**
"	26 July 80	10	12 Oct 80	88
"	31 July 80	15		cocoon failed

[1] LD 16:8, 23.0 ± 0.5°C and 60-70% R.H.

[2] from Ile Perrot except for 2 July 80 which is from Ste Anne de Bellevue

* the precise date of the larva's exit from host, in July, not known; cocoon duration based on the period August to September

** based on the period July 24 to Sept 24, at the end of which cocoon was placed in cold (5°C) 24 Sept to 13 Nov; dissected 13 Nov. and live adult found

TABLE XIX. Recovery of mature larvae of *Chrysopophthorus americanus* Mason, from males of *Chrysopa oculata* Say, and their development under laboratory and outdoor conditions

	LARVAL EMERGENCE		COCOON TREATMENTS			
				Subsequent exposure		
host collection date	date ex host	days after host capture	long days[1] experienced after spinning	days at 5°C	outdoors	Days to emergence in long-day[1]
29 June 79 *	14 July 79	15	22	144	-	14 (female)
16 July 79 *	28 July 79	12	8	168	-	(died in pupal stage)
7 Sept 79 *	15 Sept 79	8	9	112	-	(died in larval stage)
28 July 79 **	29 July 79	1	7	-	5 Aug 79 -4 Jan 80	11 (male on 15 Jan)
28 July 79 **	1 Aug 79	4	4	-	5 Aug 79 -21 Mar 80	12 (male on 2 April)

[1] LD 16:8, 20.0 ± 0.5°C, 60-70% R.H.

* from Mt. St. Hilaire

** from Ste Anne de Bellevue

TABLE XX. Incidence[1] of *Forcipomyia eques* (Johannsen) on wings of *Chrysopa oculata* Say on Mt. St. Hilaire (St. H.) and Ile Perrot (I.P.), Quebec

Collection date	Sample size		No. parasitised and sex	Parasites Per chrysopid		Per cent parasitism	
	males	females		1	2	males	females
1977 (St. H.) June 10	12	15	3m	2	1	25.0	0
23	22	19				0	0
1978 (St. H.) June 2	7	0	m	1		14.29	0
16	3	4				0	0
23	5	4				0	0
30	7	5	3m	3		42.86	0
1979 (St. H.) June 4	3	2	m	1		33.33	0
15	1	6				0	0
20	11	5	4m f	5		36.36	20.0
29	10	3	m	1		10.0	0
1978 (I.P.) July 3	4	6	m	1		25.0	0

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[1] on Mt. St. Hilaire dates beyond June are negative; no positive cases seen on Ile Perrot in 1977 and only one in 1978

TABLE XXI. Development (days) of *Chrysopa oculata* Say (from Mt. St. Hilaire, Quebec) in two types of larva-rearing cages

		Instar I	Instar II	Instar III	Prepupa	Pupa	Total
Males[1]	Mean ± S.E.	4.48 ± 0.09	3.31 ± 0.10	4.66 ± 0.11	7.24 ± 0.08	11.10 ± 0.10	30.79 ± 0.19
	N (Range)	29(4-5)	29(2-4)	29(3-6)	29(7-8)	29(10-12)	29(29-33)
Males[2]	Mean ± S.E.	5.19 ± 0.15	4.19 ± 0.12	6.08 ± 0.16	7.54 ± 0.10	11.15 ± 0.17	34.05 ± 0.17
	N (Range)	26(4-7)	26(3-5)	26(5-7)	26(7-8)	20(10-13)	20(33-35)
Difference between means		***	***	***	*	N.S.	***
Females[1]	Mean ± S.E.	4.52 ± 0.11	3.38 ± 0.11	4.86 ± 0.13	7.95 ± 0.15	11.71 ± 0.14	32.43 ± 0.25
	N (Range)	21(4-5)	21(3-4)	21(4-6)	21(7-9)	21(11-13)	21(31-35)
Females[2]	Mean ± S.E.	5.10 ± 0.12	4.10 ± 0.16	6.20 ± 0.14	8.70 ± 0.16	11.93 ± 0.13	35.93 ± 0.32
	N (Range)	20(4-6)	20(3-5)	20(5-7)	20(8-11)	14(11-13)	14(34-39)
Difference between means		***	***	***	**	N.S.	***

[1] reared in plastic vials

[2] reared in shell vials

*, **, *** significant, very significant and highly significant respectively (0.05, 0.01 and 0.001 levels; Student's t test)

TABLE XXII. Survival (l_x) in laboratory rearings[1] of *Chrysopa oculata* Say from Ile Perrot, Quebec

	Instar I	Instar II	Instar III	Prepupa	Pupa	Adult
Mean[2]	100	93.29	91.56	89.60	87.66	87.05
S.D.	0.0	7.21	8.81	9.69	10.12	10.27
Range	100.0-100.0	76.12-100.0	67.92-100.0	62.26-100.0	60.38-100.0	60.38-100.0

[1] in plastic vials

[2] based on 30 progenies
(Mean no of larvae/progeny = 64; range 32-125)

TABLE XXIII. Comparison of male and female development time (days)[1] in *Chrysopa oculata* Say, originating from Ile Perrot, Quebec

		Instar I	Instar II	Instar III	Prepupa	Pupa	Total
Males	Mean[2] ± S.E.	5.39 ± 0.11	3,58 ± 0.08	4.97 ± 0.10	6.97 ± 0.03	10.82 ± 0.11	31.74 ± 0.19
	Range	4-7	3-4	4-6	6-7	10-13	30-35
Females	Mean[2] ± S.E.	5.59 ± 0.15	3.51 ± 0.10	5.78 ± 0.12	7.89 ± 0.05	11.35 ± 0.08	34.14 ± 0.16
	Range	4-8	2-5	5-8	7-8	11-12	33-36
Difference between means		N.S.	N.S.	***	***	***	***

[1] reared in plastic vials

[2] means calculated from sample sizes of N = 38 (males) and N = 37 (females)

*** highly significant (0.001 level; Student's t test)

TABLE XXIV. Comparison of male and female development time (days)[1] in *Chrysopa oculata* Say, originating from Mt. St. Hilaire, Quebec

		Instar I	Instar II	Instar III	Prepupa	Pupa	Total
Males	Mean[2] ± S.E.	4.52 ± 0.07	3.50 ± 0.07	4.52 ± 0.08	7.05 ± 0.07	11.07 ± 0.07	30.65 ± 0.12
	Range	4-5	2-5	3-6	6-8	10-12	29-33
Females	Mean[2] ± S.E.	4.67 ± 0.07	3.54 ± 0.08	4.71 ± 0.08	7.67 ± 0.09	11.60 ± 0.09	32.19 ± 0.15
	Range	4-5	2-5	4-6	7-9	11-13	31-35
Difference between means		N.S.	N.S.	N.S.	***	***	***

[1] reared in plastic vials

[2] means calculated from sample sizes of N = 60 (males) and N = 48 (females)

***highly significant (0.001 level;Student's t test)

TABLE XXV. Comparison of male and female development time (days)[1] in *Chrysopa chi* Fitch, originating from Mt. St. Hilaire, Quebec

		Instar I	Instar II	Instar III	Prepupa	Pupa	Total
Males	Mean[2] ± S.E.	4.00 ± 0.04	3.16 ± 0.07	4.75 ± 0.11	7.31 ± 0.08	8.53 ± 0.10	27.75 ± 0.11
	Range	3-5	3-4	3-6	7-8	7-9	26-29
Females	Mean[2] ± S.E.	4.15 ± 0.10	3.15 ± 0.10	4.85 ± 0.10	7.77 ± 0.12	9.31 ± 0.13	29.23 ± 0.12
	Range	4-5	3-4	4-5	7-8	9-10	29-30
Difference between means		N.S.	N.S.	N.S.	*	***	***

[1] reared in plastic vials

[2] means calculated from sample sizes of N = 32 (males) and N = 13 (females)

*, *** significant and highly significant respectively (0.05 and 0.001 levels; Student's t test)

TABLE XXVI. Emergence (cumulative per cent of progeny) pattern in *Chrysopa oculata* Say from Ile Perrot, Quebec

		DAY NUMBER						
		I	2	3	4	5	6	7
Males	Mean[1]	5.60	15.46	26.58	34.31	41.99	47.35	50.69
	S.D.	3.99	8.41	12.92	12.37	9.32	6.62	3.25
	Range	1.64-15.79	3.28-28.95	8.57-44.74	16.67-48.65	24.07-54.05	31.48-54.05	44.44-55.56
Females	Mean[1]		1.79	7.14	17.26	26.70	35.94	42.98
	S.D.		3.08	4.88	10.45	9.49	9.58	6.06
	Range		0-7.89	1.64-13.85	2.22-33.33	14.29-41.18	25.71-51.11	34.29-51.11

[1] based on 11 progenies

TABLE XXVII. The occurrence of sperm shift in males of *Chrysopa oculata* Say

Feeding regime		AGE (DAYS POST EMERGENCE)					
		0*	1	2	3	4	5
Sucrose solution [1]	Per cent positive	0	0	66.67	93.33	93.33	84.62
	n	5	5	12	15	15	13
Sucrose solution plus live aphids [2]	Per cent positive	0	0	54.55	100.0	80.0	80.0
	n	5	11	11	12	5	10

*emergence day

[1] 10 per cent

[2] daily upon emergence

TABLE XXVIII. Ovarian development in *Chrysopa oculata* Say on a feeding regime of live pea aphids and sucrose solution[1]

	Oocytes engaged in vitellogenesis and length[2]			
Days completed on feeding regime	terminal	first subterminal	second subterminal	mature eggs in oviduct
0	-	-	-	
1	+ 2.09 - 2.78	-	-	
2	++ 2.50 - 5.84	+ 2.09 - 2.50	-	
3	++ 5.56 - 11.40	++ 2.78 - 6.26	+ 2.36 - 3.48	
4	++ 6.95 - 11.40	++ 2.50 - 5.56	++ 2.36 - 3.20	++ 10.01 - 11.40
5	++ 6.95 - 11.40	++ 2.50 - 6.67	++ 2.36 - 3.06	++ 10.01 - 11.40

[1] 10 per cent

[2] x 10^{-3} (mm)

- oocytes not engaged in vitellogenesis

\+ oocytes in early vitellogenesis - opaque to light green

++ oocytes in advanced vitellogenesis - green

TABLE XXIX. Embryonic mortality in a laboratory culture of *Chrysopa oculata* Say from Ile Perrot, Quebec

Per cent mortality	No. of crosses	Frequency
40-44	2	0.032
45-49	6	0.097
50-54	9	0.145
55-59	7	0.113
60-64	21	0.339
65-69	15	0.242
70-74	1	0.016
75-79	1	0.016

Mean (mortality) ± S.D. 59.64 ± 7.70

Range 40.8 - 78.1

n = 62 crosses over 11 generations

TABLE XXX. Embryonic mortality in a laboratory culture of *Chrysopa oculata* Say from Mt. St. Hilaire, Quebec

			PER CENT	
Cross No	Series	No eggs	fertility	embryonic mortality
	field-collected 8 Sept. 78	25	100.0	28.0
1	A (ex field-collected eggs) F_1	60	100.0	0
2	" F_1	225	95.6	44.7
3	" F_1	161	95.7	1.3
4	" F_1	312	96.5	25.6
5	B (ex Cross No 1) F_2	91	97.8	2.3
6	" F_3	74	100.0	4.1
7	" F_5		100.0	0.0
8	C (ex Cross No 2) F_2	96	99.0	40.0
9	" F_2	110	100.0	28.2
10	" F_2	96	91.7	63.6
11	" F_2	72	100.0	37.5
12	" F_2	17	88.2	20.0
13	C (ex Cross No 8) F_3	102	95.1	49.5
14	" F_3	133	99.2	52.3
15	" F_3	132	99.2	42.7
16	C (ex Cross No 13) F_4	43	86.0	64.9
	Mean (mortality in Series C) ± S.D.	44.3 ± 15.02		
	Range (n = 9)	20.0-64.9		

TABLE XXXI. Embryonic mortality in a laboratory culture of *Chrysopa chi* Fitch from Mt. St. Hilaire, Quebec

Cross No	Series	Per cent embryonic mortality
	4 wild caught females (F_0)	0.0
1	Non-diapause x Non-diapause F_1	24.5
2	" F_1	6.5
3	" F_1	13.0
4	" F_1	20.5
5	" F_1	42.3
6	" F_1	13.3
7	" F_1	0.0
8	" F_1	0.0
10	Diapause x Diapause F_1	71.4
11	" F_1	45.4
12	" F_1	82.8
13	Diapause x Non-diapause	32.1
Mean (F_1)		29.3
Range		0.0-82.8

TABLE XXXII. Observed and predicted ratios of phenotypes from matings of *Chrysopa oculata* Say originating from Ile Perrot, Quebec. Inheritance of the allelic genes B and b, determining black vs green gradate crossveins on the forewing

Cross No	Mating phenotypes	Presumed genotypes	Egg fert.	Embry. mort.	Rear success	Sex ratio m : f	Observed phenotypes and sex ratio		Predicted phenotype ratio	x^2	probability[1]
							Black gradates	Green gradates			
1	Black gradates x Black gradates	Bb x Bb	62.8	49.3	97.2	18 : 17	23 11:12	12 7:5	3:1	1.15	0.2-0.3
2	"	"	56.9	50.5	57.4	15 : 12	20 11:9	7 4:3	3:1	0.0	1.0
3	"	"	100.0	34.9	80.0	49 : 51	70 36:34	30 13:17	3:1	1.08	0.3
4	Green gradates x Black gradates	bb x Bb			93.3	41 : 43	41 26:15	43 15:28	1:1	0.01	0.9-0.95
5	"	"	86.7	50.0	96.2	14 : 11	15 8:7	10 6:4	1:1	0.64	0.3-0.5
6	Black gradates " Green gradates	Bb x bb	100.0	36.9	80.5	37 : 54	39 18:21	52 19:33	1:1	1.58	0.2-0.3

