Refuge Dynamics and Metapopulation Dynamics: An Experimental Test
Author(s): William W. Murdoch, Susan L. Swarbrick, Robert F. Luck, Sandra Walde and Dickie S. Yu
Source: *The American Naturalist*, Vol. 147, No. 3 (Mar., 1996), pp. 424-444
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: http://www.jstor.org/stable/2463216
Accessed: 05-05-2016 18:26 UTC

REFUGE DYNAMICS AND METAPOPULATION DYNAMICS: AN EXPERIMENTAL TEST

WILLIAM W. MURDOCH,[1] SUSAN L. SWARBRICK,[1] ROBERT F. LUCK,[2] SANDRA WALDE,[3] AND DICKIE S. YU[4]

[1]Department of Biological Sciences, University of California, Santa Barbara, California 93106; [2]Department of Entomology, University of California, Riverside, California 92507; [3]Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H4J1, Canada; [4]Agriculture Canada Research Station, Lethbridge, Alberta T1J4B1, Canada

Submitted October 28, 1994; Revised July 14, 1995; Accepted August 2, 1995

Abstract.—Red scale, an insect pest of citrus, is under control by the parasitoid *Aphytis melinus* in many areas, and in our study area the interaction appears dynamically stable. The bark on the interior branches and trunk of trees provides a partial refuge for red scale, which are rarely attacked there by the parasitoid. In a grapefruit grove, we carried out a two-way experiment in which we manipulated the refuge population (present or removed) and either left trees connected with the rest of the grove or isolated individual trees with cages to test for metapopulation effects. The experiment ran for 17 mo, encompassing three generations of scale. Scale density in the exterior of refuge-removed trees decreased by about 60%. However, neither removal of the refuge population nor isolation of individual trees increased the temporal variability of the scale population in the exterior or led to drift in population density. Indeed, removal of the refuge population caused a decrease in temporal variability. We conclude that stability in the control population was not maintained by either refuge or metapopulation dynamics. Reduced scale recruitment and density in the exterior of trees lacking a refuge population were associated with increased (i.e., density-dependent) scale survival that did not reflect a change in parasitism.

Explaining population regulation has been a central problem in ecology for decades (Nicholson 1933; Murdoch 1994). Older literature suggests that physical refuges from predation can stabilize or regulate populations (see, e.g., Bailey et al. 1962), while more recent attention has focused on metapopulation dynamics (see, e.g., Gilpin and Hanski 1991). In spite of their importance, these theories have rarely been tested. We report here results of a field experiment designed to test the effects of a physical refuge and metapopulation dynamics on population regulation and stability.

REFUGES

Refuges, areas in which the prey is wholly or partially free from attack by the predator, have long been thought to be a widespread source of stability in predator-prey systems. The intuitive appeal is that a refuge prevents the predator from driving the prey to extinction and can be a source of immigrants into the otherwise unstable predator-prey interaction. Experimental ecologists have rec-

Am. Nat. 1996. Vol. 147, pp. 424–444.

ognized the potentially powerful stabilizing effect of physical refuges ever since Connell's (1970) experiments on the rocky seashore. Refuges have also been shown to be stabilizing in simple Lotka-Volterra models in which the refuge can hold a fixed number of prey; this induces density dependence in the per capita prey mortality rate (Murdoch and Oaten 1975). The key to stability in simple Nicholson-Bailey models is that a fixed fraction of the prey is in the refuge (Bailey et al. 1962), which induces density dependence in the predator's (or parasitoid's) attack rate. Refuges are also stabilizing in more realistic stage-structured models (see, e.g., Nisbet et al. 1989).

In an exception to this general pattern, McNair (1986) showed in a model that, under some circumstances, letting a fraction of the prey population occupy a refuge can be either stabilizing or destabilizing. The model assumes that the fraction of prey in the refuge is not constant but increases with total prey population and that the emigration rate of prey from the refuge to the exterior also increases with prey density in the refuge. The models have density-dependent intrinsic rates of prey increase, both inside and outside the refuge, and a saturating predator functional response. Instability arises when density dependence in the refuge is weak compared with that outside the refuge. Near equilibrium, the flux of prey from the refuge accelerates with increasing prey density, which thus overwhelms the predator's functional response. A refuge with a high carrying capacity for prey thus appears to act as a source of "enrichment" that induces "paradox of enrichment" instability in the predator-prey interaction outside the refuge.

In spite of its long history, the refuge hypothesis has to our knowledge never been tested in the field, though a partial test for red scale has been carried out (Murdoch et al. 1995). We report on such a test here.

A population of California red scale (*Aonidiella aurantii*), an insect pest of citrus under successful control by the parasitoid *Aphytis melinus,* appeared to provide an excellent opportunity to explore the stabilizing role of a refuge. There is ample evidence that this highly successful biological control system is stable in the sense of showing remarkably restricted fluctuations in abundance (DeBach et al. 1971; Reeve and Murdoch 1986; Murdoch et al. 1995). Evidence has been presented (Reeve and Murdoch 1986) suggesting that stability might be induced by a physical refuge in the inside of the tree, on the bark of the trunk and interior structural branches, where parasitism by *Aphytis* was very low. The scale population in the inside of the tree was very dense, and roughly 90% of reproductive females on a tree occurred in this refuge (Murdoch et al. 1989). It has also been shown (Murdoch et al. 1995) that the scale population in the interior was extremely constant and thus could be a constant source of immigrants to the potentially unstable parasitoid-host interaction in the exterior. Argentine ants were present in the study area and are thought by biological control workers to interfere with *Aphytis,* so the ants were removed experimentally. The study provided weak support for the refuge hypothesis because the abundance of scale in the exterior of the tree fluctuated more when the refuge population was reduced in density, though the effect may have been temporary. It seems likely that the main cause

of the refuge is that *Aphytis* is much more attracted to the substrates provided by leaves, twigs, and fruit than to bark (Gregory 1985).

In the study, we tested the refuge hypothesis by physically removing the refuge population from the interior of some trees and then comparing the dynamics of the scale population in their exteriors with those in trees whose refuge population was left undisturbed. Immigration from the refuge is mainly in the form of newborn crawlers, which typically move up to about 1 m before settling. Subsequent stages are immobile, except for the adult males, which can fly.

METAPOPULATION DYNAMICS

Metapopulation dynamics has recently gained in popularity as a potential explanation for stability, or at least for population regulation and persistence (Murdoch and Oaten 1975; Gilpin and Hanski 1991). It has become a focus of conservation theory (see, e.g., Doak and Mills 1994) and may account for the persistence of biological control systems for which we otherwise have no explanation (Murdoch et al. 1985).

Metapopulation dynamics has various connotations. It commonly implies that populations go extinct in local patches that are subsequently reinvaded; spatial differences or other mechanisms maintain the ensemble of populations to create global persistence. Models of this sort predict the fraction of occupied patches (see, e.g., Levins 1970; Gilpin and Hanski 1991). An alternative approach explicitly describes population dynamics within each patch and movement of individuals between patches. Local extinction may be absent or infrequent in these models. Populations are stabilized through immigration and emigration and spatially out-of-phase fluctuations in abundance. Examples include a two-patch version of a Lotka-Volterra predator-prey model (Murdoch and Oaten 1975), simulations of Nicholson-Bailey parasitoid-host populations in a heterogeneous environment (Reeve 1988) or even in a homogeneous environment (Hassell et al. 1991), and a simulation of individual organisms in explicit space (de Roos et al. 1991). Models of this second type motivated our experiment since there is no evidence that scale are driven locally extinct, at least at the level of an individual tree.

