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Physiological benefits of nectar feeding by a predatory beetle

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Extrafloral nectar is an important food source for many animals, including predatory lady beetles (Coleoptera: Coccinellidae), although the physiological benefits of nectar consumption are poorly understood for most consumers. Under laboratory conditions, we confined new females of *Coleomegilla maculata*, a North American lady beetle, to *Vicia faba* plants with or without extrafloral nectaries for 10 days; after this, the beetles were moved onto a high-quality diet for an additional 15 days. Survival, fecundity, and oocyte size and development before and after consuming a high-quality diet were compared between treatments. Colorimetric assays were used to quantify the glycogen and lipid reserves of the beetles before and after exposure to a high-quality diet. Extrafloral nectar increased the survival of *C. maculata* by 50%, and increased fecundity by 30%, over starved individuals. Oocytes prior to and following exposure to a high-quality diet were significantly larger in females fed nectar than in females that were not fed nectar. Finally, glycogen reserves were higher following the prey-free period in the nectar-fed treatment than the starved treatment, but this deficiency did not persist once a high-quality diet was provided. We conclude that nectar improves the survival and nutrient reserves of predators during periods of prey scarcity, and that the availability of nectar during these periods improves the long-term reproductive capacity of predators.

ADDITIONAL KEYWORDS: Coccinellidae – extrafloral nectar – lady beetle – nutrient reserves – reproduction – sugar feeding – survival.

INTRODUCTION

Nectar is an important factor in mitigating interactions between plants and animals, and its availability and consumption is important to both the producer and the consumer (Lundgren, 2009b). The importance of nectar in mitigating interactions between plants and animals is best understood in cases of plant–pollinator relationships (James & Pitts-Singer, 2008). But extrafloral nectar also has important implications for the success of plants: it primarily functions as an indirect defence against herbivory by aggregating the herbivore's natural enemies (Bentley, 1977; Kost & Heil, 2005; Heil, 2007). Although nectar sometimes contains low levels of amino acids and other micronutrients (Baker & Baker, 1973), from a nutritional standpoint this substance is primarily a source of sugar (usually, mono- and disaccharides) (Baker, 1975; Adler, 2000; Petanidou, 2005). Most animals are capable of digesting simple sugars, and as such, unprotected nectar is widely acceptable and sought after by a wide range of vertebrate (Nicolson, 2007; Brown, Downs & Johnson, 2008; Fleming & Muchhala, 2008) and invertebrate animals (Pemberton & Vandenberg, 1993; Cuautle & Rico-Gray, 2003; Heil, 2007; Lundgren, 2009b). Although many animals readily consume nectar, the metabolic uses of nectars and other sugar sources remain largely unknown for many species, especially predators (Heil, 2008).

Studies have shown that different animals use nectar to fulfill various physiological functions, and invariably the importance of nectars and other sugars is dependent on the relative availability of other food sources, and on their quality, and the environmental

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conditions that they face. The benefits of nectar are most acute when other, higher quality foods are scarce. Nectar and other sugars are particularly important in fulfilling the immediate, metabolic needs of an animal, such that they can devote nutrient reserves and foods with higher nutritional quality toward nutrient-intensive functions like reproduction or diapause (Brian, 1973; Lundgren, 2009b; Taylor & Pfannenstiel, 2009). In this way, when food is limited, sugar meals can increase the likelihood of survival until other food sources become available. Nectar is molecularly simple, and most animals can use this ready source of energy with little digestive investment. As such, nectar meals are important in supporting high-energy needs like flight, foraging, or aggression (Hausmann, Wäckers & Dorn, 2005; Tschinkel, 2006; Wanner, Gu & Dorn, 2006; Grover *et al*., 2007; Taylor & Bradley, 2009; Amitai *et al*., 2010). Finally, nectar and other simple sugars are seldom nutritionally sufficient to support the reproduction of animals, but sugar meals in concert with other, higher quality foods may increase reproductive capacity over these foods on their own (Geng *et al*., 2006; Venzon *et al*., 2006; Lundgren, 2009a; Taylor & Pfannenstiel, 2009). Predatory insects are one such group of animals where nectar and sugar is believed to be an important component of their optimal diets.

