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ARTICLE

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Resource amount and discontinuity influence flight and reproduction in *Hippodamia convergens* (Coleoptera: Coccinellidae)

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Abstract

Industrial-scale agriculture creates a mosaic of large monocultures in the landscape, where seasonal cropping cycles generate discontinuous resource availability for insect predators both spatially and temporally. In this environment, selection will favor predator movement and reproductive behaviors that optimize the location and effective utilization of resource (prey) pulses that are both patchy and ephemeral in nature. Using a model system to study predator movement and reproduction, we tested how discontinuous periods of food resource access that mimic fluctuating resource populations (aphids) would influence flight behavior and reproduction of a highly mobile predator, *Hippodamia convergens* (convergent lady beetle), and possibly modify energetic trade-offs between these behaviors. Adult beetles were provided either short (3 h) or long (6 h) food pulses daily (continuous availability) or short (6 h) or long (12 h) food pulses every other day (discontinuous availability). We measured preoviposition period, fecundity, and fertility during an 18-day oviposition period, and female tethered flight activity (3 h) before and after the oviposition period. We found that discontinuous food access delayed the onset of oviposition in the high food quantity treatment; fewer females laid eggs overall, and 18-day fecundity was lower compared with continuous provision of the same food quantity. A longer preoviposition period was associated with fewer reproductive days and lower fitness. Flight distance and fecundity were negatively correlated, suggesting that energetic expenditure in flight can deplete energetic reserves otherwise used for subsequent reproduction. The negative effects of discontinuous resource access at fine temporal scales reveal how gaps in resource availability could influence lady beetle population dynamics and their ecosystem services within the agricultural landscape.

KEYWORDS
biological control, dispersal, ecological trade-offs, insect predators, temporal variability

INTRODUCTION

The negative effects of disturbance and resource fragmentation on insect biodiversity and ecosystem functions in agricultural landscapes are well documented (Angeler et al., 2016; Bianchi et al., 2009; Chaplin-Kramer et al., 2011; Haan et al., 2020; Samways, 1989; Tscharntke et al., 2012). Disturbances due to tillage, harvest, and chemical inputs can lead to direct insect mortality (Pearsons & Tooker, 2017; Tooker et al., 2020; van der Meer et al., 2020) or reduce habitat and food resources necessary for insect survival (Raven & Wagner, 2021; Wagner et al., 2021), thus decreasing ecosystem services such as biological control and pollination. Previous studies have examined the relationship between environmental disturbance and altered resource amount or quality (e.g., Karakoç et al., 2018; Ojima et al., 1994; Solbreck, 1995; Wagle & Gowda, 2018), but less information exists concerning the effects of variable access to resources, that is, resource discontinuity (Schellhorn et al., 2015; Spiesman et al., 2020; Welch & Harwood, 2014). Resource discontinuities created by disturbances can be spatial (i.e., rich resource patches are physically separated within resource matrices comprised largely of low resource regions) and/or temporal (i.e., rich resource patches are only ephemerally available) creating a landscape of unreliable resource availability in space and time. Discontinuity of resources can directly affect insect behavior and reproduction by reducing resource amount (Nicholson et al., 2021) with consequences for the population dynamics of many organisms (Holt, 2008; Yang et al., 2008) including insects (Ogilvie & Forrest, 2017). Furthermore, resource discontinuity can increase searching effort, making foraging more costly for adult predators (Forsman & Kivelä, 2021). These factors, among others, can combine to reduce the efficacy of insect-derived ecosystem services, including biological control (Schellhorn et al., 2015). Resource discontinuity is predicted to increase under climate change, as more frequent extreme weather events, including heat waves, droughts, and heavy precipitation events (Folland et al., 2002; Thornton et al., 2014) threaten to alter patterns of resource availability and stress insect communities, potentially diminishing the ecosystem services that they provide.

Insects that inhabit spatially and temporally variable resource environments face trade-offs between fitness-critical behaviors such as dispersal and reproduction. The ability of predators to track, or even anticipate, prey populations within annual crops can determine their survival and the effectiveness of their ecosystem services (Landis et al., 2000; Prasifka et al., 2004; Wissinger, 1997). For example, mobile predators may relocate to exploit alternative resources when the availability of a primary resource fluctuates capriciously (Landis et al., 2000; Wissinger, 1997), potentially incurring energetic trade-offs with other life history traits such as reproduction. Therefore, high mobility may be a prerequisite for success when generalist insect predators colonize agricultural environments, at least over short time frames (Wissinger, 1997; Xiao et al., 2017). However, flight is energetically costly, so excessive flight activity driven by food supply disruptions may diminish predator fitness and biological control services. Reproduction is also energy-intensive, and the allocation of energetic "capital" to flight may reduce the amount that can be allocated to reproduction in the future (Stearns, 1992). Considering these energetic trade-offs, any agricultural practices that minimize periods of resource scarcity within agricultural landscapes, that is, the use of cover crops, intercropping, or field crop complementarity, could reduce the energetic burden of local migrations for predators, leaving them with greater reserves to devote to foraging and reproduction when prey patches are finally encountered.

