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POPULATION ECOLOGY – ORIGINAL RESEARCH

Disease, contagious cannibalism, and associated population crash in an omnivorous bug, *Geocoris pallens*

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Abstract

Disease and cannibalism are two strongly density-dependent processes that can suppress predator populations. Here we show that California populations of the omnivorous predatory bug *Geocoris pallens* are subject to infection by a pathogen, as yet unidentified, that elicits elevated expression of cannibalism. Laboratory experiments showed that the pathogen is moderately virulent, causing flattened abdomens, elevated nymphal mortality, delayed development, and reduced body size of adult females. Infection furthermore increases the expression of cannibalism. Field populations of *Geocoris* spp. declined strongly in association with sharp increases in the expression of egg cannibalism by adult *G. pallens*. Increased cannibalism was accompanied by a strongly bimodal distribution of cannibalism expression, with some females (putatively uninfected) expressing little cannibalism and others (putatively infected) consuming most or all of the eggs present. Highly cannibalistic females did not increase their consumption of *Ephestia cautella* moth eggs, suggesting that the high cannibalism phenotype reflected a specific loss of restraint against eating conspecifics. Highly cannibalistic females also often exhibited reduced egg laying, consistent with a virulent pathogen; less frequently, more cannibalistic females exhibited elevated egg laying, suggesting that cannibalism might also facilitate recycling of nutrients in eggs. Elevated cannibalism was not correlated with reduced prey availability or elevated field densities of *G. pallens*. *Geocoris pallens* population crashes appear to reflect the combined consequences of direct virulence—adverse pathogen effects on the infected host's physiology—and indirect virulence—mortality of both infected and uninfected individuals due to elevated cannibalism expression by infected individuals.

Keywords Omnivory · Indirect virulence · Population collapse · Biological control

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Introduction

Cannibalism, once thought to be a relatively rare interaction in nature, is now recognized to be widespread among predatory and omnivorous animals (Polis 1981; Schausberger 2003; Wise 2006; Richardson et al. 2010; Pereira et al. 2017a, b). Because cannibalism is often expressed in a strongly density-dependent manner, it is expected to be an important cause of self-regulation of populations (Ricker 1954; Polis 1981; Claessen et al. 2004; Wise 2006; Richardson et al. 2010), which contributes to the stability of complex ecological networks (Barabás et al. 2017). However, demonstrating the long-term population-level consequences of cannibalism is difficult, because there is no simple experimental manipulation with which researchers can exclude cannibalistic interactions without excluding the cannibalistic species altogether; by definition, victim and exploiter are members of the same population.

Thus, we generally rely on observational studies or models to understand the longer-term and larger-scale consequences of cannibalistic interactions (e.g., Persson et al. 2003; Pereira et al. 2017a).

Disease is another widespread source of strongly density-dependent mortality in many populations. Disease and cannibalism can interact in various ways. Because a cannibalistic host population is likely to be suppressed by a pathogen or by cannibalism only when its density is relatively high, many models suggest that disease and cannibalism often will be mutually inhibitory—once either process suppresses host density, the importance of the other is lessened (Rudolf and Antonovics 2007; Bolker et al. 2008; Sadeh et al. 2016; Van Allen et al. 2017). Nevertheless, field observations and models have identified a variety of situations, some commonly encountered, in which trophic transmission of pathogens through cannibalism can elevate infection intensities and pathogen prevalence in host populations (Rudolf and Antonovics 2007; Pizzatto and Shine 2011; Sadeh and Rosenheim 2016; Sadeh et al. 2016; Whitfield et al. 2017). Furthermore, in the few systems in which it has been examined, infected hosts have also been found to increase their expression of cannibalism (Yan et al. 1994; Bunke et al. 2015).

Here we present laboratory experiments that demonstrate a causal role for a virulent infectious agent that elicits elevated expression of cannibalism in the omnivorous predatory insect *Geocoris pallens* Stål (Hemiptera: Lygaeidae). We then analyze multi-year field surveys of *Geocoris* spp. population densities and variation in cannibalism expression to determine if transient periods of elevated expression of cannibalism coincide with strong declines in *Geocoris* spp. densities. We ask a series of questions about the nature of the cannibalism-eliciting disease: (1) within high-cannibalism populations, is the distribution of cannibalism expression bimodal, with some individuals expressing very low cannibalism (putatively uninfected individuals) and other individuals expressing high cannibalism of conspecific eggs (putatively infected individuals)? (2) Within populations, do the more cannibalistic individuals often exhibit reduced fecundity, as might be expected for a virulent pathogen? (3) Do more cannibalistic individuals also consume a greater biomass of heterospecific prey, indicating a non-specific increase in predation, or do these individuals consume less heterospecific prey biomass, indicating a diet shift reflecting a specific increase in cannibalism? (4) Is elevated cannibalism associated with either higher field densities of *G. pallens* or with reduced availability of alternate prey? We conclude that strong declines in *Geocoris* spp. densities observed in the field reflect some combination of direct pathogen virulence in infected hosts, including elevated mortality and depressed fecundity, plus a contribution from 'indirect virulence,' in which infected hosts impose mortality on other members of their population (both infected and uninfected) through elevated expression of cannibalism.

Materials and methods

Study system

Geocoris pallens is a predatory bug, native to the Central Valley of California, USA, and common in both natural and agricultural ecosystems. *Geocoris* spp. are omnivores, feeding on plant-based resources, including extrafloral nectar and pollen, and directly on plant tissues (Ridgway and Jones 1968; Eubanks and Denno 1999), as well as consuming a broad array of arthropod prey, including thrips, aphids, and spider mites, which are the numerically dominant herbivores found in cotton and alfalfa (de Valpine and Rosenheim 2008). *Geocoris* spp. also consume dead arthropods and conspecifics, and can also forage for prey on the soil surface and belowground, entering through soil cracks; thus, it is challenging to characterize the full array of food resources available to these insects (Bugg et al. 1987; Takizawa and Snyder 2011; Law and Rosenheim 2013). *Geocoris* spp. lay their eggs singly, gluing them to the surface of plant structures, and eggs have no obvious defenses against predators.

Beginning in 2011, after several years of rearing different freshly field-collected *G. pallens* populations successfully in the laboratory, we observed in replicated laboratory colonies gradual increases in the insects' baseline expression of egg cannibalism, eventually leading to nearly 100% consumption of eggs and colony collapses. This phenomenon occurred despite our provisioning of diverse food resources [frozen *Ephestia cautella* (Walker) moth eggs, fresh shelled sunflower seeds (*Helianthus annuus* L.), bee pollen, fresh string beans (*Phaseolus vulgaris* L.)], and water, and was associated with extreme dorso-ventral flattening of the abdomen of some of the mid-instar nymphs, an abnormal phenotype we had never observed previously. The flattened abdomen phenotype was observed only in a minority of the nymphs, however, even as the colonies collapsed. These observations led us to hypothesize that a pathogen might be present and motivated a series of infection experiments.

Laboratory infection experiments

Experiment 1: nymph infection, abdominal flattening

The first experiment was designed to determine if a pathogen was responsible for the abnormal dorso-ventral flattening of the abdomen that we had observed. On 6 June 2013 we collected adult female *G. pallens* from a cotton field near Huron, CA. They were held singly in the laboratory for one week with excess food (*E. cautella* eggs, raw sunflower seeds,

and water) to standardize their hunger level. 300 females that laid eggs during the first week were then assayed for cannibalism expression, as follows. Females were housed singly at room temperature (25 ± 2 °C) with natural light in 60 mm-diameter Petri dishes supplied with a water vial and *E. cautella* eggs. Small paper rings were placed around each assay unit dish to prevent *G. pallens* from seeing their neighbors, as this species responds to nearby conspecifics with elevated cannibalism (Law and Rosenheim 2013). After 5 days, females were removed from the assay units, and eggs were inspected under a stereomicroscope to see if they were intact or cannibalized. *Geocoris pallens* has piercing-sucking mouthparts, and cannibalized eggs were generally completely emptied of their contents, leaving only a clean chorion. In some cases, partially-consumed eggs were also observed; these had some yolk remaining, but were obviously collapsed. Because female *G. pallens* cannot distinguish their own eggs from eggs of conspecifics (Law and Rosenheim 2013), this assay provides a measure of *G. pallens*' willingness to consume conspecific eggs.

Based on each individual's cannibalism expression, we established three groups. First, 50 of the females that expressed low cannibalism (< 11% eggs consumed) were screened in a second cannibalism assay to confirm their behavioral phenotype; 42 of these 50 females continued to express low to moderate cannibalism (< 40% eggs consumed), and their eggs were saved to produce the individuals used in the experiment as subjects. Second, the rest of the females that expressed low cannibalism (< 11% of eggs consumed) were immediately frozen at − 20 °C so that they could subsequently be homogenized, autoclaved, and then used to create the "control treatment" homogenate. Third, females who consumed > 60% of their laid eggs in the initial assay (high cannibalism) were immediately frozen at − 20 °C so that they could subsequently be homogenized and used to create the "field contamination" treatment. Because unmated females are more cannibalistic (Law and Rosenheim 2013), we verified that the highly cannibalistic females had been successfully mated by holding their uncannibalized eggs until the developing embryos' eye spots could be seen through the chorion.