The hypothesis we test is that a low level of random movement of crawlers among subpopulations is the stabilizing mechanism and that, in its absence, an isolated local population would undergo random drift. Scale crawlers move only a short distance and most probably settle on the tree in which they were born (DeBach 1958). We therefore used the individual tree as the "subpopulation" unit and tested the metapopulation hypothesis by comparing the dynamics of isolated trees with those connected with the rest of the grove through movements of individual insects.

TESTS FOR EFFECTS ON TEMPORAL VARIABILITY AND STABILITY

Relatively constant populations presumably are stable in the dynamic sense. However, the connection between the amount of temporal fluctuation observed and the population's stability is not necessarily straightforward (Murdoch 1970;

Horwood 1993; Taylor 1993). Therefore, we used two separate tests to investigate temporal variability and stability.

First, we estimated the relative temporal variability of control and treated populations, using the variance of successive log densities in each tree as the basic observation. Standard measures of temporal variability are contaminated by spatial variation, and we use an estimator that removes this contamination (Stewart-Oaten et al. 1995).

This approach assumes that the observed constancy of scale density reflected a dynamic system with a stable equilibrium that was itself relatively invariant for at least a decade or more (Murdoch et al. 1995). Further support for this interpretation is DeBach's (1958) experimental demonstration that red scale abundances returned within about 1.5 yr to their previous level after biological control was disrupted and the scale population had initially increased 20-fold in a single year.

Our second test is based on the idea that, if our manipulations had removed the important stabilizing process, the populations should have become not only unstable but unregulated. That is, we should have observed the populations undergoing increasing fluctuations that departed ever further from the original equilibrium abundance, as would occur, for example, in the basic Nicholson-Bailey model or the basic Lotka-Volterra model with time lags. We might also, or alternatively, have seen drift toward zero in scale abundance in the absence of the refuge population. Both possibilities require an estimator for the ambient equilibrium density of scale, and the best available is the density of the control population.

Relative, not absolute, abundances matter in these tests. For example, if the refuge-removed population was unregulated, the hypothesis to be tested is that $|\log \text{control} - \log \text{treatment}|$ increased with time since the imposition of treatments. If, by contrast, the exterior population remained regulated even in the absence of the refuge population, the relative difference in density should eventually reach a constant mean value. Our experiment was relatively short, so a continued increase in the log difference between treatment and control would not rule out the possibility that eventually some factor would have regulated the treatment populations. On the other hand, if the log differences between treated and control populations stopped increasing within the time of the experiment, this result would be good evidence that the treatment populations had been stabilized around their (perhaps new) equilibrium densities. A loss of regulation is also revealed by the test for a difference in temporal variability.

LIFE HISTORIES AND METHODS

Life Histories

Details of the scale's natural history are cited elsewhere (Murdoch et al. 1989, 1995; Hare et al. 1990). Female scale release several live crawlers per day and can produce 100–150 in their lifetime. The crawler is a brief dispersal stage of instar 1; most crawl a few feet before settling, but a tiny fraction become airborne. Female scale pass through three instars and two intervening nongrowing "molt"

stages. Male and female scale differentiate morphologically midway through instar 2. Males "pupate" at the end of instar 2 and emerge as winged adults, coincident with the presence of virgin female scale (i.e., instar 3); males live for only about 24 h (Moreno and Kennett 1985). We defined four stages of scale: stage 1 (instar 1 + molt 1), stage 2 (instar 2 + molt 2), stage 3 (instar 3), and mature females. Crawler-producing females were sometimes separated out from females that were mature but not yet producing crawlers. There are two scale generations per year in the study area.

Estimates of the number of degree-days needed for the development of all scale stages are available for both the laboratory and field (Yu and Luck 1988; D. S. Yu and R. F. Luck, unpublished data). Development time from crawler to production of first crawler is about 650 degree-days. *Aphytis melinus* parasitizes mainly female instar 2, male instar 2, and instar 3. Parasitism rate for all vulnerable stages was estimated from (number of parasitized hosts)/(number of parasitized hosts + number of unparasitized hosts). *Aphytis* has about three generations per scale generation.

Scale in our study area were attacked by a less important introduced parasitoid, *Encarsia perniciosi*. *Encarsia* parasitizes all stages of scale but mainly instars 1 and 2. Because parasitized hosts cannot be recognized until they reach molt 2, instar 3, or mature female stages, an index of parasitism uses (total number of parasitized)/(total number of parasitized + number of unparasitized molt 2, instar 3, and mature females) (Murdoch et al. 1995). *Encarsia* has almost two generations per scale generation (Yu et al. 1990). Larvae of this species cannot be distinguished from those of *Comperiella bifasciata,* but adults of *Comperiella* were rare.

Experimental Design and Sampling Procedures

Twenty experimental blocks were established in the grapefruit grove studied earlier (Murdoch et al. 1995). Five contiguous trees in three adjacent rows were chosen to form a 5 × 3 block. Within a given set of three rows, four blocks, each separated by an intervening 3 × 5 block, were established. This pattern was repeated in five sets of three rows of trees to give a total of 20 blocks in the experiment. A one-row buffer was left between each set of blocks. In the refuge removal treatments, the population of scale in the refuge was removed from every tree in the block. The central tree in each block was sampled.

There were four treatments in a two-way design: control, refuge population removed, caged, and caged and refuge population removed. We crossed the refuge and metapopulation treatments in our experimental design to test whether there is a statistical interaction between these "factors" and because we were interested in carrying out the refuge removal treatments both inside and outside cages. The effect of refuge removal in uncaged trees might be obscured by the immigration of organisms (especially *Aphytis*) from the refuges in surrounding trees (though we tried to prevent this occurrence by creating large experimental blocks of trees with the refuge removed). We removed this possibility by also running the experiment in cages. Because trees differed in their initial scale burden, they were divided into five groups of four trees each, ranging from those

with the heaviest to those with the lightest scale populations. We then randomly assigned trees within each group to the four treatments, so that each treatment contained trees spanning the range of initial densities.

Samples from the exterior were taken on two dates before the treatment and showed no differences, in any of the four variables examined, among the trees that were to receive different treatments: total scale density (two-way ANOVA, $P = .67$, $R^2 = 0.09$) and density of stage 1, a measure of recruitment ($P = .40$, $R^2 = 0.17$) (both $\log_{10}$ transformed), and parasitism rate by *Aphytis* ($P = .27$, $R^2 = 0.21$) or *Encarsia* ($P = .49$, $R^2 = 0.14$) (both logit transformed). There were also no significant differences in total scale density ($P = .66$, $R^2 = 0.09$) or density of stage 1 ($P = .46$, $R^2 = 0.14$) (both $\log_{10}$ transformed) in the refuge. Power to detect these initial differences (up to 60%) was low (<0.35 at $P = .05$). However, trees about to lose their refuge population had higher initial scale densities but lower posttreatment densities (see Results), so the pretreatment difference strengthens our conclusion about the refuge effect. The other difference was fleeting: trees chosen to receive cages had higher scale densities in the pretreatment period and lower densities immediately afterward and before the treatment had time to operate. Only after prolonged exposure to caging did a sustained and statistically significant increase occur (Results).

