REARING *DELPHASTUS CATALINAE* (COLEOPTERA: COCCINELLIDAE): PRACTICAL EXPERIENCE AND A MODELING ANALYSIS

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Abstract

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Delphastus catalinae (Horn) (Coleoptera: Coccinellidae) was mass reared to support field studies addressing augmentation and colonization for control of *Bemisia argentifolii* Bellows and Perring (Homoptera: Aleyrodidae) in southern California. Beetles were reared on *B. argentifolii* infested poinsettia plants grown inside greenhouses located in northern California. Potted plants, reared from rooted cuttings, were cycled through the rearing system over ca. a 12-week period, then discarded. A total of 174 245 adult beetles were harvested over a 20-week period. Each plant averaged 46 adult beetles (range 21–89) over the same period of time. Harvesting strategies were investigated using a computer simulation model based upon published and hypothesized reproduction and survivorship parameters. Results suggest that removal of approximately 50% of adults per week produced a stable and maximum production of beetles. Actual harvest rates were between 40 and 60% of available beetles. The cost of producing each adult was estimated at US$0.22, with the major cost being labor at 86% of the total.

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Résumé

Nous avons procédé à l'élevage en masse de *Delphastus catalinae* (Coleoptera: Coccinellidae) pour vérifier les données obtenues en nature sur l'augmentation et la colonisation de ces insectes destinés à assurer le contrôle de *Bemisia argentifolii*, Bellows et Perring (Homoptera; Aleyrodidae) dans le sud de la Californie. Les coccinelles ont été élevées sur des plants de poinsettia infestés de *B. argentifolii* en serre dans le nord de la Californie. Les plants en pot, cultivés à partir de boutures portant des racines, ont été gardés pendant tout un cycle, soit environ 12 semaines, puis jetés. Au total, 174 245 coléoptères adultes ont été obtenus au cours d'une période de 20 semaines. Chaque plant a donné en moyenne 46 coccinelles adultes (21–89) pendant cette période. Les stratégies de récolte des adultes ont été examinées au moyen d'un modèle de simulation à l'ordinateur basé sur des paramètres de reproduction et de survie hypothétiques ou tirés de la littérature. Les résultats indiquent que la récolte d'environ 50% des adultes chaque semaine assure une production stable et maximale de coccinelles. Les taux réels de récolte ont été de 40% à 60% des coléoptères présents. Le coût de production d'un adulte a été estimé à $0,22, la plus grande partie due à la main d'oeuvre (86% au total).

[Traduit par la Rédaction]

Introduction

Delphastus (Coleoptera) are small (0.9–1.6 mm), dark-brown to black coccinellids that have been reported attacking several species of whiteflies (Homoptera: Aleyrodidae) (Muma 1955; Gordon 1970, 1985; Hoelmer et al. 1993; Gordon 1994). It

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is the only member of the Serangiini tribe native to the Western Hemisphere (Gordon 1994). Life-history characteristics measured in laboratory and field studies suggest that some members of this genus can suppress whiteflies occurring at high densities. During laboratory studies using silverleaf whitefly, *Bemisia argentifolii* Bellows and Perring [=the *B* strain of *Bemisia tabaci* (Gennadius)] (Homoptera: Aleyrodidae) (Perring et al. 1993; Bellows et al. 1994), as prey, Hoelmer et al. (1993) found that adult *Delphastus pusillus* (LeConte) consumed 167.1 eggs or 11.6 early fourth instars per day and larvae consumed 977.5 eggs prior to pupation. In the field, *D. pusillus* was one of the most common predators associated with citrus blackfly, *Aleurocanthus woglumi* Ashby, in Florida citrus during a 2-year survey by Cherry and Dowell (1979). Cage studies in Imperial Valley, California, showed that *D. pusillus* could survive, reproduce, and suppress *B. argentifolii* during summer months (Heinz et al. 1994).

A cooperative effort between the Biological Control Program of the California Department of Food and Agriculture (CDFA) and the University of California (UC) at Davis was conducted in 1992 and 1993 to test whether inoculative releases of *D. pusillus* could suppress *B. argentifolii*, a major pest of greenhouse and field crops worldwide (Gill 1992). A recent revision of *Delphastus* by Gordon (1994) and reexamination of voucher material by the same author suggests that the tested species was actually *Delphastus catalinae* (Horn), however. The study on inoculative releases and a related project to establish *Delphastus* in *B. argentifolii* infested regions of California required large numbers of beetles for which rearing procedures have not been described. Herein, we discuss a rearing procedure that yields large numbers of *D. catalinae* for subsequent release and we describe a simple computer model for evaluating harvesting strategies of *D. catalinae* in our insectary culture.

Materials and Methods

Facilities. The CDFA Biological Control Program has greenhouse facilities for rearing natural enemies at two sites in Sacramento, California. One greenhouse site (Meadowview) is located in south Sacramento and is 10.7 × 30.5 m in size. The second site (North B Street) is located approximately 14 km north and has three houses, each 7.6 × 30.5 m. The latter greenhouses were used primarily for rearing plants free of whitefly. The Meadowview greenhouse was used for rearing whiteflies and beetles.

