Extrafloral Nectar Consumption and Its Influence on Survival and Development of an Omnivorous Predator, Larval *Chrysoperla plorabunda* (Neuroptera: Chrysopidae)

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ABSTRACT We examined the role of extrafloral nectar in the ecology of a larval common green lacewing, *Chrysoperla plorabunda* (Fitch). Larval lacewings were observed foraging freely in cotton fields and almond orchards to quantify their consumption of extrafloral nectar. Extrafloral nectar was a major component of the diet of neonate lacewing larvae foraging on cotton. Extrafloral nectar consumption increased strongly as the local availability of aphid prey declined. Lacewing larvae also fed frequently on extrafloral nectar when foraging in almond orchards. A manipulative diet experiment in the field demonstrated that in the absence of arthropod prey, extrafloral nectar contributed only slightly to neonate lacewing growth and did not support lacewing development. Nevertheless, extrafloral nectar did promote substantial longevity of first-instar lacewing larvae, which were able to maintain a high level of searching activity. Both the field experiment and a laboratory experiment showed that extrafloral nectar provides nutritional benefits that extend beyond those provided by a simple water source. Lacewing larvae are highly omnivorous: they feed on plant-based resources (extrafloral nectar), on herbivorous arthropod prey (e.g., aphids), and on other predatory or omnivorous arthropods.

KEY WORDS *Chrysoperla plorabunda*, extrafloral nectar, generalist predator, omnivory

THE ROLE OF generalist predatory arthropods in the suppression of herbivorous arthropod populations has become the subject of renewed research efforts (Murdoch 1985, Riechert and Bishop 1990, McMurtry 1992, Döbel and Denno 1994, Wiedenmann and Smith 1997). There is a growing awareness that many generalist predators consume not only a broad range of arthropod prey but also exploit plant-based resources. Generalist predators may consume pollen, floral and extrafloral nectar, and may feed directly on plant tissues (Alomar and Wiedenmann 1996, Jervis and Kidd 1996, Armer et al. 1998, Coll, 1998, Agrawal et al. 1999, Agrawal and Klein 2000). It has been hypothesized that omnivorous arthropods may be more effective regulators of herbivore populations because the diversity of used food resources may sustain omnivore populations in habitats where the availability of any particular prey species may fluctuate widely (Karban et al. 1994; Walde 1995; Settle et al. 1996; McMurtry and Croft 1997; Coll 1998; Nyrop et al. 1998; Eubanks and Denno 1999, 2000). A broad diet may be particularly important in highly disturbed environments, including many temporary agroecosystems, where specialist predators may face periodic prey shortages or even transient local extinctions of their prey resource base.

A key issue for applied insect ecologists attempting to enhance the role of omnivorous predators as biological control agents is to identify the factors that determine the densities of omnivores in agricultural ecosystems. The traditional view has emphasized the role of prey availability in defining equilibrium densities of predators (Hassell 1978). Although prey availability may not be the sole or primary factor shaping predator densities (e.g., Wise 1993; Rosenheim 1998, 2001), it is likely to be an important consideration. For omnivores, however, this resource-based approach must be expanded to incorporate the importance of plant-based foods. Thus, to begin assessing the importance of food availability as a factor shaping predator densities, we must first understand what food resources are used by predators in nature, and how different foods vary in their ability to support predator growth and development. Here we attempt to develop such an understanding of food resource use and value for the larval stages of the green lacewing, *Chrysoperla plorabunda* (Fitch).

Common Green Lacewing System. *Chrysoperla plorabunda* is a common and potentially effective generalist predator of the cotton aphid, *Aphis gossypii* Glover, in California cotton fields. Although natural densities of lacewing eggs can be very high in cotton (Rosenheim et al. 1999, Rosenheim 2001), biological control is poor, and aphid populations exhibit irruptive dynamics (University of California 1996, Rosenheim 2001).

To understand the failure of high densities of lacewing eggs to produce effective suppression of aphid populations, we previously investigated mortality factors acting on immature lacewings. Quantitative mea-

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sures of lacewing population age structure revealed that although eggs are abundant, larval stages are often rare (Rosenheim et al. 1993, 1999; Rosenheim 2001). Lacewing larvae were found to be subject to intense predation pressures from an array of generalist hemipteran predators (Rosenheim et al. 1993, 1999; Cisneros and Rosenheim 1997; see also Heinz et al. 1999). These studies led to the general hypothesis that the failure of lacewings to exert consistent, strong suppression of aphid populations was due to the action of higher-order consumers, which reduced lacewing larval stages to densities at which they were ineffective.

The traditional explanation for an age structure in which predator eggs are common but larval stages are rare is that larvae are starving due to limited prey resources. How important might the contributions of prey scarcity be in complementing the predation effects that have been documented in this system? To address this question, it is imperative first to understand what resources lacewing larvae can use in the field to survive and develop. Although much is known about the nutrition of adult lacewings (Hagen 1986), less is known about larval diet and the possible utilization of plant-based resources. Lacewing larvae have been observed to consume honeydew and floral nectar in the field (Principi 1940, Downes 1974), and laboratory studies have suggested that sugar-rich foods may enhance lacewing development (McEwen et al. 1993, 1996), but no studies have quantified nectar consumption or its role in lacewing performance in nature. Most studies view lacewing larvae as strict predators and have documented lacewing consumption of a broad array of soft-bodied arthropod prey (Principi and Canard 1984, Chang 1998).

