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Floral Resources Enhance Fecundity, but Not Flight Activity, in a Specialized Aphid Predator, *Hippodamia convergens* (Coleoptera: Coccinellidae)

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Adult aphid predators disperse across the landscape seasonally in search of prey aggregations that are patchily distributed and temporally variable. However, flight is energetically costly and consumes resources that could be invested in reproduction. *Hippodamia convergens* is an important aphid predator in North American cereal crops and other agricultural systems. Consumption of floral resources can enhance adult survival during periods of low prey availability and may improve reproductive success. We tested how an omnivorous adult diet containing floral resources (diluted honey and pulverized bee pollen) interacts with body size to influence reproduction and flight behavior compared to a prey-only diet. Two sizes of beetles were produced by controlling larval access to food—3 h daily access produced small beetles; *ad libitum* access produced large beetles with faster development. Reproductive performance was tracked for 18 days, and female flight activity was assayed via 3 h bouts of tethered flight. Diet composition and body size interacted to influence preoviposition period, with large females in prey-only treatments delaying oviposition the longest. The omnivorous adult diet improved 18-day fecundity relative to a prey-only diet, but egg fertility was unaffected. Adult size affected oviposition pattern, with small beetles laying smaller, but more numerous, clutches. Females flew up to 7 km in 6 h, but neither body size nor adult diet influenced flight distance, suggesting that all diet treatments generated energy reserves sufficient to power flights of short duration. However, pre-reproductive females flew > 60% further than they did post-reproduction, likely due to the energetic costs of oviposition. Thus, access to pollen and nectar increased reproductive success and altered oviposition patterns in *H. convergens*, indicating the importance of floral resources in the agricultural landscape to conservation of this predator and its biological control services.

Keywords: biological control, life history, energetic trade-offs, insect predators, agricultural ecology, omnivory

INTRODUCTION

The convergent lady beetle, *Hippodamia convergens* Guerin-Meneville, is a generalist insect predator that provides biological control services to agriculture throughout North America. It is primarily a predator of aphids, which adults require for reproduction (Hagen, 1962; Michaud and Qureshi, 2006), but it also preys upon the immature stages of many other agricultural pests as both larva and adult (Hodek, 1996; Michaud, 2018). It has long been associated with agricultural crops in North America, where it has proven adaptable to frequent disturbance, low plant diversity, and other characteristics of industrial agriculture (Hagen, 1962; Sloggett and Majerus, 2000). Predacious coccinellids, in general, appear well adapted to agroecosystems and often persist there at higher densities than in adjacent natural areas (Hagen, 1962; Lamb et al., 2019).

In agriculturally intensive regions of North America, large fields host successions of annual monocultures seasonally, their planting dates dictated by each crop's thermal and hydrological requirements. At landscape scale, this results in an agricultural mosaic of resource patches for arthropod herbivores and their predators that is both spatially variable and temporally dynamic across growing seasons (Bianchi et al., 2009). On the High Plains, adult *H. convergens* track aphid populations across the landscape (e.g., Prasifka et al., 2004), moving predictably between crops such as wheat and alfalfa, where overwintered beetles produce a spring generation, to summer crops such as corn and sorghum, where additional generations occur, contingent on the availability of aphids (Rice and Wilde, 1988; Nechols and Harvey, 1998; Michaud and Qureshi, 2006). They are also able to survive extended periods of prey deprivation by consuming various plant-derived resources, including tender green foliage, pollen, and nectar of both floral and extra-floral origin (Hodek, 1996; Michaud and Qureshi, 2005, 2006; Mercer et al., 2020). However, utilization of floral resources in an agricultural landscape also carries a risk of exposure to systemic insecticides now widely employed as seed treatments (Gontijo et al., 2014; Moscardini et al., 2015; Bredeson and Lundgren, 2018) in addition to foliar applications (He et al., 2012).

Supplemental foods of plant origin not only support the survival of predaceous coccinellids in the absence of animal prey (Hodek, 1996; Hatt and Osawa, 2019) they are often necessary for the beetles to achieve maximal fitness (Lundgren, 2009; Michaud, 2018; Stowe et al., 2021). Consequently, these resources are also consumed during periods of prey abundance (Berkvens et al., 2010; Hodek and Evans, 2012; Choate and Lundgren, 2013; Ugine et al., 2019), and may be selectively consumed when particular nutrients are lacking in the diet (Schuldiner-Harpaz and Coll, 2017). The inclusion of plant resources in the diet of aphidiophagous coccinellids can facilitate earlier onset of oviposition (Hatt and Osawa, 2019) and enhance egg fertility (De Clercq et al., 2005; de D'Ávila et al., 2017). Dietary self-selection of foods rich in specific macronutrients is well documented in many insects (Jensen et al., 2012), both under normal conditions (Jones and Raubenheimer, 2001; Mayntz et al., 2005), and in response to physiological deficits (Raubenheimer and Jones, 2006; Raubenheimer et al., 2007). Ratios of macronutrients in

the diet can influence insect reproduction and flight behavior by affecting the availability of metabolic precursors and titers of metabolites and hormones, as exemplified by anautogenic mosquitos (Attardo et al., 2005; Hansen et al., 2005). In the case of facultatively omnivorous predators such as *H. convergens*, the consumption of plant resources could influence energetic trade-offs between dispersal and reproduction. An improved understanding of any such tradeoffs, and the role of plant-derived nutrients in mediating them, could provide key insights for conserving the biological control services provided by these predators in agricultural landscapes.

