

Estimating Insect Flight Densities from Attractive Trap Catches and Flight Height Distributions

John A. Byers

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Abstract Methods and equations have not been developed previously to estimate insect flight densities, a key factor in decisions regarding trap and lure deployment in programs of monitoring, mass trapping, and mating disruption with semiochemicals. An equation to estimate densities of flying insects per hectare is presented that uses the standard deviation (SD) of the vertical flight distribution, trapping time, the trap's spherical effective radius (ER), catch at the mean flight height (as estimated from a best-fitting normal distribution with SD), and an estimated average flight speed. Data from previous reports were used to estimate flight densities with the equations. The same equations can use traps with pheromone lures or attractive colors with a measured effective attraction radius (EAR) instead of the ER. In practice, EAR is more useful than ER for flight density calculations since attractive traps catch higher numbers of insects and thus can measure lower populations more readily. Computer simulations in three dimensions with varying numbers of insects (density) and varying EAR were used to validate the equations for density estimates of insects in the field. Few studies have provided data to obtain EAR, SD, speed, and trapping time to estimate flight densities per hectare. However, the necessary parameters can be measured more precisely in future studies.

Keywords Estimating flight density · Flight height · Computer simulation in three dimensions · Mass trapping · Monitoring · Mating disruption

Introduction

Knowledge about densities of flying insects at particular times and places is of fundamental interest in ecology and chemical ecology, as well as in integrated pest management. Currently, there are no methods and equations that use trap catch data to estimate insect flight densities, a crucial factor in the success of mass trapping and mating disruption programs (Shorey, 1977; Cardé, 1990; Cardé and Minks, 1995; Miller et al., 2006a, b; El-Sayed et al., 2006, 2009; Byers, 2007, 2008). In order to develop methods and equations for determining flight densities from trap catch data, several parameters need to be estimated and understood. The first parameter is the *effective attraction radius* (EAR) that describes the strength of a semiochemical lure with regard to blend and release rate, which allows comparisons among species (Byers et al., 1989). The EAR is a spherical radius that would intercept the same number of insects as caught by a semiochemical-baited trap. The EAR is a spatial parameter based on catch, which conveniently substitutes in simulation models for the complex spatial dimensions of attractive odor plumes. The EAR can be determined by the catch ratio of attractive (baited) and non-attractive (blank) sticky traps, and the silhouette area of the trap (Fig. 1). In mass trapping for control of insects, the most effective lure is that with the largest EAR ascertained by field-testing the semiochemical at increasing release rates. The EAR has been used in simulation models of mass trapping and mating disruption (Byers, 2007) that are important tools of integrated pest management (Shorey, 1977; Cardé, 1990; Cardé and Minks, 1995; Miller et al., 2006a, b; El-Sayed et al., 2006, 2009; Byers, 2008). These and other studies, however, have relied upon subjectively testing densities of lures/traps by trial and error until some negative effect on mating success was observed. This approach would be more efficient with a better

J. A. Byers (✉)
US Arid-Land Agricultural Research Center, USDA-ARS,
21881 North Cardon Lane,
Maricopa, AZ 85138, USA
e-mail: john.byers@ars.usda.gov

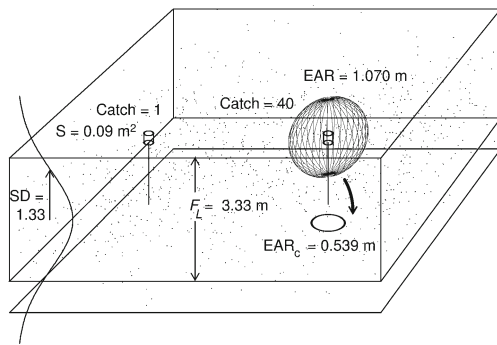


Fig. 1 Two cylindrical sticky traps, a blank catching one insect ($C_b=1$) and a pheromone trap catching 40 insects ($C_a=40$), are each 0.09 m^2 in silhouette area (S), giving a spherical $\text{EAR} = [(C_a \cdot S) / (\pi \cdot C_b)]^{0.5} = 1.070 \text{ m}$ that can be converted to a circular $\text{EAR}_c = \pi \cdot \text{EAR}^2 / (2 \cdot F_L) = 0.539 \text{ m}$ (where $F_L = SD \cdot \sqrt{2 \cdot \pi} = 3.33 \text{ m}$) (Byers, 2008). Based on the above EAR, SD, and catch of 40 given an 8 hr trap exposure with 2 m/sec flight speed, the 2D density estimate is 6.43 insects/hectare (from Eq. 6 in Results). Small dots represent 1000 insects distributed vertically in a normal distribution ($SD=1.33 \text{ m}$)

knowledge of flight densities, EAR of attractants, and use of simulation models to determine the trap density most likely to succeed in control measures (Byers, 2007, 2008).