Cotton plants produce rich supplies of extrafloral nectar. Extrafloral nectar is a rich supply of sugars but only a relatively poor source of other nutrients, such as amino acids and lipids; four of the essential amino acids required for insect development are not present (Hagen 1986). Here we address the role of extrafloral nectar in the ecology of larval *C. plorabunda.* Direct field observations were conducted on freely foraging larval lacewings to determine the composition of their diet and specifically to quantify the use of plant-based resources. A field experiment assessed the influence of extrafloral nectar consumption on lacewing survival, development, and foraging behavior. Finally, lacewing performance on diets comprising two types of extrafloral nectar was contrasted in the laboratory. The results of these investigations suggest that a basic shift is needed in the approach to the larval ecology of *C. plorabunda:* these lacewings are not just generalist predators but omnivores deriving physiologically significant resources directly from plants.

Materials and Methods

Direct Field Observations of Feeding by *C. plorabunda* Larvae: Neonate Larvae. Neonate *C. plorabunda* larvae were released in insecticide-free upland cotton fields, *Gossypium hirsutum* L., in California's Central Valley and observed to record foraging behavior. Lacewing larvae were obtained from eggs laid by adults collected in the field and held in the laboratory at 25 ± 2°C. Before releasing the lacewing larvae in the field, we identified a natural release point by selecting a plant randomly and searching the top half of the plant's canopy thoroughly for any unhatched lacewing eggs, which were marked. Only the top half of the plant was used because lacewing eggs are concentrated in the upper plant canopy (J.A.R., unpublished data), and observing larvae on foliage close to the ground can be difficult. Within a few hours or days one of the unhatched marked eggs was chosen randomly for the release location. The egg with its attached stalk was removed from the cotton plant and replaced with a reared neonate larva. Larvae were released in the field within 0–6 h of hatching and climbing down their stalks. We attempted to observe each released larva continuously from the time of release for a period of 4 h, recording its location (top of leaf, bottom of leaf, stem, fruit), behavior (resting, foraging, feeding), and the identity of all food consumed using hand-held computers (Psion Organizer 3.0, Psion, London) running behavioral event recording software (The Observer 3.0, Noldus Information Technology, Wageningen, The Netherlands). The density of *A. gossypii* on the first leaf contacted by each lacewing larva was recorded as a measure of local prey availability. These observations were repeated 10–17 times per site, at 10 different sites ($N = 136$ total larvae observed), from July to September 1995 and 1996 (see Rosenheim et al. 1999 for further details on the field sites).

Direct Field Observations of Feeding by *C. plorabunda* Larvae: All Instars. Observations were conducted on each of the three larval instars of *C. plorabunda* for periods of 1 h in insecticide-free cotton fields and almond orchards in Yolo and Solano Counties, CA, during 1996 and 1997. These observations were intended to complement the neonate observations by providing data on the full range of larval stages. Also, by observing larvae that were found in the field, we hoped to sample individuals that would exhibit a natural distribution of initial hunger levels. Observations were conducted from June to September in upland cotton, 'Maxxa', planted on the Davis campus. Observations in almonds were conducted in four commercial orchards from April to August. Almond leaves bear a pair of extrafloral nectaries located at the junction of the leaf blade and the petiole. In both crops, lacewing larvae were collected in the field by clipping whole plants (cotton) or plant-parts (almond branches), finding a larva, and transferring that larva back to an undisturbed plant in the field. Data were recorded as described above for neonates.

Field Diet Experiment. Individual neonate *C. plorabunda* larvae were confined to the lower surface of upland cotton leaves (fifth mainstem node), Maxxa, in small cages and were given access to an array of diets to evaluate the role of extrafloral nectar consumption in lacewing growth and development. Larvae were the offspring of adults collected from cotton. We used

only leaves that had minimal mite damage and whose midrib nectary was obviously wet (i.e., secreting extrafloral nectar). We cleaned leaves carefully to remove all food resources (e.g., pollen, mites, and thrips) before attaching the cages.

The cage consisted of a clear plastic 15-ml rectangular cup (3 cm wide by 4 cm long by 1.5 cm high; Bio-Serv, Frenchtown, NJ) affixed to the leaf surface with a nontoxic cement. Two ventilation openings were cut in the sides of the cup and covered with a fine mesh (70 by 200-μm openings) that excluded small arthropods. An access port was created by cutting a small hole in the cage wall and inserting a gelatin capsule. To prevent condensation in the cages, which would otherwise occur when the cages were exposed to direct sunlight, each cage was shaded by a sheet of paper.

The experiment was conducted from 27 July to 18 August 1996 in a 0.2-ha plot of insecticide-free upland cotton at the UC Davis Experimental Farm. The mean maximum daily temperature during the experiment was 35.5 ± 0.9°C, and especially hot weather occurred during the first 5 d of the experiment (mean daily high T = 37.8 ± 1.2°C).

