THE INFLUENCE OF APHID PREY CONSUMPTION ON SEARCHING BEHAVIOR, WEIGHT INCREASE, DEVELOPMENTAL TIME, AND MORTALITY OF *CHRYSOPA CARNEA* (NEUROPTERA: CHRYSOPIDAE) AND *HIPPODAMIA CONVERGENS* (COLEOPTERA: COCCINELLIDAE) LARVAE

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Abstract   *Can. Ent.* 113: 1007–1014 (1981)

The behavior of larval stages of the green lacewing, *Chrysopa carnea* Stephens, and of the ladybird beetle *Hippodamia convergens* G.-M. were studied in the laboratory. With increasing hunger level, only first instar *H. convergens* larvae spent more time searching in the upper part of alfalfa stems, where both prey aphids, *Acyrthosiphon pisum* (Harris) and *Acyrthosiphon kondoi* (Shinji), are found. All larval instars tested except first instar *C. carnea* visited more stems per unit time with increasing hunger level. The weight gain, the developmental time, and the mortality of all larvae were adversely influenced at low food levels, but differently for each predator size and species. *C. carnea* larvae had higher rates of fat body utilization and weight gain than coccinellid larvae.

Introduction

The framework. Holling (1966) formulated many of the essential behaviors which determine predator success. Since then many workers have extended his results by adding new components and have developed new predation models (see Royama 1971, Hassell 1978). Frazer and Gilbert (1976) studied the predation of the ladybird beetle *Coccinella trifasciata* Mulsant on the pea aphid, *Acyrthosiphon pisum* (Harris), using Holling's methods. This study extends this latter work to the ladybird beetle *Hippodamia convergens* G.-M. and the green lacewing, *Chrysopa carnea* Stephens, feeding on *A. pisum* and *A. kondoi* (Shinji) in California alfalfa fields. The phenology and spatial distribution of the aphids and their major predators are given by Neuenschwander *et al.* (1975) and Gutierrez *et al.* (1980) respectively.

This paper reports the effect of food availability on searching behavior, prey consumption rates, developmental times, weight increase, and survival of the larval stages of *H. convergens* and the green lacewing, *C. carnea*. These results will be used to develop parts of models describing the interaction of aphids and predators or parasites in alfalfa (cf. Gutierrez *et al.* 1980, Baumgaertner *et al.* in prep.).

Review of the hunger model. Hunger is defined as the quantity of food required to return the animal to a state of complete satiation (Holling 1966). It can be viewed as in Fig. 1, or described mathematically with equation [1] (Gutierrez *et al.* 1981):

$$0 < H_{t\triangle t} = \Omega(W)_t - Na_t - F_t + E_t + \triangle \Omega_t < (W)_{max} \qquad [1]$$

where $\Omega(W)_t$ = gut capacity at time t as a function of the predator weight
  F = weight of food in gut
  E = weight of food excreted or assimilated during $\triangle t$
  $\triangle \Omega$ = growth of the gut
  W = predator weight
  Na = weight of prey eaten.

A detailed model of the outflow (E), broken into components of assimilation, metabolic costs, and excretion and their influence on growth, development, survival, and ageing is given by Gutierrez *et al.* (1981).

Materials and Methods

Rearing the insects. Adult *H. convergens* were collected in January in an alfalfa field near Escondido, California, and *C. carnea* adults were obtained from an

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insectary colony maintained by K. S. Hagen, University of California, Berkeley. Unless otherwise reported, the predator larvae were raised in the laboratory under 14-16 h daylength and $21\pm2°C$, and kept individually in 4 ml glass vials plugged with cotton. A surplus of pea aphids raised on broad beans, *Vicia faba major* cv. Windsor, in a greenhouse was offered as prey on a stem of freshly cut alfalfa.