6–15 sibling eggs deposited by low-cannibalism females were placed in 59.2 ml plastic cups, each representing a single experimental unit, supplied with a water vial and with cotton wool to reduce hatchling cannibalism, and held at room temperature (25 ± 2 °C) and natural light. Cups were assigned to one of three treatments, each replicated 42 times: control, field contamination, and laboratory contamination. When the *G. pallens* eggs began to hatch (designated as day 1), *E. cautella* moth eggs, bee pollen, and a single raw sunflower seed were added to all cups. In all three treatments, the moth eggs, bee pollen, and sunflower seeds were coated with fluid obtained by homogenizing 25 adult female *G. pallens* obtained from either the low cannibalism females collected near Huron ("control"), high cannibalism females collected near Huron ("field contamination"), or from a collapsing laboratory colony whose females were also highly cannibalistic ("laboratory contamination"). Homogenates were prepared by grinding 25 female *G. pallens* in an Eppendorf tube in 2.5 ml of deionized water using a pestle, vortexing for 10 s, and drawing off the liquid with a micropipette. Only the homogenate for the control treatment was then autoclaved at 151 °C for 15 min.

To provide a second possible source of infection, and recognizing that *Geocoris* spp. feed on dead arthropods (Bugg et al. 1987), on day 6 each replicate cup received a single cadaver of an adult female *G. pallens* killed by freezing and obtained from the same source that was used to create the homogenate. On day 9 all food remains except cadavers were removed and replaced with fresh moth eggs, bee pollen, and sunflower seeds, treated with the appropriate homogenates. Thus, nymphal *G. pallens* had multiple possible routes of infection, and all their food sources (moth eggs, bee pollen, sunflower seeds, and conspecific cadavers) were potentially contaminated with the putative pathogen. Nymphs developed to the fourth nymphal instar between days 16 and 20, at which point each replicate cup was scored for whether at least one individual with obvious dorso-ventral flattening of the abdomen was present or not.

Experiment 2: nymph infection, virulence

The second experiment was designed to determine if the pathogen, whose presence was indicated by the first experiment, was virulent, adversely affecting survival, development rate, or growth. On 18 August 2013, adult females were collected near Huron, CA and assayed for cannibalism in the laboratory as described in Experiment 1. Females that cannibalized 100% of their eggs were kept alive at 4 °C to subsequently create an infectious homogenate. Non-cannibalistic females (0% cannibalism) were reared for 17 days and were then re-assayed for cannibalism for three days to confirm their phenotype. From this assay, eggs laid by ten females that expressed low cannibalism rates (cannibalism ≤ 17%) were held individually in 0.6 ml Eppendorf tubes to rear the experimental subjects. The infectious homogenate stock was prepared by macerating eight of the refrigerated, highly cannibalistic females individually in a chilled Eppendorf tube in 50 µl deionized water, and then pooling the resulting material. The macerate was vortexed for 10 s, pulse-centrifuged, and the supernatant then drawn off with a micropipette and combined with sucrose powder to create a 30% sucrose solution. The control treatment stock was simply a 30% sucrose solution in deionized water, without any homogenate added. These stocks were stored at 4 °C for up to 6 days, covered in aluminum foil, before being delivered to the subjects.

Eggs were observed every morning for hatching. Hatchlings were immediately fed according to their assigned experimental treatments: sucrose solution for the control treatment ($n=48$ replicates) and infectious homogenate for the pathogen exposure treatment ($n=61$ replicates; we included more replicates because we anticipated greater mortality), each delivered as a 2-µl droplet on the Eppendorf tube wall covered with a piece of filter paper to allow the nymphs to feed on it for 24 h while preventing them from getting stuck in the liquid. After the first experimental feeding, nymphs were transferred individually to 59.2 ml plastic cups, where they were reared on moth eggs, green beans, and sunflower seeds in excess, and were provided with water vials for drinking. After 1 week, a second experimental feeding involving the same treatments was delivered in new Eppendorf tubes for 48 h, followed by transferring the nymphs to new plastic cups for continued rearing. Each nymph was weighed and photographed for head width measurements 16 days after hatching, when most were in their fourth instar. Many of the individuals that expressed extreme abdominal deformations did not survive to that stage, but we examined the relationship between head width and body weight to detect more mildly deformed nymphs. Nymphs were then followed daily to record the day when they molted to the adult stage, their sex, and their mass as 1-day-old adults.

Experiment 3: Adult infection, contagious cannibalism

This experiment was designed to determine if the pathogen caused increased cannibalism expression in adult females. In August 2013, adult female *G. pallens* were collected from near Huron and Bakersfield and immediately assayed for cannibalism expression in the laboratory over 4 days. Females that consumed 100% of their eggs were held alive for 2 days at 4 °C for subsequent infectious homogenate preparation. Non-cannibalistic *G. pallens* females (0% egg cannibalism) that laid at least 8 eggs were selected as subjects for the experiment. Each female was placed individually in a 1.5 ml Eppendorf tube and then randomly allocated to one of two treatments: control, for which each female received a 2-µl droplet of 30% sucrose solution ($n=25$ replicates), and pathogen exposure, for which each female received a 2-µl droplet of infectious homogenate in a 30% sucrose solution, prepared as described in Experiment 2 ($n=24$ replicates). Adult females remained in the Eppendorf tubes for 24 h and were then introduced into two consecutive 3-day cannibalism assays.

Sampling cannibalism expression and population densities

We sampled *Geocoris* spp. populations during the summer months in cultivated fields of cotton (*Gossypium hirsutum* L. and *Gossypium barbadense* L.) and alfalfa (*Medicago sativa* L.). Sampled fields were generally insecticide-free for the entire growing season or, for some alfalfa fields, had been treated once during the late winter (often in February) for weevil control. Cotton fields sampled in 2003 were in conventional, commercial production; in this case, we sampled only in fields that had not received insecticide applications during the previous 3 weeks. Although *G. pallens* is the dominant *Geocoris* species found in both cotton and alfalfa, two other species were sometimes found: *G. punctipes* (Say), which was relatively rare in both crops, and *G. atricolor* Montandon, which was rare in cotton but sometimes more abundant in alfalfa (for details on *Geocoris* species compositions, see Online Appendix 3). Throughout this paper, when we refer to densities of "*Geocoris* spp." populations, we refer to counts of all *Geocoris* species combined. We chose often to work with combined counts, because immature *G. pallens* and *G. punctipes* are difficult to distinguish, and because *G. pallens* was almost always the dominant species. All laboratory bioassays of cannibalism expression, however, refer strictly to *G. pallens*, and we refer to these observations using the species name "*G. pallens*."

The main patterns of cannibalism expression and population densities that we attempt to document in this study became the focus of our research attention only gradually, during the course of studies that originally had different objectives. Early, informal observations, which we describe below, raised questions that led to later, more organized sampling efforts. Thus, we attempt here to reconstruct key features of the dynamics of cannibalism expression and population dynamics using a set of somewhat heterogeneous and, in some cases, repurposed datasets. We retained for analysis only those data that were gathered using substantially equivalent methods, as described below, to assure the comparability of the observations.

Sampling at the Westside site

From 2009 to 2016, *G. pallens* densities were sampled in cotton plantings grown at the University of California Westside Research and Extension Center (UC Westside REC; 36.3391, − 120.1124). Each sample consisted of 50 swings of a 38.1 cm-diameter sweep net swung across the upper canopy of a single row of cotton plants to generate a single count of nymphal + adult *Geocoris* spp. With one exception, eight such samples were taken each year on a single date between 8 and 22 July (in 2012 only four samples were taken, on 25 June).