Diet treatments were chosen to reflect the resources that lacewings had been observed feeding on during the field observations. Six diet treatments were established, and each was replicated 10 times: (1) *No Leaf.* Lacewing larvae were not given access to any source of water or food. A piece of cloth was glued to the bottom of the cage to prevent the larvae from reaching the leaf surface. (2) *Leaf Only.* Larvae were allowed access to the leaf surface but not the extrafloral nectary. The cage was glued over a section of the leaf midvein 1 cm distal of the extrafloral nectary. (3) *Water.* Larvae were provided access to the leaf surface and water. Water was delivered with a small string wick that extended from a water reservoir (a vial affixed to the leaf petiole outside the cage) and was threaded through the cage wall in a glass capillary tube and laid against the leaf. The cage was positioned over the midvein 1 cm distal of the extrafloral nectary. (4) *Extrafloral Nectar.* Larvae were given access to the leaf surface and the extrafloral nectary. The cage was positioned over the midrib at the location of the extrafloral nectary. (5) *Aphids.* Larvae were given access to the leaf surface but not the extrafloral nectary and were supplied with aphid prey. The cage was positioned over the midvein 1 cm distal of the extrafloral nectary. Ten medium to large yellow cotton aphids were added initially and restocked as needed to maintain continuous prey availability. (6) *Aphids and Extrafloral Nectar.* Larvae were given access to the leaf surface and the extrafloral nectary, and were supplied with aphid prey. This treatment was established exactly as treatment 5, except that the cage was fixed over the extrafloral nectary.

Cages were checked at 24-h intervals and the lacewing's condition (dead, alive, or lost) and activity (resting, foraging, or feeding) were recorded. The status of the extrafloral nectary (dry or wet) was recorded at the termination of each replicate. At the conclusion of each replicate, larval head-capsule size was measured to determine which individuals had molted to the second instar. Lacewing larvae in the two diet treatments that contained aphid prey were collected on day 5 of the experiment (when their growth made it difficult to supply them with an abundant supply of prey) and their live weights were recorded.

Laboratory Diet Experiment. A laboratory experiment provided a second comparison of the extrafloral nectar versus water-only diet treatments, and evaluated the quality of two types of extrafloral nectar: foliar versus bracteal extrafloral nectar. Neonate *C. plorabunda* larvae were held singly in 20-ml plastic vials with lids fitted with a ventilation opening covered with mesh. The larvae hatched from eggs laid in the laboratory by field-collected adults.

Extrafloral nectar was collected from upland cotton, Maxxa, grown in Davis. We collected extrafloral nectar using a 50-μl syringe from three sources: (1) nectaries located on undersides of leaves, on the midrib (*foliar nectaries*), (2) nectaries subtending developing flowers and fruits (=*bolls*) underneath the epicalyx bracts (*subbracteal nectaries*), and (3) nectaries below the epicalyx bract on the peduncles of flowers or fruits (*circumbracteal nectaries*). All available nectar was collected from the subbracteal and circumbracteal nectaries on a series of fruits, and combined to form a single sample, henceforth referred to as *bracteal extrafloral nectar.* To increase the efficiency of collecting foliar extrafloral nectar, fine mesh sleeve cages were tied around individual leaves to prevent the consumption of nectar by arthropods, thereby allowing the nectar to accumulate at the nectary. Extrafloral nectars were stored at –12°C until 2 h before use.

Three diet treatments were established and were replicated 10–11 times: (1) *Water Only.* Larvae were provided with access to water. Water was delivered via a small string wick that extended from a water vial outside the cage. (2) *Foliar Extrafloral Nectar Only.* Larvae were given access to two small droplets of nectar collected from foliar nectaries. (3) *Bracteal Extrafloral Nectar.* Larvae were given access to two small droplets of nectar collected from bracteal nectaries.

Vials were held at 30°C, 80% RH, and a photoperiod of 15:9 (L:D) h. Every 3 d, surviving larvae were transferred to new cages with fresh nectar droplets. The nectar remained wet and was never completely consumed by the lacewing larvae during a 3-d period. Cages were checked at 24-h intervals until all larvae died; each day, lacewing condition and behavior were recorded as in the field diet experiment. On the death of each larva, we measured head capsule size and wet weight.

