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Temperature effects on long-term population dynamics in a parasitoid–host system

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Abstract. Long-term environmental changes will likely alter the strengths of interactions between species and consequently their population dynamics, leading to changes in the stability of ecological systems. While an increasing number of empirical studies have shown that environmental changes can alter the strengths of species interactions, these studies are typically short (<1–2 generations) and therefore give only partial information about longer term population dynamics. To focus on longer term dynamics, we investigated population cycles of pea aphids and their most common parasitoid, *Aphidius ervi*, in Wisconsin, USA. Data collected over three years in alfalfa fields showed an apparent host–parasitoid population cycle. Furthermore, higher pea aphid population growth rates and increased parasitism were correlated with higher naturally occurring temperatures. While these effects were observed with seasonal fluctuations in temperature, they beg the question of how long-term changes in mean annual temperature might change aphid–parasitoid population cycles, a question which we further pursued with laboratory experiments. To quantify temperature-dependent demographic parameters, we used short-term (<1 generation) experiments conducted at 20°C and 27°C. The higher temperature increased aphid and parasitoid development rates, adult aphid life span and fecundity, and parasitoid attack rates. We then conducted multi-generation population-level laboratory experiments to reveal the effects of temperature (20°C vs. 27°C) on population dynamics. We fit the resulting time series data using a nonlinear age-structured state-space model to estimate population-level processes that could not be estimated in short-term laboratory experiments. Using the model, we parsed out the demographic rates that had the largest impacts on aphid–parasitoid population cycles. This analysis showed that there were frequent contrasts in the effects of temperature operating through different demographic rates. For example, the temperature-dependent increase in aphid development rate decreased cycle amplitude, while the increase in parasitoid attack rate increased cycle amplitude. There were also striking interactions among demographic rates. For example, the temperature-dependent increase in aphid development rate could either increase or decrease the cycle period depending on the values of other demographic rates. Although these complexities make predictions difficult, overall they suggest that increasing long-term mean temperature will decrease the period, increase the amplitude, and tend to destabilize pea aphid–*A. ervi* dynamics.

Key words: Acyrthosiphon pisum; *alfalfa;* Aphidius ervi; *climate change; ecological stability; host–parasitoid cycles; pea aphid; population dynamics; predator–prey cycles; species interactions.*

Introduction

Temperature affects almost all physiological and behavioral processes in plants and animals (Clarke 2003, Angilletta et al. 2010, Dell et al. 2011), and therefore, we should anticipate broad and complex impacts of temperature change on ecological systems (Brown et al. 2004, Tylianakis et al. 2008, Hegland et al. 2009, Kingsolver 2009, Pearson 2011). Temperature may alter demographic rates, including development rates, survivorships, and fecundities, and hence, the population growth rates of species (Frazier et al. 2006, Angilletta 2009, Doak and Morris 2010). Temperature may also affect processes that govern how species interact with each other (Gilman et al. 2010), such as predation rates (Post et al. 1999, Forchhammer et al. 2008, Barton and Schmitz 2009) and the competitive abilities of species (Park 1948, Jiang and Morin 2004, Lang et al. 2012). By changing both individual species' population growth rates and the interaction strengths among species, temperature will likely affect long-term population dynamics, that is, the characteristics of how populations fluctuate through time.

Although an increasing number of studies have shown how the direct effects of temperature on species are modified through interactions with other species (Post

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and Pedersen 2008, Tylianakis et al. 2008, Harmon et al. 2009, Hegland et al. 2009, Kordas et al. 2011, Pearson 2011), most experimental studies on species interactions have been short term, over less than a generation of the species. Therefore, these studies only investigate how temperature affects population growth rates, either directly through the physiological impacts on the focal species, or indirectly through changes in the strengths of interactions between species. Because the consequences of changes to demographic rates and species interactions play out over multiple generations, however, it is difficult to predict how short-term changes to population growth rates will affect populations in the long term (Bender et al. 1984, Ives 1995, Briggs and Borer 2005). For example, there have been numerous studies on how temperature affects the functional response that describes the rate of resource (prey) exploitation by a consumer (predator) as a function of the resource density (O'Connor 2009, Rall et al. 2010, Englund et al. 2011, Vucic-Pestic et al. 2011, Lang et al. 2012, Lemoine and Burkepile 2012, Rall et al. 2012, Sentis et al. 2012). Suppose for a given pair of consumer and resource species, higher temperatures increase the functional response, thereby leading to an overall increase in the consumption rate. While this should lead to an immediate increase in the abundance of the consumer, in the long run, it might lead to lower consumer density as the consumers depress the abundance of their resource. Thus, the short-term effects of changing demographic rates and interaction strengths do not necessarily translate into long-term population changes in a straightforward and simple fashion. Adding possible effects of temperature on multiple demographic rates, such as reproduction and mortality, leads to greater complexities in predicting the long-term consequences of changing temperature (Vasseur and McCann 2005, Vasseur and Fox 2007, O'Connor et al. 2011).

In addition to studies addressing individual species and individual species interactions, there is a growing collection of studies on community-wide responses to changing temperature (Magnuson et al. 1997, Edwards and Richardson 2004, Winder and Schindler 2004, Beveridge et al. 2010, Jeppesen et al. 2010, Burgmer and Hillebrand 2011, Winder and Sommer 2012, Werner and Matthiessen 2013). These studies characterize aggregate community responses to temperature change, such as the relative strengths of top-down vs. bottom-up effects in food webs (Hoekman 2010, Kratina et al. 2012, Shurin et al. 2012), changes in the relative biomass of different trophic levels (Ozen et al. 2013), the timing of seasonal fluctuations of species in different trophic levels (Feuchtmayr et al. 2010, Sommer et al. 2012), and changes in the composition of communities (Smol et al. 2005, Hillebrand et al. 2012). Because these studies investigate aggregate community responses, it is difficult to isolate the mechanisms underlying the observations. It is especially difficult to use aggregate community data to disentangle the possible effects of temperature on different demographic parameters and interactions between species, and hence, understand the effects of temperature on system dynamics.

Our goal here was to investigate the effects of temperature on the demographic rates and interactions between a predator and its prey. In contrast to most previous studies, we focused on endogenously driven, longer term fluctuations in population dynamics. Specifically, we asked how temperature affects predator–prey population cycles. Ecologists have long been enamored by populations that show cycles, because cycles give a clear dynamical signal suggesting tightly coupled interactions between a predator and prey (Volterra 1926, Turchin and Taylor 1992, Krebs et al. 1995). Therefore, species that show predator–prey cycles are good candidates for case studies investigating the long-term effects of temperature on species interactions. Our focus on endogenously driven population cycles places our study within the conceptual domain of ecological stability, because the stability of predator–prey systems is often measured by the tendency of prey and predator populations to cycle, and the magnitude of cycles if they occur (Elton 1958, May 1974, Hassell 1978). Thus, we addressed ecological stability not in the context of an entire ecosystem, but instead, for two species, allowing us to thoroughly explore the mechanisms that underlie any temperature-driven changes in dynamics.

We investigated the effects of temperature on the population dynamics of pea aphids (*Acyrthosiphon pisum*) and the parasitoid *Aphidius ervi*. These species are tightly coupled dynamically in the field because *A. ervi* has few other common hosts and can potentially kill a large proportion of the pea aphid population. A major difficulty in predicting the response of pea aphid–*A. ervi* dynamics to changes in temperature is that temperature will likely affect multiple demographic rates: individual growth rates, fecundity, survival of each species, and parasitism rates by *A. ervi*. These demographic rates may combine in potentially opposing ways to determine the character of population cycles. Furthermore, temperature may change the strength of density dependence in the demographic rates, which, in turn, may alter population cycles. A final complication is that temperature-driven changes in demographic rates could have different effects on different characteristics of population cycles: frequency, amplitude, cycle stability, and the ratio of mean parasitoid to mean aphid densities. We addressed all of these issues using a combination of field observations, laboratory experiments, and models fit to time series data.

Roadmap

This study brings together numerous experiments and analyses, and therefore, we give a road map. (1) We first present three years of previously unpublished field data in which there is an apparent cycle involving pea aphids and *A. ervi*. (2) We then analyzed the field data,

taking advantage of daily and seasonal fluctuations in temperature to identify effects of temperature on pea aphid population growth rates and parasitism. Although these analyses can find overall effects of temperature on pea aphid population growth rates, we cannot separate the effects of temperature on different demographic rates. For example, an increase in pea aphid population growth rate with temperature could be caused by increases in development rates, fecundity, and/or survival rates. (3) To experimentally determine the effects of temperature on individual demographic rates, we performed short-term experiments in the laboratory to measure four demographic rates that we hypothesized would affect population dynamics: aphid development rate (Elliott et al. 1995, Morgan et al. 2001), aphid fecundity and adult survival that combine to give the aphid net reproduction rate (Morgan et al. 2001, Russell and Moran 2006), parasitoid development rate, and parasitoid attack rate (Gilchrist 1996). To ensure that we saw strong effects of temperature, we performed experiments at 20°C and 27°C. The lower temperature matched the mean temperature of days when we took samples for the field data, whereas the higher temperature is close to the maximum average daily temperature; only 13 days during the field sampling had average daily temperatures exceeding 27°C. (4) How changes in demographic rates affect population cycles depends on density dependence, which is best estimated from data on long-term population dynamics. Therefore, we performed long-term laboratory experiments designed both to estimate how temperature affects density dependence and to assess the long-term dynamics of aphids and parasitoids. To match the short-term demographic experiments, we conducted the long-term experiments at 20°C and 27°C, and to expose possible temperature effects on density dependence, we conducted one set of experiments starting with initially low aphid densities and another with initially high aphid densities. (5) Both to estimate density dependence and to determine how demographic rates measured in the short-term experiments affect longer term population dynamics, we fit an age- and stage-structured nonlinear time series model to the long-term laboratory experiments. This model, tailored for pea aphids and *A. ervi* using previous knowledge about the system, made it possible to explore the relative importance of different demographic rates in explaining the differences in population dynamics observed at 20°C vs. 27°C in the long-term experiments. (6) Finally, we used the model to ask how changes in mean temperature might affect the characteristics of population cycles and the stability of the population dynamics. The context of this question was anticipating changes in dynamics caused by long-term trends in temperature, such as increases in mean annual temperatures. The model was tailored for the laboratory experiments, and we do not have enough information to quantitatively predict how temperature will likely affect pea aphids and *A. ervi* imbedded in the natural alfalfa community. Nonetheless, the model led to educated guesses about how temperature may alter the dynamics of this host–parasitoid system in the field.