The present study addressed whether resource quantity and temporal availability would influence flight capacity and reproductive success in a highly mobile insect predator, the convergent lady beetle, *Hippodamia convergens* Guerin-Meneville (Coleoptera: Coccinellidae). Although it is impossible to fully reproduce the complexity of disturbance and resource variability in the agricultural environment, controlled laboratory assays permit isolation of key factors and provide insights into their potential effects on reproduction and movement under field conditions where a multiplicity of confounding factors often impede our ability to make clear inferences. The convergent lady beetle is one of the most abundant species of coccinellid on the North American High Plains where it is a key biological control agent of important cereal aphid pests such as greenbug, *Schizaphis graminum* Rondani (Rice & Wilde, 1988), Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) (Nechols & Harvey, 1998), and sugarcane aphid, *Melanaphis sorghi* (Theobald) (Colares et al., 2015—formerly *Melanaphis sacchari* Zhentner, Nibouche et al., 2021). Although *H. convergens* can be considered a specialized aphid predator, as it relies heavily on aphids for reproduction (Michaud & Qureshi, 2006), both larvae and adults survive periods of aphid scarcity by exploiting a wide range of supplementary foods that include the immature stages of other insects and various plant-derived resources (Lundgren, 2009; Mercer et al., 2020; Stowe et al., 2021). On the High Plains, these beetles typically produce their first generation in wheat or alfalfa, the resulting adults migrating to summer crops and switching among prey types in response to their availability, ultimately reproducing in different crops than those that supported their development

(e.g., Bastola et al., 2016; Tillman & Cottrell, 2012). Spatial and temporal disturbances inherent to large-scale farming operations can increase energy demands for *H. convergens* adults by increasing both the frequency and distance of flights required to track prey populations and maximize their reproductive success. *H. convergens* are strong flyers (Hagen, 1962; Jeffries et al., 2013) and will emigrate from early season crops to later season crops even before the latter have developed large prey populations (Prasifka et al., 2004). Therefore, this species has evolved specific adaptations to exploit seasonal patterns of changing resource availability across agricultural landscapes. However, these seasonal patterns of dispersal likely represent sizable energetic costs for the migrant adults that may manifest as trade-offs in reproductive success.

We hypothesized that *H. convergens* adults fed larger quantities of food would fly greater distances and achieve higher reproductive success than those fed lower amounts, without significant effects on egg fertility or timing of oviposition. Likewise, we hypothesized that sporadic (discontinuous) access to food would reduce flight distance and female fecundity, and delay onset of oviposition relative to more continuous access. We also hypothesized that the overall quantity of food would interact with its pattern of availability, with lower quantities resulting in more severe negative effects when availability is discontinuous. Finally, because of the many ways that food amount and continuity of access could affect flight behavior and reproduction, we used a structural equation model (SEM) framework (Figure 1), to disentangle how resource amount and continuity of

access would affect the presumed energetic trade-off between flight activity and reproduction.

METHODS

Insect colony

Adult *H. convergens* beetles were collected from wheat fields at the Kansas State University Agricultural Research Center in Hays, KS, USA (38°51′32.1″ N, 99°20′07.7″ W) in June of 2020. Beetles (ca. 150) were placed in a 1-L glass mason jar covered with muslin netting and held at $24 \pm 1°C$, 50%–60% RH, and a photoperiod of 16:8 (L:D). Jars were filled with wax paper strips as harborage and provisioned with frozen eggs of *Ephestia kuehniella* every other day, with water provided on a cotton wick. Field-collected beetles are often parasitized by *Dinocampus coccinellae* Schrank (Hymenoptera: Braconidae), so the colony was inspected daily to remove any emerging wasps before they could complete pupation and emerge to attack other beetles in the colony.

A colony of greenbugs, *S. graminum*, was established from individuals collected from wheat at the same location as the beetle colony. The colony was reared on wheat seedlings grown in metal trays containing a soil/vermiculite/peat moss mixture (1/1/1). Trays were germinated in the greenhouse and infested in growth chambers under fluorescent lighting at $24 \pm 1°C$, 50%–60% RH, and a 14:10 (L:D) daylength. Wheat seedlings were infested by clipping infested wheat leaves from
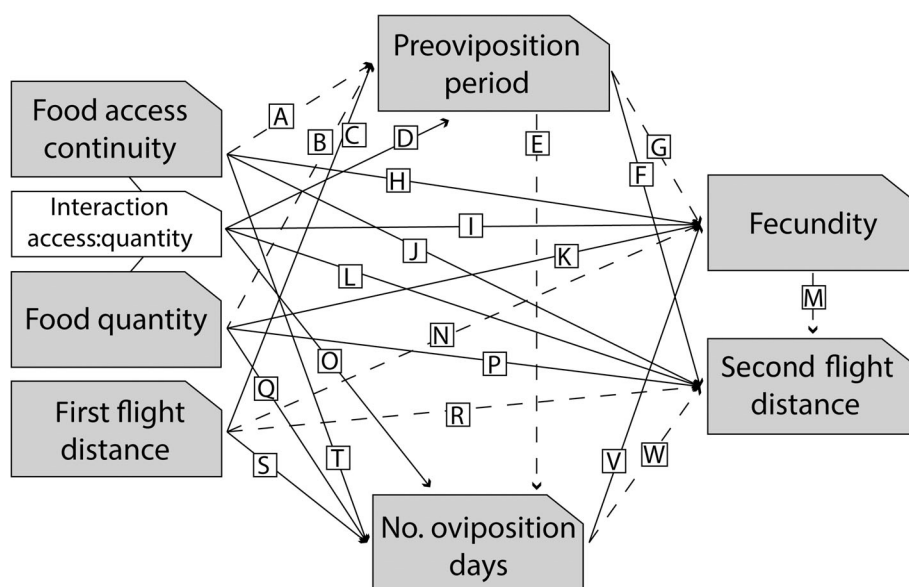
FIGURE 1 Hypothesis structural equation model: Arrows indicate directionality of hypothesized relationship, labeled with letters for identification. Solid lines denote positive influence and dashed lines indicate negative influence.

declining trays and distributing them across a new tray of seedlings at the two-leaf stage.

