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Reproductive diapause in *Hippodamia convergens* (Coleoptera: Coccinellidae) and its life history consequences

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Abstract

Adult *Hippodamia convergens* (Guerin) in reproductive diapause were collected from a spring cohort in western Kansas and held in pairs for the duration of their lives to assess female reproductive schedules under conditions of limited food availability. Environmental conditions were set to mimic natural seasonal day lengths and diurnal temperature cycles for the region. To approximate conditions of limited food availability typical of summer conditions in western Kansas, beetles were provided continuous access to sunflower petioles and periodic access to protein sources, both animal (*Ephestia kuehniella* Zeller eggs) and vegetable (bee pollen). A total of 113 out of 171 females (66.1%) became reproductive over the next five months within a mean of 55.0 ± 3.0 day. These females lived an average of 134.5 ± 4.6 day and produced a mean of 106.9 ± 11.6 eggs in a mean of 6.6 ± 0.6 day of oviposition. Thus, reproductive diapause gradually decayed over time even when females did not encounter a high quality food supply. Egg production peaked every fourth day following provision of animal protein. A subset of 20 females, randomly selected from among those still non-reproductive on August 14 and switched to an aphid diet (ad libitum provision of *Schizaphis graminum* (Rondani)) produced a mean of 654.6 ± 109.7 eggs each, almost 10 times as many as females on the maintenance diet with similar reproductive schedules. However, the longevity of greenbug-fed females was reduced by more than 30% compared to the latter group, suggesting a tradeoff between reproductive effort and survival. The costs of reproductive diapause were evident as an increased risk of mortality prior to oviposition and declining fecundity and fertility with age. Our results suggest a variable number of overlapping generations can occur annually in western Kansas, potentially as many as five.

Keywords: Diapause; Diet; Fecundity-longevity trade-off; *Hippodamia convergens*; Reproduction; *Schizaphis graminum*

1. Introduction

The convergent lady beetle, *Hippodamia convergens* (Guerin), is an important predator of cereal aphids throughout much of the High Plains region of the Central United States (Michels et al., 2001; Nechols and Harvey, 1998; Michaud and Qureshi, 2005). Principle prey species for *H. convergens* in western Kansas include the Russian wheat aphid, *Diuraphis noxia* Mordvilko, and the greenbug, *Schizaphis graminum* (Rondani). Other aphid species that sporadically serve as alternative prey include the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), and the bird-cherry oat aphid, *Rhopalosiphum padi* L., along with a number of other non-economic aphid species that feed on wild grasses and herbaceous weeds. Other coccinellid species preying on these aphids in the region include *Coleomegilla maculata* DeGeer, *Coccinella septempunctata* L., *Cycloneda munda* (Say), and *Scymnus* sp. (Rice and Wilde, 1988). Although *Harmonia axyridis* Pallas has been present in the region for a number of years, it has failed to rise to prominence in this coccinellid community as it has in many other regions throughout North America over the past decade (Colunga-Garcia and Gage, 1998; Cottrell and Yeargan, 1998; Michaud, 2002).

For several years now, we have observed *H. convergens* dominate the mixed species aggregations of coccinellids that form on sunflower plants following emigration from

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maturing wheat fields in early summer where they have completed their first generation feeding on cereal aphids. The relative predominance of *H. convergens* among the assemblage of coccinellids in wheat in this region was noted by Nechols and Harvey (1998) while evaluating natural enemy responses to *Diuraphis noxia* (Mordvilko). As wheat fields dry down in early summer, an abundance of wild *H. annuus* plants emerge in roadside habitats, as do fields of cultivated varieties grown for oil and confection markets. Coccinellid adults, along with many other insect families, can be directly observed utilizing the succulent petioles of sunflower plants as a source of hydration during summer months in this arid region. Michaud and Qureshi (2005) demonstrated that access to sunflower sap sustained the survival of *H. convergens* adults in the absence of food better than did access to distilled water. Coccinellids feeding on aphid prey do not require supplementary water (Hodek and Honěk, 1996), so the apparent importance of this 'sap drinking' behavior to multiple coccinellid species likely reflects the fact that aphid prey can be very difficult to find during hot summer months on the prairie. Sap-drinking behavior is not limited to sunflower plants and other common weed species (e.g. *Kochia scoparia* L., *Amaranthus palmeri* S. Wats) are sometimes utilized, although *H. annuus* plants seem to be the most attractive.

