Ghosts of Habitats Past: Environmental Carry-Over Effects Drive Population Dynamics in Novel Habitat

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ABSTRACT: The phenotype of adults can be strongly influenced by the environmental conditions experienced during development. Consequently, variation in habitat quality across space and through time also leads to differences in the phenotypes of adults. This could create carry-over effects where differences in the natal habitat quality of colonizers influence population dynamics in new habitats. We tested this hypothesis experimentally by simulating dispersal of *Tribolium castaneum* from low- or high-quality natal habitat into new patches of low- or high-quality habitat. Differences in the natal habitat quality of colonizers altered population growth trajectories and led to carrying capacities that differed by up to 63% within a habitat type, indicating that patch dynamics are determined by the interaction of past and current habitat quality. Interestingly, even after multiple generations, the natal habitat of colonizers determined differences in adult traits that were related to density-dependent population regulation. These changes in adult phenotype could at least partially explain why carry-over effects continued to alter population dynamics for multiple generations until the end of the experiment. These results highlight the importance of variable habitat quality and carry-over effects for population dynamics.

Keywords: habitat quality, metapopulation, carry-over effects, population dynamics, cannibalism, phenotypic plasticity.

Introduction

Predicting what factors lead to differences in the dynamics of natural populations has been a central focus of ecology. Traditionally, differences in the densities and dynamics among populations are attributed to differences in environmental conditions, and thus populations are expected to be similar if environmental conditions are identical (Pulliam 1988; Thomas 2001). Yet, increasing evidence indicates that populations experiencing similar environmental conditions can differ substantially in their dynamics (Chase 2003*a*; Benton et al. 2006; Inchausti and Ginzburg 2009). This discrepancy may in part stem from the fact that classical population models have assumed that the traits of individuals are fixed within a given environmental context. However, the traits of individuals and potentially the traits of their offspring often depend strongly on the environmental conditions they experienced in the past (Mousseau and Fox 1988; Bernardo 1996; Beckerman et al. 2002). For instance, effects from past environments (e.g., food quality or predation risk) can "carry over" to alter the phenotype of individuals colonizing a novel habitat. Thus, the traits of individuals are often the combined product of past and current environmental conditions. Consequently, the presence of such carry-over effects has the potential to alter at least transient population dynamics (Leslie 1959; Lindstrom and Kokko 2002; Beckerman et al. 2003). However, whether carry-over effects from past habitats can alter population dynamics in a novel habitat for ecologically relevant timescales remains unclear.

The effects of past conditions on individual traits are ubiquitous in natural communities. They have been termed delayed life-history effects, maternal effects, parental effects, and more, but we refer to them here more broadly as carry-over effects (Mousseau and Fox 1988; Beckerman et al. 2002). Carry-over effects occur when an environmental stimulus affects an individual's (or its offspring's) traits after leaving the stimulus or setting that produced them. Carry-over effects from past environments can sometimes result from developmental tradeoffs made during past environmental conditions (Boonstra et al. 1998; Vonesh and Bolker 2005; Hagman et al. 2009). For example, predation risk or stress at an earlier time, stage, or habitat can lead to differences in traits such as physiology and dispersal behavior later in life after the stressor is gone (Stamper et al. 2008; Stamps et al. 2009). Other mechanisms, such as macro- or micronutrient deficiency or excess (Harrison et al. 2010) and epigenetic changes to DNA expression (Shea et al. 2011), also have lasting effects on a phenotype. For instance, higher food abundance for tadpoles can increase growth rate and survival on land after metamorphosis (Chelgren et al. 2006;

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Van Allen et al. 2010), and prolonging the nonfeeding larval stage for the bryozoan *Begula neritina* can decrease adult fecundity by orders of magnitude (Burgess and Marshall 2011). Whatever the mechanism, theory suggests that carry-over effects could have lasting effects on population dynamics (Leslie 1959; Lindstrom and Kokko 2002; Beckerman et al. 2003), but this has rarely been tested experimentally (Plaistow and Benton 2009).

Current models assume that carry-over effects can alter population dynamics by affecting the quality of individuals in terms of their survival and/or fecundity (Ginzburg and Taneyhill 1994; McNamara and Houston 1996; Lindstrom and Kokko 2002; Beckerman et al. 2003; Plaistow et al. 2006; Inchausti and Ginzburg 2009; Plaistow and Benton 2009). These models suggest that differences in individual traits can destabilize transient population dynamics and result in population cycles if density and environmental quality are correlated. However, carry-over effects can alter many additional key life-history traits, including size, diet, body allometry, antipredator defenses, and dispersal propensity, to name a few (Mousseau and Fox 1998; Relyea 2001; Beckerman et al. 2003; Hagman et al. 2009; Stamps et al. 2009; Harrison et al. 2010; Shima and Swearer 2010; Burgess and Marshall 2011). Whether these different manifestations of carry-over effects can have large and qualitatively different impacts on population dynamics is unknown.

While carry-over effects can occur through a variety of routes, they are particularly likely to be important for population dynamics during the colonization of new habitat patches or when habitat quality within a patch changes rapidly due to disturbance. In such scenarios, the carry-over effects of past environments experienced by colonizers could interact with the quality of the new patch to determine whether a population can persist in the new patch and whether it will become common or rare (Norris 2005; Benard and McCauley 2008; Clobert et al. 2009). Carry-over effects may also cause phenotype environment mismatch, in which colonizers are unable to persist in their environment due to a developmental path leading to the wrong phenotype for the new environment (DeWitt et al. 1998; Marshall et al. 2010). For example, an environmentally induced antipredator phenotype may not be favorable once predators are absent or when facing a novel predator (Benard and McCauley 2008; Hoverman and Relyea 2009). Thus, knowing how past habitat quality interacts with novel habitat quality is important for understanding the dynamics of populations, given the often extensive temporal and spatial variation of habitat quality.

