

AN EXPERIMENTAL TEST OF FRAGMENTATION AND LOSS OF HABITAT WITH *ORYZAEPHILUS SURINAMENSIS*

J. S. BANCROFT¹ AND P. TURCHIN

Department of Ecology and Evolutionary Biology, U-42 University of Connecticut, Storrs, Connecticut 06269

Abstract. This research used a model experimental system to explore the joint effects of resource fragmentation and resource deterioration on population dynamics. The system provides a rapid test of conservation theory and can aid in planning for large and expensive studies. The investigation subjected the sawtooth grain beetle, *Oryzaephilus surinamensis* (L.), to five experiments in which population abundance was monitored over time. Metapopulations were created by connecting adjacent vials of flour with rubber tubes. The metapopulations were arranged in rings, and food was replenished at two-week intervals. The experiments examined populations in (1) habitats becoming increasingly fragmented, (2) dynamically fragmenting structure with concurrent loss of resources over time, (3) static structure, dynamic resource loss and differing numbers of patches, (4) static structural arrangements with dynamic resource loss that mimic resource deterioration and destruction, and (5) static arrangements of connected fragments with an equal total amount of food in a few large patches or several small patches. Time series of stage-specific abundances were compared in repeated-measures ANOVA. The results show that populations respond in nonlinear ways to both the amount of food and area provided. Within a confined area, when food is plentiful, individual interaction limits population abundance. When the amount of food is reduced, population abundance becomes food dependent. Immediate increase in immature abundance was a characteristic of fragmentation while a delayed reduction of adults was characteristic of food reduction. The stage-specific interaction at intermediate food levels shows birth and death processes that control this system, and elucidates the relationship between area and food that is integral to the dynamics of patchy populations.

Key words: grain beetle; habitat deterioration; habitat fragmentation; *Oryzaephilus surinamensis*; patch dynamics.

INTRODUCTION

Ecologists are often required to develop plans for managing endangered species where few data are available and population dynamics are poorly understood (McKelvey et al. 1993, Lamberson et al. 1994, Wallinga 1995). It is often not possible to wait until more data are collected because decisions must be made rapidly. These are the situations where general guidance from conservation theory is invaluable. However, we cannot yet claim a general understanding of the effects of habitat size, habitat quality, and patch arrangement on population dynamics of rare or endangered species (Fahrig 1997). The progress has been slow because field experimentation takes years or even decades (Debinski and Holt 2000). Laboratory experiments provide a useful approach to speeding up theory development. Popularly known as “ecology in the bottle” (e.g., Kareiva 1989, Lawler and Morin 1995), this strategy was used by empirical ecologists, such as Park et al. (1965) and Gause (1934). These empirical studies tested the ecological theory developed by Lotka (1925) and Vol-

terra (1926). The same strategy should serve us equally well during the development of the still immature field of spatial conservation biology (see Forney and Gilpin 1989, Lawler and Morin 1993, Collinge 1996, Burkey 1997). In particular, experimental measurements of the effects of space on population dynamics can inform further theoretical development in spatial conservation biology (Caughley 1994).

The main goal of our experiments was to gain an understanding of the joint effects of habitat fragmentation and habitat deterioration. This is difficult to do in the field because “habitat loss” usually affects several variables in a correlated manner (Andren 1994, Fahrig 1997), so we designed controlled experiments to disentangle these coincident effects. We used a system based on the beetle *Oryzaephilus surinamensis*, a grain pest whose short generation time and simple food requirements make it a convenient subject for laboratory experimentation. The model system was subjected to a series of laboratory experiments to tease apart the interacting effects of reduction and subdivision of food.

In practice, habitat loss is a complex manipulation of the environment and resources used by a population. It typically involves (1) habitat destruction, decrease in the total amount of resource available; (2) habitat deterioration, decrease in the density or quality of resource, and (3) habitat subdivision, decrease in spatial

Manuscript received 4 January 2001; revised 17 July 2002; accepted 4 August 2002; final version received 7 November 2002. Corresponding Editor: R. M. Nisbet.

¹ Present address: 17053 N. Shafter Ave., Shafter, California 96263. E-mail: jsb95@yahoo.com

connectivity of resource patches. Our approach was to design experiments to manipulate each of these characteristics in turn, while keeping others constant. We imposed patch architectures with habitat subdivision that was static or dynamic, which mimics barriers with little loss of habitat (e.g., roads). Food resources were held constant or reduced over time to mimic habitat deterioration, and we eliminated food in patches to represent destroyed habitat. We also used poor-quality food to imitate habitat unsuitable for reproduction. In all experiments, we quantified the effects of manipulations in patch structure and food availability with a complete census of *O. surinamensis*.

Research on the regulation and forecasting of populations has moved beyond birth and death processes and into the role of landscape arrangement and the biology of movement (see Hanski and Gilpin 1997, Tilman and Kareiva 1997, Turchin 1998). Conservation managers promote the stability and persistence of a population by facilitating larger populations and patches that are connected via dispersal. The present work provides time series data to test these predictions for spatial ecology. We describe a new system for rapidly testing the importance of environmental variables and their interaction on dynamics, and use the system to show the patterns of population change in response to environmental perturbation. The *O. surinamensis* system aids the development of a general understanding of population dynamics because the empirical time-series data can test the relationship between spatiotemporal population abundance and the behavioral mechanisms that regulate populations. These patterns can guide the design of monitoring programs to best detect population changes in small, declining populations.

In experiment 1, the "landscapes" had static structure over time. Treatments did not differ in the total amount of food, but food was subdivided into different numbers of patches (see Fig. 1). In addition, we manipulated spatial arrangement of habitat (high-quality food) and nonhabitat (poor-quality food) patches. The treatments contrasted habitat patches that were clumped with those that were evenly interspersed with nonhabitat patches. In experiments 2–5, landscapes were modified dynamically. In experiment 2, the total amount of food in the system was constant (similar to experiment 1), and we measured the effects of increasing degree of fragmentation (habitat divided into multiple patches) on population numbers. The control was nonfragmented habitat, all resources in a single patch. In experiments 3, 4, and 5, we investigated the effect of declining food resources in various fragmentation settings. Experiment 3 was similar to experiment 2, because it addressed the effect of increased fragmentation on dynamics, but in the context of decreasing food resources. In experiment 4, the degree of fragmentation did not increase in each treatment, but equal-sized patches within total populations were subjected to synchronously declining food. We wanted to under-