Flight is a behavior critical to the survival and fitness of *H. convergens* because adult beetles must track populations of their ephemeral aphid prey across large spatial scales in the agricultural landscape in order to achieve reproductive success (Hagen, 1962; Wissinger, 1997; Michaud, 2012). Dispersal by flight can be critical to biological control efficacy as insect predators move among crops, and flight behavior will have a significant impact on energy budgets (Bonte et al., 2012). Dietary effects on flight capacity could potentially affect the range of beetle movement, and thus the ability of beetle populations to track and control pest populations. As yet, relatively few studies have examined *H. convergens* flight behavior (but see Rankin and Rankin, 1980; Davis and Kirkland, 1982; Abdel-Wahab et al., 2017), and none have addressed the potential of plant-derived resources to affect flight capacity. The present study was designed to examine how access to floral resources might affect flight capacity and distance flown by *H. convergens* females, and how the energy expended in flight might exact a cost in terms of reproductive performance. Because body size is a key morphological trait that affects both wing loading (Byrne et al., 1988), and potential fecundity (Vargas et al., 2013), we created two size classes of adult beetles by controlling larval access to food. We hypothesized that both larger adult size and access to floral resources would benefit reproductive success, and enable beetles to fly longer distances when compared to smaller beetles, and those with access only to prey. We also hypothesized a negative correlation between flight distance and reproductive success, a trade-off that should be more pronounced in smaller beetles with fewer energy reserves. Finally, we used structural equation modeling to explore direct and indirect relationships between adult body size, diet composition, and reproductive and flight metrics to determine if early energy expenditures influence later performance.

MATERIALS AND METHODS

Insect Colonies

Adult *Hippodamia convergens* beetles (ca. 120 individuals) were collected from wheat fields at the Agricultural Research Center-Hays, in Hays, Kansas (38°51′32.1″N 99°20′07.7″W) in early June, 2020. Beetles were placed in a 1 L glass mason jar covered with muslin netting and held in a climate-controlled growth chamber set to 24 ± 1°C, 50–60% RH, and a 16:8 (L:D) photoperiod. Wax paper strips were placed in the jar as harborage, water was provided on a cotton wick, and 10–20 mg of

frozen eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) were added to the jar every 48 h. Because *H. convergens* are often parasitized by *Dinocampus coccinellae* Shrank (Hymenoptera: Braconidae), the colony was examined daily for the first week to remove all emerging parasitoid larvae before they could pupate or energy as wasps. Under these conditions, beetles remain in reproductive diapause and can be held for extended periods (Michaud and Qureshi, 2006).

A colony of greenbug, *Schizaphis graminum* Rondani, was established from material collected from the same wheat field as the beetles. Aphid colonies were reared in metal trays of wheat seedlings in a mixture of soil, vermiculite, and peat moss (1/1/1). Trays were germinated in a greenhouse and then were moved to growth chambers set to $22 \pm 1°C$, 50–60% RH, and a 16:8 (L:D) photoperiod. Plants were infested at the 2-leaf stage by spreading infested wheat cuttings over fresh trays of seedlings.

Experimental Beetles

For the experiment, parental females ($n = 29$) were isolated in plastic Petri dishes (5.5 cm diam) and held in a climate-controlled growth chamber under the same conditions as the stock colony. Females were provisioned with greenbugs *ad libitum* to induce oviposition and the fertility of each female was confirmed by verifying the eclosion of eggs in her initial clutches. Once a sufficient number of fertile females were ovipositing ($n = 29$), a single day's oviposition was collected from each for incubation. were collected from eclosing clutches on 18 September, 2020. Neonate larvae were permitted to consume their chorions and disperse from their natal egg mass before they were collected and isolated in Petri dishes (as above). Neonates observed cannibalizing conspecific eggs or other larvae were excluded from the experiment, as cannibalism can alter developmental times (Michaud and Grant, 2004; Bayoumy and Michaud, 2015). Each larva was labeled according to maternal lineage ($n = 29$) to ensure that similar numbers of offspring from each lineage were assigned to each treatment (ca. $n = 24$ couples, per treatment), and that sibling adults were never paired together within treatments.

