

STUDIES ON THE BIOLOGY OF THE CHRYSOPIDAE  
II. THE FEEDING BEHAVIOR OF THE  
ADULT OF *CHRYSOPA CARNEA* (NEUROPTERA)<sup>1, 2</sup>

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INTRODUCTION

Although it has long been known that the larvae of the Chrysopidae are obligate predators of small, soft-bodied arthropods, the feeding habits of their adults have never been studied in detail. The adults of such species as *C. chi* Fitch, *C. incompleta* Banks, *C. oculata* Say, *C. nigricornis* Burmeister, and *C. quadripunctata* Fitch are believed to feed primarily, like their larvae, on living prey (Smith, 1922; Burke and Martin, 1956; MacLeod, unpubl.) On the other hand, adults of a number of other species, including *C. carnea* Stephens, will not accept such food, although several other substances are readily consumed.

Smith (1922) maintained adults of *C. carnea* (= *C. ploribunda* Fitch) on a weak sugar solution plus crushed aphids, but he did not ascertain the separate contributions of these dietary items toward adult survival or toward yolk deposition in the female. Finney (1948), whose studies were the first to be directed toward developing methods for the mass rearing of *C. carnea* for biological control, found that a diet consisting solely of honey resulted in a very low level of oviposition, but when this food was supplemented with a coxoid honeydew a much higher level was achieved. Neumark (1952) reported obtaining similar "high" levels of oviposition using aphid honeydew as the sole food, while Sundby (1966, 1967) was successful in maintaining adults and securing reasonable numbers of eggs from females which were fed upon a diet of honey and pollen.

As Finney's mass rearing procedures had proven uneconomical because of the difficulty of obtaining adequate supplies of honeydew, Hagen (1950) investigated several alternatives. After establishing that the difference in the fecundity of adults fed either honey or honeydew alone was not due to quantitative or qualitative differences

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in the carbohydrate components, he supplemented the honey diet with several synthetic foods known to contain high proportions of proteins (or their products of hydrolysis) and B-complex vitamins. All were found to raise egg production well above the level obtained on honey alone.

This early work led to further efforts toward developing highly nutritious, semi-defined, laboratory diets which would permit the efficient mass rearing of large numbers of adults (Finney, 1950; Burke and Martin, 1956; Hagen and Tassen, 1966, 1970; Ridgeway *et al.*, 1970).

None of these investigations attempted to determine the natural feeding habits of the adults of *C. carnea*. We have therefore centered our attention on a qualitative attempt to discover the food utilized by adults under natural conditions. This has involved an analysis of the gut contents of field-collected individuals and observations on the feeding behavior of adults in the field. In addition, as large numbers of wild adults were found feeding on corn pollen during the summer, we have investigated the efficiency of this material as food.

#### MATERIALS AND METHODS

Since it has been suggested that honeydew is an important natural food of *C. carnea* (Hagen, 1950; Neumark, 1952), we began our study with a microscope examination of leaf-surface honeydew in order to obtain a standard of comparison for our study of gut contents. This was carried out using two methods. In the first, leaves covered with honeydew were washed in a beaker containing distilled water, and the washings were then poured into a centrifuge tube and spun down. The pellet was placed in a drop of warm glycerine jelly on a microscope slide, a cover slip was added, and the preparation was gently squashed to flatten it. The second method utilized unfed, lab-reared adults which were permitted to feed on leaves covered with fresh honeydew, and an examination was then made of the slide-mounted gut contents. In these preparations the crop, midgut, and hindgut were removed in an isotonic 0.75% NaCl solution (MacLeod, unpublished) and these were mounted directly into glycerine jelly as described above. Studies of the gut contents were also made from similar whole mounts of the crop, midgut, and hindgut of 133 field-collected individuals which had been collected at various times throughout the year. These samples were taken, depending on the season, from woodlands or agricultural fields