Lady beetles are a conspicuous and widespread group of insects that occur in many temperate food webs. Although best appreciated as predators of other insects, most lady beetles are more accurately described as omnivores (Hagen, 1962; Hodek & Honěk, 1996; Lundgren, 2009a). Lady beetles regularly supplement their diet with fungal spores, pollen, fruit, vegetation, and sugar (Forbes, 1883; Triltsch, 1999; Lundgren, Razzak & Wiedenmann, 2004; Moser, Harwood & Obrycki, 2008; Lundgren *et al*., 2011). Although nectar consumption by lady beetles is often observed under field conditions (Ewing, 1913; Stephenson, 1982; Pemberton & Vandenberg, 1993; Ricci, Ponti & Pires, 2005), very little quantitative, field-based data are available on how often lady beetles consume nectar and other sugar sources under field conditions, or what the implications of this nutrition are for lady beetle life histories. Using gut content analysis, Seagraves *et al*. (2011) found that many of the lady beetle species within an agroecosystem frequently consumed fructose, a plant-based sugar, and these authors suggested that sugar feeding had an important place in the diets of these insects. The current study is aimed at substantiating that nectar feeding affects the survival, reproductive capacity, and nutrient reserves of the common North American lady beetle, *Coleomegilla maculata*, when this predator is food limited in the laboratory. To accomplish this, we selected the extrafloral nectary (EFN)-bearing plant *Vicia faba* as a model system. This plant has well-characterized stipular nectaries that are clearly distinguished from surrounding tissues by their deep violet coloration (Davis, Peterson & Shuel, 1988). Several recent studies have used this plant to investigate the importance of EFN in plant–insect interactions (Mondor & Addicott, 2003; Katayama & Suzuki, 2004; Mondor, Tremblay & Messing, 2006; Laird & Addicott, 2007; Jaber & Vidal, 2009). Several coccinellid species have been observed to consume nectar from *V. faba* in the field (Pemberton & Vandenberg, 1993), and *C. maculata* readily locates and consumes EFN from this plant's nectaries (J.G.L., pers. observ.). Although *C. maculata* is an important predator in many systems, it best represents the more omnivorous species along the dietary continuum within predaceous insects (Evans, 2009; Giorgi *et al*., 2009; Lundgren, 2009a).

MATERIAL AND METHODS

Organisms

The *C. maculata* specimens used in this study originated from a population collected in Beltsville, MD, USA, that had been reared continuously, but that also received annual infusions of field-collected individuals. The experimental beetles had been reared from the eggs of 30 females on water and an excess of Lundgren's Super C. mac diet (Lundgren *et al*., 2011). Mean ± SEM wet weight at eclosion was equivalent in the two treatments ($F_{1,118} = 0.33$; $P = 0.57$). Each newly eclosed beetle was given an initial meal of three *Myzus persicae* (Sulzer, 1776), and was randomly transferred to one of the treatments within 2 days of eclosion.

Fava beans (*V. faba* L.) were produced in a glasshouse in soil mix (field soil, peat moss, and vermiculite in a 4 : 2 : 1 ratio), and were watered daily. When the plants had between three and six nodes with fully expanded leaves, their root masses were submerged in water to clean the excess soil from the roots, and then individual plants were placed in a 50-mL plastic centrifuge tube filled with water. Parafilm (Pechiney Plastic Packaging, Menahsa, WI, 54952) was wrapped over the tube opening and around the plant stem. On half of the plants, exposed extrafloral nectaries were covered with small pieces of Parafilm; the other half of the plant population had a similar-sized piece of Parafilm wrapped around randomly selected stems and petioles. Each plant was then placed individually into a plastic cup (710 mL; Solo, Urbana, IL, USA) with the tube protruding through a hole in its bottom. An identical cup was placed mouth-to-mouth with the cup holding the plant (these were then sealed with

Parafilm), and a mesh screen was placed over the top of the enclosure.

Nectar consumption by predators

The frequency of nectar consumption by *C. maculata* females was assessed using the cold anthrone test. Three prey-free *V. faba* plants (at least at the six-leaf stage) were placed into a single cage ($30 \times 30 \times 51$ cm); these plants were actively secreting extrafloral nectar. Forty *C. maculata* females were released into the cage and allowed to feed for 24 h. Following this exposure, the beetles were recollected, surface washed with water, and frozen at –20 °C until they could be processed.