Larvae were reared on frozen eggs of *E. kuehniella* and provided water on a small cube of sponge, both refreshed daily. Larvae assigned to the "small adult" treatment were permitted access to food for only 3 h daily (although water remained continuously available), whereas those assigned to the "large adult" treatment had *ad libitum* access to food. Upon pupation, each petri dish was cleaned of any remaining food to prevent consumption by newly emerged adults and ensure an accurate fresh weight at emergence could be obtained. Adult beetles were all sexed and weighed (within 24 h of emergence) on an analytical balance (Mettler Toledo, AG285, Columbus, OH). Non-sibling beetles from the same treatment were then paired in ventilated snap cap vials (5 cm diam × 9 cm ht).

Both small adult pairs ($n = 48$) and large adult pairs ($n = 48$) were further divided into two groups each, one receiving an omnivorous diet, the other receiving a prey-only diet, both provided *ad libitum*. The omnivorous diet consisted of greenbugs, provided on excised leaves of their host plant, frozen *E. kuehniella* eggs, pulverized bee pollen, dilute honey on a sponge cube (1:2 honey:water), and water on another

sponge cube, all provided *ad libitum*. In contrast, the prey-only diet lacked the floral resources and consisted of only greenbugs on wheat foliage, frozen *E. kuehniella* eggs, and water on a sponge cube, all provided *ad libitum*. Both greenbugs and water were refreshed daily, whereas *E. kuehniella* eggs, bee pollen, and diluted honey were refreshed every third day. Initially, all beetle pairs were maintained in reproductive diapause for 18 days by withholding the greenbug component of the diet, as female *H. convergens* reared on *E. kuehniella* eggs do not become gravid until provisioned with aphids *ad libitum* for 3–4 days (Michaud and Qureshi, 2006). This was done so that we could flight-test all females on a similar time frame both before and after a period of reproduction.

Experimental Design

The experiment was organized in a 2 × 2 factorial design with adult size (large vs. small) and adult diet (omnivorous vs. prey-only) as independent factors, yielding four treatments: (1) small, omnivorous couples (SO, $n = 25$), (2) small prey-only couples (SP, $n = 24$), (3) large omnivorous couples (LO, $n = 25$), and (4) large prey-only couples (LP, $n = 25$).

Flight Assays

Flight mills ($n = 16$) were constructed, modified from the design of Attisano et al. (2015), which allowed measurement of total flight distance when connected to recording software. A small spot of magnetic primer (Rust-oleum magnetic primer) was applied to the distal portion of the right elytra of each beetle using a wooden toothpick. After the paint dried (ca. 24 h), each female was attached to a small neodymium magnet on the end of a flight mill arm, where she flew at will in a 10 cm diameter circle in a climate controlled growth chamber set to $24 \pm 1°C$ and 50–60% RH. The flight mill arm rotated freely around a frictionless magnetic bearing and distance flown was measured by an infrared light sensor that tracked each revolution of the arm. Data was recorded continuously from the sensors using an Arduino MEGA 2560 REV3 single board microcontroller and terminal program (CoolTerm). For the initial flight test, each female was placed on a mill for a total of 3 h, then returned to her dish. Following 18 days of oviposition, tallied consecutively from production of her first clutch, each female was flown for another 3 h period.

Reproduction

Following the addition of greenbugs to the diets, females in both diet treatments were monitored daily for oviposition. Egg clusters, usually laid on the opaque lids of the vials, were collected and held until eclosion under the same physical conditions as the stock colony. The number of eggs in each clutch (daily oviposition) was counted before and after eclosion to obtain total fecundity and egg fertility for each female. This continued for a period of 18 days, a period that is usually sufficient to detect any dietary effects on reproductive success (Michaud, 2005). Females were held together with males from pair formation until the end of the experiment to maximize female fertility. Females that did not oviposit within 30 days after access to greenbugs were concluded to be non-reproductive and completed their second flight test. These non-reproductive females ($n = 2$) were excluded

from reproductive analysis, but included in flight observations, as they expressed the lowest reproductive effort.

Statistical Analysis

All data passed tests for equality of variance (Levene's test) and normality (Shapiro-Wilk test) and were analyzed by two-way ANOVA, followed by a Bonferroni test to separate means. Preoviposition period was tallied for each female as the no. days from first provision of greenbugs to the first day of oviposition, 18-days fecundity as the total number of eggs laid in 18 days, counted from first oviposition day, and egg fertility as the percentage of all eggs hatching. Oviposition days were tallied as the total number of days, out of 18, on which at least one egg was laid. Flight distance was tallied as the total number of revolutions completed on the flight mill, multiplied by the circumference of the mill arm. We also used linear regression to test for relationships between pairs of continuous response variables, and a paired t-test to compare distances flown by beetles pre- and post-oviposition.