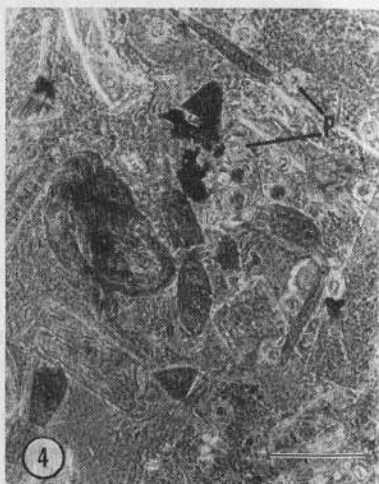
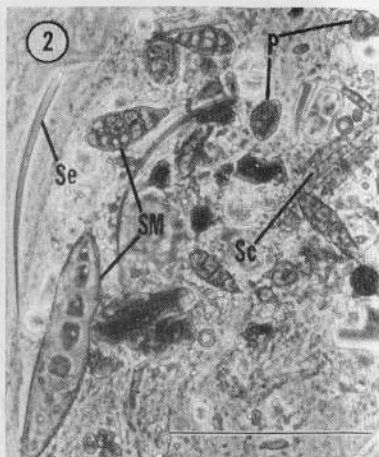
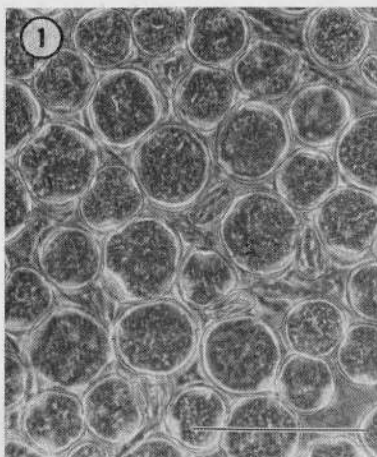
at several localities in Champaign County, Illinois during 1970 (Table 1).

An experiment examining the nutritive value of corn pollen utilized the offspring of 20 females collected at Urbana, Illinois on 15 June 1970 and maintained as a mass culture in an environmental chamber at  $25 \pm 1^\circ\text{C}$  and at a photoperiod of  $\text{LD} = 16/8$ . The females had constant access to water and a food consisting of a 1:1:1 volumetric mixture of Food Wheast®, sucrose, and water (Hagen and Tassen, 1970; Ridgway *et al.*, 1970). A sufficient number of eggs for the experiment was collected from a single night's oviposition and these were placed singly in cotton-stoppered, two-dram shell vials. The rearings were carried out at the temperature and photoperiod experienced by the adults in the mass culture, as described previously (MacLeod, 1967), except that vials containing the immature stages were kept in a desiccator over a saturated solution of KBr which maintained a relative humidity of 80%. Upon emerging, the young adults were immediately divided by sex, and 40 of each sex were randomly distributed among the four diet groups shown in Table 2. Each group, still maintained under the same temperature and photoperiodic regimen as before, was provided daily with fresh food. The hand-collected pollen was fed dry, while the sucrose was presented in the form of a highly concentrated solution absorbed in a small cotton pledget. A cotton pledget saturated with water was also available in all four groups at all times.

The efficiency of these diets was measured by an examination of the condition of the reproductive system five days after eclosion. In males it was noted whether sperm had shifted from the testis to the seminal vesicle. This is an important initial step in the ontogeny of full reproductive activity by the male (MacLeod, 1967; Sheldon and MacLeod, in prep.). In the females the basal diameter of the largest ovariole in each ovary was measured,<sup>4</sup> the number of mature eggs (diam.  $\geq 0.41$  mm) was noted, and the number of yolky oocytes was counted. These scores, indicating the degree of development of the female reproductive system, should be excellent indicators of the adequacy of the diet since the process of yolk deposition is undoubtedly responsible for the largest nutritional require-

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<sup>4</sup>The number of ovarioles per ovary in *C. carnea* is nearly always 12. We have occasionally encountered specimens with 11 ovarioles in one ovary and 12 in the other, but this is the greatest departure from the normal 12/12 state which we have observed. When yolk synthesis is underway, all of the ovarioles of a female are similarly active and usually they all have a similar basal diameter.



ment placed on females. All measurements of ovarioles and oocytes were made in isotonic NaCl Ringer's solution. The results were analyzed using Student's *t* test.