Statistical Analyses. Nonparametric regression was used to examine the association between the time spent feeding on extrafloral nectar and the density of aphids on the first leaf contacted. Multiple regression was used to assess the joint influences of aphid availability and total lacewing foraging time (independent variables) on the time lacewings spent consuming extrafloral nectar (dependent variable). Because the

Table 1. Food resources consumed by neonate *Chrysoperla plorabunda* larvae foraging freely in cotton

Resource	Number of *C. plorabunda* observed feeding on resource	Mean number of prey consumed (or feeding bouts on plant-based resources) per lacewing (±SE)	Mean time(s) feeding on resource per lacewing (±SE)
		Arthropod prey	
Aphis gossypii	72	1.037 ± 0.118	969.9 ± 123.8
Tetranychus spp. motile stage	11	0.132 ± 0.040	20.8 ± 6.8
Whitefly (nymphs plus adults)	6	0.044 ± 0.016	40.7 ± 21.8
Thrips	5	0.052 ± 0.026	15.2 ± 8.3
Tetranychus spp. egg[a]	3	0.044 ± 0.028	1.1 ± 0.7
Geocoris sp. egg	2	0.015 ± 0.007	23.0 ± 17.9
Chrysoperla sp. egg	1	0.007 ± 0.007	16.9 ± 16.9
Orius sp. nymph	1	0.007 ± 0.007	2.5 ± 2.5
Unknown prey[b]	25	0.250 ± 0.056	43.7 ± 10.8
		Plant-based resource	
Extrafloral nectary	29	0.265 ± 0.047	14.7 ± 3.3
Leaf vein	6	0.044 ± 0.016	4.7 ± 2.8

Focal observations lasted an average of 3.30 ± 0.10 h ($n = 136$).

[a] Mite eggs were difficult to see in the field without interfering with foraging lacewing; thus, these figures should be viewed as lower estimates of mite consumption.

[b] These prey were generally too small to identify reliably in the field while they were being consumed. Many instances of predation on mite eggs may be included here.

distribution of nectar feeding times was highly nonnormal, the two-part procedure recommended by Conover (1999) was followed. First, the standard parametric multiple regression was conducted. Then each variable was rank-transformed separately before conducting the regression; this transformation produces a robust analysis that is less sensitive to outliers or other deviations from a normal distribution (Conover 1999). Survival analysis using the Kaplan–Meier product limit survival curve (SAS Institute 1995) was used to examine the influence of diet on lacewing larva longevity; this analysis allowed us to use data from replicates that were censored due to lacewing larva escapes from cages before death. The sequential Bonferroni technique was used to adjust the critical significance levels for multiple pairwise comparisons (Rice 1989). Throughout the text, means are presented ±1 SE

Results

Direct Field Observations: Neonate Larvae. Some of the focal observations were truncated because lacewings were lost from view or were killed by other predators before the 4-h observation was completed; the resulting mean duration of observations was 3.30 ± 0.10 h ($N = 136$). The primary food resource used by neonate lacewing larvae was soft-bodied arthropod prey, including both herbivorous and omnivorous species (Table 1). Lacewing larvae also frequently consumed extrafloral nectar: 21.3% (29/136) of the larvae fed on extrafloral nectar. The mean duration of an extrafloral nectar feeding bout was 54.2 ± 8.9 s ($n = 36$). Thirty-three of the 36 nectar feeding bouts were at foliar nectaries, whereas the remaining three were on circumbracteal nectaries; rare instances of feeding on subbracteal extrafloral nectaries might also have occurred, but because these nectaries are located underneath the bracts, the larvae were out of view when foraging there. A few lacewings ($N = 6$) also were observed inserting their mandibles into leaf veins (mean bout duration = 115.8 ± 47.6 s, $n = 6$).

We observed a total of 182 prey attacked and consumed by lacewings, of which 141 (77.5%) were aphids. The local availability of aphid prey was estimated by counting aphids on the first leaf contacted by the neonate lacewings (this was either the leaf onto which lacewings were released or the first leaf contacted by lacewings that were released onto plant stems or fruits; lacewings spent an average of 71.2% of the total observation period on this first-contacted leaf). The time spent consuming extrafloral nectar was correlated negatively with the density of aphids on the first-contacted leaf (Spearman's rank correlation, $r_s = -0.29$, $N = 136$, $P < 0.001$), indicating a shift from the utilization of arthropod-based resources to the utilization of plant-based resources as prey availability declined (Fig. 1).

The negative correlation between local aphid density and consumption of extrafloral nectar could be produced by either of two nonmutually exclusive processes. First, the amount of time lacewings spent actively foraging decreased as local aphid density increased ($r_s = -0.47$, $N = 136$, $P < 0.001$). Thus, it is possible that lacewings simply had fewer encounters with extrafloral nectaries when aphid prey were more abundant. Second, it is possible that lacewing larvae that succeeded in consuming aphid prey might either reject opportunities to feed on extrafloral nectar or might take shorter nectar-feeding bouts. To distinguish these two possibilities, we conducted multiple regression analyses to assess the influences of local aphid density and total foraging time (the independent variables) on the time spent consuming extrafloral nectar (the dependent variable). Because the distribution of nectar feeding times across replicates was highly non-normal, we followed the procedure recommended by Conover (1999): we first conducted the standard, parametric multiple regression proce-