[1] acceptable at the 0.05 level and greater

TABLE XXXIII. Observed and predicted ratios of phenotypes from matings of *Chrysopa oculata* Say, originating from Mt. St. Hilaire, Quebec. Inheritance of the allelic genes *B* and *b*, determining black vs green gradate crossveins on the forewing

Cross[*] No	Mating phenotypes	Presumed genotypes	Rear. success	Sex ratio m : f	Observed phenotypes Black gradate	 Green gradate	Pred. ratio	x^2	Probability[**]
1	Green gradate x Black gradate	*bb* x *Bb*	98.3	32:27	24	35	1:1	1.69	0.1-0.2
2	"	"	66.7	12:10	11	11	1:1	0.0	1.0
3	"	"	75.0	15:15	14	16	1:1	0.03	0.7-0.9
4	Black gradate x Green gradate	*Bb* x *bb*		7:6	7	6	1:1	0.0	1.0
5	"	"		9:12	11	10	1:1	0.0	1.0
6	Black gradate x Black gradate	*Bb* x *Bb*	96.2	17:34	38	13	3:1	0.0	1.0

[*] embryonic mortality associated with these crosses is included in Table XXX, Crosses 1, 2, 5, 6, 8 and 3 respectively

[**] acceptable at 0.05 level and greater

TABLE XXXIV. Observed and predicted ratios of phenotypes from matings of *Chrysopa oculata* Say from Ile Perrot, Quebec. Inheritance of the allelic genes *B* and *b*, determining black *vs* green gradate crossveins on the forewing, and of the allelic genes *A* and *a* determining respectively, presence of the sub-antennal facial band and spots

Cross No	Mating phenotypes	Presumed genotypes	PERCENTAGE		
			Egg fertility	Embryonic mortality	Rearing success
1	Green grad. Fac. band x Green grad. Fac. band	bbAA x bbAA	100.0		100.0
2	"	"	100.0	40.8	97.8
3	"	"	80.2	42.4	83.7
4	"	bbAA x bbAa	95.5	53.0	97.1
5	"	bbAa x bbAa		47.4	60.6
6	"	"	97.6	46.8	68.2
7	Green grad. Fac. spots x Green grad. Fac. band	bbaa x bbAA	91.8	53.8	94.4
8	Black grad. Fac. spots x Black grad. Fac. spots	Bbaa x Bbaa	99.1	68.4	65.7
9	"	"	92.8	60.0	55.6
10	"	"	99.3	55.6	70.3
11	"	"	97.7	58.5	81.5
12	"	"	96.8	64.4	96.9
13	"	"	64.0	49.2	78.8
14	"	"	81.6	61.3	75.0
15	"	Bbaa x BBaa	85.6	68.4	59.2
16	"	BBaa x Bbaa	95.5	62.1	84.5
17	Black grad. Fac. band x Green grad. Fac. band	BbAa x bbAa	89.2	64.6	94.3
18	"	"	82.3	50.0	94.4
19	"	"	95.0	65.4	94.4
20	"	"	95.6	55.9	88.1
21	"	"	91.1	57.8	95.3
22	Green grad. Fac. band x Black grad. Fac. band	bbAa x BbAa	93.8	60.8	95.7
23	"	"	96.5	50.0	85.4
24	"	"	100.0	48.4	90.6
25	"	"	84.5	54.1	82.2
26	Black grad. Fac. spots x Green grad. Fac. band	Bbaa x bbAa		51.3	97.1
27	Black grad. Fac. band x Green grad. Fac. spots	BbAa x bbaa	99.4	56.1	88.2
28	Green grad. Fac. spots x Black grad. Fac. band	bbaa x BbAa			69.2
29	Black grad. Fac. band x Black grad. Fac. spots	BbAa x Bbaa	98.9	55.3	88.1
30	Black grad. Fac. band x Black grad. Fac. band	BbAa x BbAa	100.0	47.7	84.6
31	"	"	98.0	48.0	75.6

TABLE XXXIV. (cont'd) Observed and predicted ratios of phenotypes from matings of *Chrysopa oculata* Say from Ile Perrot, Quebec. Inheritance of the allelic genes B and b, determining black *vs* green gradate crossveins on the forewing, and of the allelic genes A and a determining respectively, presence of the sub-antennal facial band and spots

Cross No	Sex ratio m : f	Observed phenotypes and sex ratio Black gradates Fac. band	 Fac. spots	 Green gradates Fac. band	 Fac. spots	Predicted ratio of phenotypes	x^2	Prob. (p)[1]
1	56 : 65	x	x	121	x	100 per cent		
2	55 : 33	x	x	88	x	100 per cent		
3	23 : 18	x	x	41	x	100 per cent		
4	38 : 29	x	x	67	x	100 per cent		
5	25 : 32	x	x	43	14	3:1	0.0	1.0
				18:25	7:7			
6	20 : 24	x	x	31	13	3:1	0.273	0.5-0.7
				14:17	6:7			
7	16 : 18	x	x	34	x	100 per cent		
8	20 : 24	x	33	x	11	3:1	0.0	1.0
9	7 : 13	x	16	x	4	3:1	0.067	0.7-0.9
10	25 : 20	x	40	x	5	3:1	3.9	<0.05
11	22 : 22	x	36	x	8	3:1	0.757	0.3-0.5
12	16 : 15	x	24	x	7	3:1	0.011	0.9-0.95
13	12 : 14	x	16	x	10	3:1	1.846	0.1-0.2
14	3 : 6	x	6	x	3	3:1	0.0	1.0
15	14 : 15	x	29	x	x	100 per cent		
16	15 : 12	x	27	x	x	100 per cent		
17	19 : 14	9	7	17	0	3:1:3:1	8.77	<0.05
18	31 : 37	12	12	44	0	3:1:3:1	30.5	<0.001
19	27 : 41	15	15	38	0	3:1:3:1	23.9	<0.001
20	36 : 22	16	15	27	0	3:1:3:1	18.3	<0.001
21	18 : 20	10	8	20	0	3:1:3:1	10.6	<0.05
22	22 : 23	9	10	26	0	3:1:3:1	17.6	<0.001
23	15 : 20	10	7	18	0	3:1:3:1	8.5	<0.05
24	20 : 9	6	11	12	0	3:1:3:1	20.5	<0.001
25	20 : 17	8	7	22	0	3:1:3:1	13.1	<0.001
26	18 : 16	6	9	5	14	1:1:1:1	5.765	0.1-0.2
		1:5	4:5	3:2	10:4			
27	32 : 28	3	27	30	0	1:1:1:1	49.2	<0.001
28	11 : 7	0	9	9	0	1:1:1:1	18.0	<0.001
29	18 : 19	11	16	10	0	3:3:1:1	11.79	<0.01
30	33 : 30	33	10	20	0	9:3:3:1	10.04	<0.05
31	30 : 28	32	12	14	0	9:3:3;1	4.65	0.1

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[1] acceptable at the 0.05 level and greater

TABLE XXXV. Observed and predicted ratios of phenotypes from matings of *Chrysopa oculata* Say from Ile Perrot, Quebec: segregation distortion

Cross No from Table XXXIV	Presumed mating genotypes	Observed progeny phenotypes				Normally expected phenotype ratio	New predicted phenotype ratio[1]
		Black gradate facial band	Black gradate facial spots	Green gradate facial band	Green gradate facial spots		
17	BbAa x bbAa	9	7	17	0	3:1:3:1	3:1:2
18	idem	12	12	44	0	idem	idem
19	"	15	15	38	0	"	"
20	"	16	15	27	0	"	"
21	"	10	8	20	0	"	"
22	bbAa x BbAa	9	10	26	0	"	"
23	idem	10	7	18	0	"	"
24	"	6	11	12	0	"	"
25	"	8	7	22	0	"	"
27	BbAa x bbaa	3	27	30	0	1:1:1:1	1:1:1
28	bbaa x BbAa	0	9	9	0	idem	idem
29	BbAa x Bbaa	11	16	10	0	3:3:1:1	3:2:1
30	BbAa x BbAa	33	10	20	0	9:3:3:1	7:1:1
31	idem	32	12	14	0	idem	idem

[1] based on three classes of gametes from the double heterozygote after selective elimination of the ba

TABLE XXXVI. Observed and predicted ratios of phenotypes from matings of *Chrysopa oculata* Say, originating from Ile Perrot, Quebec. Inheritance of the post-antennal spot in the green gradate phenotype (*bb*)

Cross No	Mating phenotypes and presumed genotypes	PERCENTAGE			Sex ratio	Observed phenotypes and sex ratio		Predicted ratio of phenotypes	x^2	Probability*
		Egg fert.	Embry. mort.	Rearing success	m : f	spot present	spot absent			
1	Spot absent x spot present (- -) (+ -)	91.8	53.8	94.4	20 : 23	21 12:9	22 8:14	1:1	0	1.0
2	Spot present x spot present (+ -) (+ -) (from Cross No 1)	84.0	51.4	66.7	6 : 6	6 3:3	6 3:3	3:1	2.78	0.1
3	Spot absent x spot absent (- -) (- -) (from Cross No 1)	25.1	56.0	81.8	8 : 10	X	18	100 per cent		
4	Spot present x spot absent (+ -) (- -) (from Cross No 2)	97.6	46.8	68.2	20 : 24	24 8:16	20 12:8	1:1	0.2	0.5 - 0.7

* acceptable at 0.05 level and greater

TABLE XXXVII. Frequency of characters not usually associated with the green-gradate and black-gradate phenotypes of *Chrysopa oculata* Say

Phenotype	Character	Number observed and frequency within phenotypes Ile Perrot, 1977		Mt. St. Hilaire, 1977	
Green gradate	Post-antennal spot absent	36	0.3130	17	0.2099
	Two pairs post-antennal spots (as in black-gradate phenotype)	1	0.0087		
	Black on basicardo of maxilla (as in black-gradate phenotype)			5	0.0617
Black gradate	The immediate post-antennal spot absent	6	0.0769	17	0.1006
	"*Illepida* condition" - the post-antennal spots fuse to form lines	9	0.1154	6	0.0355
	Black absent on basicardo of maxilla (as in green-gradate phenotype)	3	0.0385	10	0.0592

TABLE XXXVIII. Frequency of the allelic genes *B* and *b*, determining black vs green gradate crossveins in *Chrysopa oculata* Say, on Ile Perrot, Quebec

Population			Green gradates (*bb*)	Black gradates (*BB*, *Bb*)	p (*b*)	q (*B*)
1977	Overwintering generation	No. collected	87	41		
	(May 30-July 18)	Frequency	0.67969	0.32031	0.82443	0.17557
	F_1	No. collected	28	37		
	(July 25-Sept 6)	Frequency	0.43077	0.56923	0.65633	0.34367
1978	Overwintering generation	No. collected	44	20		
	(May 29-July 24)	Frequency	0.68750	0.31250	0.82916	0.17084

TABLE XXXIX. Frequency of the allelic genes *B* and *b*, determining black vs green gradate crossveins in *Chrysopa oculata* Say, on Mt. St. Hilaire, Quebec

Population			Green gradates (*bb*)	Black gradates (*BB*, *Bb*)	p (*b*)	q (*B*)
1977	Overwintering generation	No. collected	33	53		
	(June 10-July 15)	Frequency	0.38372	0.61628	0.61945	0.38055
	F_1	No. collected	48	116		
	(July 29-Sept.2)	Frequency	0.29268	0.70732	0.54100	0.4590
1978	Overwintering generation	No. collected	40	29		
	(June 2-July 21)	Frequency	0.57971	0.42029	0.76139	0.23861
1979	Overwintering generation	No. collected	42	40		
	(June 4-July 19)	Frequency	0.51220	0.48780	0.71568	0.28432
	F_1	No. collected	56	111		
	(July 26-Sept. 13)	Frequency	0.33533	0.66467	0.57908	0.42092

TABLE XL. Frequency of the allelic genes *A* and *a*, determining respectively, presence of the sub-antennal facial band and spots, in *Chrysopa oculata* Say, on Mt. St. Hilaire, Quebec

Population			Facial spots (*aa*)	Facial band (*AA,Aa*)	p (*a*)	q (*A*)
1977	Overwintering generation	No. collected	1	85		
	(June 10-July 15)	Frequency	0.01163	0.98837	0.10783	0.89217
1978	Overwintering generation	No. collected	1	68		
	(June 2-July 21)	Frequency	0.01449	0.98551	0.12039	0.87961
1979	F_1	No. collected	1	166		
	(July 26-Sept.13)	Frequency	0.00599	0.99401	0.07738	0.92262
	MEAN	FREQUENCY			0.10187	0.89813

TABLE XLI. Observed progeny phenotypes[1] from matings[2] of Chrysopa chi Fitch from Mt. St. Hilaire, Quebec. Inheritance of obligatory diapause[3]

Cross No	F	Mating phenotypes	PERCENTAGE			OBSERVED PROGENY PHENOTYPES		Expected progeny ratio	x^2*	p
			Egg fertility	Embryonic mortality	Rearing success	Non-diapause	Diapause			
	F_o	(4 field-collected females)	100.0	0.0	100.0	45 (32:13)	26			
1	F_1	Non-diapause x Non-diapause	86.0	24.5	70.3	20 (13:7)	6	3:1	0.0	0.95-1.0
2	F_1	idem	100.0	6.5	92.9	34 (20:14)	5	3:1	2.47	0.1 -0.2
3	F_1	"	88.5	13.0	95.5	48 (27:21)	16	3:1	0.0	0.95-1.0
4	F_1	"	92.9	20.5	53.3	14 (9:5)	2	3:1	0.75	0.3 -0.5
5	F_1	"	100.0	42.3	72.7	5 (2:3)	3	3:1	0.17	0.5 -0.7
6	F_1	"	85.7	13.3	80.8	19 (13:6)	2	3:1	2.92	0.05-0.1
7	F_1	"	100.0	0.0	86.7	25 (13:12)	1	3:1	5.13	0.01-0.05 N.S.
8	F_1	"	97.2	0.0	82.9	29 (12:17)	0			
9	F_2	Non-diapause x Non-diapause (from Cross 3)				4	3	9:7	0.0	1.0
10	F_1	Diapause x Diapause	92.1	71.4	50.0	1 (1:0)	4	1:3	0.0	0.95-1.0
11	F_1	idem	98.0	45.4	37.7	8	12	1:3 1:1	1.67 0.45	0.1 -0.2 0.5
12	F_1	"	97.1	82.8	48.6	1 (1:0)	16	1:3	2.37	0.1 - 0.2
13		Diapause x Non-diapause (F_o) (ex Cross 9)	86.9	32.1	63.9	16 (8:8)	7	3:1	0.13	0.7-0.9

[1] sex ratio in parenthesis

[2] progeny rearings conducted under LD 16:8, 23.0 ± 0.5^{o}C and 60-70% R.H.