Surveys of *Geocoris* spp. densities and prey availability

We conducted field surveys of *Geocoris* spp. densities and prey availability across the Central Valley during

1993–1994, 1997–1998, and 2003 in cotton, before the crash of *Geocoris* spp. populations that we document here, and again during 2015–2017 in both cotton and alfalfa, after most of the population densities had recovered. We included alfalfa in the later surveys because cotton plantings had decreased by ca. 80% during the intervening years, making it difficult to find suitable collecting sites. *Geocoris* spp. population densities were estimated using sweep nets, as described above, with ca. 9 sweep net samples conducted per site (mean ± SD = 9.0 ± 1.8; range = 3–11). Although during 1993–1994 populations were sampled weekly through the summer, for the analyses presented here we chose the sample taken closest to July 20 to provide single density estimates that could be compared directly with the 2015–2017 surveys, in which fields were sampled just once between June and Sept, but mostly in mid-late July (see Online Appendix 1 for details of sampling locations and dates). At most sites, subsamples of *Geocoris* spp. adults were returned to the laboratory to determine species composition. To estimate the abundance of the dominant herbivore prey available to *Geocoris* spp., including the western flower thrips *Frankliniella occidentalis* (Pergande), spider mites *Tetranychus* spp., and aphids (on cotton *Aphis gossypii* Glover; on alfalfa *Acyrthosiphon pisum* Harris, *Aphis craccivora* Koch, and *Therioaphis maculata* (Buckton), we took leaf samples (1993–1994, 1997–1998, and 2015–2017). In cotton, we took 50 main-stem leaves from the fifth node below the plant terminal, whereas in alfalfa we took 30 stems, cut near the plant crown. Leaf samples were stored in 70% ethanol in plastic bags and refrigerated. Samples were processed by hand, rinsing all leaf surfaces over a fine mesh sieve (11.8–15.7 mesh per mm) to collect all motile arthropods for counting under a stereomicroscope.

Cannibalism assay

We quantified cannibalism expression by returning field-collected adult female *G. pallens* to the laboratory and testing them singly in the simple assay described above (Experiment 1). Bioassay methods varied somewhat across years; here we describe the common elements and the main between-year changes, with additional details presented in Online Appendix 1.

Adult female *Geocoris* spp. were field collected with a sweep net from cotton or alfalfa and transported to the laboratory in a cooler. We assayed cannibalism in adult *G. pallens* by introducing females singly into small assay units (35 ml plastic vials in 2010; 60 mm Petri dishes in all other years) provided with food and held at room temperature (25 ± 2 °C) and natural light.

The foods provided varied across years; in 2008–2009 all females were held for a day with water and excess eggs of *E. cautella* moths prior to the cannibalism assays to standardize hunger level, and then given a 2-cm slice of string bean during the assay as a source of water and nutrients. In 2010 *E. cautella* eggs and water were provided both before the assay (for one to several days) and during the assay. From 2013 to 2017 females were generally kept in a cooler or a refrigerator (4 °C) for not more than 24 h prior to being introduced directly into the cannibalism assay; the only exception involved females from just two populations sampled in 2013 that were fed prior to cannibalism assays (water vial; a raw, shelled sunflower seed; raw honeybee pollen; *E. cautella* eggs) for 6 days prior to the assays, in order to standardize their hunger. From 2013 to 2017, females in cannibalism assays were provided with a 2-cm slice of string bean, a sunflower seed, excess *E. cautella* eggs, and in some cases a water vial as an additional source of water.

Females were generally held in the assay units for 3 days (sometimes other durations; only 3-day assays were included in the analyses of between-population differences in cannibalism expression), during which they laid eggs singly. Eggs never completed their development and hatched during the short assays, and no other source of mortality could be confused with cannibalism. Nearly all eggs, including those deposited by females expressing high levels of cannibalism, developed eye-spots when checked a few days after the cannibalism assay was scored, indicating that females were almost universally mated and were laying viable eggs. The total number of eggs laid provided a measure of short-term fecundity.

To assess the possibility that *G. pallens* that consumed more of their own eggs were also consuming more heterospecific prey, we quantified consumption of *E. cautella* eggs during one of the cannibalism assays. While testing the Huron1 field population collected on 16 May, 2013, *E. cautella* eggs were provided in a small plastic dish, which we weighed to the nearest 0.01 mg immediately before and after the assay.

Statistical analyses

All analyses were performed in R version 3.3.3 (R Core Team 2017). Between-treatment comparisons of proportions (sibships or individuals expressing abdominal flattening in Experiments 1 and 2, respectively, and survival to adulthood in Experiment 2) were performed using *Z* tests or Fisher's exact tests. Nymph body condition at 16 days was analyzed using general linear models, by regressing log-transformed body weight versus head width, and testing for difference in slopes between treatments. Nymph development time and size at adulthood in Experiment 2 were analyzed using two-way ANOVA, testing for the combined effects of treatments and sex. Cannibalism expression was compared across treatments in Experiment 3 using a Wilcoxon rank-sum test. To test for changing expression of cannibalism over time from

2009 to 2017, we built a generalized linear mixed model (GLMM) with fixed effects of year and crop (alfalfa versus cotton), a random effect for population, binomially distributed error (eggs either are, or are not, cannibalized), and a logit link. Only cannibalism assays of 3-day duration were used in this analysis. To assess changes in mean *Geocoris* spp. densities found in sweep sample counts at the UC Westside REC, we constructed a generalized linear model (GLM) with main effect for year and Poisson-distributed error (log link). To examine if mean *Geocoris* spp. population densities observed before the population crash (1993–2003) differed from densities after the crash (2015–2017), we constructed another GLMM using a categorical fixed effect to compare pre- versus post-crash, a fixed effect for crop of origin (alfalfa versus cotton), a random effect for population, and a Poisson-distributed error with log link function. To test for bimodal distributions of cannibalism expression within sampled populations, we computed Hartigans' dip test statistic for unimodality using the package diptest (Maechler 2016). We tested populations from which ≥ 9 individuals were tested in cannibalism assays of any duration (1–5 days). Multiple linear regression was used to examine the influence of mean cannibalism expression by a population on the bimodality of the distribution of cannibalism expression within that population, while controlling for effects of variable sample sizes. Univariate linear regression was used to test the relationship between within-population variation in consumption of conspecific eggs (cannibalism) versus consumption of heterospecific eggs (*E. cautella* moth eggs). A GLM was used to test for an association between within-population variation in short-term fecundity and cannibalism expression, using binomially distributed error and a logit link function. Finally, regression was used to ask if between-population variation in cannibalism expression was associated with availability of prey (multiple linear regression, with independent variables for counts of thrips, spider mites, and aphids) or field densities of *G. pallens* at the collection site (univariate linear regression). All GLMs and GLMMs were built using the lme4 package (Bates et al. 2017).

Results

Experiment 1: nymph infection, abdominal flattening

Of the 43 sibships tested in each treatment, only 5 sibships in the control treatment presented at least one nymph with a dorso-ventrally flattened abdomen, whereas 25 and 21 sibships presented at least one deformed individual in the laboratory contamination and field contamination treatments, respectively (Z tests: $\chi^2 = 20.7$, $P < 0.0001$, and $\chi^2 = 14.3$, $P = 0.0002$, respectively). These results establish that a contagious factor was responsible for the flattened abdomen symptom that we had observed associated with the highly cannibalistic, collapsing laboratory colonies of *G. pallens*.

Experiment 2: nymph infection, virulence

16 days after hatching, *G. pallens* nymphs with severely dorso-ventrally flattened abdomens were observed more frequently in the pathogen exposure treatment (7 of 61, 11.5%) than in the control treatment (1 of 48, 2.1%; one-tailed Fisher's exact test, $P = 0.038$) (Fig. 1a). Mortality of nymphs prior to reaching the adult stage was also significantly elevated in the pathogen exposure treatment compared to the control treatment (Fig. 1a; Z test: $\chi^2 = 9.6$, $P = 0.002$). Nymph body condition at 16 days was significantly lower in the pathogen exposure treatment than in the control treatment (Fig. 1b; linear model, head width by homogenate treatment interaction: $P = 0.033$; model fit: $R^2 = 0.66$, $F_{3,74} = 47.1$, $P < 0.0001$). Nymphs in the pathogen exposure treatment also required significantly longer to reach the adult stage (Fig. 1c; $F_{1,53} = 6.1$, $P = 0.016$); males developed more slowly than females ($F_{1,53} = 5.8$, $P = 0.019$). Finally, pathogen exposure in nymphs reduced the body size of the resulting adult females ($t = 2.88$, $P = 0.006$), but not males ($t = 0.45$, $P = 0.65$; Fig. 1d, main effect of sex, $P < 0.0001$, sex by treatment interaction $P = 0.024$). These results establish that the *G. pallens* pathogen is moderately virulent, reducing a range of fitness-related metrics.

Experiment 3: adult infection, contagious cannibalism

In the first cannibalism assay, which covered days 1–3 after applying the experimental treatments, *G. pallens* exposed to the pathogen expressed significantly more cannibalism (mean ± SE % eggs eaten = 37.4 ± 6.9%, median = 31.0%) than did *G. pallens* that fed on the control sucrose solution (mean 21.2 ± 6.1%, median = 5.6% eggs cannibalized; Wilcoxon's $W = 198$, $P_{1-\text{tailed}} = 0.019$; Fig. 2). This effect was short-lived, however, as cannibalism expression during the second assay, which covered days 4–6 after applying the treatments, no longer differed (mean ± SE, 27.8 ± 8.6%; median 0% for the pathogen-exposed females and mean 27.2 ± 8.0%; median 5% for the control females, $W = 217$, $P_{1-\text{tailed}} = 0.39$). Thus, the pathogen appeared to elicit a transient pulse of elevated cannibalism in *G. pallens*. A second adult infection experiment, which we do not present because of unacceptably high mortality during the infection protocol, produced similar results (data not shown).