Coll and Guershon (2002) reviewed the various ways plants may be utilized by omnivorous insects, but did not mention sap-feeding by predatory species. Schmidt (1992) surveyed coccinellid abundance on 76 plant species in Germany (mostly common weeds) and found strong evidence of patterns of plant association and avoidance. Associations with plants did not seem to be driven entirely by prey availability as fully 40% of the beetles surveyed occurred on plants without any aphids. The use of plant sap by lady beetles is perhaps an important aspect of coccinellid ecology in arid habitats that has been largely overlooked. Sunflower sap, in particular, may be exceptionally suitable as a source of hydration, and possibly some nutrition, for both predaceous and parasitic insects. Royer and Walgenbach (1991) catalogued a large number of predaceous arthropods in North Dakota associated with sunflower plants in various growth stages. Suter (1988) found that sowing 2–3 sunflowers in every 100 m^2 of corn increased the abundance of beneficial insects (coccinellids, syrphids, lacewings and predatory Hemiptera) compared to a corn monoculture. Pilson (2005) documented the attractiveness of sunflower sap to a wide range of insects once stems had been gouged open by *Euphora inda* (Coleoptera: Scarabaeidae). We have now documented sap-drinking behavior on cultivated sunflowers by adult lacewings (Neuroptera), flies (Diptera), beetles (Coleoptera) of diverse families, and Hymenoptera, including a plethora of wasp and ant species.

The predominance of *H. convergens* in the assemblage of coccinellids in grassland ecosystems of the High Plains (Rice and Wilde, 1988; Nechols and Harvey, 1998; Brewer and Elliott, 2003) is suggestive of unique ecological adaptations that provide it with substantial survival and/or reproductive advantages over other species. Use of sunflowers is not unique to *H. convergens* and virtually all coccinellid species in the region appear to engage in this behavior. Aphids tend to be scarce during hot summer months but other, less suitable, sources of animal protein are probably available, especially the eggs of a wide range of lepidopteran species that are laid on the foliage of various herbaceous plants throughout the season. Similarly, pollen of a variety of wild and cultivated flowering plants is available periodically throughout the summer and is known to serve as an important food supplement for adult coccinellids during periods when animal prey are scarce (Hodek and Honěk, 1996). Although *H. convergens* females readily consume copious amounts of pollen, this food alone is insufficient to support the maturation of their eggs (J.P. Michaud, unpublished data).

The ability of first generation *H. convergens* adults to undergo reproductive diapause in response to limitations in the quality and availability of food may represent a significant adaptation not shared by other species (Michaud and Qureshi, 2005). Induction of reproductive diapause in response to food limitation has also been demonstrated for *Harmonia sedecimnotata* F. (Zaslavski et al., 1998). Adult *H. convergens* can use limited food resources to develop fat bodies in their haemolymph and delay onset of reproduction until a high quality food source, such as a large colony of a suitable aphid species, is encountered. Previously, Michaud and Qureshi (2005) demonstrated that immediate provisioning of greenbug, *S. graminum*, to first generation adult females prevented most from entering diapause, whereas provisioning of greenbugs after several weeks on a maintenance diet caused a significant proportion to break diapause within a few days. Here, we examine complete reproductive and life history schedules of a first generation (spring) cohort of *H. convergens* adults under environmental conditions replicating seasonal norms for western Kansas. The insects were subjected to a diet treatment designed to simulate limited availability of plant and animal protein sources using types of food likely available to adult beetles throughout summer and fall (pollen and eggs of Lepidoptera). Partway through the summer, a subsample of beetles was switched to an ad libitum diet of greenbug to simulate encounter with a rich prey patch so that its effects on reproductive diapause, oviposition, and overall reproductive success could be observed.