The circular EAR (termed EAR_c), used in encounter-rate simulations of mass trapping in two dimensions (2D), is not identical to the spherical EAR obtained from insect catches in the field (Byers, 2008, 2009). A transformation of EAR is necessary (Fig. 1) to obtain an accurate EAR_c for 2D simulations. This conversion equation requires an estimation of the effective flight layer (F_L), which reflects the vertical layer where the particular insect species flies in search of mates and host plants. Essentially, if the vertical flight density distribution described by the standard deviation (SD) is squeezed into a layer of uniform density equal to that at the mean flight height, then the thickness of this layer is the F_L (Byers, 2008, 2009). However, the F_L does not describe a real layer, so hereafter to avoid confusion the F_L will be replaced with its equivalent, which is $SD \cdot \sqrt{2 \cdot \pi}$. It is expected that the SD is a species characteristic that might vary somewhat due to habitat, but otherwise would often be quite different for each species, as indicated by SD-analyses of 116 species from previous studies (Byers, 2011).

Although more than 100 publications report trap catches of insects at different heights, the mean flight height or its SD have seldom been estimated (Byers, 2011), probably because iterative equations to calculate SD require inputting data for every insect caught (possibly thousands). By using an iterative algorithm, however, the SD can readily be determined (Byers, 2011). Knowledge about the mean flight height \pm SD is not only useful in models, but can be applied in practice when deploying semiochemically baited traps for monitoring, mating disruption, and mass trapping. For

example, Byers et al. (1989) estimated flight densities of spruce bark beetles, *Ips typographus* L., searching for host trees in Denmark. The densities were estimated in 2D (per hectare) by placing sticky-traps of known radius on metal poles throughout the flight volume (0.7 to 11.5 m high), and recording the number of beetles trapped over time. In these experiments during the spring swarming flight (May 17, 19, 20, 21, and 22, 1984), an estimated 38, 5, 55, 32, and 90 beetles per hectare were in continuous flight each day, respectively.

The first objective of the present investigation was to develop the equations necessary to obtain density estimates of flying insects from a combination of data including (1) catches on passive sticky traps at three or more heights to determine mean height and \pm SD, and (2) catches on attractive and passive sticky traps to determine EAR and EAR_c . The equation for estimating densities in 2D also depends, in part, on the average flight speed, which is affected by both the insect's inherent flight speed in still air and the average wind speed.

The second objective addressed herein was to validate the density equation, and explore parameter effects by simulation of flying insects in three dimensions (3D). Simulated individuals can fly anywhere, but the population maintains a specified mean flight height, and a normal vertical distribution of flight heights (Byers, 2009, 2011). During these simulated population flights under constant parameters for number per area, flight speed, trap EAR, and exposure time, the stochastic catches on a spherical trap at the mean flight height were counted and compared to predicted results from the density equation. The simulation results should indicate the reliability and variability of the density estimates.

My third objective was to use the equations developed in the study to determine 2D insect densities from previous publications reporting passive and attractive trap data.

Methods and Materials

Equations for Estimating Densities of Insects per Hectare The trap catch data and a series of equations are presented that allow estimation of flight density in two dimensions, i.e., number per hectare. The equations are based on trap catch at several heights, and on data from a passive sticky trap placed at the mean flight height. The same equations, with little modification, can be used for chemically or visually attractive traps.

Given a passive cylindrical sticky trap, if its radius is 0.15 m and the height is 0.3 m, then the area S of the silhouette, as seen from a horizontal direction, is $S = 2 \cdot ra$

$d_{\text{ius}} \cdot \text{height} = 0.09 \text{ m}^2$. Using these values, the spherical effective radius, ER, of the trap is simply:

$$\text{ER} = \sqrt{S/\pi} = 0.169 \quad (1)$$

The mean flight height (\bar{h}) and SD of a particular insect species is found from catches on a series of passive traps placed at several heights (at least three) using the following formulas (Byers, 2011):

$$\bar{h} = \text{sum}x/n \quad (2)$$

$$\text{SD} = \sqrt{(n \cdot \text{sum}x^2 - (\text{sum}x)^2)/(n \cdot (n - 1))} \quad (3)$$

where $\text{sum}x = \sum_{i=1}^t \sum_{j=1}^{c_i} h_i$, $\text{sum}x^2 = \sum_{i=1}^t \sum_{j=1}^{c_i} h_i^2$, and $n = \sum_{i=1}^t c_i$ with t = number of trap levels, h_i = height of trap level, c_i = catch at trap level, and i = trap level. In previous studies (Byers, 2008, 2009), $F_L = \text{SD} \cdot \sqrt{2 \cdot \pi}$ was used in an equation to convert spherical to circular radii. However, since F_L is a mathematical construct and not a real flight layer, while SD describes a real distribution, subsequent equations are in terms of SD.

The ER in three dimensions is converted to a circular effective radius ER_c in two dimensions (Byers, 2008, 2009) by the following formula:

$$\text{ER}_c = \pi \cdot \text{ER}^2 / (2 \cdot \text{SD} \cdot \sqrt{2 \cdot \pi}) \quad (4)$$

The two-dimensional density D_2 of flying insects is then found from:

$$D_2 = C / (2 \cdot \text{ER}_c \cdot T \cdot V \cdot K) \quad (5)$$

where C is the catch on the trap ($K=1$) or traps ($K>1$) in the field, T is the seconds of trap exposure, and V is the average velocity (m/s) of the flying insects (K was added to equation 2 of Byers et al., 1989). Thus, if $\text{ER}=0.169 \text{ m}^2$ and $\text{SD}=1.67 \text{ m}$ then $\text{ER}_c=0.01075 \text{ m}$. Given that $C=4$, $K=1$, $T=3600 \text{ sec}$, and $V=2 \text{ m/sec}$, then $D_2=0.0258 \text{ insects per m}^2$ or $258 \text{ insects per hectare}$. In 3D at the trap level, there are $D_2 / (\text{SD} \cdot \sqrt{2 \cdot \pi}) = 0.0062 \text{ insects per m}^3$ (Byers, 2009, 2011).