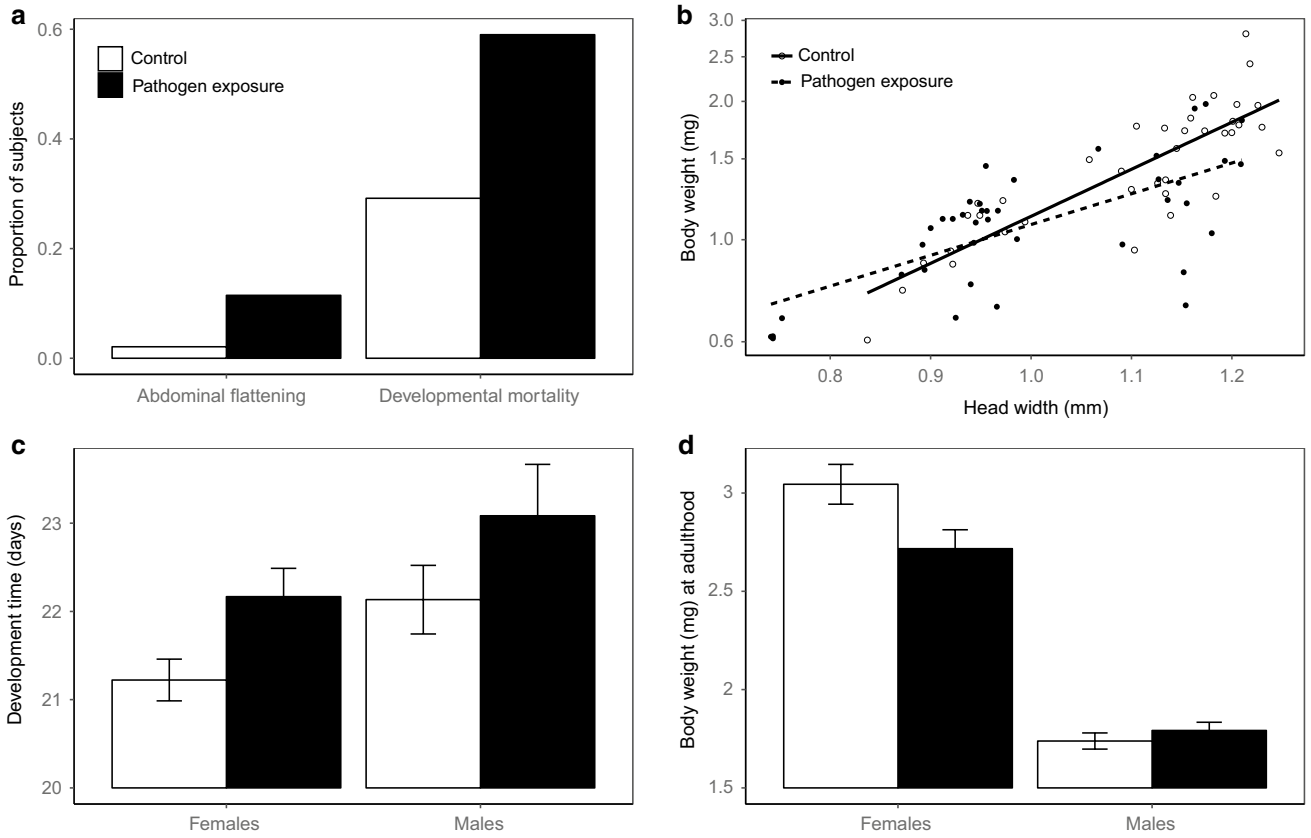

Fig. 1 Experiment 2, nymph infection, virulence. Effects of pathogen exposure on **a** proportions of nymphs that expressed extremely dorsoventrally flattened abdomens at age 16 days, and mortality between hatching and reaching the adult stage; **b** body condition of nymphs at age 16 days, measured as the relationship between body weight and head width; **c** development time of nymphs from hatching to adulthood; and **d** body weights of 1-day-old adult females and males

Informal observations of *Geocoris* spp. population crash

Informal observations described in full in Online Appendix 2 led us to hypothesize a widespread collapse of *G. pallens* populations in California's Central Valley that coincided with an increase in cannibalism expression. In brief, the following were the key observations: (1) between 2007 and 2008, *G. pallens* populations in the Davis area crashed and remained at very low densities through 2017; (2) in 2008 we moved our collection sites for *G. pallens* south ca. 115 km to the Los Baños–Firebaugh area; between 2010 and 2011, populations there also collapsed; (3) in 2012 we moved our collections an additional 90 km south to Huron; in 2013 we detected very high levels of cannibalism in multiple populations there, and by 2014 populations in that region (western Fresno County) had also collapsed; (4) by 2015–2017, most but not all of *G. pallens* populations in the Central Valley had recovered.

Population crash at the Westside site

Geocoris spp. population densities in cotton at Westside collapsed during 2012–2013 (GLM, effect of year, $P < 0.001$; Fig. 3a). This population collapse mirrored the drop in *Geocoris* spp. densities that we recorded informally across many sites in the Central Valley. The collapse in *Geocoris* spp. densities also coincided with strongly elevated mean cannibalism expression by *G. pallens* females (Fig. 3b); cannibalism varied significantly across years (GLMM, $F = 4.56$, $P < 0.001$) but did not vary between females collected from alfalfa versus cotton ($F = 0.002$, $P = 0.97$). For 2013, when the population reached its lowest density at Westside, our estimate of cannibalism was for a population sampled near Huron, ca. 25 km further south; thus, the high cannibalism coincided both temporally and, approximately, spatially with the strong decline in *Geocoris* spp. densities. Other fields sampled in the Huron area during 2013, but using cannibalism assays of different durations and thus not included in

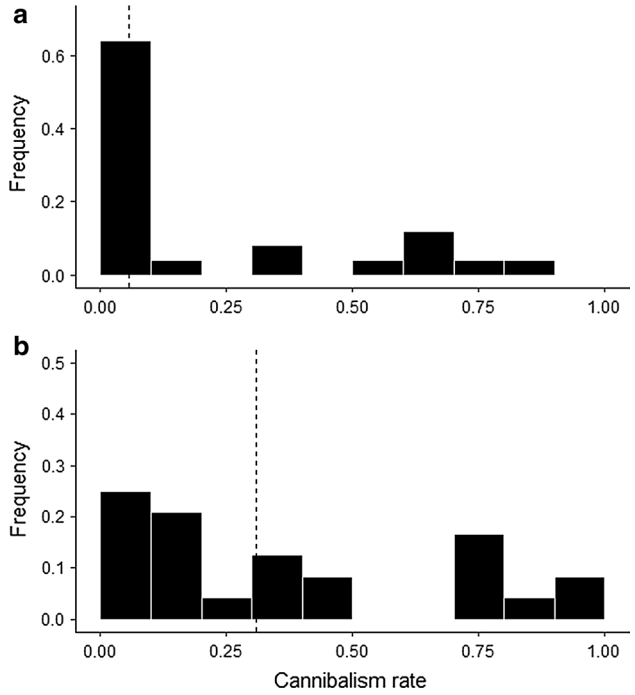

Fig. 2 Experiment 3, adult infection, contagious cannibalism. Distribution of cannibalism rates across days 1–3 post-infection, **a** control; **b** pathogen exposure. Vertical dashed lines indicate medians

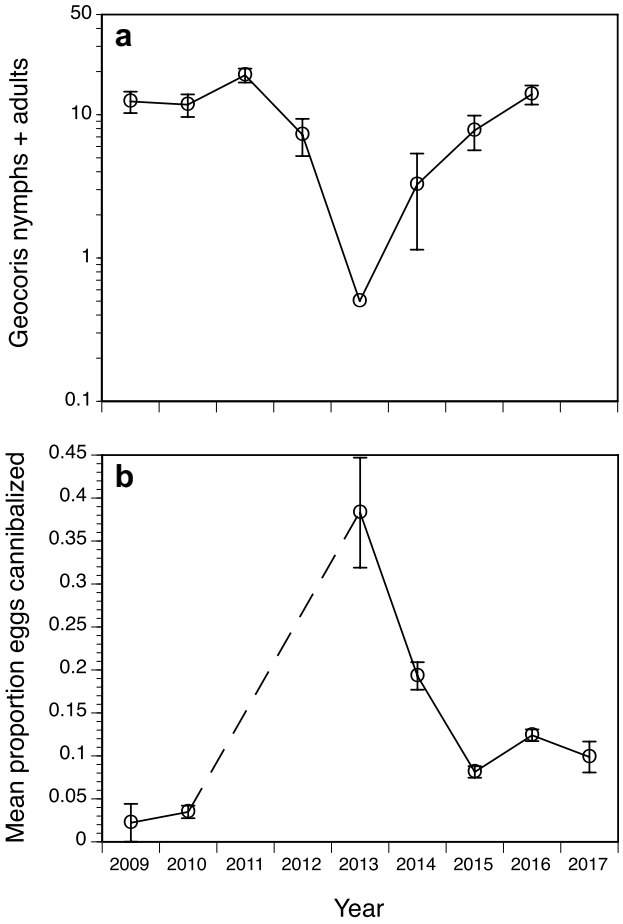

Fig. 3 **a** Mean densities of *Geocoris* spp. motile stages (nymphs + adults) per sweep net sample in cotton fields grown at the University of California Westside Research and Extension Center (log scale). **b** Mean cannibalism expression (proportion of eggs laid that were subsequently cannibalized during a 3-day assay) for *G. pallens* females sampled from cotton or alfalfa in California's Central Valley. Cannibalism data reflect the means across all individuals tested within the indicated year using 3-day assays, as described in Appendix 1. Shown are means ± 1 SE

the Fig. 3 data, exhibited similarly elevated cannibalism (see below), and had crashed by 2014.