Field observations of feeding behavior were carried out at night in both forest edge and field communities using a Burgess "Safari Light" with a "cool white" bulb for illumination. This method has the advantage over a regular flashlight of uniformly illuminating a broad area rather than casting a narrow beam. A few individuals seemed to be disturbed by this procedure as they took wing and flew toward the light; however most were apparently undisturbed and seemed to continue their normal activities.

### RESULTS

*Analysis of Gut Contents.* Honeydew, a secretion emitted from the anus of various Homoptera, consists largely of unabsorbed plant sap to which certain excretory products may be added by some species. From the leaf washings we found that many foreign objects are rapidly trapped in honeydew, the most obvious of these being minute, nonorganic fragments such as small particles of rock, and such other objects as pollen grains, spores of various types, and portions of insect cuticle (particularly exuviae of aphids and lepidopteran scales). The quantity of pollen present varies in proportion to the amount being produced in the near vicinity. Also directly associated with the honeydew are sooty-molds (Dematiaceae) grow-

#### Figures 1-4

Photomicrographs of selected areas of the midgut contents of species of *Chrysopa* illustrating the principal types of digestive debris found in *C. carnea* and in the predaceous species *C. nigricornis* and *C. oculata*. All figures are prints from polaroid negatives made through a Zeiss Photomicroscope using phase optics. The scale lines in figs. 1, 3, and 4 represent 0.1 mm. The scale of fig. 3 is the same as that of fig. 4.

Fig. 1. *Acer saccharum* pollen from *C. carnea*. The gut contents of this individual consisted almost exclusively of this single species of pollen. Fig. 2. Residue of honeydew feeding from *C. carnea*. Visible are fruiting bodies of sooty-molds of the genera *Helminthosporium* and *Alternaria*, pollen grains, and a lepidopteran scale. Also visible are setae derived from integumental grooming. Fig. 3. Cuticular remains, mostly antennal fragments, from *C. nigricornis*. Also present are a few scattered pollen grains and fruiting bodies from the sooty-molds *Alternaria* and *Fumago*. Fig. 4. Cuticular remains from *C. oculata*, including the tarsal tips and pre-tarsal claws from several legs and antennal fragments. A few pollen grains are also visible. In both figs. 3 and 4 the irregular dark objects are the fragments of darkly pigmented cuticle.

Abbreviations: P—pollen grain Se—seta; Sc—lepidopteran scale; SM—fruiting body of a sooty-mold.

ing directly on the surface of the honeydew. Fruiting bodies of *Alternaria* spp. are very common, with *Piricauda* spp., *Helminthosporium* spp., and *Fumago* spp. somewhat less abundant.

In addition to the presence of honeydew in the gut of most adults examined, many individuals were also found to contain a considerable amount of pollen (fig. 1). We considered an individual to be feeding selectively on pollen whenever we found compact masses of one species of pollen predominating in the gut (Table 1, columns 3 and 4), while individuals were considered to be feeding largely on honeydew when only occasional, scattered pollen grains, usually of several different species, were present along with the other honeydew materials mentioned above (Table 1, column 2). Of the 133 specimens examined, 48 had a sufficient amount of one type of pollen in the gut to indicate preferential feeding. Several species of pollen were detected in these individuals, including (at various times of the year) *Catalpa bignonioides*, *Acer saccharum*, *Ulmus* sp., *Carya* sp., *Celtis occidentalis*, *Zea mays*, and a monoporate type of grass pollen. In most of these cases the gut contained evidence of honeydew in addition to the pollen. Only five of these 48 individuals were found with nearly pure pollen. Of the remaining 85 specimens (Table 1, columns 1 and 2) most had a few scattered pollen grains representing several plant species.