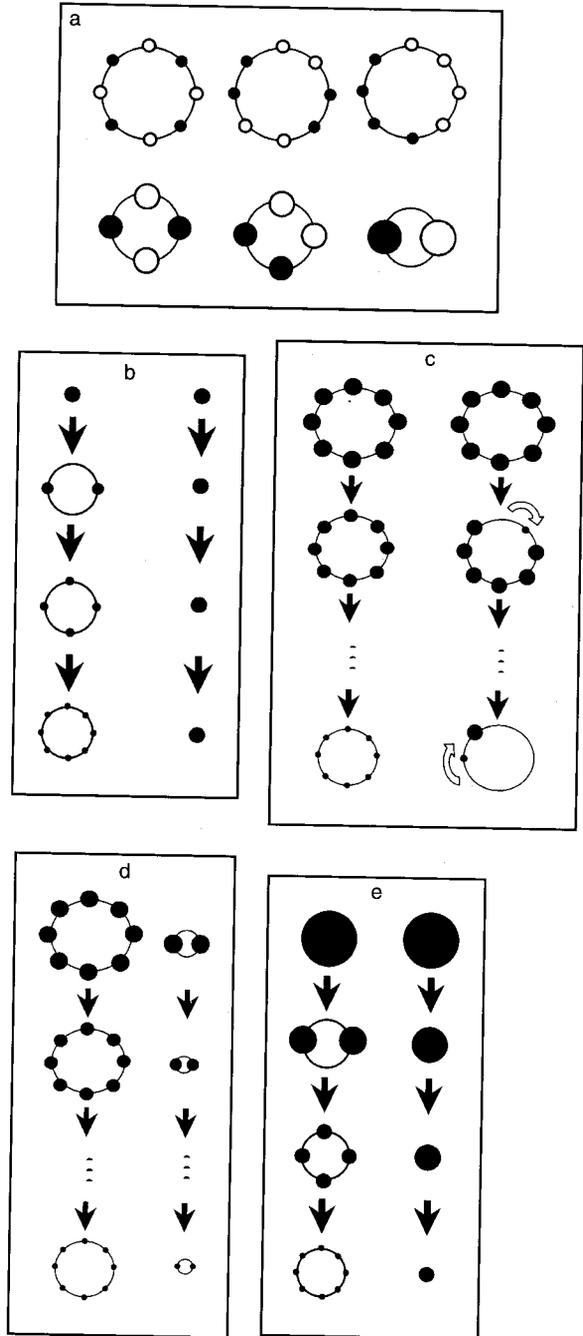


FIG. 1. Experimental treatments. Solid circles represent high-quality food, and hollow circles represent poor-quality food. Arrows represent time progression. (a) Design to examine effects of patch size and arrangement in subdivided populations with equal total resource. (b) Design to examine effects of fragmentation of patch populations with equal total resource. (c) Design to examine effects of co-occurring fragmentation and loss in patch populations with equal total resource. (d) Design to examine effects of the number of patches on patch populations when patch food is reduced over time. (e) Design to examine effects of contrasting types of food reduction on total population dynamics. Food is reduced evenly over time as in habitat deterioration or in "patch-by-patch" reduction as in habitat destruction.

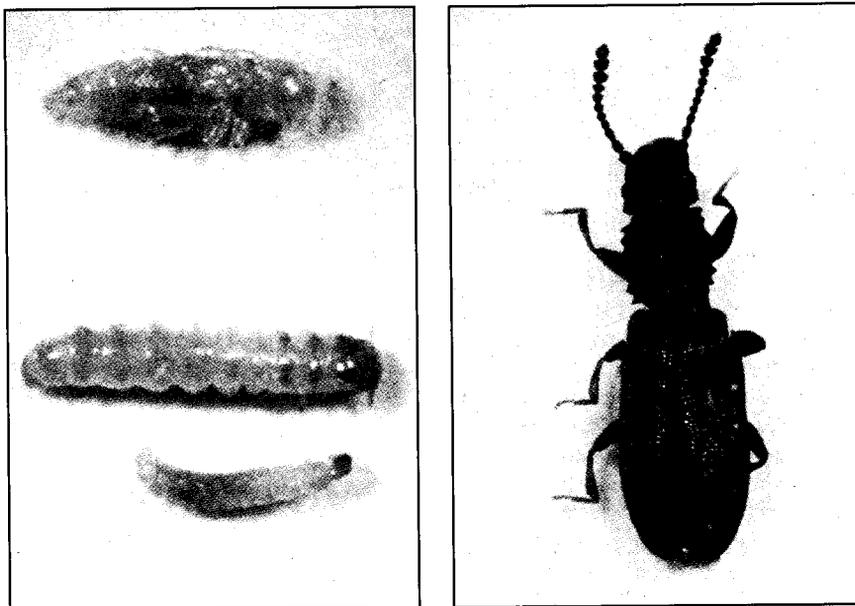


PLATE 1. The stages of the *O. surinamensis* are (left, from top to bottom) pupa, fourth instar, second instar; and (right) adult. Pupa is shown in ventral view, and fourth and second instar are dorsal views.

stand how the number of patches would affect beetle abundances *within* patches. The fifth experiment tested the effect of spatial extent of habitat loss: spatially uniform deterioration vs. "patch-by-patch" destruction. The partitioning of food among patches differed between treatments, but the total amount of food in each treatment was equal at a given time.

METHODS

The empirical system

Oryzaephilus surinamensis belongs to the subfamily Silvanidae of Cucujidae (Borror et al. 1989). It is a worldwide pest of stored grain and can rapidly increase in numbers if unchecked. Its larval stage usually passes through four instars (Collins et al. 1989; see Plate 1). In our system, development lasts ~3, 13, and 5 d for the egg, larval, and pupal stages, respectively. A number of studies of *O. surinamensis* have characterized reproduction and mortality at various temperatures and humidities and in various grains (Back 1926, Thomas 1940, Howe 1956, Prus 1966, Ciesielska 1990, Jacob and Fleming 1989, Beckett and Evans 1994). Bancroft (2001) has previously measured the rates of oviposition, mortality, and dispersal in response to conspecific density. With ample resources, females lay ~1 egg/d and live several months. Beetles readily dig through the food, which becomes degraded by feces over time. As food becomes degraded, oviposition and larval growth will stop and cannibalism will reduce survival. The dispersal rate is quite low in this system (3×10^{-5} adults per adult per day), and crowded conditions with limited food are known to induce dispersal. Within single con-

tainers, starvation and cannibalism are known to be the mechanisms that regulate abundance in this system.

General methods

We conducted all experiments in an environmental chamber kept at $33 \pm 1^\circ\text{C}$ and $65 \pm 10\%$ R.H. The "habitat" was 95% wheat flour and 5% brewers' yeast by mass (Park 1965). This diet is highly favorable for survival and reproduction and allows indefinite maintenance of beetle populations under our laboratory conditions. In addition, we used "nonhabitat" consisting of powdered cane sugar (dextrose). This diet sustains adults but prevents successful reproduction. We used black film vials (2.54 cm diameter) as "patches". Every two weeks or about half the generation time (Bancroft 2001), investigators sieved and counted all larvae, pupae, and adults. Live beetles were placed into a clean vial with fresh food. Patches were connected in "stepping stone" fashion with black latex tubes that allowed beetles to pass to the neighboring patches.

We normalized distributions of adults, pupae, and larvae with a $\ln(x + 1)$ transform of abundance. Populations in which patches died out were excluded from analyses of patch dynamics. We used a repeated-measures analysis of variance (SAS 1998) to compare populations in the treatments unless otherwise noted. Where treatment effects were significant ($P < 0.05$), we employed Tukey's hsd to identify significant differences among treatment levels. The first experiment established long-term abundance among stages within a patch; the mean values were used to estimate stable initial conditions in experiments 2–5.