Structural equation modeling (SEM) was employed to characterize direct and indirect relationships between independent variables (body size, adult diet) and components of female fitness (preoviposition period, no. oviposition days, fecundity, egg fertility) and flight performance (pre- and post-ovipositional flight distances). Categorical experimental predictors were coded for adult size as 0 (small) and 1 (large), and diet treatment as 0 (prey-only) and 1 (omnivorous). Maximum likelihood methods were used for model selection with goodness of fit assessed by Akaike's Information Criterion (AIC) in a step-wise process. Model selection began using the complete hypothesized model with influence expected between all biologically feasible pathways, then removing non-significant relationships at each step, beginning with the highest p-value. We also used tests of directed separation to identify factors whose addition (or reintroduction) could improve model fit. The AIC value of each successive model was consulted at each step of the model selection process to assess goodness of fit and models with AIC decreases > 2 were considered better fit. Models with AIC value changes < 2 were differentiated by parsimony (Burnham and Anderson, 2002; Grace, 2006). R version 4.0.3 was used to conduct all analyses in the piecewise SEM package (Lefcheck, 2016).

RESULTS

Larvae restricted to 3 h daily food access were smaller at adult emergence than those reared with *ad libitum* access to food; females weighed less (16.4 ± 0.3 mg vs. 21.7 ± 0.3 mg, $F = 119.7$; df = 1, 97; $P < 0.001$), and developed more slowly (22.5 ± 0.2 day vs. 19.0 ± 0.1 day; $F = 218.7$; df = 1, 97; $P < 0.001$).

Both adult size ($F = 11.01$, df = 1, 95; $P = 0.001$) and adult diet ($F = 4.95$; df = 1, 95; $P = 0.028$) affected how long females took to begin oviposition after they began receiving greenbugs, but these factors did not interact significantly ($F = 2.47$; df = 1, 95; $P = 0.119$). Females in the LP treatment took longer to begin oviposition than females in other treatments, the latter

being not significantly different from each other (**Figure 1**). Similarly, adult size ($F = 5.64$; df = 1, 95; $P = 0.020$) and adult diet ($F = 5.43$; df = 1, 95; $P = 0.022$) affected the number of oviposition days in the 18 days observation period, again without any significant interaction between factors ($F = 0.001$; df = 1, 95; $P = 0.981$). Females in the SO treatment laid clutches on more days than did females in the LP treatment, with other treatments not significantly different (**Figure 2**). The 18-days fecundity of females was not affected by adult size ($F = 3.30$; df = 1, 95; $P = 0.073$), but strongly affected by adult diet ($F = 13.06$; df = 1, 95; $P < 0.001$), without any interaction between these factors ($F = 0.91$; df = 1, 95; $P = 0.343$). Fecundity was higher in the SO treatment than in either the SP or LP treatments, with no other differences among treatments significant (**Figure 3**). Egg fertility averaged 62.8 ± 2.9% (mean ± SE) and was unaffected by body size ($F = 2.19$; df = 1, 95; $P = 0.142$) or adult diet ($F = 0.16$; df = 1, 95; $P = 0.687$).

Neither adult body size ($F = 0.001$; df = 1, 95; $P = 0.975$) nor adult diet ($F = 0.17$; df = 1, 95; $P = 0.685$), affected the initial (pre-reproductive) flight distance of females, although the interaction term between these factors was marginally significant ($F = 3.72$; df = 1, 95; $P = 0.057$). Similarly, the distance flown by females after an 18-days reproductive period was unaffected by adult body size ($F = 2.12$, df = 1, 95; $P = 0.815$) or adult diet ($F = 0.06$; df = 1, 95; $P = 0.148$. Female flight activity varied greatly, with total distance flown ranging from < 5 m to > 7 km. Beetles flew significantly further on their first test than on their second ($t = 5.93$; df = 1, 98; $P < 0.001$; **Figure 4**). Regression analysis revealed that preoviposition period was negatively correlated with both number of oviposition days ($F = 45.35$; df = 1, 97; $P < 0.0001$; $r^2 = 0.32$) and 18-days fecundity ($F = 29.38$; df = 1, 97; $P < 0.0001$; $r^2 = 0.02$). However, fecundity was not correlated with flight distance, whether pre-reproductive ($F = 0.11$, df = 1, 97; $P = 0.741$) or post-reproductive ($F = 0.19$, df = 1, 97; $P = 0.277$).