Density can more readily be estimated from a trap with a lure attractive to the particular insect species. First, calculate an EAR from an attractive trap placed at the mean flight height as shown in Byers (2008, 2009). For example, assuming the same catch occurred on a blank trap ($Cb=4$) of the same size as above, and $Ca=80$ were caught on the attractive trap, then $\text{EAR} = [(Ca \cdot S) / (\pi \cdot Cb)]^{0.5} = 0.757 \text{ m}$. Substituting EAR for ER in Eq. (4), then $\text{EAR}_c=0.215 \text{ m}$ and this is substituted for ER_c in Eq. (5), where $C = Ca$, gives the same $D_2=0.0258 \text{ per m}^2$ with the same above parameters. This means that EAR converted to EAR_c can

be used to estimate 2D densities much more easily since catch is more readily obtained on an attractive trap than on a blank trap. The EAR and EAR_c need to be estimated previously from an attractive trap catch compared to the blank trap catch ($Cb>0$; Byers et al., 1989), as well as the SD from a series of trap heights and catches (Byers, 2008, 2009, 2011). Once the SD and EAR/ EAR_c are estimated for a particular attractant release rate, subsequently only an attractive trap is needed to calculate the density of flying insects.

Equation (5) requires the average flight speed of the insects, which can be estimated by the flight speed in still air (for bark beetles this is about 1.6 m/sec, Byers et al., 1989). However, wind speed will affect flight speed either additively when the insect flies with the wind, or negatively when the insect flies upwind. Assuming most insects fly in all possible horizontal directions with respect to moderate wind speed as observed for moths, flies, and bark beetles (Elkinton and Cardé, 1983; Judd and Borden, 1988, 1989; Byers et al., 1989), then the affect of wind on average flight speed appears complex. Given that wind speed can range from 1 to 5 m/sec and the insect flies at 2 m/sec in still air, the average flight speed can be calculated by computer (from Eq. 7 in Results).

Simulation of Flight Densities and Catch on a Spherical Trap in 3D Insects were simulated in a volume with X-axis (xa), Y-axis (ya), and Z-axis (za) of $50 \times 50 \times 10 \text{ m}$, respectively. Various numbers of insects were placed initially at random according to a specified normal distribution of SD (Byers, 2001). Insects flew in a correlated random walk using spherical (x, y, z) coordinates (Hearn and Baker, 1994). The walk progressed as a series of steps, each of length *step* (0.1 m), and 6° standard deviation of angular turns as in Byers (2001, 2009, 2011). Insects rebounded at random angles when striking the volume sides, and rarely when intercepting the ground and top boundaries. The coordinates of insects were transformed to 3D perspective coordinates when viewing the simulations (p. 57, Adams, 1987). Insects flew within the volume such that the population had a mean height of $za/2$ and was distributed normally with $\text{SD}=1.67 \text{ m}$, as accomplished by an algorithm in Byers (2009, 2011). Insects flew at 2 m/sec for 1 hr except when the period of simulation was varied. The algorithm to determine whether insects entered or passed through the spherical EAR of a trap was as described in Byers (2009, 2011). Insects that were caught on the trap were replaced at random according to the population distribution within the volume to maintain a constant density. Simulations and calculations, for general demonstration on the Internet with a web browser (<http://www.chemical-ecology.net/java2/den-2d.htm>), were programmed in QuickBASIC 4.5 (Microsoft Corp., Redmond, WA, USA) as well as Java 6.0 (Oracle, Redwood City, CA, USA).

Estimating Densities from Insect Catch Studies in the Literature The scientific literature was explored (BIOSIS Previews) for articles that reported catch on traps at three or more heights in which catch diminished with height. These data were used to determine the mean height of flight and SD. These parameters were calculated previously (Tables 1–3 in Byers, 2011), but only the data on unattractive traps (his Table 3) were further analyzed to determine densities with Eq. (5). The catch at the mean flight height was estimated from the normal equations (Byers, 2011). In addition, some of these studies also reported catch on an attractive sticky trap as well as on a blank sticky trap that caught at least one insect in order to find an EAR. In studies where an attractive-colored sticky card was used (Gillespie and Vernon, 1990), the height by width area S is calculated for all possible angles that insects can intercept the trap giving $S = 0.637 \cdot height \cdot width$ (Byers et al., 1989). Attractive-colored cross-pane barrier traps (Zhang et al., 2011) have a mean interception area of $S = 0.9 \cdot height \cdot width$ (Byers, 2009). The formulas for cards and cross-pane traps also work for attractive odors. Using the attractive catch, EAR, and SD, it is possible to calculate densities per hectare (Eq. 6 in Results).