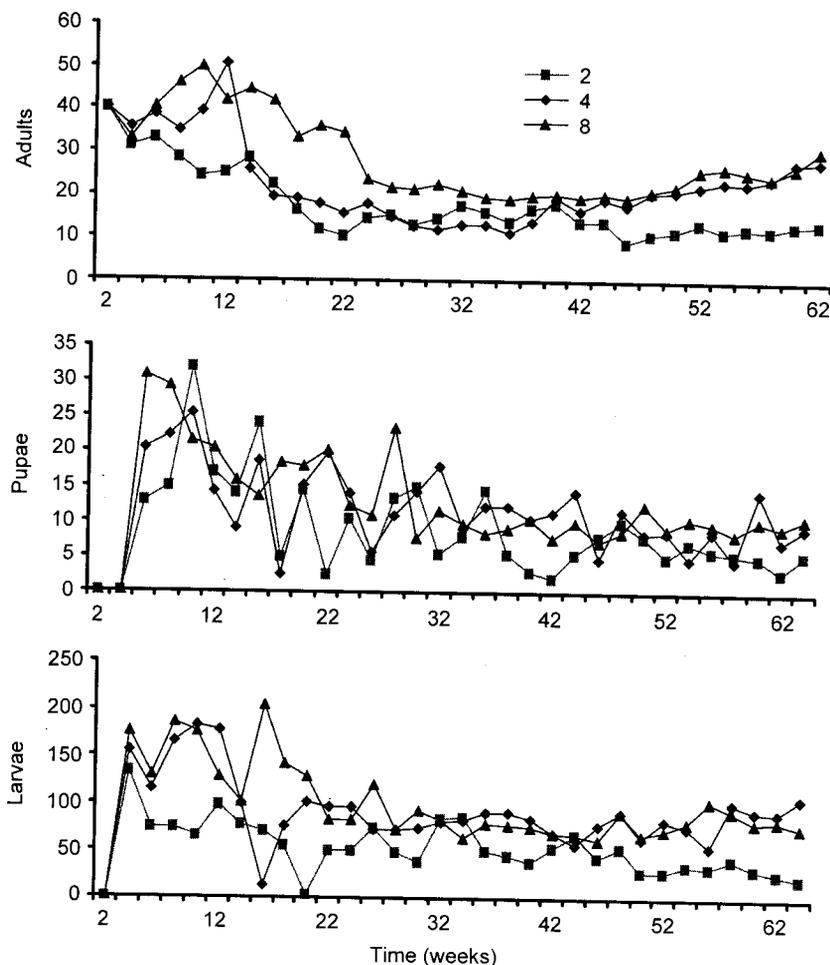


FIG. 2. Average stage abundance for experiment 1, with two-, four-, and eight-patch experimental treatments (key to symbols in top panel: "2" = two-patch treatment, etc.). Abundances in four-patch and eight-patch treatments were greater than those in the two-patch treatment.

Experiment 1: Effects of fragmentation and spatial arrangement

Methods.—The experiment measured how total metapopulation abundance is affected by two variables, spatial arrangement and number of patches in a metapopulation (see Fig. 1). We equally divided a total of one gram of high-quality and one gram of poor-quality food among patches in each metapopulation (see *General methods*). Beetles inhabited two, four, or eight interconnected patches. A two-patch metapopulation had one gram of food in each patch. A four-patch metapopulation had one-half gram of food in each patch: two with wheat-yeast and two with sugar. An eight-patch metapopulation had one-quarter gram of food in each patch: four with wheat-yeast and four with sugar. With the second variable, we compared sequences of clumped patches in of the same food type to interspersed patches of alternating food types. We nested the arrangement of patches within the number of patches because, for example, a two-patch system had to

alternate the two food types. We monitored two replicates for each of the six treatments. The effects on total abundance were also linked to correlations in patch abundance. We calculated autocorrelations of abundance for interconnected patches. The correlation coefficients for patch censuses were calculated for lags across time and space for each population ring, and values >0.2 were considered significant. Finally, we calculated the coefficient of variation ($CV = \text{ratio of standard deviation to mean}$) for stabilized populations of each patch and population to compare the relative fluctuation of abundances among the treatments.

Results.—Each time series had 32 censuses over 16 mo. All beetles in patches containing sugar died out before six months, and no beetles were subsequently found to disperse into these patches. Total abundance varied significantly with patch size ($P < 0.01$, see Fig. 2), but surprisingly, the populations fragmented into many small patches had higher abundance than those with few large patches. Paired comparisons showed

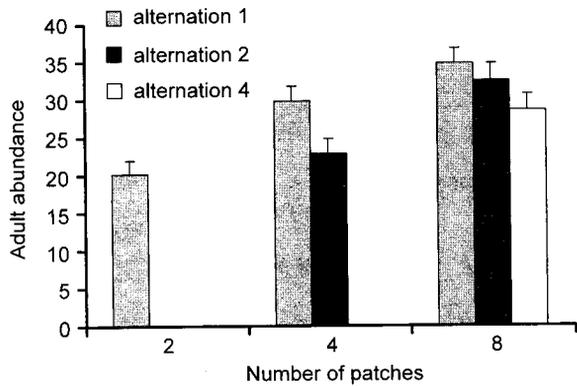


FIG. 3. Average adult abundance in experiment 1, categorized by sequential alternation of patch quality and number of patches in the metapopulation. Error bars show $+1$ SE. Greater abundance was observed in even alternating patches and, to much greater extent, in populations with larger numbers of patches (more area).

that the two-patch treatment had significantly fewer beetles than either of the four-patch and eight-patch treatments (both $P < 0.01$), but abundance between the four-patch and eight-patch treatments did not differ ($P = 0.06$). The increase in alternation structure caused a mild decrease in beetle abundance ($P < 0.01$, see Fig. 3), but paired comparisons within the size categories showed no effect of alternation structure ($P = 0.11$). Larger area per unit of food, and to a lesser extent the even distribution of high-quality food patches, caused larger populations.

The relative independence of patches was also explored with spatiotemporal autocorrelation, and we only report coefficients for adults because their results were the strongest. The temporal correlation in the large 1-g patch began at $r = 0.58$ at lag 1 and declined to $r = 0.19$ at lag 5. All autocorrelation coefficients exhibited an exponential decay over time lags, which is characteristic of an autoregressive (breeding) process. The autocorrelation coefficients did not differ due to alternation structure but did show a strong pattern according to the size of the population's patches. The 0.5-g patches had significant temporal correlation (>0.2) to lag eight or four months. However, the small, 0.25-g patches had significant correlation until lag 12. The pattern across space was the opposite. The correlation of first spatial lag was $r = 0.42$ in 0.5-g patches and only $r = 0.18$ in the 0.25-g patches. Larger patches had greater spatial autocorrelation but lower temporal autocorrelation.

Each cv was calculated from time step 12 on for both patches and total populations. Because the cv of each beetle stage was included in the analysis, the means reported below are stage adjusted (least-squares mean). For patch abundance, the cv values did not differ among patch sizes ($P = 0.18$), but were significantly different among alternation structures ($P < 0.01$). Coefficients of variation were 0.80, 0.54, and 0.51 for four-patch, two-patch, and one-patch alter-

nations. Paired comparisons showed that the four-patch cv was greater than the two- or one-patch alternation. However, total populations showed a different cv according to patch size ($P < 0.01$) but not alternation structure ($P = 0.55$). Coefficients of variation were 0.51, 0.21, and 0.16 for eight-patch, four-patch, and two-patch populations. Paired comparisons showed that the eight-patch cv was greater than that for the four- or two-patch alternation. Larger patches had a lower cv, and contiguous patches of high-quality diet had a greater cv.