Methods

Study system

The pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), is an Old World species introduced to North America in the 19th century (Hagen et al. 1976). It attacks a wide variety of legumes, including peas, beans, clover, and alfalfa (lucerne). Pea aphids reproduce rapidly and asexually in the summer, with parthenogenic females producing as many as eight nymphs per day (Hutchinson and Hogg 1984, 1985). Alate (winged) adults occur at low frequency throughout the summer, typically when densities reach high levels (Gross et al. 2005). The last generation of the autumn consists of females and males, and mated females produce eggs that survive the winter (Blackman and Eastop 1984).

Aphidius ervi (Haliday) (Hymenoptera: Braconidae) is a solitary endoparasitoid of aphids. Following its introduction in the 1950s and 1960s for use as a biological control agent of pea aphids, *A. ervi* proliferated to become the dominant pea aphid parasitoid throughout much of North America (Gonzalez et al. 1978, Danyk and Mackauer 1993). *A. ervi* attacks all pea aphid instars, although it has highest attack rates on second and third instars (Ives et al. 1999). The parasitoid larva develops inside the still-living aphid before killing the host and forming a mummy containing the developing pupa. Although small, adults are capable of movement at rates that will easily allow them to traverse multiple fields over the course of a day (Olson et al. 2000).

Alfalfa (*Medicago sativa*) is the fourth most important crop in the USA in terms of acreage, and is a perennial crop that supports a diverse community of herbivores and natural enemies. It is typically harvested two to three times per summer, with harvesting causing high pea aphid mortality (Ives et al. 2000, Rauwald and Ives 2001).

For the laboratory experiments, we followed the standard practice of using fava beans rather than alfalfa. Because alfalfa is a perennial, it grows slowly in the laboratory and never reaches the size of plants in the field. Furthermore, there is high heterogeneity among potted alfalfa plants, which introduces uncontrollable variability unlike that found in the field. Finally, alfalfa is susceptible to thrips outbreaks in the laboratory. Pea aphids collected from alfalfa in the field readily establish on fava beans in the laboratory, and we have never encountered differences in overall demographic rates following the transfer between these host plants. Therefore, fava beans give a good laboratory model system for pea aphids and *A. ervi*.

Field data

To obtain pea aphid densities and parasitism rates, we sampled 7 alfalfa fields in 1995 and 12 fields in 1996 and 1997. The fields were distributed across the 800-ha Arlington Agricultural Research Station, near Arlington, Wisconsin, USA. We used a combination of fields with established alfalfa and fields planted that year. Established fields were harvested three times, and newly planted fields were harvested twice per growing season.

Pea aphids were sampled with sweep nets, with 20–80 sets of 10 sweeps per sample depending on the abundance of aphids. Data presented are in terms of the average numbers of aphids per set of 10 sweeps. In 1995, the percentage of parasitism was calculated by counting the numbers of aphids and mummies on 50 to 200 stems of alfalfa, with the percentage of parasitism estimated as mummies/(mummies + aphids). In 1996 and 1997, the percentage of parasitism was determined both by counting numbers of aphids and mummies, and by dissecting 50 to 100 adult pea aphids and counting second- and third-instar parasitoids. When both types of samples were taken simultaneously, they were averaged, because the sampling techniques were statistically indistinguishable (paired Wilcoxon signed rank test, $N = 45$, $P = 0.74$). Both measurements were underestimates of the actual percentage of aphids that are killed by parasitism because parasitism is only detected during a portion of the parasitoid's life stages (mummies for mummy counts and instars II–III for dissections).

We analyzed field data with two objectives. First, we investigated the long-term population dynamics of pea aphids and *A. ervi* in the field. Alfalfa fields are harvested throughout the season, which causes high mortality of aphids and immature parasitoids. Furthermore, aphids and parasitoids move among fields. These factors make it impossible to see long-term population-level dynamics from observations in a single field. Therefore, to show the data clearly, we combined data from all fields. Second, we analyzed the data for evidence that temperature affected demographic rates. Because the data consisted only of pea aphid counts and estimates of the percentage of parasitism, we could not measure aphid survival and fecundity, aphid and parasitoid development rates, or parasitoid attack rates directly. Nonetheless, we could determine whether aphid population growth rates, an amalgamation of all individual aphid demographic parameters, depended on temperature. We could similarly investigate whether the decrease in aphid population growth rates with increasing parasitism depended on temperature.

The data set consisted of 296 field-sample points in which we had sweep-net samples; these were used to show the long-term dynamics in the field. For analyses of changes in aphid abundances and parasitism between samples, we restricted the data to samples separated by 12 or fewer days, of which there were 165 samples. The removal of points due to missing parasitism and samples $\geq$12 d apart was biased against samples with low aphid abundances, although there was little bias in mean daily temperatures; the average mean daily temperatures recorded at the nearby Dane County Regional Airport (located 20 km away) were 19.9°C for all samples, and 20.3°C for samples used for analyses.

We analyzed the field data with the statistical model

$$x(t+\Delta t) = x(t)\exp\left[r(T)(1-\beta\log(x(t)))\Delta t - \frac{a(T)Y(t)\Delta t}{g+X(t)} + cH(t) + \varepsilon(t)\right] \quad (1)$$

where $x(t)$ is the abundance of aphids (number per 10 sweeps) in the sample taken at time t, Δt is the time to the next sample from the same field, $T(t)$ is the mean daily temperature averaged over the 12 d preceding $t + \Delta t$, $X(t)$ and $Y(t)$ are the average abundances of aphids and parasitoids (calculated as the percentage of parasitism multiplied by the abundance of aphids) among all samples taken within 12 d but not including the sample taken at $t + \Delta t$, and $\varepsilon(t)$ represents residual variation. The intrinsic rate of increase for the aphids, $r(T) = \exp(r_0 + r_1 T(t))$, is assumed to depend exponentially on temperature. This exponential form is a close approximation to the thermal performance equation given by Boltzman's factor (Gillooly et al. 2001); furthermore, the exponential form fit the data better (had higher likelihood) than a linear equation of temperature on the intrinsic rate of increase. We incorporated density-dependent population growth with the term $(1 - \beta\log(x(t)))$ that decreases with log(aphid density) at a rate proportional to β; thus, larger values of β correspond to stronger density dependence, because the per capita population growth rate decreases more rapidly with log(density). We also investigated a linear dependence on aphid density $x(t)$, but the log-linear expression fit the data slightly better (had higher likelihood). The parasitoid attack rate, $a(T) = \exp(a_0 + a_1 T(t))$, also depends exponentially on temperature. Because parasitoids move readily among fields, we assumed that the parasitoid attack rate depends on the average numbers of parasitoids in samples between t and $t + \Delta t$, $Y(t)$. The parasitoid is assumed to have a type II functional response governed by the parameter $g \geq 0$. In this formulation, $1/g$ is proportional to the host "handling time" (Hassell 1978), so lower values of g correspond to greater saturation of the attack rate at higher aphid density. We parameterized the functional response in terms of g rather than the handling time, because the nonlinear model fitting converged on $g = 0$; the model using handling time $1/g$ did not converge. To model mortality of aphids during harvesting, $H(t)$ is a categorical variable that equals one when harvesting occurs between t and $t + \Delta t$, and zero otherwise. Thus, mortality during harvesting equals $\exp(c)$. We assumed that the residual variance $\varepsilon(t)$ follows a Gaussian distribution, and because samples were taken consecu-

tively from the same fields, we assumed that within fields values of $\varepsilon(t + \Delta t)$ and $\varepsilon(t)$ are autocorrelated with autocorrelation coefficient ρ.

To fit Eq. 1, we used nonlinear maximum likelihood regression with the nlme function in the nlme package of the R statistical computing language version 3.0.2 (R Development Core Team 2012); R code is provided in the online Supplement. Rather than use the t values reported in this package, we used likelihood ratio tests, which were more conservative (gave larger P values) and should be more robust to nonlinearities in the model than the approximate t values and standard errors produced by nlme.

Laboratory experiments: demographic rates

We first performed short-term ($\leq$1 generation) laboratory experiments to estimate pea aphid development and reproduction (survival and fecundity) rates. Previous experiments demonstrated that temperature can affect these demographic rates (Elliott et al. 1995, Gilchrist 1996, Morgan et al. 2001, Russell and Moran 2006), but the quantitative relationships measured have varied among studies, pea aphid populations, and clones (Lamb et al. 1987). We also performed short-term experiments to estimate parasitoid development times and attack rates.

We performed experiments at 20°C and 27°C; the former is roughly the mean average daily temperature over the field data set, and the latter is near the maximum average daily temperature over the same time period. Temperatures above 30°C may cause decreases in aphid reproduction (Russell and Moran 2006, Harmon et al. 2009), but because heat shocks are rare in Wisconsin, we selected temperatures below the heat-shock threshold. We selected only two temperatures because our objective was to provide demographic data to match long-term experiments on population dynamics carried out at 20°C and 27°C, rather than to estimate the full temperature-performance curves of aphids and parasitoids. Logistics restricted the long-term experiments to two temperatures. We selected the relatively high temperature of 27°C to ensure strong responses that we would have the statistical power to identify.

To determine the effect of temperature on aphid development, survival, and fecundity, we placed single first-instar aphids into individual plastic containers with a pair of fava bean leaves kept moist with water-soaked cotton. Every day, the instar of the aphid was determined and the leaves replaced. Once aphids reached adulthood, the containers were examined every day for offspring until the adult aphid died; any offspring were counted and removed. Totals of 72 and 76 aphids were used at each of 20°C and 27°C, although mortality reduced the numbers to 60 and 70 individuals surviving to adulthood at 20°C and 27°C, respectively.

To assess parasitoid development rates, 25 aphids in instars II to IV were added to single fava bean plants enclosed by cages consisting of transparent plastic tubes. Aphids were allowed to acclimate for 2 h, after which a single mated female *A. ervi* was added to the cage. Parasitoids were removed after being allowed to parasitize aphids for 24 h in a common greenhouse environment. Half of the plants were then placed in a growth chamber at 20°C, while the other half were placed at 27°C. Plants were checked daily for the presence of mummies. Totals of 134 and 206 parasitoids survived to mummy formation at 20°C and 27°C, respectively, and totals of 90 and 179 emerged as adults, respectively.

To determine if the temperature experienced by adult parasitoids while foraging affects the attack rate of *A. ervi* on pea aphids, we enclosed single fava bean plants in plastic tubes and inoculated plants with 25 pea aphids in instars II to IV. After 2 h, a single mated female *A. ervi* was added to each plant. Half of the plants were placed in a growth chamber maintained at 20°C, and the others were placed in a growth chamber at 27°C. After 24 h, parasitoids were removed, and the plants were placed in a greenhouse so that the development of parasitoids in both treatments occurred in the same environment. Plants were checked daily for mummies for 14 d. Two sequential blocks of this experiment were conducted, for a total of 38 and 34 replicates at 20°C and 27°C, respectively. All demographic data were analyzed using generalized linear models assuming a quasi-Poisson distribution (Bates et al. 2008, R Development Core Team 2012).