Recovery of *Geocoris* spp. populations

Population surveys of *Geocoris* spp. revealed that densities largely recovered across the Central Valley following the population crash (Figs. 3, 4). Mean *Geocoris* spp. densities were not significantly different before versus after the crash (GLMM, $F = 17.32$, $P = 0.22$) and did not differ between the two sampled crops (alfalfa vs. cotton, $F = 2.92$, $P = 0.09$).

Within-population distribution of cannibalism expression

The within-population distributions of cannibalism expression observed during 2008–2010 were consistently unimodal (7/7 tests not significantly different from unimodal, Fig. 5). Although sample sizes were small, no high-cannibalism females were observed in 2008 or 2009. During 2010, however, we recorded a small proportion of more cannibalistic females for the first time (Fig. 5d, g). The greatly increased mean expression of cannibalism observed in 2013–2014 (Fig. 3b) was associated with the appearance, within populations, of a class of females that expressed very high levels of cannibalism (Fig. 6), producing a significantly bimodal distribution (unimodality rejected for 5/7 populations, Fig. 6). As cannibalism expression returned to lower values and population densities recovered during 2015–2017, nearly all populations returned to unimodal distributions of cannibalism expression (35/37 populations not significantly different from unimodal, Figs. 7, S1, S2 in Electronic Supplementary Material, ESM). Across all populations tested from 2008 to 2017, the dip test statistic for non-unimodality (D) was significantly positively correlated with mean cannibalism expression in the population (Fig. 8); thus, populations with elevated cannibalism appeared to contain a class of highly cannibalistic females, rather than showing an increase in cannibalism expression by all population members.

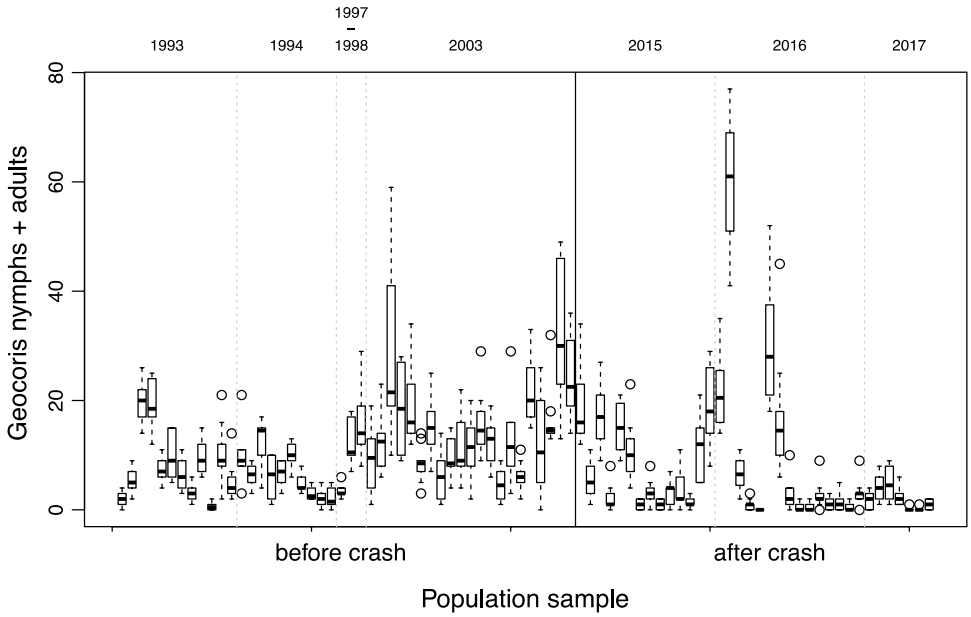

Fig. 4 Boxplot for density of *Geocoris* spp. populations sampled using sweep nets in cotton and alfalfa fields growing in California's Central Valley before (1993–2003) and after (2015–2017) a population crash associated with elevated cannibalism. Heavy black bars indicate the median values; the top and bottom of each box indicate the 25th and 75th percentiles; the whiskers indicate the most extreme values observed within 1.5 times the interquartile range of the box; circles indicate all values outside the whiskers. The locations of all sampled populations are given in Online Appendix 3

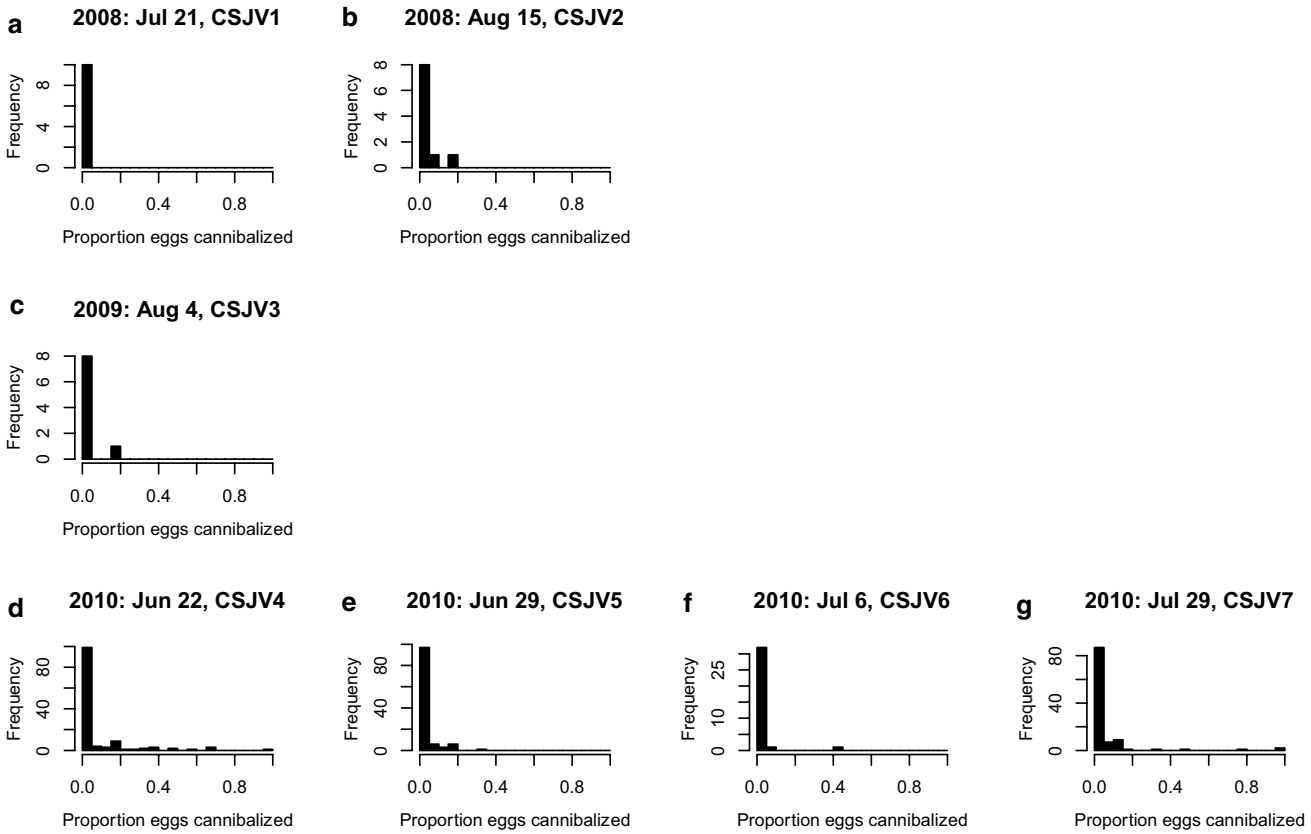

Fig. 5 Distribution of cannibalism expression within populations of *G. pallens* collected in cotton grown in the central San Joaquin Valley (CSJV), 2008–2010. The hypothesis of unimodality for the distribution of cannibalism values cannot be rejected for any population: **a** $N=10$, $D=0.05$, $P=1.00$; **b** $N=10$, $D=0.06$, $P=0.99$; **c** $N=9$, $D=0.06$, $P=1.00$; **d** $N=129$, $D=0.03$, $P=0.83$; **e** $N=113$, $D=0.04$, $P=0.32$; **f** $N=34$, $D=0.02$, $P=1.00$; **g** $N=109$, $D=0.04$, $P=0.30$. See Online Appendix 1 for additional details on site locations and assay methods