Experiment 2: Effects of fragmentation, constant amount of food

Methods.—This experiment tested whether increasing habitat fragmentation without habitat loss negatively affects population abundance. These time-varying treatments, as opposed to experiment 1, show the time varying response of *O. surinamensis* stage abundance. Specifically, we subdivided the same amount of food into progressively greater numbers of patches. Both the experimental and control treatments (see Fig. 1) started in one patch with 0.4 g of food. Pilot experiments suggested that 0.4 g of food/vial is enough to maintain a stable beetle population over many generations. We inoculated each patch with 12 adults and 48 larvae. The experimental treatment consisted of doubling the number of patches for the first three censuses. At each doubling, we equally split the replacement food and beetle population in each patch between two new patches (see Fig. 1). Thus, after the first split there were two patches with 0.2 g of food in each, after the next split there were four patches with 0.1 g, and finally there were eight patches with 0.05 g in each vial. We censused the system for three further periods to check for long-term effects. In the control treatment, we simply placed the existing population into the new vial supplied with 0.4 g of food. Each treatment had five replicates.

Results.—Progressively subdivided populations had greater abundance than nonfragmented populations ($P < 0.01$ level, see Fig. 4). By the fourth census, pupae had significantly greater abundance in the fragmentation treatment than that in the nonfragmented control ($P < 0.01$). Large variation in immature abundance was in contrast to the stable, delayed divergence in adult numbers.

Experiment 3: Effects of fragmentation, decreasing amount of food

Methods.—This experiment mimicked human activities that destroy and fracture habitat that wild animals use. We subjected 10 populations to declining food resources. Five nonfragmented populations were compared to five undergoing habitat fragmentation (see Fig. 1). We initiated all populations with 3.2 g food, 37 adults, and 100 larvae. At each census, we halved the replacement food but did not remove beetles. In the non-subdivided populations, the amount replacement

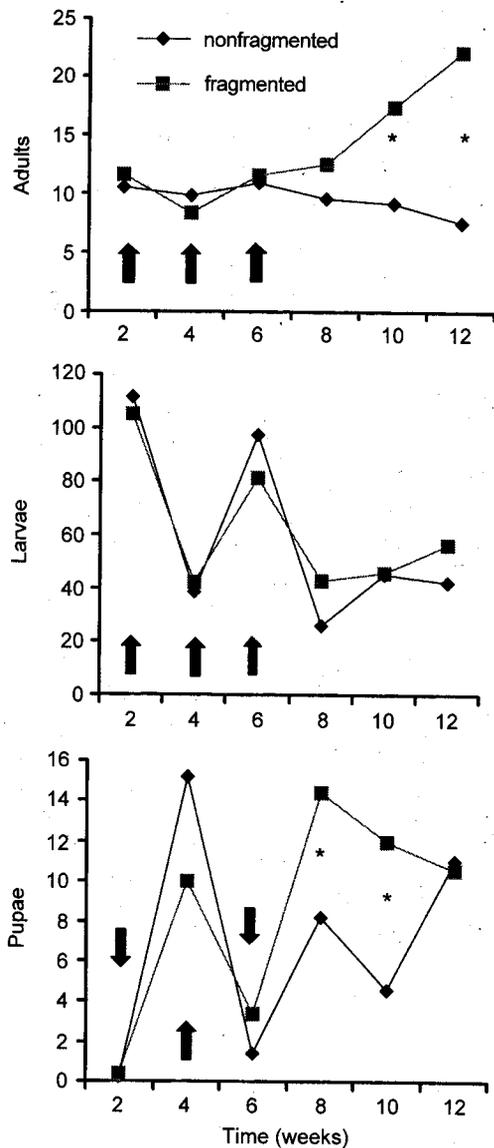


FIG. 4. Average abundance for experiment 2, with adults, larvae, and pupae for the experiment's control and treatment. An asterisk (*) denotes treatment difference at that census interval ($P < 0.05$). Arrows indicate fragmentation treatments. Strong effects of fragmentation appeared well after the fragmentation stopped.

food after three census periods was maintained at 0.4 g for three more census periods. In the fragmented populations, we split the beetles between two connected patches of 0.8 g food each. We repeated this splitting procedure through eight-patch metapopulations with 0.05 g of food. We censused the eight-patch metapopulation three more times. This procedure tested the combined effects of fragmentation and resource loss on *O. surinamensis* abundance.

Results.—The fragmented system had significantly larger populations than nonfragmented populations ($P < 0.01$, see Fig. 5). Pupal abundance was significantly

greater in the fragmentation treatment by the third census ($P < 0.01$), while adult and larval abundance in fragmented populations did not become significantly greater than the controls after the fifth and sixth census, respectively (both $P < 0.01$). The effect of spatial subdivision counteracted the effect of reduced food resources.

Experiment 4: Effects of number of patches in a metapopulation on patch abundance, decreasing amount of food

Methods.—This experiment tested the effects of the number of interconnected patches on *O. surinamensis* abundance within patches (see Fig. 1). The first treatment had five replicates of eight-patch systems. The other treatment had 10 replicates of two-patch systems. Each patch started with 0.25 g of food, 10 adults, and 20 larvae. At each census, we decreased the amount of food by 0.05 g per patch. The reduction in food stopped with 0.05 g per patch and three censuses were taken at that level.

Results.—Effects of number of *O. surinamensis* per patch differed significantly between the two-patch and eight-patch treatments ($P < 0.01$, see Fig. 6). Interestingly, we found no clear pattern showing consistently greater populations in one treatment. Decline in abundance for eight-patch populations was delayed compared to two-patch populations. Unlike previous experiments, no differences were detected after the reduction in food stopped.

Experiment 5: Effects of even reduction vs. patch by patch destruction

Methods.—This experiment contrasted the effects of even resource deterioration in all the patches of a metapopulation vs. contiguous destruction of entire patches (see Fig. 1). We set up 10 eight-patch metapopulations with 0.25 g of food per patch. Each patch was initiated with 10 adults and 20 larvae. Each treatment had five replicates. In one treatment, we reduced the amount of food in each patch at a rate of 0.05 g per patch at each census. In the other treatment, we eliminated food from patches, one at a time. We lowered the amount of the metapopulation's replacement food by 0.4 g per census and repeated this procedure sequentially from patch to patch. After four censuses, three more censuses were taken with 0.4 g remaining to observe long term effects.

Results.—Contiguous loss of resource from patch to patch caused significantly lower populations than reduction in all patches ($P < 0.01$, see Fig. 7). The abundance of larvae was significantly greater in the first census ($P < 0.01$). After the third census, adult abundance in the treatment with even reduction became greater than the treatment with contiguous destruction ($P < 0.01$). Numbers of larvae and pupae gave an early indication of treatment differences that was opposite of the final census.