Hunger. Hunger as a function of starvation time was studied for both species of newly hatched larvae and for the last feeding larval stages (i.e., 3rd instar *C. carnea* and 4th instar *H. convergens*). The larvae were fed a surplus of aphids for 24 h, starved for various time periods at 21°C, and then weighed in gelatin capsules on a Cahn electrobalance accurate to 0.015 mg. The larvae were then fed for 3 h and reweighed. Nine to 12 larvae were tested per trial.

Hunger and searching behavior. The influence of age and hunger on searching was studied in an artificial arena consisting of a 24×24 cm plexiglass plate with eight equidistant (3.8 cm) small holes in its center placed over a water filled tray. A 24 cm high alfalfa stem was inserted in each hole into the water. Individual predator larvae treated as described above were placed half way up one of the alfalfa stems. Groups of 10 larvae of the same age (1st and 2nd *C. carnea* and 1st and 4th *H. convergens*) were starved at 21°C for 0, 4, or 24 h, respectively. Each insect was then observed for 45 min and the time spent searching in the upper half of the plants and the number of stem visits were recorded. Larvae leaving stems were moved with a camel's-hair brush back to the center of a stem. Observation times were converted to day-degrees (Gilbert *et al.* 1976) above the developmental thresholds for *H. convergens* (9.0°C) and *C. carnea* (8.3°C) (see Butler and Dickerson 1972 and Butler and Ritchie 1970 respectively). The proportion of the time spent searching the upper half of the stems (T*) was used to measure site preference. Arcsin transformations were made to facilitate statistical analyses (Zar 1974). Values outside the range of two standard deviations from the mean were omitted. The data on number of stems visited per larvae (V) were subjected to analysis of variance.

Fat body utilization. Since the guts of these predators are empty after 24 h starvation at 21°C, weight losses after that time were assumed to be due to respiration (Gutierrez *et al.* 1981.). The weight decreases for eight 3rd instar *C. carnea* and twelve 4th instar *H. convergens* were measured until the first larvae died. The repeated observations were made with the same individuals and are therefore not independent, but this was accounted for in the analyses (Thoeni 1970).

Hunger and development. Effects of limiting food supply (N_a, Fig. 1) on the larval biology have been investigated by Sundby (1966) and Simpson and Burkhardt (1960) for both *C. carnea* and *H. convergens* larvae. Little, however, is known about its effect on larval weight increase, developmental time, and mortality. To do this, aphids were sorted according to size (small 0.04 mg and medium 0.5 mg/ each) by passing them through two sieves (0.83 mm and 1.4 mm mesh). First instar *C. carnea* larvae were fed small nymphs; all others were fed medium size nymphs.
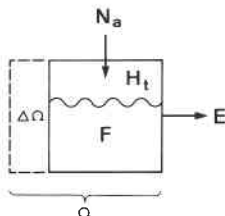

FIG. 1. Hunger at time t (H_t) defined as the quantity of food required to fill the gut (Ω). N_a = weight of prey eaten, F = food in the gut, E = outflow (excretion, assimilation, respiration).

Within each instar, different groups of larvae were fed different rates of aphids. Only predators maintained on an abundance of food were used in these studies. The larvae were weighed daily, and those dying before completion of the instar were replaced. The highest individual weight achieved before pupation was used as the final weight for that individual. The within instar maximum weight was the mean value between the weight on the day before and after molting. The weight gained by each individual during the instar was divided by their initial body weight, and positive ratios were plotted against the number of aphids offered per day. Nine to 41 individuals at each prey density were tested.

Results and Discussion

Hunger and development. The weight increase during the feeding period divided by the initial weight (i.e., the hunger index H*) is a measure of the amount of food consumed. Holling's (1966) hunger curve was fitted to these data (Fig. 2) for each instar (Table I) with an algorithm written by G. Smith (pers. comm.):

$$H^* = H^*_{max} (1 - \exp(-K \cdot t))\qquad\qquad [2]$$

where H^*_{max} = maximum hunger index (gut empty)
        K = constant
        t = starvation time in hours at 21°C.