Results

Equations for Estimating Densities of Insects per Hectare The EAR_c does not need to be calculated explicitly to calculate 2D density because the EAR and SD can be used instead. Using EAR for ER in Eq. (4) gives the equation $EAR_c = \pi \cdot EAR^2 / (2 \cdot SD \cdot \sqrt{2 \cdot \pi})$ that, when substituted into Eq. (5), gives the final portion of Eq. (6) in terms of EAR and SD:

$$D_2 = C / (2 \cdot EAR_c \cdot T \cdot V \cdot K) = C / (\pi \cdot EAR^2 \cdot T \cdot V \cdot K / (SD \cdot \sqrt{2 \cdot \pi})) \tag{6}$$

The density in 3D at the trap would be $D_3 = C / (T \cdot V \cdot K \cdot \pi \cdot EAR^2)$, which yields values identical to $D_2 / (SD \cdot \sqrt{2 \cdot \pi})$.

Assuming insects fly in all horizontal directions with respect to the wind while searching (Elkinton and Cardé, 1983; Judd and Borden, 1988, 1989; Byers et al., 1989), then many possible ground speeds are possible depending on the direction of flight with respect to wind direction (Fig. 2, bottom right inset). The average ground speed (\bar{s}) that results from all possible directions of insect flight for a

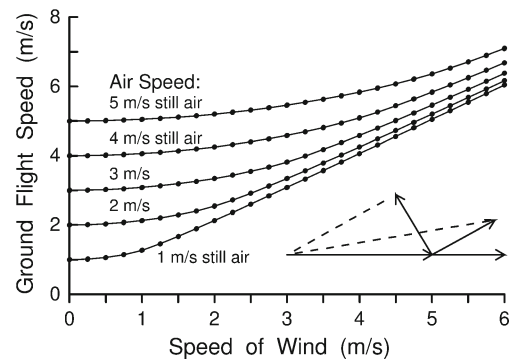


Fig. 2 Relationship between wind speed and ground flight speed when insect flies at 1 to 5 m/sec in still air (air speed); results generated by Eq. (7). Insert at lower right shows three possible ground flight speeds (3 m/sec straight line and dashed lines of 2.91 m/sec and 1.73 m/sec) based on vectors of air speed in still air (2 m/sec) and wind speed (1 m/sec)

speed in still air (s_i) of 2 m/sec and a wind speed (s_w) of 2 m/sec is found from the equation:

$$\bar{s} = \frac{1}{n} \sum_{a=0}^n \sqrt{s_i^2 + s_w^2 - 2 \cdot s_i \cdot s_w \cdot \cos(a \cdot \pi/n)} \tag{7}$$

where $n=1000$, giving 2.54 m/sec ground flight speed with the above values. Equation (7) was used with varying wind speed and flight speed to show graphically the effects on the average ground flight speed (Fig. 2).

Simulation of Flight Densities and Catch on a Spherical Trap in 3D The simulations attempted to fly a population of insects of known constant density in a volume ($X=50, Y=50, Z=10$ m). The population of individuals flies at a mean height of $Z/2$ and exhibits a normal distribution about the mean height with $SD=1.67$ m. The insects can be caught by a spherical trap of specified EAR placed at the mean flight height (5 m) in the center of the volume. The catch on the trap at the end of the simulation ($T=3600$ sec, with insects taking 72,000 steps of 0.1 m each) was used with the appropriate parameters in Eq. (6) to calculate the number of insects per hectare (means and 95 % CL, Fig. 3). The dashed line is the density of insects maintained throughout the simulations (10 insects in the volume gives 40 per hectare). As can be seen (Fig. 3), the means calculated from the catches are near the expected values of 40 or 160 per hectare. The 95 % CL is larger when the trap EAR is smaller since more variation in catch is expected on smaller traps.

When the time of exposure of the 0.5 m EAR trap was increased, there was no effect on the calculation of density, which was kept constant at 160 per hectare (Fig. 4). The 95 % CL of the means overlap the expected density, with generally more variation at the shorter exposures, an expectation when traps are not exposed long enough. Equation (6) predicted the densities of insects per hectare based on the

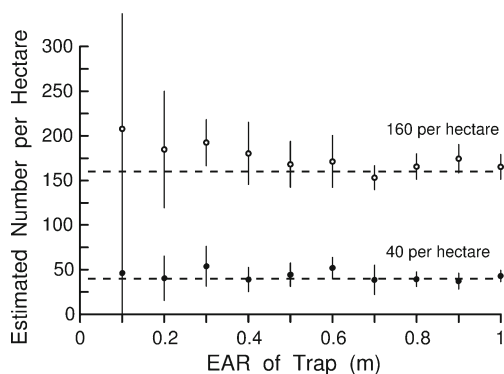


Fig. 3 Mean density of insects (number per hectare) flying at 2 m/sec calculated from catches on a trap of varying EAR exposed for 1 hr in simulations ($N=8$ each point) in three dimensions with constant densities of 40 or 160 insects per hectare (bars represent 95 % CL). The dashed lines indicate the expected values

trap catches of a spherical trap of 0.5 m EAR during an hour exposure when the simulated density of insects was increased from 10 to 100 in the volume (Fig. 5). The number per hectare is four times the number simulated since the volume represents one fourth of a hectare in surface area. The 95 % CL variation did not decrease with higher numbers of simulated insects as might be expected from the results on increasing EAR and exposure period. In fact, the larger numbers caught simply allowed more variation about the means, as seen when comparing the means for 40 and 160 densities in Fig. 3. These simulation results, which aim to represent stochastic processes in nature, show that the equations are valid assuming catch, mean ground speed, exposure period, and EAR were obtained with reasonable accuracy.