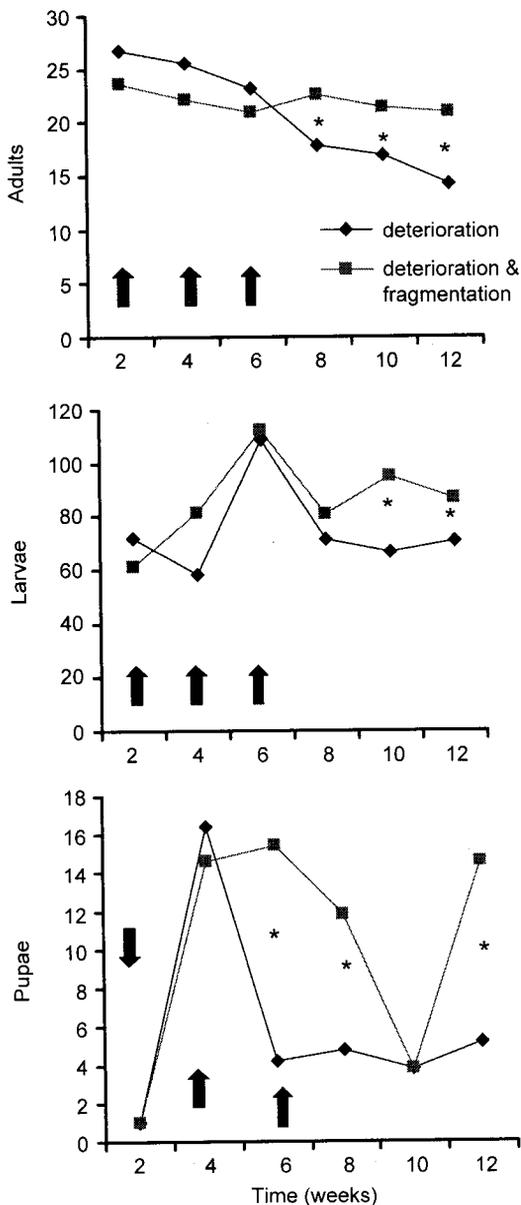


FIG. 5. Average abundance for experiment 3, with number of adults, larvae, and pupae for the experiment's control and treatment. An asterisk (*) denotes treatment difference at that census interval ($P < 0.05$). Arrows indicate food reduction and fragmentation treatments. Pupal abundance was an early indicator of treatment differences with fragmentation somewhat counteracting resource reduction.

General results across experiments

Only 6% of all patches (15 of 247) in our experiments died out, and all were low food treatments. Six extinctions occurred in 0.25 g patches from experiment 1, and the rest occurred in 0.05 g patches in experiments 2–5.

We estimated rates of birth and death in each replicate of each experiment (Table 1). Again, we used a repeated-measures analysis of variance to compare

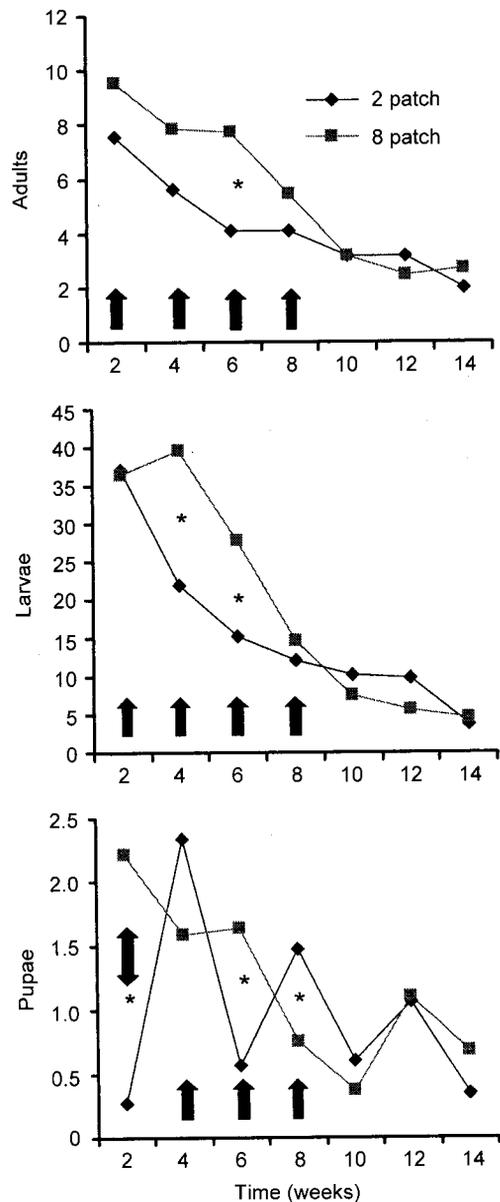


FIG. 6. Average abundance for experiment 4, with adults, larvae, and pupae for the 2- and 8-vial experimental treatment rings. An asterisk (*) denotes treatment difference at that census interval ($P < 0.05$). Arrows indicate food reduction treatments. Immature stages indicated treatment differences during food reduction but not after abundance stabilized.

treatments. We analyzed the rates of mortality (using arcsine square-root transform). In experiment 1, spatial subdivision and patch arrangement had no significant effect on any of the four rates. Reproduction from the fragmentation experiments (experiments 2 and 3) were analyzed together to see if the rates differed between the experiments as well as between each experiment's treatment and its control. Of the four rates in Table 1, only per capita rate of larval productivity showed a significant difference ($P < 0.01$), with a large increase

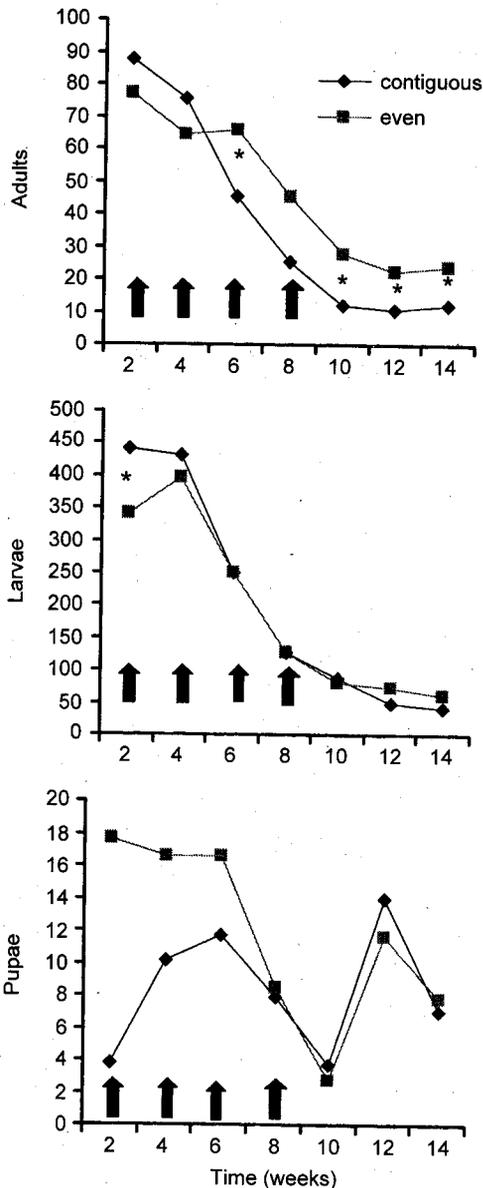


FIG. 7. Average abundance for experiment 4, with adults, larvae, and pupae for even and contiguous reduction in experimental treatment rings. An asterisk (*) denotes treatment difference at that census interval ($P < 0.05$). Arrows indicate food reduction treatments. Larval abundance in the first census gave a false indication of final abundance differences.

in the fragmentation treatment at the second census (see Fig. 8a). In experiment 4, the number of patches caused no significant rate changes. Rates of adult mortality, larval production showed a strong effect of the type of loss ($P < 0.01$ and $P = 0.02$, respectively, see Fig. 8b and 8c). Mortality rate in the deterioration treatment was half that of the destruction treatment.