The guts of the insects were dissected microscopically, and were each placed in a 1.5-μL micocentrifuge tube with 50 μL of saline solution [750 mg $NaCl_2$ (product #S271; Fisher Chemical Company, Fair Lawn, NJ, USA), 350 mg KCl (product #P217; Fisher), and 280 mg $CaCl_2$ (product #349615000; Acros Organics, NJ, USA) in 1 L water]. The insects were ground with a plastic pestle and then vortexed in 450 μL of methanol-chloroform (2 : 1) for 10 s. The samples were centrifuged for 4 min at 16 100 *g*, and 200 μL of the supernatant was added to each of two glass test tubes (one for testing fructose content and one for use as the no-anthrone control). The fluids were reduced to approximately 50 μL at 90 °C, at which time 950 μL of anthrone solution (a 72% sulfuric acid solution with 750 mg of anthrone; product #319899; Sigma-Aldrich, St Louis, MO, USA) or sulfuric acid solution only was added to each tube and vortexed for 10 s. To quantify the fructose content, a sugar absent in insects that have not consumed plant material or exudates, the subsamples were held at 34 °C for 1.5 h (cold anthrone test). Optical densities (OD) at 625 nm of a 200-μL aliquot of each sample were recorded from 96-well plates using a spectrophotometer (BioTek μQuant; Winooski, VT, USA). Samples were considered as positive if their optical densities exceeded the level of the no-anthrone control by three times the standard deviation of a starved beetle control series run on the same plate ($N = 8$). These unfed beetles have a low but detectable OD, with slight variation among them. The frequency of the 40 beetles testing positive for fructose was recorded.

Nectar availability and fitness parameters

One-hundred and twenty *C. maculata* females were randomly and evenly assigned to *V. faba* plants with exposed or covered EFNs; a timetable of the following experimental procedures is presented in Table 1. This experiment was conducted in two replicates of 30 individuals per treatment because of constraints on the resources available. Specimens were examined every 48 h for mortality during this period. Plants were replaced as needed, and the occasional new nectaries were covered with Parafilm as the plants grew. Beetles were reared with just the plant and a water-saturated cotton wick for 10 days. Following this exposure, the females were split into two treatments. The first was frozen at –80 °C to determine the effects of nectar availability on fat/glycogen levels and ovarial maturation.

Table 1. Timetable of procedures enacted over the 25-day experiment

	Day of experiment	Sample size	Experiment event	Additional details
Nectar phase	1–10	T1: 60	Females (2-days old) were randomly assigned to two treatments and	Survival monitored daily
		T2: 60	received no other food aside from the plant for 10 days	
	10	T1: 28	Initial cull of beetles	Initial oocytes measured
		T2: 14		Initial nutrient contents measured
High-quality diet phase	10–12	T1: 27	Females were mated	Switched to high-quality diet
		T2: 17		
	12–25		Maintained individual females on high-quality diet	Daily fecundity and survival was monitored
	25	T1: 27	Remaining beetles killed	Final oocytes measured
		T2: 13		Final nutrient contents measured

Note that this experiment was replicated twice using equal initial sample sizes of 30 beetles per treatment, per replicate. The treatments varied only during the nectar exposure phase of the experiment. Here, treatment 1 (T1) beetles received plants with the nectaries exposed, whereas T2 beetles received plants with the nectaries covered.

The second cohort was mated for 24 h with two males from the colony per female, and then daily oviposition rates and survival were recorded for 14 days. During this period, females received unlimited access to Lundgren's Super C. mac diet, three *M. persicae* every 2 days, and a water-saturated wick, and were housed in a 6-cm diameter plastic Petri dish (#08-757-13A; Fisher Scientific, Pittsburgh, PA, USA). Following their oviposition period, this cohort of females was frozen at –80 °C for subsequent analyses to determine whether nectar availability had any lasting effects on egg maturation and nutritional status.