Plant Culturing. Beetles were reared on *B. argentifolii* infested poinsettia plants, *Euphorbia pulcherrima* Willd. (Euphorbiaceae). Poinsettias were used because *B. argentifolii* reproduced well on these plants, they are easy to culture and handle, they are relatively free of secondary pests, and they are commercially available. Two cultivars of poinsettia, both highly susceptible to *B. argentifolii*, were used for rearing, Angelica White in 1992 and Annette Hegg in 1993. The latter was found to sustain higher numbers of immature whiteflies. Commercially purchased rooted cuttings were grown in a commercial mix of of 48% peat : 45% perlite : 7% sand following standard propagation practices (Jall et al. 1993). Plants were maintained at 28–30°C during the day and 24–26°C during the night. We used a 14L:10D photoperiod during the winter and spring months; natural light was used during summer months. Potted plants were grown for 4–6 weeks at the North B Street greenhouse until they reached an approximate height of 15 cm and were then transported to the Meadowview greenhouse. Plants were pinched back to the first fully mature leaf just prior to being moved into the whitefly culturing room. This removal of plant tissue made for a shorter, stiffer plant that could withstand greater shaking and handling associated with rearing of *D. catalinae*.

Insect Culturing. The Meadowview greenhouse has three rearing rooms, each separated by a wall of glass and brick. *Delphastus catalinae* and *B. argentifolii* were reared independently in separate rooms. The whitefly rearing room contained eight 2.4 × 1.2 m benches and lighting and temperature regimes as described above. On each bench, 50 plants were spaced equidistant from each other and were held in the room for approximately 4 weeks prior to their movement to the beetle-rearing room. This period permitted regeneration of the whitefly culture and thorough infestation of the plants with immature whiteflies.

Whitefly-infested plants within the beetle-rearing room were spaced equidistantly on 2.4 × 1.2 m greenhouse benches covered with fine-mesh plastic cloth, which prevented beetles from dropping to the greenhouse floor. The culture was initialized with approximately 1200 male and 1200 female adult beetles over a 4-week period. The beetle-rearing room of the greenhouse was maintained during the day at 26.5–29.5°C and during the night at 24–26°C. Approximately 200–500 plants were used to maintain beetles at any one time during maximum beetle production, July through September. Host plants typically remained in the beetle culture for 4 weeks, the period of time when more than 75% of whitefly nymphs and eggs were consumed. Every week approximately 50 new plants heavily infested with whiteflies were added to the beetle production room and 50 were removed. To insure beetles always had a constant and unlimited food source, an entire potted plant was disposed of when it no longer supported visibly high densities of whitefly nymphs and eggs, or when the plants were senescent.

A large number of beetle larvae pupated inside crevices on the sides and bottoms of plant pots. Therefore pots of destroyed plants were retained among the new host plants until adults emerged.

Collection and Monitoring of Beetles. Beetles were collected once a week for shipment to field sites. In 1993, prior to collection, we estimated the number of adult beetles in the greenhouse in an effort to maximize the number of beetles that could be removed while maintaining the highest sustainable yields. We removed from 40 to 60% of the total available adults. Beetle densities were estimated by sampling from three plants on each of six benches ($n = 18$) using the same technique as that used when collecting beetles for shipment to field sites. Individual plants were shaken by hand for up to 5–10 s over a sheet of paper. Dislodged beetles were counted and, with the aid of an electric vacuum pump, aspirated directly into 0.5-L plastic bottles used to deliver them to the field.

The larval population was also monitored weekly in 1993 to forecast the production of adults and monitor the status of the beetle population. Larvae were sampled by removing three leaves haphazardly from each of three plants on a maximum of six benches. Larvae were counted directly from leaves without magnification.

Delphastus catalinae **Population Model.** Prior to the 1993 rearing season, a computer population model was created to predict the initial growth of the *D. catalinae* population for planning purposes. The form of the model was a distributed delay, discrete, constant temperature, daily iterated approximation for the continuous growth process of the beetle population (Berry and Stinner 1992). Estimates for growth and mortality parameters were obtained from Hoelmer et al. (1993) and personal observations (C.H. Pickett). Although Hoelmer et al. (1993) report on values for *D. pusillus*, we believe they can represent those for *D. catalinae*, since the two species are closely related. Because the greenhouse had a constant-temperature regime on a daily basis, the model iterated on both a daily and physiological time basis. The average daily temperature was approximately 26–28°C. This corresponded well with the constant-temperature (28°C)

TABLE 1. Parameter values in the *Delphastus* model

Parameter	Value	Source
Longevity of adult	Male 44.8 days at 28°C; female 60.5 days at 28°C	Hoelmer et al. 1993
Developmental time from oviposition to eclosion	21.0 days at 28°C	Hoelmer et al. 1993
Pupal development time	6.0 days at 28°C	Hoelmer et al. 1993
Eggs laid per day	3 at 28°C	Hoelmer et al. 1993
Developmental distribution lag and advancement	0.0725	L.T. Wilson (personal communication), based on other insects
Egg mortality	0.5 over the stage duration	K.A. Hoelmer (personal communication)
Larval and adult mortality	0.01 per day	K.A. Hoelmer (personal communication)

studies of Hoelmer et al. (1993). The *C* computer language code for the model is included in the Appendix. Table 1 shows the parameters in the model and their derivations. As in the actual greenhouse production effort, the model was initialized with 1200 adult male and 1200 adult female *D. catalinae*. The model initially assumed unlimited availability of whiteflies to *D. catalinae*, as was observed to be the case for the previously described mass-rearing program. However, the model was modified to decrease fecundity by calculating a multiplicative fecundity scaler in the following density-dependent manner: the multiplicative fecundity scaler is 1 if the number of adult beetles per plant ≤200, 2 – [(number of adults per plant)/200] if the number of adult beetles per plant is less than 400 and greater than 200, and 0 if the number of adult beetles per plant ≥400. The relationship was derived from the average number of whiteflies per plant and the known consumption rates of the adult females (Hoelmer et al. 1993).