We tested how such environmentally mediated carry-over effects alter population dynamics by independently manipulating the past habitat quality of colonizers and the habitat quality of newly colonized patches in an experimental flour beetle system. Our results indicate that population dynamics in colonized patches were driven by the interaction of carry-over effects from the past habitat of colonizing individuals and the quality of the habitat that was colonized. These differences in dynamics were likely driven by short-term changes in fecundity and lasting cross-generational changes in cannibalism behavior, a novel trait for carry-over effect studies. As a consequence, long-term population sizes and life-history traits within populations differed significantly among patches with similar habitat quality. This emphasizes the need to account for carry-over effects in the dynamics of populations in temporally and spatially variable environments.

Methods

Study Organism

Tribolium castaneum is a cosmopolitan pest of stored grains and dry goods. It has a typical beetle life cycle, in which larvae hatch from eggs and then go through a number of instars over three or more weeks before pupating. The pupae metamorphose into adults in under a week. Adults begin to senesce after approximately 3 months but can live much longer under some conditions (Kollros 1944; Walter 1990). The entire life cycle takes place in wheat flour, under decaying tree bark, or in almost any dried good (Zeigler 1976). Larval and adult flour beetles are cannibalistic on eggs and pupae, and confined flour beetle populations are often largely regulated through cannibalism (Park 1957; Sokoloff et al. 1965). Wild *T. castaneum* disperse away from their natal habitat shortly after reaching reproductive maturity, possibly to avoid intense cannibalism on eggs by developing larvae (Zeigler 1976). *Tribolium castaneum* can disperse through flight and by walking but are also frequently dispersed by being moved during any life stage in flour and other dry goods (Zeigler 1976; Ridley et al. 2011).

Experimental Setup for Population Dynamics

Beetles used in this experiment originated from stocks kept in wheat flour for many years at the USDA Agricultural Research Service (ARS) station at Kansas State University. Before being used in this experiment, *T. castaneum* were kept on wheat flour in stock containers at ambient lab temperatures (23°–25°C and 10%–30% humidity) for 9 months. F_0-generation *T. castaneum* used in this experiment were raised from eggs that were randomly collected from stock colonies. Eggs were separated and individually hatched in trays containing 60 wells with 1.5 g of either unbleached organic white wheat flour with 5% brewer's yeast (henceforth, wheat) or organic whole oat flour (oat)

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at 24°–26°C and 25%–30% humidity. Wheat provides a high-quality habitat for *T. castaneum* growth, while oat flour is a relatively low-quality habitat (Park 1948; Via 1991).

Within 2–4 days after emergence, three virgin flour beetles of each gender were placed into an 8-dram vial containing 6 g of either wheat or oat flour. This mimicked the natural tendency of *T. castaneum* to disperse into a novel habitat after metamorphosis (Zeigler 1976) and resulted in a 2 × 2 full factorial design manipulating the colonizers' natal habitat (wheat or oat) and the habitat they colonized (wheat or oat). This design could also imitate a situation in which disturbance dramatically lowers population size and either alters or does not change the local habitat quality. Due to differences in survival and sex ratios, there were different numbers of replicates in each treatment.

These populations were allowed to grow naturally over 133 days under the same temperature, humidity, and light conditions as their natal habitat. Every 19 days (the development time of *T. castaneum* in low-quality habitat divided by 2) from their starting date, populations were sifted to enumerate larvae, pupae, live adults, and dead adults for each population. At each check, all mature adults in a population were grouped and weighed to the nearest tenth of a milligram. For logistical reasons, it was unfeasible to count eggs and recently hatched larvae, which were too small to see without magnification. Dead adults were removed to record adult mortality. Dead larvae and pupae are consumed by larvae and adults, so they were not recoverable. Vials then received 6 grams of new flour of their respective habitat type (wheat or oat), and all larvae, pupae, adults, and eggs were returned. This procedure resulted in seven equally timed checks of all flour beetle populations during the 19-week course of the experiment. This period of time allowed populations in wheat to complete two generations and enter a third before the experiment ended, while populations in oat did not enter a third generation. Note that a generation in a confined flour beetle population is often much longer than egg-to-adult development time since a cohort of larvae can consume new eggs and preclude successful recruitment of new larvae.

Analysis

Our aim was to characterize multiple levels of population and individual traits to understand how carry-over effects from the natal habitat of six colonizers could scale up to affect multigenerational population dynamics.

Overall Population Dynamics

Adult Population. Mature adult flour beetles are the main dispersal stage, are long lived, and, unlike other stages, are invulnerable to cannibalism, so we focused on this stage for most analyses. Dynamics of adult beetles were analyzed in two sections, a growth phase and a carrying capacity phase. The growth phase for all populations occurred when the first cohort of larvae produced in all populations metamorphosed into the F_1 (first generation) adult generation. After the growth phase, adult population size was stable despite fluctuating larval abundance. We considered a lack of significant change in population size over two or more generations to indicate a quasi-stable carrying capacity (Chase 2003*b*). The growth rate of adult population size during the growth phase was estimated using linear regression of adult population size over time from time zero to the census at the end of the growth phase, with the intercept forced to 6 (the number of colonizers present at time zero). Due to differences in development rate, the growth phase ended at census 3 in wheat colonization habitat (WW), 4 in wheat-to-oat populations (WO), and 5 in oat-to-oat populations (OO; fig. 1). For statistical analysis, a small constant (0.1) was added to all population growth coefficients, since one population had a negative growth rate. The effects of population history on population growth rate were then fitted with a generalized linear model (GLM) using fixed effects of natal habitat, colonization habitat, and their interaction with gamma errors and an inverse-link function. Carrying capacity population sizes were estimated by taking the mean of the last three adult population size counts for each replicate. The effects of population history on carrying capacity were then fitted using $\log_e$-transformed mean population size using a GLM with fixed effects of natal habitat, colonization habitat, and their interaction with Gaussian errors.

Juvenile Stages. To gain more insight into population dynamics, we also analyzed numerical changes in juvenile stages. Unlike adult dynamics, larval and pupal numbers in all treatments never settled to a carrying capacity and instead cycled with each generation's reproductive pulses. As a result, they were not suitable for any linear or autoregressive repeated measures or averaging approach. Thus, we compared larval and pupal densities across treatments using bootstrapped 95% confidence intervals penalized for multiple comparisons across all treatments and time steps using Bonferroni correction. As a result, differences among error bars within and between censuses are statistically significant at $\alpha < 0.05$.