Females were thawed and their ovarial status was examined before quantifying their lipid and glycogen levels. The head, legs, wings, and elytra were removed from each female in saline solution. The ovaries were carefully excised from each female, and stained for 2 min in methylene blue solution [290 mg methylene blue (product #414241000; Acros Organics) in 1 L water]. The lengths and widths of the three largest follicles in each of the two ovaries were measured microscopically (at 80× magnification, with six follicles from each beetle). The volume of each follicle was calculated as a cylinder, $h \times \pi r^2$, and an average egg volume per female was generated. The remaining corpse and any body fat in the saline solution was moved into a 1.5-mL microcentrifuge tube and refrozen at –20 °C for subsequent nutrient analysis.

The levels of lipids and glycogen found in each corpse were quantified using the colorimetric assays developed by Van Handel (1985a, b). Specifically, each insect (and saline solution) was crushed into a 1.5-mL microcentrifuge tube containing 300 μL of methanol-chloroform (2 : 1) using a sterile plastic pestle. The mixture was centrifuged at 16 100 *g* for 4 min, and the resulting supernatant and pellet were separated into glass test tubes. To quantify the lipid content of the beetle, 40 μL of sulfuric acid was added to the supernatant, and the solution was heated for 2 min at 90 °C. The tubes were cooled on ice, and 975 μL of vanillin-phosphoric acid reagent (600 mg vanillin in 100 mL water, diluted in 400 mL of 85% phosphoric acid; vanillin product #V10-100; Fisher Chemical) was added to each tube. The solution was incubated at approximately 23 °C for 25 min, after which 200 μL was added to the 96-well plate. The optical density was recorded at 490 nm on a spectrophotometer. For a positive control, 200 μL of virgin olive oil [109 μL oil (Italica Imports, Scarsdale, NY, USA) in 100 mL of chloroform] was added to eight wells of the plate. No-lipid controls (200 μL vanillin reagent only) were added to five wells as a negative control. Next, the pellet produced from the original methanol-chloroform extraction was subjected to a hot anthrone assay to quantify the glycogen content of each beetle. Specifically, 975 μL of anthrone reagent was added to each tube, and the resulting mixture was heated at 90 °C for 15 min. Following incubation, 200 μL of each sample was loaded onto a 96-well plate, and optical density was recorded at 630 nm using a spectrophotometer (BioTek μQuant). For a positive control, 200 μL of glycogen solution [25 mg glycogen (from oyster, type II; Sigma-Aldrich) in 25 mL water] was added to eight wells of the plate. No-glycogen controls (200 μL anthrone reagent only) were added to five wells as a negative control.

Data analysis

Survival over the 25-day experiment was compared between the treatments using the non-parametric Mantel test statistic; survival of the cohort killed directly after exposure to the plants was included in the analysis as censored data points. Models were run with and without the latter cohort and the same patterns emerged, regardless of their inclusion. Fecundity (total number of eggs laid) per unit body weight and absorbances from the lipid and glycogen assays (following consuming high-quality diet) were compared between treatments using ANOVA. The number of days until first oviposition event and absorbances from the lipid and glycogen assays (before the high-quality diet) were compared between treatments using Kruskal–Wallis non-parametric ANOVAs, because these data did not conform to parametric ANOVA assumptions. A repeated-measures ANOVA was used to compare the effects of treatment on oocyte size: treatment and replicate were between-subjects effects; oocyte (the six largest from each female were measured), replicate, and treatment were within-subject effects. Data were pooled across replicate unless replicate was determined to be a significant factor, in which case it was included in the analysis. General linear models were created to describe the relationships between absorbances of glycogen and lipid assays and the mean size of oocytes per female both before and after consumption of a high-quality diet. Additional regressions were created to compare these nutrient statuses with the number of eggs laid during the observation period.

RESULTS

Nectar consumption by caged *C. maculata*

Upon release into the cage with *V. faba* plants, we saw several of the 40 females aggregate to the extrafloral nectaries to feed. After 24 h of exposure, 82.5% of *C. maculata* females tested positive for the consumption of fructose.