2. Materials and methods

On 5 June, 2005, we estimated relative coccinellid species abundance locally by counting adult beetles in naturally occurring aggregations on cultivated sunflowers, *H. annuus*, at the Agricultural Research Station at Hays, Kansas. Subsequently, we collected more than 500 adult *H. convergens* by tapping them off plant petioles into ventilated Plexiglass containers, transported them to the laboratory, and then transferred them to 9 cm diameter plastic Petri dishes in groups of 10–15 per dish. We knew from previous work (Michaud and Qureshi, 2005) that adult females collected from sunflowers at this time of year are not yet gravid, having recently emigrated from mature wheat fields as newly emerged adults. Mating pairs were isolated as quickly as they formed and transferred to 5.5 cm diameter plastic Petri dishes until a total of 247 pairs were isolated. Each dish was immediately provisioned with an excised segment of sunflower petiole (ca. 4 cm long) and a measure of frozen eggs of *Ephestia kuehniella* Zeller (ca. 10 mg). The sunflower petiole segments were replaced every 2 days with material harvested from cultivated fields. On every third day, each dish received a measure of bee pollen (ca. 10 mg), and every sixth day, another measure of *E. kuehniella* eggs. All insects were transferred to clean dishes every sixth day. This feeding cycle was designed to simulate sporadic access to limited sources of vegetable and animal protein that we anticipated would represent the field situation for a majority of beetles during summer months in the High Plains. This feeding cycle is henceforth referred to as the 'maintenance diet'. Sunflower stalks were discontinued on 11 September and replaced with water encapsulated in polymer beads (Hydrocapsules©, ARS Laboratories, Gainesville, Florida) since little succulent plant material remains available in fall, although beetles may still have periodic access to moisture in the form of dew. Provision of pollen was discontinued after 7 October on the rationale that natural pollen sources would no longer be available in the field beyond this date.

All dishes were labeled with a number corresponding to the female. When any female died, she was immediately weighed, dissected to determine the presence or absence of mature eggs in her ovaries, and the male held separately until it could be re-paired with a widowed female. In this manner, all females had virtually continuous access to a male for the entire course of the experiment and no female was ever held without a male for more than a few days.

Dishes containing beetle pairs were laid out on a series of trays and held in a climate-controlled growth chamber. Day length was adjusted weekly to correspond to that of particular dates at 40° latitude according to Beck (1968) and an oscillating temperature cycle was maintained with an amplitude of ca. 10 °C corresponding to long-term average values for the region obtained from weather records at Agricultural Research Center—Hays, albeit without the occasional extreme temperatures often experienced in High Plains summer conditions. These climatic conditions were adjusted every two weeks to correspond to average seasonal values and are summarized in Table 1 for the entire experiment. All dishes were examined daily for oviposition. Eggs were usually attached directly to the surface of the plastic dishes and were harvested by simply changing the beetle pair to a new dish inscribed with the female's reference number. Eggs were labeled with date and female number and then held until eclosion under the same environmental conditions as the adults, whereupon the total number of eggs and hatching larvae were counted.

Table 1
Monthly means of diurnal temperature oscillations and daylengths experienced by pairs of *H. convergens* adults monitored for reproductive activity over a six month period

Month	Mean minimum temperature (°C)	Mean maximum temperature (°C)	Mean median temperature (°C)
June	13.9	24.3	19.1
July	14.0	24.4	19.2
August	12.6	24.1	18.3
September	11.4	23.7	17.6
October	7.2	20.3	13.7
November	6.5	16.3	11.8

Date	Daylength
6/6–6/14	14:50
6/15–6/30	15:01
7/1–7/14	14:58
7/15–7/31	14:43
8/1–8/14	14:18
8/15–8/31	13:46
9/1–9/14	13:03
9/15–9/30	12:31
10/1–10/14	11:44
10/15–10/31	11:14
11/1–11/14	10:29
11/15–11/30	9:57

Female fertility was calculated as the proportion of her eggs that hatched.

Large colonies of greenbug, *S. graminum* 'biotype I', were reared on trays of sorghum, *Sorghum bicolor* (L.) Moensh, in a greenhouse. On 14 August, a series of 20 pairs of beetles were selected at random from among those in which females had yet to oviposit. These beetle pairs were henceforth provided with an ad libitum diet of greenbug (introduced on excised sorghum leaves) daily for the next two months, or as long as the female remained alive.

Voucher specimens of beetles were placed in the Kansas State University Museum under Lot. 177. Life history and reproductive data were compared between various treatment groups by one-way ANOVA, followed by a Tukey test for means separation in cases where three groups were compared. Longevity and reproduction data for greenbug-fed females were compared to two groups of maintenance diet females, those reproducing earlier than the mean of greenbug-fed females (18 August), and those beginning oviposition on or after 18 August).