The first indication of preferential pollen feeding in our samples occurred in the middle of April and coincided with the early spring flowering of a number of forest trees. Some preferential pollen feeding continued throughout the spring and summer and was particularly noticeable in samples from agricultural fields taken when the extensive stands of field corn tasselled. This utilization of corn pollen was confirmed both by examination of the gut contents of the specimens collected on the corn and by direct field observation of feeding adults.

The frequent presence of a characteristic type of insect seta in the gut contents at first suggested that either *C. carnea* was picking up a very common type of seta from the debris on the honeydew or that occasional arthropods were being taken for food (fig. 2). The origin of these setae was ultimately found to be from the grooming of their own integument, as we recovered large numbers of such setae from the gut contents of a lab-reared individual that had been fed only sucrose. This origin was substantiated by a microscopic examination of the integument, which showed that most of the body setae are identical to those recovered from the gut.

Table 1. Analysis of the gut contents of 133 field-collected specimens of *Chrysopa carnea*. Individuals in column (2) contained only the residues of honeydew feeding; those in columns (3) and (4) contained compact masses of single species of pollen, and are inferred to have fed preferentially on pollen. The proportions of pollen present in columns (3) and (4) are visual estimates of the total volume of the slide-mounted gut occupied by pollen. The July-August samples are from agricultural (corn) fields; all other samples from woodland habitats.

Date of Sample (1970)	(1) Gut Empty	Gut with Residues of Feeding			Total
		(2) Honeydew Remains Only <sup>a</sup>	Pollen Present		
			(3) Pollen < ½ volume	(4) Pollen > ½ volume	
February	6	0	0	0	6
April 1-15	3	25	0	0	28
April 16-30	10	21	10	17	58
May	0	4	3	2	9
June	1	1	1	2	5
July-August	0	0	0	8	8
September	0	4	3	2	9
November	10	0	0	0	10

<sup>a</sup>If pollen present, only a few scattered grains of several species.

*Pollen Feeding Experiment.* In all 40 of the males the sperm shift had taken place by day five, and no other obvious differences between the dietary groups were present. The results for the females, summarized in Table 2, show an obvious dietary effect. We found that both pure corn pollen and pure sucrose resulted in significantly less oocyte development compared to the two combined or to Food Wheat® alone. This was true in comparisons of the mean ovariole diameter, the mean number of yolky oocytes, and the mean number of mature eggs per female ( $P < 0.05$  in all cases, except in the three cases where  $\bar{sx}$  is zero and where a  $t$  test cannot be made. In these cases the differences are obvious.) Even though by itself corn pollen seems to be a poor diet, it is significantly better than sucrose alone with respect to the ovariole diameter and the number of yolky oocytes ( $P < 0.05$  in both cases). No statistical comparison was made between these two groups for the number of mature eggs as only a single individual (pollen fed) had matured any. The diets of pollen plus sucrose vs. Food Wheat® were not found to differ in any of the three parameters examined.

*Field Observations.* The observations made in the field were consistent with the data derived from the study of the gut contents. Direct observation of the feeding of adults on pollen in the spring was not possible because of the low numbers of *C. carnea* present in the habitats sampled and the high frequency of nights too cool for extended activity of the chrysopids. During the middle of the summer a large number of adults were found feeding at night on corn pollen. They were either directly on the tassels or were on the leaves feeding on shed pollen which had accumulated, primarily in the mid-rib depression. On warm, calm nights during the peak of pollen production there were at times as many as two or three individuals per corn plant, and as many as 200-300 individuals could be collected in an hour. Feeding of adults on honeydew was also observed on several occasions during the summer. These observations, made at night, revealed that the adults simply walk along leaf surfaces, stopping periodically to scrape at them. Consistently, a close examination of each area where a chrysopid had stopped revealed a concentration of honeydew.