Survival

Coleomegilla maculata exposed to extrafloral nectaries had higher survival rates than those exposed to covered nectaries (Mantel $\chi^2_1 = 18.56$, $P < 0.001$). Mean (95% CI) survival times were 23.63 ± 1.18 and 16.23 ± 2.11 days for *C. maculata* exposed to and restricted from nectar, respectively (Fig. 1). There were no long-term survival benefits of nectar being available after the two cohorts were moved to high-quality diets.

Fecundity

Nectar-exposed females laid significantly more eggs over 25 days than females without access to nectar ($F_{1,37} = 3.58$; $P = 0.066$) (marginally so). No eggs were laid during the exposure to nectar treatments. The mean (SEM) numbers of eggs laid per beetle were 155.12 ± 14.57 and 111.92 ± 23.13 eggs for beetles exposed to and restricted from nectar, respectively. Those exposed to nectar also laid eggs significantly sooner than those restricted from nectar (Mann–Whitney U statistic = 87.00, $\chi^2_1 = 5.75$, $P = 0.02$). The times to first clutches after mating were 4.8 ± 0.4 and 6.2 ± 0.7 days for females exposed to and restricted from nectar, respectively.

Oocyte status

Directly after exposure to the plants, and before being fed the high-quality diet, females exposed to nectar had developed significantly larger oocytes than those with no nectar (treatment, $F_{1,38} = 4.18$, $P = 0.048$; replicate, $F_{1,38} = 0.04$, $P = 0.85$; interaction, $F_{1,38} = 3.13$, $P = 0.09$). Oocyte volumes were approximately 0.022 ± 0.004 and 0.012 ± 0.002 mm^3 for females exposed to nectar and restricted from nectar, respectively. There were no fully developed oocytes in either treatment at this stage of the experiment.

Even after exposure to the high-quality diet for 15 days, oocytes were significantly larger in nectar-exposed females than in females restricted from nectar, and this relationship was affected by replicate (treatment, $F_{1,36} = 3.78$, $P = 0.06$; replicate, $F_{1,36} = 9.61$, $P = 0.004$; interaction, $F_{1,36} = 0.98$, $P = 0.33$). Oocyte volume was approximately 0.50 ± 0.03 and 0.42 ± 0.06 mm^3 for females exposed to nectar and restricted from nectar, respectively. These sizes represent oocytes that are nearing full development.

Nutrient status

Directly following exposure to the plants, there was significantly more glycogen (Mann–Whitney U statistic = 329.00, $\chi^2_1 = 12.59$, $P < 0.001$), but not lipid (Mann–Whitney U statistic = 253.00, $\chi^2_1 = 2.32$, $P = 0.12$), detected in the females exposed to nectar than in females restricted from it. After consuming the high-quality diet for 15 days, females had similar glycogen ($F_{1,38} = 0.86$, $P = 0.36$) and lipid ($F_{1,38} = 0.06$, $P = 0.82$) contents (Fig. 2).

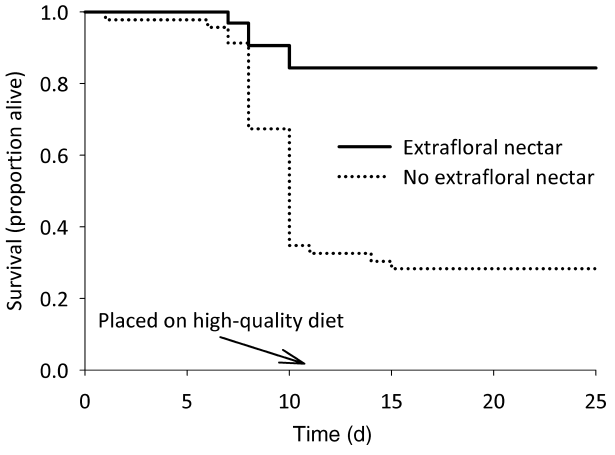

Figure 1. Survival plot of *Coleomegilla maculata* females that were, or were not, exposed to extrafloral nectaries of *Vicia faba*. The exposure period was 10 days, after which point the beetles were mated and transferred onto a high-quality diet. Sample sizes for the two treatments were $N = 32$ and 46 for nectar-exposed and nectar-restricted treatments, respectively.