Table I. Parameter estimates for hunger curves (H^*_{max}, K) and hunger levels (HL) reached after a 4 h and 24 h starvation period at 21°C. H^*_{max} = maximum hunger index, K = constant, HL = H^*/H^*_{max} with H^* = hunger index after a given starvation period

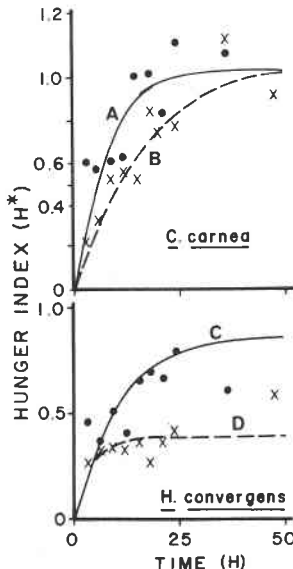| Species	Instar	H^*_{max}	K	HL	
				4 h	24 h
C. carnea	1	1.09	0.13	0.40	0.95
	3	1.10	0.06	0.21	0.76
H. convergens	1	0.73	0.14	0.34	0.92
	4	0.39	0.32	0.72	1.00

FIG. 2. Hunger index (H* = weight increase/initial weight) of starved 1st (A, ●) and 3rd (B, x) instar *C. carnea* larvae and 1st (C, ●) and 4th (D, x) instar *H. convergens* larvae on starvation time in hours at 21°C. (Data based on 9–12 individuals for each starvation period.)

Early chrysopid larval stages tend to become hungry faster than late instars (Fig. 2), but this trend was not observed for *C. convergens*. The gut size of *C. carnea* larvae relative to the body size appears to be greater than in coccinellids. In all but *C. carnea* 3rd instar larvae, the gut was nearly empty after a 24 h starvation period. The hunger level $(0 < HL = H^*/H^*_{max} < 1)$ is an index of the gut fullness, and is calculated for a 4 h and 24 h starvation period (Table 1).

Hunger and searching behavior. Groups of about 10 individuals were observed at three different hunger levels (HL). Larvae that were always in contact with prey aphids were considered to have a 0 hunger level. Both the relative time spent searching in the upper plant regions (T*) and the number of stems visited (V) at HL (0, 4, and 24 h) were examined via analysis of variance (Table II). Only first instar *H. convergens* larvae spent more time searching in the upper half of the alfalfa stems at high hunger levels (Fig. 3(A); Table II). The average time spent searching the plant region occupied by aphids was 27% and 35% for first and second instar *Chrysopa*, respectively, and from 12% to 57% for first and 37% for fourth instar *H. convergens*. All predator stages tested (except first instar *C. carnea* larvae) visited more stems at high hunger levels, than at low levels (Fig. 3(B); Table II). In general both early and late larval stages of *H. convergens* visited more stems per time period than corresponding *C. carnea* stages. However, on a per mg body weight basis early stages of both species were more active than later stages (Fig. 4), and *C. carnea* larvae visited more stems than the comparable stage coccinellid larvae. Many natural enemies concentrate their search in an area where prey has been found previously, and this behavior is thought to be advantageous for parasites or predators attacking aggregated insects (Dixon 1959). At zero hunger coccinellid larvae were less active than *Chrysopa* larvae (Fig. 4).
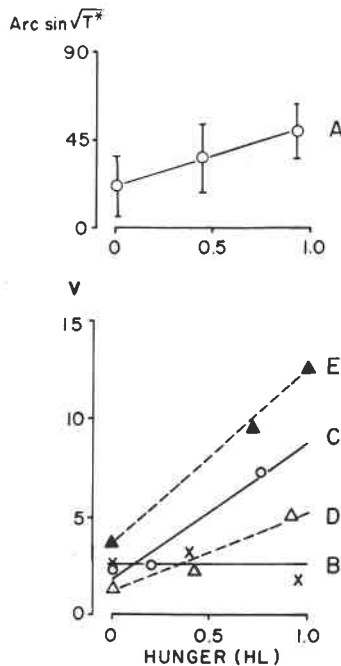

FIG. 3. Searching behavior with changing hunger level (HL). The relative time spent searching in the upper regions of the plant by *H. convergens* 1st instar larvae (T* = time searching in upper half of the stems/total observation time, A: Arcsin $\sqrt{T^*}$ = 21.7+30.6•HL). The number of stems visited per day-degree (V) by 1st and 3rd instar *C. carnea* (B: V = 2.6 and C: V = 1.7+7.1•HL) and 1st and 4th instar *H. convergens* (D: V = 1.0+3.9•HL, and E: V = 3.6+8.7•HL) larvae.