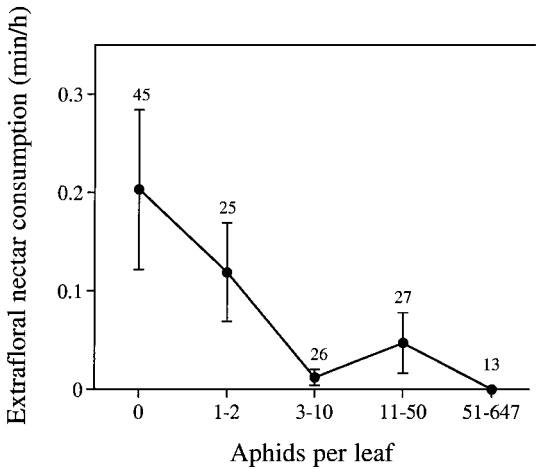

Fig. 1. Influence of aphid prey availability on the consumption of extrafloral nectar by neonate *Chrysoperla plorabunda* larvae (minutes spent consuming extrafloral nectar per hour that the larva was observed). Means ±1 SE; numbers are sample sizes.

dure (for which we log-transformed local aphid density) and then repeated the analysis after rank-transforming all the variables (both independent and dependent). The standard multiple regression showed that foraging time was the sole significant predictor of extrafloral nectar feeding ($F = 5.75$, df = 1, $P < 0.05$); partial correlation coefficient = 0.20); once foraging time was entered into the regression model, aphid density failed to explain a significant amount of the residual variance ($F = 1.04$, df = 1, P = not significant; partial correlation coefficient = −0.09). The multiple regression on the rank-transformed data yielded entirely congruent results: foraging time was again the sole significant predictor of nectar feeding ($F = 12.8$, df = 1, $P < 0.001$), and local aphid density did not explain a significant amount of the residual variance ($F = 2.8$, df = 1, P = not significant).

Direct Field Observations: All Instars. Only a single instance of extrafloral nectar consumption was observed when first-, second-, and third-instar lacewing larvae ($N = 15$) were observed foraging on cotton in the field (Table 2). Seven of the 11 (63.6%) lacewings observed foraging freely in almond orchards for 1 h consumed extrafloral nectar (Table 2). The proportion of lacewing larvae consuming extrafloral nectar in almonds was greater than that observed in cotton ($G = 10.0$, $P < 0.01$).

Field Diet Experiment. No mortality was observed through day 5 of the experiment in either of the treatments in which aphid prey were provided. The four diet treatments that did not include aphid prey had significantly different effects on neonate lacewing survival (log-rank test, $\chi^2 = 22.7$, df = 3, $P < 0.001$). Lacewing larvae lived an average of 1.5 ± 0.2 d in the no-leaf treatment, 1.3 ± 0.2 d in the leaf only treatment, 1.9 ± 0.1 d in the water treatment, and 12.9 ± 2.0 d in the extrafloral nectar treatment (Fig. 2). In

Table 2. Extrafloral nectar feeding by *Chrysoperla plorabunda* larvae observed foraging freely in the field during 1-h focal observations

Instar	No. of larvae observed	Mean ± 1 SE number of extrafloral nectar feeding bouts	Mean time per feeding bout, s
		Cotton fields	
First	8	0	0
Second	3	0	0
Third	4	0.25 ± 0.025	43
		Almond orchards	
First	2	2.0 ± 2.0	43.8 ± 32.3
Second	5	3.2 ± 2.1	23.4 ± 7.6
Third	4	0.5 ± 0.3	20.5 ± 9.5

four of the 20 replicates in which lacewings were given access to the foliar nectary, the nectary ceased secreting nectar during the trial: one replicate of the aphids plus extrafloral nectar (dry by day 5) and three replicates of the extrafloral nectar treatment (dry by days 1, 14, and 19). Thus, the one larva that died immediately in the extrafloral nectar treatment was actually deprived of access to nectar, and otherwise the larvae in this treatment showed 100% survival through day 5, just as did those larvae given aphid prey. There was no significant difference between the no-leaf and leaf-only treatments (log-rank test, $\chi^2 = 0.8$, df = 1, P = not significant). Lacewings in the water treatment exhibited significantly reduced mortality compared with the leaf-only treatment ($\chi^2 = 7.8$, df = 1, $P = 0.005$). The longevity of larvae in the extrafloral nectar treatment was significantly greater than that observed in the leaf-only treatment ($\chi^2 = 15.4$, df = 1, $P < 0.001$) but only marginally nonsignificantly greater than that observed in the water treatment ($\chi^2 = 3.9$, df = 1, $P = 0.048$).

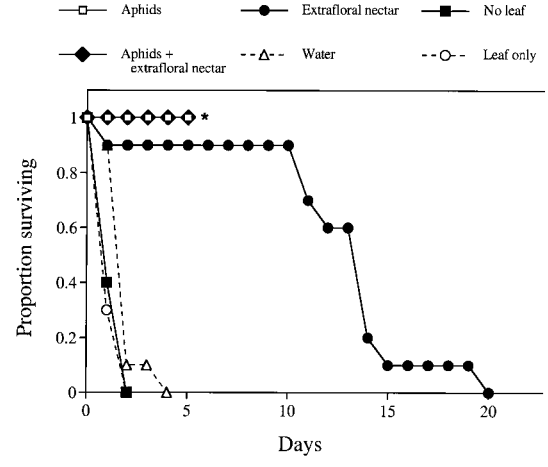

Fig. 2. The proportion of *Chrysoperla plorabunda* larvae surviving in small cages in the field under six diet treatments. * Indicates that two of the treatments (aphids, aphids + extrafloral nectar) were terminated on day 5 of the experiment.