Harvesting Strategies. The *D. catalinae* population growth model was used to investigate hypothetical harvesting strategies. Specifically, we compared a "constant-number" beetle harvesting strategy versus a "constant-percentage" beetle harvesting strategy. The constant-number harvesting strategy was modeled by removing a fixed number of beetles at 7-day intervals. The constant-percentage harvesting strategy was modeled by removing a fixed percentage of beetles at 7-day intervals. The optimal number of beetles removed, and when, were calculated by running the appropriate version of the model for approximately 20 values and observing which gave the most constant harvest, and the largest total harvest of adult beetles over the season.

Results

Production of Beetles. A total of 174 245 adult beetles were collected during the summer of 1993. Usually 10 000 adult beetles per week were collected through August 1, and on average 6374 per week thereafter (SEM = 1340, *n* = 10; Fig. 1*a*). Practical experience and preliminary simulation runs indicated that approximately 50% of the adult population could be collected without causing a reduction in yield of adults. Estimates of the proportion of individuals harvested from the beetle population varied between 25 and 78% (Fig. 1*b*; *n* = 16).

The number of adult beetles per plant over the same period varied between 20 and 90: half the values were within 20% of the mean, 46.4 per plant (Fig. 2*a*). The total number of beetles in the greenhouse usually varied directly with the number per pot.

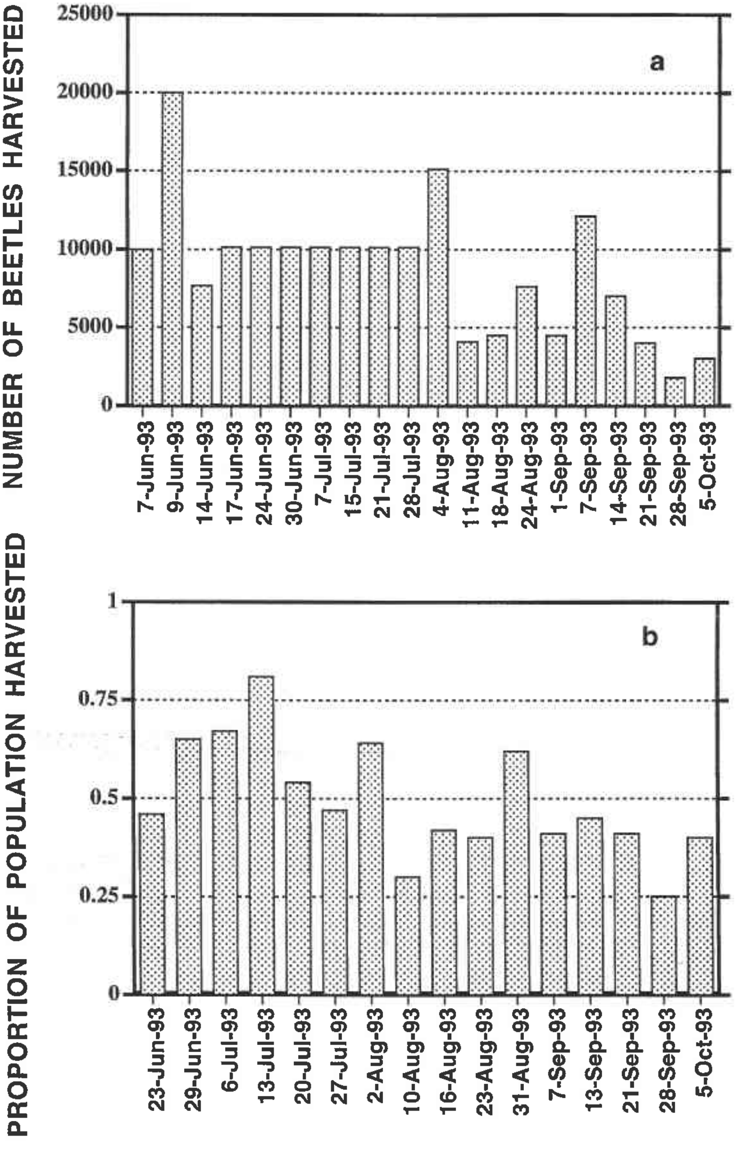

FIG. 1. Collection of adult *Delphastus catalinae* during 1993. (*a*) Total number of beetles harvested. (*b*) Proportion of available population harvested.

This was expected because the number of potted plants within the rearing facility remained fairly constant most weeks at 50 per table.

The larval population dynamics in 1993 show three distinct peaks (Fig. 2*b*). These are 26 and 29 days apart, approximating a generation period at greenhouse temperatures (Hoelmer et al. 1993). No significant correlation was detected between mean larvae and adults sampled on the same date, or between larvae and adults sampled 1, 2, and 3 weeks later ($p > 0.05$). However, adult beetles increased significantly, following each peak in larval density.