The treatments were established in August 1987. The refuge (interior) of a tree is the bark surface covering the trunk and structural branches interior to the most recent four flushes of growth. In the refuge-removed treatments, all 15 trees in the block had the refuge population removed so that scale could not migrate from the refuges in nearby trees onto the refuge-removed sample tree in the center. We removed the refuge population in the sample tree by scrubbing the bark with plastic pot scrubbers. In the remaining trees the refuge population was killed by spraying the interior with 1% oil in water, which eradicates scales. The interior was sampled thereafter every 2–6 mo using 10 1-cm^2-core random samples stratified into high- and low-density classes (Murdoch et al. 1995). Refuge-removed sample trees were rescrubbed every 6 mo, and the nonsample trees were reoiled after 1 yr. Scrubbing reduced scale density in the refuge, averaged over the whole treatment period, to 6% of that in control trees.

The cage treatment consisted of caging only the sample tree in the center of the block. The cage consisted of fine-mesh (0.2-mm) organdy cloth hung on a framework of polyvinyl chloride piping that enclosed the tree. The cage had a small opening at the top to minimize microclimate effects. Clear plastic sticky traps were continuously in place around the top opening of all cages. No scale or *Aphytis* were ever captured on the traps, and we conclude that movement into and out of cages was negligible. The individual tree was chosen as the unit for the metapopulation treatment because it appears that most of the scale born on a tree live their entire life there (DeBach 1958).

Maximum temperatures were marginally but significantly lower (difference = 0.65°C; paired t-test, $t = 2.94$, $P = .004$), and minimum temperatures were marginally but significantly higher (difference = 0.75°C; paired t-test, $t = 6.66$, $P = .0001$) inside the cage. Light levels were significantly higher inside cages, probably because some branches were trimmed to fit the cage over the tree (27.3

vs. 14.5 microeinsteins $m^{-2}s^{-1}$, $t = 4.61$, df = 17, $P = .0003$). However, the higher readings were still much lower than readings outside the tree canopy (1,800 microeinsteins $m^{-2}s^{-1}$).

Scale in the exterior were sampled by taking twigs at randomly chosen heights and compass directions in a tree. Ten twig samples, each consisting of the three most recent growth flushes, were taken from each tree once a month over most of the experiment.

We calculated the number of red scale degree-days between successive sampling dates using temperatures recorded hourly in the grove with a Datapod DP 220 (Omnidata International, Logan, Utah) placed within the canopy of one of the sample trees. The recorder did not operate on some days, and then temperatures were estimated from those recorded at a nearby weather station. Degree-days were calculated from the relationship between scale development rate and temperature developed previously (Yu and Luck 1988).

The experiment was run for 17 mo, or about three generations of scale, nine of *Aphytis,* and six of *Encarsia.*

Statistical Analyses

Since initial properties (scale density, number of recruits, and parasitism rates) were indistinguishable among trees that were to be assigned to different treatments, we tested for treatment effects by comparing data taken from the posttreatment period. Unless otherwise stated, we included all posttreatment dates in testing for the effect of treatment. The first posttreatment sample was taken only 28 d (193 degree-days) after treatment, so older scale stages were certainly survivors from the pretreatment period. However, the main burst of fall 1987 recruitment was counted on the first posttreatment sampling day, and these recruits made up the bulk of the populations even on this first date.

Counts of total live scale from all samples within a tree on a date were averaged to give five replicate observations (trees) of scale density (mean number per twig) on each date in each treatment. To estimate the effects of treatments on scale density, we averaged the density in a tree over the posttreatment period and used a two-way ANOVA on $\log_{10}$ of these time averages. The time average of the untransformed data is obviously most affected by periods of high density, namely, the three recruitment periods, but two other transformations that weighted the time averages differently gave similar results. The first transformation divided each observation on a date by the largest value observed on that date, which gave an estimate of the relative effect of treatment and weighted each date equally regardless of absolute abundance. The second, the square-root transformation, is a compromise that gives more weight to dates with more scale, but it is less severe in this regard than the untransformed data. We report only results based on logs of the untransformed time-averaged data.

We wanted to determine whether parasitism rate responded to any experimentally induced change in mean scale density. Parasitism was often poorly estimated on individual trees, especially in winter when hosts were rare. We therefore calculated the time-averaged fraction parasitized in each tree in the posttreatment period by dividing the total number of hosts parasitized over the period by the

total number available over the period. This is a weighted average of posttreatment parasitism rate in each tree. Tests for the effects of treatments on parasitism rate included only data starting on the second posttreatment date, because the vulnerable stages prior to that date included survivors from the pretreatment period. We replicated the test using data from only the last 6 mo of the experiment to test for effects after treatments had been in place for a year. The fraction parasitized was arcsine transformed for statistical analysis.

To estimate relative temporal variability, we calculated the variance of the logarithms of successive estimated population sizes, $V(\log N_t)$, as described by Stewart-Oaten et al. (1995). Temporal variation in the estimated population mean includes temporal variation in the true population mean—the component of interest—and a contamination contributed by spatial variability among samples taken on each date, which must be removed. In addition, estimating the log of the true population mean on a date as the log of the mean density of samples introduces a bias caused by Jensen's inequality (i.e., the mean of the log of a variable will be less than the log of the mean). The effect of Jensen's inequality is corrected by calculating the log (base e) of the density on date t as

$$L_t = \log_e(N_t) + (s^2_{N_t}/2r_tN_t^2), \tag{1}$$

where r_t is the number of samples at date t, N_t is the mean of samples at date t, and $s^2_{N_t}$ is the variance of samples at date t. The spatial variance on date t is

$$s^2_{L_t} = s^2_{N_t}/r_tN_t^2. \tag{2}$$

Thus, the estimate of true temporal variability is

$$V(\log_e N_t) = \Sigma (L_t - \bar{L})^2/(T - 1) - \Sigma (s^2_{L_t})/T, \tag{3}$$

where ($\bar{L}$ is the mean of L_t's over all dates and T is the number of dates sampled. We were interested in measuring temporal variance as $\log_{10}$ because most common measures of temporal variability as the standard deviation of the logarithms of successive population sizes are calculated as $\log_{10}$. To convert $V(\log_e N_t)$ from $\log_e$ to $\log_{10}$, we multiplied $V(\log_e N_t)$ by $(\log_{10}e)^2$. The value of $V(\log N_t)$ was estimated separately for each tree, which thus provided five replicate estimates for each treatment. (The conversion to $\log_{10}$ was done incorrectly in Murdoch et al. 1995, p. 214. Their statistical conclusions remain unchanged, but the estimates of temporal variability are about 0.24 higher than reported for the ant exclusion and control trees in the exterior. In the interior, the correct numbers are 0.19 for the ant exclusion trees and 0.07 for the control trees.)