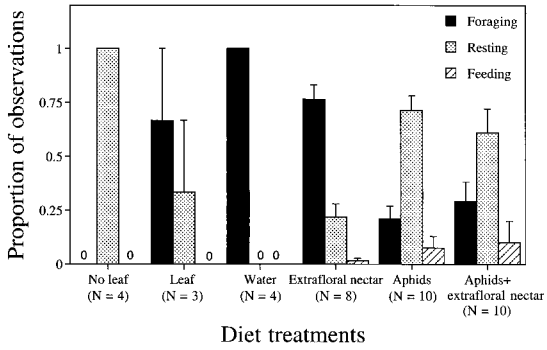

Fig. 3. Behavior of larval *Chrysoperla plorabunda* observed in small cages in the field and given access to different diets. Behavior was observed daily; shown are means ± 1 SE. *N* = the number of replicates in which the larva lived long enough to be observed at least once.

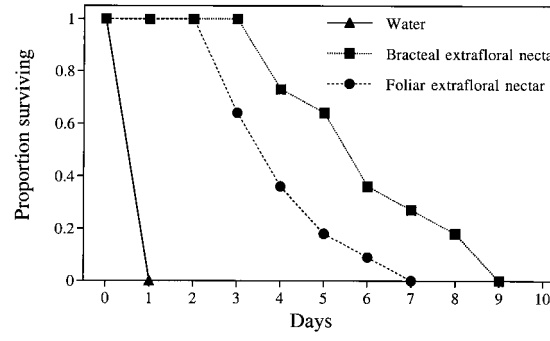

Fig. 4. Survivorship of larval *Chrysoperla plorabunda* fed different diets in the laboratory.

The diet treatments also had significant effects on larval development, as measured by the probability of lacewings reaching the second instar. None of the larvae in the no-leaf, leaf-only, or water treatments ever molted to the second instar. Similarly, no larvae in the extrafloral nectar treatment molted to the second instar, including those individuals that lived for more than 2 wk. In contrast, 100% (8 of 8) of lacewings in the aphids treatment and 78% (7 of 9) of lacewings in the aphids + extrafloral nectar treatment reached the second instar during the first 5 d of the experiment. The proportions of lacewings reaching the second instar in the aphids and aphids + extrafloral nectar treatments were not significantly different (G = 0.9, *P* = not significant). There was also no significant difference between the day 5 live weights of lacewings in the aphids treatment (mean = 1.09 ± 0.10 mg, *N* = 8) versus the aphids + extrafloral nectar treatment (mean = 1.26 ± 0.20 mg, *N* = 9) ($t = -0.77$, df = 15, *P* = not significant).

Larvae in the extrafloral nectar treatment spent a significantly greater proportion of their time actively foraging (mean = 0.77 ± 0.07, *N* = 8) than did larvae in diet treatments including aphid prey (aphids and aphids + extrafloral nectar treatments combined: mean = 0.25 ± 0.05, *N* = 20; $t = 5.4$, df = 26, $P < 0.001$; Fig. 3). Neonate larvae in the no-leaf, leaf-only, and water treatments all stopped foraging and died within an average of 1–2 d, but as with larvae in the extrafloral nectar treatment, foraging activity was high until the larvae were very near to death (larvae in the no-leaf treatment were all alive but moribund when checked on day 1). Thus, the extrafloral nectar supported not only substantial longevity but also a prolonged period of intense foraging activity.

Laboratory Diet Experiment. *Chrysoperla plorabunda* larvae lived an average of 1.0 ± 0.0 d on water (*n* = 10), 4.2 ± 0.4 d on foliar extrafloral nectar (*n* = 11), and 6.2 ± 0.6 d on bracteal extrafloral nectar (*n* = 11) ($\chi^2 = 35.6$, df = 2, $P < 0.001$; Fig. 4). The water-only treatment was significantly different from each of the extrafloral nectar treatments ($P < 0.001$). Lacewings lived significantly longer on bracteal extrafloral nectar than on foliar extrafloral nectar ($\chi^2 = 6.4$, df = 1, $P < 0.05$).

No larvae reached the second instar on the water or nectar diets. Wet weight of the freshly dead (less than 24 h postmortem) larvae on the water treatment (mean = 9.9 ± 0.7 mg) was significantly lower than the weight of the freshly dead larvae on the foliar extrafloral nectar (mean = 15.0 ± 0.6 mg) and bracteal extrafloral nectar (mean = 16.3 ± 1.0 mg) treatments (both $P < 0.001$), further indicating that the extrafloral nectar was providing resources other than water. Postmortem wet weights of larvae in the leaf versus bracteal extrafloral nectary treatments were not significantly different ($t = -1.1$, df = 20, *P* = not significant).

Foraging activity data were not obtained for larvae in the water-only treatment because all larvae died before the first daily observation. Larvae spent a large proportion of their time foraging in both of the extrafloral nectar treatments (foliar extrafloral nectar: 0.50 ± 0.06, *N* = 11; bracteal extrafloral nectar: 0.62 ± 0.06, *N* = 11; the two means are not significantly different: $t = -1.3$, df = 20, *P* = not significant; Fig. 5).