The variability in adult *D. catalinae* population dynamics within the rearing facility suggested that their current population size might have been influenced by the

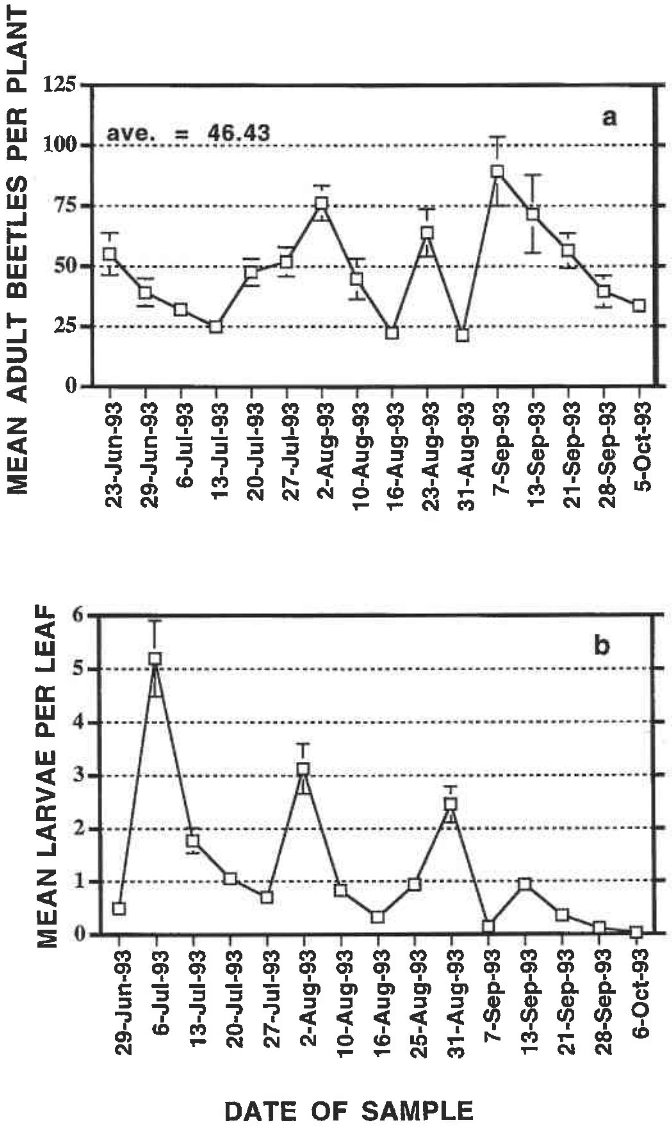

FIG. 2. Production of *Delphastus catalinae* in beetle-rearing room. (*a*) Mean (± SEM) number of adults per plant. (*b*) Mean (± SEM) number of larvae per leaf.

percentage of beetles collected at an earlier date. We tested this hypothesis by plotting the total number of adult beetles in the production room versus the proportion collected 3–5 weeks earlier (about one generation). A negative correlation would be expected if the number collected was a factor in future beetle densities, i.e. the higher the number collected, the fewer to produce future progeny. However, a slightly positive correlation was detected for current beetle population densities and the proportion of the population harvested 4 weeks earlier ($r = 0.56$, $p = 0.03$) (SAS Institute Inc. 1989). No significant correlations were apparent when the proportion of beetles collected in the rearing room was plotted against those harvested 3 and 5 weeks earlier ($p > 0.25$).