[3] expressed in the prepupal stage

[*] includes Yate's correction factor

TABLE XLII. Termination of obligatory diapause in *Chrysopa chi* Fitch: regression analysis

Weeks at 5^{o}C	Days to pupation	Duration(days) of pupal stage	Total days to emergence	Per cent emergence
16	19	13	32	12.5
18	20 20 15 m' 16	11 11 9 m' 10	31 31 24 m' 26	36.36
20	12 m' 15 15 23	9 m' 11 12 11	21 m' 26 27 34	80.0
21	8 m' 7 m' 9 8 11 8 9	10 m' 11 m' 10 10 12 11 10	18 m' 18 m' 19 18 23 19 19	87.5
26	7 m' 7 m' 8 8 8 9 8 8	9 m' 9 m' 9 9 10 9 10 10	16 m' 16 m' 17 17 18 18 18 18 18	100.0
Slope (m)	-1.11252	-0.20303	-1.28978	8.82937
Intercept (b)	35.82697	14.67445	50.00360	-115.08120
n	24	24	25	5
Corr. coeff. (r)	-0.73813	-0.60128	-0.77289	0.89582
r^2	0.54484	0.36154	0.59736	0.80249
t^t	-5.13163	-3.52960	-5.84143	3.49130
significance	***	**	***	*
For x = 16, y =	18.02665	11.42597	29.36712	26.18872
For x = 21, y =	12.46405	10.41082	22.91822	70.33557

m'= male specimen; when not so indicated the data pertain to females

* significant (p = 0.974)

** very significant (p = 0.998)

*** highly significant (p = 0.999)

TABLE XLIII. Termination[1, 2] of obligatory diapause in *Chrysopa chi* Fitch: summarised data

		EMERGENCE		DEVELOPMENT[3]		
Weeks at 5°C	No treated	No	Per cent	Days to pupation	Duration (days) of pupal stage	Total days to emergence
16	8	1	12.5	19.0	13.0	32.0
18	11	4	36.36	17.75 ± 2.63 (15-20)	10.25 ± 0.96 (9-11)	28.0 ± 3.56 (24-31)
20	5	4	80.00	16.25 ± 4.72 (12-23)	10.75 ± 1.26 (9-12)	27.0 ± 5.35 (21-34)
21	8	7	87.5	8.57 ± 1.27 (7-11)	10.57 ± 0.79 (10-12)	19.14 ± 1.77 (18-23)
26	9	9	100.0	7.88 ± 0.64 (7-9)	9.38 ± 0.52 (9-10)	17.33 ± 0.87 (16-18)

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[1] LD 16:8; 23.0 ± 0.5°C and 60-70% R.H. subsequent to cold treatment.

[2] Pupation is taken as an indicator of diapause termination and is recognised by the appearance of a black area (moulted skin) at one pole of the cocoon

[3] Mean ± S.D., Range in parenthesis

Fig. 1 Population dynamics of _Chrysopa_ _oculata_ Say and _Chrysopa_ _chi_ Fitch on Ile Perrot, Quebec: 1977 and 1978

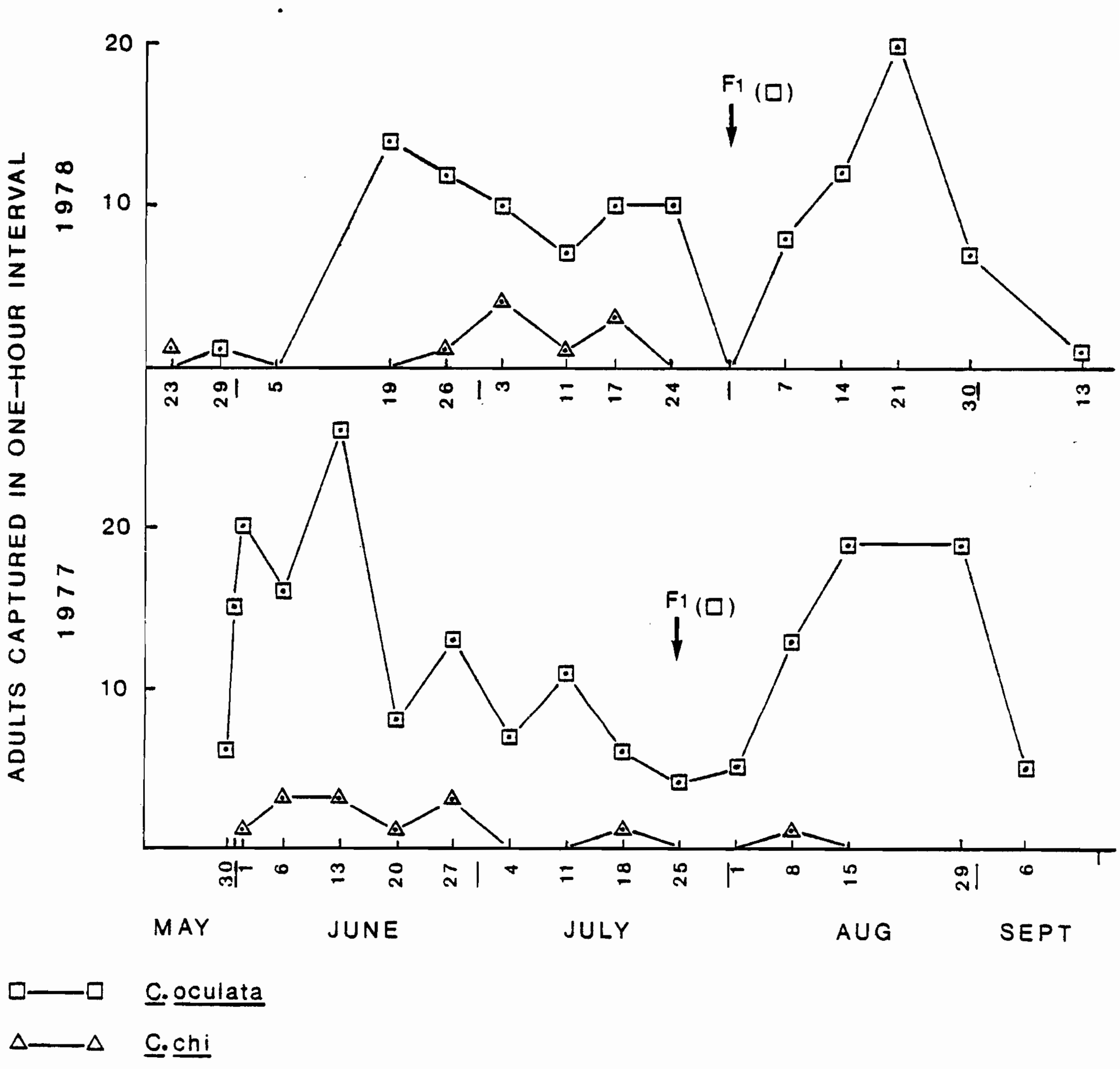

Fig. 2 Population dynamics of <u>Chrysopa oculata</u> Say and <u>Chrysopa chi</u> Fitch on Mt. St. Hilaire, Quebec: 1977

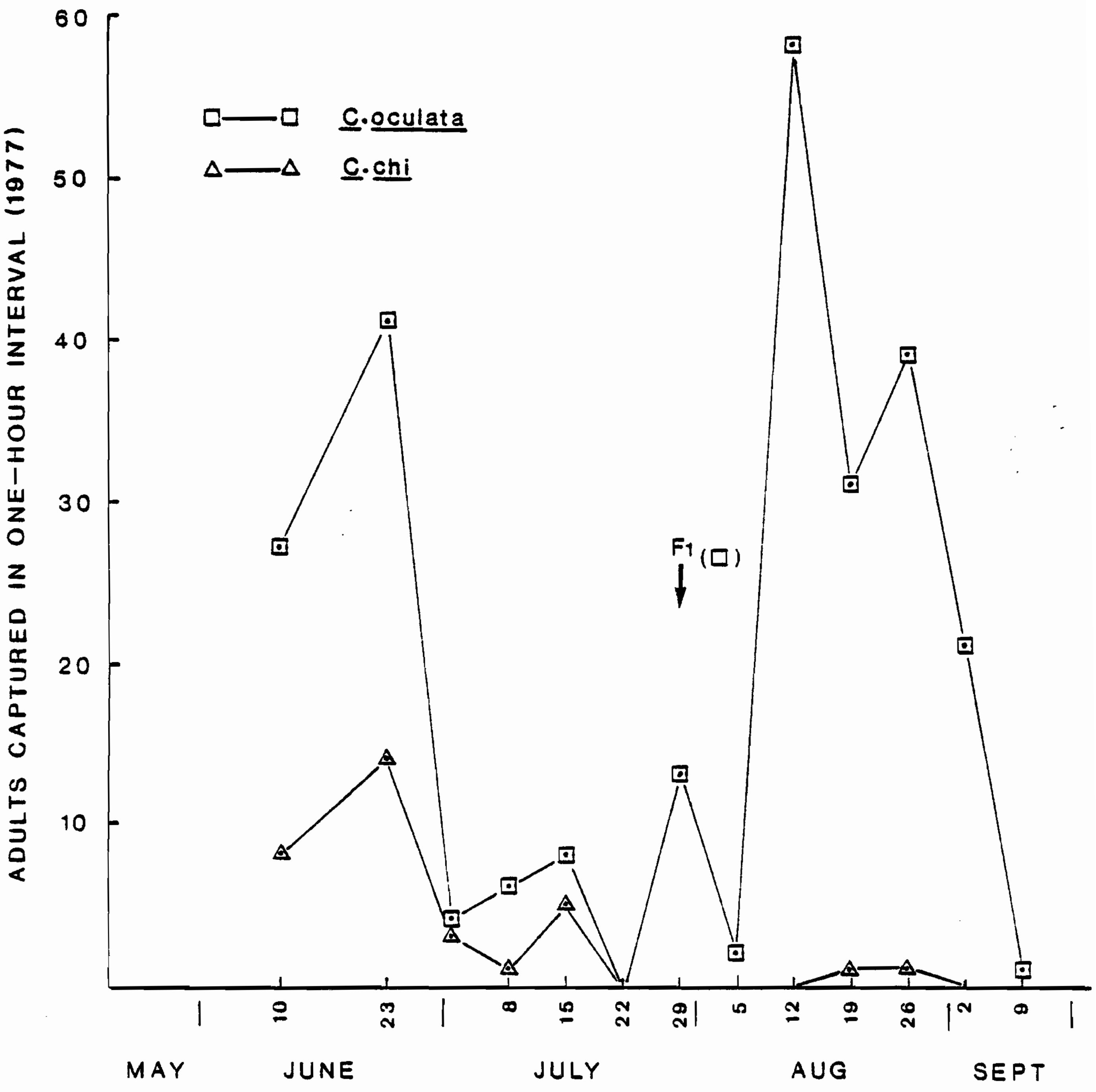

Fig. 3 Population dynamics of <u>Chrysopa</u> <u>oculata</u> Say and <u>Chrysopa</u> <u>chi</u> Fitch on Mt. St. Hilaire, Quebec: 1978 and 1979