Laboratory experiments: population processes

We conducted long-term laboratory cage experiments to determine the effect of temperature on pea aphid–*A. ervi* density dependence and population dynamics. In the first set of cages, eight square pots, each containing a fava bean plant, were placed into four $30 \times 60 \times 60$ cm cages enclosed with fine mesh screening. The bases of the plants were surrounded with plastic collars coated with fluon, a slippery substance, to reduce the movement of aphids between plants. Two of the cages were maintained in one growth chamber at 20°C, while the other two were kept in a chamber at 27°C. Four randomly selected plants in each cage were inoculated with 10 aphids of mixed instars. Aphids were allowed to acclimate for 4 h, and then two mated female *A. ervi* were added to each cage; two more were added after 2 d and 4 d, for a total of six females released into each cage. Every 2–3 d, adult and juvenile aphids and mummies were counted. Under laboratory conditions, aphid populations can reach sufficient levels to kill potted plants. Therefore, if the aphid population on a single plant had dropped by 25% or more since the previous observation, or if the population had decreased for two consecutive observations, the plant was replaced with a young fava bean. When a plant was replaced, any remaining aphids were removed with the plant. Any mummies were left in the cage by removing leaves from

plants and placing them on the cage floor. This was done to mimic conditions expected in the field, in which mummies (being inactive) survive even after the plant they are on dies.

For a second set of long-term cages, we introduced parasitoids after allowing aphids to reach high densities; thus, the two sets of initial conditions (low aphid and low parasitoid densities, and high aphid and low parasitoid densities) bracket the possible initial aphid densities. This design gave us more statistical power to identify possible temperature-mediated density dependence affecting the population dynamics. Aphid populations were allowed to grow in the absence of parasitoids until day 35, at which point aphid populations in both 20°C and 27°C treatments had reached a steady state. Then five mated female *A. ervi* adults were added to each cage; five more were added on day 40. The experiment was terminated six weeks after the addition of parasitoids, as no unparasitized aphids remained in the cages at 27°C.

In the first set of cages (with low initial aphid densities), plants were replaced, on average, every 39.2 d over the 77 d of the experiment, while in the second set, plants were replaced on average every 8.8 d over the 82 d of the experiment. In both cases, there was no statistically significant difference in plant replacement between 20°C and 27°C treatments ($t_{30} = 0.82$, $P = 0.42$; $t_{30} = -0.65$, $P = 0.52$). The much higher replacement rate in the second set of cages was due to the much higher aphid densities.

Population model

We built an age- and stage-structured model of pea aphid–*A. ervi* population dynamics that incorporated the data collected from the laboratory experiments on demographic and parasitoid attack rates. Specifically, the development rates of aphids and parasitoids, the adult survival and fecundity of aphids, and the relative attack rates at 20°C vs. 27°C were assigned values from the demographic experiments. The model is both age and stage structured to allow for different development rates; time is iterated daily, and aphids and parasitoids remain in different stages according to their development rates. Aphids are divided into stages corresponding to instars, and adults (instar V) are assumed to follow different survival and fecundity schedules at the two temperatures. In addition, aphids experience density-dependent survival. Previous work (Rauwald and Ives 2001) showed that, under benign conditions, parasitized aphids have the same survival as unparasitized aphids (until they are killed by the parasitoid), although parasitized aphids can have higher mortality when stressed (removed from plants); thus, we assumed that parasitized aphids may have higher density-dependent mortality than unparasitized aphids. Once parasitoids reach the mummy stage, they experience density-independent mortality and emerge according to the development schedule given by the demographic laboratory experiments. Adult parasitoids attack aphids at temperature-dependent rates given by the short-term laboratory experiments and experience density-independent mortality. In addition to the effects of temperature on the demographic rates measured in the short-term experiments, we assumed that temperature can affect aphid density dependence in pea aphid population growth, and aphid and parasitoid density dependence in the parasitoid attack rate.

The model is

$$\begin{aligned}
\mathbf{X}(t+1) &= S(z(t)) \cdot \mathbf{A}(x(t), Y_{\mathrm{m}}(t) \,|\, T) \cdot (\mathbf{L}(T)\mathbf{X}(t)) \cdot e^{\boldsymbol{\varepsilon}(t)} \\
Y_1(t+1) &= S_{\mathrm{y}}(z(t)) \cdot (1 - \mathbf{A}(x(t), Y_{\mathrm{m}}(t) \,|\, T))' \mathbf{L}(T)\mathbf{X}(t) \\
Y_i(t+1) &= s_i S_{\mathrm{y}}(z(t)) Y_{i-1}(t) e^{\boldsymbol{\varepsilon}(t)} \qquad \text{for } (i = 1, \ldots, m_1) \\
Y_i(t+1) &= Y_{i-1}(t) \qquad \text{for } (i = m_1 + 1, \ldots, m - 1) \\
Y_{\mathrm{m}}(t+1) &= \left(s_{\mathrm{y}} Y_{\mathrm{m}}(t) + \frac{1}{2} Y_{\mathrm{m}-1}(t) \right) e^{\boldsymbol{\varepsilon}_{\mathrm{y}}(t)} \qquad (2)
\end{aligned}$$

where $\mathbf{X}(t)$ is a vector giving the number of aphids in each age class on day t, $Y_i(t)$ is the number of parasitoids in age class i, m_1 is the number of days parasitoids remain within still-living aphids, m is the number of days for adult parasitoid emergence, the dot indicates element-by-element multiplication (Schur product), and the prime symbol denotes the matrix transpose. Aphid survival and reproduction are given in the Leslie matrix $\mathbf{L}(T)$ that depends on temperature T and was parameterized from the individual laboratory experiments. The functions $S(z(t))$ and $S_{\mathrm{y}}(z(t))$ give the survivals of aphids and parasitized aphids as they depend on the density of unparasitized plus parasitized aphids $z(t)$. The parasitoid attack rate depends on temperature T, and the proportion of aphids escaping parasitism, $\mathbf{A}(x(t), Y_{\mathrm{m}}(t) \,|\, T)$, is assumed to be aggregated according to a negative binomial distribution and depends on the density of parasitoid adult females $Y_{\mathrm{m}}(t)$, the total density of aphids $x(t)$ (to allow for a type II functional response), and the stage of the aphid. Once parasitized aphids turn into mummies (after m_1 days), mummies are assumed to have 100% survival. The adult parasitoids have daily survival s_{y}, and adult females appear as mummies emerge at day m with a sex ratio of 1/2. Process error (environmental + demographic stochasticity) was included as the random variables $\boldsymbol{\varepsilon}(t)$ and $\boldsymbol{\varepsilon}_{\mathrm{y}}(t)$.

The model was iterated on a daily time scale; initial explorations using shorter time steps gave similar results. The daily time step required rounding aphid development times in different instars to the nearest day. At 20°C, development times for instars I–IV were 2 d, while at 27°C development times were 1 d for instars I–III and 2 d for instar IV. The age-structured Leslie matrix for pea aphids is

$$\mathbf{L}(T) = \begin{pmatrix} 0 & f_1 & f_2 & \cdots & f_{n-1} \\ s_1 & 0 & 0 & & 0 \\ 0 & s_2 & 0 & & 0 \\ \vdots & & & \ddots & \vdots \\ 0 & 0 & \cdots & s_{n-1} & 0 \end{pmatrix} \quad (3)$$

where s_i and f_i are age-specific survivorships and fecundities, respectively. The demographic parameters s_i and f_i within $\mathbf{L}(T)$ are different when measured at different temperatures ($T = 20$°C or 27°C). We included juvenile instar survivorships of 0.97 and 0.98 for 20°C and 27°C, respectively, that were recorded in the laboratory experiments. Adult aphid survival and fecundity were interpolated from the demographic laboratory data using cubic splines. Parasitoid development times were obtained from the experiments, rounded to the nearest day. The intrinsic rate of increase of the aphid population was calculated as the principle eigenvalue of $\mathbf{L}(T)$.

The model includes intraspecific density dependence such that survival of aphids diminishes with increasing density; previous experiments showed that in similar laboratory situations density dependence primarily operates on survival rather than fecundity (Ives and Settle 1996). Let X_i ($i = 1, \ldots, n$) be the number of aphids in age group i, and let Y_i ($i = 1, \ldots, m$) be the number of parasitoids in age group i, with the element Y_m corresponding to adults. If z denotes the total number of unparasitized and parasitized but still-living aphids, then

$$z = \sum_{i=1}^{n} X_i + \sum_{i=1}^{m_1} Y_i. \quad (4)$$

We assumed that aphid intraspecific density dependence depends on the number of both unparasitized and parasitized aphids according to the function

$$S(z) = \left(1 + \frac{z}{K}\right)^{-1} \quad (5)$$

where smaller values of the parameter K correspond to stronger density dependence.

We assumed that the attacks of parasitoids on aphids are aggregated, so that the probabilities of attack are given by the $n \times 1$ vector $\mathbf{A}(x, Y_m \mid T)$ that depends on the total number of aphids $x = \sum_{i=1}^{n} X_i$, the number of adult female parasitoids Y_m, and temperature T. The elements of $\mathbf{A}(x, Y_m \mid T)$ are

$$\left(1 + \frac{a\alpha(T)p_i Y_m}{k(hx+1)}\right)^{-k} \quad (6)$$

where a is a parameter governing the overall attack rate, $\alpha(T)$ scales the attack rate according to temperature T, p_i is the relative attack rate on aphids in stage i, h is the handling time that makes the attack rate depend on aphid density, and k is the aggregation parameter of the negative binomial distribution. For p_i, we used previously reported relative attack rates of 0.12, 0.27, 0.39, 0.16, and 0.06 for instars I–V, respectively (Ives et al. 1999). We assumed that parasitized aphids experience aphid density-dependent survival given by

$$S_y(z) = \left(1 + \frac{z}{K_y}\right)^{-1}. \quad (7)$$

This has the same form as aphid density-dependent survival, but replaces K with K_y so that the strength of density dependence affecting parasitized aphids is estimated separately from that affecting unparasitized aphids.