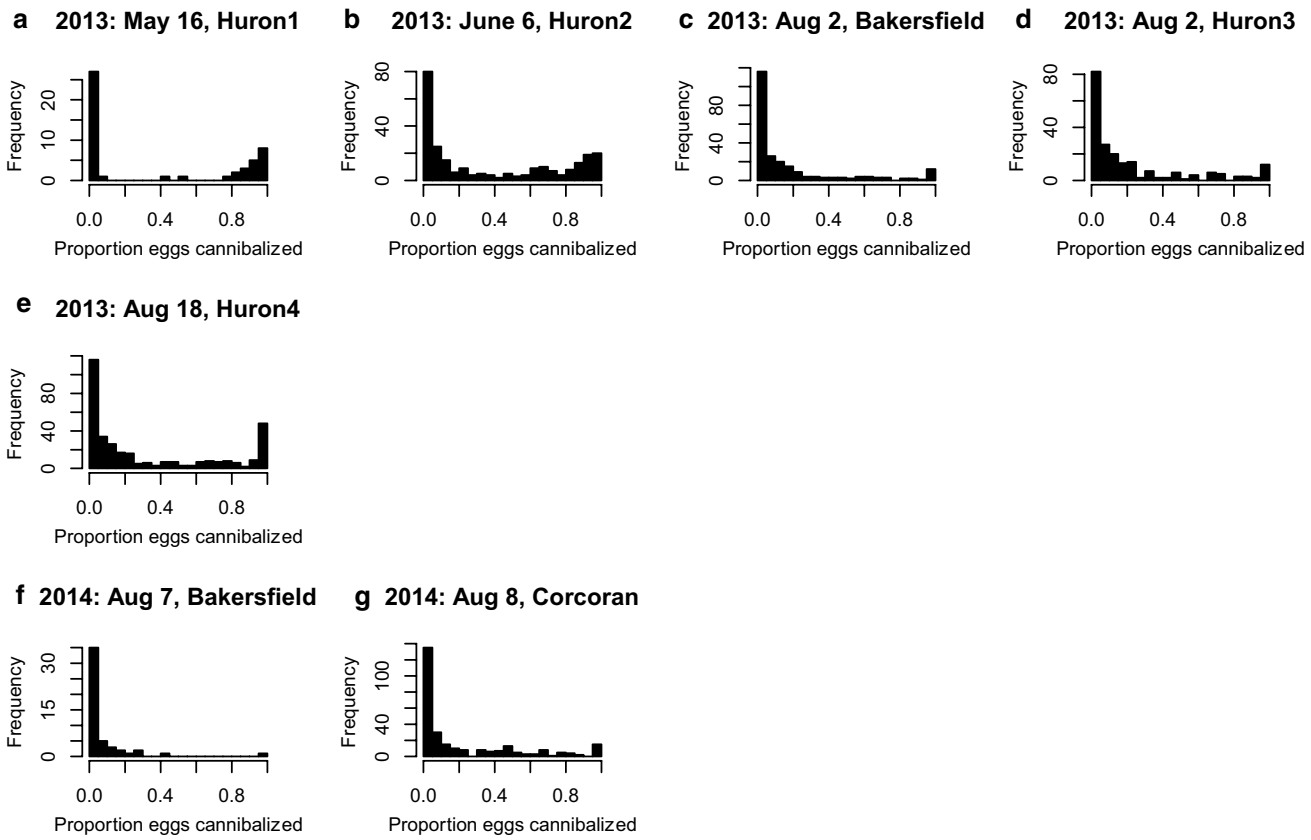

Fig. 6 Distribution of cannibalism expression within populations of *G. pallens* collected in cotton grown in the San Joaquin Valley, 2013–2014. The hypothesis of unimodality for the distribution of cannibalism values was rejected for five of the seven populations shown: **a** $N=49$, $D=0.147$, $P<0.0001$; **b** $N=252$, $D=0.063$, $P<0.0001$; **c** $N=236$, $D=0.029$, $P=0.19$; **d** $N=211$, $D=0.042$, $P=0.009$; **e** $N=338$, $D=0.068$, $P<0.0001$; **f** $N=50$, $D=0.082$, $P=0.008$; **g** $N=278$, $D=0.030$, $P=0.08$. See Online Appendix 1 for additional details on site locations and assay methods

Consumption of heterospecific vs. conspecific eggs by highly cannibalistic females

Females that consumed a larger proportion of their own eggs showed no increase in their consumption of heterospecific (*E. cautella*) eggs; instead, the data actually suggest the reverse: a slight decrease in the consumption of *E. cautella* eggs (Fig. 9; linear regression, $R^2=0.079$, $N=49$, $P=0.05$). Thus, highly cannibalistic females were exhibiting a selective increase in the consumption of conspecific prey, and may have been trading off increased consumption of conspecific prey for a decreased consumption of heterospecific prey.

Relationship between cannibalism expression and short-term fecundity

We used generalized linear models to ask if there was any relationship, within populations, between cannibalism expression and short-term fecundity (i.e., the number of eggs laid by *G. pallens* during the cannibalism assay). The results were mixed. During 2008–2010, when cannibalism expression was generally very low and all *G. pallens* females were fed *E. cautella* eggs ad libitum prior to the assays to standardize hunger levels, we found no significant relationships between cannibalism and fecundity ($P \geq 0.10$, $n=7$ populations tested). During 2013–2014, when cannibalism expression was elevated, two populations were fed *E. cautella* eggs ad libitum prior to the cannibalism assays to standardize hunger; one population exhibited a strong negative relationship between cannibalism and fecundity (Fig. 10a); such a relationship might be expected if a pathogen that infects *G. pallens* reduces their fecundity and makes them more cannibalistic. A second population, however, exhibited a noisier but significant positive relationship (Fig. 10b). All of the remaining assays were performed with females taken directly from the field and not fed before the assays to standardize hunger. Results were again variable: during 2013–2014; we observed three significant negative relationships and two significant positive relationships. During 2015–2017, we

