BIOLOGICAL CONTROL **6,** 35–44 (1996)
Article No. 0005

Quantifying Movement of a Minute Parasitoid, *Anagrus epos* (Hymenoptera: Mymaridae), Using Fluorescent Dust Marking and Recapture

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Received January 20, 1995; accepted June 26, 1995

A mark–recapture methodology is presented for quantifying dispersal parameters for small hymenopteran parasitoids. Results of studies using this methodology are presented for the egg parasitoid *Anagrus epos* (Hymenoptera: Mymaridae) dispersing in grape vineyards in California. *A. epos* was found to exhibit some upwind displacement in all three mark–recapture trials and strong directional upwind displacement in one of the trials. A preliminary estimate of 520 m^2/day is suggested for the diffusion rate of *A. epos* in mid-summer at high host densities. The high mobility and directionality exhibited by this parasitoid support concerns regarding dispersal of biocontrol agents away from target areas following augmentative releases. Application of this methodology to other small parasitoids should be feasible and will contribute to effective augmentative biological control.

KEY WORDS: ***Anagrus epos;* egg parasitoid; mark–recapture; diffusion; mobility; fluorescent dust marking.**

INTRODUCTION

The implementation of biological control strategies using entomophagous arthropods almost invariably relies upon the movement of the control agent. Biocontrol agents released in augmentative programs must spread from release points and subsequently occupy the target area over which control is desired. In "classical" biological control programs (Caltagirone, 1981), establishment is dependent on the agent (1) dispersing from release locations, (2) locating overwintering sites, and (3) dispersing from overwintering sites to locate and exploit host/prey. In habitat management approaches the control agent must disperse from the vegetation providing overwintering sites or complementary resources to exploit host/prey on nearby crops.

Despite the critical role of movement in biological control, there is minimal information on the flight behavior and mobility of biocontrol agents. Upon implementation of a biocontrol program it is rarely known, for example, how rapidly the control agent is distributing throughout the target area for which control is desired or what proportion of the released individuals remain within the target area. It is also generally not known how physical factors such as wind, temperature, and vegetation structure are influencing the patterns of distribution. Wind is likely to be a particularly important factor for minute parasitic Hymenoptera (e.g., trichogrammatids; Pedgley, 1982; Keller *et al.*, 1985); it is as yet unclear whether these small organisms are always carried downwind or whether upwind displacement, such as in anemotaxis, is possible under some conditions. The movement behavior of biocontrol agents is likely to vary between species and release conditions and will, in part, determine the degree of control achieved as a result of the biological control intervention. For example, researchers evaluating the augmentation of *Trichogramma* spp. in cotton concluded that the rate of movement of individuals following release, and in particular their tendency to remain in the target control area, represents a critical gap in information that limits our ability to successfully understand and implement augmentation methodologies (Keller *et al.*, 1985; Goodenough and Witz, 1985).

An established methodology for quantifying insect mobility is the use of mark–recapture data to obtain an estimate of the "diffusion" parameter, *D* (Kareiva, 1982; Wetzler and Risch, 1984; Rudd and Gandour, 1985; Plant and Cunningham, 1991). The diffusion parameter represents the random component of movement independent of other forces acting on the organism such as prevailing winds, attraction toward particular habitats or food sources, or repulsion from conspecifics (Okubo, 1980). Application of this approach to quantifying the mobility of insects, and of biological control agents in particular, has two primary benefits: (1) it provides a common measurement of mobility that can be compared across taxonomic groups and across experimental conditions (assuming pitfalls in recapture meth-

1049-9644/96 $12.00

odology are avoided—see Kareiva, 1981), and (2) the parameter D can be used directly in a modeling framework to predict the distribution of insects at time $t > 0$ given a known distribution at time $t = 0$. Estimates of D have been obtained for many herbivorous insects using this approach, but for only a handful of entomophagous insects (see Corbett and Plant, 1993).

A particularly important group of biological control agents for which we have found no published estimates of the diffusion parameter are the minute parasitic Hymenoptera. For example, members of the families Trichogrammatidae, Encyrtidae, Aphelinidae, Aphidiidae, and Mymaridae. These parasitoids are typically very small ($\leq$1 mm) and delicate in structure, which makes experimental manipulations of any sort challenging. The conventional methods of marking are not feasible for these organisms. It is difficult to apply a mark directly to individuals. Direct applications of fluorescent powders are likely to have severe negative impacts on survivorship and behavior. Some researchers have attempted to overcome this obstacle through using patterns of egg parasitism as an indicator of adult distribution patterns (Yu *et al.,* 1984; Smith, 1988). While this approach can provide a gross indication of mobility, it has two serious shortcomings: (1) the relationship between instantaneous adult distribution and the distribution of parasitism events is indirect and dependent on many interacting factors, making it difficult to obtain a meaningful estimate of mobility that can be compared with other experimental results (see Kareiva, 1981); and (2) it can only be applied when the background parasitism rate is extremely small relative to that produced by the released individuals. Radioactive (Stern *et al.,* 1965) and trace-element (Jackson *et al.,* 1988) labeling have been successfully used to label minute Hymenoptera. Radioactive labeling is generally not feasible as a result of environmental concerns. Trace-element labeling shows great promise in quantifying movement of small Hymenoptera, but not all researchers will be equipped or inclined to learn and apply this methodology.

In this paper we present a methodology for quantifying the mobility of the minute egg parasitoid *Anagrus epos* Girault (Hymenoptera: Mymaridae) that circumvents the difficulties stated above. The essence of this proposed methodology is that, rather than attempting to apply marks to individuals directly, plant material containing parasitized host eggs is treated with fluorescent powder and parasitoids "mark themselves" in the process of emerging from the host. A similar approach has been used to label bark beetles emerging from logs dusted with fluorescent powder (Cook and Hain, 1992) and to label a parasitoid of tephritid fruit flies emerging from dusted puparia (Messing *et al.,* 1993). Appropriate analysis of recapture data obtained with this method will yield an estimate of the diffusion rate. In addition, recapture data can be used to evaluate and quantify directional displacement, such as in response to wind.