The random variable $\boldsymbol{\varepsilon}(t)$ describing the effect of demographic and environmental stochasticity on aphids that has two components, $\boldsymbol{\varepsilon}(t) = \boldsymbol{\varepsilon}_d(t) + \boldsymbol{\varepsilon}_e(t)$. Fitting the model to the time series data requires assuming that $\boldsymbol{\varepsilon}(t)$ has a normal distribution (Harvey 1989). Therefore, we approximated demographic stochasticity by assuming that $\boldsymbol{\varepsilon}_d(t)$ has a normal distribution with mean zero and variance $\min((1 + z(t))^{-1}, 1/2)$ which approximates the variance of a Poisson distribution with mean z. To allow for greater than Poisson variability that results from environmental stochasticity, we assumed that $\boldsymbol{\varepsilon}_e(t)$ has a normal distribution with mean zero and variance σ_x^2. We assumed a correlation ρ between all elements of $\boldsymbol{\varepsilon}_e(t)$ to account for different age classes responding in a similar way to environmental fluctuations. Parasitized aphids experienced exactly the same environmental variation as unparasitized aphids. Finally, variation in adult female parasitoids was modeled in the same way as that for aphids, with a demographic stochasticity term having variance $\min((1 + Y_m(t))^{-1}, 1/2)$ and an environmental stochasticity term with variance σ_y^2.

Because we used normal distributions to approximate demographic and environmental stochasticity, it is possible for aphids and parasitoids to "spontaneously appear" when the estimate of $\boldsymbol{\varepsilon}(t)$ is large. To disallow this possibility, the number of aphids and parasitized aphids in a given age class on day t was not allowed to exceed the number in the preceding age class on day $t - 1$. While fitting the model to the data, this was rare, occurring on $<3\%$ of the age class-days.

In the model, there are four parameters that govern density dependence: the strength of density dependence affecting unparasitized (K) and parasitized (K_y) aphids, the degree of aggregation in the negative binomial distribution (k), and the handling time that determined the strength of the type II functional response (h). To account for the possibility of these parameters differing between 20°C and 27°C, we introduced additional parameters ΔK, Δk, and Δh that give the difference in values of the parameters between 20°C and 27°C. We assumed that the temperature dependence in K_y was proportional to the temperature dependence in K; thus, $\Delta K_y/K_y = \Delta K/K$. Furthermore, we did not include a parameter Δa because the effect of temperature on the overall parasitoid attack rate was independently estimated in the short-term demographic experiments.

There are an additional three parameters governing the variability of the system: the environmental variability affecting unparasitized and parasitized aphids (σ_x^2), the correlation between instars (ρ), and the environmental variability affecting adult parasitoids (σ_y^2).

We fit the model to the long-term experimental data using a nonlinear state-space approach (Harvey 1989). In addition to the process error, the state-space model includes measurement equations for the sampling of aphids and mummies, specifically

$$x^*(t) = \left(\sum_{i=1}^{n} X_i(t) + \sum_{i=1}^{m_l} Y_i(t)\right) e^{\gamma_x(t)}$$

$$y^*(t) = \left(\sum_{i=m_l+1}^{m-1} Y_i(t)\right) e^{\gamma_y(t)}. \quad (8)$$

Here, $x^*(t)$ is the observed number of aphids (both unparasitized and parasitized, since they cannot be visually distinguished) in a sample. Note that even though the model has both age and stage structure, the observations were made only on the total number of aphids, and therefore, the total numbers of parasitized and unparasitized aphids in the model were summed for the model fitting. Observations were assumed to be made with measurement error given by the zero-mean normal random variable $\gamma_x(t)$. We estimated the standard deviation of γ_x as 0.2015 by performing a repeatability trial on aphid densities between 2 and 440 per plant. There was no relationship between the variance and the mean log(number of aphids per plant). The observed number of mummies, $y^*(t)$, was assumed to be given by a normal random variable $\gamma_y(t)$ whose variance σ_m^2 was estimated during the fit of the time series data. In addition, we fit the mean value of $\gamma_y(t)$, M, because the model consistently overestimated the observed number of mummies in the time series. This was not unexpected, because mummies can occur in places on the plants, such as underneath leaves, where they cannot be seen during our sampling from a distance outside the cages.

The state-space model was fit to the data using an extended Kalman filter that propagates the variances of the state variables through the nonlinear equations using stepwise linear approximations (Harvey 1989). Because the model is iterated on a short, daily time scale, the linear approximations were accurate. The extended Kalman filter produces an estimate of the negative log-likelihood function that we minimized to obtain the maximum likelihood (ML) parameter estimates. In addition to the six biological parameters, three parameters giving difference between 20°C and 27°C and three process error parameters, there are two measurement error parameters, σ_m^2 and M, making a total of 14 parameters estimated from the data. The statistical significance of departures from zero of the three parameters ΔK, Δk, and Δh was assessed using likelihood ratio tests. We fit the model to data from all of the long-term population cages (eight time series) simultaneously. These analyses were performed in MATLAB version R2012b (Mathworks 2012), which is provided in the online Supplement.

The laboratory experiments on demographic rates gave four sets of parameters each measured at 20°C and 27°C (aphid development rate, aphid fecundity and survival, parasitoid development rate, and parasitoid attack rate). To provide a statistical assessment of the effects of temperature-dependent demographic rates on the long-term dynamics, we compared (1) the fit of the model to the time series using the demographic parameters estimated at the same temperatures as the population cages, with (2) the fit of the model when parameter sets were switched (i.e., the demographic rates estimated at 20°C were used in the model to fit the population dynamics observed at 27°C, and vice versa). When refitting the model, we included ΔK, Δk, and Δh so that there could still be differences between these parameters at 20°C and 27°C. Standard likelihood ratio tests cannot be performed for this comparison, because the two models are not nested; we therefore used two other statistical comparisons. Vuong's closeness test (Vuong 1989) is based on the asymptotic approach of the point-wise log-likelihood ratios to a Gaussian distribution. This test, however, has been shown to have low power when the distribution of point-wise log-likelihood ratios is leptokurtic (Clarke 2007, Clarke and Signorino 2010), as is strongly the case for our model (results not presented). Therefore, we also performed Clarke's distribution-free test for non-nested models (Clarke 2007) that depends on the median of the point-wise log-likelihood ratios.

Results

Field data

To identify the among-field population dynamics of pea aphids and *A. ervi*, we averaged samples both among fields and among three consecutive sample days over the each of the three study years (Fig. 1A). The averaged data gave apparent pea aphid–*A. ervi* cycles that suggest a strong impact of parasitism on aphid dynamics over broad spatial and temporal scales. These cycles are not caused by the harvesting of alfalfa fields, because fields were harvested largely asynchronously (Fig. 1B, histograms). In fact, if data were only available for a single field (Fig. 1B, black lines), the harvesting events would have obscured the cycles that are only clearly evident in the data when the data are averaged among fields. Furthermore, the cycles were not caused by seasonal changes in temperature (Fig. 1C). In 1995, peak temperatures occurred in August coincident with a trough in aphid density; in 1996, temperatures were uniformly high throughout July and August, while aphid densities rose and then fell; and in 1997, aphid densities rose in parallel with temperature until mid-July.

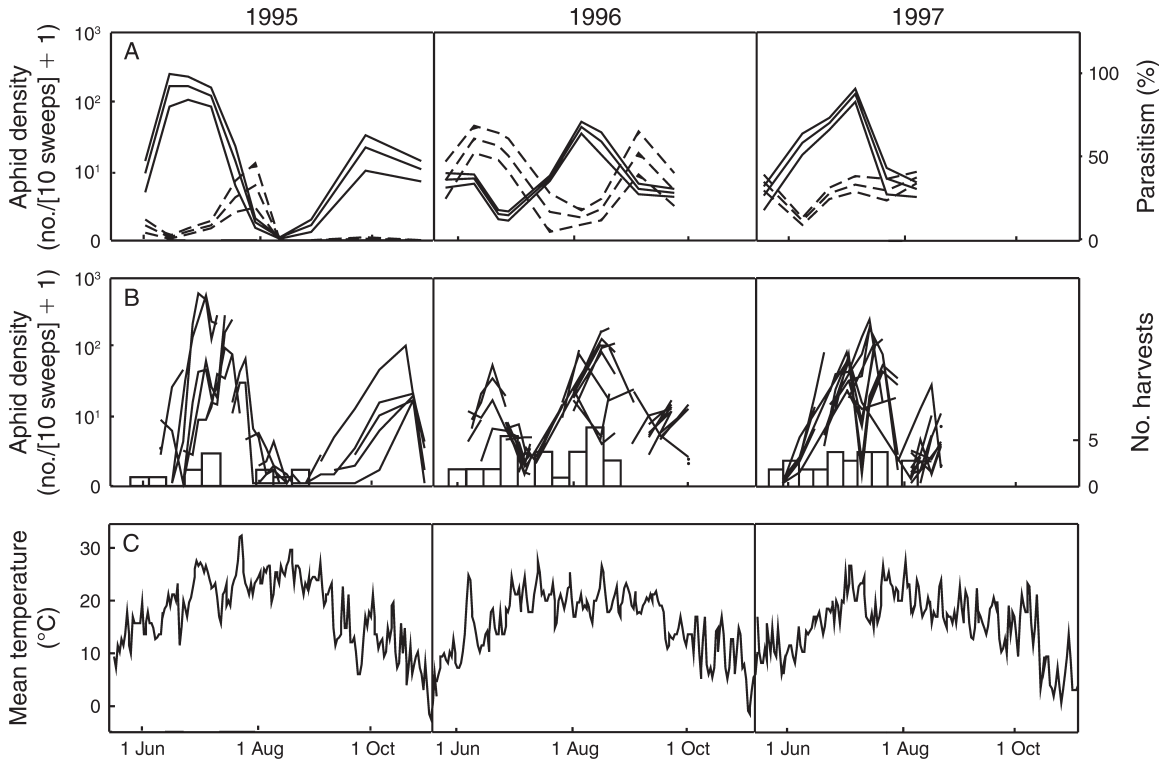

FIG. 1. (A) Pea aphid (*Acyrthosiphon pisum*) densities (solid lines) and the percentage of parasitism (dashed lines) in 7 (1995) and 12 (1996–1997) alfalfa (*Medicago sativa*) fields at the Arlington Agricultural Research Station, near Arlington, Wisconsin, USA. Aphid densities and parasitism were averaged among fields for three consecutive sample dates (1–2 week intervals). Mean values are given by the central lines, with ±SE given by the upper and lower lines. (B) Aphid densities in each of the sample fields. Data from the same field within a harvesting cycle are joined by a line, with breaks in the lines corresponding to harvesting. Histograms give the numbers of fields harvested in each interval. (C) Mean daily temperatures recorded at a nearby weather station (Dane County Regional Airport).