3. Results

3.1. Relative abundance

A total of 454 adult coccinellids were tallied on cultivated sunflower plants on 6 June, 2005. The relative composition of species was 74.4% *H. convergens*, 20.3% *C. septempunctata*, 2.6% *C. munda*, 1.8% *C. maculata*, and 0.9% *H. axyridis*.

3.2. Longevity

Larvae of the parasitoid *Dinocampus coccinellae* (Shrank) (Hymenoptera: Braconidae) emerged from a total of 90 beetles (18.2%) over a period of 31 days after collection (43 males, 47 females). The sex of parasitized beetles was determined by dissection and their surviving mates were re-paired with others of the opposite sex. Data for parasitized beetles were excluded from all analyses. The cumulative survival of unparasitized beetles on the maintenance diet varied between males and females, the former tending to die somewhat sooner (Fig. 1). Females receiving the greenbug diet demonstrated a steeper mortality curve than did their counterparts that had been non-reproductive for the same period (up to August 18) but remained on the maintenance diet. There were significant differences in longevity among groups of females that were transferred to the greenbug diet ($n = 20$), reproductive on the maintenance diet beginning oviposition earlier than greenbug-fed females ($n = 113$), and 3) reproductive on the maintenance diet but not beginning oviposition earlier than greenbug-fed females ($n = 28$) ($F = 14.742$; $df = 2{,}130$; $P < 0.001$). Greenbug-fed females lived an average of 118.1 ± 8.4 day, significantly less than the 171.1 ± 6.0 day lifespan of females on the maintenance diet that were non-reproductive up to the same date (Tukey test, $\alpha < 0.05$). Females on the maintenance diet that reproduced on an earlier schedule than greenbug-fed females were not significantly different in longevity from them, but were significantly shorter-lived than the group of maintenance diet females with late reproductive schedules (Tukey test, $\alpha < 0.05$). Twelve of the 20 females fed greenbug (60%) died with fully developed eggs in their ovaries, compared with only 17 (15%) of reproductive females on the maintenance diet.

3.3. Reproduction

A total of 113 out of 171 females (66.1%) on the maintenance diet became reproductive during the course of the experiment and their onset of oviposition over the course of the experiment is depicted in Fig. 2. Total egg production by all females on the maintenance diet is depicted throughout the course of the experiment in Fig. 3. Egg pro-

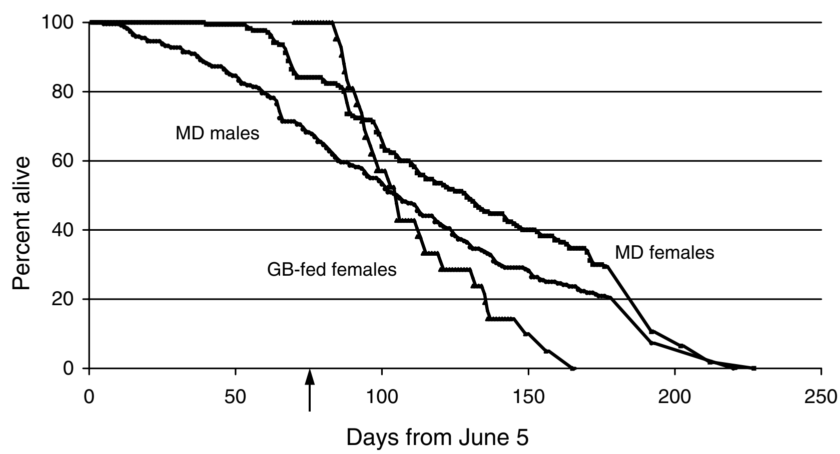

Fig. 1. Cumulative mortality of male and female *H. convergens* receiving a maintenance diet (MD-females and MD-males) comprising limited access to sub-optimal food (eggs of *E. kuehniella* once every 6 days followed by pollen 3 days later, with continuous access to sunflower petioles). GB-fed females were switched to an ad libitum diet of greenbug, *S. graminum*, refreshed daily, on August 14 (arrow), prior to any oviposition.