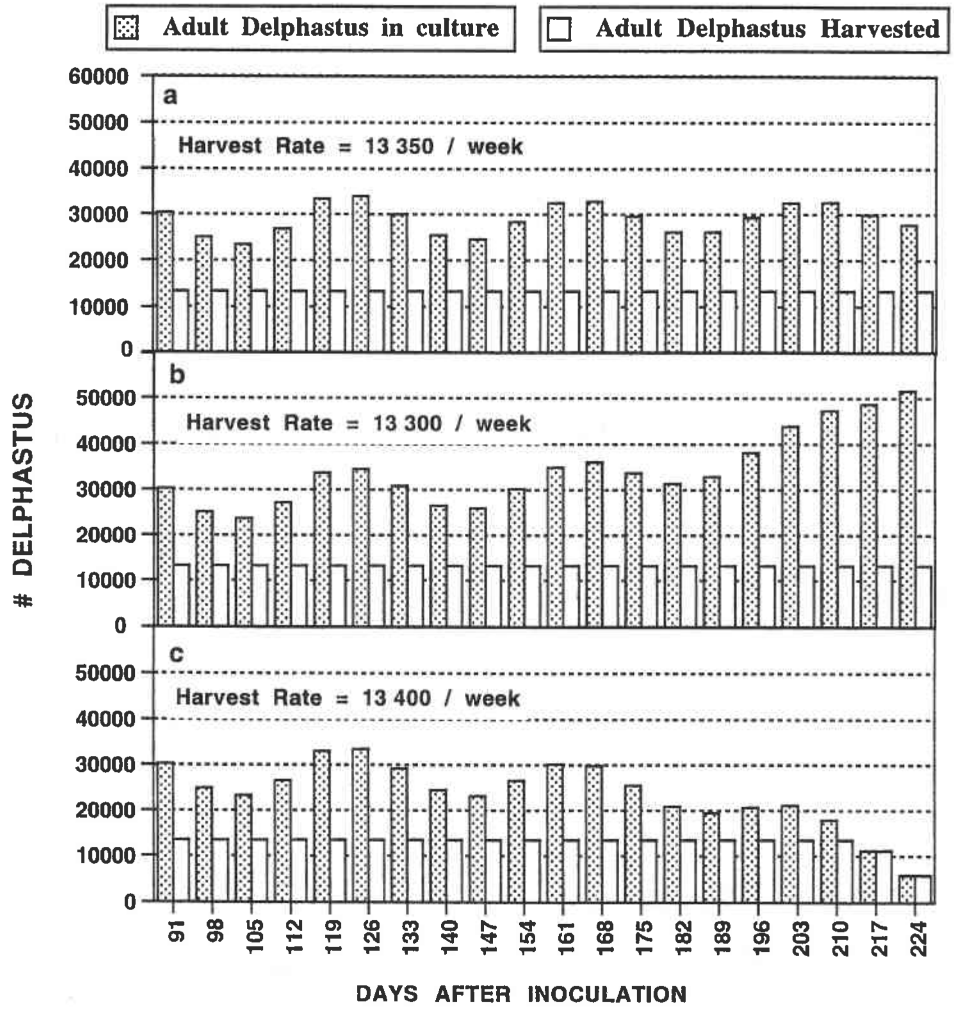

FIG. 3. Number of harvested adult beetles, calculated weekly by the population model under a constant-number harvest scheme: (*a*) 13 350 per week, (*b*) 13 300 per week, and (*c*) 13 400 per week.

Modeling Results. Initially the model was created and run to suggest the first beetle harvesting date. Not surprisingly, the model showed, prior to harvesting, an exponential increase in the number of adult beetles which was cyclic, and predicted that sufficient numbers of beetles would be available for harvesting after about 10 weeks or roughly three generations.

Using a constant number of harvested beetles, modeling results suggested that the removal of 13 350 *D. catalinae* per week caused the model population to enter into the most stable, moderately fluctuating cycle, which extended well beyond the 5-month harvesting period (Fig. 3*a*). However, small deviations from this rate (e.g., 50 per week) cause the model population to eventually increase (Fig. 3*b*) or to gradually die out (Fig. 3*c*) towards the end of the harvest period.

A scheme in which a constant proportion of adult beetles is removed (e.g., 50%) resulted in a different number of beetles being harvested each week. At a harvest rate of 48.6% the fluctuations in numbers removed were most dampened and approached a

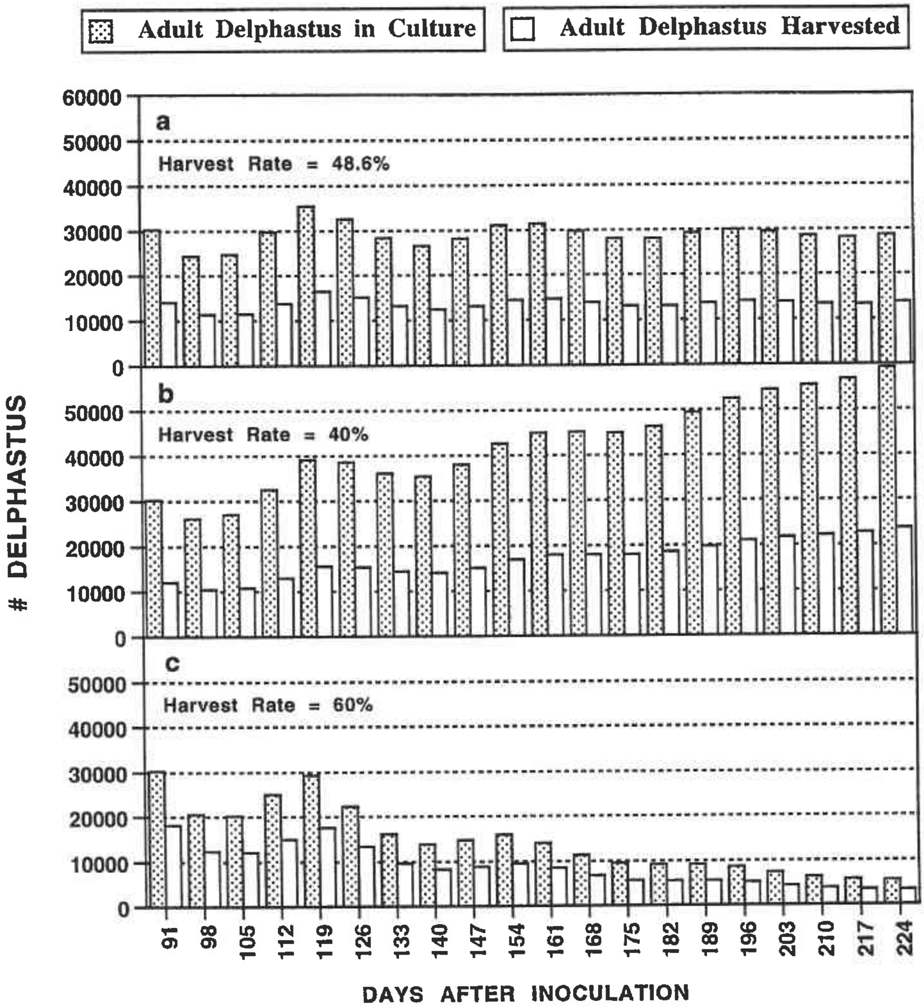

FIG. 4. Number of harvested adult beetles, calculated weekly by the population model under a constant-proportion harvest scheme: (*a*) 48.6% per week, (*b*) 40% per week, and (*c*) 60% per week.