Experimental insects

Maternal females ($n = 12$) were removed from the stock colony and isolated in plastic Petri dishes (5.5 cm diameter) where they were provided greenbugs ad libitum to induce oviposition. After the fertility of each female was confirmed by observing the eclosion of several clutches, offspring from two successive days of oviposition were collected from each female. Eclosing neonates were allowed to disperse naturally from their egg clusters before they were isolated in Petri dishes (as above). This allowed teneral larvae time to harden their cuticles and consume their chorions, as occurs naturally. The maternity of each larvae was tracked so that progeny of each cluster could be distributed equally among treatments, and no siblings would be paired for reproduction.

All neonate larvae were reared under the same environmental conditions as the adult colony, with ad libitum access to frozen *E. kuehniella* eggs and water provided in a small square of sponge, both refreshed daily. Once larvae pupated, any remaining food was removed from the dishes and pupae were monitored daily until emergence, whereupon adults were sexed and weighed on an analytical balance (Mettler Toledo, AG285, Columbus, OH, USA) within 24 h. Pairs of non-sibling adults were established in ventilated snap-cap plexiglass vials (4.9 cm diameter × 9.0 cm height) where they remained for 12 days to permit maturation and mating. During this period, they were provisioned with frozen *E. kuehniella* eggs (ca. 5 mg), fresh foliage of wheat seedlings, pulverized bee pollen, diluted honey (1:2 honey:water) on a small cube of sponge, and water on a second cube. No aphids were provided during this maturation period to prevent oviposition prior to the flight assays and the imposition of treatments. All plant resources were refreshed daily, *E. kuehniella* eggs were provided every 3 days, water and diluted honey as required. This diet was designed to mimic patterns of food availability under field conditions when first-generation adults emigrate from natal fields and remain in reproductive diapause prior to encountering aphid populations that support their ovariole maturation and oviposition (Michaud & Qureshi, 2006).

Assays of flight behavior

A series of flight mills were constructed, modified from the instructions provided by Attisano et al. (2015), which allowed beetles to fly in a 10-cm-diameter circle. A small dot of magnetic paint (Rust-Oleum magnetic primer) was placed on the right elytra of each female beetle using a toothpick. After allowing 24 h for the paint to dry completely, each female was then magnetically attached to a flight mill arm via a small neodymium magnet. Flight tests were conducted in a climate-controlled growth chamber set to $24 \pm 1°C$ and 50%–60% RH. Each beetle was attached to one end of a rotating arm with the opposite end passing through an infrared sensor to record the number and timing of revolutions. This information was collected via an Arduino MEGA 2560 REV3 single-board microcontroller and a terminal program (CoolTerm) for data collection. After flying for a total of 3 h, each female was returned to their container with their mate and assigned to one of four food access treatments, as described below. Female beetles were flown once just before beginning the reproductive diet, and again immediately after they completed the 18-day oviposition period, measured from their first day of oviposition, and the total distance flown by each female was recorded for both dates.

Food access treatments and experimental design

The experiment was constructed as a 2×2 factorial design, with varying resource amount (high vs. low) and resource access (continuous vs. discontinuous) to separate the effects of these two aspects of resource availability (quantity and period of access) on flight behavior and subsequent reproductive success. Mature lady beetle couples were randomly assigned to one of four food access treatments: (1) high amount, continuous availability, "HC" ($n = 21$ couples with access to 6 h of ad libitum food daily); (2) low amount, continuous availability, "LC" ($n = 25$ couples with access to 3 h of ad libitum food daily); (3) high amount, discontinuous availability, "HD" ($n = 22$ couples with access to 12 h of ad libitum food every other day); and (4) low amount, discontinuous availability, "LD" ($n = 26$ couples with access to 6 h of ad libitum food every other day). Food access treatments were designed to provide 24 h of cumulative food access in high food treatments and 12 h of cumulative food access in low food treatments during each 48-h period. The prey components comprised *S. graminum* aphids provided on excised wheat seedling leaves and frozen *E. kuehniella* eggs (ca. 5 mg), both refreshed at the start of each feeding period. Manipulation of available food biomass is difficult when aphids are used as prey because nymphal instars vary greatly in size and apterous adults continue to reproduce even when

removed from host plants. Therefore, we opted to control periods of access to ad libitum food rather than trying to estimate the biomass of aphids or other foods consumed: an approach that has been successfully used in previous work (e.g., Vargas et al., 2013).