Structural equation modeling indicated no significant effect of pre-reproductive flight on subsequent reproductive success or flight behavior (**Figure 5**, Fisher's $C = 10.5$, df = 22, $P = 0.98$). Adult size and diet both influenced the preoviposition period, with large adult size delaying onset of oviposition ($\beta_A = 0.32$, $P = 0.001$) and the omnivorous diet accelerating it ($\beta_D = -0.21$, $P = 0.020$). Omnivory also had a direct positive effect on fecundity ($\beta_H = 0.16$, $P = 0.004$) in addition to its indirect positive effects on fecundity via effects on preoviposition period ($\beta_C = -0.54$, $P < 0.001$) and number of oviposition days, the latter having a direct positive effect on fecundity ($\beta_F = 0.80$, $P < 0.001$). Delayed onset of oviposition was also associated with greater post-reproductive flight distance ($\beta_B = 0.27$, $P = 0.008$). Fertility and fecundity were positively correlated with one another ($\beta_G = 0.29$, $P = 0.002$) and fertility was positively correlated with post-reproductive flight distance ($\beta_E = 0.21$, $P = 0.04$).

DISCUSSION

The omnivorous adult diet resulted in greater female fecundity than did the prey-only diet, supporting our initial hypothesis,
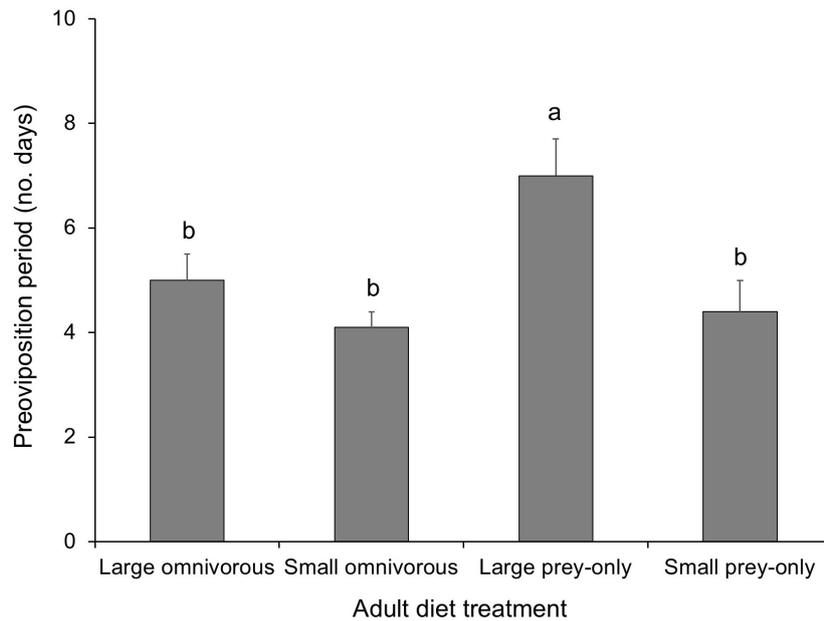
FIGURE 1 | Mean (+ SE) preoviposition periods, of large (*ad libitum* larval food access) and small (3 h daily larval food access) *Hippodamia convergens* pairs subjected to one of two different adult diet treatments: omnivorous (pollen, honey, *Schizaphis graminum* and *Ephestia kuehniella* eggs), or prey-only (*S. graminum* and *E. kuehniella* eggs). Treatments bearing the same letter were not significantly different (Tukey's test, α = 0.05).
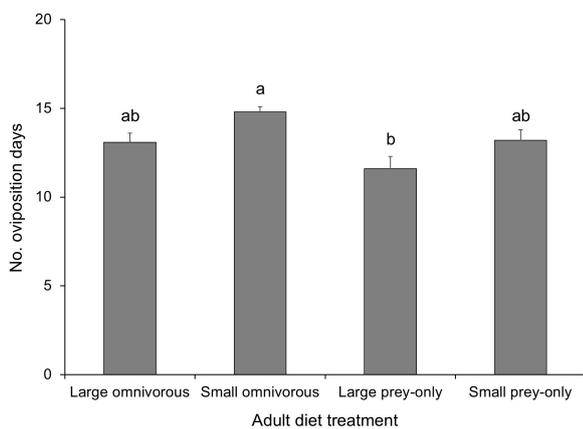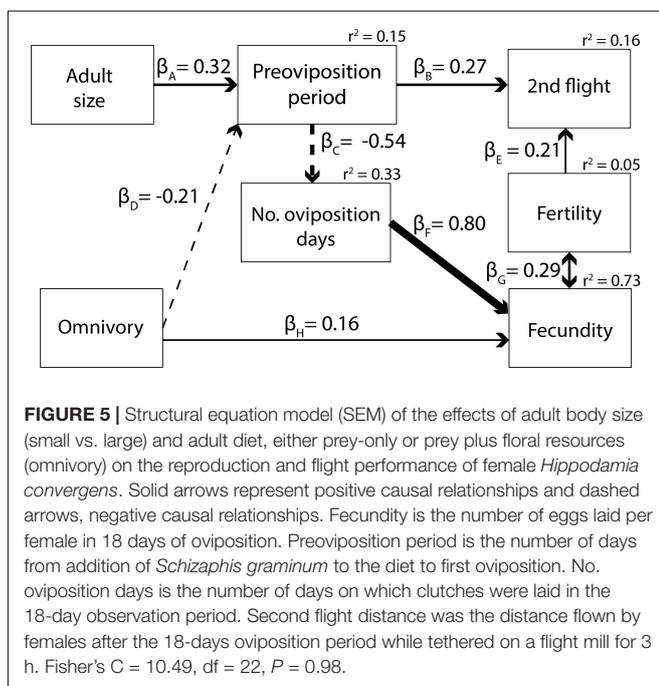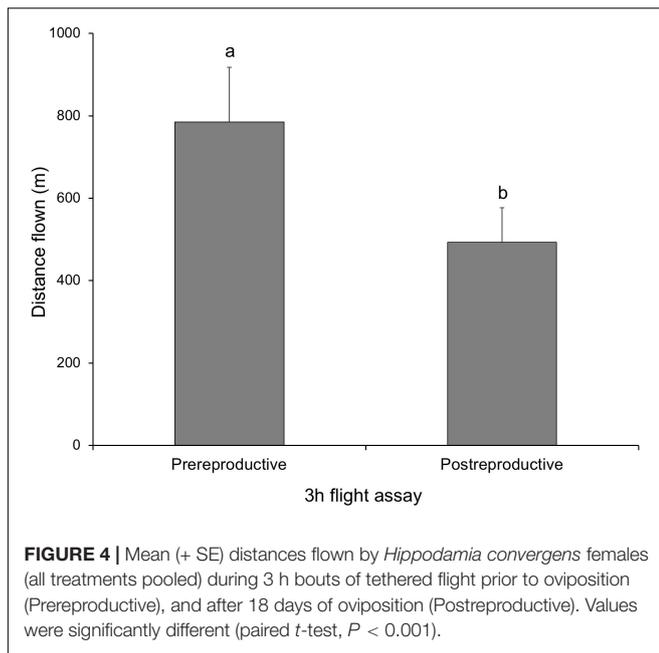