constant value (Fig. 4*a*). Deviations in harvest percentage (ca. 10%) from this stable value caused the population and harvest numbers to gradually increase (40% harvest rate, Fig. 4*b*) or to progressively decrease (60% harvest rate, Fig. 4*c*).

Another issue, in addition to production stability, is maximizing the total number of beetles produced throughout the season. When removing the same number of adult *D. catalinae* each week, a harvest rate of 13 350 beetles per week resulted in the maximum total seasonal beetle production of 266 000 beetles (Fig. 5*a*). When removing the same proportion of adult beetles each week, a 14% harvest rate led to a maximum total seasonal production of 705 000 beetles (Fig. 5*b*). The constant, low proportion of harvested beetles early in the season allowed the population to build to higher numbers towards the end of the season. This finding suggests that a low harvest rate throughout the season maximizes total production, but is based on the model assumption of unlimited food during the production period. In our greenhouse production we were constrained by the number of plants we could supply and the ability of the whiteflies to maintain adequate densities.

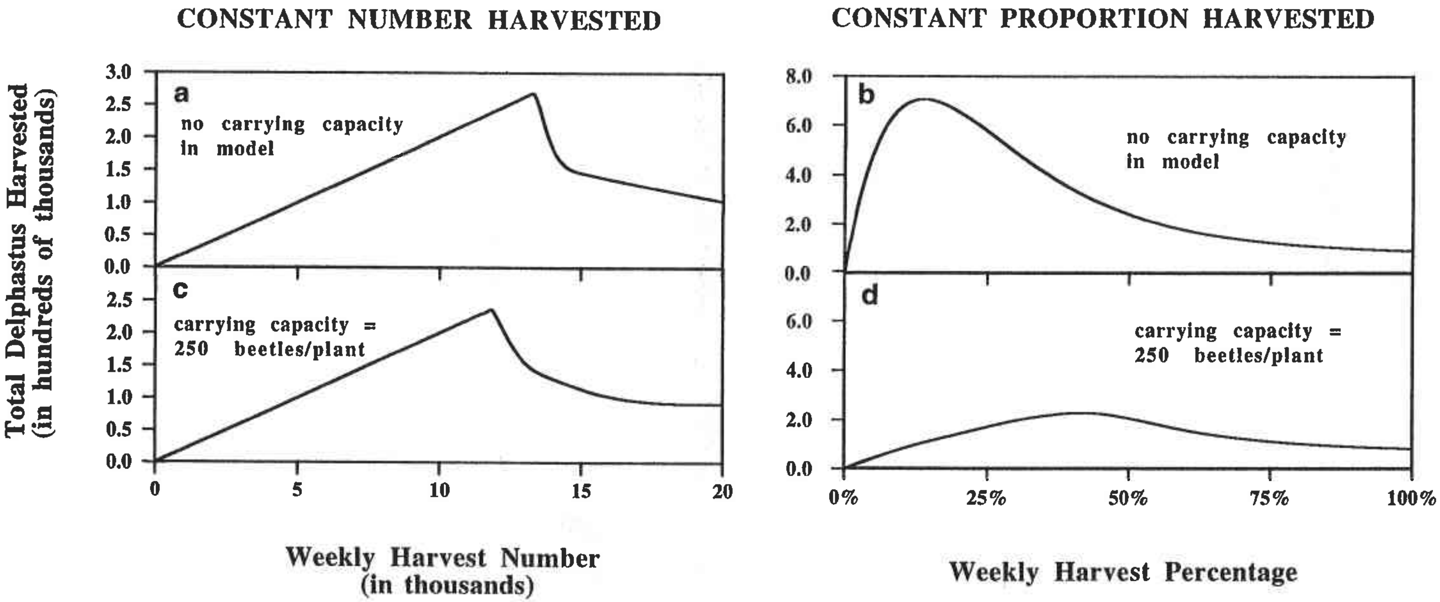

FIG. 5. Total number of beetles harvested throughout the season as a function of (*a*) weekly harvest number, no carrying capacity; (*b*) weekly harvest percentage, no carrying capacity; (*c*) weekly harvest number, carrying capacity of 250 beetles per plant; and (*d*) weekly harvest percentage, carrying capacity of 250 beetles per plant.

TABLE 2. Cost of producing adult *Delphastus catalinae* in summer 1993

	Cost (US$)
Personnel	
One permanent employee (three-quarters time)	23 000
Two technicians (half-time each)	10 000
Subtotal	33 000
Materials	
Plants (Annette-Hegg, dark red)	4 275
Soil	450
Pots	427
Fertilizer	300
Subtotal	5 452
Total	38 452
Cost per beetle through September 1993[a]	0.22

[a] Derived as (total production cost in US$) / (total number of adult beetles collected) = 38 452 / 174 245.