Statistical analysis of changes in aphid abundance showed that higher temperature within seasons was associated with higher aphid per capita population growth rates ($r_1 = 0.057$, $\chi^2_1 = 7.06$, $N = 165$, $P < 0.001$; Table 1) and greater effects of parasitism ($a_1 = 0.191$, $\chi^2_1 = 19.7$, $N = 165$, $P < 0.0001$). For these analyses, we set $g = 0$, because it was not statistically different from zero ($\chi^2_1 = 0.58$, $P > 0.4$). The estimate $g = 0$ implies that parasitism is ratio dependent, depending on the ratio of parasitoids to aphids over the range of aphid densities occurring in the field. The analysis also showed a large effect of harvesting on aphid abundance ($c = -2.40$, $\chi^2_1 = 17.02$, $P < 0.0001$, corresponding to a survival of $\exp(c) = 0.09$) and strong intraspecific density dependence ($\beta = 0.21$, $\chi^2_1 = 60.7$, $P < 0.0001$). This density dependence is likely due to natural enemies, especially ladybeetles, that we know exert strong density-dependent mortality on pea aphids (Snyder and Ives 2003, Harmon et al. 2009).

TABLE 1. Maximum likelihood parameter estimates for the statistical model of temperature-dependent pea aphid (*Acyrthosiphon pisum*) population dynamics in the field at the Arlington Agricultural Research Station, near Arlington, Wisconsin, USA (Eq. 1).

Parameter	Value	SE	χ^2	P	Description
c	−2.40	0.57	17.2	0.0001	harvesting mortality
r_0	−2.13	0.53	⋯	⋯	$r(T) = \exp(r_0 + r_1 T(t))$
r_1	0.057	0.026	7.06	0.001	
β	0.21	0.018	60.7	0.0001	aphid density dependence
a_0	−4.50	1.025	41.9	0.0001	$a(T) = \exp(a_0 + a_1 T(t))$
a_1	0.191	0.045	19.7	0.0001	
ρ	−0.048	⋯	⋯	⋯	autocorrelation

Notes: $N = 165$, and groups (fields) = 30. Ellipses show where no test was performed on the parameter.

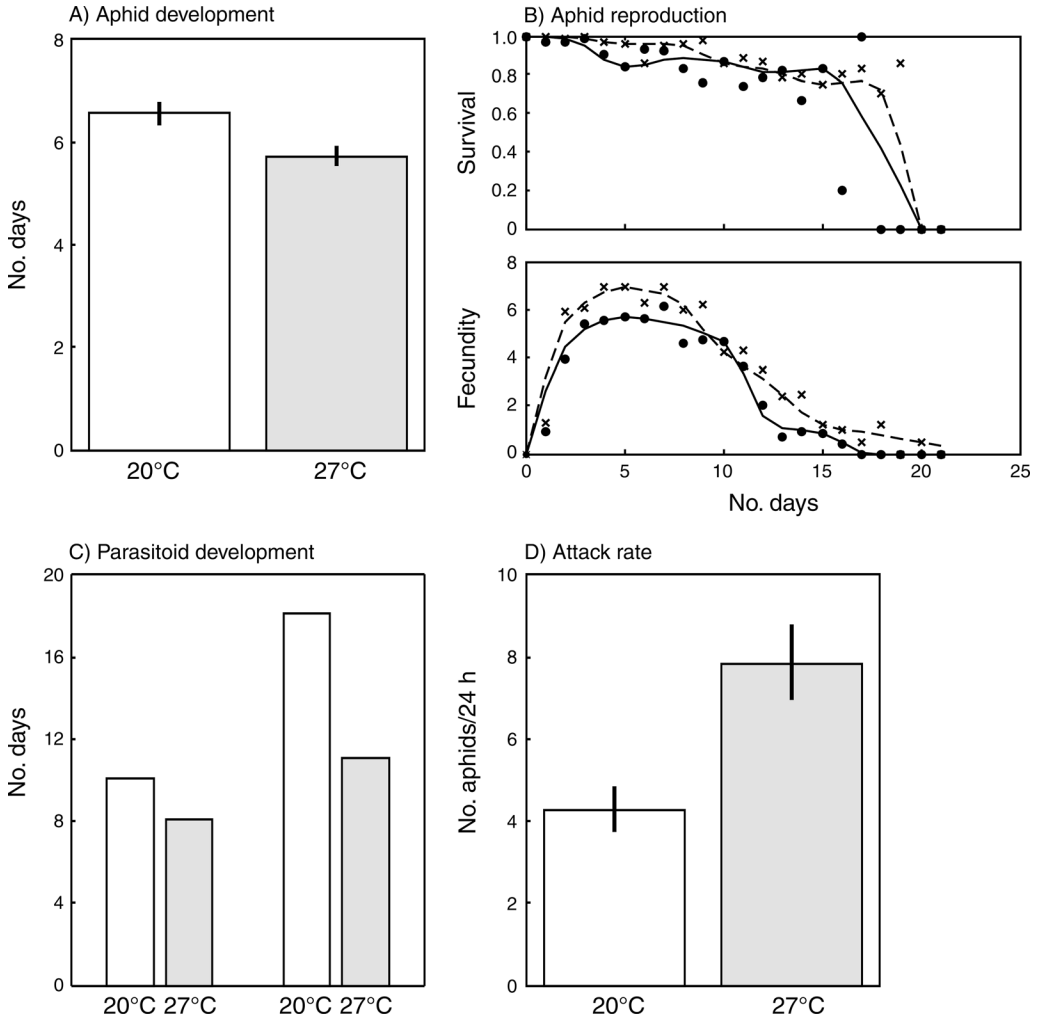

FIG. 2. Temperature effects on aphid (*A. pisum*) and parasitoid (*Aphidius ervi*) demographics. (A) Aphid development time to adulthood (mean ± SE). (B) Adult survival (upper panel) and fecundity (lower panel) at 20°C (solid line and circles) and 27°C (dashed line and x's). (C) Parasitoid development time (SE bars are so short they are not visible). (D) Parasitoid attack rates (number of aphids parasitized in 24 h, measured by numbers of mummies ± SE).

Laboratory experiments: demographic rates

The short-term (≤1 generation) estimates of demographic rates of pea aphids and *A. ervi* showed large effects of temperature (Fig. 2). At 20°C, mean aphid development time, from birth to adult, was longer (6.56 vs. 5.73 d, generalized linear model [GLM] with a quasi-Poisson distribution, $t_{131} = 5.78$, $P < 0.0001$); increased development time was found for all instars (Table 2). At 20°C, adult life span was shorter (8.65 vs. 11.89 d; GLM, $t_{128} = 4.00$, $P < 0.0001$) and fecundity was lower (41.9 vs. 58.4 offspring; GLM, $t_{117} = 3.25$, $P = 0.002$). Overall,

TABLE 2. Pea aphid instar-specific development times at 20°C and 27°C.

Effect	Instar I	SE	Instar II	SE	Instar III	SE	Instar IV	SE
20°C	0.38*	0.080	0.33*	0.090	0.38*	0.087	0.87*	0.078
27°C	0.25*	0.081	0.19*	0.089	0.23*	0.087	0.75*	0.078
Block	0.015	0.034	0.099**	0.037	0.042	0.040	−0.15**	0.034

Notes: A generalized linear model assuming a quasi-Poisson distribution for the development time was fit with a categorical "block" term. Asterisks for treatments correspond to the difference between 20°C and 27°C treatments. Values reported are $\log_e$(days). $N = 72$ and 76 individuals for 20°C and 27°C treatments, respectively, for instar I, although sample sizes dropped to $N = 60$ and 70 by instar IV due to mortality.

* $P < 0.05$; ** $P < 0.01$.

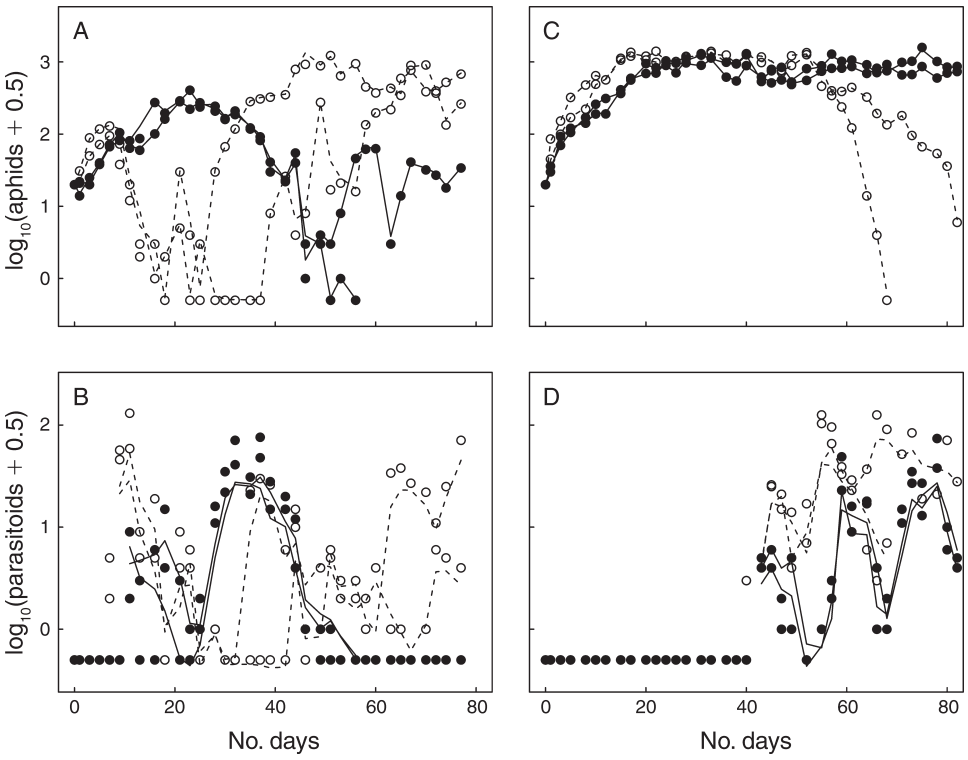

FIG. 3. Long-term aphid–parasitoid dynamics at 20°C (solid lines, solid circles) and 27°C (dashed lines, open circles) in laboratory cages. In panels (A) and (B), two cages were run at each temperature, and parasitoids were introduced immediately after aphids. In panels (C) and (D), parasitoids were introduced to two cages at each temperature starting at day 35. Lines give model fits to the data.

the demographic differences produced daily intrinsic rates of population increase of 1.29 and 1.46 at 20°C and 27°C, corresponding to population doubling times of 2.71 and 1.82 d, respectively.