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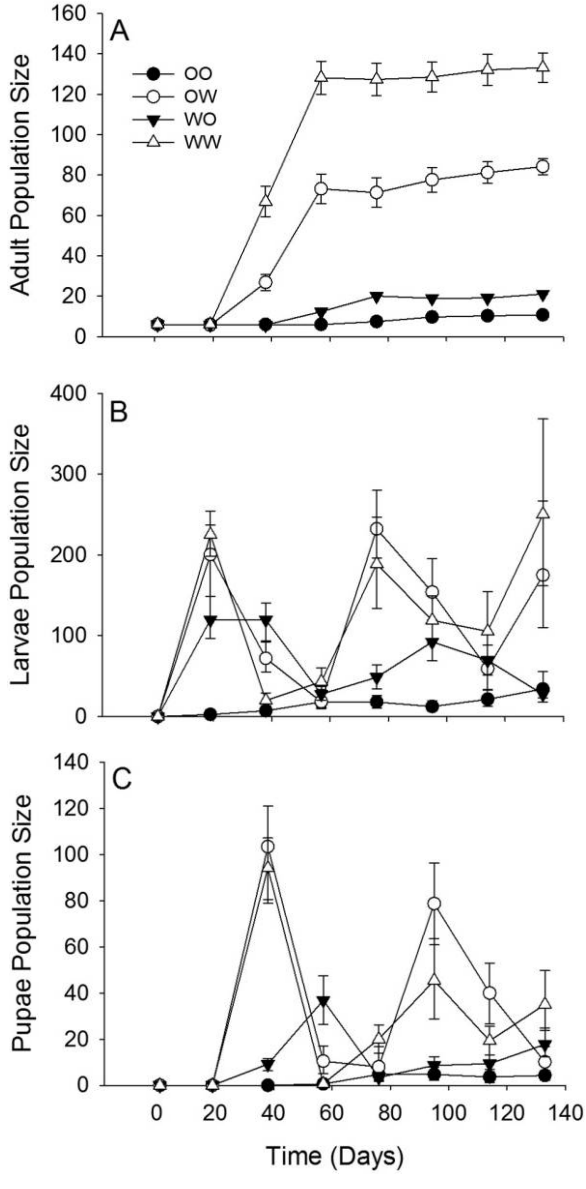

Figure 1: *Tribolium castaneum* population dynamics for the adult stage (*A*), the larval stage (*B*), and the pupal stage (*C*) under different habitat histories. The first letter of the key abbreviations indicates natal habitat type (low quality: O = oat, high quality: W = wheat; see methods for details), and the second indicates colonization habitat type. Adult stages show mean and ±1 SE. Larval and pupal density show mean and 95% confidence intervals corrected for multiple comparisons at all time steps so that any nonoverlap of confidence intervals indicates differences at $P = .05$.

Demographic Rates

To gain insight into the demographic processes driving adult population dynamics (growth and carrying capacity phases), we used a combination of population census data and cannibalism assays to estimate F_1 larval production (a composite of fecundity and egg cannibalism determining reproductive success of colonizers), F_1 larval survival to adulthood, adult mortality rates across all censuses, and egg production and cannibalism rates at the end of the experiment.

F_1 Larval Abundance. During the F_1 generation, the production of larvae was balanced by the number of eggs laid and consumed by the initial six adults, as well as the survival of early instar larvae. To see if these factors could be important in adult population growth, we tested for differences in F_1 maximum larval population using a Monte Carlo randomization routine with 10,000 permutations in SAS software (Casell 2002). These tests and the others in these sections used natal habitat and colonization habitat as fixed factors, each with two habitat quality levels, and their interaction. F_1 maximum larval population was defined as the highest number of larvae counted in a replicate container at any time step during the F_1 generation after any cannibalism or mortality of eggs that may have occurred (i.e., it is the highest point of the first peak in fig. 1*B*). Any single larval period was longer than the 19-day duration between steps at our temperature levels, so this should closely approximate the true maximum (Walter 1990).

F_1 Larva-to-Adult Survival. Carry-over effects of past habitats could manifest and affect population dynamics through impacts on survival at any stage. Larvae that survived to be counted in F_1 abundance above must then survive the later larval instars and through the challenges of pupation and metamorphosis to become adults. Both the initial six adults and large larvae could cannibalize pupae and soft new adults as well. F_1 larval survival was estimated by dividing the number of new adult recruits at the end of the growth phase by the maximum number of F_1 larvae. Thus, survival from the larval stage includes late larval and pupae survival as well as recently emerged (<3 days old) adult survival. Larval survival rates between treatments were compared using a Monte Carlo randomization routine with 10,000 permutations in SAS software (Casell 2002). All adult population growth during the growth phase consisted of F_1 recruits.

Adult Mortality. Adult mortality was calculated as the proportion of unique adults that had died by the end of the experiment (i.e., total dead divided by the sum of total dead and alive at the last census). Differences in adult proportional death rates are largely driven by the deaths of recently emerged adults, which are soft and still vulnerable to cannibalism. The fixed effects of natal habitat, colonization habitat, and their interaction were fitted to

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adult death rates using a GLM with Gaussian-distributed errors.