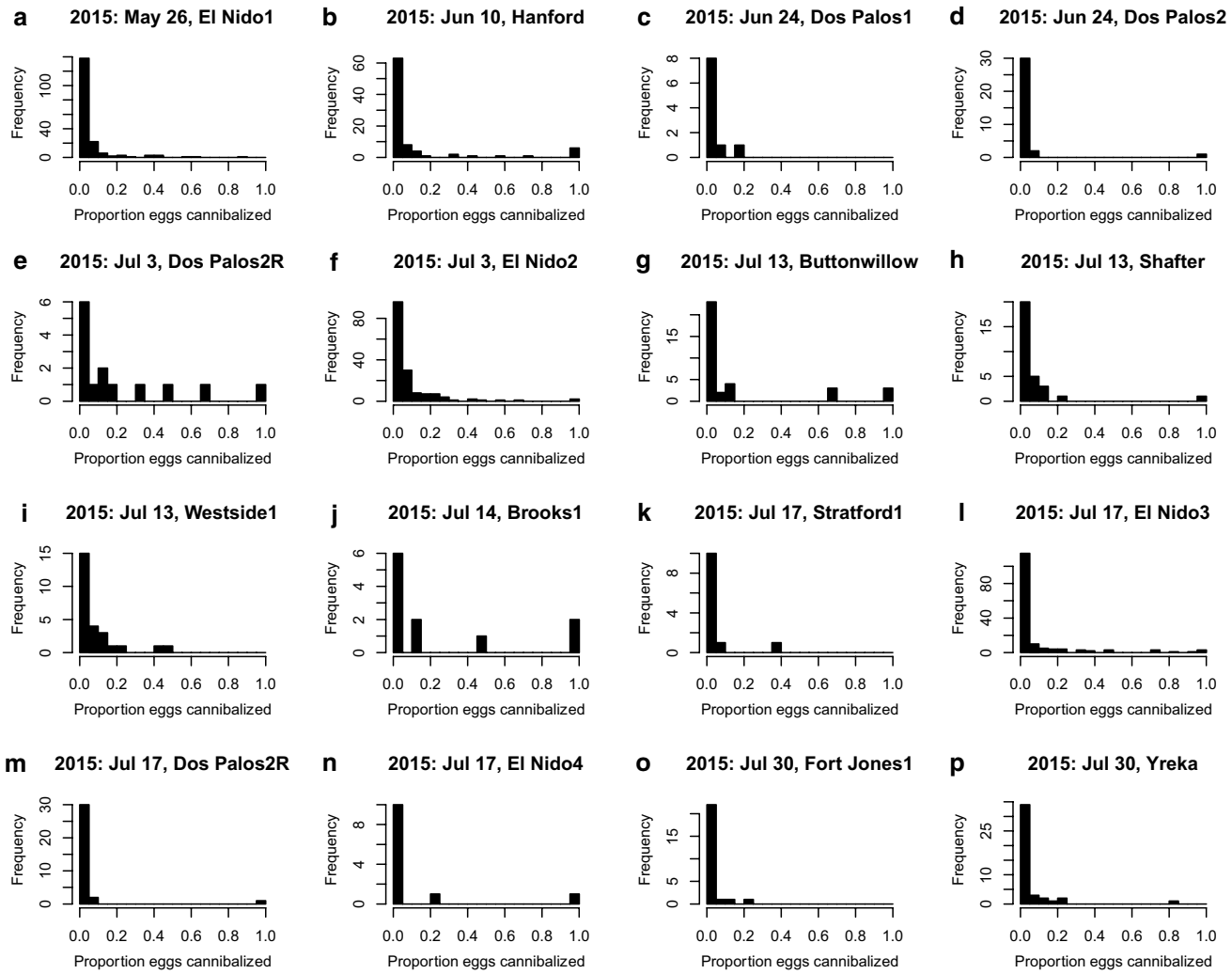

Fig. 7 Distribution of cannibalism expression within populations of *G. pallens* collected in alfalfa and cotton grown in the Central Valley, 2015. The hypothesis of unimodality for the distribution of cannibalism values was rejected for only 1 of the 16 populations shown (see **f**): **a** $N=181$, $D=0.037$, $P=0.08$; **b** $N=87$, $D=0.034$, $P=0.67$; **c** $N=10$, $D=0.050$, $P=1.00$; **d** $N=33$, $D=0.022$, $P=1.00$; **e** $N=14$, $D=0.071$, $P=0.81$; **f** $N=160$, $D=0.052$, $P=0.003$; **g** $N=35$, $D=0.052$, $P=0.66$; **h** $N=30$, $D=0.059$, $P=0.58$; **i** $N=26$, $D=0.079$, $P=0.20$; **j** $N=11$, $D=0.091$, $P=0.59$; **k** $N=12$, $D=0.052$, $P=0.99$; **l** $N=154$, $D=0.024$, $P=0.079$; **m** $N=33$, $D=0.022$, $P=1.00$; **n** $N=12$, $D=0.042$, $P=1.00$; **o** $N=25$, $D=0.042$, $P=0.003$; **p** $N=35$, $D=0.052$, $P=0.99$. See Online Appendix 1 for additional details on site locations and assay methods

observed a total of 17 significant negative relationships, two significant positive relationships, and 18 non-significant associations (data not shown). For the 2015–2017 assays, in which hunger was not standardized, a negative relationship could reflect within-population variation in hunger, with hungrier females expressing more cannibalism and laying fewer eggs. Thus, while there is a preponderance of evidence supporting a negative relationship between cannibalism and short-term fecundity, the handful of positive relationships suggests that some process, such as more rapid recycling of nutrients in eggs through cannibalism, may also be operating in some populations.

Cannibalism expression, *G. pallens* density, and prey availability

Between-population variation in mean expression of cannibalism by *G. pallens* adult females was not explained by either the density of *G. pallens* ($R^2=0.0013$, $N=27$, $P=0.86$; Fig. S3 in ESM), the density of all *Geocoris* spp. combined ($R^2=0.0002$, $N=27$, $P=0.94$), or the availability of the numerically dominant prey [thrips, aphids, or mites, tested as separate independent variables with crop

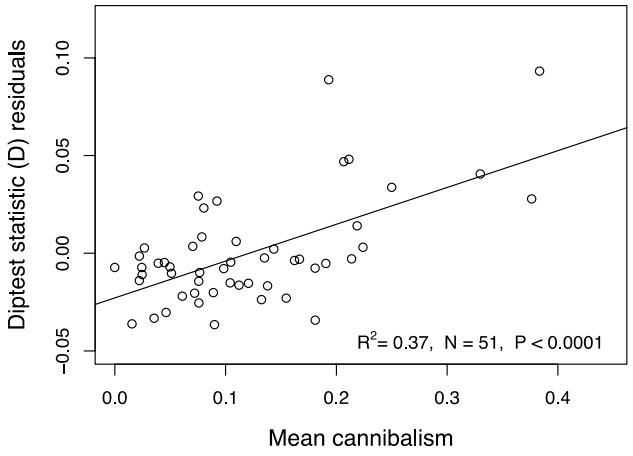

Fig. 8 Relationship between mean cannibalism expression and bimodality of the within-population distribution of cannibalism expression for 51 populations of *G. pallens* sampled from 2008 to 2017. The dip test statistic (*D*) quantifies the degree to which a distribution deviates from unimodality. A multiple regression showed that *D* was significantly influenced by mean cannibalism expression (regression coefficient = 0.220 ± 0.0037 (SE), $t = 6.00$, $P < 0.0001$) and by sample size, *N* (the number of *G. pallens* assayed per population; coefficient = −0.000178 ± 0.000038, $t = -4.68$, $P < 0.0001$). To display just the effect of mean cannibalism, we plot here the residuals from a linear regression of *D* on *N* versus the mean cannibalism expression for the population

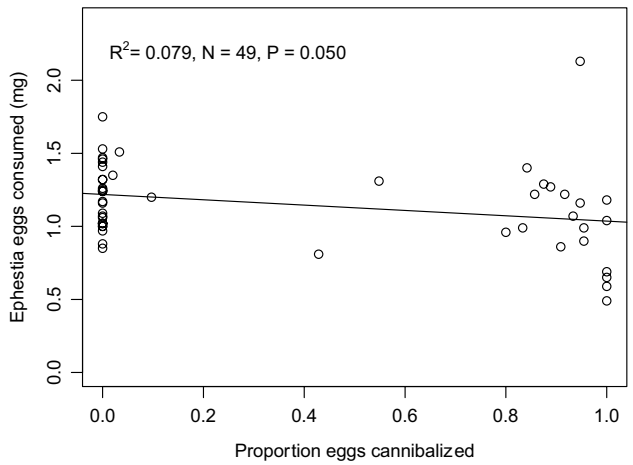

Fig. 9 Consumption of heterospecific prey (*E. cautella* eggs) by female *G. pallens* who varied in their consumption of conspecific prey (their own eggs). The negative relationship shown here suggests that the highly cannibalistic females are expressing a specific increase in cannibalism rather than a non-specific, global increase in consumption of all prey (conspecific + heterospecific)

(alfalfa vs. cotton) as a categorical variable, or as a single summed density estimate ($R^2 = 0.001$, $N = 28$, $P = 0.87$); Fig. S4 in ESM].

Discussion

Infection experiments conducted in the laboratory demonstrated that highly cannibalistic *G. pallens* collected from the field harbored a moderately virulent pathogen; nymphs exposed to this pathogen exhibited flattened abdomens, increased mortality, slowed development, and reduced growth. Adults exposed to the pathogen showed elevated cannibalism expression, although only as a transient response. Our field survey data describe a spike in cannibalism expression in field-collected *G. pallens* that was associated with a strong decline in *Geocoris* spp. densities. Increased cannibalism was associated with a shift from a unimodal to a bimodal distribution of cannibalism within field populations, and, in particular, with the appearance of a class of females that were exceptionally cannibalistic, eating most or all of the eggs that they laid. More cannibalistic females did not increase their consumption of *E. cautella* moth eggs, suggesting that the high cannibalism phenotype reflects a breakdown of restraint against eating conspecific eggs, rather than an increase in consumption both conspecific and heterospecific prey. Highly cannibalistic females often exhibited reduced egg laying, but sometimes showed the reverse. Variation in cannibalism expression did not appear to be associated with variation in either *G. pallens* density or prey availability.

Signature of a pathogen involvement?