Dates on which no scale were found in a tree pose severe difficulties because log density is undefined. This outcome occurred on five dates spread over four trees. Stewart-Oaten et al. (1995) discuss possible corrective measures, none of which is truly satisfactory. They note that the standard procedure of choosing a constant to add to all observations involves a purely arbitrary choice—which nevertheless can have a large effect on the estimate. Mosteller and Tukey (1977) recommend (but do not justify) adding one-sixth of the smallest observation. We report results for a range of constants, as recommended by Stewart-Oaten et

al. (1995). We also analyzed two-date running averages, which is a preferred alternative.

To test whether the abundance of treatment populations drifted ever farther from the control trees with time, we first calculated the mean scale density on each date across all samples from all five trees in each treatment. We then calculated the absolute value of the difference $|\log_{10}(\text{control}) - \log_{10}(\text{treatment})|$ for each date and regressed these differences against time. The differences on each date are probably not statistically independent, so the variance in the regression may be underestimated; the test is therefore more sensitive to an increase in difference between control and treatment than it would otherwise be.

We calculated an index of survival rate between scale stages as follows. First, for each tree, we averaged the density of scale in the earlier stage over sample dates chosen so that all scale in the stage were produced after the treatment had been imposed and would have developed into the later stage during the experiment. Next, for each tree we also averaged the density of the later scale stage, beginning with the first date when all of them had to have recruited in the posttreatment period and ending with the final sample. We then divided mean density of the later stage by mean density of the earlier stage, for each tree. The index was logit transformed for analysis of survival from stage 1 to the mature female stage because the index was usually less than 0.1. In all other cases the index was arcsine transformed.

RESULTS

Effects on Average Red Scale Density and Recruitment

Removing the refuge populations reduced total live scale density, averaged over the posttreatment period, by about 60%, and the effect was statistically significant (fig. 1; table 1*A*). The difference was not restricted to periods of generally high density: it was still statistically significant in the low-density winter months (table 1*B*). Adding cages increased the average total live scale density over the posttreatment period by 38%, but the difference was not statistically significant and was small in winter (table 1*A*, *B*). The interaction between the two treatments was not significant in this or any of the analyses to follow.

The above analysis looked at all posttreatment dates. However, older scale present in the first few posttreatment dates had recruited before the treatments were imposed. We therefore repeated the analysis on total live scale (excluding crawler-producing females, which are potentially long-lived), starting 635 degree-days (see Life Histories and Methods) after the treatments were imposed. The results were very close to those seen over the whole period, except that the cage effect was statistically significant (table 1*C*).

We also analyzed density by stage to determine whether treatment effects were consistent across stages. We delayed the starting dates for older stages so that the scale included in the analysis most likely were recruited after imposition of treatments. The density effects were dependent on scale stage, and the patterns were different in the refuge-removed and cage-added treatments.

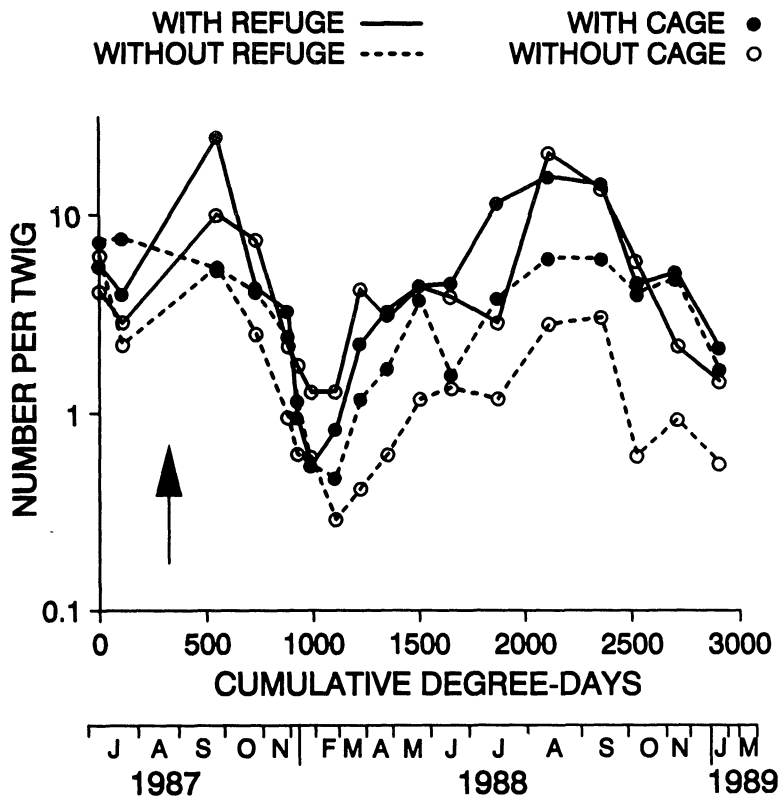

FIG. 1.—The effect of removing the scale refuge population and of caging on the total live scale density in the exterior of trees. Each value is based on the mean density per twig found in the five trees in each treatment. Note that the *Y*-axis is logarithmic. The *X*-axis shows both real time and physiological time since start of the experiment in degree-days. The arrow shows when the treatments were imposed.

The density of stage 1 averaged over the whole posttreatment period, which represents total recruitment, was reduced by 70% on the average when the refuge population was removed, and the difference was statistically significant (fig. 2; table 2*A*). Recruitment was 26% higher in caged than in uncaged trees, but this difference was not statistically significant (table 2*A*).

The effect of the refuge removal treatment became progressively smaller in the successive scale developmental stages. While density reduction in the refuge-removed populations was 70% in stage 1, the percentage declined in each successive scale stage and was only 25% in mature females, at which point it was not statistically significant (table 2). We discuss this pattern further in the section Regulation of Refuge-Removed Populations.

In contrast to these results and the nonsignificant effect of caging on total scale density, a significant cage effect was seen in the later scale stages. As noted above, stage 1 density in caged trees exceeded that in noncaged trees by only about 26%. The increase was about the same in stage 2. However, by stage 3 the

TABLE 1

TWO-FACTOR ANOVA OF EFFECTS OF REFUGE AND CAGING ON THE DENSITY OF TOTAL LIVE SCALE

SOURCE	ANOVA RESULTS		CHANGE IN DENSITY	
	P	R^2	Treatment	Percentage Change
A. Density of all stages of scale averaged over the entire posttreatment period (September 1987–January 1989):				
Model	.002	.60		
Refuge	.0004		Refuge removed	−62
Cage	.12		Cage added	+38
Refuge × cage	.35			
B. Density of all stages of scale averaged over low-density winter months (December 1987–April 1988):				
Model	.02	.45		
Refuge	.005		Refuge removed	−56
Cage	.49		Cage added	+ 8
Refuge × cage	.21			
C. Density of all stages of scale, excluding crawler-producing females, averaged over a period starting 635 degree-days after treatments were imposed (February 1988–January 1989):				
Model	.0002	.69		
Refuge	.001		Refuge removed	−64
Cage	.035		Cage added	+31
Refuge × cage	.12			

NOTE.—Data were $\log_{10}$ transformed for analysis. The percentage reduction in the refuge-removed treatment is based on the comparison between the average density in 10 trees with the refuge population removed and 10 trees with the refuge population present. The percentage added in the cage-added treatment is based on the comparison between the average density in 10 trees with cages and 10 trees without cages.

density in cages was more than 100% greater than that in noncaged trees, and by the mature female stage it was more than 300% greater; differences in both later stages were highly statistically significant (table 2*C*, *D*). These results imply a higher survival rate of later scale stages in caged trees.