Cannibalism and Egg Production Assays. Fecundity and cannibalism rates together largely determine carrying capacity for confined *Tribolium castaneum* (Park 1957; Sokoloff et al. 1965). Thus, to gain more insight into what factors lead to observed differences in carrying capacity, we randomly selected 10 populations from each treatment for a trial of cannibalism rates and fecundity at the end of the experiment. Six individual beetles were randomly chosen without regard to their sex from each of the selected populations and put into an 8-dram vial with 6 g of flour matching the habitat of the chosen population. These "trial" containers also contained 20 *T. castaneum* eggs from stock populations marked with neutral red dye. The 40 resulting trial vials were placed in a cooler under the same environmental conditions as the colonization populations. After 22 hours, all trial vials were examined for the number of remaining red eggs and for the number of new, undyed eggs. Fresh eggs were counted as reproductive events from our assay beetles, while missing red eggs were assumed to be cannibalized. Since it is possible that assay beetles could eat their own eggs, we checked for correlations between fresh eggs produced and red eggs consumed. There was no significant correlation between the two (Pearson's $r = -0.26$, $P = .118$). Cannibalism and fecundity rates were tested for differences among individuals from each natal and colonization habitat using ANOVA. These tests used fixed effects of natal habitat, colonization habitat, and their interaction. Fecundity rates were $\ln+1$ transformed to meet assumptions of equal variance.

General Methods of Analyses

Significant models and ANOVA were followed by post hoc comparisons of all treatments using planned contrasts with Benjamini-Hochberg correction for false discovery rate (Benjamini and Hochberg 1995). These results are shown when required for interpretation of the models. Unless otherwise stated above, all tests were performed in R, version 2.13.0 (R Development Core Team 2011), and included the library nlme (Pinheiro et al. 2011). Results are presented with mean ± standard errors unless otherwise noted, and all statistical tests were two-tailed.

Results

Natal Habitat Development

Colonizing beetles that developed in high-quality natal habitat emerged approximately 10 days before beetles in low-quality habitat (high-quality [wheat] mean: 27.3 ± 0.33 days, low-quality [oat] mean: 37.8 ± 0.6 days, $t = -15.28$, corrected df = 7.811, $P < .001$). Survival was equal between high-quality and low-quality natal habitats (high-quality mean: 0.81 ± 0.07, low-quality mean: 0.76 ± 0.08, $t = 0.528$, corrected df = 9.789, $P = .61$). The average mass of beetles colonizing from high-quality natal habitat was 3% greater than the mass of colonizers from low-quality habitat (2.14 ± 0.013 mg vs. 2.07 ± 0.019 mg, $P = .005$). The colonizers' natal habitat continued to be important for individual mass in subsequent generations (see appendix). This indicates that wheat is higher-quality habitat for individual beetle development. Low-quality habitat did not reduce individual beetle survival outside of a population setting.

Overall Population Dynamics

Adult Population. Populations founded by colonists from high-quality habitat increased at a greater rate during the growth phase in both colonization habitats (natal habitat likelihood ratio test [LRT] = 54.52, df = 1, $P < .001$). Additionally, populations in high-quality habitat increased by more than an order of magnitude greater than populations in low-quality habitat (mean slope of growth in high-quality habitat = 2.53, mean slope in low-quality habitat = 0.13; colonization habitat LRT = 379.73, df = 1, $P < .001$). However, the interaction between natal habitat and colonization habitat was also significant (LRT = 45.98, df = 1, $P < .001$), indicating that their effects were not independent (fig. 1*A*).

While colonizing high-quality habitat (wheat) always resulted in a significantly larger adult carrying capacity regardless of natal habitat quality (mean of wheat colonization habitats = 106.1 ± 6.6 vs. oat = 14.9 ± 1.6; $F_{1,56} = 315.74$, $P < .001$; fig. 1*A*), adult carrying capacity was also significantly larger within a colonization environment type if the colonizers developed in high-quality habitat (WW carrying capacity adult population = 131.3 ± 7.2 vs. OW = 81 ± 4.9, and WO = 19.7 ± 1.5 vs. OO = 10.3 ± 1.1; $F_{1,56} = 40.08$, $P < .001$; fig. 1*A*). While natal habitat and colonization habitat both affected carrying capacity population size, they did not interact during the carrying capacity phase ($F_{1,56} = 1.59$, $P = .2121$). As a consequence, carrying capacity was determined by current and past habitat quality (of colonizers). Overall, all individual treatments differed significantly from each other (post hoc test: all $P < .05$) in both the growth and carrying capacity phases, indicating that each combination of past and current habitat quality led to different population dynamics within a patch.

Juvenile Stages. Comparisons of corrected 95% confidence intervals in figure 1*B* and 1*C* indicate that larval and pupal

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dynamics did not differ significantly among the natal habitat types of the colonizers in high-quality colonization habitat but led to significant differences in low-quality habitat (i.e., WO and OO; fig. 1*B*, 1*C*). Populations in low-quality habitat founded by colonizers from high-quality habitat exhibited larval and pupal dynamics that appeared similar to dynamics in high-quality habitat but at a lower wavelength and amplitude. Any cycling for populations in low-quality habitat founded by colonizers from low-quality habitat occurred very slowly and at much lower amplitude than other treatments (corrected 95% confidence intervals; fig. 1*B*, 1*C*).

Demographic Rates

F_1 Larval Abundance. Peak abundance of F_1 larvae was significantly influenced by natal habitat, colonization habitat, and their interaction (randomization test with 10,000 resamples; all $P < .001$; fig. 1*B*). Populations that colonized high-quality habitat showed three times higher larval recruitment than populations in low-quality habitat. Within low-quality habitats, though, populations founded by colonizers from high-quality habitat (WO) produced almost seven times as many F_1 larvae than populations founded by colonizers from low-quality habitat (OO). These results are consistent with the growth phase of adult population dynamics and clearly indicate a strong carry-over effect of natal habitat for beetles colonizing low-quality habitat.

F_1 Larva-to-Adult Survival. Larval survival to adulthood was only affected by colonization habitat and its interaction with natal habitat (randomization test with 10,000 resamples; natal habitat $P = .15$, colonization habitat $P < .001$, interaction $P < .001$; fig. 2*A*). Using planned contrasts, individual treatments did not show significant differences among colonizers' natal habitat quality in the same colonization habitat (in high-quality habitat: WW mean survival = 0.62, SE = 0.025; OW survival = 0.52, SE = 0.028, $P = .0548$; and in low-quality habitat: OO survival = 0.19, SE = 0.026; WO survival = 0.16, SE = 0.012, $P = .0529$), but all other treatment combinations were significantly different at $P < .001$.