#### DISCUSSION

*The seasonal nutritive cycle of C. carnea.* The probable use of honeydew as a natural food by *C. carnea* was pointed out by both Hagen (1950) (who used the synonym *C. californica* Coq. for this species) and Neumark (1952). That honeydew has a high food



value has been demonstrated by several authors who have noted the presence of the mono- and disaccharides fructose, glucose, and sucrose and such trisaccharides as raffinose and gluco-sucrose. Several more-complex sugars are also present along with many of the essential amino acids (Gray and Fraenkel, 1954; Ewart and Metcalf, 1956, Auclair, 1958; Burns and Davidson, 1966). All of these analyses were based on pure honeydew collected shortly after deposition, so that there was no chance for the contaminants which we have mentioned above to have developed on it. The quantitative nutrient content of honeydews found under natural conditions should vary considerably from that noted above depending on the amount of sooty-mold and trapped pollen which is present since Todd and Bretkerick (1942) have shown that both of these materials contain considerably more amino acids than are present in pure honeydew.

Many of the data relating to the chemical composition of different pollens (Todd and Bretherick, 1942; Free, 1970) have indicated the presence of rather high proportions of carbohydrates. Thus in an analysis of pollens from 26 different plant species, Todd and Bretherick (1942) found mean values of 25.71% reducing sugars, 2.71% non-reducing sugars, and 2.55% starch along with mean values of 21.60% crude protein, 4.96% lipids ("ether extract"), 2.70% ash, and 11.19% water. These analyses, however, were based on pollens which had been collected by bees, the workers of which add various amounts of honey and nectar to the pollen during the process of collection and storage (Ribbands, 1953 and references therein), so that the true carbohydrate content of bee-collected pollen is actually lower. Such lower values are shown in a similar analysis of six species of hand-collected pollen, in which Todd and Bretherick (1942) found a mean percentage of only 2.59% reducing sugars, while the absolute amounts of the other major constituents were of approximately the same order of magnitude as those in the samples of pollen collected by bees. Comparisons made between the different species of these hand-collected pollens show that there is some interspecific variation in the proportions of the major nutrients, particularly starch, and it is obvious that only detailed studies of specific pollens can determine their exact nutritional characteristics.

The low proportion of carbohydrate reported for most pollens is consistent with the results of the only other study which has examined the effectiveness of pollen as a complete diet for females of *C. carnea* (Sundby, 1967). This work indicated a carbohydrate inadequacy for such a diet, since, although there was a low level of oviposition after feeding on (timothy) pollen, a considerably higher level was

Table 2.—The effect of diet on the reproductive maturation of lab-reared females of *Chrysopa carnea*.

Diet <sup>a</sup>	Mean Ovariole Diameter	Mean Number of Yolky Oocytes per Female	Mean Number of Mature Eggs per Female
Pollen Only	0.21 ± 0.03mm <sup>b</sup>	4.6 ± 1.08	0.2 ± 0.20
Sucrose Only	0.14 ± 0.01mm	0.7 ± 0.47	0.0 ± 0.00
Sucrose + Pollen	0.41 ± 0.00 mm	28.0 ± 2.42	12.2 ± 1.67
Wheast®	0.41 ± 0.00 mm	26.5 ± 2.14	12.4 ± 1.5

<sup>a</sup> N = 10 females per dietary group

<sup>b</sup> The ovariole diameter in a teneral or diapausing female is approximately 0.07 mm; in a field-collected, reproductively active female it is about 0.41 mm. The standard error of the mean is given for each group.