The objectives of this paper are: (1) to evaluate the potential of this proposed methodology for studying movement of minute parasitic Hymenoptera; (2) to quantify mobility of and to assess directional displacement by the egg parasitoid *A. epos;* and, (3) to suggest a computational procedure for estimating rates of diffusion and directional displacement based on recaptures obtained with this method.

MATERIALS AND METHODS

Mark–Recapture Methodology

A. epos is a major mortality factor for the grape leafhopper (GLH), *Erythroneura elegantula* (Homoptera: Cicadellidae), an important pest of vineyards in the western United States (Doutt and Nakata, 1973). The studies presented here were conducted in grape vineyards in California's San Joaquin Valley as part of an effort to better understand the dynamics of this parasitoid/herbivore interaction. GLH lays its eggs directly within leaf tissue just beneath the leaf surface. *A. epos* females oviposit inside these eggs through the leaf surface, resulting in a single adult *A. epos* emerging from the parasitized egg. This aspect of their biology suggests a means of indirect marking. Specifically, leaves containing parasitized eggs with *A. epos* in an advanced stage of development can be collected from the field and treated with fluorescent powder. Adult *A. epos* emerging from dusted leaves will then "self-mark" by picking up a small amount of powder during and following emergence.

Grape leaves were treated with fluorescent dust as follows. All leaves for a mark–recapture trial (up to 1000 leaves) were collected over a period of a few hours. Individual leaves collected were from the middle to lower (i.e., older) section of a cane and exhibited a moderate amount of GLH damage (as indicated by stipling on the upper surface of leaves). Use of these characteristics maximizes the number of parasitized eggs collected. These leaves were then quickly transported in coolers to the lab and kept refrigerated until treated with fluorescent powder. "Fire Orange" fluorescent powder from Day-Glo Color Corp. (Cleveland, Ohio; Product Code: AX-14-N) was used in all mark–recapture trials. The powder was first dispersed in a "carrier" medium of ground walnut husks (purchased at a local pet shop) to achieve light and uniform application of the powder over the whole leaf surface. Roughly 75 to 100 ml of powder was mixed into approximately 1 kg of walnut husk grinds in a plastic bag. Four or five leaves were placed into a bag at a time and gently rolled in the medium for approximately 1 min. Subsequent to dusting, leaves were placed in "emergence boxes" at roughly 100 leaves per box.

Emergence boxes consisted of 25.4 × 30.5 × 40.6-cm cardboard boxes, lined with plastic to minimize leaf desiccation, and having four 1-in.-diameter holes cut out to allow escape of emerged *A. epos*.

Preliminary testing was conducted in the lab to determine the success of the marking technique. *A. epos* were collected from emergence boxes in vials, released into rearing cages, and subsequently captured on 7.6 × 12.7-cm yellow cards coated on both sides with "Stickem Special." *A. epos* captured on sticky-cards were examined under a dissecting scope using high intensity fiber-optic lighting.

Mark–Recapture Trials

1991. One mark–recapture study was conducted during August 1991 in a block of Chardonnay near the intersection of Rd. 25 and Hwy. 113 in Yolo Co., California. On August 14, 400 grape leaves were collected and placed in cold storage. On August 19 leaves were dusted with fluorescent powder and placed in four emergence boxes as described above. On the morning of August 21 these emergence boxes were placed in the field by suspending them from trellis wires beneath the grape canopy. The boxes were deployed immediately adjacent to one another.

To recapture marked *A. epos*, a grid of 7.6 × 12.7-cm yellow cards, coated on both sides with Stickem Special, was established with the emergence boxes at the center of the grid. The use of yellow cards is not expected to significantly influence or bias the recapture of *A. epos* since cards were placed within a dense canopy and any attraction would have occurred only within a short radius immediately around the card. One hundred and one cards were deployed in a "compound" grid as follows: (1) 81 cards in a 9 × 9 grid with 1 card placed within the canopy of each vine, (2) an additional 20 cards in a 4 × 5 grid with cards placed in-between vines at the center of the larger grid (see Fig. 2). Both vinerows and vines in this block are spaced 2.74 m apart. Cards were initially put out immediately after the emergence boxes were placed in the field on the morning of August 21. Cards were subsequently replaced at 24-h intervals for the next 4 days, with the final set of cards being taken down on the morning of August 25, for a total of 4 days of sampling. The average daily maximum temperature over these 4 days was 34.2°C. All captured *A. epos* were examined under a dissecting microscope at 50× using high-intensity fiber-optic illumination to determine whether they were marked with fluorescent powder.

1992. Two mark–recapture studies were conducted during July 1992 in vineyards near Lodi, California. For the first study (trial I), 1000 leaves were collected on July 13. Leaves were dusted with fluorescent powder and placed in emergence boxes on July 13 and 14. Ten boxes, each with 100 dusted leaves, were deployed on the afternoon of July 15 in a French Colombard block near the intersection of Kettleman and Alpine Rds. (east of Lodi, CA). For the second study (trial II), 1000 leaves were collected on July 20. Leaves were dusted with fluorescent powder and placed in emergence boxes that same day. On the morning of July 21, 10 emergence boxes were placed in a French Colombard block near the intersection of Davis and Woodbridge Rds. (west of Lodi, CA). All emergence boxes were suspended beneath the grape canopy immediately adjacent to one another, in five pairs arranged vertically (but separated to allow escape of *A. epos*).