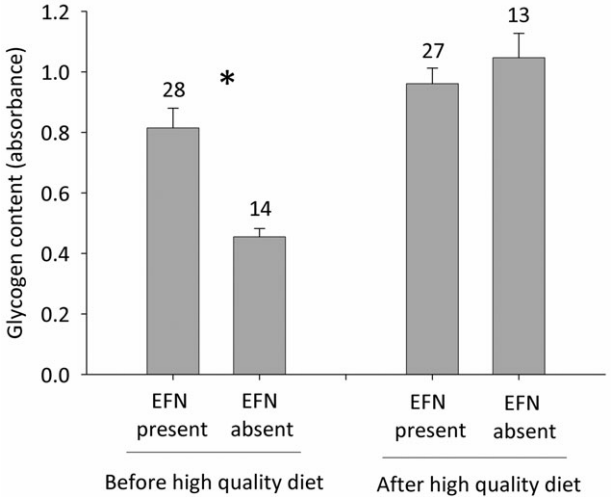

Figure 2. Glycogen content (assessed using the hot anthrone assay) of *Coleomegilla maculata* females exposed to extrafloral nectar or not before and after being reared on a high-quality diet. The exposure to nectar was for a period of 10 days. Sample sizes for each treatment are noted above the bars.
*Significant difference between the two nectar treatments ($P = 0.001$).

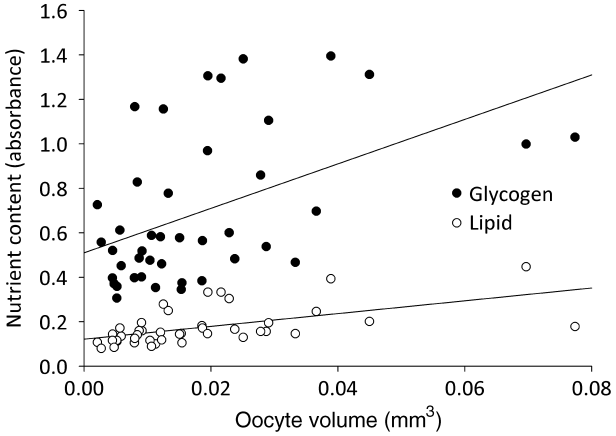

Figure 3. Relationships between glycogen and lipid reserves and the sizes of oocytes found in *Coleomegilla maculata*. Nutrient contents were assessed using the hot anthrone assay and vanillin assay, respectively. The oocyte volume per female was the mean of the six largest oocytes present in the ovaries. Each data point represents information gathered from a single female.

Glycogen ($F_{1,40} = 12.56$, $P = 0.001$) and lipid ($F_{1,40} = 18.38$, $P < 0.001$) contents prior to the consumption of the high-quality diet were strongly correlated with mean oocyte sizes at the time of dissection (Fig. 3). This was also true after the consumption of the high-quality diet for 10 days. Glycogen ($F_{1,38} = 5.56$, $P = 0.02$) and lipid ($F_{1,38} = 6.18$, $P = 0.02$) contents following the consumption of the high-quality diet were strongly correlated with mean oocyte sizes. Also, glycogen ($F_{1,38} = 5.56$, $P = 0.02$) and lipid ($F_{1,35} = 12.66$, $P = 0.001$) contents following the consumption of the high-quality diet were strongly correlated with the number of eggs laid over the observation period.

DISCUSSION

The current work showed that the predator *C. maculata* readily consumes extrafloral nectar in the laboratory (83% of individuals had consumed plant-based sugars within 1.5 h of collection), and that this nectar consumption increases survival, increases long-term fecundity, and improves the nutrient status of this predator over starved individuals. Sugar consumption by parasitoids in the field is relatively well studied (Wäckers & Stepphun, 2003; Heimpel *et al*., 2004; Lavendero *et al*., 2005; Lee, Andow & Heimpel, 2006), but predators have largely escaped quantitative assessments on the frequency of sugar consumption under field conditions (but see Taylor & Pfannenstiel, 2008). Seagraves *et al*. (2011) found that coccinellids frequently consumed sugar in *Glycine max* (soybean) fields of North America, and recorded that 22% of *C. maculata* adults had eaten fructose within 1 h of collection; applying sucrose to the foliage increased the frequency of detection to 78% of specimens. The laboratory assays conducted for the current study provide an additional basis for why sugar, and nectar in particular, is a frequent component of natural enemy diets in the field.