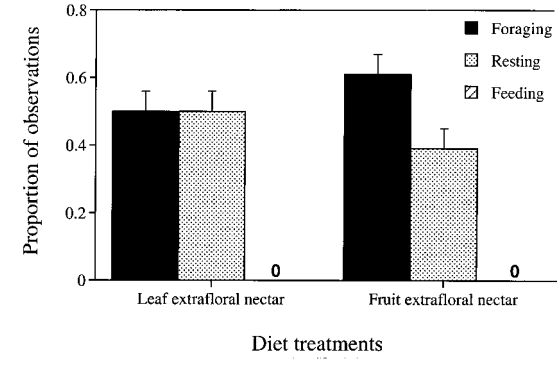

Fig. 5. Behavior of larval *Chrysoperla plorabunda* (*n* = 10 or 11 per treatment) observed in the laboratory and given access to different diets. Behavior was observed daily; means ± 1 SE.

Discussion

Our observations of lacewing larvae foraging freely in the field have confirmed the generally held view that these arthropods are generalist predators, consuming a broad array of soft-bodied arthropod prey (including both strict herbivores and omnivores). The observations also produced a less-anticipated result, that the lacewing diet also includes plant-based food resources: extrafloral nectar was used widely by lacewing larvae foraging on both cotton and almonds. This is the first quantitative demonstration that the larval stages of a green lacewing are omnivorous. The observation of extensive nectar feeding in almonds as well as in cotton suggests that nectar consumption may be a relatively general feature of lacewing biology rather than being linked specifically to cotton.

The consumption of extrafloral nectar in cotton increased strongly as the availability of aphid prey decreased. This trade-off between the consumption of prey and extrafloral nectar did not, however, appear to reflect a 'decision' by lacewings to reject opportunities to feed on extrafloral nectar when aphid prey were abundant. Instead, our regression analyses of factors controlling the time spent feeding on extrafloral nectar suggested the following chain of causation: (1) lacewings that have access to many aphids spend less time foraging, and (2) lacewings that spend less time foraging encounter the extrafloral nectaries less often, and therefore consume less extrafloral nectar. Thus, we suggest that foraging time mediates the trade-off between the consumption of prey and the consumption of extrafloral nectar. Because this result is based upon correlative rather than experimental data, we suggest that it be viewed as a tentatively supported hypothesis, pending additional experimental work.

The conclusion that lacewing larvae are omnivorous is only important if the plant-based foods support lacewing foraging activity, survival, or development. Our field and laboratory diet experiments were designed to answer questions about the functional significance of plant-based resources. Our field observations revealed that a small proportion of neonate lacewing larvae (6 of 136) inserted their mandibles into leaf veins; were these lacewings obtaining important resources from the veins? The field experiment suggested that the leaf vein did not support lacewing survival; all of the larvae in the 'no leaf' and the 'leaf only' treatments were dead within 2 d, and the treatments were statistically indistinguishable. Thus, the function of piercing the leaf vein remains unknown. Leaf veins did not appear to provide a source of water, because when lacewings were given an artificial water supply they exhibited substantially enhanced longevity compared with the 'leaf only' treatment. Extrafloral nectar consumption provided benefits that extended beyond those provided by water alone; both the field and laboratory experiments showed that lacewings given access to extrafloral nectar lived much longer than those given only water. Although the laboratory experiment showed that lacewings were able to use nutrients present in extrafloral nectar to grow slightly, both the field and the laboratory experiments showed that lacewings fed only extrafloral nectar were unable to molt to the second instar. Nevertheless, extrafloral nectar did allow lacewings to forage intensively for more than 10 d; such sustained foraging should provide excellent opportunities for lacewing larvae foraging in nature to locate even low-density prey.

First-instar lacewing larvae given access to abundant aphid prey did not show any additional benefits from having access to foliar extrafloral nectar; thus, nectar does not appear to provide important nutrients beyond those supplied by aphid prey. However, our observation that bracteal nectar supports greater longevity than foliar nectar suggests that within-plant variation in extrafloral nectar quality may be significant, and we did not test the possibility that bracteal nectar might enhance an aphid-based diet. Further work is needed to examine this possibility, as well as the value of feeding on extrafloral nectar by later larval instars.

We conclude that lacewing larvae are true omnivores, feeding on plant-based resources (extrafloral nectar), on herbivorous arthropod prey (e.g., aphids), and on other predatory or omnivorous arthropods (including *O. tristicolor* and *Geocoris* sp.). Thus, both the larval and the adult stages of lacewings (Hagen 1986) may benefit significantly from consuming plant-based resources.