To more realistically investigate the full range of possible harvesting strategies, it was necessary to include a density-dependent mechanism in the model which would limit the reproduction rate of *D. catalinae* as they increased in number past a "carrying capacity" of the individual plants. Based on observed *Delphastus* and whitefly densities in the greenhouse and laboratory studies (K.A. Hoelmer, personal communication) we included a function in the model which caused a linearly progressive downscaling of beetle reproduction and survival as the population increased between 200 and 400 beetles per plant. Under the constant-number harvest scheme the inclusion of a downscaling function caused only a small change in model behavior, with the maximum seasonal harvest dropping to 223 000 beetles achieved at a removal of 11 800 per week (Fig. 5*c*). The inclusion of a downscaling function in the model for a proportional removal of beetles caused a larger change in the maximum seasonal beetle production, dropping to 227 000, and was achieved with a weekly harvest of 40% (Fig. 5*d*).

Cost of Production. The total cost of producing an adult beetle in 1993 was estimated at US$0.22 (Table 2). This figure underestimates the total cost because it does not account for maintenance, rent, and energy costs, figures that were unobtainable. However, the labor costs may be inflated because they include work required in the initialization of plant and insect cultures. During the first 5 months of the year, beetles were not being produced, only plants and whiteflies. Another compounding problem was contamination of our whitefly culture by *Encarsia formosa* Howard and *Encarsia pergandiella* Howard (Hymenoptera: Aphelinidae). Several times during the summer leaves were examined and between 50 and 70% of fourth instar or pupae were parasitized. As a result, much higher numbers of whitefly-infested plants were needed to maintain the beetle culture than would have occurred in the absence of these parasitoids. Costs were inflated by this source of contamination because of the increased number and handling of plants.

Discussion

Preparation for beetle production began 6 months before the first group of adult *D. catalinae* was collected. A substantial amount of time was required for growing plants and whiteflies to maintain beetle cultures. Simulation studies and prior experience indicated that three generations of beetles, corresponding to about 10 weeks, were needed before a large and rapidly increasing *D. catalinae* population was present.

Much of the variability in the adult population probably represents generational oscillations in the adult and larval populations over time (Fig. 2). The adult beetle population density varied less than anticipated considering the large number of individuals being removed weekly, and the continual addition and removal of plants from production rooms. The modeling results suggest that adult harvesting actually stabilized the population dynamics and is supported by an analysis of the greenhouse beetle populations. Harvesting higher numbers of beetles did not suppress future population densities.

Monitoring the dynamics of the larval population density may prove useful for rearing beetles. Future numbers of adult beetles may be related to current numbers of larvae. Peaks in larval populations were usually followed by a large increase in adult beetle numbers. Although larval and adult numbers were not correlated, peaks in larval densities may be used as one of several indicators of culture viability. If a population model is being used to assist in determination of harvesting tactics, it would be important to sample larvae and even eggs in addition to adults.

A critical issue facing any rearing operation of natural enemies as described in this paper is the optimal ratio of predator to prey. By removing too many beetles at any point in time, production rate (i.e., number of new beetles produced per week) may drop and the whiteflies could increase to levels that will kill plants. By maintaining a beetle population density that is too high, their source of food (whitefly nymphs) may be depleted to levels difficult to manage. The weekly removal of 49.3% of the adult population averaged over the collection phase of beetle production, June–October, resulted in a stable population of beetles, i.e., varied less than 10% of the mean (heavily infested plants were being moved into the beetle-rearing room weekly). Results from the modeling investigation suggest that harvesting 48.6% of the adults weekly (Fig. 4*a*) would provide a relatively constant supply of beetles and maximize total beetle production over the season given limitations on the amount of food supplied to the beetles.

Although *D. pusillus* have been shown to suppress *B. argentifolii* populations on poinsettia, tomatoes, and cotton (Heinz and Parrella 1994; Heinz et al. 1994; Heinz and Zalom 1996), the costs associated with the releases were high. Our estimated US$0.22 per adult is higher but similar to that charged by commerical insectaries. They charge between US$0.08 and US$0.16 per adult, depending on quantity purchased (J. Davis, personal communication). The high cost of rearing this predator will likely limit its use to high-value crops and greenhouse production. The major source of cost in our rearing was labor, which made up 86% of the total. Mechanization of rearing procedures or artificial diets would greatly reduce this cost. Increased demand and industry competition could further decrease the production costs, as has been seen in the commercial production of predacious mites. The cost for predacious mites has been reduced by up to 50% over the last 10 years, dropping from US$10.00 to US$15.00 per 1000 to US$5.00 to US$10.00 per 1000 (G. Scriven, personal comunication). Work by others (M. Rose, personal communication; Heinz and Parrella 1994) has shown that whitefly and other homopteran pests of greenhouse and interior-scape plants can be controlled using periodic releases of natural enemies. Malls, office buildings, and commercial greenhouse flower production all have pest problems that are difficult to control using insecticides because of human health risks. Under these situations, commercial use of *Delphastus* spp. for whitefly control would be feasible and desirable.