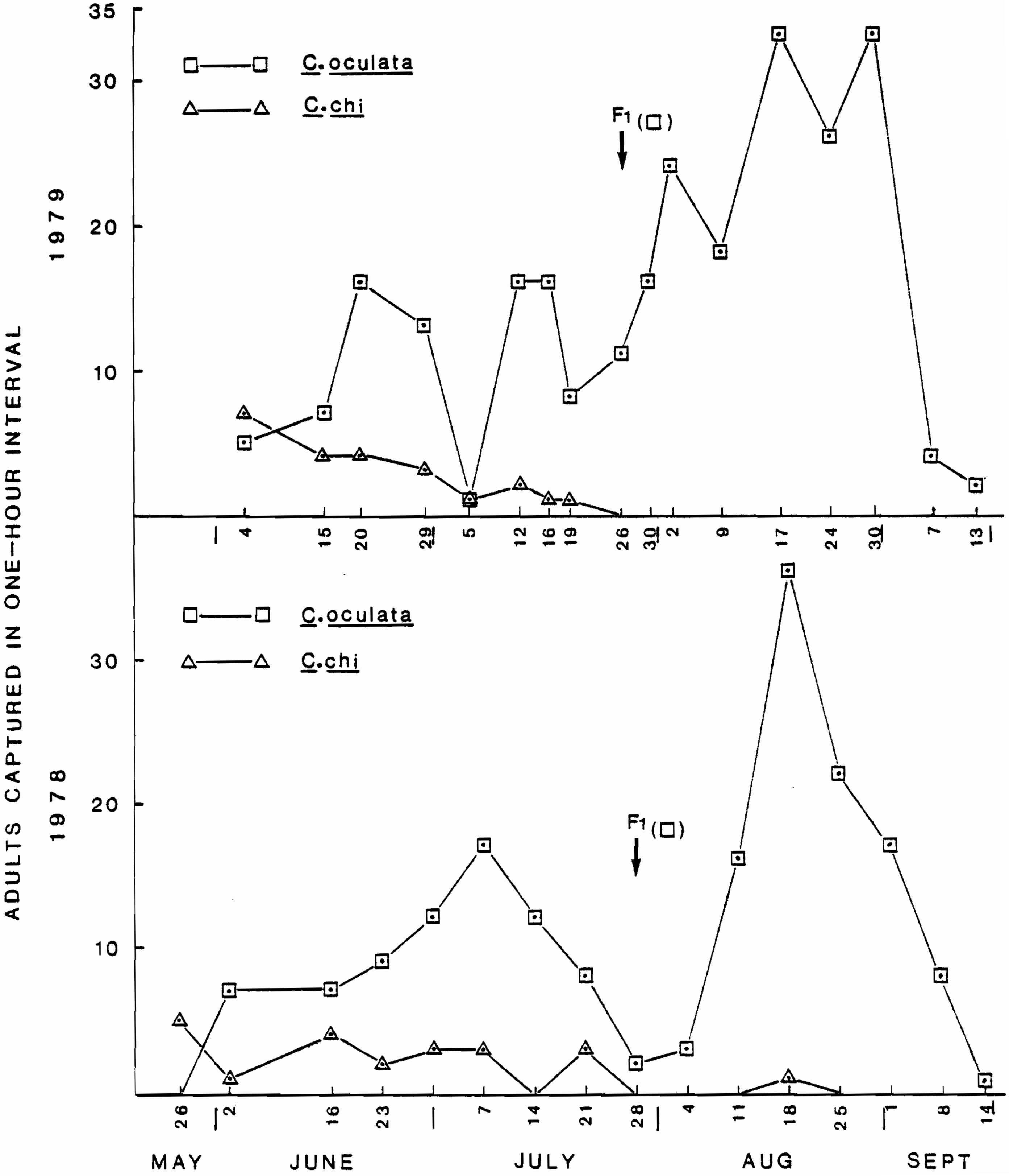

Fig. 4 Oviposition rhythm of field-collected *Chrysopa oculata* Say and *Chrysopa chi* Fitch under field conditions: 16-17 July 1978

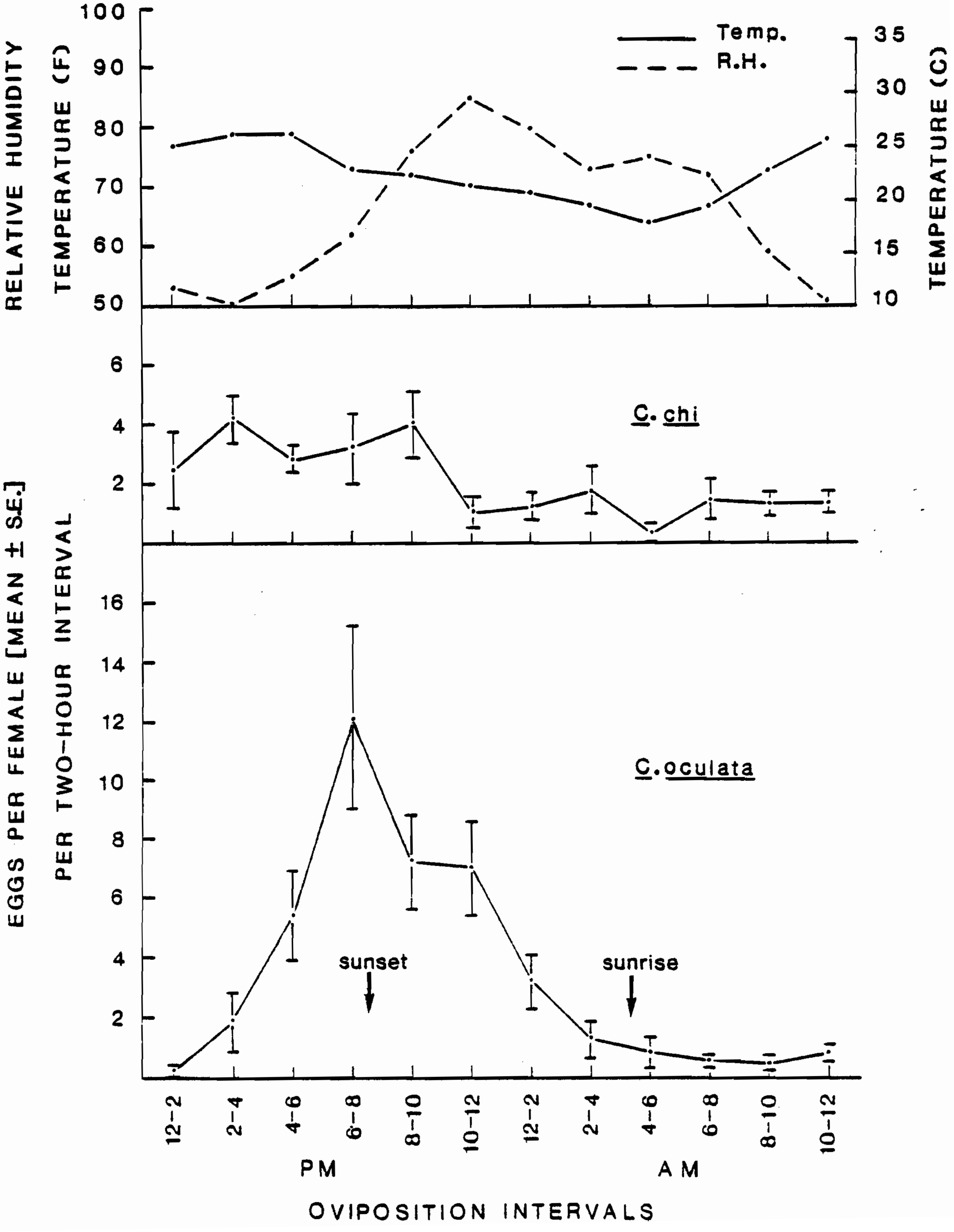

Fig. 5 Oviposition rhythm of field-collected *Chrysopa oculata* Say and *Chrysopa chi* Fitch under field conditions: 21-22 June 1979

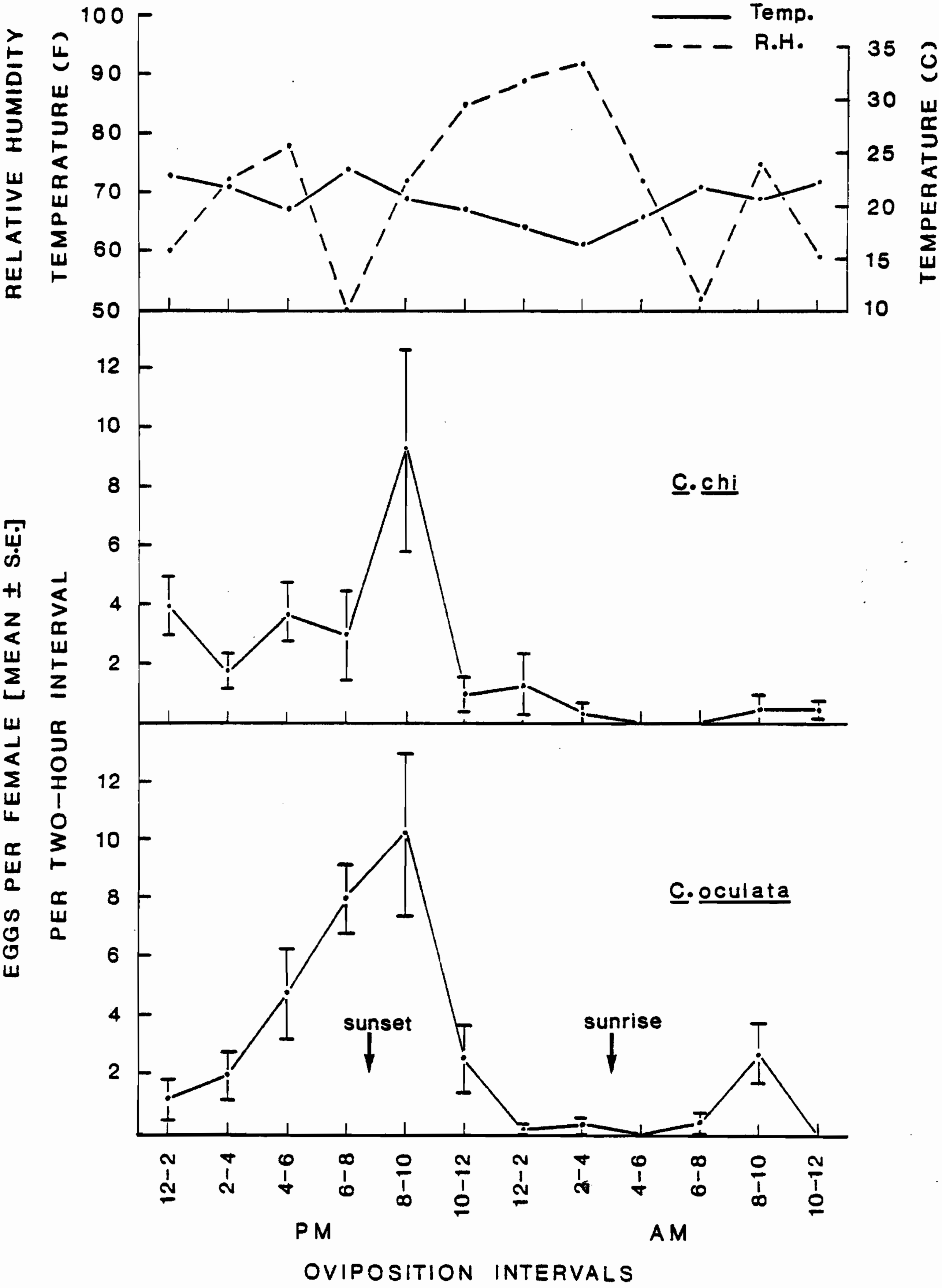

Fig. 6 Survival (lx) in Laboratory rearings of *Chrysopa oculata* Say from Ile Perrot, Quebec

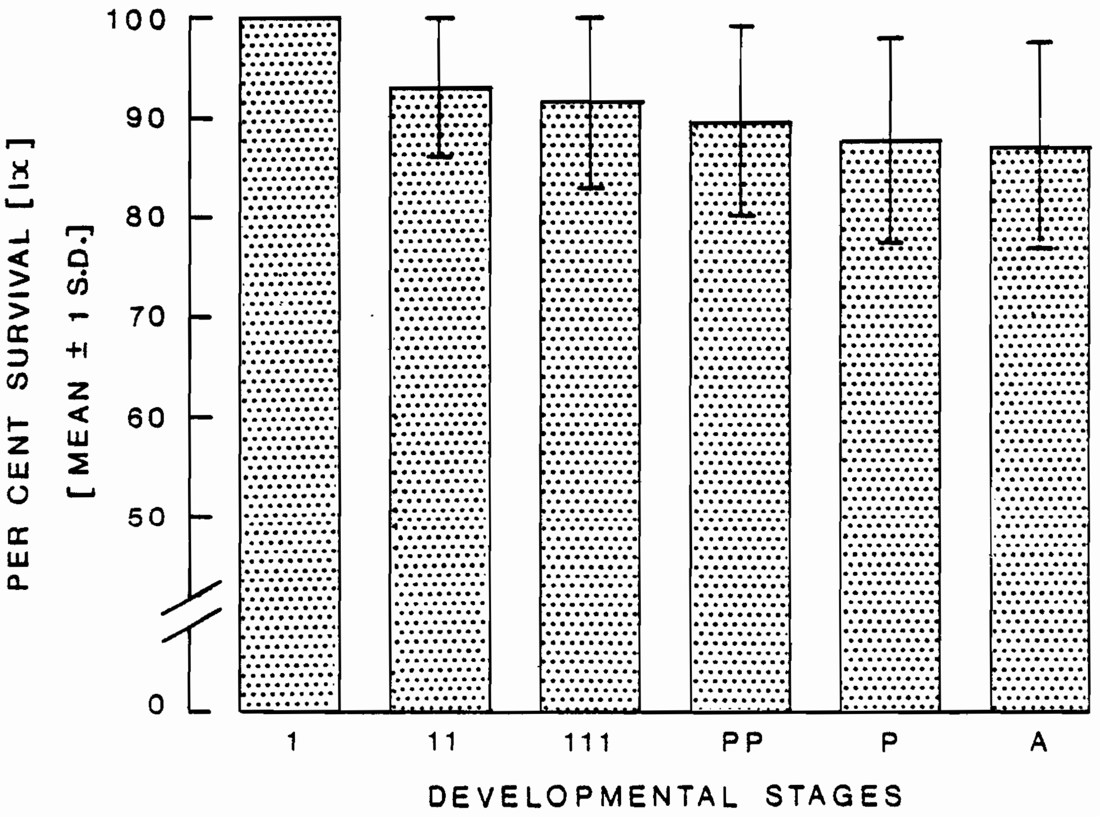

Fig . 7 Emergence pattern in laboratory rearings of <u>Chrysopa</u> <u>oculata</u> Say from Ile Perrot, Quebec