Adult Mortality. Over the 19 weeks of the experiment, natal habitat quality did not have a consistent effect on proportional adult death rate in all treatments ($F_{1,56} = 0.121$, $P = .729$), but colonization habitat ($F_{1,56} = 16.958$, $P < .001$) and the interaction term ($F_{1,56} = 60.264$, $P < .001$) were significant. Interestingly, this is because adult death rates were only dependent on the colonization habitat when the colonists came from low-quality natal habitat. Populations founded by colonizers from high-quality habitat did not show significantly different adult mortality regardless of current habitat quality (post hoc test: $P = .094$), while adult mortality of populations founded by colonizers from low-quality habitat differed by fivefold ($P < .005$) among current environments (fig. 2*B*). Furthermore, the mortality rates for populations from low-quality habitat differed significantly within a given habitat from populations founded by colonists from high-quality habitat, though in opposite directions (fig. 2*B*).

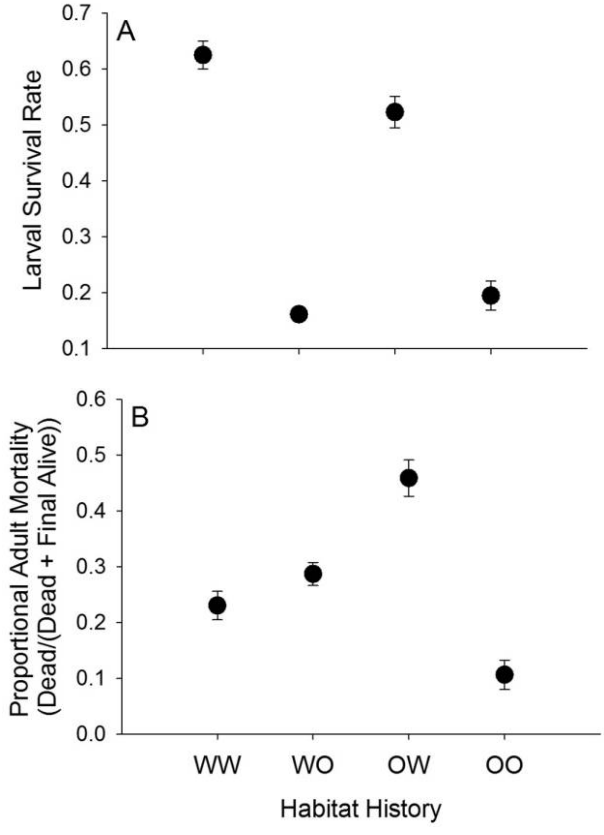

Figure 2: Effects of different habitat history for mean (±1 SE) F_1 larval survival to adulthood (*A*) and mean (±1 SE) proportional adult mortality through the entire experiment (*B*). For habitat history notation, see figure 1.

Cannibalism and Egg Production Assays. After 133 days of the experiment, the fecundity rate of individuals within populations did not show any carry-over effects but only differed among colonization habitat types that beetles were then in (natal habitat: $F_{1,34} = 0.005$, $P = .94$; colonization habitat: $F_{1,34} = 6.581$, $P = .01$; interaction: $F_{1,34} = 0.066$, $P = .79$; fig. 3*A*). Cannibalism rate, however, did not differ among colonization habitats but instead differed only among natal habitats of the colonizers (natal habitat: $F_{1,34} = 8.82$, $P = .005$; colonization habitat: $F_{1,34} = 0.382$, $P = .54$; interaction: $F_{1,34} = 0.042$, $P = .84$; fig.

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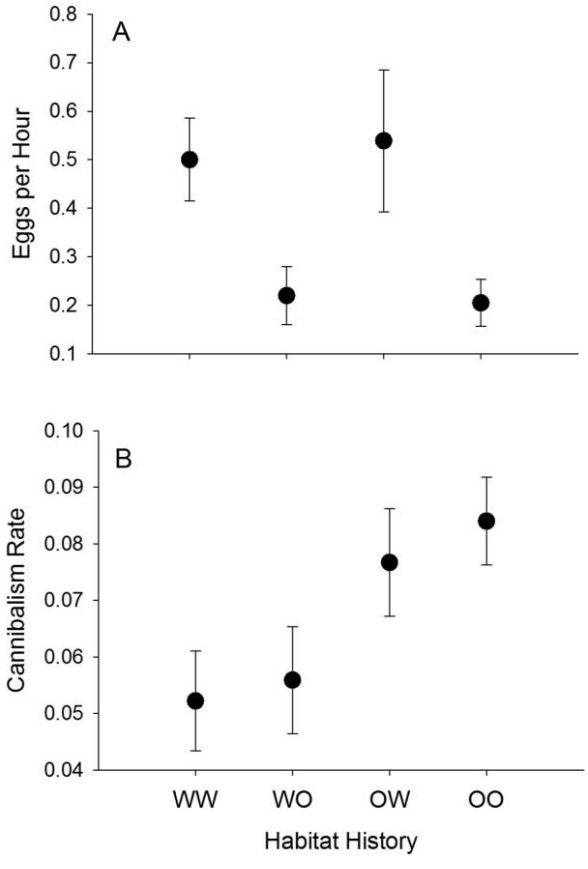

Figure 3: Effects of different habitat history on *Tribolium castaneum* (*A*) mean (±1 SE) hourly fecundity per beetle and (*B*) mean (±1 SE) cannibalism rate, calculated as $-1/(N \times t) \times \ln(\text{initial eggs/final eggs})$ (Sonleitner 1961). For habitat history notation, see figure 1.

3*B*). Cannibalism rates were 33% higher for beetles from populations founded by colonizers from low-quality natal habitat. Due to the high population growth in high-quality colonization habitat, it is very unlikely that this pattern could be driven by original colonists that lived through the experiment.