FIGURE 2 | Mean (+ SE) number of oviposition days (no. days on which clutches were laid out of 18 days of observation) for large (*ad libitum* larval food access) and small (3 h daily larval food access) *Hippodamia convergens* pairs subjected to one of two different adult diet treatments: omnivorous (pollen, honey, *Schizaphis graminum* and *Ephestia kuehniella* eggs), or prey-only (*S. graminum* and *E. kuehniella* eggs). Treatments bearing the same letter were not significantly different (Tukey's test, α = 0.05).
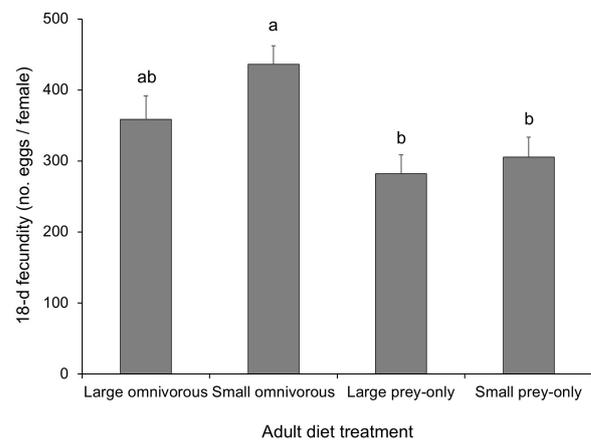
FIGURE 3 | Mean (+ SE) 18-days fecundities of large (*ad libitum* larval food access) and small (3 h daily larval food access) *Hippodamia convergens* pairs subjected to one of two different adult diet treatments: omnivorous (pollen, honey, *Schizaphis graminum,* and *Ephestia kuehniella* eggs), or prey-only (*S. graminum* and *E. kuehniella* eggs). Treatments bearing the same letter were not significantly different (Tukey's test, α = 0.05).

and confirming that floral resources complement the nutrition provided by prey, and are essential to maximal reproductive success in this species. Previous studies have similarly concluded that plant-derived foods generally enhance the performance of predatory coccinellids relative to prey-only diets (Lundgren, 2009), including *H. convergens* (Stowe et al., 2021). Supplemental (plant-derived) foods have long been recognized

for their importance to coccinellid survival during periods of prey scarcity (Hodek, 1996; Michaud and Qureshi, 2005), but may also provide phytosterols, key requirements for development and reproduction that insects are unable to synthesize endogenously (Levinson, 1962; Behmer and Nes, 2003; Pilorget et al., 2010). Furthermore, feeding on carbohydrates can increase lipid reserves, which can improve insect longevity and overwintering

FIGURE 4 | Mean (+ SE) distances flown by *Hippodamia convergens* females (all treatments pooled) during 3 h bouts of tethered flight prior to oviposition (Prereproductive), and after 18 days of oviposition (Postreproductive). Values were significantly different (paired *t*-test, $P < 0.001$).