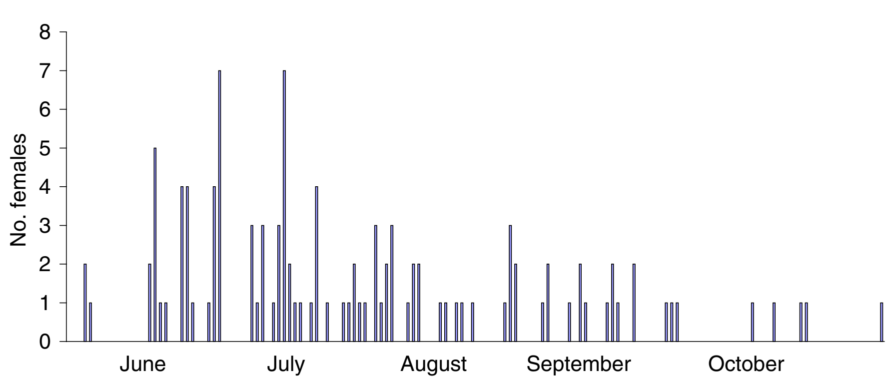

Fig. 2. Numbers of females receiving a maintenance diet (eggs of *E. kuehniella* once every 6 days followed by pollen 3 days later) that initiated oviposition on particular dates over the course the experiment ($n = 113$ females total). The first date of oviposition was 9 June, 3 days after collection and the last day was 3 November, 152 days after collection.

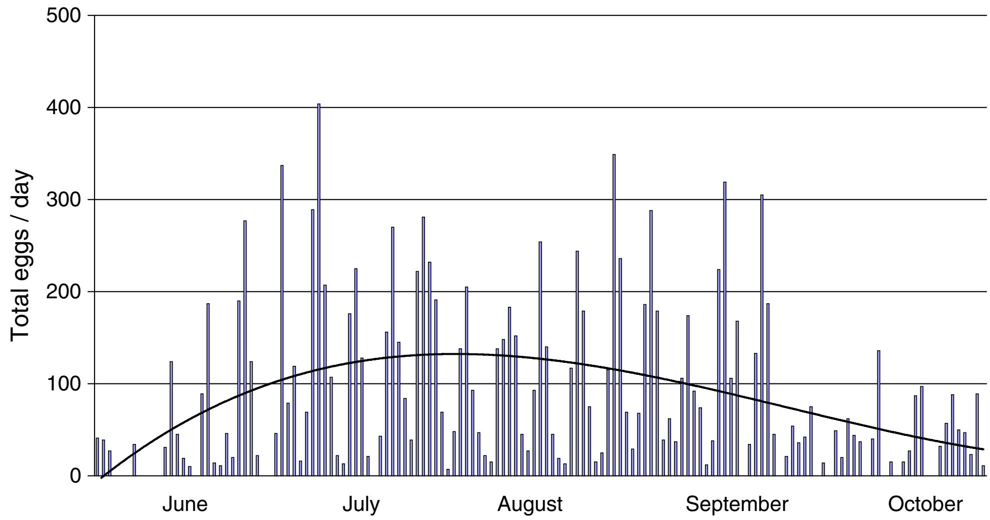

Fig. 3. Temporal distribution of reproductive effort (total number eggs/day) by a cohort of *H. convergens* females on a maintenance diet (eggs of *E. kuehniella* once every 6 days followed by pollen 3 days later) over a period of 5 months. The data were generated by a total of 113 females with variable longevity and onset of reproduction.

duction followed a distinct periodicity with respect to food supply, an ovipositional peak occurring every four days after provisioning with *Ephestia* eggs (Fig. 4). These females lived an average of 134.5 ± 4.6 day and produced a mean of 106.9 ± 11.6 eggs in a mean of 6.6 ± 0.6 day of oviposition that yielded a mean of 72.3 ± 7.9 larvae. Female oviposition on the greenbug diet, summed over all females, is depicted as a function of female reproductive life in Fig. 5.