Discussion

When individuals develop under different environmental conditions, they often differ in their adult phenotypes. We found that such differences can lead to carry-over effects that generate unique population dynamics in novel patches for several generations. Populations started by colonists from high-quality habitat had both significantly higher initial population growth trajectories and multigenerational carrying capacities (by up to 63%) than populations initiated with colonists from low habitat quality. Furthermore, the phenotype of individuals (in terms of fecundity, cannibalism rate, death rate, and adult body mass) in each population was influenced by interactions between the past habitat of colonizers and the current habitat quality. The significant differences in the general phenotype among these populations at the end of the experiment were surprising and suggest that alternative carrying capacities could persist for many additional generations. These results indicate the importance of accounting for environmental carry-over effects mediated by phenotypic differences in the traits of colonizers for the dynamics of populations.

Initial Population Growth

For many species, carry-over effects can generate large differences among individuals in important traits such as fecundity. For instance, developmental history or past experiences can result in large fecundity differences for individuals or cohorts of bryozoans (Burgess and Marshall 2011), birds (Norris 2005), mammals (Hamel et al. 2009), and numerous others (reviewed in Harrison et al. 2010). Thus, carry-over effects could be expected to influence at least initial population dynamics in a new environment. However, whether the signal of such carry-over effects is strong enough against the more immediate current environment is less certain. In our experiment, the natal habitat of colonizers resulted in substantial differences in population growth beyond the strong effects of the current environment. Populations started by colonizers that developed in high-quality natal habitat grew twice as much as those started by colonizers in low-quality habitat during the first generation. Indeed, it is expected that the latter populations would be much less likely to persist in the long term or be able to recover from any negative perturbation than the former populations. Smaller population size and lower growth rates together increase extinction risk for populations (Griffen and Drake 2008, 2009). This suggests that carry-over effects not only can influence fecundity rates but also may determine colonization success and local extinction risk.

The carry-over effects on initial population growth observed in our study likely arose from changes in multiple life-history traits. Population growth and regulation of flour beetles is typically governed by the balance between egg production and cannibalism of eggs and pupae (Park 1961). *Tribolium castaneum* has been shown to increase cannibalism rates and decrease fecundity in our low-quality habitat, oat flour (Via 1991). We observed a marked increase in the fecundity of beetles colonizing low-quality habitat from high-quality habitat during the first generation, but fecundity rates were identical within a current habitat after two or three generations. While sex ratios

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were even at the start of the experiment, we did not monitor this over time. Although flour beetles typically produce even numbers of male and female offspring, the results of equal fecundity within but not between current habitat types could still potentially be driven by unobserved differences in sex ratio as well as current habitat quality effects. While carry-over effects alter fecundity for many animals (Harrison et al. 2010), this has only once been demonstrated for individuals of a different flour beetle species. Long-term adult exposure to low-quality "conditioned" wheat flour for *Tribolium confusum* resulted in a temporary decline in individual fecundity that was regained after nearly 2 months back in fresh wheat flour (Park 1935). Thus, differences in initial population growth in our experiment were likely caused by carry-over effects of natal habitat quality on both fecundity and cannibalism rate for the colonizers.

Long-Term Dynamics/Carrying Capacity

Although carry-over effects may lead to differences in initial population growth, it has been unclear whether such differences should be transient or whether they should have persistent effects on long-term population dynamics. Theory and empirical work suggest that initial differences in population characteristics such as individual phenotype or density can have lasting effects on dynamics (Leslie 1959; Beckerman et al. 2002; Lindstrom and Kokko 2002; Chase 2003*b*; Benton et al. 2006; Inchausti and Ginzburg 2009). However, previous experimental tests of carry-over effects on population dynamics found only dampening transient effects (Benton et al. 2005, 2008; Plaistow and Benton 2009), no effects (Banks and Powell 2004), or population cycles caused by patch dynamics (Ginzburg and Taneyhill 1994). In contrast to these studies, we found that within a given habitat quality, adult populations remained constant after one generation of population growth but at different densities, depending on the colonists' natal habitat. While adult population size within a treatment remained constant (and largely within individual replicates as well; B. G. Van Allen, unpublished data), the production of juveniles' stages continued in cycles (fig. 1). Thus, we consider that most of our populations reached a quasi-stable carrying capacity during the experiment (Chase 2003*b*). Additionally, adult cannibalism rates, death rates, and individual body masses all continued to be strongly affected by colonizer history 4 months and multiple generations after colonizing a new habitat. Persistent differences in population traits within identical habitats have been shown to occur due to invader biomass (Chase 2003*b*) or genetic founder effects (Agashe et al. 2011; Shine et al. 2011). The duration (in terms of generation time) of our study is comparable to the duration of other experimental studies of factors influencing population dynamics (Chase 2003*b*; Banks and Powell 2004; Benton et al. 2005, 2008; Plaistow and Benton 2009). To the best of our knowledge, however, this study is the first to report persistent differences in carrying capacity due to environmental carry-over effects.

While this study provides the first clear evidence that carry-over effects due to differences in developmental history can alter long-term population dynamics and carrying capacity, it is also important to understand the mechanisms responsible for this pattern. While average differences among current habitat types (i.e., low- vs. high-quality habitats) could be explained by the corresponding differences in fecundity observed at the end of the experiment, this does not explain why populations within a habitat showed no signs of convergence in adult population size. Flour beetle populations with a given fecundity rate have carrying capacities set by their cannibalism rates (Park 1957; Stevens 1989). Indeed, individuals born in either habitat during the experiment to colonizing parents from low-quality habitat showed 33% higher cannibalism rates than individuals with parents from high-quality habitat at the end of the experiment. To see whether this could generate observed differences in adult population densities in the experiment, we simulated population dynamics using a simple model that captures the two most important aspects of flour beetle population dynamics, fecundity and cannibalism: $N_t = N_{t-1} + rN_{t-1} \times \exp(-cN_{t-1})$, where r is fecundity and c is cannibalism rate. We found that while holding fecundity constant within habitat treatments (as suggested by our fecundity estimates), differences in cannibalism rate of approximately 50% can account for the observed differences in long-term population dynamics within a common current habit for populations with differing natal habitats. While the difference is just higher than the upper 95% confidence limit of our cannibalism assay (mean: 0.334; 95% CI: 0.218–0.462), this is expected since our cannibalism assay only measured egg cannibalism rates, while the model implicitly attributes all forms of density-dependent mortality to cannibalism rates, including other cannibalistic interactions between stages (e.g., adults cannibalizing pupae). Given that the propensity for cannibalism is a general behavioral trait of individuals, it is reasonable to assume that other cannibalistic interactions showed similar patterns. Thus, our results suggest that the interaction between history of populations (i.e., past habitat affecting cannibalism rate) and the current habitat (i.e., fecundity) largely determined the population carrying capacity in all treatments.