Estimating Densities from Insect Catch Studies in the Literature Over 100 articles were found on insect flight heights of which only about 60 were suitable for estimating SD (Tables 1–3 in Byers, 2011). Of these, about 30 species

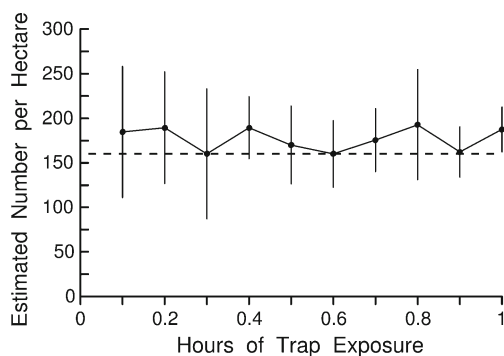


Fig. 4 Mean density of insects (number per hectare) flying at 2 m/sec calculated from catches on a trap of EAR=0.5 m exposed for varying periods of time in simulations ($N=8$ each point) in three dimensions with a constant density of 160 insects per hectare (bars represent 95 % CL). The dashed lines indicate the expected values

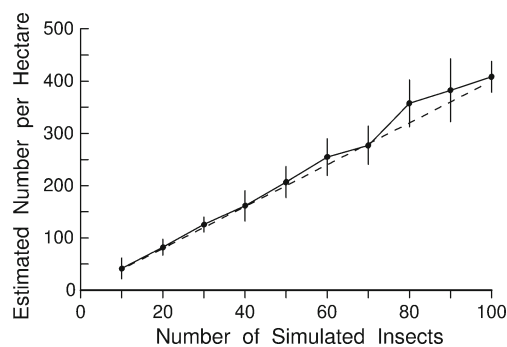


Fig. 5 Mean density of insects (number per hectare) flying at 2 m/sec calculated from catches on a trap of EAR=0.5 m exposed for 1 hr in simulations ($N=8$ each point) in three dimensions with varying densities of insects per simulation volume (one fourth hectare; bars represent 95 % CL). The dashed line indicates the expected values

were caught on passive (blank) traps, and the catch at the mean flight height (estimated from normal equations in Byers, 2011) was used to calculate densities per hectare (Table 1) using Eqs. (4) and (5). These 30 species were matched with studies that had determined EAR from an attractive trap and a blank trap (preferably sticky traps) of reported dimensions, with the blank trap or traps catching >0 insects. Of these matches, only a few species were found that met these requirements to allow estimation of 2D densities (Table 2) from attractive traps using Eq. (6). These examples show how density can be estimated and serve as a model for future work.

Discussion

Equations (5) and (6) were derived in part from the equation: $\text{Density} = \text{catch} / (2 \times \text{radius} \times \text{time} \times \text{speed})$ presented in Byers et al. (1989) who were unaware of an earlier equation by Holling (1959) for calculating densities. Holling's type I functional response equation calculates how many prey would be eaten by a predator (or caught on sticky trap) as $H_a = aH$, where H_a is catch per time, H is prey density, and a is attack rate. In the case of traps, the attack rate, a , would be the diameter of the trap ($2R$) times average speed of the insects times the exposure time. Equations (5) and (6) simply solve for H (which is D_2 here). However, the trap's radius R that was implicit in Holling's equation is not appropriate in 3D with different vertical flight distributions. Thus, R is corrected by using SD (Eq. 3) to calculate ER (Eq. 1) and ER_c (Eq. 4) for passive traps to find insect densities by Eq. (5). If the vertical flight SD of a species and the EAR of an attractive trap are known, then densities are calculated via Eq. (6).

In order to estimate densities of flying insects over a certain length of time, one can use passive sticky traps.

Table 1 Estimation of mean density of insects (n/hectare) based on published data for non-attractive traps (window, sticky card, cross-barrier, or sticky cylinder) at various heights