DISCUSSION

Our experiments were designed with the assumption that food was the limiting resource. We obtained puzzling results because, contrary to our expectations, fragmented populations had larger abundances than nonfragmented populations. In hindsight, there are actually two resources: food and space. Either food or space could be the resource setting population abundance depending on which resource is in short supply. When food is plentiful, populations build up, then crowding causes beetles to interfere with one another. Splitting food into smaller packages, by increasing the number of patches, relieves the intensity of the competition for space. As a result, the total abundance in the metapopulation increases even though the amount of food is kept constant. However, if food is split up into packages that are too small, there is not enough food to propagate a minimum number of individuals necessary to sustain a population in each patch. In short, our results delineate the resource trade-off between amount of food and amount of space.

The effect of subdivided food in the experiments caused a pattern in beetle abundances that seems to challenge predictions of conservation theory. The theory suggests that contiguous habitat will maintain larger populations than fragmented habitat (Doak et al. 1992, Soule and Simberloff 1986). The usual rationale is that in small fragmented populations, organisms have trouble finding mates (Park 1933). However, we found greater survival rates in fragmented patches. Within patches, *Orizaephilus surinamensis* beetles interact freely and utilize any food that is provided (Bancroft 2001). However, with larger amount of food per patch, greater beetle crowding increases cannibalism by active stages of beetles on inactive stages. The pattern of alternation structure suggests that dispersal to neighboring patches of high quality lowers abundance. The complex effects of population synchrony vary among biological systems, and no simple generalizations have

TABLE 1. Per capita vital statistics. Equations were used on data from each experiment. Overall average and standard deviation are shown for experiment 1.

Vital rate	Equation†	Average	SD
Larvae production	L_t/A_{t-1}	3.84	3.51
Pupae production	P_t/L_{t-1}	0.019	0.45
Pupal survival	$1 - ((A_t + D_t - A_{t-1})/P_{t-1})$	0.35	0.40
Adult mortality	D_t/A_{t-1}	0.28	0.28

† Key to variables: A = adults, D = dead, L = larvae, P = Pupae, t = time. Where division by zero occurred the value was omitted.

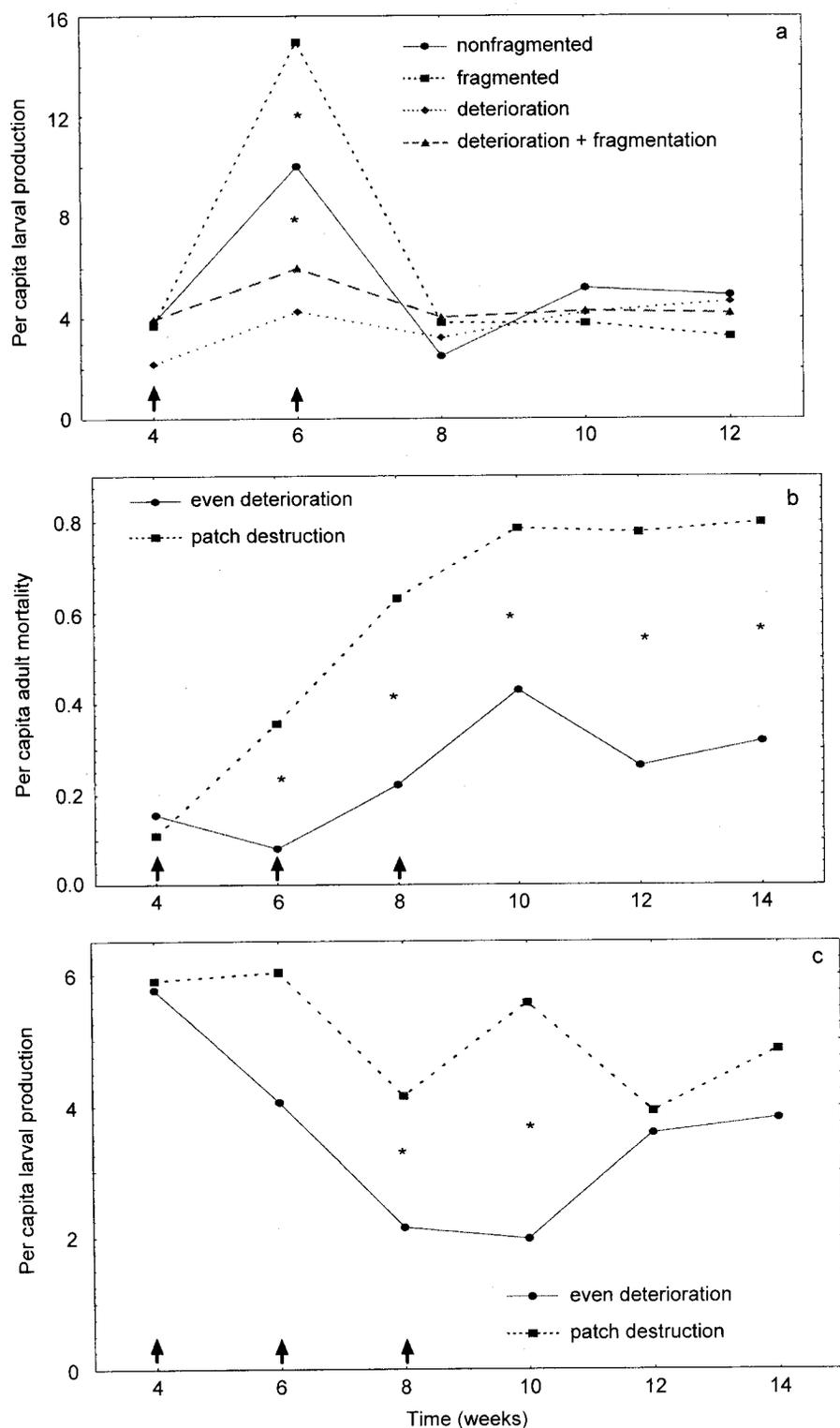


FIG. 8. (a) Rates of larval production in experiments 1 and 2. (b) Rates of adult mortality in experiment 4. (c) Rates of larval production in experiment 4. An asterisk (*) denotes treatment difference at that census interval ($P < 0.05$). Arrows indicate food reduction treatments. Larval production showed a characteristic increase due to fragmentation, and adult mortality and larval production both provide strong indications for food reduction.

yet been discovered (Matter 1997, Lande et al. 1999). Dispersal behavior links with the spatiotemporal autocorrelation of patches and with total population. Surprisingly, the small dispersal rate caused a significant synchrony among patches and affected abundance of the entire population. The strongest temporal correlation was found in 0.25 g patches, which suggests longer adult longevity in these relatively uncrowded patches. *O. surinamensis* has a strong dispersal response to crowding (Bancroft 2001), and this corroborates our observation of more than twice the spatial correlation in the crowded 0.5 g patches. Finally, the larger CV in small patches supports our patch extinction results and conservation efforts to increase populations abundance as a buffer against extinction risk.