That cannibalism rates at the end of the experiment (after 4 months and multiple generations) were solely dependent on the colonizers' natal habitat is surprising, since the offspring usually vastly outnumbered initial colonizers

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and developed in a current habitat that was often different from the colonizers' natal habitat. The parents of all colonizing beetles were randomly selected from the same stock habitat, suggesting that this is not a genetic effect. However, the colonizers themselves were raised in different habitats. The observed difference could therefore be some type of epigenetic effect on the germ line of individuals that depended on the habitat they developed in and led to maternal effects on the phenotype of their offspring. Environmentally induced maternal effects, which can last multiple generations, are common in insect and vertebrate organisms and can represent an adaptive attempt to match offspring phenotype to changing environmental conditions (Rossiter 1996; Mousseau and Fox 1998; Fox and Savalli 2000; Plaistow et al. 2006). Alternatively, the differences in the initial population dynamics and density-dependent feedbacks within a habitat could have selected for different cannibalistic phenotypes. This would suggest that the carry-over effect of the colonizers' natal habitat on cannibalism rates at the end of the experiment could be a product of the interactions between individuals in the experimental populations rather than a product of the actual habitat quality they were living in. Interactions between colonizers and their offspring in new populations could generate strong selective pressures in colonized patches since carry-over effects are still strong and density changes rapidly (Lankau and Strauss 2011). Continuous feedbacks between the environment, carry-over effects, and selection have been seen in insect host expansions (Fox and Savalli 2000), selection for life-history strategy in spadefoot toads (Pfennig and Martin 2009), and in many other systems (Lambrinos 2004; Carroll et al. 2007). Thus, we could speculate that feedbacks between past environment and current within-population interactions set stable cannibalism rates across generations in each treatment. This feedback could be due to long-lasting epigenetic or nutritional maternal effects, strong selection, or phenotypic plasticity due to interactions between the colonizer generation and their offspring.

Cannibalism between life stages and generations could explain the presence of lasting feedbacks on phenotype in our flour beetle populations. This could help explain why strong initial carry-over effects altering population size in experiments with the soil mite *Sancassania berlesei* often largely attenuate over a similar number of generations to our study (Benton et al. 2005, 2008; Plaistow and Benton 2009). Unlike our study species, *S. berlesei* is not cannibalistic and has a relatively short adult life span relative to the juvenile stages, which potentially reduces interactions between stage classes (10–25 days and 90+ days for adults and 4–50 days and 25–55 days for larvae of *S. berlesei* and *Tribolium castaneum*, respectively; Walter 1990; Plaistow et al. 2007; this study). Previous studies show that experimentally selected differences in cannibalism rates among flour beetle populations can persist for 60 generations in lab populations, leading to long-term differences in population densities (Stevens 1989). Cannibalism is a common life-history trait in nature (Fox 1975; Polis 1981), but it has received no attention in previous studies on carry-over effects. Thus, the life history of a species could moderate the interactions between past and current environment for population dynamics. However, feedbacks between carry-over effects and selection could occur in any situation where novel habitat and interactions meet, such as during species invasions and in metapopulations with changing habitats or species patch occupancy.

Implication for Metapopulation Dynamics

Classical metapopulation theory typically assumes that fitness of individuals that colonize new patches is only determined by the quality of the colonized patch and does not differ among individuals (e.g., Hanski 1994; Mouquet et al. 2006). We have shown that individuals that developed in high-quality habitat founded populations that reached higher equilibrium population sizes in either high-quality or low-quality habitat. This indicates that high-quality habitat patches within a metapopulation can potentially increase the mean fitness of individuals in low-quality patch populations by providing high-quality migrants. It also suggests that the average fitness and size of populations in all patches could decline if the amount of low-quality habitat available for a metapopulation increases and individuals immigrate from low-quality patches. Observational and modeling studies with migratory birds make similar predictions on habitat quality and average fitness of spatial populations (Norris 2005; Reid et al. 2006).

Shifts from a developmental habitat to another habitat are common for many species that disperse between patches during the adult or juvenile stage. More than 80% of animal taxa have complex life cycles and have some sort of shift in habitat usage from the juvenile to adult stages (e.g., almost all marine invertebrates, amphibians, insects, most marine fish, and more; Werner 1988). Similarly, animals such as birds, mammals, and reptiles that do not have complex life cycles still frequently disperse or migrate during their lives. Carry-over effects operate at the individual level and are separate from any density-dependent effects of habitat quality that are already known to affect metapopulation persistence (Pulliam 1988; Hanski 1994; Harrison et al. 1997; Thomas 2001). The dispersal behavior of an organism can itself be altered by carry-over effects as well, which may alter the regional impacts of carry-over effects (Benard and McCauley 2008; Clobert et al. 2009; Stamps et al. 2009). Thus, carry-over effects are

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likely to be common in many species, and our results suggest that they have the potential to affect metapopulation dynamics.

Outlook for Natural Systems

Carry-over effects have the potential to alter the phenotype of almost all living organisms. Survival rate and fecundity are two traits that are influenced by past experiences in our study and in many other taxa (amphibians: Smith 1987, Semlitsch et al. 1988; arthropods: Plaistow and Benton 2009; birds: Reid et al. 2006, Van de Pool et al. 2006; bryozoans: Burgess and Marshall 2011; fish: Shima and Swearer 2010; mammals: Hamel et al. 2009; polychaetes: Allen and Marshall 2010, and many others). For many taxa, such as birds and mammals (Reid et al. 2006; Hamel et al. 2009), these phenotypic changes, which develop early in life, last for a lifetime and move with the individual into new habitats. Traits besides survival and fecundity, such as cannibalism in this study, can be affected as well for some organisms, which may have novel effects on population dynamics.