Reproduction

Following the 12-day maturation period, beetle pairs were supplied with greenbugs ad libitum on the excised leaves of their host plants to induce oocyte maturation in females, which requires 3–4 days (Michaud & Qureshi, 2006). Couples were checked everyday for oviposition and egg clutches were collected by simply moving adult beetles to a clean snap-cap vial. All egg clusters were held until eclosion under the same environmental conditions as the stock colony so that fecundity and egg fertility could be recorded for each beetle pair. Males were kept together with females throughout the observation period to ensure female fertility was maintained. Reproduction was recorded for 18 days for each couple, counted from the first oviposition day, a period long enough to capture any effect of treatment on reproductive success (Michaud, 2005) as fecundity declines rapidly in coccinellid females (Dixon & Agarwala, 2002). Females that failed to lay any eggs within 30 days after provision of the reproductive diet were recorded and excluded from analysis of reproductive performance data as including nonreproductive adults in measures of ovipositional timing and fecundity would skew treatment means and variance.

Statistical analysis

We analyzed treatment effects of resource continuity and amount on preoviposition period, fecundity, egg fertility, total oviposition days, and flight distance using separate two-way ANOVAs followed by Tukey's honestly significant difference for post hoc multiple comparisons. Preoviposition period was calculated for each female as the number of days from provision of the reproductive diet (i.e., *S. graminum* provided ad libitum) until the first clutch was laid. Oviposition days were tallied for each female as the number of days on which at least one egg was laid. Clutches were considered the total number of eggs laid by a female in 1 day. Fecundity was tallied as the total number of eggs laid, and egg fertility as the percentage of eggs hatching. Flight distance was calculated by counting the number of flight mill revolutions and multiplying by revolution circumference. All data passed tests for equality of variance (Levene's test) and normality (Shapiro–Wilk test) prior to the performance of ANOVA.

To examine the direct and indirect relationships between feeding treatment and fitness metrics (preoviposition period, fecundity, egg fertility, and oviposition days), and flight, we used a SEM framework. Experimental treatments were coded as 0 (low food quantity) and 1 (high food quantity) and resource access as 0 (discontinuous) and 1 (continuous). We predicted direct relationships between food quantity, food access continuity, the interaction between food access continuity and quantity, and reproduction timing and amount and post-reproductive flight distance (Figure 1, paths A, B, D, H, I, J, K, L, M, O, P, Q, and T). We also expected higher pre-reproductive flight distance, reproduction, and post-reproductive flight distance would each inversely influence later performance in these metrics (Figure 1, paths C, N, R, and S). Initial flight distance was included as a covariate in the SEM selection process because the initial flight distances may indicate intrinsic variation in flight capacity among females. Finally, we were interested in relationships between fitness and flight (Figure 1, paths E, F, G, M, V, and W), specifically, whether trade-offs existed between energy expended in flight effort and reproduction, which could diminish the availability of energetic reserves available for subsequent flight and/or reproductive effort.

Model selection was performed using maximum likelihood methods and linear relationships between variables were determined using bivariate scatterplots. We assessed the overall goodness of fit using Akaike information criterion (AIC) in a step-wise process of elimination. At each step, nonsignificant relationships were removed starting with higher order interaction terms the highest p values in the coefficient list. Instances where non-hypothesized direct relationships were significant or marginally significant, predictors were returned to the model starting from the lowest available p value. At each step, AIC was consulted and only steps that reduced ΔAIC >2 were retained. For models with similar AIC values (Δ <2), the more parsimonious model was chosen (Burnham & Anderson, 2002; Grace, 2006). All analyses were conducted in R version 4.0.3 using the piecewise SEM package (Lefcheck, 2016).
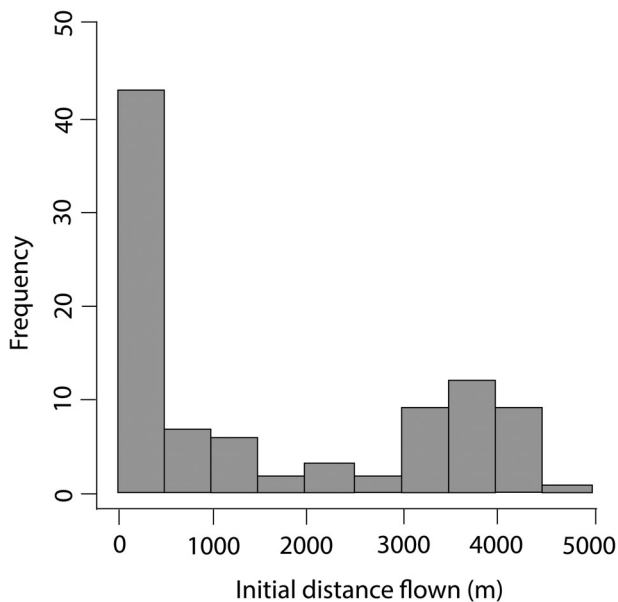
RESULTS

A total of 300 larvae were reared to adulthood, with 12 deaths and 1 escape yielding 287 adults. The average time from oviposition to adult emergence was 23.0 ± 1.0 days. Females had greater fresh weight at emergence than males (20.6 ± 2.6 mg vs. 16.3 ± 1.8 mg, $F_{1,285} = 273.1$, $p < 0.005$). The reproductive performance experiment was conducted with non-sibling couples assigned to each of the four treatments (HC, $n = 21$; HD, $n = 22$; LC, $n = 25$; LD, $n = 26$). Initial flight distances flown by females showed a

bimodal distribution (Figure 2), with most females flying only a short distance, and a subset exhibiting greater flight propensity, flying between 3.5 and 4 km in a 3-h test period.