Females receiving the greenbug diet beginning August 14 began oviposition a mean of 3.8 ± 0.2 day later. There was significant variation among groups of females in the mean numbers of eggs ($F = 54.007$; $df = 2{,}130$; $P < 0.001$) and larvae ($F = 40.292$; $df = 2{,}130$; $P < 0.001$) they produced. Females receiving the greenbug diet produced a mean (±SEM) of 654.6 ± 109.8 eggs and a mean (±SEM) of 451.0 ± 92.2 larvae, significantly more (Tukey test, $\alpha < 0.05$) than females on the maintenance diet that began reproduction prior to August 18 (mean ± SEM = 121.0 ± 14.8 eggs and 82.7 ± 10.1 larvae) or after August 18 (mean ± SEM = 64.2 ± 9.7 eggs and 40.7 ± 6.7 larvae). Differences between the latter two groups were not significant for either eggs or larvae (Tukey test, $\alpha > 0.05$). There was no difference in fertility among the three groups ($F = 1.534$; $df = 2{,}130$; $P = 0.220$).

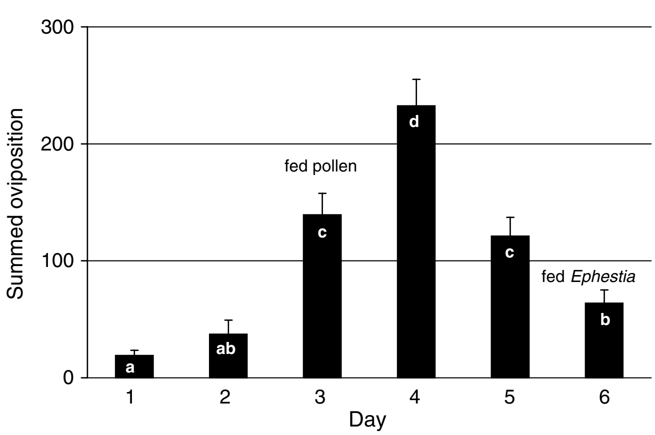

Fig. 4. Summed egg production (mean ± SEM) by *H. convergens* females ($n = 113$) over 135 days as a function of food provisioning showing a peak in oviposition every fourth day following provision with animal protein. Females paired with males were held on a 6-day feeding cycle (eggs of *E. kuehniella* once every 6 days followed by pollen three days later) with continuous access to sunflower petioles. Means bearing the same letter were not significantly different (Tukey test, $\alpha > 0.05$).

Date of first reproduction among females on the maintenance diet was negatively correlated with both lifetime fecundity ($F = 20.23$; $df = 111$; $P < 0.001$; $r^2 = 0.154$) and mean fertility ($F = 3.98$; $df = 111$; $P = 0.048$; $r^2 = 0.035$). There was no significant relationship between fecundity and fertility ($F = 1.70$; $df = 111$; $P = 0.195$), between fecundity and longevity ($F = 3.51$; $df = 111$; $P = 0.64$), or between fecundity and death weight ($F = 0.73$; $df = 111$; $P = 0.395$). However, there was a strong positive correlation between fecundity and number of reproductive days for both females on the maintenance diet ($F = 1201.82$; $df = 111$; $P < 0.001$; $r^2 = 0.915$) and those receiving greenbug ($F = 60.88$; $df = 18$; $P < 0.001$; $r^2 = 0.772$). The last date on which any viable eggs were laid was 3 November, suggesting that a mean temperature of 12 °C might represent a threshold below which oviposition does not occur.

4. Discussion

Aestivation has been inferred to represent an adaptation to hot dry summers (Masaki, 1980). The reproductive diapause of *H. convergens* falls short of true aestivation in that the beetles remain active, but a similar function can be inferred, that of enhancing adult survival during periods of low prey availability that are typically associated with