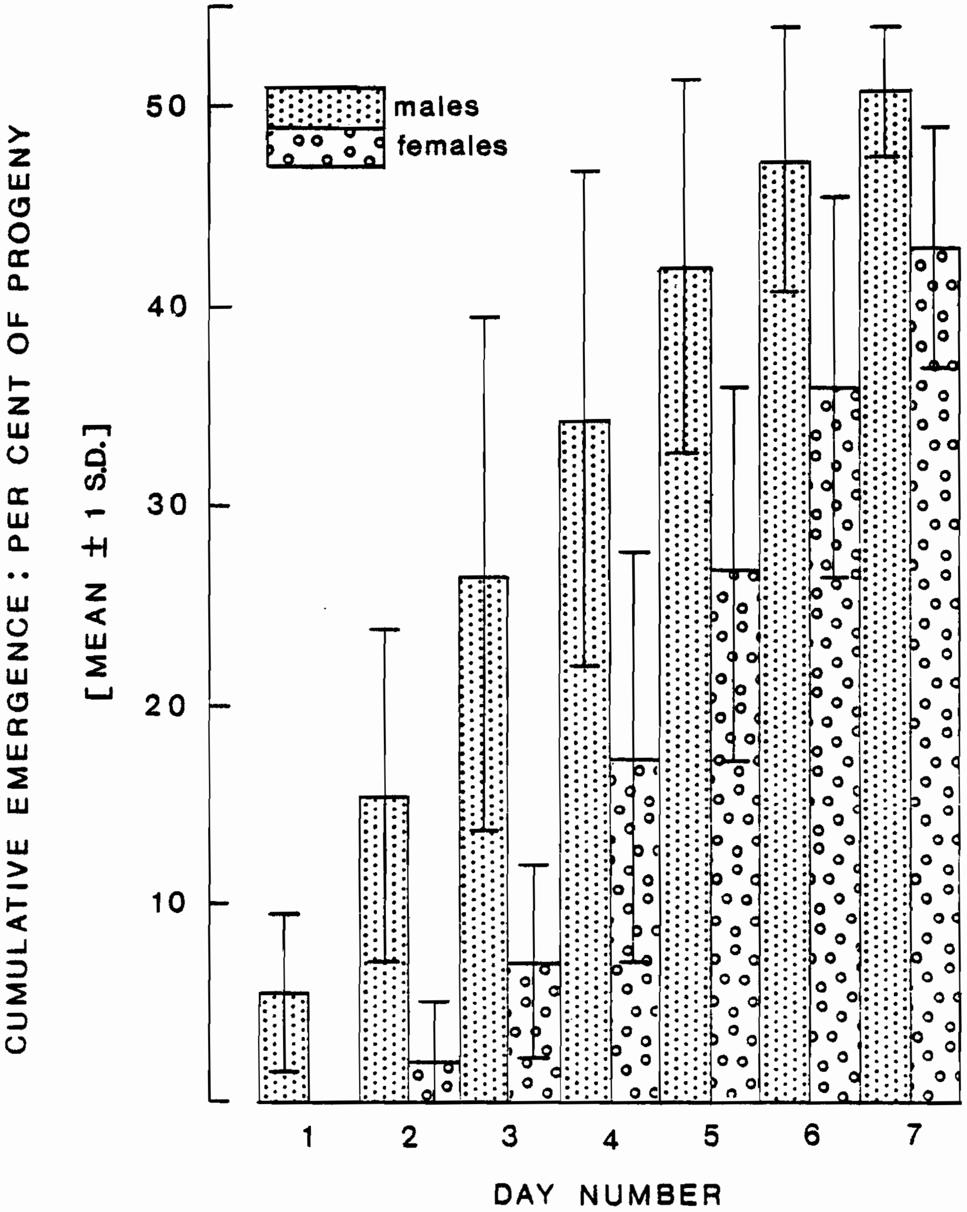

Fig. 8 Frequency distribution of embryonic mortality in a laboratory culture of _Chrysopa_ _oculata_ Say from Ile Perrot, Quebec

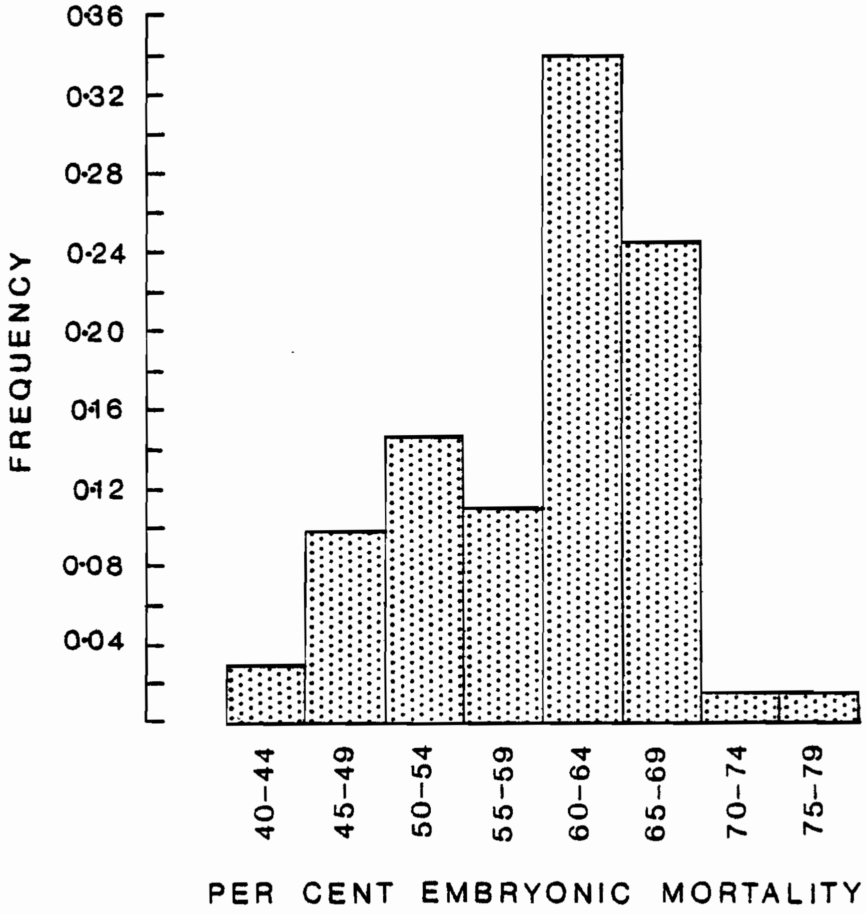

FIG. 9. FOREWING OF <u>CHRYSOPA</u> <u>OCULATA</u> SAY

[x12]

[Terminology after Adams <u>Bull. Mus. comp. Zool. Harv.</u> 135(4): 215-238 (1967).]

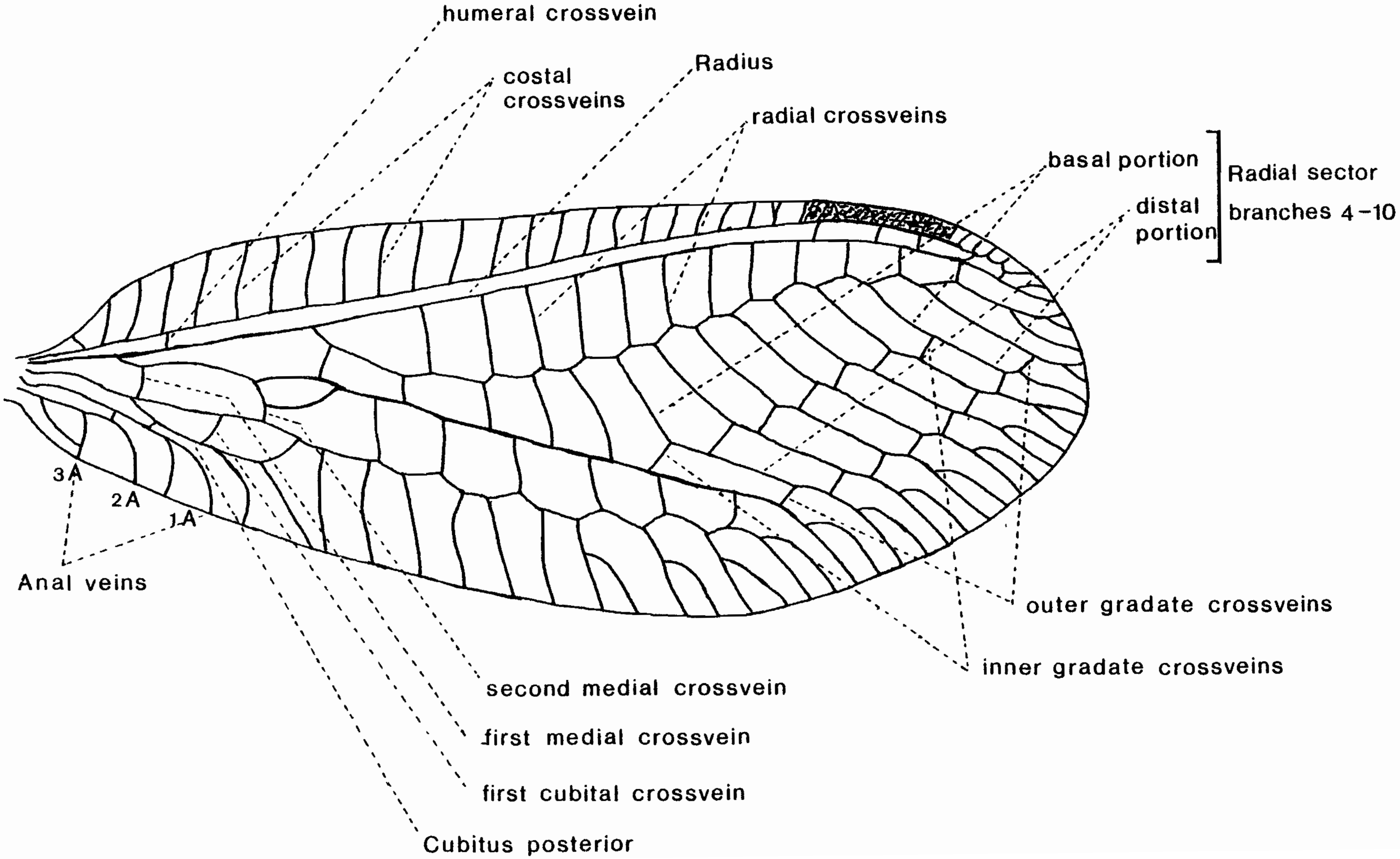

Fig. 10 Phenotypes of *Chrysopa oculata* Say

a (X 25) Head of the green-gradate, facial-band phenotype (*bbAA*). Arrows indicate facial band and the single pair of post-antennal spots usually associated with green gradates.

b (X 50) Maxilla (ventral view) showing black-pigmented basicardo (arrow) in the black-gradate (*BB* and *Bb*) phenotype.

c (X 25) Head of the black-gradate (*BB* and *Bb*) phenotype (also homozygous dominant, *AA*, for facial band), showing the two pairs of post-antennal spots (arrows) usually associated with black gradates.

d (X 25) Head of the black-gradate, facial spots phenotype (*BBaa* and *Bbaa*), showing reduction of the facial band to an inter-antennal and a pair of sub-antennal spots.

e (X 25) Expression of the facial band (arrow) in facial band heterozygotes (*Aa*).

f (X 25) Expression of facial spots (*aa*) in the green-gradate (*bb*) phenotype.