The exact implications of carry-over effects for population dynamics in natural systems will likely depend on more than the biology of the organisms affected. It is important to caution that not all individuals in a patch will always have the same developmental history and that other context-dependent factors such as strong density dependence could mask the expression of carry-over effects at the population level (Benton et al. 2006; Plaistow and Benton 2009). As a result, we expect the impact of environmental carry-over effects on population dynamics to be most recognizable when the difference between habitat qualities is clear, initial population sizes are small, and population structure is cohort based so that many individuals have similar developmental histories. Given these conditions, carry-over effects are likely to be especially important for species that have a limited or patchy distribution at the regional scale or when patches are frequently disturbed or go extinct and are recolonized. Thus, carry-over effects are also likely to play an important role in the dynamics of rare species and invasive species at their invasion front. Under certain habitat and population structures, however, carry-over effects could be regionally important for very abundant species as well. The ubiquity of variation in habitat quality, disturbance, and dispersal suggests that carry-over effects could affect the dynamics of populations to the point of producing alternative stable states in similar habitats. Our results thus highlight the importance of incorporating carry-over effects into models of population dynamics to more accurately predict the context-dependent dynamics of natural systems.

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APPENDIX

Average Beetle Mass across 19 Weeks

The effects of carry over from the natal and colonized habitats were tested on average beetle mass in each colonized replicate using a repeated-measures linear mixed effects model with continuous first-order autoregressive correlations and random effects of population ID and fixed effects of natal habitat, colonization habitat, time, and their interactions. A nonsignificant third-order interaction was removed from this test, and the model was run again.

Across the 19 weeks of the experiment, the average mass of beetles in colonization habitat fluctuated (fig. A1). Natal habitat quality ($F_{1,56} = 16.8$, $P < .001$) and time ($F_{1,357} = 42.07$, $P < .001$) were significantly associated with beetle mass across the 19 weeks of the experiment, while colonization habitat was not a significant first-order effect ($F_{1,56} = 1.2$, $P = .278$). Colonization habitat did, however, affect adult beetle mass, but this depended on the natal habitat of colonists (colonization × natal habitat $F_{1,56} = 4.52$, $P = .0379$) and time of population censuses (colonization habitat × time $F_{1,357} = 12.12$, $P < .001$). The effect of natal habitat did not vary across the different population censuses (natal habitat × time $F_{1,357} = 0.78$, $P = .377$). Average beetles in low-quality habitat populations founded by low-quality colonizers remained roughly the same low mass during the experiment (initial mass of 2.07 ± 0.028 mg to a final mass of 2.08 ± 0.054 mg each). Interestingly, the average mass of a beetle in a population in the same low-quality habitat that was colonized by high-quality dispersers stayed high and increased slightly by the end of the experiment (initial mass 2.14 ± 0.02 mg standard error, final mass 2.2 ± 0.015 mg each). This was despite average adult population size tripling with all new individuals developing in low-quality habitat.

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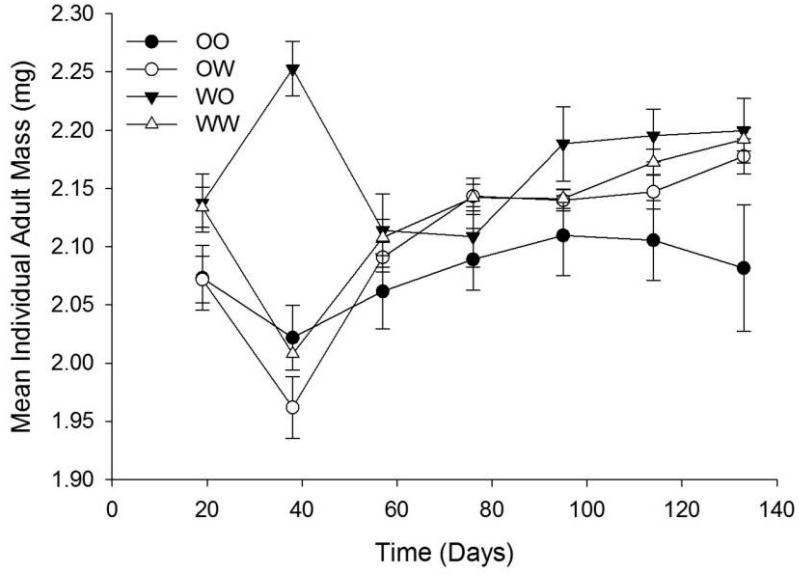

Figure A1: Mean individual adult mass of flour beetles from populations with different habitat histories over 19 weeks. Error bars are ±1 SE.

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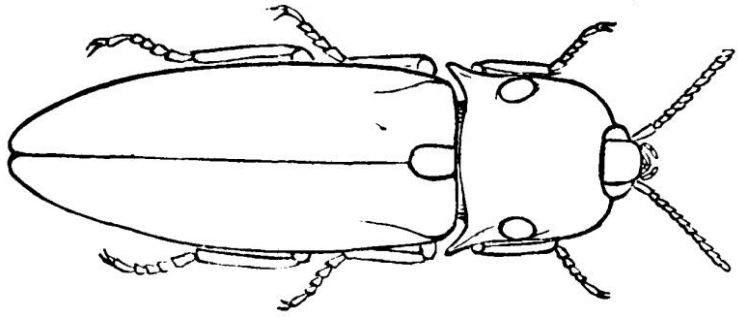

"But few of the many thousands of organized beings that cover the earth are endowed with the power of becoming luminous, and it is because their number is so limited, and consequently that they fall so seldom under our observation, that our wonder is so great upon beholding them. ... At the head of the list of light-giving creatures, and far exceeding them all in the amount and intensity of its phosphorescence, stands the West Indian Fire Beetle." From"The Cucuyo; or, West Indian Fire Beetle" by G. A. Perkins (*American Naturalist*, 1868, 2:422–424).

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