Several of our observations from the field are consistent with the involvement of a pathogen. First was the sudden strong decline of *Geocoris* spp. densities in Central Valley populations. *Geocoris pallens* had been an abundant and ubiquitous generalist predator, whose extremely generalist diet (Crocker and Whitcomb 1980) and strong self-regulation by cannibalism (Law and Rosenheim 2011) had appeared for many years to support stable population densities, even in the face of strong fluctuations in prey availability (Rosenheim 2005; de Valpine and Rosenheim 2008). Nevertheless, *G. pallens* suddenly exhibited dramatic population collapses. The density observed at Westside in 2013 was lower than any of the 50 cotton populations sampled in earlier years (Figs. 3a, 4). Exceptionally low densities were recorded informally at many other sites in the Central Valley, starting in Davis in 2008. The more variable densities observed after the population crashes (Fig. 4) may reflect either the ongoing effects of the factor(s) causing the crash or also, possibly, more variable *Geocoris* spp. population dynamics in alfalfa compared to cotton, given that alfalfa fields are mowed approximately monthly during the growing season.

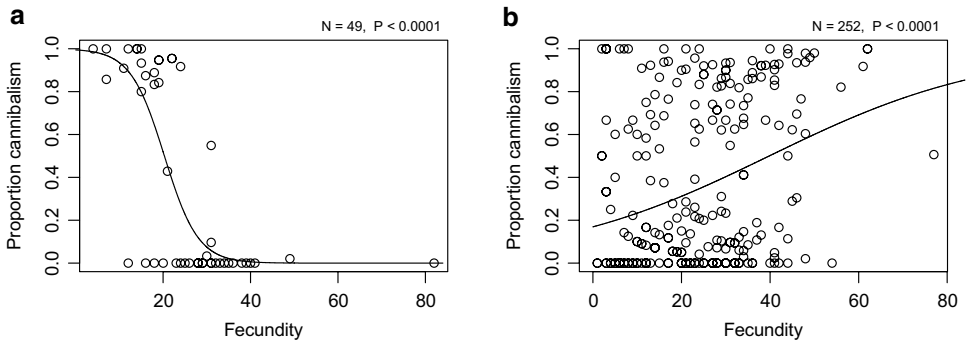

Fig. 10 Relationship between variation in cannibalism expression and short-term fecundity within field-collected populations of *G. pallens*; populations collected from two cotton fields near Huron **a** 16 May, 2013 (see Fig. 6a; eggs laid over 3 days); and **b** 6 June, 2013 (see Fig. 6b; eggs laid over 4–5 days). For both samples, female *G. pallens* were held in the laboratory with water, a sunflower seed, bee-collected pollen, and *E. cautella* eggs ad libitum for 6 days before the cannibalism assay to standardize hunger level. Shown are data points with GLM model fit (logit link)

Second, our informal sampling suggested a gradually expanding region of *G. pallens* population collapse. Beginning in Davis in 2008, the region of depressed densities extended southwards over a period of years.

Third, our assays revealed elevated cannibalism in field-collected *G. pallens* and the appearance of bimodal distributions of cannibalism expression. Our working hypothesis is that the bimodality stems from a mixture of low cannibalism (putatively uninfected) and high cannibalism (putatively infected) individuals. A related hypothesis is that infections of varying intensity could generate a continuum of elevated cannibalism expression.

Fourth, we observed a frequent, although not universal, association between elevated cannibalism expression and reduced egg-laying by *G. pallens*. This could reflect the impact of a moderately virulent infection. The minority of populations in which we observed a weak association of elevated cannibalism with enhanced egg laying might be consistent with cannibalism promoting nutrient recycling by adult females, supporting their short-term fecundity. Such a possibility has long been suggested (e.g., Polis 1981), but the few experimental tests of this hypothesis have provided only equivocal support (Lourdais et al. 2005; Hood 2012).

Finally, we observed a recovery in the densities of many, although not all, *Geocoris* spp. populations. Persistent suppression of *Geocoris* spp. populations in the Davis-Winters area, which is ongoing, and elevated cannibalism expression at nearby sites where *Geocoris* spp. population densities are partly recovered (Brooks populations; Figs. 7j, S2b), are consistent with the idea that the Davis-Winters area may be a continuing focus of activity for the pathogen. Consistent with this suggestion, sampling during the summer of 2018 revealed that the Brooks population of *Geocoris* spp. has now collapsed (data not shown).

Ongoing work, now focused on a complex of RNA viruses, is striving to characterize the pathogen(s) involved in the cannibalism-eliciting disease. We are also working to solve a problem that has plagued our laboratory studies of *G. pallens* cannibalism expression since 2012, namely that when we rear *G. pallens* nymphs from eggs to adults in the laboratory, the resulting adults are invariably highly cannibalistic, whether we experimentally expose them to the pathogen (data not shown) or not. This might reflect cross-contamination of individuals in control and pathogen exposure treatments, or the impact of some other aspect of long-term laboratory culture that stresses *G. pallens*, resulting in elevated cannibalism. Our future work will test the hypothesis that it is the nymphal stage that is most susceptible to the pathogen (nymphs displayed both the most striking physical symptoms of infection and also showed substantially increased mortality; those nymphs that displayed the flattened abdomen symptom but that survived were morphologically normal as adults), whereas adults may be only moderately susceptible, or may rapidly clear infections.

Infection as a cause of elevated cannibalism expression

Disease is not generally regarded as an important driver of increased cannibalism (Polis 1981; Wise 2006; Schausberger; Richardson et al. 2010); instead, for uninfected members of a host population, the risk of contracting an infectious pathogen is viewed as a cost and deterrent of cannibalism (Pfennig 1997; Pfennig et al. 1998; Bolker et al. 2008). Infected hosts do, however, frequently exhibit alterations in other behaviors, reflecting either (i) adaptive host behaviors that defend against the pathogen, (ii) adaptive pathogen manipulations of the host that enhance pathogen transmission to new hosts, or (iii) non-adaptive side-effects of infection (Thomas et al. 2012; Poulin and Maure 2015). Neither of the adaptive scenarios seems likely for highly

cannibalistic *G. pallens*. Although the consumption of conspecific eggs could provide nutritional advantages for *G. pallens*, the small and stable home foraging range of this species (unpubl. data) coupled with *G. pallens* females' inability to distinguish her own eggs from those laid by other females, seem likely to produce a significant risk of filial cannibalism (Rudolf et al. 2010; Law and Rosenheim 2013). Thus, fitness benefits from elevated cannibalism of eggs seem unlikely. Similarly, increased cannibalism by infected *G. pallens* seems unlikely to enhance the fitness of the infecting pathogen, as such cannibalism would remove what would otherwise be a pool of suitable hosts. Finally, if the pathogen is transmitted vertically, whether trans-ovarially or through other mechanisms (Ebert 2013), then filial cannibalism would also directly interrupt pathogen spread.

The most parsimonious explanation may, therefore, be that elevated expression of cannibalism is a non-adaptive side-effect of infection (Bunke et al. 2015). Such infection-driven cannibalism may be widespread due to a two-step chain of causality:

Step 1: Infection causes nutritional stress. This is nearly universally observed in host–parasite interactions (Schmid-Hempel 2011). Metabolic stress can result from infection either because the host mounts a metabolically costly immune response to infection, or because the pathogen redirects host nutrients to its own reproduction.

Step 2: Nutrient stress causes elevated cannibalism expression. This is nearly universally observed in cannibalistic species (Polis 1981; Wise 2006; Scharf 2016; Orrock et al. 2017; Pereira et al. 2017b).

Because both Steps 1 and 2 are observed so frequently, we hypothesize that the link between infection and cannibalism expression may be widespread, especially when the infected host is not so physically impaired that it cannot mount an attack, and when the cannibalistic population includes an exposed and poorly defended life stage.

Collapse of *Geocoris* spp. populations

The population collapses described here are likely to reflect the combined impacts of two processes. The first is the direct virulence of the pathogen, which may reduce the fitness of infected hosts through increased mortality, slowed development of immature stages, and reduced fecundity of adult females (Figs. 3, 10a). The second is what we can call "indirect virulence," in which infected individuals impose mortality on other members of the *G. pallens* population, including both infected and uninfected individuals, through cannibalism. For a disease to lead to substantially increased mortality of uninfected individuals is a surprising outcome. We can imagine scenarios in which a pathogen that is only mildly virulent to its host might still impose strong, suppressive effects on its host population by triggering extensive cannibalism. Virulence in pathogens is often moderated by inherent trade-offs: a too-virulent pathogen risks killing its host before it has time to be transmitted to additional hosts (Alizon et al. 2009; Redman et al. 2016). Thus, the optimal level of virulence is often intermediate. Intense indirect virulence, however, in which an infected host imposes mortality on uninfected individuals around it, could be sustained over much of the infected host's lifespan if direct virulence is weak. Thus, indirect virulence might break the normal trade-off, especially if the infected host is mobile enough that it can move away from locations where it might suppress densities of conspecifics, thereby retaining opportunities for disease transmission to new hosts. Exploring the population-dynamic implications of such indirect virulence is an important future research goal.

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Author contribution statement JAR, AS, NB, MCM, TM, RK, WBH, and YHL conceived the idea for the study and designed the work; all authors collected the data; JAR and AS analyzed the data and led the writing with input from all authors.

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