Fewer females broke reproductive diapause in the LD treatment than in any other treatment ($\chi^2 = 10.47$, df = 3, $p = 0.015$). Among reproductive females, food quantity and access period interacted to influence pre-oviposition period ($F_{1,78} = 7.0$, $p = 0.037$). The HC treatment produced the shortest preoviposition period, and the HD and LD treatments the longest, with the LC treatment intermediate and not significantly different from other treatments (Figure 3). Fecundity was significantly increased by continuity of food access ($F_{1,78} = 19.4$, $p < 0.001$) and food quantity ($F_{1,78} = 9.0$, $p = 0.004$, Figure 4), but these two factors did not interact ($F_{1,78} = 0.102$, $p = 0.75$). The HC treatment produced the highest fecundity, followed by the HD treatment, with the LD treatment yielding the lowest, and the LC treatment intermediate between HD and LD. Egg fertility was affected by food quantity ($F_{1,78} = 20.2$, $p < 0.001$) but not by continuity of food access ($F_{1,78} = 1.3$, $p = 0.49$), with low food quantity reducing egg fertility relative to high (Figure 5). Post-oviposition flight distance was not significantly affected by food quantity ($F_{1,90} = 0.6$, $p = 0.65$) or continuity of food access ($F_{1,90} = 0.6$, $p = 0.45$), nor did the two factors interact significantly ($F_{1,90} = 0.6$, $p = 0.74$).

Our best fit SEM (Fisher's $C = 13.85$, df = 12, $p = 0.31$, Figure 6) revealed the various direct and indirect ways that food amount and continuity of access affected reproduction and flight. We found that both food
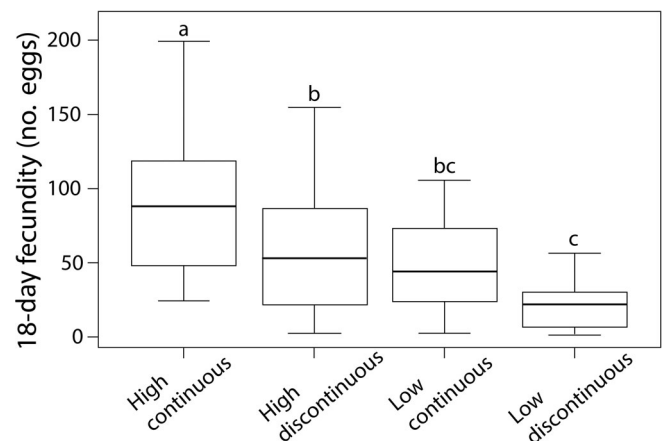
amount (standardized path coefficient, $\beta_D = 0.26$, $p = 0.03$) and pre-reproductive flight distance ($\beta_L = 0.32$, $p = 0.005$) directly increased post-reproductive (second) flight distance ($R^2 = 0.23$). On the other hand, continuity of food access influenced post-reproductive flight distance only indirectly via its effects on preoviposition period and number of oviposition days (paths $J \rightarrow N \rightarrow R$). In particular, food
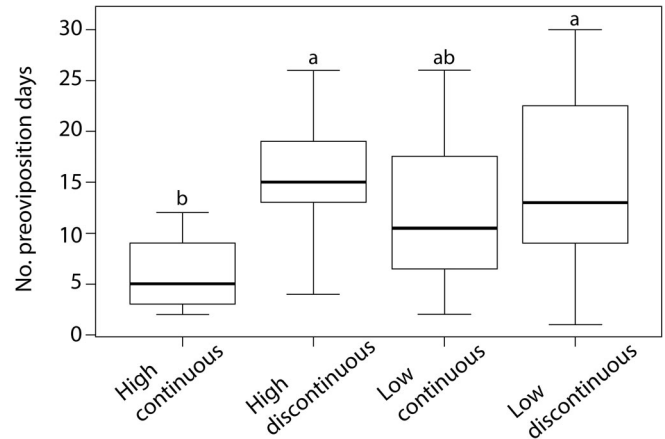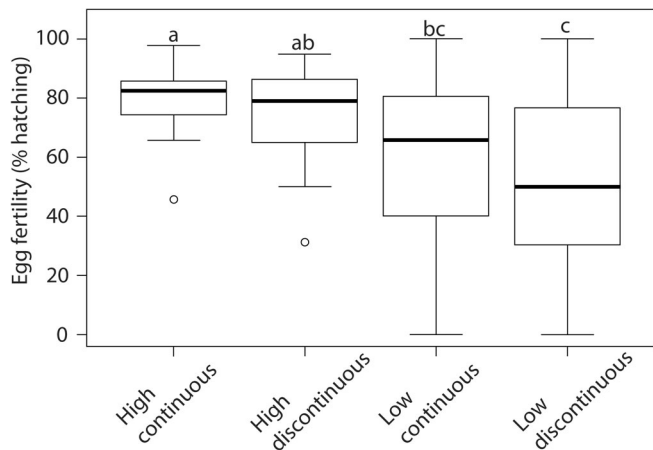

FIGURE 3 Median preoviposition periods, with interquartile range, of female *Hippodamia convergens* subjected to four different food supply treatments (high continuous = access to 6 h of ad libitum food daily; high discontinuous = access to 12 h of food every other day; low continuous = access to 3 h of ad libitum food daily; and low discontinuous = access to 6 h of food every other day). Treatments bearing the same letters were not significantly different (Tukey's test, $\alpha = 0.05$).