In both of these studies, marked *A. epos* were recaptured on 25.4 × 25.4-cm yellow cards, coated on both sides with petroleum jelly, deployed in a grid with the emergence boxes at the center. Seventy cards were put out in a 7 × 10 grid with cards placed in the canopy of every other vine. At both sites vinerows were spaced 3.65 m apart and vines were spaced 2.44 m apart. Cards were put out 24 h after the emergence boxes were placed in the field and left in place for a total of 4 h. Average hourly temperature during this 24-h period for trial I was 23.4°C, with a maximum of 32.6°C; for trial II the average was 20.4°C, with a maximum of 30.1°C. All captured *A. epos* were examined under a dissecting microscope at 50× using high-intensity fiber-optic illumination to determine whether they were marked with fluorescent powder.

Analysis of Recaptures

Descriptive recapture patterns. Conventionally, mark–recapture results are summarized by generating parameters such as mean squared displacement, horizontal variance in recaptures, and kurtosis of the recapture distribution, ultimately leading to an estimate of the diffusion rate of dispersing insects (Kareiva, 1982; Wetzler and Risch, 1984). Calculation of these parameters is based on the presumption of an underlying Gaussian distribution of recaptures. Such a distribution is expected when marked individuals are released simultaneously and subsequently move randomly and independently of one another (Kareiva, 1982). These assumptions are violated by the nature of releases in this study: marked *A. epos* emerge from boxes over time following their placement in the field. Such a situation results in a nonGaussian pattern of recaptures (Okubo, 1980). The appropriate equation for this situation is used to estimate diffusion from our recapture data and will be discussed in detail below.

To assess directional tendencies of movement, the mean angle of displacement was calculated for recapture data following Zar (1984). A χ^2 analysis was performed for each recapture data set to determine if there were significant differences in the probability of *A. epos* movement upwind versus downwind. This χ^2 analysis was done as follows. Data for hourly wind

speed and direction recorded at nearby weather stations were obtained from the California Irrigation Management Information System (California Dept. of Water Resources). The average wind direction was calculated for the period over which dispersal was monitored in each mark–recapture trial. A line was drawn through the origin, i.e., the location of emergence boxes, perpendicular to the average wind direction. Recaptures were then classified as occurring upwind or downwind of the release point based on their position relative to this line and a χ^2 analysis performed to determine whether these recaptures occurred randomly with respect to wind direction.

Estimation of diffusion and advection. Movement of an insect can be described quantitatively by estimating parameters of diffusion and advection, which characterize the overall mobility of an insect and the strength of directional tendencies in movement, respectively (Okubo, 1980; Kareiva, 1981; Plant and Cunningham, 1991). Parameters for diffusion and advection of *A. epos* under the conditions of the mark–recapture trials were estimated by fitting a mathematical model to the recapture data of each trial. The differential equation describing diffusive movement with advective flow in two dimensions is

$$\frac{\partial n}{\partial t} = -c\left(\frac{\partial n}{\partial x}\cos\phi + \frac{\partial n}{\partial y}\sin\phi\right) + D\left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2}\right), \quad [1]$$

where n is insect density. Assuming that all marked individuals are released instantaneously at position $x = y = 0$ and at time $t = 0$, the equation describing the distribution of individuals at time $t > 0$ is

$$n(t, x, y) = \frac{n_0}{4\pi Dt}\exp\left[-\frac{((ct - x\cos\phi - y\sin\phi)^2 + (-x\sin\phi + y\cos\phi)^2)}{4Dt}\right]. \quad [2]$$

The parameters in these equations are: the diffusion rate, D; the advection rate, c; the angle of advection, θ; and the number of released individuals, n_0. This equation has been used by Plant and Cunningham (1991) to estimate diffusion and advection parameters for the Mediterranean fruit fly (*Ceratitis capitata* Wied.), where large numbers of marked individuals were released simultaneously in mark–recapture studies.

In our methodology, marked individuals are not released simultaneously, but rather emerge over time from boxes following their placement in the field. Obtaining an appropriate model for this situation requires a modification to Eq. [2]. Specifically, the continuous release situation can be approximated by assuming that a continuous release is analogous to a sequence of instantaneous releases that occur at discrete, closely spaced intervals of time. Such an approach is referred to as "superposition" (Okubo, 1980) and is represented by

$$n(t, x, y) = \sum_{k=1}^{m}\frac{Qs}{4\pi D(sk)} \times \exp\left[-\frac{((sk - x\cos\phi - y\sin\phi)^2 + (-x\sin\phi + y\cos\phi)^2)}{4D(sk)}\right], \quad [3]$$

where s is the interval between instantaneous releases and $m = t/s$. This new model replaces t with (sk) and n_0 with (Qs), where Q is the rate of emergence of marked individuals per unit of time. When $s = t$, Eq. [3] simplifies to Eq. [2]. In the limit, as s goes to zero, this equation will yield the integral of Eq. [2] with respect to time. We have opted, rather than integrating, to utilize the discrete version, Eq. [3], as our model to fit. This is primarily because of the flexibility that this approach provides: any appropriate solution of a diffusion-based model which assumes instantaneous release can be substituted into Eq. [3] without requiring the analytical solution of its integral.