Species	Mean height of catch \pm SD (m) ^a	Catch at mean height ^b	Trap area S (m ²) ^c	ER _c (m) ^d	Hours of trapping (N) ^e	Density (number per hectare) ^f
Hemiptera:						
<i>Alydus eurinus</i> (Say) ^g	1.35 \pm 1.03	76	0.37	0.072	1400 (4)	0.26
<i>Sinea diadema</i> (F.) ^h	1.29 \pm 0.87	27	0.37	0.085	600 (4)	0.18
<i>Sinea spinipes</i> (Herrich-Schaeffer) ^h	4.06 \pm 2.06	6	0.37	0.036	900 (4)	0.06
<i>Nabis americanoferus</i> Carayon ⁱ	2.48 \pm 1.83	13	0.37	0.040	600 (4)	0.19
<i>Nabis roseipennis</i> Reuter ⁱ	3.07 \pm 1.76	27	0.37	0.042	600 (4)	0.37
<i>Orius insidiosus</i> (Say) ⁱ	3.45 \pm 1.81	1109	0.37	0.041	600 (4)	15.72
<i>Antillocoris pilosulus</i> (Stål) ^j	4.27 \pm 1.80	66	0.37	0.041	2100 (4)	0.27
<i>Crophius disconotus</i> (Say) ^j	3.09 \pm 1.76	18	0.37	0.042	900 (4)	0.17
<i>Geocoris punctipes</i> (Say) ^j	2.37 \pm 1.74	19	0.37	0.042	1300 (4)	0.10
<i>Corythucha ciliata</i> (Say) ^k	4.27 \pm 1.75	15	0.37	0.042	300 (4)	0.42
<i>Gargaphia solani</i> Heidemann ^k	1.85 \pm 1.50	29	0.37	0.049	900 (4)	0.22
<i>Amnestus basidentatus</i> Froeschner ^l	4.63 \pm 1.43	168	0.37	0.051	600 (4)	1.89
<i>Amnestus pallidus</i> Zimmer ^l	3.51 \pm 1.85	21	0.37	0.040	600 (4)	0.31
<i>Amnestus spinifrons</i> (Say) ^l	3.33 \pm 2.02	15	0.37	0.036	450 (4)	0.31
<i>Brochymena quadripustulata</i> (F.) ^l	3.01 \pm 1.17	179	0.37	0.063	900 (4)	1.10
<i>Euschistus servus</i> (Say) ^l	2.12 \pm 1.54	41	0.37	0.048	1350 (4)	0.22
Diptera:						
<i>Leptoconops noei</i> Clastrier et Coluzzi ^m	2.11 \pm 0.50	1365	0.0382	0.015	35 (3)	1194.50
<i>Leptoconops irritans</i> (Noé) ^m	2.12 \pm 0.59	332	0.0382	0.013	35 (3)	340.72
<i>Bibio johannis</i> (L.) males ⁿ	0.71 \pm 0.42	2374	0.04	0.018	225 (72)	11.22
<i>Bibio johannis</i> (L.) females ⁿ	0.88 \pm 0.45	183	0.04	0.017	225 (72)	0.93
<i>Sergentomyia bedfordi</i> Newstead in open ^o	2.85 \pm 2.13	9	0.637	0.060	14 (5)	3.00
Above in wooded area ^o	4.80 \pm 2.69	38	0.637	0.047	14 (5)	16.11
<i>Sergentomyia antennatus</i> New. in open ^o	2.17 \pm 1.94	9	0.637	0.065	14 (5)	2.85
Above in wooded area ^o	2.85 \pm 2.72	23	0.637	0.047	14 (5)	9.58
Coleoptera:						
<i>Hoplia spectabilis</i> Medvedev ^p	0.87 \pm 0.76	2423	0.135	0.035	75 (3)	421.99
<i>Hylurgops palliatus</i> (Gryllenhal) ^q	4.98 \pm 2.63	16	0.09	0.007	6 (3)	177.50
<i>Ips typographus</i> (L.) males ^q	4.63 \pm 2.66	9	0.09	0.007	30 (3)	20.17
<i>Ips typographus</i> (L.) females ^q	4.63 \pm 2.85	9	0.09	0.006	30 (3)	21.83
<i>Tomicus piniperda</i> (L.) ^q	5.98 \pm 3.00	2	0.09	0.006	12 (3)	10.37
<i>Trypodendron domesticum</i> (L.) ^q	2.82 \pm 1.67	5	0.09	0.011	6 (3)	33.72
<i>Cryphalus abietus</i> (Ratz.) ^q	3.44 \pm 2.73	46	0.09	0.007	6 (3)	542.54
<i>Pityogenes bidentatus</i> (Herbst) ^q	3.10 \pm 1.62	7	0.09	0.011	6 (3)	48.08
<i>Pityogenes chalcographus</i> (L.) ^q	6.89 \pm 2.90	13	0.09	0.006	6 (3)	166.53
<i>Pityogenes quadridens</i> (Hartig) ^q	4.08 \pm 2.80	9	0.09	0.006	6 (3)	105.28
<i>Balanogastriis kolae</i> (Desbr.) ^r	0.68 \pm 0.44	395	0.057	0.026	150 (3)	47.28

^a Calculated from Eqs. (2) and (3)

^b Estimated from normal equations (Table 3 in Byers, 2011)

^c Based on equations to calculate S for either flat, cross-barrier, or cylindrical traps as presented in Methods

^d Using Eq. (1)

^e Rough estimate of trapping times based on trap days and 5 hr flight per day, N = number of trap stations

^f Average density over trapping period as estimated from Eq. (6) with V assumed at 1 m/sec in all cases, T in seconds from trapping hours, and N was number of traps at each height level

^g McPherson and Weber, 1981a; ^h McPherson and Weber, 1981b, ⁱ c, ^j d, ^k e, ^l 1980, ^m Carrieri et al., 2007, ⁿ D'Arcy-Burt and Blackshaw, 1987,

^o Basimike et al., 1989, ^p Zhang et al., 2011, ^q Byers et al., 1989, ^r Ivbijaro and Daramola, 1977

Table 2 Densities of flying insects calculated from Eq. (7), using EAR and EAR_c of semiochemicals or colors attractive to various species based on passive and active catches of sticky traps, SD ($SD = F_L /$ $\sqrt{2 \cdot \pi}$ from Table 1 in Byers, 2011), and estimated average flight speed (V) of 2 m/sec for Scolytidae and Scarabaeidae, and 0.5 m/sec for Thripidae (trapping exposure times from literature unless specified)