Table II. Searching behavior at different hunger levels (HL) : T^* = relative time spent searching in the top area of the alfalfa stems, V = the number of stems visited per day-degree, CV = coefficient of variation, Diff = differences between hunger levels, and significance (s) and not significant (ns) at $P < 0.05$. (N = 10 for each instar/hunger level)

Species	Instar	HL	Arcsin $\sqrt{T^*}$	Diff	CV	V	Diff	CV
C. carnea	1	0.00	24.20		0.74	2.67		1.13
		0.40	30.87	ns	0.79	3.29	ns	0.74
		0.95	38.88		0.70	1.97		0.65
	2	0.00	33.30		0.64	2.28		0.65
		0.21	39.63	ns	0.41	2.43	s	0.59
		0.76	34.56		0.59	7.33		0.61
H. convergens	1	0.00	20.39		0.80	1.33		0.65
		0.44	34.01	s	0.51	2.20	s	0.62
		0.97	49.14		0.29	5.07		0.56
	4	0.00	34.21		0.39	3.70		0.61
		0.72	36.66	ns	0.22	9.53	s	0.46
		1.00	41.61		0.40	12.54		0.69

Fat body utilization. The fraction of initial body weight lost during a starvation period with empty gut appears to be highest for older *Chrysopa* larvae (Fig. 5). It has been demonstrated in the previous experiment that calculated on a per unit body weight basis they are more active than coccinellids. Respiration losses were therefore expected to be greater.
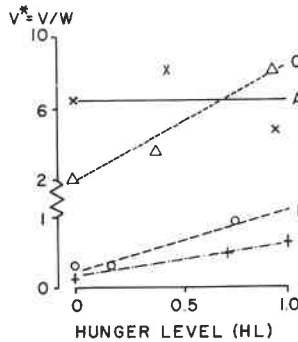

FIG. 4. Searching behavior with changing hunger level (HL). For each larval stage observed, the number of stems visited per day-degree (V) was divided by the average wet weight: A: $V^* = 6.4$ and B: $V^* = 0.2+0.9 \cdot HL$ for *C. carnea* 1st and 3rd instar larvae respectively, and C: $V^* = 1.6+6.2 \cdot HL$ and D: $V^* = 0.2+0.4 \cdot HL$ for *H. convergens* 1st and 4th instar larvae respectively.
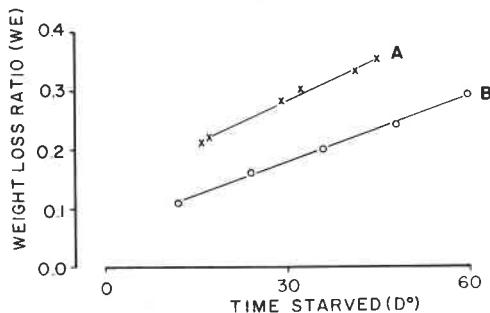

FIG. 5. Weight loss ratio (WE = weight decrease/initial weight) during starvation of eight 3rd instar *C. carnea* larvae (A: WE = $0.14+0.0047 \cdot D°$) and twelve 4th instar *H. convergens* larvae (B: WE = $0.068 + 0.0037D°$).