The parameters D, c, θ, and Q were estimated for each of the two 1992 mark–recapture trials by fitting Eq. [3] to recapture data using the Nelder–Mead method (Press *et al.*, 1988). Parameter estimation was not done for 1991 recapture data. The fact that cards were left out for 24 h at a time in 1991 violates the assumptions of Eq. [3]; in 1992, however, cards remained out for only 4 h, providing data on distribution for a short time period (Kareiva, 1981). The Nelder–Mead procedure uses a geometrically based algorithm to find the parameter values that result in a minimum sum of the squared deviations between observed and predicted. This method is particularly appropriate for Eq. [3] since it does not make special assumptions concerning the nature of the function being minimized and, more importantly, it does not require the solution of partial derivatives, as do many least-squares minimization procedures (Press *et al.*, 1988). Prior to model fitting, absolute recaptures were converted to densities by dividing by the mean area per trap. To obtain predicted values, Eq. [3] was evaluated using $s = 0.001$ days.

A shortcoming of the Nelder–Mead method is that it does not generate confidence intervals for estimated parameters. Variability in the recaptures between adjacent traps, however, suggested the potential for a large amount of uncertainty in our parameter estimates. To address this problem we implemented a "bootstrap-like" procedure to evaluate this uncertainty (Dixon, 1993). Specifically, traps were grouped into 35 pairs, with 7 pairs of adjacent traps for each of the five trap rows (Figs. 3 and 4). It was then assumed that each trap position could have received either one of the two recapture values for its respective pair. Based on this assumption, 100 hypothetical data sets were randomly

generated from the recapture data of each trial. D, c, θ, and Q were then estimated for each of these hypothetical data sets and frequency distributions obtained for each parameter.

RESULTS

Success of Marking A. epos

Examination of individual *A. epos* on test cards indicated that particles of fluorescent dust were detectable on greater than 85% of *A. epos* emerging from boxes of dusted grape leaves. These particles were detectable at a magnification of 50 times, but not at lower magnification. The majority of marked individuals had one or a few minute particles of dust caught in wing hairs. A smaller number had a small particle of dust on the thorax. Some *A. epos* had one or more fluorescent dust particles immediately adjacent to them on the card, within a few millimeters, but none detectable on the body of the insect. These individuals were also considered as "marked." None of the marked individuals had more than a few dust particles, suggesting that there would be minimal effects on behavior or survivorship. During one of the preliminary lab tests, traps were placed in rearing cages 48 h after test individuals had been released into the cage. Fluorescent dust was detectable on roughly 70% of *A. epos* on these traps indicating that, under laboratory conditions, the fluorescent mark is retained by most individuals for extended periods following emergence. Attempts to utilize UV light to enhance the detection of marked individuals were not successful. Due to the minute size of dust particles comprising a "mark," the fluorescent powder was easier to detect under high-intensity illumination with high magnification than with UV light.

Recapture Patterns

A. epos marked with fluorescent dust were recaptured throughout the trapping grids, including traps most distant from the emergence boxes, in all three mark–recapture trials (Figs. 2–4). A total of 141 individuals were recaptured during the 4 days of trapping in the 1991 trial; 90 and 65 individuals were recaptured in the two 1992 trials during the 4 h of trapping for each trial. In both 1992 trials, marked individuals were recaptured on traps furthest away from the emergence boxes, 24.5 m, 24 h following the initiation of emergence. Thus, *A. epos* is capable of dispersing at least 24.5 m/day and will retain fluorescent dust over this distance and time period.

Wind directions were consistent during the period that dispersal was monitored for each of the mark–recapture trials. The mean hourly wind direction over the 4 days of the 1991 trial was 263° (i.e., direction wind flowing toward; N = 0°, E = 90°, etc.) and was significantly clumped relative to a uniform distribution of wind directions ($z = 4.24$; $P < 0.02$). The mean hourly wind directions for the 24 h from initiation of emergence to the time of recapture during 1992 mark–recapture trials I and II were 97° and 22°, respectively (Fig. 1). Both estimates were significantly clumped relative to a uniform distribution of wind directions ($z = 13.9$, $P \ll 0.001$; $z = 4.27$, $P < 0.02$, respectively). Average hourly wind speed during trial I was 1.92 m/s with a maximum of 4.1 m/s at 1800 h (July 15) and a minimum of 0.5 m/s at 0400 h (July 16). Average hourly wind speed during trial II was 1.89 m/s with a maximum of 4.3 m/s at 1700 h (July 21) and a minimum of 0.6 m/s at 2200 h.

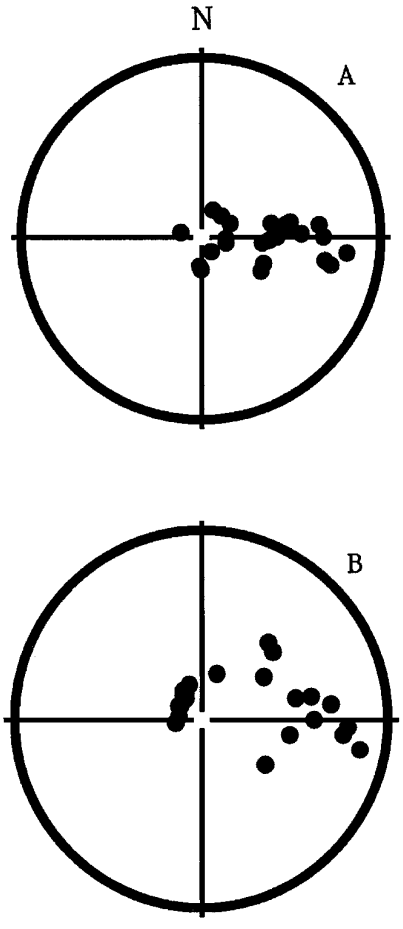

FIG. 1. Distribution of hourly wind directions and speed for 1992 mark–recapture trials (A) I and (B) II. Vector drawn from origin to point indicates direction and magnitude of wind. North is at 0°; west is at 270°. Maximum wind speed for trial I and trial II are 4.1 m/s and 4.3 m/s, respectively.