FIGURE 5 | Structural equation model (SEM) of the effects of adult body size (small vs. large) and adult diet, either prey-only or prey plus floral resources (omnivory) on the reproduction and flight performance of female *Hippodamia convergens*. Solid arrows represent positive causal relationships and dashed arrows, negative causal relationships. Fecundity is the number of eggs laid per female in 18 days of oviposition. Preoviposition period is the number of days from addition of *Schizaphis graminum* to the diet to first oviposition. No. oviposition days is the number of days on which clutches were laid in the 18-day observation period. Second flight distance was the distance flown by females after the 18-days oviposition period while tethered on a flight mill for 3 h. Fisher's C = 10.49, df = 22, $P = 0.98$.

survival (He and Sigsgaard, 2019), and can be rapidly oxidized to provide energy for flight (Toprak, 2020; Wang et al., 2020). The benefits of omnivory likely occur independent of prey diversity in the diet, as animal and plant-derived foods typically supply key macronutrients in differing ratios (Raubenheimer and Jones, 2006; Raubenheimer et al., 2007). Macronutrient ratios have been shown to affect growth, development, and survival in phytophagous coccinellids (Wang et al., 2018) and other insect herbivores (Behmer, 2009), and arthropod predators often forage selectively to balance their intake of protein, lipids

and carbohydrates (Mayntz et al., 2005; Jensen et al., 2012). For example, a prey-only diet will be high in protein, which can reduce net energy intake due to digestive costs, and alter activity levels (e.g., Koemel et al., 2019).

Our hypothesis that large body size would result in greater female fecundity was not supported, seemingly contradicting previous work that examined the effect of *H. convergens* body size on fecundity over longer time frames (Vargas et al., 2012a,b), although plant resources were not provided in those experiments. Adult size only had a marginal effect on fecundity within the 18-days observation period, and in the opposite direction of that expected, being highest for small females. This result may reflect fewer days of oviposition by LO and LP pairs within the period of observation, and/or delayed onset of oviposition in LP pairs. Oviposition days were strongly correlated with fecundity in the SEM model, and previous work has shown that daily fecundity peaks later in large *H. convergens* than in smaller ones (Vargas et al., 2012b), so a longer period of observation could reveal different body size effects. Fertility was unaffected by either diet or adult size, contradicting our hypothesis that larger body size would benefit fertility. Once again, this result likely reflects the limited time frame of our observations. Maternal body size has no discernable effect on *H. convergens* egg fertility early in reproductive life, but its effects become more pronounced with advancing age, as fertility declines faster in both large and small females than in those of intermediate size (Vargas et al., 2012b).

Our hypothesis that access to floral resources would positively affect reproductive success was supported. Large beetles fed a prey-only diet experienced delayed onset of oviposition relative to those receiving the omnivorous diet, suggesting that nutrients provided by floral resources enabled beetles to begin maturing eggs sooner when body size was large. However, the large beetles produced in this experiment are likely uncommon in nature, where food-limitation is the norm for most larvae at some point in development. If reproductive traits have evolved to be adaptive for the average body size, a large body size may impose some costs. Large individuals may have higher maintenance requirements than small ones, such that the soma of large beetles may (initially) take precedence over the gonads when certain key nutrients become limiting, as likely occurred in the prey-only treatment.

Despite the fact that body size and adult diet affected beetle reproductive parameters, neither treatment generated any significant variation in the distance flown by females on flight mills, either in pre- or post-reproductive tests. In large part, this was due to immense variation among females in total flight activity, which ranged from < 5 m to > 7 km. Rankin and Rankin (1980) similarly reported large variation in distances flown by tethered *H. convergens* beetles, with 90% of individuals stopping after 30 min, while the remaining 10% were still flying after 12 h. We infer that *H. convergens* populations consist of individuals that vary greatly in intrinsic flight propensity, and that additional variation was probably contributed by differences in physiological state, despite our best efforts to standardize beetle age and rearing conditions. Maes et al. (2014) showed that body size was positively correlated with greater flight distance in both *Harmonia axyridis* Pallas and *Cryptolaemus montrouzieri*

Mulsant, although not in *Adalia bipunctata* (L.), so it is possible our observation period was not sufficiently long to resolve a body size effect. Although nectar can be an essential source of energy fueling flight in many insects, including Diptera (Dunn et al., 2020), Hymenoptera (Suarez et al., 2005), and Lepidoptera (Su et al., 2021), most of the energy obtained by nectar feeding is stored as lipids in the fat body, the "coordination center" of lipid metabolism in insects (Toprak et al., 2020), and lipids are the energy currency of sustained flight in most insects (Canavoso et al., 2003; Van der Horst et al., 2003). Our results indicate that *H. convergens* adults do not require access to sugar to fuel flight, but likely rely upon stored lipids, as do most other insects (Arrese and Soulages, 2010; Toprak, 2020). Some of these lipid reserves may be accumulated during larval development, and in the case of some Coleoptera, almost entirely (e.g., Tussey et al., 2018; Dvoracek et al., 2020), thus rendering adults less dependent on floral resources. This could be adaptive for *H. convergens*, given that adult beetles may need to make long distance migratory flights across landscapes where flowers are unavailable, such as after emergence from hibernation or aestivation (Hagen, 1962).