FIGURE 2 Frequency distribution of distances flown during first 3-h flights by pre-reproductive *Hippodamia convergens* females.

FIGURE 4 Median 18-day fecundities (number of eggs), with interquartile ranges, of female *Hippodamia convergens* subjected to four different food supply treatments (high continuous = access to 6 h of ad libitum food daily; high discontinuous = access to 12 h of food every other day; low continuous = access to 3 h of ad libitum food daily; and low discontinuous = access to 6 h of food every other day). Treatments bearing the same letters were not significantly different (Tukey's test, $\alpha = 0.05$).

access continuity decreased the pre-ovipositional period ($\beta_J = -0.041$, $p < 0.001$), whereas greater pre-ovipositional period, in turn, decreased the number of oviposition days


FIGURE 5 Median egg fertility (% eggs hatching), with interquartile range, of female *Hippodamia convergens* subjected to four different food supply treatments (high continuous = access to 6 h of ad libitum food daily; high discontinuous = access to 12 h of food every other day; low continuous = access to 3 h of ad libitum food daily; and low discontinuous = access to 6 h of food every other day). Treatments bearing the same letters were not significantly different (Tukey's test, $\alpha = 0.05$). Open circles represent outliers.

($\beta_N = -0.45$, $p < 0.0001$). The number of oviposition days positively influenced 18-day fecundity ($\beta_F = 0.79$, $p < 0.0001$) but was negatively correlated with total post-reproductive flight distance ($\beta_R = -0.32$, $p = 0.011$ and $R^2 = 0.03$, $p = 0.036$, Figure 7), suggesting possible trade-offs between flight and fecundity.

Although both food quantity and access affected fecundity and flight, the magnitude of the effect of food quantity on fecundity ($\Sigma\beta_{quant-fecund} = 0.316$, Table 1) and flight ($\Sigma\beta_{quant-flight} = 0.132$) was more than twice that of food access ($\Sigma\beta_{access-fecund} = 0.145$, $\Sigma\beta_{access-flight} = -0.05$) for our specific levels of variance. Food quantity also affected fecundity (range $\beta_{fecund} = 0.14$–0.61, $R^2 = 0.77$) more than it affected flight distance (range $\beta_{flight} = -0.05$ to 0.132, $R^2 = 0.23$).

DISCUSSION

Both higher food quantity and higher continuity of access increased female fitness via effects on oviposition behavior. Fewer females became reproductive in the LD treatment than in any other treatment, suggesting that resource quantity in this treatment was close to the lower limit for reproduction in this species. Higher food quantity increased the number of oviposition days, whereas greater food continuity accelerated the onset of
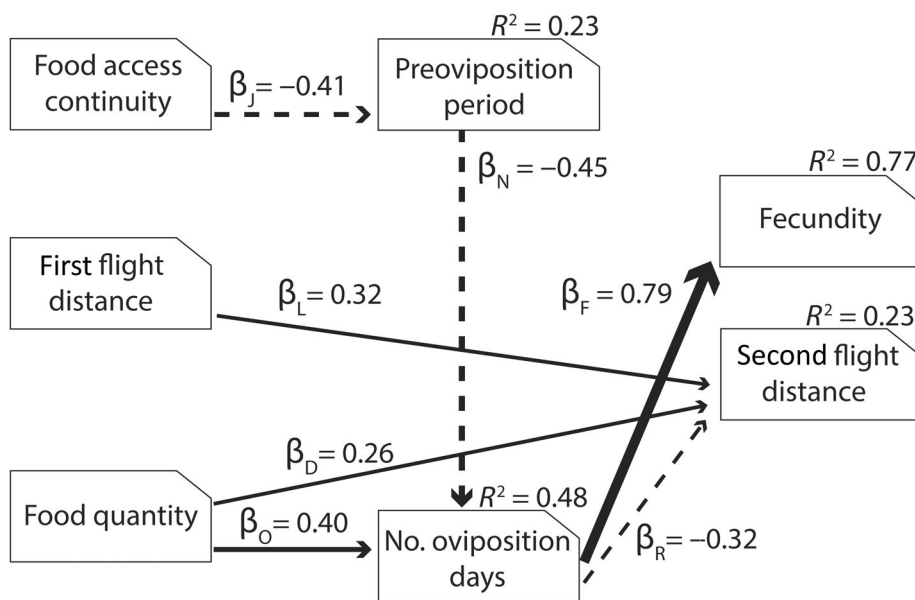

FIGURE 6 Structural equation model of the effects of food treatments (food access continuity and food quantity) on flight performance and reproduction of female *Hippodamia convergens*. Solid arrows represent positive causal relationships and dashed arrows represent negative causal relationships. Values are standardized path coefficients (β) with line sizes scaled to illustrate standardized coefficients. Coefficient of determination (R^2) values indicate the proportion of the variation explained by the model. Fecundity is the number of eggs laid per female in 18 days of oviposition. Preoviposition period is the number of days from provision of the reproductive diet (greenbugs) to first oviposition. No. oviposition days is the number of days on which clutches were laid in the 18-day observation period. Flight distance is the total distance flown (in meters) during a 3-h period on a tethered flight mill. Model fit: Fisher's $C = 13.85$, df $= 12$, $p = 0.31$.