The mean direction of displacement from the emergence boxes for the 1991 trial was 2.8° (Fig. 2; N = 0°, E = 90°, etc.). Using the average wind direction as a reference, 59.6% of recaptures were upwind of the emergence boxes. A χ^2 test resulted in rejection of the hypothesis that dispersal was random with respect to wind direction ($\chi^2 = 4.84$, $P < 0.05$). The mean direc-

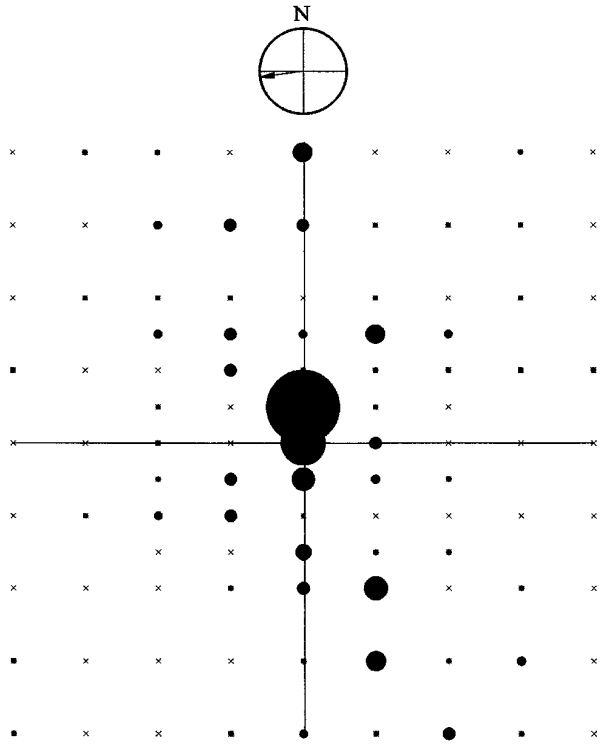

FIG. 2. Distribution of recaptures in 1991 mark–recapture trial. Largest symbol represents 20 individuals; smallest symbols represent 1 individual; crosses indicate trap positions at which no individuals were recaptured. North is at top of figure; arrow indicates average direction wind flowing toward during 4 days of emergence.

tion of displacement for the 1992 mark–recapture trials I and II were 317° and 239°, respectively (Figs. 3 and 4). These average directions are generally upwind with respect to the prevailing winds over the period that dispersal was monitored. Using the average wind direction as a reference, 72.3% of recaptures were upwind of the emergence boxes in mark–recapture trial I of 1992, and 72.2% were upwind in trial II. For both of these recapture patterns, a χ^2 test resulted in rejection of the hypothesis that dispersal was random with respect to wind direction ($\chi^2 = 12.94$, $P < 0.001$; $\chi^2 = 17.78$, $P \ll 0.001$, respectively).

Diffusion and Advection Estimates

The least-squares estimates for D, c, θ, and Q are shown in Table 1. For both mark–recapture trials, Eq. [3] does a better job of explaining the recapture data than does the mean. However, the correlation between predicted and observed recaptures is low. Our least-squares parameter estimates, therefore, must be considered as preliminary approximations of the movement characteristics of *A. epos*.

Recapture rates per trap were generally low, with a large number of zero values, a small number of nonzero values, and a large amount of variability in recaptures

TABLE 1

Estimates of Parameters of Eq. [3] Using Nelder–Mead, Least-Squares Minimization Procedure

Trial	D (m^2/day)	c (m/day)	θ	Q	RSS	RSS-μ	r
1992 I	47.8	10.6	347°	54.7	0.290	0.411	0.580
1992 II	522.6	164.6	239°	546.4	0.464	0.548	0.479

Note. RSS is the residual sum-of-squares agaisnt the fitted model. RSS-μ is the residual sum-of-squares agaisnt the mean recaptures per trap. r is the correlation coefficient between predicted and observed recaptures.

between adjacent traps (Figs. 3 and 4). This suggests that there is a large degree of uncertainty in our least-squares estimates of D. This is borne out by the distribution of our "bootstraped" estimates of D (Fig. 5). Simulated data sets from trial I generated estimates of D that are distributed relatively evenly across the interval from 30 to 1000 m^2/day. Given the large variability in bootstrapped estimates based on trial I we have minimal confidence in the "best-fit" value of 47.8 m^2/day (Table 1). Estimates of D based on trial II, on the other hand, were highly clumped around the

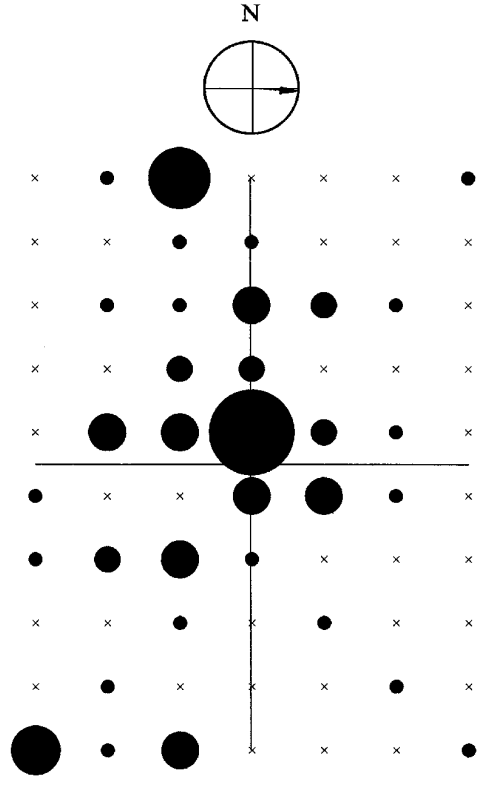

FIG. 3. Distribution of recaptures in mark–recapture trial I, 1992. Largest symbol represents seven individuals; smallest symbols represent one individual; crosses indicate trap positions at which no individuals were recaptured. North is at top of figure; arrow indicates average direction wind flowing toward during 24 h of emergence.