Species and conditions	Insect catch		Trap area S (m ²)	EAR (m)	SD (m)	EAR _c (m)	Density (n per hectare)
	Blank	Active					
Scarabaeidae							
<i>Hoplia spectabilis</i> Medvedev ^a							
Yellow cross-panel	1867	12448	0.135	0.54	0.76	0.237	144.82
White cross-panel	1867	9274	0.135	0.46	0.76	0.176	144.82
Blue cross-panel	1867	5944	0.135	0.37	0.76	0.113	144.82
Host Plant	288	405	0.135	0.25	0.76	0.050	78.19
Host plant + 200 <i>Hoplia</i>	288	509	0.135	0.28	0.76	0.063	78.19
Curculionidae (Scolytinae)							
<i>Tomicus piniperda</i> L.							
Scots pine log I ^b	52	623	0.06	0.48	3.00	0.048	283.25
Log I + 30 males + 30 females ^b	52	774	0.06	0.53	3.00	0.059	283.25
(+)-3-Carene ^b	7	48	0.06	0.36	3.00	0.027	19.06
(+)- α -Pinene ^b	7	60	0.06	0.40	3.00	0.034	19.06
(-)- α -Pinene ^b	7	79	0.06	0.46	3.00	0.045	19.06
Terpinolene ^b	7	104	0.06	0.53	3.00	0.059	19.06
Scots pine Log II ^b	7	256	0.06	0.84	3.00	0.146	19.06
April 15, Monoterpenes ^c	2.33	27	0.09	0.58	3.00	0.069	67.69
April 21, Monoterpenes ^c	1	19	0.09	0.74	3.00	0.114	29.06
<i>Ips typographus</i> L.							
High release pheromone ^d	6	753	0.06	1.55	2.75	0.546	3.74
Medium release pheromone ^e	7	80	0.06	0.47	2.75	0.050	4.37
May 17, Pheromone ^f	5.67	194	0.09	0.99	2.75	0.223	241.5
May 20, Pheromone ^f	16.67	269	0.09	0.68	2.75	0.105	426.01
May 22, Pheromone ^f	8.5	215	0.09	0.85	2.75	0.165	402.26
<i>Ips paraconfusus</i> Lanier							
Log + 50 males ^g	1.27	339	0.1185	3.17	5.14 ^h	1.228	2.13
Thripidae							
<i>Frankliniella occidentalis</i> (Pergande) ⁱ							
Blue card (greenhouse I)	29	639	0.0046	0.18	0.39	0.051	693.47
Yellow card (greenhouse I)	29	529	0.0046	0.16	0.39	0.042	693.47
Yellow card (greenhouse II)	-	71	-	0.16	0.39	-	97.11 ^j

^a Zhang et al. (2011): passive catch on black cross-panel trap, host plant was *Dasiphora fruticosa* (L.) Rydb. (Syn. *Potentilla fruticosa* L.) tested 4 d × 6 h, N=3; colored traps in pastureland, 7 d × 6 h, N=6

^b Byers et al. (1985): released about 30 mg each compound/day; Scots pine (*Pinus sylvestris* L.) Log I tested 2 d × 8 h, Log II and chemicals (30 mg each compound/day) tested 4 d × 8 h, N=2 in all cases

^c Byers et al. (1989): released about 10–20 mg/day of (+)- α -pinene, (-)- α -pinene, and (+)-3-carene, and 3–5 mg/d of terpinolene, 240 min trapping each date, N=1

^d Schlyter et al. (1987): high release of 57 mg 2-methyl-3-buten-2-ol (MB)/day and 1 mg (4S)-*cis*-verbenol (cV)/day at 12 m trap separation, 16 d × 8 h, N=2

^e Schlyter et al. (1987): medium release: 5.8 mg MB/day and 1 mg cV/day, 16 d × 8 h, N=2

^f Byers et al. (1989): medium release MB and cV, trapping times as indicated in their Table 1, N=1

^g Byers (1983): ponderosa pine log (*Pinus ponderosa* Laws.), passive catch average of 15 traps on row 3; 9 d × 10 h, N=1

^h Gara (1963)

ⁱ Gillespie and Vernon (1990): passive catch average of green and black sticky traps at 2.4 m height and average F_L , 1 d × 10 h, N=5

^j Density estimated in second greenhouse from catch and yellow card's EAR in first greenhouse, N=5

These should be nearly invisible to the insects of interest in order to obtain an accurate density estimate. The most appropriate insects are those with limited visual acuity with interommatidial angles $>2^\circ$, including many herbivorous beetles, aphids, thrips, whiteflies, and true bugs (Land, 1997). Also, nocturnally flying insects would not avoid clear sticky traps under low light conditions. In addition, the SD must have been previously calculated from trap catches at several heights. The mean flight height also is obtained from these data so that the density-monitoring trap can be placed at this height. The habitat where densities are measured should be the same as where SD was obtained, since this value can sometimes vary depending on the habitat. For example, over open areas of grass, some species had mean flight heights that were lower than when flying in orchard/wooded areas (analyzed in Byers, 2011). In most cases, there were little or no differences in vertical flight distributions between the sexes of a species, but in species with sex-specific behaviors or territoriality there were significant differences (Byers, 2011). In the present study, only vertical distributions sampled with passive traps were used because a few insects appear to alter their vertical flight distribution when semiochemical lures are used at all trap heights (Byers et al., 1989; Byers, 2011). In most studies though, visible or olfactory attractants at all trap heights on the poles did not appear to affect the flight height distribution compared to passive traps (Byers, 2011).