Although recruitment and total live scale density, averaged over the whole posttreatment period, were not significantly greater in caged trees, the implied pattern of increased survival rate in cages (table 2) might have led ultimately to higher total scale densities, had the experiment continued. This possibility is supported by the following analysis. We compared density of scale stages 1 + 2 + 3 in the fall (October–January) period immediately following imposition of treatments with those in the same period of the next year. In the first year the density in cages was 8% lower than in noncaged trees (not a statistically significant difference; table 3*A*). One year later, however, the density in caged trees was 71% higher than in noncaged trees, a statistically significant difference (table 3*B*). By contrast, the refuge effect occurred quickly and remained constant: the

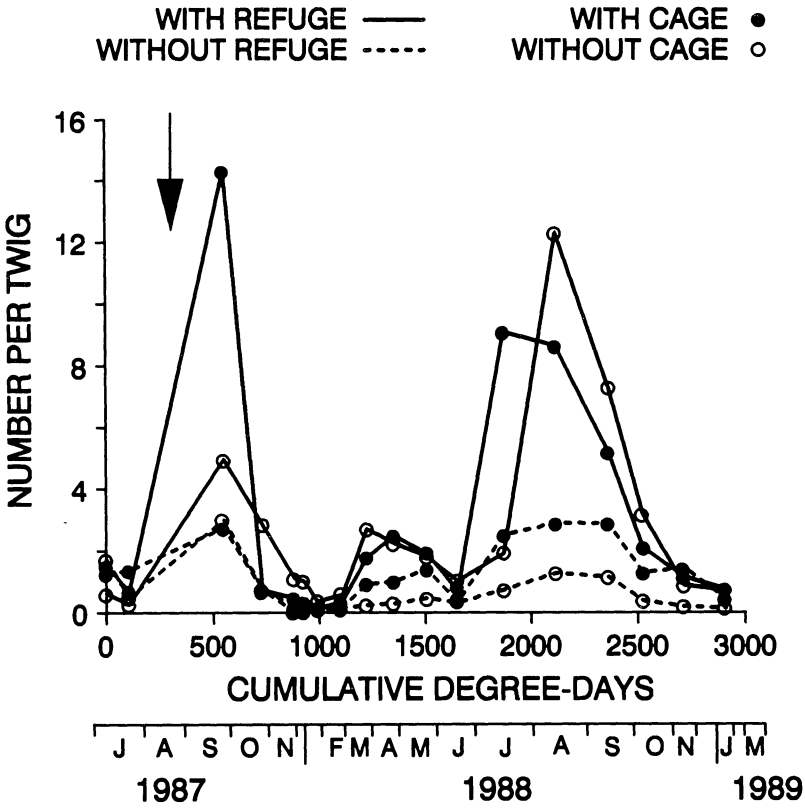

FIG. 2.—The effect of removing the scale refuge population and of caging on the recruitment of scale as measured by the abundance of stage 1 scale in the exterior of trees. Each value is the mean density per twig found in the five trees in each treatment. The *X*-axis shows both real time and physiological time since start of the experiment in degree-days. The arrow shows when the treatments were imposed.

reduction in scale density in refuge-removed trees was the same in both years (table 3*A*, *B*).

Effects on Temporal Variability of Red Scale

Our estimates of temporal variability are based on the variance of successive $\log_{10}(N_t)$, corrected for spatial variation, where N_t is the mean number of live scale per twig on a tree (see Life Histories and Methods). Five of the N_t values were zero: no scale were found in samples from each of four trees in the refuge-removed treatment on one date, and for one of these trees this also occurred on the next date.

We first treated the zero observations by the preferred approach of taking two-date running averages of successive densities and using these averages as the observations (Life Histories and Methods). This approach removed all zeros except for the tree with zeros on two consecutive dates. When this tree was

TABLE 2

TWO-FACTOR ANOVA OF EFFECTS OF REFUGE AND CAGING ON THE DENSITY OF STAGES OF SCALE

SOURCE	ANOVA RESULTS		CHANGE IN DENSITY	
	P	R^2	Treatment	Percentage Change
A. Stage 1, averaged over sample date 1 (193 degree-days after treatments were imposed) through the end of the experiment:				
Model	.003	.57		
Refuge	.0004		Refuge removed	−70
Cage	.38		Cage added	+26
Refuge × cage	.35			
B. Stage 2, averaged over sample date 2 (375 degree-days after treatments were imposed) through the end of the experiment:				
Model	.007	.66		
Refuge	.0001		Refuge removed	−57
Cage	.069		Cage added	+22
Refuge × cage	.11			
C. Stage 3, averaged over sample date 3 (524 degree-days after treatments were imposed) through the end of the experiment:				
Model	.004	.55		
Refuge	.01		Refuge removed	− 42
Cage	.004		Cage added	+111
Refuge × cage	.77			
D. Mature female stage, averaged over sample date 5 (635 degree-days after treatments were imposed) through the end of the experiment:				
Model	.0001	.72		
Refuge	.46		Refuge removed	− 25
Cage	.0001		Cage added	+334
Refuge × cage	.33			

NOTE.—Stage 1, instar 1 + molt 1; stage 2, instar 2 + molt 2; stage 3, instar 3. Data were $\log_{10}$ transformed for analysis. The percentage reduction in the refuge-removed treatment is based on the comparison between the average density in 10 trees with the refuge population removed and 10 trees with the refuge population present. The percentage added in the cage-added treatment is based on the comparison between the average density in 10 trees with cages and 10 trees without cages.

excluded from the analysis, refuge removal was found to have significantly *reduced* temporal variability. The refuge removal effect was significant, but the cage effect was not (table 4*A*).

We then included the tree omitted earlier and, to remove the zero observation, added a constant to each of the running averages, using a range of constants from 0.006 (about 1/6 of the lowest observed density) to 0.12 (about three times the smallest observation). Only with the smallest constants (≤ 0.01) was the tree with a zero observation a clear outlier. Results were consistent for all constants except the smallest: temporal variability was again lower in refuge-removed treatments,

TABLE 3

TWO-FACTOR ANOVA OF EFFECTS OF REFUGE AND CAGING ON THE DENSITY OF STAGES 1, 2, AND 3 SCALE AT THE BEGINNING AND END OF THE EXPERIMENT

SOURCE	ANOVA RESULTS		CHANGE IN DENSITY	
	P	R^2	Treatment	Percentage Change
A. Year 1, averaged over October 26, 1987, through February 1, 1988:				
Model	.16	.27		
Refuge	.047		Refuge removed	−43
Cage	.40		Cage added	− 8
Refuge × cage	.46			
B. Year 2, averaged over October 10, 1988, through January 23, 1989:				
Model	.008	.51		
Refuge	.01		Refuge removed	−46
Cage	.025		Cage added	+71
Refuge × cage	.16			

NOTE.—Data were $\log_{10}$ transformed for analysis. The percentage reduction in the refuge-removed treatment is based on the comparison between the average density in 10 trees with the refuge population removed and 10 trees with the refuge population present. The percentage added in the cage-added treatment is based on the comparison between the average density in 10 trees with cages and 10 trees without cages.

and the effect was always statistically significant (table 4*B* shows the results when 0.04, the lowest observed density, was added as a constant). Caging never had a significant effect (table 4*B*).