What do these observations say about the likelihood that lacewing larvae are experiencing mortality due to starvation under natural field conditions in the cotton agroecosystem? If one assumes that the diet experiments produced natural levels of nectar availability to lacewings (see below), it seems likely that extrafloral nectar would allow lacewings to survive through transient periods of prey scarcity. Lacewing development was arrested when larvae fed on extrafloral nectar in the absence of arthropod prey, with larvae remaining in the first instar for up to 19 d (Fig. 2). (Development can proceed from neonate larva to the pupal stage in approximately 12 d when prey are abundant [Zheng et al. 1993]). Two forms of evidence derived from earlier work suggest that lacewings forage quite efficiently for aphid prey on cotton plants. First, direct field observations of neonate lacewings showed that they can achieve near-maximal rates of aphid consumption even when aphid densities are quite low (four aphids per leaf; see Rosenheim et al. 1999). Second, field experiments showed that lacewing survival and development are not significantly enhanced when aphid densities are increased experimentally from 5 to 10 aphids per leaf to >100 aphids per leaf (Rosenheim 2001), suggesting that aphid prey are not limiting at the lower densities. Together, these results suggest that the scarcity of aphid and other arthropod prey would have to be severe (i.e., less than four aphids per leaf) and prolonged (≥2 wk) before prey limitation would produce substantial lacewing starvation.

Several caveats are in order, however. The diet experiments provided ad libitum access to nectar; the cages facilitated the location of the extrafloral necta-

ries by lacewings (by caging the lacewings on a small section of the leaf harboring the nectary) and excluded all other arthropods known to consume extrafloral nectar. Although casual observations of cotton plants during the mid- and late season yield the impression of high availability of extrafloral nectar, and the observations reported above show that even the smallest lacewing larvae are able to locate the foliar extrafloral nectaries, it is also clear that many other arthropods use this nectar resource (Yokoyama 1978, De Lima and Leigh 1984). The possibility that exploitative competition could drive levels of nectar availability below those required by lacewing larvae (or other arthropods) has not been explored. Ants are known to be among the most dominant consumers of extrafloral nectar (Koptur 1992). Although ants (mostly *Solenopsis xyloni* McCook) are sometimes observed on cotton plants feeding at nectaries, ant populations are strongly suppressed by soil tillage in cotton fields, and ants are rarely present on more than a small minority of plants within a field (J.A.R., unpublished data). It has been demonstrated, however, that the quantity and sugar content of extrafloral nectar in leaf nectaries varies seasonally (Yokoyama 1978). The volume of extrafloral nectar produced by some *Gossypium* spp. may also increase following herbivory (Agrawal and Rutter 1998). The laboratory diet experiment reported here demonstrates variation in the quality of extrafloral nectar: nectar secreted by the foliar nectaries, which is produced in greatest abundance during July and August (Yokoyama 1978), was a lower-quality resource than the nectar secreted by the subbracteal and circumbracteal nectaries, which continues to be produced in large quantities until the crop is harvested (unpublished data). Thus, both the quality and quantity of extrafloral nectar available to lacewing larvae may vary seasonally and as a result of competition with the local arthropod community.

The hypothesis that lacewings are starving under field conditions needs to be evaluated against the backdrop of lacewing omnivory. Because lacewings exploit a diversity of food resources, it may be difficult to quantify meaningfully the availability of usable foods. An approach to assessing food limitation that focuses on the physiological state of the lacewing therefore may be preferable to one focusing on the food resources. Body condition indices (Jakob et al. 1996), physiological condition bioassays (Bilde and Toft 1998), and simple biochemical assays to quantify carbohydrate or fat reserves (e.g., Yuval et al. 1994, Ellers et al. 1998) may be valuable tools for assessing food limitation.

The highly variable duration of lacewing larval instars revealed by the field diet experiment and by previous studies (Zheng et al. 1993) suggests the hypothesis that resource availability and higher-order predation may interact in their effect on lacewing survival. Lacewings that survive periods of prey scarcity by consuming extrafloral nectar will remain in the highly vulnerable neonate larval stage for an extended period, because extrafloral nectar does not support lacewing development. These lacewings whose development is suspended are likely to be exposed to an amplified risk of predation. For example, given a previously estimated rate of predation for neonate *C. plorabunda* larvae of 0.0202 predation events per hour, the probability that a lacewing would reach the age of 12.9 d (the mean age attained by neonate lacewings given access to nectar) is only 0.19% (i.e., one in 520 individuals). Thus, as has been observed in other predator-prey and host-parasitoid systems (Krebs et al. 1995, Benrey and Denno 1997), effects of resources and effects of predators may be functionally integrated, and it may be most meaningful to consider their joint effects rather than attempting to consider them in isolation.

The results reported here for *C. plorabunda* adds to the growing appreciation of the ecological significance of the catholic diets displayed by omnivorous arthropod predators. Lacewing larvae, like other better-studied omnivorous taxa, such as thrips (Agrawal et al. 1999, Agrawal and Klein 2000), true bugs (Alomar and Albajes 1996, Coll 1998), and phytoseiid mites (McMurtry and Croft 1997, Nyrop et al. 1998), are able to shift between a diet comprised of arthropod prey and one composed of plant-based resources during periods of prey scarcity. This ability may be central to the success of lacewings in highly disturbed annual agroecosystems, where arthropod prey populations may fluctuate widely and transient periods of prey scarcity are common.

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