In the fragmentation experiments (2 and 3), the response in the number of pupae was the earliest indication that the treatments differed from the controls. Although adult populations varied little the effects on immature abundance was pronounced. The dampened fluctuations at the end of the experiment suggested that the immature stages exhibited transient dynamics, although we can not rule out more complex dynamics (oscillations and chaos). The added area per unit food suggests beetles pupate more successfully at low adult densities. This is corroborated by experiments with refugia used by *Tribolium castaneum* pupae to prevent cannibalism by adults (Beckett and Evans 1994, Benoit et al. 1998). Finally, adult abundance diverged from controls only after fragmentation treatments ceased. Both the number of patches and type of loss experiments (4 and 5) contrasted with the fragmentation experiments. Experiment 5, which contrasted habitat deterioration and destruction, showed that populations with degraded habitat generally had greater abundance than those with contiguous loss; these results agree with experiments suggesting that a large amount of deteriorated habitat may be preferable to small amounts of prime habitat (Ostfeld et al. 1985, Robinson et al. 1992). Both experiments 4 and 5 showed that changes in abundance of immatures (and for experiment 5, adults) may provide an early warning to the occurrence of resource perturbation. These experiments demonstrate a characteristic pattern in stage abundance in response to the resource perturbation (Hastings and Higgins 1994). This is encouraging because characteristic differences in population abundance may exist for other systems, which can facilitate mechanistic understanding of their decline.

Our results show this is a sensitive method for detecting changes in local populations in conjunction with resource perturbations. Changes in the vital rates (Fig. 8) provided the first indication that the population was responding to increased area. The rates of reproduction show a significant increase that was not detected in the analysis of stage abundance (Figs. 4 and 8a). The sudden increase in immature production would be expected in a species that is spreading out from a confined area.

We believe that low larval production in the deterioration treatment was due to the lingering survival of adults beyond reproductive age. In comparison, adult mortality was an early indicator of patch destruction, while patch deterioration caused fluctuations around the mean mortality (Fig. 8b). In natural systems, census of immature and adults stages may be very difficult, and the sampling error associated with each will make these calculations difficult. However, monitoring individual vital rates is the only option in many species, and our results show that vital rates are a good indicator of environmental change.

The pattern of decline in our experiments suggests how habitat managers can counteract similar patterns in endangered species. By turning our results around, we can generalize for survey design and management actions. Decline in immature abundance suggests area reduction and efforts to increase space and patch connectivity may be of primary importance. Conversely, greater population variation (due to patch isolation) and loss of reproductive stages may suggest a decline in habitat quality. Clearly, the strength of these effects depend on factors in the *O. surinamensis* systems such as crowding, mobility of adults, and the relative importance of food quality for immatures and reproductives. Because these experiments are not possible with endangered species, we must rely on experimental tests to understand how key mechanisms that mediate regional abundance link to population trends and environmental perturbation (Eveleigh and Chant 1982, Caro and Laurenson 1994, Caughley 1994).

In field populations, the cause of differences among mean abundances may not be known. Generally, populations that fluctuate more (higher variance) may have a lower means because they must grow out of low ebbs (Taylor 1961, Ruel and Ayers 1999). In experiment 1, means of population variance for transformed adult abundance were 0.26, 0.28, and 0.17 for two-, four-, and eight-patch populations, respectively. A simple ANOVA of our three patch sizes did not show differences among variances ($P = 0.81$). Before applying the variance stabilizing transformation, there was a common increasing trend in variance with mean. Although variance may account for differences in mean abundance of field systems, our experiments suggest deeper understanding of the interaction between species and environmental perturbation would be more predictive (Sawyer 1989, Yamamura 1990).

This system is amenable to studies of environmental perturbation that cause population decline. The importance of catastrophes has become prevalent in conservation biology and this *O. surinamensis* system is well suited for tests of catastrophe theory (Lockwood and Lockwood 1991, Lande 1993, Akcakaya and Baur 1996, Root 1998). Our experiments controlled subdivision and patch size with balanced treatments, but this system provides a powerful method to investigate source-sink dynamics (Diffendorfer 1998). Patches of

differing number and amount of food could be connected, and the timing of food replenishment could be altered in order to detect effects among patches with strong asymmetries in resources. Furthermore, demographic variability and population genetics can easily be monitored in time series experiments. The extinction vortex for small populations is caused by the positive feedback of individual variation in reproductive success and expression of deleterious alleles. Experimental manipulation of *O. surinamensis* is simple and can provide a definitive link from behavior (Pierce et al. 1983) and genetics (Brown et al. 1997) to the emergent dynamics on a population.

Conservation theory stands to benefit from empirical tests (DeAngelis and Gross 1992, Debinski and Holt 2000). We have linked theory to conservation biology using controlled experiments that cannot be performed with endangered species or in landscape-sized systems. Natural populations are increasingly subject to habitat deterioration, destruction, and fragmentation. Our system acts as an analogy for studying of landscape-level resource perturbations and provides quantitative measures of the effects of fragmented habitat patches. We show the trade off between resources, and how dispersal creates strong effects on population abundance when induced by crowding. We suggest that scientists working on other systems carefully consider possible limiting resources and their interacting effects (Tilman 1988, O'Neill 1989). Obviously, long-term monitoring and knowledge of the causes of population change will be critical for informed management action. These experiments complement monitoring efforts by promoting data collection that may test overlooked resource interactions and may identify mechanisms of regional population regulation. In general, our approach provides empirical evidence for theory development that improves our ability to rapidly assess population dynamics.

ACKNOWLEDGMENTS

Voucher specimens of *O. surinamensis* were deposited in the University of Connecticut Research Collection of Insects. We thank two anonymous reviewers for comments that helped improve the paper.