Finally, we used the standard approach of adding a constant to each of the observed N_t values, without taking running averages and using the same range of constants as previously. No significant treatment effects were detected, regardless of the constant added: all P values were greater than .15. (Table 4*C* shows the results when 0.04 was the added constant.) Small constants, however, severely distorted the data and illustrate the problem with this standard approach. For example, for constants less than 0.02, while observations from most trees still lie clustered together, three of the four trees containing zero observations were very distant outliers. The effects were not significant, however, even though these outliers increased the mean temporal variability in refuge-removed treatments.

Thus, the experimental results reject both of the main hypotheses: temporal variability was not increased by cutting the exterior population off from either the interior refuge population or from the rest of the grove. Indeed, removing the refuge seems to have reduced variability.

Effect on Regulation

A nonregulated population should drift ever further from equilibrium over time. To test whether this occurred in the scale populations, particularly in trees lacking a refuge population, we asked whether their relative abundance drifted further from that of the control populations over time (see Life Histories and Methods).

TABLE 4

TWO-FACTOR ANOVA OF EFFECTS OF REFUGE AND CAGING ON THE TEMPORAL VARIABILITY OF SCALE POPULATIONS IN THE EXTERIOR OF TREES

SOURCE	ANOVA RESULTS		REFUGE EFFECT		CAGE EFFECT	
	P	R^2	Refuge	No Refuge	No Cage	Cage
A. Temporal variability calculated from two-date running averages of successive scale densities for each tree:*						
Model	.03	.44	.169	.104	.121	.154
Refuge	.01		(.018)	(.012)	(.020)	(.018)
Cage	.11					
Refuge × cage	.96					
B. Temporal variability calculated from two-date running averages with a constant of 0.04, the lowest observed density, added to each two-date average for each tree to remove the zero:						
Model	.15	.27	.161	.106	.124	.143
Refuge	.04		(.017)	(.017)	(.021)	(.017)
Cage	.43					
Refuge × cage	.57					
C. Temporal variability calculated with a constant of 0.04, the lowest observed density, added to density of each tree on each date to remove zeros:						
Model	.71	.08	.192	.176	.166	.202
Refuge	.65		(.017)	(.030)	(.024)	(.024)
Cage	.31					
Refuge × cage	.74					

NOTE.—Temporal variability was calculated using three methods. Refuge and cage effects are the means (1 SE of the mean) of temporal variability in the 10 trees in each treatment.

* The tree with zero density on two consecutive dates was deleted.

None of the treatment populations diverged increasingly from the control with time (fig. 3). After the initial reduction in density, the (log) refuge-removed populations paralleled the control closely and did not show evidence for a drift toward zero (fig. 1). This analysis, plus the analysis of temporal variability, shows that the treatment populations were quickly regulated after the treatments were imposed (further evidence is the constant refuge effect shown in table 3).

Regulation of Refuge-Removed Populations

The above results show that the refuge was not the mechanism that stabilized the populations. Scale abundance was at least as stable in the absence of the refuge population, even though the treatment led to a large reduction in recruitment. Such a reduction in recruitment should lead to a drift toward zero in the absence of some other density dependence in the system. The above analysis of stage-specific densities strongly suggests that survival rate to the mature female stage was higher in refuge-removed trees, which reflects density dependence. The implication here is that, were the density of scale to be reduced through

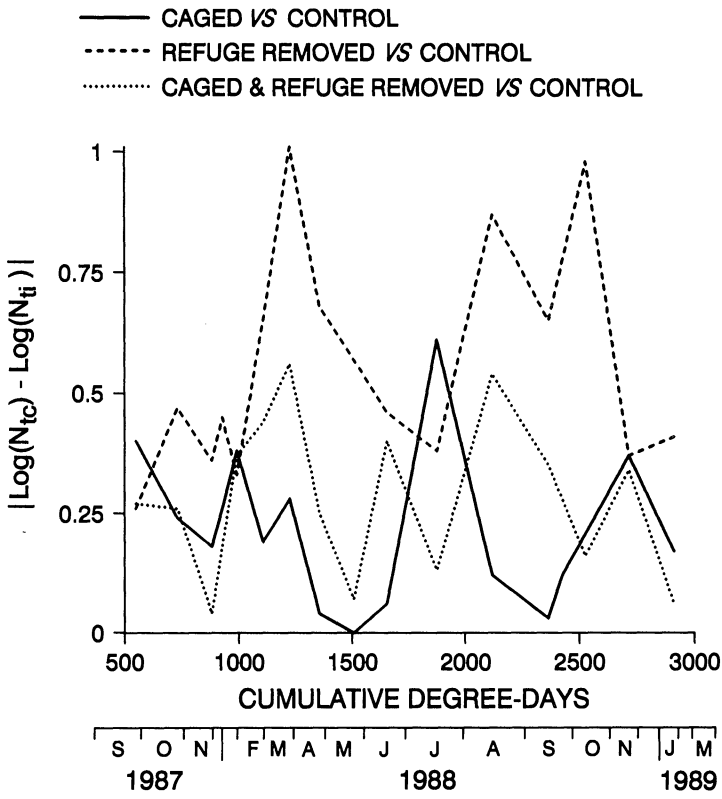

FIG. 3.—Absence of drift in scale population density, with time, in the three treatments. Each point measures the relative difference between the density in a treatment and the control density on a date and is $|\log_{10}(N_{t,c}) - \log_{10}(N_{t,i})|$, where $N_{t,c}$ is the mean number of live scale in control trees on date t, and $N_{t,i}$ is the mean number in trees in treatment i on date t. Results of regression of difference vs. time: caged vs. control, $P = .45$, $R^2 = 0.04$; refuge removed vs. control, $P = .29$, $R^2 = 0.08$; caged and refuge removed vs. control, $P = .90$, $R^2 = 0.001$. Only the posttreatment period is shown.

natural causes, there would be compensatory survival. The density dependence cannot have been caused by a response of scale emigration rate to change in scale density because these stages are immobile.

We next ask whether the survival rate of scale from stage 1 to the mature female stage was higher in refuge-removed treatments than in the refuge-present populations (see Life Histories and Methods for calculations). Scale in refuge-removed trees survived about twice as well on the average as did those in refuge-present trees, and the difference was significant (table 5*A*).

A stage-by-stage analysis of survival rate showed that the increase in survival in trees lacking a refuge population was greater in the later stages. The proportion of scale surviving from stage 1 to stage 2, and from stage 2 to stage 3, was about 20% higher in refuge-removed trees, but survival from stage 3 to the mature female stage was about 50% higher in refuge-removed trees (table 5).