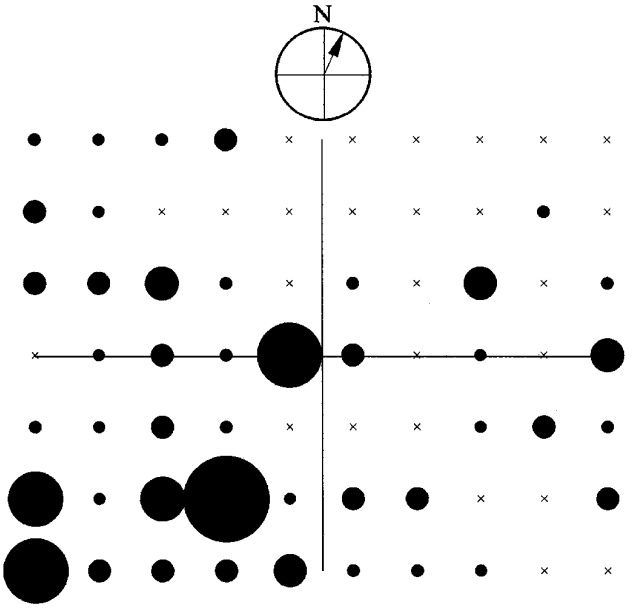

FIG. 4. Distribution of recaptures in mark–recapture trial II, 1992. Largest symbol represents eight individuals; smallest symbols represent one individual; crosses indicate trap positions at which no individuals were recaptured. North is at top of figure; arrow indicates average direction wind flowing toward during 24 h of emergence.

best-fit value of 522.6 m^2/day with 33% of the estimates falling between 500 and 1000 m^2/day. The high frequency at the upper end of the distribution (Fig. 5B) represents a long tail of estimates between 15,000 and 50,000 m^2/day; this is not surprising given the numerous large recapture values in the SW quadrant of the trapping grid in this trial. Given the high frequency of bootstrapped estimates at the least-squares estimate for trial II, and the substantial overlap with this value of bootstrapped estimates from trial I, we propose 520 m^2/day as a valid, albeit preliminary, estimate of the

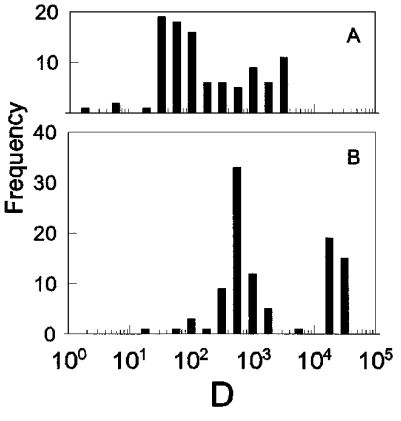

FIG. 5. Frequency distribution of diffusion rate (D = m^2/day) estimated from simulated data sets generated from recapture data from 1992 trial (A) I and (B) II. Each distribution is based on a total of 100 simulated data sets.

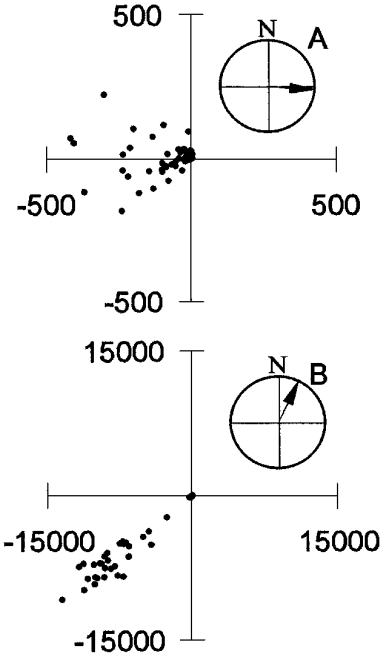

FIG. 6. Frequency distribution of advection vectors (combined c(= m/day) and θ) estimated from simulated data sets generated from recapture data from 1992 trial (A) I and (B) II. Each distribution is based on a total of 100 simulated data sets. North is at top of figure; arrows indicate average direction wind flowing toward during 24 h of emergence.

mobility of *A. epos* in grape vineyards under midsummer conditions—i.e., relatively high temperatures and high host abundance.

The least-squares estimates of c and θ (Table 1), and the variability in advection vectors (c and θ combined) obtained from simulated data sets (Fig. 6), indicate displacement of *A. epos* in an upwind direction. The magnitude and angle of advection is consistent with the descriptive assessment of directional movement (Fig. 6). This upwind displacement was particularly strong in trial II, with 90% of the estimates of c being greater than 130 m/day.

DISCUSSION

Movement Characteristics of A. epos

Mobility, in terms of diffusion rate, has been quantified for only a small number of entomophagous arthropods (Table 2). We have found no estimates of D for parasitic Hymenoptera. Using 520 m^2/day as a preliminary estimate of mobility, *A. epos* is clearly at the upper end of mobility for known entomophagous arthropods and is in the range of such herbivores as the tarnished plant bug and the cabbage root fly. (Note that the estimates of D in Table 2 for coccinellid species represent nonmigratory foraging movement rather than migratory dispersal, which would exhibit mobility many

TABLE 2

Estimated Diffusion Rates for Selected Arthropod Species

Species	D (m^2/day)	Source
Galandromus occidentalis (Acari: Phytoseiidae)	0.2	Rabbinge and Hoy (1980)[a]
Geocoris spp. (Hemiptera: Lygaeidae)	1.8	Rudd and Gandour (1985)
Coleomegilla maculata (Coleoptera: Coccinellidae)	4.1	Weltzler and Risch (1984)
Phylotreta cruciferae (Coleoptera: Chrysomelidae)	38.3	Kareiva (1982)
Pterostichus spp. (Coleoptera: Carabidae)	60.0	Gordon and McKinlay (1986)[a]
Lygus lineolaris (Hemiptera: Miridae)	150.0	Fleischer *et al.* (1988)[b]
Delia brassicae (Diptera)	240.0	Banks *et al.* (1988)
Anagrus epos (Hymenoptera: Mymaridae)	522.6	This study
Ceratitis capitata (Diptera: Tephritidae)	5793.0	Plant and Cunningham (1991)

Note. Entomophagous species are shown in bold type.