To compare the effects of temperature on per capita aphid population growth rates measured in the laboratory vs. in the field, we calculated the predicted values of r from Eq. 1: $r = 0.372$ and 0.554 at 20°C and 27°C, respectively, for a difference of 0.18. The intrinsic rates of increase calculated from the laboratory experiments (Eq. 3) at 20°C and 27°C were 1.29 and 1.46, respectively. These intrinsic rates of increase are higher than the per capita population growth rates estimated in the field, as is expected because aphids experience high predation rates in the field from predators other than *A. ervi*. Nonetheless, the difference is $1.46 - 1.29 = 0.17$, showing that the effect of temperature on the per capita population growth rate is comparable to that found in the field, 0.18.

Mean parasitoid development times from egg to emergence as adults were longer at 20°C (18.1 vs. 11.1 d; GLM, $t_{249} = 9.59$, $P < 0.0001$). When we measured the attack rates by mated females on 25 aphids, the number of aphids parasitized in 24 h was lower at 20°C (4.26 vs. 7.82 aphids; GLM, $t_{69} = 4.68$, $P < 0.0001$).

Laboratory experiments: population processes

To assess the effects of temperature on pea aphid–*A. ervi* dynamics, we conducted long-term cage experiments lasting at least six pea aphid generations. The population dynamics exhibited were different at 20°C vs. 27°C (Fig. 3). For the first set of cages in which aphids and parasitoids were introduced simultaneously, aphid populations rose slowly in the two replicated cages at 20°C, reaching a peak at roughly 20 d, coincident with the initial emergence of the second generation of parasitoids (Fig. 3A, B). After 40 d, the aphids were kept in check by parasitoids. In the two replicated cages at 27°C, the parasitoid population rose more rapidly and caused strong suppression of aphids. This suggests that, at higher temperatures, the population cycle has shorter period and greater amplitude (leading to greater suppression of aphids). Because the initial populations of aphids were small, the second generations of *A. ervi* were also small, and consequently aphid populations were able to escape parasitoid control. The parasitoid populations remained small, only recovering in one of the two cages at 27°C by the end of the experiment.

In the second set of cages, aphid populations were allowed to reach carrying capacity before parasitoids were introduced. At 27°C, *A. ervi* caused a rapid decline in the aphid populations, while at 20°C parasitoid

TABLE 3. Maximum likelihood parameter estimates for Eq. 1 fit to eight time series from cages at 20°C and 27°C (Fig. 3).

Parameter	Estimate	Description
a	2.32	parasitoid attack rate
K	0.000467	aphid density dependence
K_y	1.57 K	parasitized aphid density dependence
k	0.35	parasitoid aggregation
h	0.008	handling time at 20°C
Δh	0.021	difference in handling time at 27°C
s_y	0.69	parasitoid adult daily survival
σ_x	0.44	environmental standard deviation for aphids
ρ	1.0	environmental correlation among instars
σ_y	0.70	environmental standard deviation for parasitoids
M	−0.22 (=log[0.80])	mummy observation error offset
σ_m	16.8	mummy observation error standard variation

Notes: There was no statistically significant difference in K and k between 20°C and 27°C ($\Delta K = 3.0 \times 10^{-5}$, $\chi^2 = 0.16$, $P = 0.69$; $\Delta k = 0.14$, $\chi^2 = 1.94$, $P = 0.16$), while Δh was significant ($\chi^2 = 4.40$, $P = 0.036$). Parasitoids were *Aphidius ervi*.

densities increased slowly (Fig. 3C, D), again suggesting more rapid aphid–parasitoid cycling at high temperature. In both sets of cages, variation between replicates was low, except at high temperature when aphids and parasitoids were introduced simultaneously (Fig. 3A, B); in this case, demographic stochasticity associated with very small parasitoid populations likely caused variation in the recovery of the aphid and parasitoid populations (see *Population model* below).

Fitting the model (Eq. 2) to the time series from all eight long-term experimental cages together (Fig. 3) demonstrated that the differences in demographic rates (Fig. 2) could explain the differences in observed dynamics. The model explained 84% and 69% of the variance in aphid and parasitoid (mummy) abundances, which includes variation among treatments and replicates. The plotted lines give the "updated" fits of the model to the data; these are the values of parasitized and unparasitized aphid abundance, $\sum_{i=1}^{n} X_i(t) + \sum_{i=1}^{m_l} Y_i(t)$, and mummy abundance, $\sum_{i=m_l+1}^{m-1} Y_i(t)$, after these estimates have been updated using the data (Eq. 8). Thus, the lines give at each data point the best estimated value from the model, taking into account both process error (environmental and demographic stochasticity) and observation error (Harvey 1989).

The parameter estimates obtained from the model fitting give information about the population-level, density-dependent processes underlying the dynamics (Table 3). There was no statistically significant difference in K between 20°C and 27°C ($\Delta K = 3.0 \times 10^{-5}$, $\chi^2 = 0.16$, $P = 0.69$). The strength of density dependence experienced by parasitized aphids was roughly equal to that experienced by unparasitized aphids, $K_y = 1.57\ K$; interpretation of this difference is difficult, because higher parasitism generally occurred at lower aphid densities when there is less aphid density dependence, which would lead to larger K_y. Parasitoids showed aggregation in attacks among aphids, $k = 0.35$, and there was no difference in the aggregation parameter between 20°C and 27°C ($\Delta k = 0.14$, $\chi^2 = 1.94$, $P = 0.16$). The parasitoid attack rate showed a type II functional response, with a value of $h = 0.008$ at 20°C and $h + \Delta h = 0.029$ at 27°C. The statistically significant difference in the handling time with temperature ($\chi^2 = 4.40$, $P = 0.036$) implies that parasitoids experienced greater saturation of their attack rate with aphid density at higher temperature.

Parameters involving the stochastic components of the model were also estimated. There was lower environmental process error variance estimated for aphids ($\sigma_x = 0.44$) than the adult parasitoids ($\sigma_y = 0.70$). A high correlation between process errors affecting different age classes of aphids (both unparasitized and parasitized) is expected biologically, although the very high estimated value of $\rho = 1.0$ was largely an artifact of the fitting procedure; all aphids were aggregated into a single value, $x^*(t)$ (Eq. 8), and without separate measurements of different age groups, it is statistically difficult to estimate how fluctuations in these groups are correlated. There was high measurement error variance for mummies ($\sigma_m = 16.8$), and the offset in the measurement of mummies, $M = -0.22$, implies that, on average, the probability of observing a mummy is 0.80 (=exp[–0.22]), the probability of observing an aphid.

To fit the model to the data, we not only estimated the parameters in Table 3; we also used results from the short-term experiments on demographic rates at 20°C and 27°C (Fig. 2). To assess the importance of temperature on the fit of the model acting through these demographic rates, we refit the model reversing the four demographic rates measured at different temperatures. The resulting log-likelihood of the best-fitting model was 29.2 lower than the model fit with the correct demographic rates, representing a significant loss of fit by Vuong's closeness test ($Z = 2.05$, $P = 0.04$; Vuong 1989). This difference was more significant ($P = 0.00044$) in Clarke's distribution-free comparison test for nonnested models (Clarke 2007), whose assumptions are

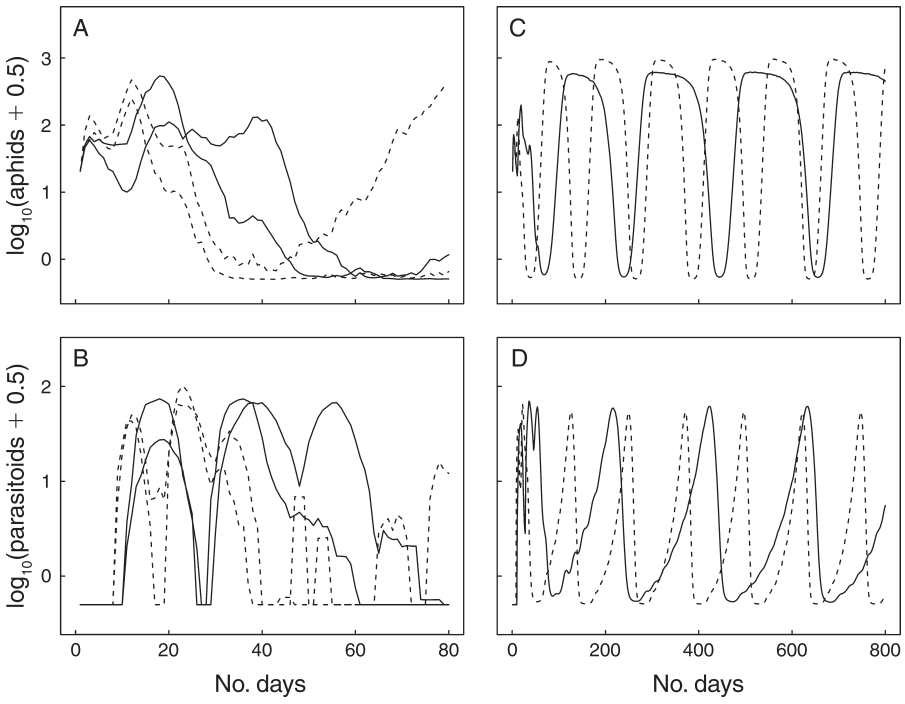

FIG. 4. Examples of simulated trajectories of (A, C) aphids and (B, D) parasitoids at 20°C (solid lines) and 27°C (dashed lines) from the laboratory model. In panels (A) and (B), the simulations were performed including demographic stochasticity in parasitoids by treating attacks on aphids at different instars as Poisson random variables and adult parasitoid mortality as a binomial random variable. The initial numbers of aphids and parasitoids were chosen to match those in the long-term experiment cages with low initial aphid densities (Fig. 3A, B). Environmental variation was set at 50% that estimated in the model (Table 3), and observation error was set to zero. In panels (C) and (D), population dynamics were simulated without demographic and environmental stochasticity, and observation error. Model parameters are given in Table 3; although in panels (A) and (B) $\sigma_x = 0.22$ and $\sigma_y = 0.35$, and in panels (C) and (D) $\sigma_x = \sigma_y = 0$.

better met by the data than those of Vuong's closeness test.