TABLE 5

TWO-FACTOR ANOVA OF EFFECTS OF REFUGE AND CAGING ON THE SURVIVAL RATE OF SCALE

	ANOVA RESULTS		REFUGE EFFECT		CAGE EFFECT	
SOURCE	P	R^2	Refuge	No Refuge	No Cage	Cage
A. Survival rate from stage 1 to mature female:						
Model	.0004	.67	.05	.10	.04	.10
Refuge	.001		(.01)	(.02)	(.01)	(.02)
Cage	.003					
Refuge × cage	.12					
B. Survival rate from stage 1 to stage 2:						
Model	.070	.35	.68	.82	.69	.81
Refuge	.063		(.07)	(.05)	(.04)	(.07)
Cage	.064					
Refuge × cage	.46					
C. Survival rate from stage 2 to stage 3:						
Model	.004	.56				
Refuge	.025		.23	.28	.22	.29
Cage	.007		(.02)	(.02)	(.02)	(.02)
Refuge × cage	.049					
D. Survival rate from stage 3 to mature female:						
Model	.051	.38	.28	.43	.25	.46
Refuge	.083		(.06)	(.08)	(.06)	(.07)
Cage	.028					
Refuge × cage	.57					

NOTE.—Index of survival rate is (time-averaged density of later stage)/(time-averaged density of earlier stage). Data were logit transformed for the analysis of survival rate from stage 1 to mature female stage and arcsine square-root transformed for all other analyses. Refuge and cage effects are untransformed means (1 SE of the mean) of survival rate in the 10 trees in each treatment.

Caging and Survival Rate

Caging also increased scale survival rate, as suggested by the stage-by-stage analysis of scale densities. Survival rate from stage 1 to mature female was more than twice as high in caged as in uncaged trees, and the effect was statistically significant (table 5*A*).

As in the case of refuge removal, the increase in relative survival induced by caging was larger in later developmental stages of the scale. Survival from stage 1 to stage 2 was only 17% higher in cages, 32% higher from stage 2 to stage 3, and 84% higher from stage 3 to the mature female stage (table 5).

This effect of caging on scale survival may have been a consequence of the cage itself rather than the isolation of the trees from the rest of the grove. Scale need to reinsert their mouthparts after each molt, and caging may have affected either the scales, by increasing humidity, or substrate quality, by increasing the light level (see Life Histories and Methods). Alternatively, caging may have reduced immigration of predators, but we have no observations on this possibility. Again, the effect cannot be explained by a reduction in emigration of scale, since they are immobile in these stages.

TABLE 6

TWO-FACTOR ANOVA OF EFFECTS OF REFUGE AND CAGING ON THE FRACTION OF TOTAL HOSTS PARASITIZED BY *APHYTIS* OR *ENCARSIA*

SOURCE	ANOVA RESULTS		REFUGE EFFECT		CAGE EFFECT	
	P	R^2	Refuge	No Refuge	No Cage	Cage
A. Fraction of total hosts parasitized by *Aphytis* from October 1987 to January 1989:						
Model	.79	.06	.21	.24	.21	.23
Refuge	.40		(.02)	(.02)	(.01)	(.02)
Cage	.59					
Refuge × cage	.92					
B. Fraction of total hosts parasitized by *Encarsia* from October 1987 to January 1989:						
Model	.94	.02	.24	.26	.24	.26
Refuge	.76		(.02)	(.08)	(.02)	(.03)
Cage	.75					
Refuge × cage	.68					
C. Fraction of total hosts parasitized by *Aphytis* from August 1988 to January 1989:						
Model	.47	.09	.21	.21	.19	.23
Refuge	.80		(.02)	(.03)	(.02)	(.03)
Cage	.25					
Refuge × cage	.84					
D. Fraction of total hosts parasitized by *Encarsia* from August 1988 to January 1989:						
Model	.57	.07	.29	.31	.33	.27
Refuge	.77		(.03)	(.04)	(.04)	(.03)
Cage	.32					
Refuge × cage	.93					

NOTE.—Data were arcsine square-root transformed. Refuge and cage effects are the untransformed means (1 SE of the mean) of parasitism rate in the 10 trees in each treatment.

Role of Parasitism

A reduction in parasitism rate in the scale in the exterior of the trees, in response to the reduced density of early stages of scale, would be evidence that density-dependent parasitism played a role in regulating the refuge-removed scale populations at their observed low densities. There is no convincing evidence, however, that parasitism by either *Aphytis* or *Encarsia* was density-dependent. Average parasitism rates over the whole experiment, and in the last 6 mo, were not statistically distinguishable among treatments (table 6).

DISCUSSION

This experiment shows that the constancy and stability of red scale populations cannot be explained by a partial refuge from parasitism or by metapopulation dynamics, at least at the spatial scales at which we tested these two hypotheses.

We cannot, of course, exclude the possibility that experiments done at a different spatial scale would give a different answer, though we tried to choose the spatial scale that was ecologically relevant. Our experiment focused on the dynamics of the population in the exterior of the tree because this is where the predator-prey interaction takes place. It is also, from an agricultural point of view, where the pest is important.

The refuge result is especially surprising. We had thought the refuge population was a source of stability because it is a source of scale recruits to the population in the exterior of trees, and we showed earlier that scale density in the refuge is quite invariant (Murdoch et al. 1995). However, removal of the refuge population, which makes up about 90% of the entire population (Murdoch et al. 1989), caused a reduction, rather than an increase, in the temporal variability of the exterior population, and it did not cause that population to drift in abundance. Two caveats may be in order. First, our measure of the degree of instability is the amount of temporal variability of population density; an experiment using capacity to return to equilibrium following perturbation could give a different result. Second, the exterior population was sparser when the refuge was removed and might therefore be more vulnerable to stochastic events with the potential for causing local extinction, though there were at least 1,200 scales in the exterior of all but one of the trees.

As far as we know, this is the only experiment testing the effect of a refuge on population dynamics. It does not establish that refuges typically are not stabilizing, but it does call into question the prevalent notion that refuges probably are stabilizing. The higher variability in exterior populations connected to a refuge may have resulted from the larger recruitment peaks, driven by influxes of crawlers from the refuge.

McNair's (1986) models are unique in predicting that a refuge with prey moving into and out of it can in some cases destabilize an otherwise stable predator-prey interaction. However, the process envisaged by McNair is probably not operating in this system. His models require that instability of the prey population in the refuge is much further below the limit set by its resources than that in the exterior, and that as a consequence the refuge population shows much weaker density dependence. The opposite seems to be true in our system. First, scale density in the refuge is about 100 times higher than in the exterior (Murdoch et al. 1989, 1995). Second, the abundance of scale in the refuge population is much more constant through time than that in the exterior (Murdoch et al. 1995).