[a] D calculated from data provided on mean displacement using Eq. [6.11] in Kareiva (1981).

[b] D calculated from hours and B provided in Table 2 (1984 experiment, Day 2), using Eq. [12] in Rudd and Gandour (1985).

orders of magnitude higher.) This relative mobility for a parasitic hymenopteran is consistent with the fact that flight, rather than cursorial movement, is a significant component of host-finding behavior. The fact that mobility of *A. epos* is potentially one or two orders of magnitude greater than predatory coccinellids or big-eyed bugs is a nontrivial result. Such differences would, for example, result in quite different rates of dispersal from release points following an augmentative release. Corbett and Plant (1993) have demonstrated that such differences in mobility can also have important implications for how entomophagous insects respond to the spatial distribution of resources within an agricultural system. Our estimate of D is only for the conditions under which our mark–recapture trials were conducted. Mobility of *A. epos* will likely vary for different times of the season or for different locations as a result of differences in temperature, wind patterns, or host abundance. Indeed, the difference in best-fit estimates of D between trials I and II may in part be due to actual differences in mobility between these sites, although the variability in estimates of D for trial I does not definitively permit this conclusion (Fig. 5A).

A. epos, like most egg parasitoids, is a minute insect, being less than 0.5 mm in length. As such, one would expect its flight speed to be low, and therefore its ability to fly against prevailing winds to be rather limited (Chapman, 1982). Nevertheless, there was a significant upwind component in the dispersal of *A. epos* for all mark–recapture trials. Studies on the dispersal of *Trichogramma* spp., another minute egg parasitoid, following inundative releases have found that (1) when there is clear directional displacement it is in a downwind direction, and (2) upwind displacement is not prohibited by moderate wind speeds of less than 3.0 m/s (see Keller *et al.*, 1985, for review). For example, Hendricks (1967), in release–recapture studies with *T semifumatum* within cleared out areas of a cotton field, observed strong downwind displacement at wind speeds between 3 and 5.5 m/s but variable directional displacement at wind speeds of 3 m/s or less (measured at the study site). Smith (1988), using "sentinel" egg masses to monitor dispersal of *T. minutum* released in a white spruce plantation, found variable directional displacement at wind speeds up to 2.8 m/s (measured ca. 15 km from the study site). Thus the upwind displacement observed for *A. epos* in our studies, at wind speeds less than 4 m/s and averaging 1.9 m/s, is not inconsistent with the dispersal ability exhibited by *Trichogramma* spp.

The prevailing wind speed and direction recorded at weather stations does not necessarily represent that experienced by insects dispersing within a crop. Wind speed is modified in the layer immediately above a crop canopy; within a crop canopy wind speed quickly drops and approaches zero near the ground (Rosenberg, 1974). Crop canopies of different structure produce different effects on wind patterns both above and within them. The *T. minutum* dispersing within a white spruce plantation (Smith, 1988), for example, likely experienced wind speeds much reduced with respect to prevailing winds. Sylven (1970) found that radioactively labeled brassica pod midges (*Dasyneura brassicae;* Diptera: Cecidomyiidae) dispersed downwind above a cereal crop canopy but upwind within the canopy, perhaps in response to differences in wind speeds above and within the canopy. In our studies, *A. epos* may have dispersed above or below the height of the vineyard canopy following emergence, and would have experienced differing wind patterns accordingly.

Based on these considerations we can pose the following hypotheses to account for the upwind displacement of *A. epos* observed in our studies. (1) *A. epos* may disperse primarily above the vineyard canopy and against prevailing winds. This would be feasible especially if *A. epos* avoids dispersal at times of peak wind speed, as do some *Trichogramma* species (Keller *et al.*, 1985). (2) *A. epos* may preferentially disperse beneath the top of the vineyard canopy where wind speeds are lower and upwind flight is easier. Such a tendency has been documented for *Trichogramma pretiosum* dispersing in cotton following augmentative releases (Keller and Lewis, 1985). (3) Sudden changes in the vertical profile of vegetation can produce turbulence effects (Lewis and Dibley, 1970; Rosenberg, 1974). If there are strong turbulence effects between vinerows then individual *A. epos* may be carried passively in a direction

opposite to the prevailing winds. More studies are needed to evaluate these hypotheses for *A. epos* and for other small Hymenoptera. It would be especially useful to obtain vertical profiles of wind speed, direction, and turbulence during release–recapture studies for different crops. If *A. epos* truly engages in preferential upwind movement, this raises the possibility of oriented movement toward host patches based on chemical cues.