Nectar consumption increases predator survival when prey is scarce. Several studies have documented the importance of sugar consumption to predatory animals when alternative foods are scarce (Lundgren, 2009a, b; Taylor & Pfannenstiel, 2009; Patt *et al*., 2011). These sugar sources come in the form of floral and extrafloral nectar sources, and from honeydew produced by sternorrhynchan herbivores. Sugar meals improve survival in spiders (Araneae), predatory mites, lacewings (Neuroptera: Chrysopidae; Hemerobiidae), predatory heteropterans (Heteroptera: Anthocoridae; Geocoridae), parasitoid wasps (Hymenoptera: Parasitica), and lady beetles (amongst many other taxa) under laboratory conditions. Although nectar is nutritionally simple, with access to extrafloral nectar *C. maculata* had a 50% higher survival rate compared with those without access to nectar (Fig. 1). Indeed, only 15% of the individuals fed sugar died over the 10-day period of stress. It is also noted that the effects on survival in the nectar-free treatment were quickly remedied by providing the beetles with a high-quality diet. Thus, the survival data set indicates that sugar feeding is important in delaying starvation when access to high-quality foods like prey is scarce.

Although nectar on its own is seldom sufficient for predatory animals to produce viable offspring (but see Nomikou, Janssen & Sabelis, 2003), it plays a role in enhancing long-term reproductive capacity when high-quality foods become available. Egg production in animals typically requires protein or lipids. But even diets of rudimentary nutrition may enable the initiation of oogenesis (van Rijn & Tanigoshi, 1999), or at least stop egg resorption during starvation (Heimpel, Rosenheim & Kattari, 1997). Thus, although sugar-only diets do not permit oviposition in the short term, these sugar meals may have important implications for the long-term reproductive potential of a predator when prey is scarce or of poor quality (McMurtry & Scriven, 1964; Evans, 2000; Taylor & Pfannenstiel, 2009) – a concept noted for coccinellids decades ago (Hemptinne & Desprets, 1986; Hodek & Honěk, 1996). Indeed, a recent meta-analysis showed that sugar and nectar increased the reproductive output of coccinellid females in the laboratory over those fed only on prey (Lundgren, 2009a). In a more directed examination of the benefits of sugar (and nectar specifically) for reproduction, the current study revealed that oocytes were 45% larger

in females with access to nectar directly following the 10-day period of prey scarcity compared with females without access to sugar. Moreover, these effects during the starvation period have lasting effects on the fecundity of the female, even after she feeds on a high-quality diet (these results are similar in some parasitoids; Hagley & Barber, 1992). Nectar consumption during the time of food scarcity increased the fecundity of females by 30% over the observation period, relative to those without access to nectar, and the oocytes in nectar-fed females were 16% larger than those in the nectar-starved females, even after a high-quality diet was given to both cohorts. We conclude that feeding on nectar when prey is scarce has lasting benefits to the reproductive potential of this predator.

Both survival and reproduction are tied to the nutrient reserves of a female, and nectar consumption can preserve nutrient reserves over that experienced by starved individuals. Essentially, sugars from nectar are able to accommodate many of the immediate nutritional needs of an insect, and thereby may help reduce the reliance on storage molecules like lipids and glycogen to maintain the physiological status of an insect during starvation. In our study starved females had similar lipid contents, but glycogen was reduced by 45% over 10 days in nectar-starved females compared with nectar-fed females (Fig. 2). Access to a high-quality diet for 15 days remedied any nutrient deficiencies in the starved cohort. These results are different from earlier studies involving parasitoid wasps: in those insects, lipids and glycogen were quickly depleted during starvation, but the availability of sugar was able to defray the depletion of both lipids and glycogen (Olson *et al*., 2000; Lee, Heimpel & Leibee, 2004). The strong relationships between fecundity and ovarial status and storage nutrients are easily seen in the positive and significant correlations between these two fitness metrics (Fig. 3). Our data are in line with the hypothesis that the positive effects of nectar feeding on survival and reproductive capacity are driven in part by the ability of these insects to maintain their glycogen reserves.

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