Fig. 10 Phenotypes of *Chrysopa oculata* Say

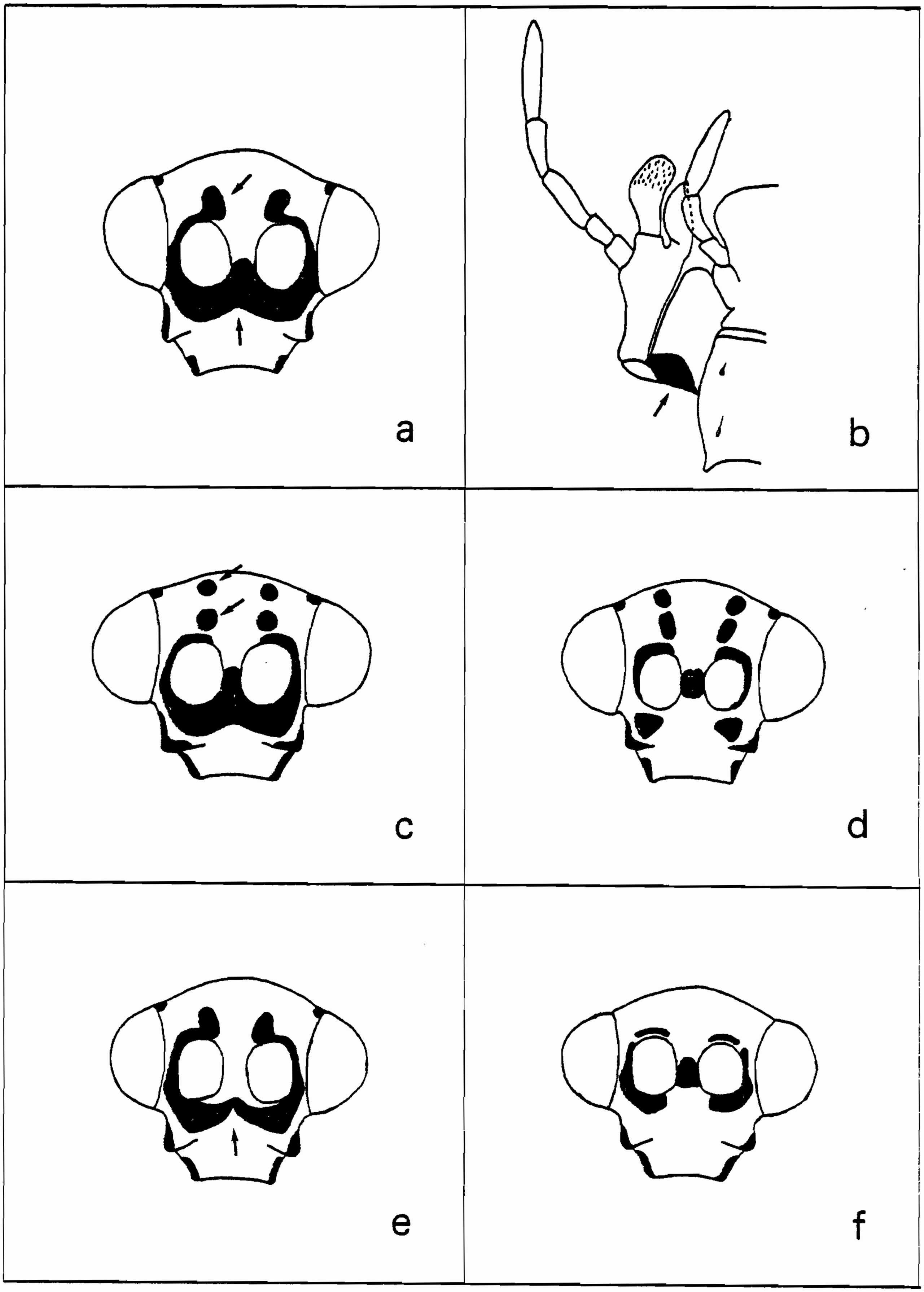

Fig. 11 Seasonal change in frequency of the allelic genes B and b, determining black *vs* green gradate crossveins in *Chrysopa oculata* Say, on Ile Perrot and Mt. St. Hilaire, Quebec

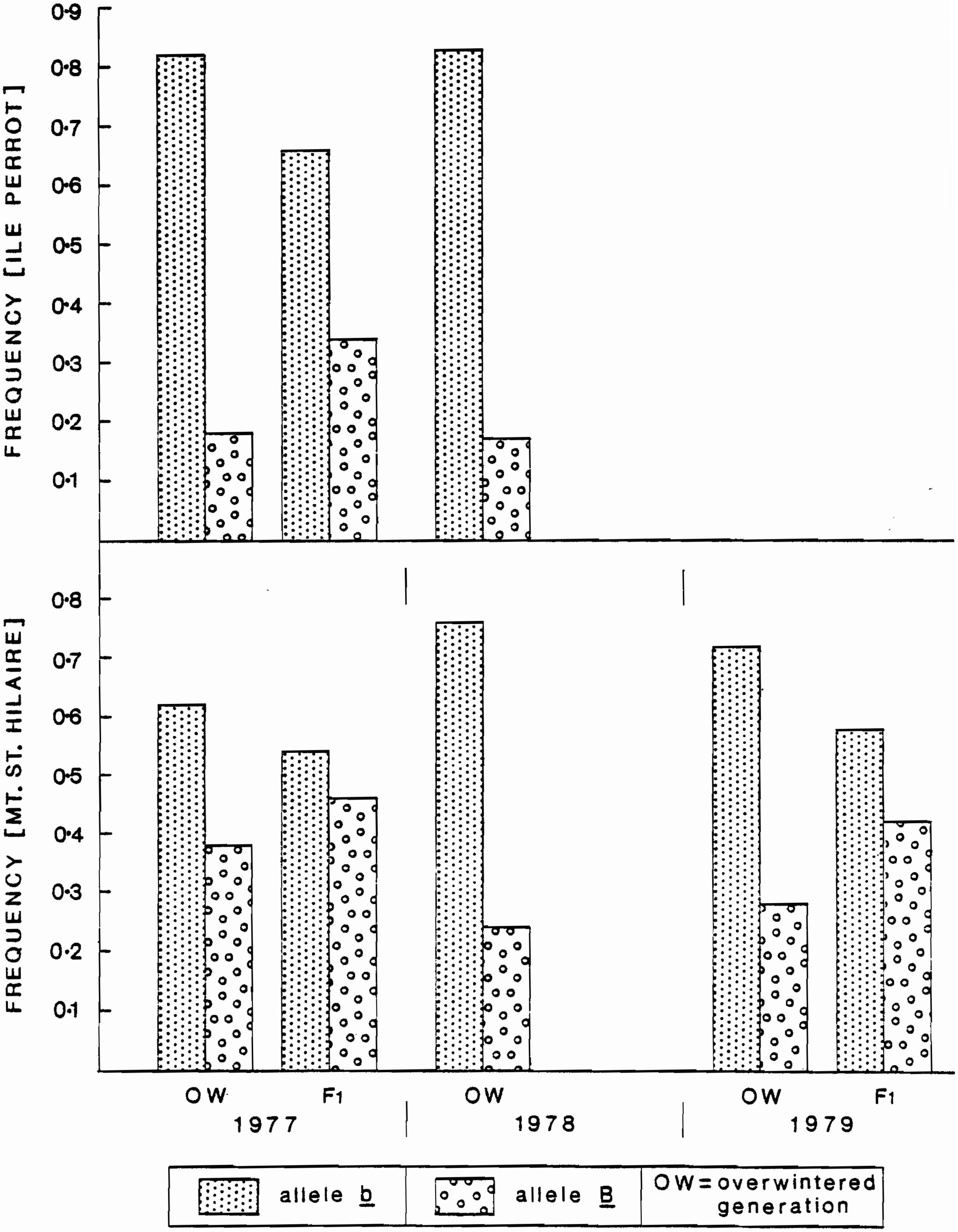

Fig. 12 Termination of obligatory diapause in prepupae of *Chrysopa chi* Fitch. The effect of cold exposure on emergence (Fig. 12.1), days to pupation, duration of pupal stage and overall development time (Fig. 12.2)

FIG 12·1

FIG 12·2

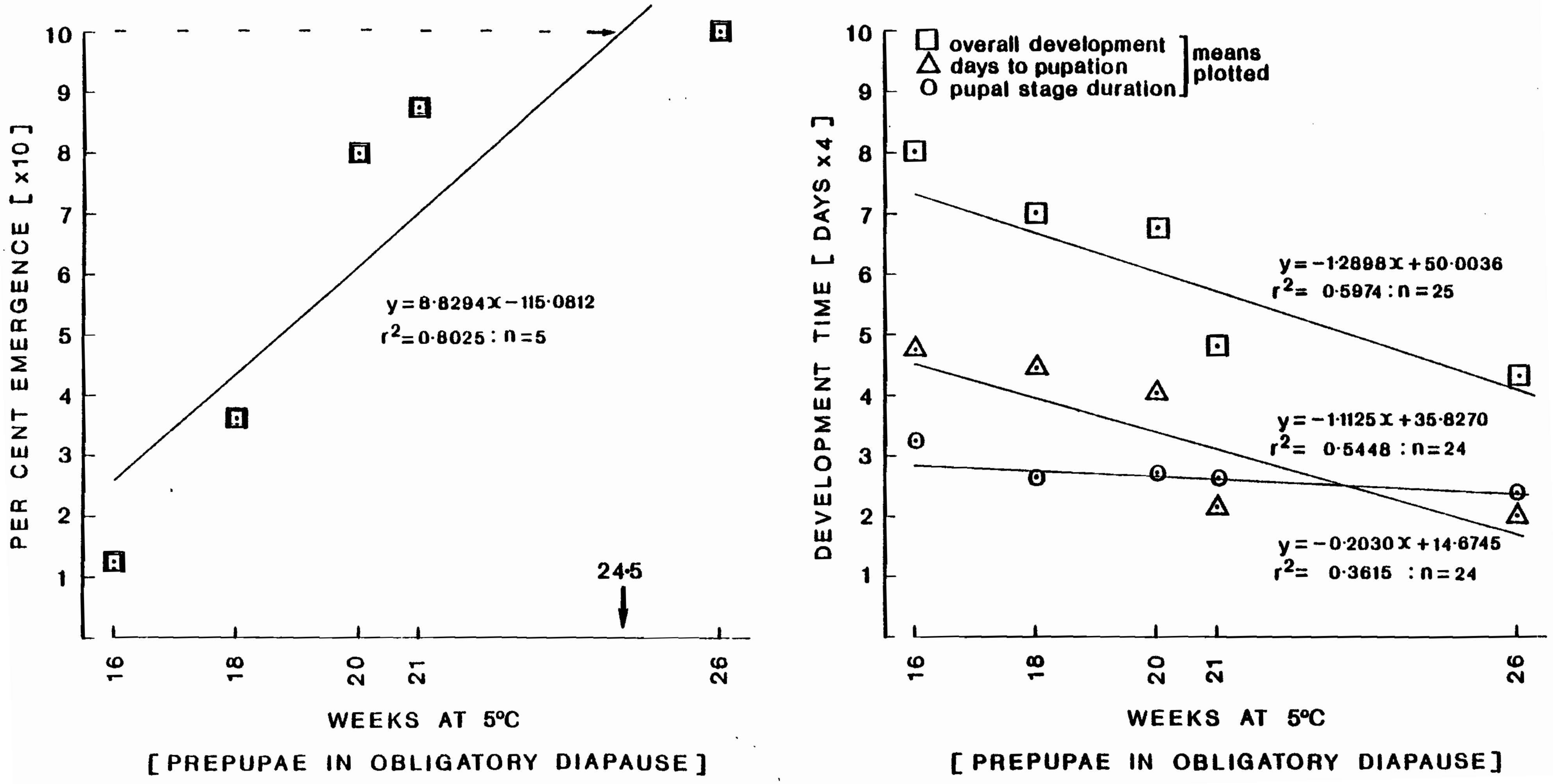

Plate 1 *Chrysopophthorus americanus* Mason, a parasite of adults of *Chrysopa oculata* Say: host pathology and parasite developmental stages.

a *C. oculata* host (male) showing exit wound made by parasite.

b Trophamnion cells (X 200).

c Head capsule of first instar larva of *Ch. americanus* (X 400).

d Egg of *Ch. americanus* (X 60).