LITERATURE CITED

- Akçakaya, H. R., and B. Baur. 1996. Effects of population subdivision and catastrophes on the persistence of a land snail metapopulation. *Oecologia* **105**:475–483.
- Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**:355–3366.
- Back, E. A. 1926. Biology of the sawtoothed grain beetle, *Oryzaephilus surinamensis*. *Linnaean Journal of Agricultural Research* **33**:435–452.
- Bancroft, J. 2001. Population regulation and intraspecific interaction with experimentally limited habitat. *Environmental Entomology* **30**:1061–1072.
- Beckett, S. J., and D. E. Evans. 1994. The demography of *Oryzaephilus surinamensis* (L.) (Coleoptera, Silvanidae). *Journal of Stored Product Research* **30**:121–137.
- Benoit, H. P., E. McCauley, and J. R. Post. 1998. Testing the demographic consequences of cannibalism in *Tribolium confusum*. *Ecology* **79**:2839–2851.
- Borror, D. J., C. A. Triplehorn, and N. F. Johnson. 1989. An introduction to the study of insects. Harcourt Brace College Publishers, Fort Worth, Texas.
- Brown, R. J., C. Malcolm, P. L. Mason, and R. A. Nichols. 1997. Genetic differentiation between and within strains of the saw-toothed beetle, *Oryzaephilus surinamensis* (Coleoptera: Silvanidae) at RAPD loci. *Insect Molecular Biology* **6**:285–289.
- Burkey, T. V. 1997. Metapopulation extinction in fragmented landscapes: using bacteria and protozoa communities as model ecosystems. *American Naturalist* **150**:568–591.
- Caro, T. M., and M. K. Laursen. 1994. Ecological and genetic factors in conservation: a cautionary tale. *Science* **263**:485–486.
- Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* **63**:215–244.
- Ciesielska, Z. 1990. Dynamics and expansion of populations of stored product beetles. Pages 498–507 in *Proceedings of the Sixth International Working Conference on Stored-product Protection*.
- Collinge, S. K. 1996. Ecological consequence of habitat fragmentation: implications for landscape architecture and planning. *Landscape and Urban Planning* **36**:59–77.
- Collins, P., J. C. Mulder, and D. Wilson. 1989. Variation in life history parameters of *Oryzaephilus surinamensis* (L.) (Coleoptera: Silvanidae). *Journal of Stored Product Research* **25**:193–199.
- DeAngelis, D. L., and L. J. Gross, editors. 1992. Individual based models and approaches in ecology: populations communities and ecosystems. Chapman and Hall, London, UK.
- Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology* **14**:342–355.
- Diffendorfer, J. E. 1998. Testing models of source-sink dynamics and balanced dispersal. *Oikos* **81**:417–432.
- Doak, D. F., P. C. Marino, and P. M. Kareiva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. *Theoretical Population Biology* **41**:315–336.
- Eveleigh, E. S., and D. A. Chant. 1982. Experimental studies on acarine-predator interactions: distribution of search effort and predation rates of a predator population in a patchy environment (Acarina: Pytoseiidae). *Canadian Journal of Zoology* **60**:3001–3009.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* **61**:603–10.
- Forney, K. A., and M. E. Gilpin. 1989. Spatial structure and population extinction: a study with *Drosophila* flies. *Conservation Biology* **3**:45–51.
- Gause, G. 1934. *The struggle for existence*. Dover, Baltimore, Maryland.
- Hanski, I., and M. Gilpin, editors. 1997. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California.
- Hastings, A., and K. Higgins. 1994. Persistence of transients in spatially structured ecological models. *Science* **263**:1133–1136.
- Howe, R. W. 1956. The biology of the two common storage species of *Oryzaephilus* (Coleoptera, Cucujidae). *Annals of Applied Biology* **44**:341–355.
- Jacob, T., and D. A. Fleming. 1989. The difference in the developmental period and mortality of some field strains of *Oryzaephilus surinamensis* (L.) at constant temperatures (Coleoptera: Silvanidae). *Journal of Stored Product Research* **25**:73–76.

- Kareiva, P. 1989. Renewing the dialogue between theory and experiments in population ecology. Pages 68–87 in J. Roughgarden, R. May, and S. Levin, editors. *Perspectives in ecological theory*. Princeton University Press, Princeton, New Jersey.
- Lamberson, R. H., B. R. Noon, C. Voss, and K. S. McKelvey. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the Northern Spotted Owl. *Conservation Biology* 8:185–195.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142:911–927.
- Lande, R., S. Engen, and B.-E. Saether. 1999. Spatial scale of population synchrony: environmental correlation and density regulation. *American Naturalist* 154:271–281.
- Lawler, S. P., and P. J. Morin. 1993. Food web architecture and population dynamics in laboratory microcosms of protists. *American Naturalist* 141:675–686.
- Lawler, S. P., and P. Morin. 1995. Food web architecture and population dynamics: theory and empirical evidence. *Annual Review of Ecology and Systematics* 26:505–529.
- Lockwood, J. A., and D. R. Lockwood. 1991. Rangeland grasshopper (Orthoptera: Acrididae) population dynamics: insights from catastrophe theory. *Environmental Entomology* 20:970–80.
- Lotka, A. 1925. *Elements of physical biology*. Williams and Wilkins, Baltimore, Maryland.
- Matter, S. 1997. Population density and area: the role of between- and within-patch processes. *Oecologia* 110:533–538.
- McKelvey, K., B. R. Noon, and R. H. Lamberson. 1993. Conservation planning for species occupying fragmented landscapes: the case of the Northern Spotted Owl. Pages 424–450 in J. K. P. Kareiva and R. Huey, editors. *Biotic interactions and global change*. Sinauer Press, Sunderland, Massachusetts.
- O'Neill, R. V. 1989. Perspectives in hierarchy and scale. Pages 147–163 in J. Roughgarden, R. M. May, and S. A. Levin, editors. *Perspectives in ecological theory*. Princeton University Press, Princeton, New Jersey.
- Ostfeld, R. S., W. Z. Lidicker, and E. J. Heske. 1985. The relationship between habitat heterogeneity, space use, and demography in a population of California voles. *Oikos* 45:433–442.
- Park, T. 1933. Studies in population physiology. *Journal of Experimental Zoology* 65:17–42.
- Park, T., D. B. Mertz, W. Grodzinski, and T. Prus. 1965. Cannibalistic predation in populations of flour beetles. *Physiological Zoology* 38:289–321.
- Pierce, A. M., J. H. Borden, and A. C. Oehlschlager. 1983. Effects of age and population density on response to beetle and food volatiles by *Oryzaephilus surinamensis* and *T. mercator* (Coleoptera; Cucujidae). *Environmental Entomology* 12:1367–1374.
- Prus, T. 1966. Emigrational ability and surface numbers of adult beetles in 12 strains of *Tribolium confusum* and *T. castanum* Herbst (Coleoptera, Tenebrionidae). *Ekologia Polska ser. A* 14:547–588.
- Robinson, G. R., R. D. Holt, M. S. Gaines, S. P. Hamburg, M. L. Johnson, H. S. Fitch, and E. A. Matinko. 1992. Diverse and contrasting effects of habitat fragmentation. *Science* 257:524–526.
- Root, K. V. 1998. Evaluating the effects of habitat quality, connectivity, and catastrophes on a threatened species. *Ecological Applications* 8:854–865.
- Ruel, J. J., and M. P. Ayers. 1999. Jensen's inequality predicts effects of environmental variation. *Trends in Ecology and Evolution* 14:361–366.
- SAS Institute. 1998. Version 8. Cary, North Carolina.
- Sawyer, A. J. 1989. Inconsistency of Taylor's b: simulated sampling with different quadrat sizes and spatial distributions. *Researches in Population Ecology* 31:11–24.
- Soule, M., and D. Simberloff. 1986. What do genetics and ecology tell us about the design of nature refuges? *Biological Conservation* 35:19–40.
- Taylor, L. R. 1961. Aggregation, variance, and the mean. *Nature* 189:732–735.
- Thomas, E. L. 1940. The influence of temperature, moisture, and food upon the development and survival of the saw-toothed grain beetle. *Journal of Agricultural Research* 60:605–615.
- Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, New Jersey.
- Tilman, D., and P. Kareiva, editors. 1997. *Spatial ecology*. Princeton University Press, Princeton, New Jersey.
- Turchin, P. 1998. *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. Sinauer Associates, Sunderland, Massachusetts.
- Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. *Nature* 118:558–600.
- Wallinga, J. 1995. The role of space in plant population dynamics: annual weeds as an example. *Oikos* 74:3370–383.
- Yamamura, K. 1990. Sampling scale dependence of Taylor's power law. *Oikos* 59:121–125.