Effects of hunger on larval development. For each larval stage, the ratio of weight increase/weight at the beginning of the instar (i.e., WR), developmental time (DT) in days at 21°C and the survival rate per instar (SR) were described as functions of food availability (mass of aphids offered per day):

$$WR = WR_{max} (1 - exp (-K_1 \cdot F)) \tag{3}$$

$$DT = \begin{cases} DT_{min} + (1/F^{K_2}) \\ \\ DT_{min} + 1/(F+K_2) \text{ (}H.\text{ convergens 3rd instar)} \end{cases} \tag{4}$$

$$SR = A(F/(K_3+F)) \tag{5}$$

where WR_{max} and DT_{min} are the values calculated with a surplus of food, A and K_i are constants and F is the number of aphids (0.04 and 0.5 mg each) for *C. carnea* 1st instar and for the remaining larvae respectively. The fits of all functions to the data ([3], [4], [5]) using least square methods (Jennrich 1977) are satisfactory (Figs. 6, 7; Table III).

In both species, WR, DT and SR appeared to be generally affected at similar low food levels. Both species except first instar *C. carnea* suffered similar low mortalities (5%) when offered a surplus of food (Figs. 6, 7). The low survival rate of first instar *C. carnea* probably was due to the quality of the food and not to the amount eaten (K. S. Hagen, pers. comm.). To demonstrate the response of both species to decreasing food supply, development and survival were calculated ([3], [4], [5]) for a food level that would ensure a 75% weight increase in one instar period (Table IV). *C. carnea* larvae had lower instar-survival rates, and their developmental times were longer relative to *H. convergens* as the food became scarce (Table IV), perhaps due to higher respiration costs (see above) which causes *C. carnea* larvae to die quicker than coccinellid larvae when food is limited.

Food requirements. Knowing the weight of the newly hatched larvae (0.1 mg for *C. carnea* and 0.2 mg for *H. convergens* respectively) we can calculate the total weight (W) for all instars (i) under conditions of surplus food:

$$W_{i+1} = W_i \cdot WR_{max,i} \tag{6}$$

where W_i is initial weight of instar i, and $WR_{max,i}$ is the weight gain ratio given a surplus of food ([3]). The weight of the larvae (W) can also be described as a function of physiological age in day-degrees (D°) and the weight (Wo) of the newly hatched larvae (Fig. 8):

$$W_t = Wo \cdot exp (K_4 D°) = exp (-K_5 + K_4 D°) \tag{7}$$

where K_4 and K_5 are constants.

Table III. Parameter estimates of the effects of food supply (e.g., 3, 4, 5 per day) on predator larval stages kept at 21°C

Species	Instar	Weight increase ratio (WR) (eq. [3])		Developmental time (DT) (eq. [4])		Survival (SR) (eq. [5])	
		WR_{max}	K_1	DT_{min}	K_2	A	K_3
C. carnea	1	6.22	2.06	5.29	2.12	0.84	0.84
	2	3.07	2.12	4.77	3.13	1.01	0.34
	3	3.55	0.23	5.84	2.88	0.92	0.01
H. convergens	1	4.29	0.79	3.96	1.50	0.98	0.47
	2	2.20	0.63	2.60	0.86	1.06	0.47
	3	2.15	0.67	3.30	−0.35[a]	0.91	0.002
	4	1.87	0.61	7.48	0.37	0.97	0.42