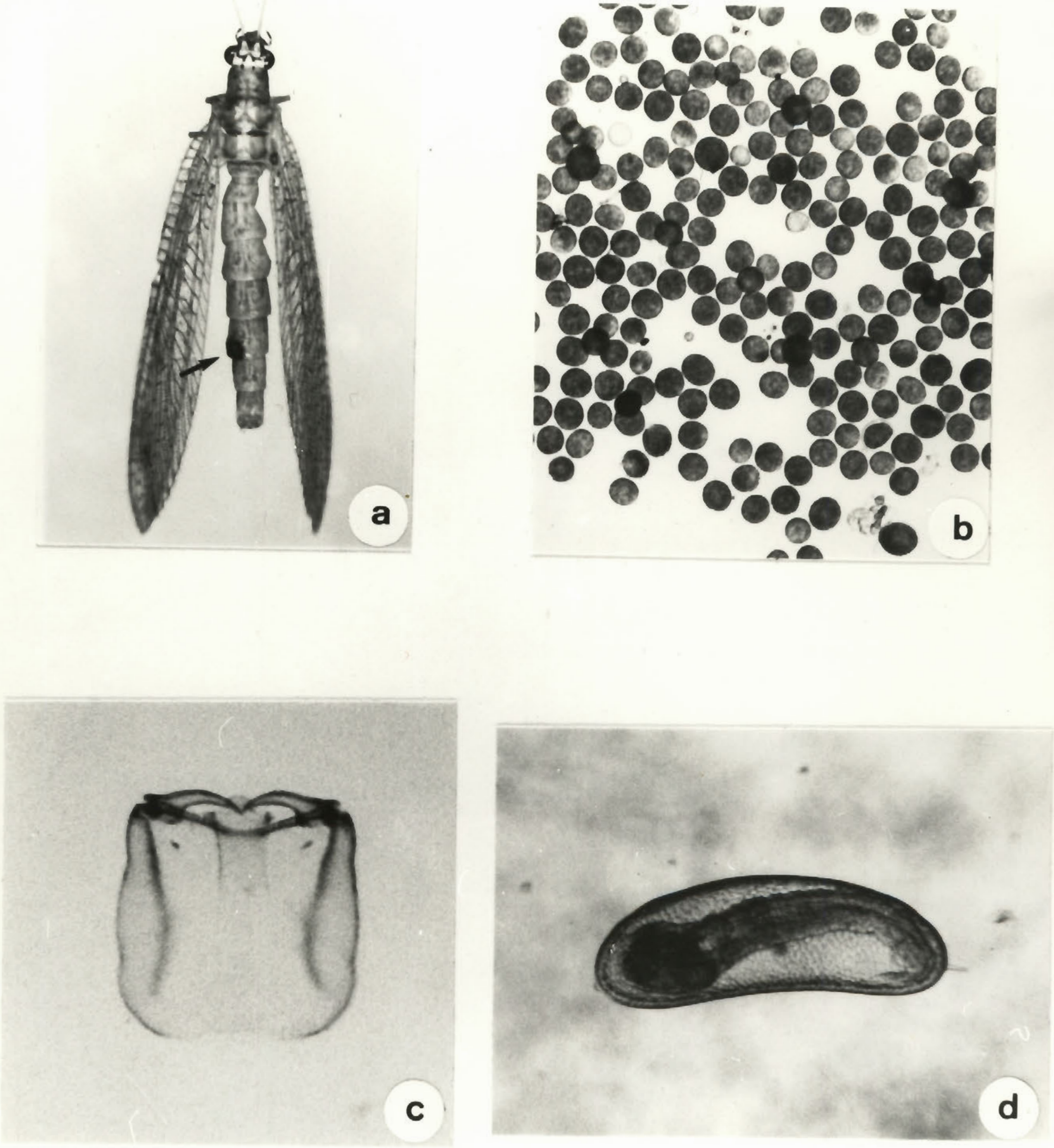

PLATE I

Plate 2 *Chrysopophthorus americanus* Mason, a parasite of *Chrysopa oculata* Say: developmental stages.

a First instar larva - dorsal view (X 200).

b First instar larva - ventral view (X 200).

c Penultimate larva.

d Cocoon.

e Adult.

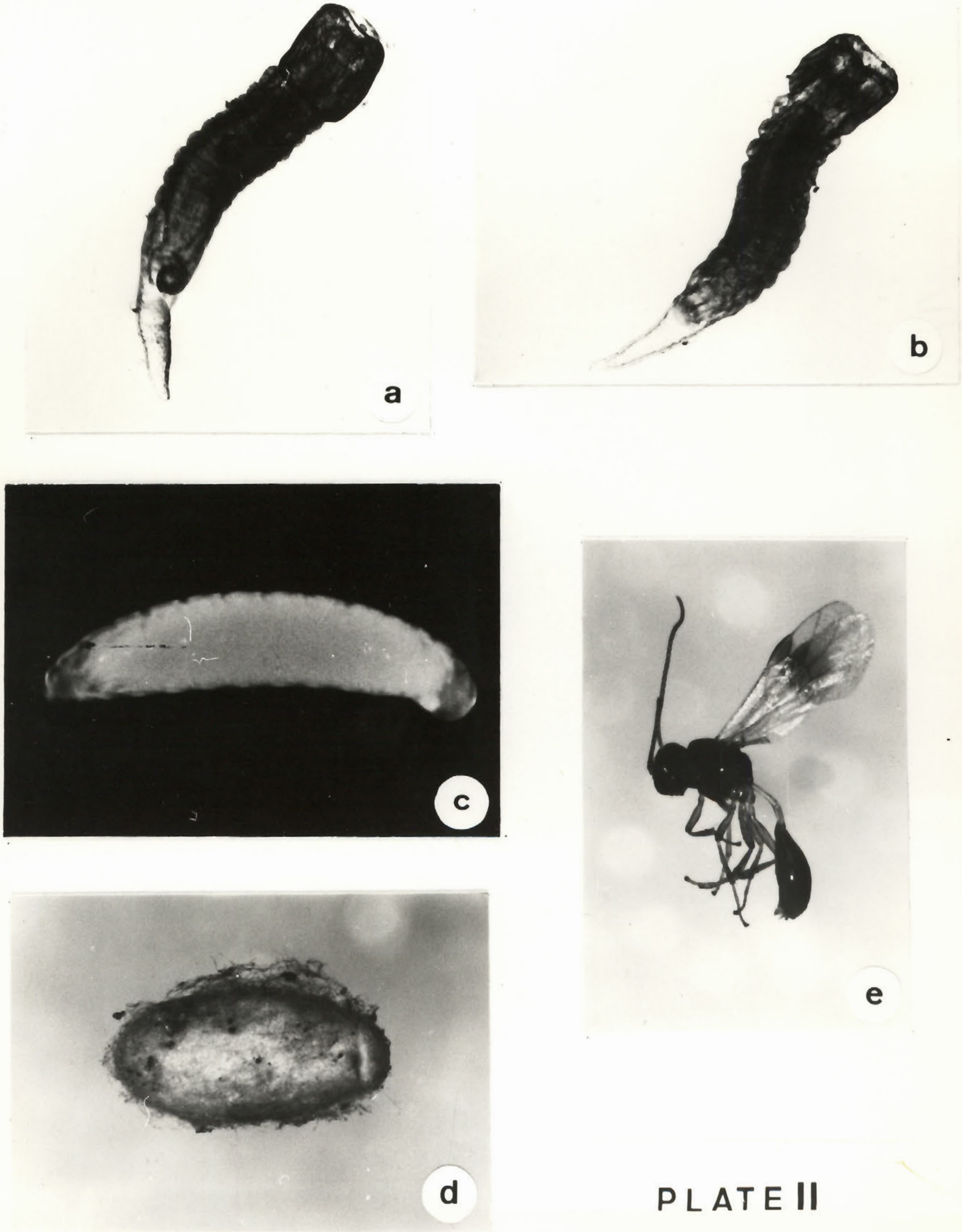

PLATE II

Plate 3 Intracellular bacteria (Rickettsia?) in gonads of *Chrysopa chi* Fitch.

a-c (in testes) X 5000

d (in testes) X 8000

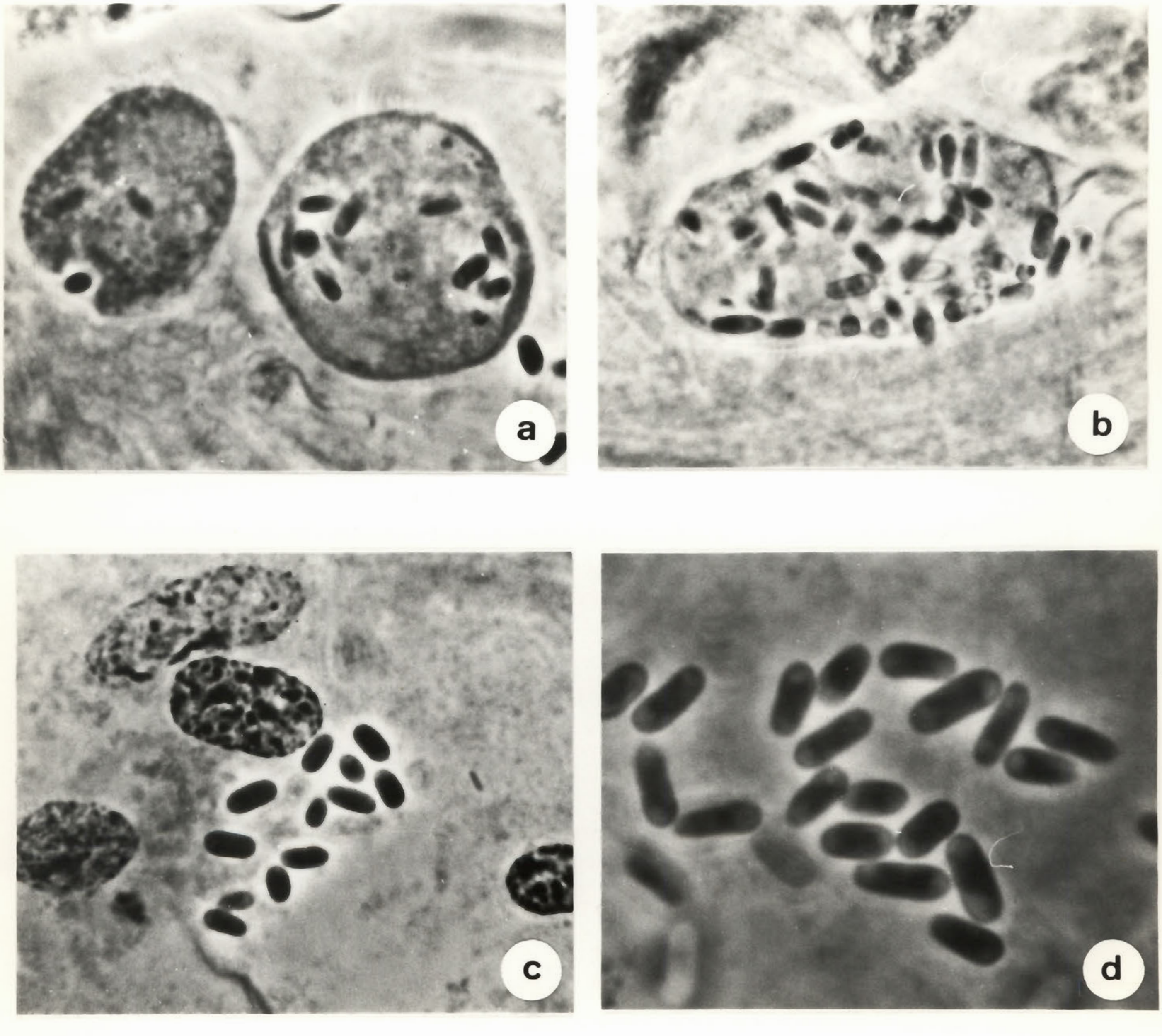

PLATE III

Plate 4 Chromosomes of *Chrysopa oculata* Say

a	Spermatogonial metaphase	X 8000
b	Male karyotype	X 8000
c	Oogonial metaphase	X 8000
d	Female karyotype	X 8000
e	Metaphase I (male)	X 5000
f	Metaphase II (male)	X 8000
g	Diakinesis in male (7 elements)	X 5000
h	Diakinesis in male (7 elements in cell on extreme right)	X 2000
i	Late diakinesis in male (X and Y associated)	X 8000

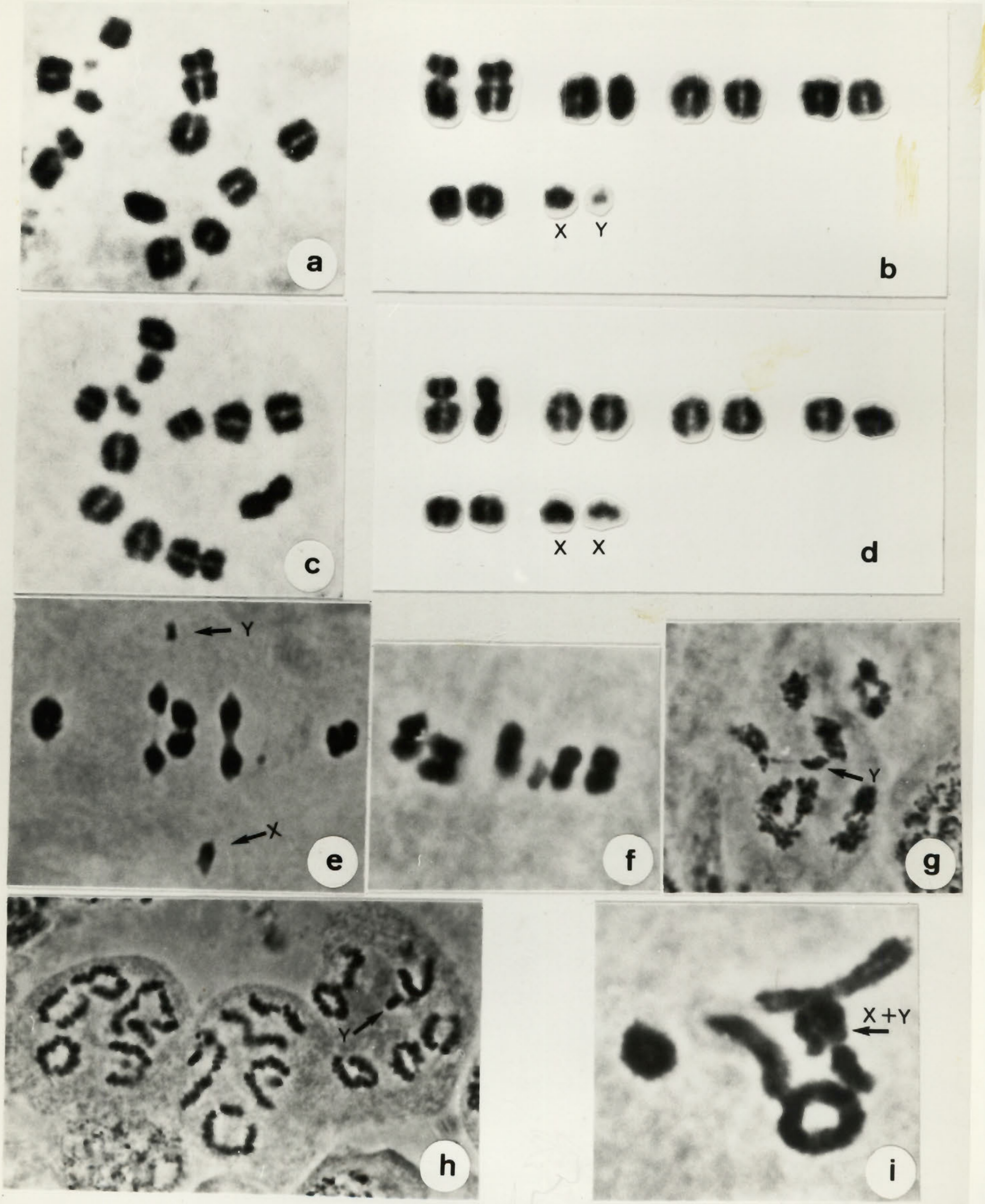

PLATE IV

Plate 5 Chromosomes of *Chrysopa chi* Fitch.