Population model

We analyzed the model fit to the laboratory data in order to explore the effects of temperature on the dynamics operating through different demographic rates. The populations in the laboratory cages (Fig. 3) were not sustained beyond two to three cycles, potentially due to demographic stochasticity associated with small population sizes. To investigate this, we simulated data from low aphid density as in the first set of long-term laboratory experiments (Fig. 3A, B). For these simulations, we incorporated demographic stochasticity by explicitly treating parasitoid attacks and adult parasitoid mortality as discrete events with probabilities given by the state-space model; thus, attacks were Poisson distributed and mortality was binomially distributed. This contrasts the version of the model use for fitting the data; for fitting with a Kalman filter, the model necessarily approximated demographic stochasticity as a normal distribution (Harvey 1989). Although the simulation model discretized the parasitoid population so that parasitoids could go extinct, we did not discretize the aphid population in order to retain the structure of the remainder of the model as it was fit to the data, although we decreased the environmental variation to emphasize the demographic stochasticity by reducing σ_x and σ_y by 50%. Fig. 4A, B gives two representative simulated data sets at each of 20°C and 27°C starting at the same initial aphid and parasitoid densities, but experiencing different sequences of stochastic demographic and environmental events. Parasitoids sometimes went extinct, but not always, indicating the importance of demographic stochasticity for parasitoid dynamics. In general, the simulations showed qualitatively similar patterns to the data, although given their stochastic nature, we would not expect exactly the same patterns as in the experimental data. Furthermore, simulations were very sensitive to the initial conditions, including not only the size of the aphid and parasitoid populations, but also the initial aphid age structure (results not shown). We also simulated the alternate case in which aphid abundances were initially allowed to reach high values (Fig. 3C, D), and these showed the anticipated small effects of demographic stochasticity (results not shown). A practical lesson from the simulations is that we cannot expect laboratory populations to persist in the long term for this host–parasitoid system due to the combination of demo-

TABLE 4. Fits of the stage-structured model to time series data from eight cages maintained at 20°C and 27°C (Fig. 3).

Aphid development	Aphid reproduction	Parasitoid development	Parasitoid attack rate	LLR
				0
X				11.10
	X			0.31
		X		25.22
			X	4.21
X	X			15.37
X		X		18.37
	X	X		19.28
X			X	8.47
	X		X	3.09
		X	X	38.63
X	X	X		21.58
X	X		X	11.53
X		X	X	26.67
	X	X	X	33.44
X	X	X	X	29.15

Notes: Fits were performed while switching the demographic parameters estimated from separate experiments (Fig. 2). Thus, for the "Aphid development" column, an X indicates that the development time estimated at 20°C (Fig. 2A) was used in fitting the model to time series data generated at 27°C (Fig. 3). The final column gives a measure of the fit of the model in terms of the log-likelihood ratio (LLR) of the fitted model. "Aphid reproduction" represents the combined effect of temperature on adult aphid survival and fecundity (Fig. 2B).

graphic stochasticity and the small populations generated by strongly cyclic dynamics.

Inference about the characteristics of the population cycles that would occur with larger populations in a uniform environment can be obtained by simulating the model without demographic and environmental stochasticity, and observation error. When the sizes of the simulated populations are sufficient to ensure that extinction of the parasitoid does not occur, the populations show sustained cycles (Fig. 4C, D). The period was 211 days when simulated for parameter values at 20°C and shortened to 130 days at 27°C, while the amplitude measured as the ratio of maximum to minimum aphid abundances increased from 1.7 to 9.6×10^4. This indicates that increasing temperature will likely shorten the period and increase the amplitude of pea aphid–*A. ervi* population cycles.

While these simulations suggest that the overall effect of increasing temperature will be to decrease cycle period and increase cycle amplitude, they give no indication of which specific demographic processes might be responsible. We investigated how the four demographic rates (aphid development, parasitoid development, aphid reproduction, and parasitoid attack; Fig. 2) separately affected the population cycles in two ways. The first estimated the magnitude of the effects of different demographic rates by measuring the fit of the model to the time series data while switching one-by-one the demographic rates measured at 20°C with those measured at 27°C. To compare the fits of the model, we used the log-likelihood ratio (LLR) between the "correct" model (with demographic rates appropriately matched with the temperature of the cages) and the models with switched demographic rates; the greater the value of LLR, the poorer the fit of the models with switched parameters. Comparing the models shows that aphid and parasitoid development rates had greater impacts on the observed dynamics in the laboratory cages than aphid reproduction and parasitoid attack rates, because switching either aphid or parasitoid development rates between their values estimated under 20°C and 27°C caused the largest decreases in the fit of the models (Table 4). There were also interactions between different demographic rates. For example, respectively, aphid development and aphid reproduction rates lowered the log-likelihoods by 11.10 and 0.31 individually, but by 15.37 together. This type of interaction suggests that the effect of one demographic rate on the dynamics is contingent on the values of the other demographic rates.

As a second assessment of the effects of temperature on population dynamics through the four different demographic rates, we computed five characteristics: (1) the cycle frequency, (2) the cycle amplitude, (3) the magnitude of the dominant eigenvalue of the Jacobian matrix at the stationary point (May 1974), (4) the Lyapunov exponent for the stable limit cycle (Guckenheimer and Holmes 1983, Strogatz 1994), and (5) the ratio of the mean parasitoid abundance to the mean aphid abundance. We performed this analysis on each of $2^4 = 16$ models in which demographic rates measured at 20°C and 27°C were switched. To factor out the temperature dependence of the parasitoid handling time h, we set $\Delta h = 0$ and refit all of the other parameters to the long-term cage data; this gives a "neutral" background of parameter values for the comparison among demographic rates measured in the short-term experiments (Fig. 2). In two parameter scenarios (those with 27°C aphid development, and 20°C parasitoid development and attack rate) the parasitoid went extinct, and these were excluded from all calculations except for (3) and (5). For each of the five measures of dynamics, we paired scenarios that differed in only one demographic rate (e.g., pairing 27°C aphid development rate, 27°C aphid reproduction, 20°C parasitoid development rate, 20°C attack rate with 20°C aphid development rate, 27°C aphid reproduction, 20°C parasitoid development rate, 20°C attack rate) and computed the difference in the measured values (Fig. 5).

Temperature-dependent aphid and parasitoid development rates had the greatest average effect on the frequency of the population cycles, with more rapid cycles occurring at 27°C (Fig. 5A). The greatest effects on cycle amplitude occurred through aphid development and the parasitoid attack rate (Fig. 5B), with these effects in the opposite direction. Higher temperature acting through the attack rate increased the magnitude of the dominant eigenvalue of the Jacobian matrix at the stationary point, corresponding to an increase in the rate at which trajectories diverged from the equilibrium (Fig.

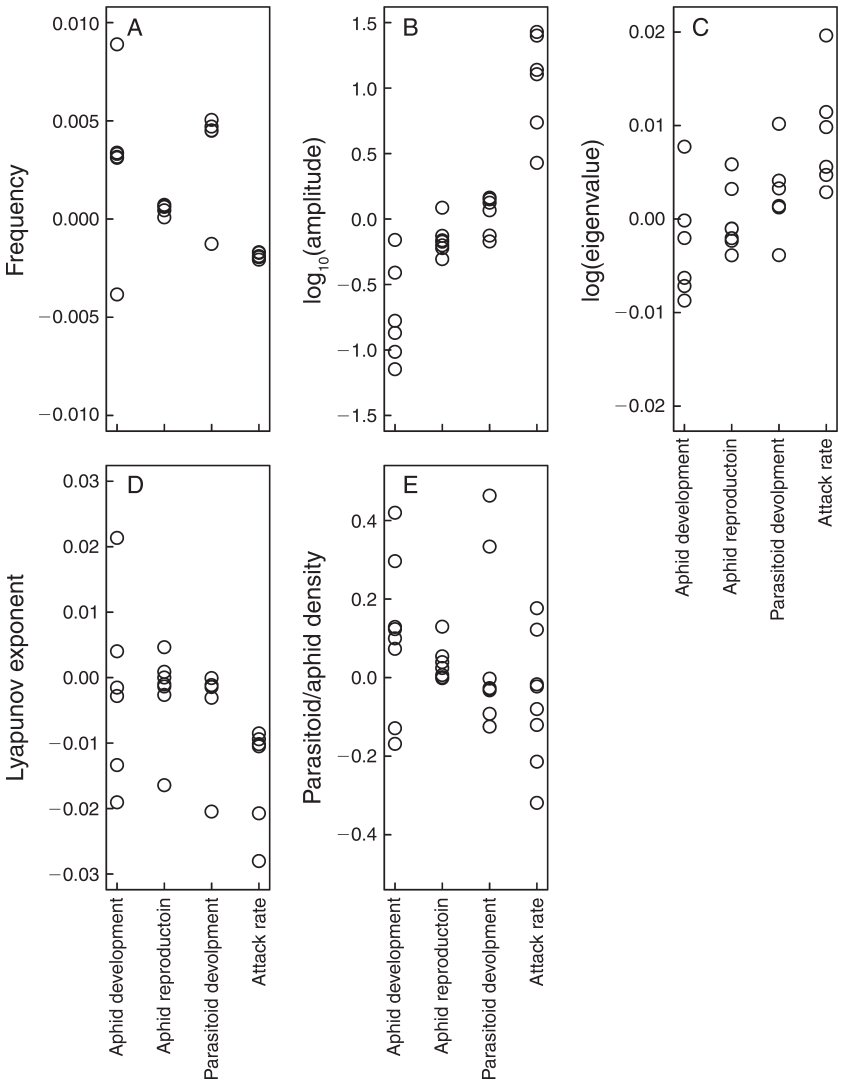

FIG. 5. To partition the effects of the four demographic effects of temperature (Fig. 1), we simulated the model switching the demographic rates measured at 20°C and 27°C to give 16 (=2^4) scenarios, and then computed (A) the cycle frequency, (B) the cycle a amplitude, (C) the magnitude of the dominant eigenvalue of the Jacobian matrix at the equilibrium point, (D) the Lyapunov exponent for the stable limit cycle, and (E) the ratio of the mean parasitoid abundance to the mean aphid abundance. The results are graphed as the difference between these measures at 27°C and 20°C for each of the pairs of models that differ in only the demographic rate in question.

5C). The temperature-dependent increase in the attack rate decreased the Lyapunov exponent, which measures the rate at which trajectories converge to a stable, but not necessarily stationary structure, in this case the stable limit cycle; values below zero correspond to a stable limit cycle, and the lower the value, the more rapidly trajectories approach the limit cycle (Fig. 5D). The temperature-dependent effect of the attack rate on the Lyapunov exponent is consistent with the result found for the eigenvalue (Fig. 5C); the higher attack rate makes population trajectories both leave the stationary point (higher eigenvalue) and approach the stable cycle more rapidly (lower Lyapunov exponent). Finally, rapid parasitoid development (27°C) had the greatest effect on increasing the mean abundance of parasitoids relative to the mean abundance of aphids (Fig. 5E).