[a]For more than 0.35 aphid/day.
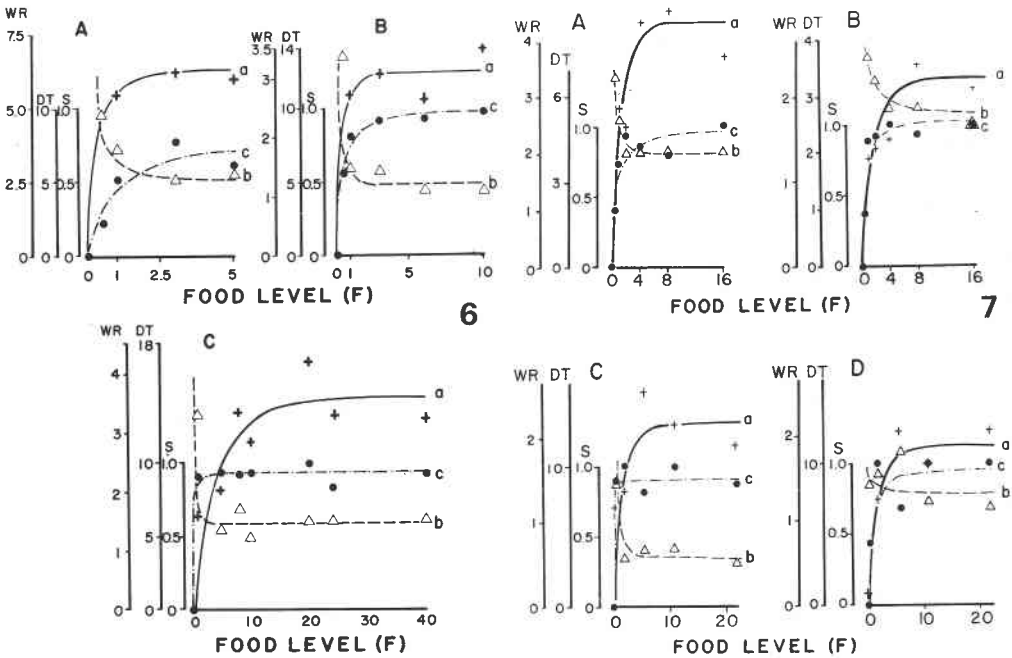
Figs. 6–7. The effects of limiting food (F = number of aphids offered per day at 21°C) on weight increase ratio (WR, a), developmental time (DT, b) and survival (S, c) of (6) (A) 1st, (B) 2nd, and (C) third instar *C. carnea* larvae and of (7) (A) 1st, (B) 2nd, (C) 3rd), and (D) 4th instar *H. convergens* larvae. The stages prior to the ones tested were fed to satiation, hence there was no carryover effect due to inadequate food supply.

Table IV. The responses of various larval stages to limiting food supply: (1) food levels (FL = number of small (*) or medium size aphids selected (eq. [3], [4], [5]) to ensure an arbitrarily 75% weight increase for all stages, (2) DF = developmental time at FL/developmental time with a surplus of food, and (3) S = instar survival rate at FL

Species	Instar	(1) Food level (FL)	(2) Development factor (DF)	(3) Survival (S)
C. carnea	1	0.67*	1.44	0.37
H. convergens		1.75	1.11	0.77
C. carnea	2	0.65	1.81	0.66
H. convergens		2.20	1.20	0.87
C. carnea	3	6.03	1.00	0.92
H. convergens		2.07	1.18	0.91
H. convergens	4	2.27	1.10	0.82

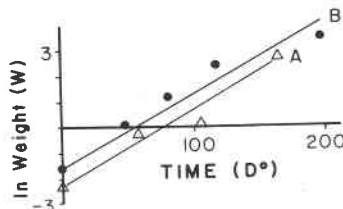Fig. 8. The pattern of $\log_e$ maximum weight (W) over time in D° of growing *C. carnea* (A: *ln* W = −2.3+0.031·D°) and *H. convergens* (B: *ln* W = −1.6+0.028·D°) larvae offered a surplus of prey at 21°C.

Summary

The rate of weight gain was slightly higher for *C. carnea* larvae than for coccinellids. It is known that the aphids are of relatively low nutritional value for *C. carnea* larvae (K. S. Hagen, pers. comm.), and hence qualitatively better food than aphids is required to meet their high respiration rates and adequate growth, development, and survival rates of *C. carnea* larvae especially of the 1st instars. Furthermore, aphids are aggregated (Gutierrez *et al.* 1980) and *Chrysopa* larvae appear to search less efficiently among prey occurring in colonies (see above). We suggest therefore that the polyphagous *C. carnea* larvae are much less adapted to aphid prey than is the stenophagous *H. convergens*.

Acknowledgments

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