a	Spermatogonial metaphase	X 8000
b	Male karyotype	X 8000
c	Oogonial metaphase	X 8000
d	Female karyotype	X 8000
e	Metaphase I (male)	X 8000
f	Metaphase II (male)	X 8000
g	Pachytene (male)	X 5000
h	Diakinesis (male)	X 2500
i	Diakinesis (male)	X 5000

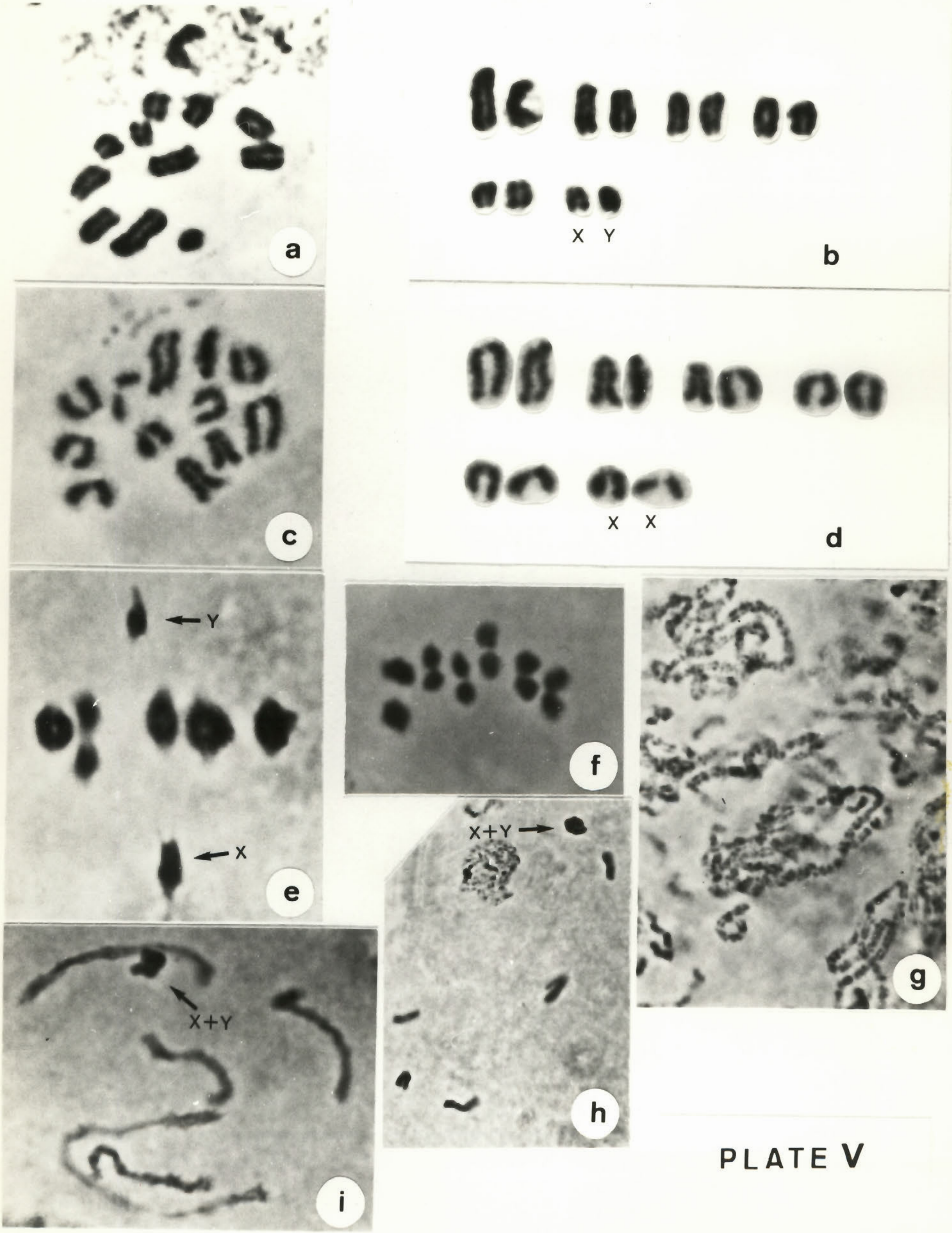

PLATE V

Plate 6 Chromosomal translocations (indicated by arrows) in *Chrysopa oculata* Say.

a-e	Metaphase I plates: translocations in the Mt. St. Hilaire culture	X 5000
f, g, i	Metaphase I plates: translocations in the Ile Perrot culture	X 5000
h	Premetaphase I showing double translocation (Ile Perrot culture)	X 5000

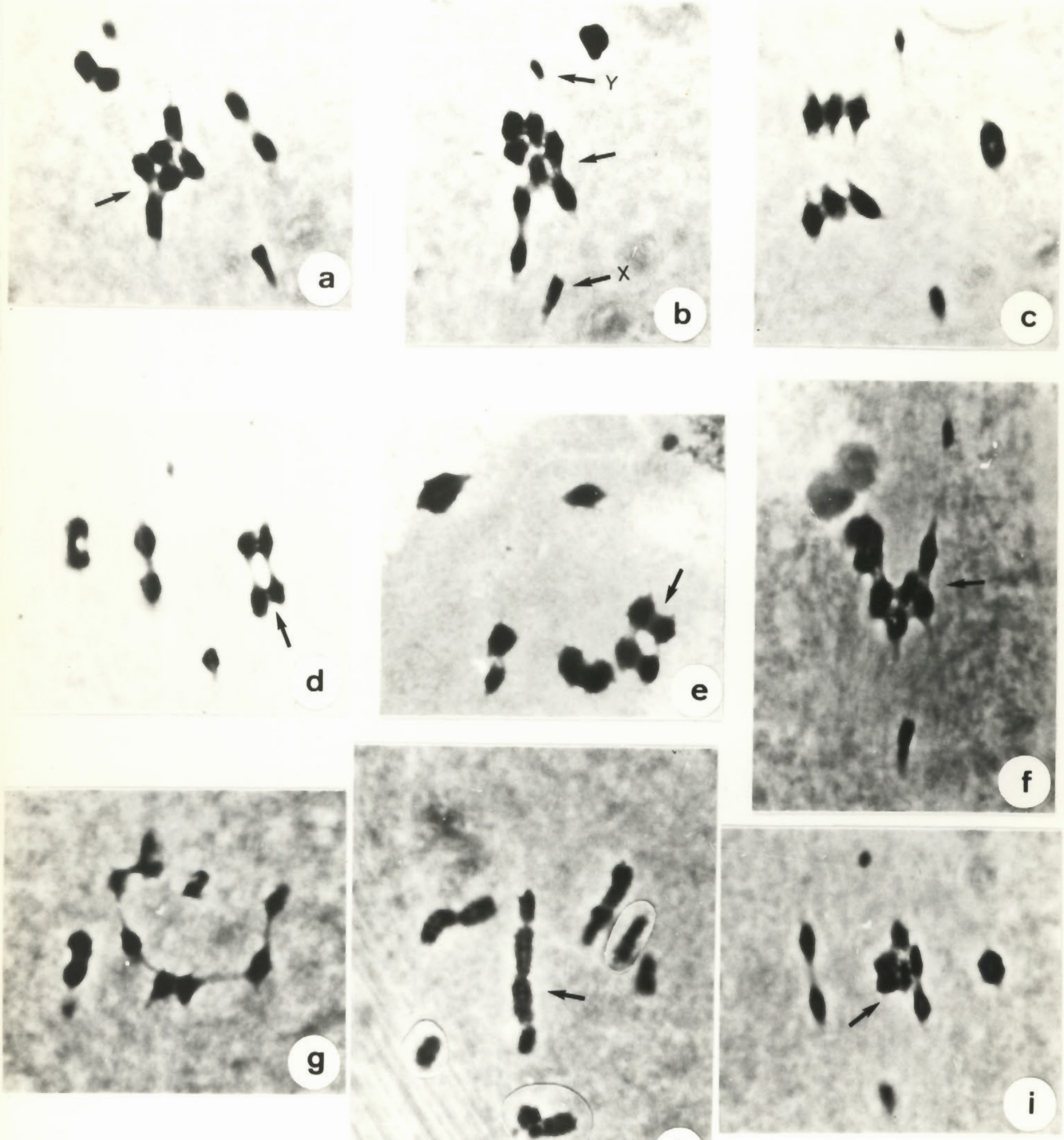

PLATE VI

Plate 7	Chromosomal translocations (indicated by arrows) in <u>Chrysopa</u> <u>chi</u> Fitch.

a-d	Metaphase I plates: translocations in the Mt. St. Hilaire culture (a-c, X 5000; d, X 8000)
e-g	Metaphase I plates: translocations in field-collected (Ile Perrot) material. (e, g, X 8000; f, X 5000)

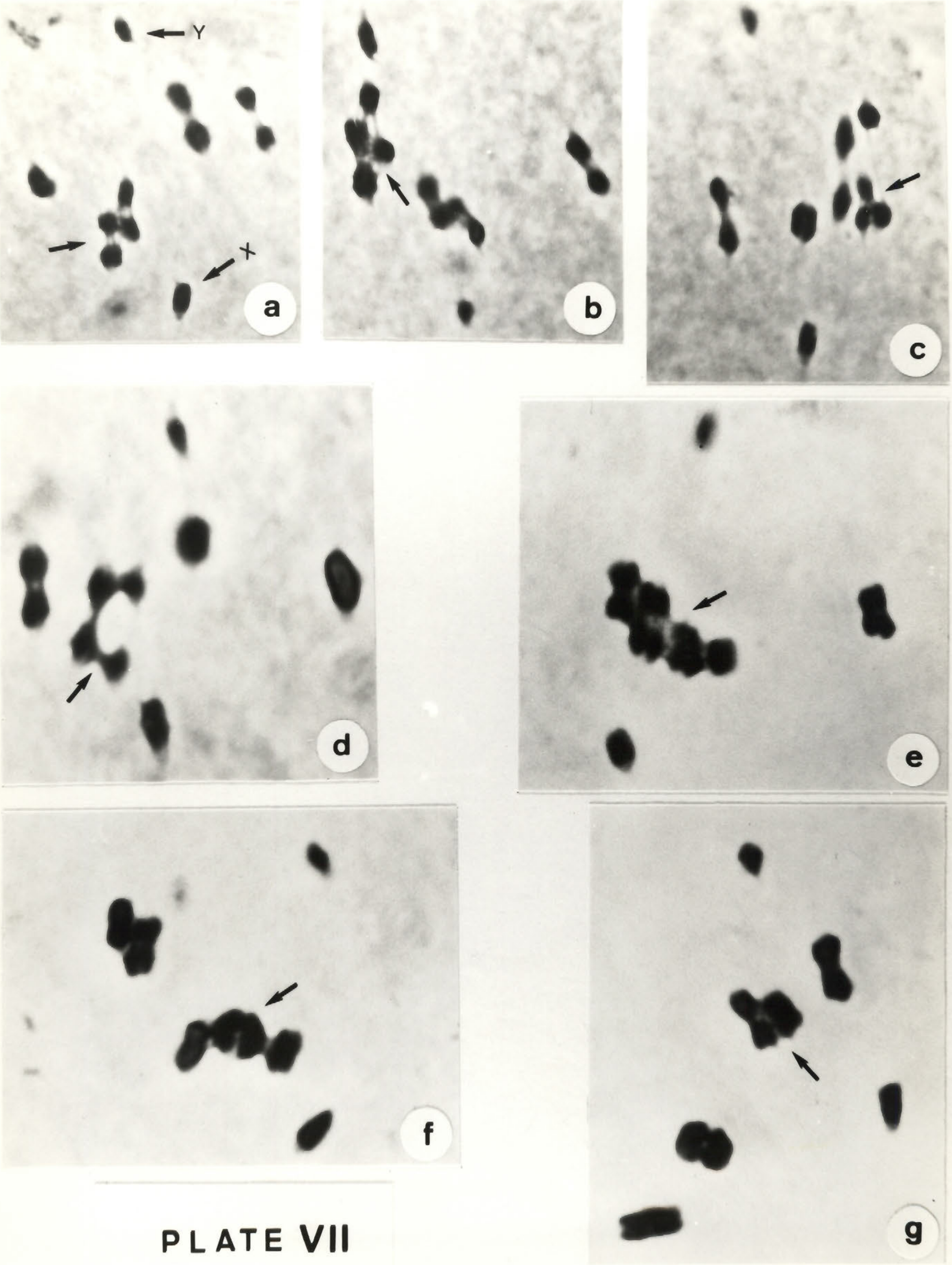

PLATE VII