oviposition. These results supported our initial hypothesis that both continuity of food access and food quantity affect female fitness. According to our piecewise SEM, the quantity of resource provided affected the oviposition amount (i.e., number of oviposition days), whereas continuity of resource access affected the timing of oviposition onset (i.e., preoviposition period). Food resources have clear bottom-up effects on insect predators (Agrawal et al., 1999; Alomar & Weidenmann, 1996; Polis & Winemiller, 1996), but past work has focused mostly on resource quantity and quality, whereas the effects of access continuity on insect predators has received less study (Rosenheim, 2001). The SEM indicated that resource quantity has stronger effects on both flight distance and reproductive performance compared with resource continuity for the levels examined here, although both predictors were influential. Discontinuity of resources may alter population persistence (Fahrig, 2002; Gibson et al., 2013), erect barriers to movement between prey patches (Henle et al., 2004), or create "bottlenecks" or

"interruptions" that delay reproduction or diminish population fitness (Schellhorn et al., 2015). A delay in onset of reproduction can slow population growth without necessarily affecting individual fecundity (Houston & McNamara, 1999; Millon et al., 2010). However, we examined only two levels of resource discontinuity and amount in the present study, and a complete understanding of their potential effects on predator population dynamics would require examination of a wider range of variation and combinations of these factors.

Onset of oviposition was delayed by resource discontinuity, especially when food quantity was high. Whereas HC beetles were the first to begin laying eggs, HD beetles were the last, and LC and LD females began laying eggs sooner than HD females. The greatest difference in timing of oviposition onset occurred in high food treatments, whereas low food treatments were intermediate. The delayed onset of oviposition observed in the HD treatment relative to the LD treatment suggests that the physiological impact of food supply interruptions on oocyte maturation is greater when females are acclimated to higher prey densities (greater food quantity) and would suggest that oviposition may begin earlier under conditions of resource discontinuity when the overall supply of prey is limited. However, the life history impacts of resource quantity and continuity of access are likely to vary with the amount of variance in each component, so results would likely differ according to both the amplitude and periodicity of food access cycles. Delayed reproduction in response to environmental variability and resource discontinuity has been documented in many insects (e.g., Johnson et al., 2016) and other animals (owls in Millon et al., 2010, and bats in Nurul-Ain et al., 2017). Delayed or reduced reproduction can extend lifespan (Holliday, 1989; Michaud & Qureshi, 2006; Speakman & Mitchell, 2011) but also carries fitness costs (Clutton-Brock, 1984; Viallefont et al., 1995). In *H. convergens*, long periods of reproductive diapause in summer extend lifespan, but reduce lifetime fecundity (Michaud & Qureshi, 2006). All organisms must balance current reproductive effort against the potential benefits of longer survival and future reproductive success under (possibly) more favorable conditions (Hadley et al., 2007;
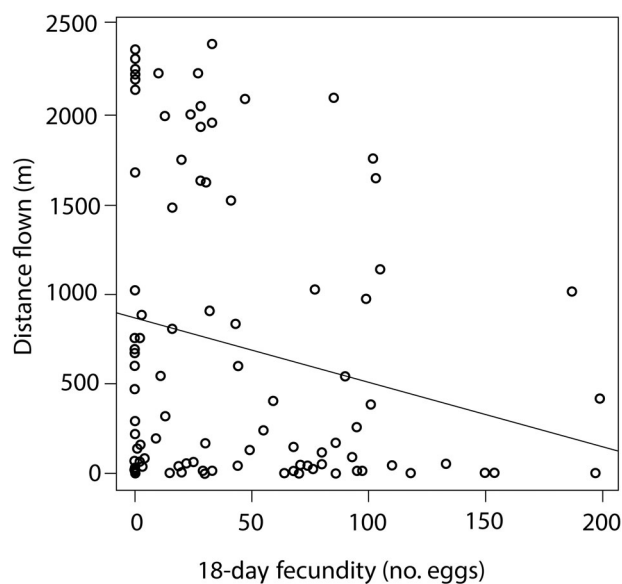
FIGURE 7 Linear regression of post-reproductive flight distances covered by *Hippodamia convergens* females on their 18-day fecundities. Equation: $y = -7.26x + 1744.2$. $R^2 = 0.036$, $p = 0.036$.

TABLE 1 The direct, indirect, and total effects of food quantity and continuity on fecundity and flight.

Variable	Fecundity			Flight		
	Indirect	Direct	Total	Indirect	Direct	Total
Quantity	0.32	...	0.32	−0.13	0.26	0.13
Continuity	0.15	...	0.15	−0.06	...	−0.06

Note: Indirect effects were calculated as the product of structural equation model β coefficients while the total effects were the sum of the direct and indirect effects. Ellipses (...) represent no direct effects observed.

Roff, 1993; Stearns, 1992; Williams, 1966). Although delayed onset of oviposition reduced the initial 18-day period of fecundity measured in our study, discontinuous access to high prey densities may signal that better oviposition opportunities lie ahead, and so represent an adaptive response that averts excessive premature egg production. Measurement of female reproductive performance over a longer period might elucidate longer-term impacts of these treatments on lifetime reproductive success.