The dimensions of the density-monitoring trap are easily measured, as well as the time of trap exposure. Average wind speed, but not direction, also need to be measured during the trapping period. Measurement of flight speed in still air would make estimates more accurate for a particular insect species, and then ground flight speed adjusted based on the observed average wind speed using Eq. (7). This procedure would allow more accurate estimates of density as compared to most previous studies where these parameters have been ill defined. Values for flight speed in still air and wind speed giving ground flight speeds (Fig. 2) can be reasonably assumed, based on the species and conditions tested. In any case, these two parameters can be measured.

A more efficient way of estimating densities is to use attractive traps since more insects are caught than with passive traps. Again, the SD must have been calculated previously, and the wind speed, time of trapping, and flight speed in still air is important to measure as precisely as possible. In addition, an EAR needs to be estimated prior to monitoring flight densities. The larger the passive trap catch, the more reliable and accurate the EAR estimate. Therefore, it is advisable to deploy several passive traps in order to obtain a sufficient catch for a reliable average to compare to the active trap catch. The magnitude of the EAR depends on the abilities of the species in question to find the attractant, and on the attractant's qualities (e.g., spectral

reflectance; chemical components, and release rates). The EAR is a function of the ratio of catch on attractant and passive traps, and the effective radius of the passive trap. The EAR, being a ratio of trap catch, is expected to be robust and not affected by changes in population density. This has been shown previously in simulations (Byers, 2008, 2009), and is indicated from EAR calculations of trap data (Table 2). The EAR of attractive odors also is defined by a specified release rate, which would not be maintained by evaporative dispensers if temperature declines. Thus, flight density measurements are valid only under temperature conditions similar to those under which the EAR was obtained for a particular dispenser/release rate.

Other environmental factors may alter the EAR for chemical lures by altering the insect's flight height and orientation efficiency. The flight height and/or orientation efficiency is influenced by wind speed and wind turbulence in different habitats, which could affect EAR magnitude and reduce accuracy of density estimates. Further work is needed to test the variability of EAR estimates; however, some data are available for comparisons (Table 2). For example, bark beetles (*T. piniperda*) attracted to freshly cut host logs on different occasions had EAR of 0.48, 0.53, and 0.84 m; bark beetles (*I. typographus*) attracted to a specific release rate of aggregation pheromone had EAR of 0.68, 0.85, 0.99 m; scarab beetles (*H. spectabilis*) attracted to host plants had EAR of 0.25 and 0.28 m; and western flower thrips (*F. occidentalis*) attracted to yellow colored traps in two greenhouses had identical EAR of 0.16 m. In some species, the EAR for pheromone baits would be expected to be different for each sex, such as the sexes of *Ips* bark beetles that respond differentially to aggregation pheromone. The males avoided the highest pheromone concentrations indicating resident males, while females were attracted to high pheromone concentrations (Byers, 1983; Schlyter et al., 1987).

Different baits with different EAR calculated in the same experiment will report the same density (Table 2), since the catch on the attractive trap is used for both the density and EAR calculation. In practice, the measurement of density should be based on a previous EAR determination (which might involve several attractive and passive traps), and then only one attractive trap need be set up in any area in the future to estimate flight densities based on the catches. Multiple traps can be averaged to increase the accuracy, since flight densities vary locally and temporally. In one study, however, a "medium" and a "high" release rate of synthetic pheromone gave two different EAR for *I. typographus* in the same forest area, and the densities calculated were remarkably similar (4.37 and 3.74 beetles per hectare, Table 2), as should occur if the density methods are valid. These densities represent the average flight density over a 16-day period in 1982, but if most flight occurred over 4 days (not unusual for middle Sweden), then the densities

would be four times higher. The daily densities over a week period in May 1984 were certainly higher (241 to 426 beetles per hectare, Table 2) in Denmark as beetles were emerging from large piles of tree trunks after clear-cut operations.

When using passive traps to estimate densities, it is probably more important to place them at the mean flight height than when using traps with semiochemical lures in which insects can be attracted from different heights by following odor plumes or by visual attraction. Many previous studies were found in which proportions of catch were reported without total number. In these cases, SD can be calculated, but no calculation of trap catch at the mean flight height, or at any height is possible; thus, no densities can be estimated. The density estimates are for the flying population, and do not count resting insects. For moths, density measurements with EAR of pheromone are for flying males, including the entire population during the night in many species. Since the sex ratio is about 1:1 in moths, then the female population that is resting can also be estimated as equal to that found for the males. In any case, the flight density should correlate well with the total population density.

The equations presented here provide new methods to estimate flight densities for many insect species in the field. Additionally, estimates of flight densities of pest insects in agricultural systems obtained by other methods can be entered into computer models of mating disruption and mass trapping developed earlier (Byers, 2007). Even without such use in models, knowledge of flight population densities is critical to efficient deployment of lures and traps in monitoring, mating disruption and mass trapping (El-Sayed et al., 2006, 2009).

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