Dispersal by flight is energetically costly and is expected to reduce the energy available for subsequent foraging behavior and/or reproduction (Stearns, 1992). The SEM results revealed direct, but weak, relationships between post-reproductive flight distance and both length of the preoviposition period and egg fertility, implying that both delayed onset of oviposition and higher egg fertility were associated with greater flight activity in gravid females. More significantly, the shorter distances flown by females post-reproduction suggest that egg maturation depleted the energy reserves available for flight. This result stands in contrast with the findings of Stewart and Gaylor (1994) for the tarnished plant bug, *Lygus lineolaris*; older bugs flew greater distances than preproductive ones. Our adult diet treatments did not impact energy reserves sufficiently to affect flight activity within a 3 h period, nor did this period of flight deplete energy reserves sufficiently to negatively affect subsequent reproductive capacity. These results are consistent with a long-range dispersal capability in this species, with much longer periods of flight required before energetic demands become significant.

Apparent trade-offs between flight ability (or energetic expenditure on flight) and reproductive effort have been reported in many insects (Zera and Harshman, 2001). For example, Guerra and Pollack (2007) showed that flight ability was negatively correlated with male courtship singing in the cricket *Gryllus texensis*. Roff (1986) compared 22 species of wing-dimorphic insects and found that brachypterous female morphs were more fecund and had earlier onset of reproduction than macropterous morphs, and Zera and Denno (1997) showed that flight capability carries reproductive costs for males as well as females. In the present study, we found that post-reproductive flight distance was positively correlated with preoviposition period in the SEM model, the latter being negatively correlated with number of oviposition days, and thus with fecundity, results that are also consistent with a trade-off between reproductive effort and energy expenditure on flight.

The quality of the natal patch is known to have strong carryover effects on dispersal capacity. For example, high emigration rates of the backswimmer *Notonecta undulata* are associated with development in patches of high quality (Baines and McCauley, 2018). Because the quality of the developmental environment has the potential to shape adult phenotypes, it can have cascading effects on population dynamics and community structure that extend to landscape scales (Van Allen and Rudolf, 2013, 2016). Carryover effects of natal patch quality on body size and life history parameters will have significant implications for *H. convergens* population dynamics and the predation services this species provides in the agricultural landscape, as successive generations colonize different crops that vary in the quality of resources they provide. Thus, the provision of floral resources either within, or adjacent to, crop fields will help sustain the vigor of *H. convergens* populations, and the efficacy of their biological control services. These services extend beyond control of aphids to the consumption of many other pests in their early life stages, even though the latter may not support beetle reproduction (Michaud, 2018).

Our results illustrate the importance of floral resources to the fitness of arthropod predators that provide biological control services as they migrate across the agricultural landscape. Broadleaf plants have distinct, usually brief, flowering seasons, so a diversity of species that vary in flowering phenology will be required to ensure these resources are available over extended periods (Bianchi et al., 2006). Many cultural practices have the potential to support, or disadvantage, populations of coccinellids and other generalist predators in the landscape and warrant careful assessment of their ecological impacts. For example, over-zealous control of all broadleaf plants on roadsides and marginal lands constitutes an unnecessary reduction of potential floral diversity in the service of cultural expectations, with no direct impact on crop production. Also concerning is the increasingly wide-spread use of insecticidal seed treatments. This practice not only impacts predators negatively via prey deprivation during crop establishment, but creates various routes of direct and indirect exposure for beneficial species, with both lethal and sublethal consequences (Seagraves and Lundgren, 2012; Gontijo et al., 2014; Moscardini et al., 2015; Bredeson and Lundgren, 2018, 2019). In contrast, farmer tolerance of flowering broadleaf plants in marginal and uncultivated areas, and the planting of cover crops as an alternative to sterile, "chem-fallow" periods that create starvation conditions for all arthropods, represent feasible approaches to supplement valuable floral resources for predator populations as they move among crops in the agricultural landscape.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

HS and JPM conceived and designed the experiment with conceptual contributions from TK. HS conducted the

experiments and compiled the data. HS and TK analyzed the data and constructed the SEM. HS and JPM wrote the manuscript in consultation with TK. All authors contributed to the article and approved the submitted version.

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