achieved when pollen (of an unstated species) was supplemented with honey. We found a similar marked increase in the reproductive potential of females in the present study when our experimental diet of corn pollen was supplemented with sucrose (Table 2) In this case, however, the carbohydrate inadequacy of corn pollen was unexpected since hand-collected samples of this pollen have been shown to have the exceptionally high value of 36.59% carbohydrate (Todd and Bretherick, 1942). This large proportion of carbohydrate is due primarily to a high content of starch, 22.4% (as opposed to 2-3% found in other hand-collected pollens), and the proportions of reducing and non-reducing sugars, 7.31% and 6.88% respectively, are much lower and closer to the means of other hand-collected pollens. The results of a separate study on the utilization of dietary starch by adult chrysopids, which we initiated after the surprising results from the corn pollen experiments were obtained and which will be published elsewhere, show that in *C. carnea* a large proportion of the starch incorporated into experimental diets remains in an unaltered form in the feces. These findings suggest that the large quantity of starch present in corn pollen is nutritionally unavailable to *C. carnea* and that the lower concentrations of sugars which are present provide an insufficient carbohydrate source for maximal egg production.

The importance of pollen in the natural diet of *C. carnea* can be

best appreciated when it is considered in conjunction with the seasonal cycle of this species. The adults undergo a reproductive diapause during the cold months of the year (MacLeod, 1967; Tauber *et al.*, 1970), and in the early fall migrate from the field communities into the forest edge areas (Zelený, 1965; Sheldon and MacLeod, in prep.) where they eventually enter the leaf litter and spend the winter. Dissections show that throughout the winter the gut is largely empty, most individuals containing only a few scattered setae, pollen grains, and sooty-mold fragments. There is no evidence of extensive feeding. It seems likely that this material represents the undigested residue of feeding late in the autumn, particularly as it is difficult to account otherwise for the presence of pollen in the gut contents at this time. During unseasonably warm periods of the winter there is some movement of the adults within the litter and a few may temporarily leave this habitat and fly about, so that some of this particulate matter which we have seen in our winter dissections may derive from mid-winter feeding on persistent honeydew containing pollen grains and mold fragments. Dissections made during December and January of 1969-1970 do, however, demonstrate the long-term persistence of the residue of late autumn feeding, since this interval had not been interrupted by warm periods. The gut contents of active mid-winter individuals sometimes include a large amount of clear liquid, which suggests that they imbibe free water at this time.

With the arrival of warmer weather in the early spring, the adults move out of the litter and begin to search for food. The specimens in the early spring samples in our study (Table 1—April 15) show typical honeydew remains in their gut contents, although most specimens are far from full. There is no honeydew production at this time of the year, and the source of this material in the gut remained an enigma until we noticed that early spring adults could be beaten, with considerable success, from the dry, persistent leaves of such tree species as *Quercus alba* and *Q. palustris*. Since many of these leaves had areas of what appeared to be old honeydew on their surfaces, we placed a number of such leaves in a cage with newly emerged, lab-reared adults. An examination of the gut contents of these adults 24 hours later gave results qualitatively identical to what we had encountered in the guts of our field-collected samples. We have not determined the nutritional adequacy of old honeydew, and it is possible that such other food sources as fermenting sap flows, where one might expect to find similar contaminants to those found on honeydew, are the actual

sources of the gut contents of our early spring adults. The congregating behavior of the adults and the feeding behavior of our lab-reared series suggest otherwise, however, and it is likely that an analysis of the nutritional content of the honeydew from last-year's leaves would show that, although limited in amount, this is potentially an important initial food source for early spring insects.

By the middle of April the pollen production of a number of forest trees begins and this provides focal points of large sources of food which are apparently heavily utilized by the adults of *C. carnea*. The importance of this early pollen becomes evident when the dietary requirements of the females are considered. Males are probably able to complete their reproductive maturation on a smaller energy budget than females, since spermatogenesis is completed in the pupal stage (MacLeod, unpubl.) and, upon adult eclosion, the males have only to shift the mature sperm from the testes to the seminal vesicle (MacLeod, 1967), secrete spermatophores, and mate. Females, on the other hand, have large, continuing nutritional requirements associated with the synthesis of yolk. The spring pollen should provide an energy source adequate for the males to initiate reproductive activity, while it conceivably also provides a sufficient source of carbohydrate and amino acids for the production of a limited number of eggs by the females. When it becomes possible for the adults to supplement their pollen diet with a more nearly optimal carbohydrate source such as fresh honeydew or, possibly, nectar, our experiments indicate that this combination should then constitute an excellent diet for maximal reproductive activity. Obviously, as noted above, the nutritional adequacy of this early pollen probably varies from one plant species to another.