The refuge removal treatment did show that scale survival in the exterior increased in a density-dependent way when scale density and recruitment were reduced. We could not detect a density-dependent response in parasitism rate that could have accounted for this change in survival rate, and we do not know what caused it. It does not seem likely that the mechanism involves density dependence internal to the scale population. Hare et al. (1990) have shown no effect of scale density on scale survival in experimental cohorts of scale protected in the field from *Aphytis,* and other predators, over a range of densities higher than those in our experiment. In addition, DeBach's (1958) insecticide experiment showed that removal of *Aphytis* (and perhaps other unmeasured changes) led to

enormous increases in scale density, so density dependence within the scale population cannot be the main explanation for the general maintenance of scale around a low stable equilibrium. The suppression of scale to that low equilibrium, however, appears to be caused mainly by *Aphytis* (DeBach et al. 1971). Occasional individuals of the predatory beetle, *Rhyzobius lophanthae,* were seen, and this species might cause density-dependent mortality. However, it is also known that *Rhyzobius* is not an effective control agent for scale (DeBach et al. 1971). Other predators of scale, such as lacewings, are rare in the grove.

We were not surprised by rejection of the metapopulation hypothesis because we have not seen evidence for out-of-phase fluctuations in different parts of the grove. DeBach (1958) also commented that fluctuations in scale abundance in different parts of groves were largely in synchrony. No evidence was found (Walde 1994) for metapopulation dynamics in mite populations in an apple orchard. In a literature survey Harrison (1991) found few examples (a frog, a butterfly, a lousewort, and moss), on the basis of purely observational evidence, of natural populations that might persist via metapopulation dynamics. However, Hanski et al. (1994) provide observations and a model of a butterfly population, which may be another example.

Our experiment has produced a crucial result for future experimental work in this system: scale populations in isolated trees lacking a refuge population remained both stable and temporally quite invariant. Thus, whatever the stabilizing mechanism, it operates on a small spatial scale. The tree can thus be used as the experimental unit.

ACKNOWLEDGMENTS

We thank A. Stewart-Oaten for statistical advice. We are grateful to N. J. Gotelli and an anonymous reviewer for comments. This work was supported by National Science Foundation grants BSR-891774 and DEB93-06354 and U.S. Department of Agriculture grant 90-37153-5237.

LITERATURE CITED

Bailey, V. A., A. J. Nicholson, and E. Williams. 1962. Interaction between hosts and parasites when some host individuals are more difficult to find than others. Journal of Theoretical Biology 3:1–18.

Connell, J. H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecological Monographs 40:49–78.

de Roos, A. M., E. McCauley, and W. G. Wilson. 1991. Mobility- versus density-limited predator-prey dynamics on different spatial scales. Proceedings of the Royal Society of London B, Biological Sciences 246:117–122.

DeBach, P. 1958. The role of weather and entomophagous species in the natural control of insect populations. Journal of Economic Entomology 51:474–484.

DeBach, P., D. Rosen, and C. E. Kennett. 1971. Biological control of coccids by introduced natural enemies. Pages 165–194 *in* C. B. Huffaker, ed. Biological control. Plenum, New York.

Doak, D. F., and L. S. Mills. 1994. A useful role for theory in conservation. Ecology 75:615–626.

Gilpin, M., and I. Hanski, eds. 1991. Metapopulation dynamics: empirical and theoretical investigations. Academic Press, London.

Gregory, W. A. 1985. In-flight response of citrus-inhabiting *Aphelinidae* (Hymenoptera) to trap colors and plant structures. Ph.D. diss. University of California, Riverside.

Hanski, I., M. Kuussaari, and M. Nieminen. 1994. Metapopulation structure and migration in the butterfly *Melitaea cinxia*. Ecology 75:747–762.

Hare, J. D., D. S. Yu, and R. F. Luck. 1990. Variation in life history parameters of California red scale on different citrus cultivars. Ecology 71:1451–1460.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Pages 73–88 *in* M. Gilpin and I. Hanski, eds. Metapopulation dynamics: empirical and theoretical investigations. Academic Press, London.

Hassell, M. P., H. N. Comins, and R. M. May. 1991. Spatial structure and chaos in insect population dynamics. Nature (London) 353:255–258.

Horwood, J. 1993. Comment: population variance and deterministic stability analysis. Journal of Animal Ecology 62:588–591.

Levins, R. 1970. Extinction. Pages 77–107 *in* M. Gesternhaber, ed. Some mathematical problems in biology. American Mathematical Society, Providence, R.I.

McNair, J. N. 1986. The effects of refuges on predator-prey interactions: a reconsideration. Theoretical Population Biology 29:38–63.

Moreno, D. S., and C. E. Kennett. 1985. Predictive year-end California red scale (Homoptera: Diaspididae) orange fruit infestations based on catches of males in the San Joaquin Valley. Journal of Economic Entomology 78:1–9.

Mosteller, F., and J. W. Tukey. 1977. Data analysis and regression: a second course in statistics. Addison-Wesley, Reading, Mass.

Murdoch, W. W. 1970. Population regulation and population inertia. Ecology 51:497–502.

———. 1994. Population regulation in theory and practice. Ecology 75:271–287.

Murdoch, W. W., and A. Oaten. 1975. Predation and population stability. Advances in Ecological Research 9:1–131.

Murdoch, W. W., J. Chesson, and P. L. Chesson. 1985. Biological control in theory and practice. American Naturalist 125:344–366.

Murdoch, W. W., R. F. Luck, S. J. Walde, J. D. Reeve, and D. S. Yu. 1989. A refuge for red scale under control by *Aphytis:* structural aspects. Ecology 70:1707–1714.

Murdoch, W. W., R. F. Luck, S. L. Swarbrick, S. J. Walde, D. S. Yu, and J. D. Reeve. 1995. Regulation of an insect population under biological control. Ecology 76:206–217.

Nicholson, A. J. 1933. The balance of animal populations. Journal of Animal Ecology 2:132–178.

Nisbet, R. M., W. S. C. Gurney, W. W. Murdoch, and E. McCauley. 1989. Structured population models: a tool for linking effects at individual and population level. Biological Journal of the Linnean Society 37:79–99.

Reeve, J. D. 1988. Environmental variability, migration, and persistence in host-parasitoid systems. American Naturalist 132:810–836.

Reeve, J. D., and W. W. Murdoch. 1986. Biological control by the parasitoid *Aphytis melinus*, and population stability of the California red scale. Journal of Animal Ecology 55:1069–1082.

Stewart-Oaten, A., S. J. Walde, and W. W. Murdoch. 1995. Estimation of temporal variability in populations. American Naturalist 146:519–535.

Taylor, A. D. 1993. Comment: population and stability: a response to Horwood. Journal of Animal Ecology 62:592–593.

Walde, S. 1994. Immigration and the dynamics of a predator-prey interaction in biological control. Journal of Animal Ecology 63:337–346.

Yu, D. S., and R. F. Luck. 1988. Temperature dependent size and development of California red scale (Homoptera: Diaspididae) and its effect on host availability for the ectoparasitoid *Aphytis melinus*. Environmental Entomology 17:154–161.

Yu, D. S., R. F. Luck, and W. W. Murdoch. 1990. Competition, resource partitioning and coexistence of an endoparasitoid *Encarsia perniciosi* and an ectoparasitoid *Aphytis melinus* of the California red scale. Ecological Entomology 15:469–480.

Associate Editor: Nicholas J. Gotelli