Although there are consistent patterns for the effects of some demographic parameters on some measures of population dynamics (Fig. 5), the most impressive pattern is the variation in the effects of one demographic rate depending on the values of the other demographic rates; this variation is indicated by the differences among points for each demographic rate (columns in the panels of Fig. 5). For example, consider the range in values for the change in cycle frequency caused by the difference in aphid development rate at 27°C vs. 20°C; this difference ranged from −0.0038 to 0.0089 (first column in Fig. 5A). Table 5 gives the other demographic

TABLE 5. Period and frequency of population cycles in the simulations using demographic rates calculated from short-term laboratory experiments at 20°C and 27°C (Fig. 2).

Aphid development	Aphid reproduction	Parasitoid development	Attack rate	Period	Frequency
20°C	27°C	20°C	27°C	153	0.0065
27°C	27°C	20°C	27°C	370	0.0027
20°C	20°C	20°C	27°C	155	0.0064
27°C	20°C	20°C	27°C	65	0.0153

Note: These comparisons correspond to the maximum and minimum differences in cycle frequency appearing in the first column of Fig. 5A.

rates underlying the extremes of −0.0038 and 0.0089. The only difference between the case in which increasing the aphid development rate to its 27°C level causes a 0.0038 decrease in frequency from the case in which there is a 0.0089 increase is the aphid reproduction rate; the aphid reproduction rate (adult survival and fecundity; Fig. 2B) is that observed at 27°C and 20°C, respectively. Thus, the effect of aphid development rate on cycle frequency is highly contingent on the aphid reproduction rate. Patterns like this occur throughout Fig. 5.

DISCUSSION

When anticipating the consequences of climate change, ecologists have focused on changes in the spatial distribution of species, changes in phenologies, and changes in species abundances (Root et al. 2003, Parmesan 2006, Tylianakis et al. 2008, Pearson 2011). Climate change may also modify population dynamics (how population densities change through time). We have shown that higher temperatures may cause aphid–parasitoid populations to cycle with higher frequency and amplitude, clear signatures of changes in long-term population dynamics.

A difficulty in predicting the consequences of temperature change on population dynamics is that temperature will change many demographic rates, and each of these changes may have different effects on population dynamics (Kendall et al. 1999, Wearing et al. 2004, Murdoch et al. 2005, Cobbold et al. 2009). Our analyses of the pea aphid–*A. ervi* system show that, at best, few simple generalities can be divined. In the detailed stage and age-structured model fit to laboratory data, aphid survival and fecundity rates, parasitoid attack rates, and aphid and parasitoid development rates all changed population cycles in different ways; in some cases, in opposite ways that counterbalance each other (Table 5, Fig. 5). For example, the temperature-dependent increase in the aphid development rate decreased the amplitude of the cycles, while the temperature-dependent increase in the parasitoid attack rate increased the amplitude (Fig. 5B). Furthermore, the same change in a demographic rate could have different effects on different measures of population dynamics. For example, the increase in the parasitoid attack rate with increasing temperature destabilized the system by increasing the departure rate from the equilibrium (Fig. 5C), yet sometimes increased and sometimes decreased the ratio of parasitoids to aphids (Fig. 5E). Finally, there may be interactions among demographic rates. For example, the effect of the aphid development rate on cycle frequency can be positive or negative, depending on the other demographic rates (Fig. 5A, Table 5). These results caution against any blanket predictions about the consequences of mean annual temperatures, such as that global warming will make species show greater population fluctuations. The prediction devils are in the demographic details.

There have been several attempts to generate mathematical generalities about the consequences of temperature change on consumer–resource dynamics (Vasseur and McCann 2005, O'Connor et al. 2011, Binzer et al. 2012). These involved assuming that modeled demographic rates depend on temperature in a way predictable from metabolic rates (e.g., Gillooly et al. 2001). One conclusion from these studies is that assumptions about which rates depend on temperature can reverse conclusions. For example, Vasseur and McCann (2005) concluded that higher temperatures would destabilize consumer–resource interactions and lead to cycles, whereas Binzer et al. (2012) found that higher temperatures would be stabilizing. The source of this difference was the assumption by Binzer et al. (2012) that temperature increases density dependence (decreases the carrying capacity) of the resource species. While we support the exploration of models to investigate the possible theoretical effects of temperature on population dynamics, we suspect the ultimate conclusion will be that generalities are difficult to generate. Thus, we see the need for experimental case studies in which the mechanisms underlying temperature-dependent population dynamics are investigated in detail.

Although predicting the response of population dynamics to temperature changes will be hard, it is not impossible given sufficient investment in observations, experiments, and modeling. Direct and indirect interactions among species must be quantified, and the interplay among them must be understood. The only way to do this is through the integration of models and data, and we advocate for fitting models to time series data as we did here. This approach is distinct from obtaining parameter estimates and then plugging them into models. The advantage of fitting time series is that the data being fit with a model then contain information

about the dynamics themselves. This ensures that the dynamics found in the model have their ultimate origin in the data. Also, fitting a model to time series data makes it possible to statistically test the quantitative effects of temperature on population dynamics.

Our detailed experiments to quantify demographic rates showed strong effects of temperature. At 27°C, aphid development time from birth to adulthood was reduced to 87% of the rate at 20°C, adult life span was 37% longer, and fecundity was 39% greater. These changes in pea aphid demographic rates were large, leading to a reduction in the population doubling time from 2.71 d at 20°C to 1.82 d at 27°C. While we anticipated the decrease in development time, we did not anticipate the increases in adult life span and fecundity. The effect of higher temperature to increase adult life span is the opposite from that anticipated from theory (Amarasekare and Savage 2012) and found previously for pea aphids (Morgan et al. 2001), and we do not have an explanation for why our (statistically very strong) results differ.

The effects of temperature were even larger on *A. ervi* demographic rates. Parasitoid development times from egg to emergence as adults at 27°C were 60% the value at 20°C, and the short-term (24 h) parasitoid attack rate increased by 84%. There was an additional temperature-dependent effect on parasitoids that was found by fitting the model to the time series produced in the long-term laboratory experiment: The handling time in the functional response equation increased, indicating that the attack rate decreased more rapidly with aphid density at 27°C than at 20°C. This is not surprising, because at 27°C the overall attack rate was nearly double the attack rate at 20°C (Fig. 2D). *A. ervi* attack rates are likely to be limited by the time it takes females to mature eggs (Ives et al. 1999), and if this egg maturation rate does not increase strongly with temperature, then females will experience a greater proportional reduction in their attack rate at 27°C, leading to a higher estimate of h.

We assessed the importance of the demographic rates at 20°C vs. 27°C for population dynamics by comparing the fit of the population dynamics model (Eq. 2) to the long-term experimental data when the demographic rates either matched or mismatched the temperature of the long-term data (Table 4). The loss of statistical fit caused by mismatching demographic rates, especially aphid and parasitoid development rates, shows broad consistency between the short-term experiments to measure demographic rates and the long-term experiment to measure population-level dynamics. Although the short-term experiments gave detailed individual-level information, there are nonetheless several factors that they did not capture, but that might have been important for long-term dynamics. The temperature at which parasitoids developed could have affected adult size and/or fitness (Ellers et al. 2001, Colinet et al. 2007). The adult size of pea aphids decreases with both crowding and temperature (Murdie 1969), and this could indirectly lead to smaller parasitoid adults, which suffer a fitness cost (e.g., Cloutier et al. 2000). De Sassi et al. (2012) found for lepidopteran parasitoids that temperature-dependent changes in community-level average host size changed the parasitism rate. Similarly for pea aphids, temperature, by increasing the intrinsic rate of increase of pea aphids, might increase the proportions of the pea aphid population in instars II and III which are preferred by *A. ervi* females (Sequeira and Mackauer 1992, Ives et al. 1999). Therefore, temperature-driven changes in the aphid age structure might affect parasitism rates, although this effect is already accounted for in the stage-structured model (Eq. 1). Temperature could also affect the survival of parasitoids that we could not pick up in our experiments; we did not explicitly investigate this possibility because adult parasitoid fitness is notoriously difficult to study (e.g., Gilchrist 1996). An additional effect of temperature might be to reduce the resistance of pea aphids to parasitism. Recent studies have shown that bacterial symbionts within pea aphids can kill parasitoid eggs (Oliver et al. 2003, 2005, Degnan et al. 2009), but that this defense is compromised at higher temperature (Bensadia et al. 2006). Despite these, and probably other, effects of temperature on pea aphid–*A. ervi* interactions, the strong statistical consistency between short-term and long-term experiments suggests that the short-term experiments captured many of the important effects of temperature.

We have focused on understanding the dynamics of aphids and parasitoids in the laboratory, and extrapolating to population dynamics outside the laboratory is more tenuous. In field data collected over three years, we showed that higher daily temperatures were associated with higher aphid per capita population growth rates and higher parasitoid attack rates, consistent with the effects of temperature that we measured in the laboratory. These temperature effects in the field, however, were measured from short-term pea aphid dynamics and parasitism, taking advantage of daily/seasonal temperature fluctuations. The question we address with the long-term laboratory experiments and model is how longer term changes in mean temperature affect population dynamics by changing demographic rates and species interaction strengths. We do not have full information on all of the possible effects of temperature on pea aphids and *A. ervi* to predict in detail the response of population dynamics in the field to changes in long-term mean temperatures (e.g., increases in mean annual temperature). The laboratory experiments were conducted at only two fixed temperatures that were selected to be far enough apart (20°C vs. 27°C) to elicit strong effects of temperature. Consequently, we have no detailed demographic information about the effects of daily and seasonal fluctuations in temperature, or of winter, on pea aphid–*A. ervi* dynamics. Furthermore, temperature will likely affect all species in the

food web containing pea aphids (Cardinale et al. 2003, Snyder and Ives 2003), with the net effect on pea aphid dynamics contingent on numerous species of natural enemies in addition to *A. ervi*.

Despite the unknowns about temperature effects in the entire alfalfa–pea aphid–*A. ervi* system, our results give a qualitative expectation: Increasing temperature will lead to more rapid and higher amplitude fluctuations in pea aphid and *A. ervi* populations in the field, and increasing temperature will tend to destabilize the dynamics. We think that the question of whether similar conclusions will likely be found in other systems is still very open. The lesson that we learned, that the effect of temperature on long-term population dynamics will depend on how temperature affects all demographic rates and, in turn, how these alter species interactions, will likely be true in all systems. But the details of these temperature-dependent changes will be key to predicting how temperature change will alter the character of the dynamics of interacting species.

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Supplemental Material

Supplement

R computer code for estimating the population growth rate of aphids and parasitism rates from three years of field data (Eq. 1, Fig. 1), and MATLAB computer code for fitting the data from the long-term cage experiments (Eqs. 2–9, Fig. 3) using a nonlinear state-space model (*Ecological Archives* M084-016-S1).

Data Availability

Data associated with this paper (Figs. 1, 2, and 3) have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.h73b0