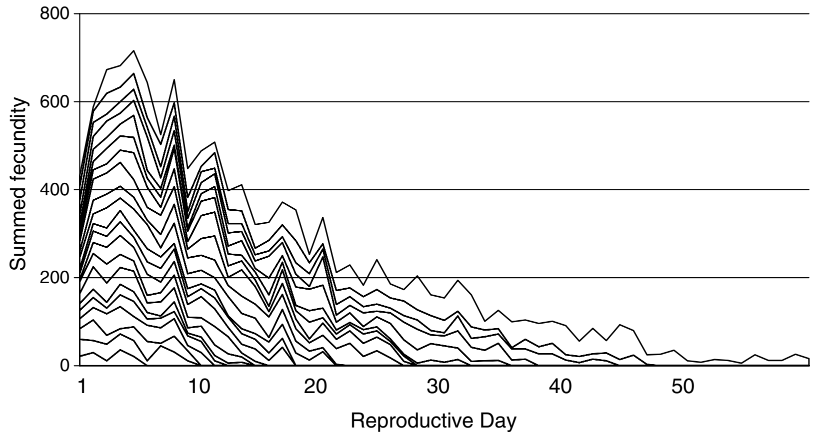

Fig. 5. Stacked line graph of egg production by *H. convergens* females ($n = 20$) that received an ad libitum diet of greenbug, *S. graminum*. Data for various females are aligned according to their first date of reproduction and summed on the *y*-axis in order of fecundity to demonstrate the triangular shape of the female fecundity function under conditions of unlimited food supply.

very hot weather in the region. Food limitation has been found to be a regulating factor for aestival diapause in relatively few insects (Nechols et al., 1999). Zaslavski et al. (1998) demonstrated a similar effect for *H. sedecimnotata* and Tauber and Tauber (1973) found that food was an important determinant of diapause induction and termination in a California strain of *Chrysoperla carnea* (Neuroptera: Chrysopidae), another relatively specialized aphid predator. Thus, food-regulated diapause could be a particular adaptation of predators specializing on prey such as aphids that exhibit seasonally unpredictable cycles of abundance.

Because of the facultative nature of reproductive activity in *H. convergens*, only the spring generation of overwintered adults is likely to reproduce as a comparatively synchronous cohort. Our data suggest that subsequent generations overlap as a function of two factors: (1) variation in the foraging success of first generation females in finding patches of suitable prey sufficient to terminate reproductive diapause directly and, (2) variation among females in spontaneous diapause termination when such patches are not encountered. Thus, *H. convergens* could potentially complete as many as five generations per year if suitable prey remained continuously available throughout the season, a highly unlikely circumstance in most years. These inferences are supported by the previous observations of Hagen (1962) that *H. convergens* can have a variable number of generations per year in California depending on the availability of suitable aphid prey.

Although some non-reproductive females on the maintenance diet were able to survive to an age of at least eight months, all were dead by mid-January. Our experimental beetles were subjected to a relatively moderate range of winter temperatures and at least two additional months survival would be needed for beetles to reach spring conditions suitable for reproduction. Therefore, it seems unlikely that first generation adults, even those able to maintain reproductive diapause throughout summer and fall, could survive to overwinter successfully and contribute offspring to the next spring generation. We conclude that a minimum of two generations per year appear necessary for the persistence of *H. convergens* populations in the High Plains region of the United States.

Largely as a result of the great variation in onset of reproduction among individual females experiencing food limitation (Fig. 2), we would expect *H. convergens* populations to normally exhibit an extended distribution of reproductive activity through summer and fall, somewhat similar to that depicted in Fig. 3. However, food sufficient to induce egg production is not necessarily sufficient to ensure female reproductive success—the local food supply at oviposition sites must be adequate to support the completed development of larvae. Even in years when suitable prey are never sufficiently abundant to directly induce diapause termination, variation in onset of reproduction under conditions of food-limitation will ensure that the reproductive effort of some subset of females coincides with the period of best prey availability for larvae, whenever this happens to occur in the course of the growing season. Thus, in certain years, a small proportion of spring generation females may contribute a large proportion of progeny to subsequent generations.

A wide range of coccinellid species can be observed exploiting sunflowers for their sap during summer months and this behavior has been previously documented (Michaud and Qureshi, 2005). Three of every four coccinellid adults tallied in our sunflower field were *H. convergens*, reflecting the relative dominance of this species among the assemblage of aphidophagous coccinellids inhabiting western Kansas (Rice and Wilde, 1988; Nechols and Harvey, 1998). To the best of our knowledge, summer diapause in response to food limitation has not been reported in any of the other five species commonly found in our region of study. Reproductive diapause in response to food limitation may therefore comprise an important life history trait that contributes to the success of *H. convergens* in the arid High Plains region of the Central United States and its significance as an important predator of cereal aphids (Brewer and Elliott, 2003).