After their initial, preferential pollen feeding, the adults appear to disperse within the woodlands and into other habitats (Sheldon and MacLeod, in prep.) where they probably feed opportunistically on both honeydew and pollen. Near the middle of the summer, in our area of study, there is again a sharp increase in pollen feeding at the time of anther anthesis of the field corn. This is followed in the late summer by a decreased pollen utilization, which probably corresponds to a reduction in the availability of pollen, until by late fall only honeydew remains are present in the gut analyses.

In connection with the suggestion made above that *C. carnea* is probably unable to utilize starch as a carbohydrate source, it is perhaps noteworthy that, other than corn pollen, none of the major food sources which we have found this species to utilize contain much starch. The failure of *C. carnea* to make use of starch may

indicate the evolutionary loss of this ability, since the present ecology of this species provides adequate simple sugars from honeydew and seldom brings adults into contact with foods containing large concentrations of starch.

*Notes on the feeding behavior of other Nearctic Chrysopidae.* *C. carnea* is one of a large number of chrysopids which seem to feed opportunistically either as "leaf scrapers" or on pollen. Unlike such predators as *C. nigricornis* and *C. oculata*, which usually have numerous, obviously chewed fragments of cuticle in addition to pollen and portions of sooty-molds in their gut (figs. 3, 4), these non-predaceous species lack arthropod fragments other than lepidopteran scales ingested during honeydew feeding and the setae scraped from their own cuticle during grooming.

By an examination of gut contents we infer the absence of predation and an extensive reliance on the leaf-scraping habit in a rather large number of Nearctic species of several genera, including the close taxonomic relatives of *C. carnea* within the genus *Chrysopa*. These close relatives, which comprise the Carnea Group (Subgenus *Chrysopa*, *sens. str.*, MacLeod, unpubl.), include *C. downesi* Smith, *C. externa* Hagen, *C. harrisi* Fitch, and *C. rufilabris* Burmeister. The feeding behavior of *C. comanche* Banks and *C. mohave* Banks, which are western members of this group, have not yet been examined by us. Although *C. rufilabris* has been reported by Smith (1922) to be predaceous and to feed readily on aphids, we have been unable to confirm this. Our analyses of the gut contents of field-collected specimens of this species fails to indicate predatory food habits and we have not been able to entice them to feed on aphids in the laboratory. Burke and Martin (1956) were also unable to observe feeding of *C. rufilabris* on aphids.

Limited field observations on feeding adults and studies of gut contents of several species of *Chrysopiella* and of *Eremochrysa fraterna* Banks suggest that these species feed exclusively on pollen.

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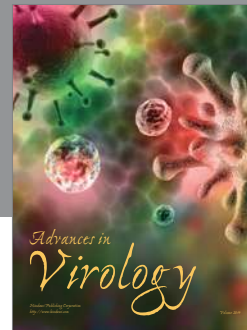
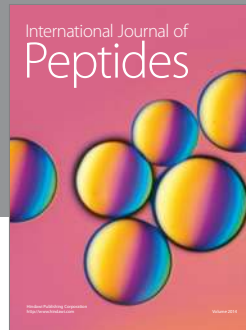
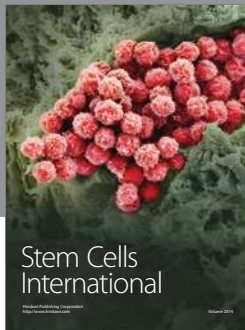
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