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Appendix

***C* Language Computer Code for the *Delphastus catalinae* Simulation Model.** The graphical output code has been removed for brevity. Model structure and algorithms are explained in the text. Model parameter sources are presented in Table 2. This listing contains algorithms for both constant-rate and constant-number harvesting. Only one of these code blocks was activated at a time.

```
#include < c:\tc\include\math.h >
#include < c:\tc\include\graphics.h >
#include < c:\tc\include\conio.h >
#include < c:\tc\include\stdio.h >
#include < c:\tc\include\stdlib.h >
```

```
main(int argc,char *arvc[])
{
int driver,mode,j,z,zz,xx,a,s,b,w,day;
float egglarv[21],pupae[6],males[70],females[70],el,p,mf,eps,epsc,x,numharv,
harvrate,r,x1,x2,eggmort,eggs,take,scaler,total;
char zname1[20],zname2[20],zname3[20],zname4[20],sdum[10];
FILE *fp1,*fp2,*fp3;
/***********************************************************
Parameters
***********************************************************/
harvrate = atof(arvc[1]);
take = atof(arvc[2]);
eps = 0.075;
epsc = 1.0 - (2.0 * eps);
eggmort = 0.5;
eggs = 3.0;
survive = 0.99;
/***********************************************************
Open Files
***********************************************************/
if ((fp1 = fopen("del.ini","r")) = = NULL) {
printf(“Cannot open input file \n");
exit(1); }
if ((fp2 = fopen("del.out","w")) = = NULL) {
printf("Cannot open output file \n");
exit(1); }
if ((fp3 = fopen("harv.out","w")) = = NULL) {
printf("Cannot open output file \n");
exit(1); }
/***********************************************************
read in population initializations from file - del.ini
***********************************************************/
fscanf(fp1,"%s",sdum);
fscanf(fp1,"%s",sdum);
for (s = 0; s < 21; s++) { fscanf(fp1,"%s %f",sdum,&egglarv[s]); }
for (s = 0; s < 6; s++) { fscanf(fp1,"%s %f",sdum,&pupae[s]); }
for (s = 0; s < 70; s++) { fscanf(fp1,"%s %f",sdum,&males[s]); }
for (s = 0; s < 70; s++) {fscanf(fp1,"%s %f",sdum,&females[s]); }
fclose(fp1);
/***********************************************************
A PASS FOR EACH NEW DAY
***********************************************************/
total = 0.0;
for (day = 0; day < 230; day++) {
/***    age the adults population    ***/
for (s = 69; s > = 0; s--) {
males[s] * = eps;
if(s > 0) males[s] + = epsc * males[s-1]*survive;
if(s > 1) males[s] + = eps * males[s-2]*survive;
females[s] * = eps;
if(s > 0) females[s] + = epsc * females[s-1]*survive;
```

```
if(s > 1) females[s] + = eps * females[s-2]*survive;
}
males[1] + = 0.5 * eps * pupae[5]*survive;
males[0] + = 0.5 * epsc * pupae[5]*survive;
males[0] + = 0.5 * eps * pupae[4]*survive;
females[1] + = 0.5 * eps * pupae[5]*survive;
females[0] + = 0.5 * epsc * pupae[5]*survive;
females[0] + = 0.5 * eps * pupae[4]*survive;
for (s = 5; s > = 0; s--) {
pupae[s] * = eps;
if(s > 0) pupae[s] + = epsc * pupae[s-1];
if(s > 1) pupae[s] + = eps * pupae[s-2];
}
pupae[1] + = eps * egglarv[20]*survive;
pupae[0] + = epsc * egglarv[20]*survive;
pupae[0] + = eps * egglarv[19]*survive;
for (s = 20; s > = 0; s--) {
egglarv[s] * = eps;
if(s > 0) egglarv[s] + = epsc * egglarv[s-1];
if(s > 1) egglarv[s] + = eps * egglarv[s-2];
}
/***   generate output totals   ***/
el = p = mf = 0.0;
for (s = 0; s < 21; s++) { el + = egglarv[s]; }
for (s = 0; s < 6; s++) { p + = pupae[s];}
for (s = 0; s < 70; s++) { mf + = (males[s]+females[s]); }
/***   females lay their eggs   ***/
/***   density dependence   ***/
scaler = 2 - (mf/200);
if (mf < = 200) con = 1;
if (mf > = 400) con = 0;
for (s = 69; s > = 5; s--) { egglarv[0] + = eggs * eggmort * scaler * females[s]; }
/***   harvesting every seven days if constant rate   ***/
numharv = 0.0;
r = harvrate;
if((fmod(day,7) = = 0)&&(day > 90)) {
vv + = 1;
for (s = 69; s > = 0; s--) {
numharv + = (females[s] * r) + (males[s] * r);
females[s] * = (1-r);
males[s] * = (1-r); }
total + = numharv; }
/***   harvesting every seven days if constant number   ***/
/*numharv = 0.0;
r = take/mf;
if (r > 1.0) r = 1;
if((fmod(day,7) = = 0)&&(day > 90)) {
for (s = 69; s > = 0; s--) {
numharv + = (females[s] * r) + (males[s] * r);
females[s] * = (1-r);
males[s] * = (1-r); }
```

```
total + = numharv; } */
} /* end daily loop */
fclose(fp2);
return 0;
}
```