Pairs of *H. convergens* were observed mating frequently from their date of collection until late in life, and in many cases long after the female ceased oviposition, suggesting that sexual activity is entirely unaffected by reproductive diapause. The fitness benefits of female promiscuity have been previously demonstrated in other aphidophagous coccinellids (Majerus, 1994) and such promiscuity could give rise to sperm competition. By re-pairing widowed females in the experiment, we reduced the likelihood that female fecundity or fertility would ever be limited by sperm availability, although we were unable to control for possible variation in male fitness that may have affected female reproductive performance via effects on sperm quality.

Hippodamia convergens females that were switched to an ad libitum greenbug diet after more than two months of reproductive diapause initiated a burst of reproductive effort, beginning an average of four days later, that subsequently tapered off through the remainder of their reproductive life (Fig. 5). This distribution of reproductive effort is consistent with the triangular fecundity function inferred by Dixon and Agarwala (2002) for coccinellid females, reflecting a maximal reproductive effort shortly after onset of reproduction that declined gradually with age. Similarly, ovipositing females on the maintenance diet required four days to effectively convert animal protein into eggs (Fig. 4), suggesting that this period may reflect the time required by the female reproductive system to respond to a favorable change in diet. Regression analyses revealed that fecundity varied as a function of the number of days a female produced a clutch, but was not correlated with either female weight or longevity, suggesting that body size bore no relation to female fitness.

Fully one third of females on the maintenance diet never became reproductive even though they survived for an average of 147 days. These could represent a sub-group of strongly diapausing females that will only become reproductive if and when an adequate supply of the preferred prey is encountered. Alternatively, they may represent a sub group of individuals intrinsically unable to mature eggs on the sub-optimal maintenance diet.

The strategy of delaying onset of reproduction through reproductive diapause (even though resources are available for some egg production) can only comprise an adaptive strategy if two conditions are met: (1) females are able to extend their life by doing so, and thus increase their chances of encountering an optimal prey patch, and (2) if the reproductive success obtainable in a rich patch of optimal prey is sufficiently large to balance the risks associated with delayed onset of reproduction. Individuals of both sexes died at a relatively constant rate throughout the course of the experiment, although males began dying earlier than females (Fig. 1), suggesting that the risk of mortality was relatively constant throughout adult life even in the absence of exposure to predation. The steeper mortality curve of females on the greenbug diet in comparison with those on the maintenance diet is likely indicative of the physiological costs associated with their high reproductive effort. Comparison of longevity between greenbug-fed females and those that also diapaused for at least two months but never received greenbug prey revealed that the latter lived an average of 45% longer than the former, confirming that females on the maintenance diet increased their lifespan by forgoing or reducing reproduction under sub-optimal conditions. Furthermore, greenbug-fed females were four times more likely to die with mature eggs left in their ovaries, suggesting that their cause of death was often due to failure of physiological processes unrelated to reproduction.

The negative correlations observed between date of onset of reproduction and both fecundity and fertility are likely indicative of the costs of reproductive diapause that appear to increase with female age. The longer females delay onset of reproduction, the lower their intrinsic reproductive potential and the greater their risk of dying without progeny. The fact that two thirds of females on the maintenance diet eventually terminated diapause even though optimal conditions were not encountered suggests a tendency for reproductive diapause to decay over time as a function of female age, independently of other factors. However, females that received the greenbug diet after more than two months in diapause produced more than five times the eggs of those on the maintenance diet that initiated reproduction earlier, and almost 10 times as many as those initiating reproduction later. The most fecund female on the greenbug diet produced more than four times the eggs of the most fecund female on the maintenance diet even though she began reproduction more than two months later in life.

Clearly, the reproductive diapause of *H. convergens* meets the criteria necessary for it to be considered an adaptive female strategy. Even though the strategy is time-limited because of the inevitable decline in female reproductive potential with age, female lifespan can be effectively extended by delaying the onset of reproduction and female fitness can be increased by 5- to 10-fold provided a rich patch of suitable prey is eventually encountered. Variation among females in the strength of reproductive diapause likely results in a broad temporal distribution of reproductive activity in the population throughout the summer and fall in most years when prey availability is sporadic. Flexibility in the reproductive schedule of female *H. convergens*, at both the level of the individual and the population, may well be a key life history feature determining its relative importance as a biological control agent of cereal aphids in the arid High Plains region of the United States.

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