The high mobility and the strength of directional displacement exhibited by *A. epos* in this study could have important implications for the efficacy of augmentative releases of small parasitoids. Substituting the least-squares parameter estimates for D, c, and θ from 1992 trial II into Eq. [2], we can predict the distribution of *A. epos* following an augmentative release (Fig. 7). The great majority of individuals that were released at the center of a hypothetical 100 × 100-m (1 ha) block of grapes have dispersed out of the block 2 days after the release. (We assume in this exercise that the "target" block is surrounded by grapes—e.g., other growers' vineyards.) Concerns regarding the dispersal of parasitoids released in augmentation programs have been raised by other researchers. For example, Keller *et al.* (1985), in a review of dispersal of *Trichogramma* spp. in augmentative releases, conclude that dispersal out of the area targeted for control was a major concern and needed further investigation. Our results support this concern and indicate that studies of dispersal behavior of released parasitoids will be essential to the successful design of augmentation programs.

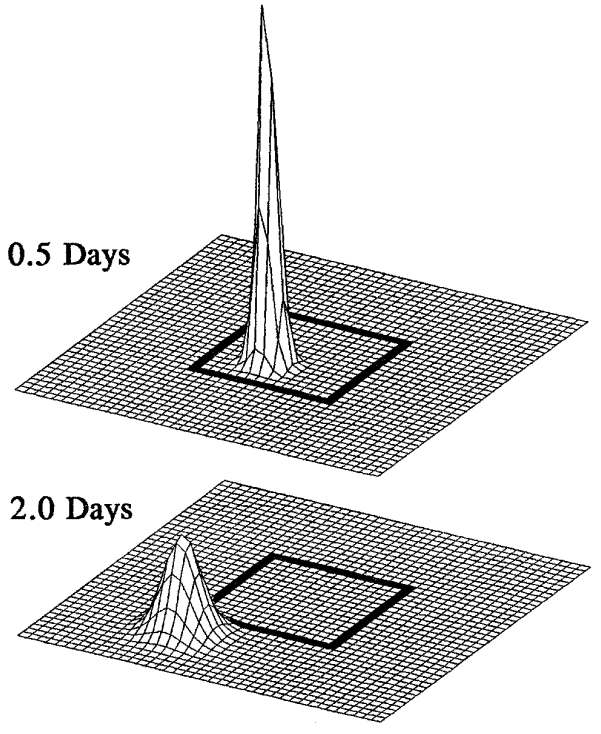

FIG. 7. Predicted distribution of *Anagrus epos* released in a hypothetical augmentative release at 0.5 and 2 days following release. Release occurs at the center of a hypothetical 100 by 100-m block of grapes, indicated by square on lower graph. "Target" block is assumed to be surrounded by grape vineyards.

Mark–Recapture Methodology

Our mark–recapture methodology was successful at marking a minute parasitic hymenopteran wasp and allowing a preliminary, quantitative assessment of its mobility and directional displacement. The treating of a "medium" containing parasitized host eggs with fluorescent dust resulted in a high proportion of adults marked with small but detectable amounts of fluorescent powder. Messing *et al.* (1993) applied fluorescent dust to *Diachasmimorpha longicaudata* Ashmead (Hymenoptera: Braconidae) puparia and found (1) a decrease in survivorship from approximately 96 to 88% and (2) a decrease in percentage recapture per trap from 0.013 to 0.002% as a result of labeling. This supports the general concern that application of fluorescent powders can have negative impacts on survivorship and behavior of small insects. To the extent that our labeling technique significantly affected survivorship and dispersal, or that there was loss of marks over time under field conditions, it has resulted in a conservative estimate (i.e., an underestimate) of the mobility of *A. epos*.

The research presented here is a preliminary application of this methodology. As such there are many aspects that can and should be improved upon in future work. Most importantly, a much higher number of recaptures is required to obtain an accurate estimate of movement parameters. Clearly, it would have been highly desirable to have collected and treated a much larger number of grape leaves. Also, it is not known what proportion of mature *A. epos* survived and subsequently emerged from the emergence boxes. Attention to factors affecting this survivorship, as well as maximizing the amount of host medium treated, should greatly increase the number of parasitoids marked and recaptured.

By far the largest cost of this research was in time spent examining traps for marked *A. epos*. There were substantial existing populations of *A. epos* when and where our mark–recapture trials were conducted. Thus, it was necessary to examine a large number of *A. epos* to find a relatively small number of marked individuals. Careful choice of timing and location of mark–recapture trials should minimize this cost in future studies. In addition, development of techniques that allow rapid detection of extremely small amounts of fluorescent powder would be highly desirable.

With attention to some of these logistical factors, it should be possible to apply this methodology effectively and efficiently to the study of movement of many other small parasitoids. Such studies would increase our understanding of the population ecology of parasitic

Hymenoptera and improve our ability to use these organisms as effective biological control agents.

ACKNOWLEDGMENTS

We thank: B. C. Murphy (Department of Entomology, UC Davis) for valuable suggestions concerning the labeling methodology; and A. Okubo (Marine Science Research Center, SUNY Stony Brook) and R. E. Plant (Department of Agronomy and Range Science, UC Davis) for assistance in developing the computational procedures. We also thank S. Cheykin, J. Tecklenberg, and J. Lundquist for their hospitality and assistance in carrying out the mark–recapture studies in their vineyards. Kimberly Steinmann and Lisa K. Miller spent countless hours examining *A. epos* for the presence of fluorescent powder, and their sacrifice is gratefully acknowledged. This work was supported by a USDA Western Regional IPM Program grant to J. A. Rosenheim and by a USDA NRICGP grant to A. Corbett.

Ode to *Anagrus*

How long has it been since I did last behold thee?

Thy wings: Soft and delicate as the feathers upon the crown of a downy chick.

Thy antennae: No less beauteous than the beaded pearls that would adorn the graceful neck of a fair princess.

Thy legs: That of the doe in springtime as she doth bound through the deepest evergreen forests.

So many hours have I spent gazing into the eternal mysterious deep pools of darkness in thy eyes.

Thou art truly the most noble of all bugs on sticky-cards squashed beneath saran-wrap. —K. Steinmann

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