Egg fertility declined in low food quantity treatments, but was not affected by continuity of access. This result could reflect reduced egg or sperm viability due to nutrient limitation. Although differences in food quantity or quality do not always affect egg fertility in *H. convergens* (e.g., Stowe et al., 2021; Vargas et al., 2012a), effects can appear over longer observational periods, as egg fertility declines as a function of maternal age in both very large and very small females, and eggs get progressively smaller with age in the case of the latter (Vargas et al., 2012a, 2012b). Any reduction in egg fertility may also improve the survival of siblings, given that cannibalism of infertile eggs within hatching clusters provides a valuable food source for eclosing larvae within hatching clusters (Michaud & Grant, 2004; Osawa, 1992). Although it is unclear if a fraction of each cluster may be left intentionally unfertilized to serve as "trophic eggs" (e.g., Perry & Roitberg, 2005), sibling egg cannibalism does occur in *H. convergens* (Bayoumy & Michaud, 2015) and could serve to raise maternal fitness when prey density is low.

Studies on the energetic trade-offs associated with flight and fitness have historically focused on investment in wing development in species with wing polymorphism (e.g., Harrison, 1980; Roff, 1986; Zera & Denno, 1997) and very few have examined those associated with flight effort expended by individuals (but see Guerra & Pollack, 2009). Although flight behavior is complex and comprises multiple related metrics such as bout length, distance, and flight propensity, in the present study, we used total flight distance as a metric for energy expenditure, with the expectation that trade-offs would be manifest in reproductive effort (amount of oviposition). The SEM revealed that the initial distance flown by pre-reproductive females was negatively correlated with their fecundity during the observation period, and that post-reproductive flight distance decreased with an increasing number of reproductive days, rather than with increased fecundity per se. The relationship between reproductive effort and flight capacity persisted even when considered in isolation, as the total distance flown was negatively correlated with fecundity. These findings are generally consistent with our hypothesis of an energetic trade-off between flight activity and reproductive effort. Longer, or more frequent, flights will also expose insects to increased predation risk, exhaustion, and physical damage (Bonte et al., 2012) while reducing the energy reserves needed for survival and reproduction (Guerra & Pollack, 2009; Schmid-Hempel et al., 1985). Interestingly, pre-reproductive flight and post-reproductive flight distance were positively correlated. Although this finding contradicts our hypothesis that greater initial flight distance would decrease subsequent flight distance, it is consistent with our inference that substantial variation exists among females with respect to intrinsic flight propensity, as environmental uncertainty in the agricultural landscape would likely counter any normalizing selection around some universally optimum mean. We also suspect that the experimental flight period provided in the experiment was insufficiently demanding to produce any negative effect on later flight activity. Many females remained actively flying at the end of the 3-h flight period, suggesting that energy reserves were not exhausted. A flight duration of approximately 60 min appears typical for large coccinellid species (Maes et al., 2014), although some *H. convergens* adults (ca. 10%) may fly for as long as 12 h in a single bout (Rankin & Rankin, 1980). Future investigations of possible trade-offs between flight and reproduction in this species should increase flight periods or induce repeated bouts of flight to increase energetic expenditure.

Agricultural systems present high levels of resource variability for predators and pests due to harvest cycles and other human disturbances. Conservation practices have primarily focused on increasing resource amount and diversity to support insect communities within agroecosystems (Power, 2010). More recently, continuity of access to resources has been increasingly recognized as important to the efficacy of natural biological control and other ecosystem services (Angeler et al., 2016; Cateau et al., 2018; Cohen & Crowder, 2017; Egli et al., 2020; Iuliano & Gratton, 2020; Kennedy et al., 2016; Schellhorn et al., 2015; Spiesman et al., 2020). A more even distribution of supplemental resources across the landscape would complement efforts to increase the amount and quality of these resources. More continuous availability of food resources has been shown to decrease emigration in planthoppers (Denno et al., 1991) and certain pollinators (Nicholson et al., 2021). Our results reveal that more continuous feeding by predatory beetles leads to earlier oviposition and more oviposition days. Increased resource continuity could be provided by the judicial planting of cover crops, management of non-crop habitat, or even crop field arrangement in the landscape, to materially improve the effectiveness of natural enemies, independent of the absolute amount of resources provided. (Bianchi et al., 2006; Landis et al., 2000; Rayl

et al., 2018; Rusch et al., 2010; Tscharntke et al., 2005). We conclude that spatial and temporal continuity of resources across the landscape should be considered in concert with absolute resource amounts in order to conserve populations of generalist insect predators like *H. convergens* and the biological control services they provide in agriculture.

This study illustrates how the interactive and complex nature of resource access (i.e., amount and access variability) may alter various aspects of *H. convergens* behavior and fitness. Complex behavioral and fitness trade-offs exist between various resource needs in insect predators, both with respect to resource amount and resource access continuity. The various ways that resources influence natural enemy responses provide opportunity for improvements to land management success. An understanding of these effects could provide novel and nuanced ways to support crucial ecosystem services. Biological control agents benefit from increased resource availability, and as sustainable agricultural systems are expected to increasingly rely on biological control services, we might increase these benefits by considering resource availability in time and space. Conservation of native natural enemies, especially generalist insect predators like *H. convergens*, might be substantially improved by increasing resource continuity across the landscape and throughout the year, resulting in better control of the pests that threaten agricultural ecosystems. Improving resource continuity on the landscape must be considered in concert with resource amount to maximize the survival and population growth of generalist insect predators like *H. convergens*.

AUTHOR CONTRIBUTIONS

All authors conceived of the study and designed the experiment collectively. Hannah E. Stowe performed the experiments and collected the data. Hannah E. Stowe and Tania N. Kim analyzed the data and conducted model selection. All authors contributed equally to writing the manuscript.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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