

Analysis of Vertical Distributions and Effective Flight Layers of Insects: Three-Dimensional Simulation of Flying Insects and Catch at Trap Heights

JOHN A. BYERS¹

US Arid-Land Agricultural Research Center, USDA-ARS, 21881 North Cardon Lane, Maricopa, Arizona 85138

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ABSTRACT The mean height and standard deviation (*SD*) of flight is estimated for over 100 insect species from their catches on several trap heights reported in the literature. The iterative equations for calculating mean height and *SD* are presented. The mean flight height for 95% of the studies varied from 0.17 to 5.40 m, and the *SD* from 0.12 to 3.83 m. The relationship between *SD* and mean flight height (*X*) was $SD = 0.711X^{-0.7849}$, $n = 123$, $R^2 = 0.63$. In addition, the vertical trap catches were fit to normal distributions and analyzed for skew and kurtosis. The *SD* was used to calculate an effective flight layer used in transforming the spherical *effective attraction radius* (*EAR*) of pheromone-baited traps into a circular *EAR_c* for use in two-dimensional encounter rate models of mass trapping and mating disruption using semiochemicals. The *EAR/EAR_c* also serves to reveal the attractive strength and efficacy of putative pheromone blends. To determine the reliability of mean flight height and *SD* calculations from field trapping data, simulations of flying insects in three dimensions (3D) were performed. The simulations used an algorithm that caused individuals to roam freely at random but such that the population distributed vertically according to a normal distribution of specified mean and *SD*. Within this 3D arena, spherical traps were placed at various heights to determine the effects on catch and *SD*. The results indicate that data from previous field studies, when analyzed by the iterative equations, should provide good estimates of the population mean height and *SD* of flight.

KEY WORDS mean flight height, computer simulation in three dimensions, movement algorithms, mating disruption, mass trapping

A large number of studies in entomology have determined the catch of insects on traps placed vertically at several heights (over 60 studies will be analyzed here). The purpose of the previous work was 1) to find the best height to place traps or semiochemical lures for monitoring and control (mass trapping and mating disruption, and 2) to determine the natural heights at which insects fly while searching for mates or hosts. However, surprisingly few studies have determined mean height of flight or calculated the vertical standard deviation, *SD*, of flight distribution. Notably, Zhang et al. (2011) and earlier McPherson and Weber (1980; 1981a,b,c,d,e 1990) reported mean flight height and *SD*, which require iterative equations as will be presented here. In many previous studies, a standard deviation was reported for the mean of trap catches at a particular height, but not the mean height of flight and *SD* that are based on a range of trap heights weighted by the catch numbers at each height. Because samples of *n* can be hundreds to thousands of insects caught on several trap heights, it may have seemed too laborious to use the iterative calculations for these two parameters, however, these calculations

become practical with a simple computer routine outlined in the current study.

Knowledge about the mean flight height and *SD* is applied in practice when deploying traps and semiochemical lures in mating disruption and mass trapping for control of a number of pest insects as discussed by several authors (Cardé 1990; Cardé and Minks 1995; Miller et al. 2006a,b; El-Sayed et al. 2006, 2009; Byers 2007, 2008). Mating disruption attempts to uniformly distribute many point sources of semiochemical, usually sex pheromone, throughout the area to confuse the insect's orientation to natural odors. The two major mechanisms of disruption, not mutually exclusive, appear to waste the responding sex's time and energy on "false-plume following" to synthetic lures and to adapt insect receptors so they either no longer function or camouflage the natural odor plumes. In mass trapping, moderate doses are released from lures in traps distributed over the area to catch the responding insects.

Most studies on mating disruption and mass trapping have more or less guessed at the density of lures and traps necessary to achieve successful control, adjusting densities and lures based on population levels by means of trial and error. This approach likely will

¹ Corresponding author, e-mail: john.byers@ars.usda.gov.

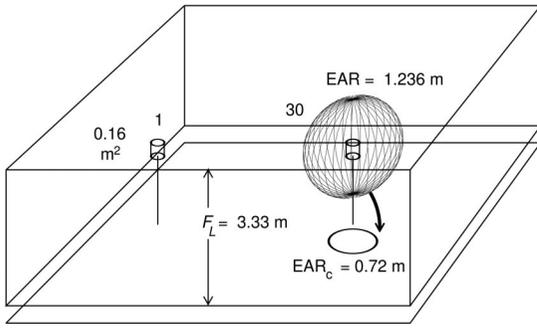


Fig. 1. Two cylindrical sticky traps, a blank catching one insect ($Cb = 1$) and a pheromone trap catching 30 insects ($Ca = 30$), are each 0.16 m^2 in silhouette area (S), giving a spherical $EAR = [(Ca \cdot s) / (\pi \cdot Cb)]^{0.5} = 1.236 \text{ m}$ that can be converted to a circular $EAR_c = \pi \cdot EAR^2 / (2 \cdot F_L) = 0.72 \text{ m}$ based on a flight layer (F_L) of 3.33 m (Byers 2008).

continue but might become more efficient with better understanding from simulation models. A key parameter in recent models of mating disruption and mass trapping (Byers 2007) is the effective attraction radius (EAR), an index of the ability of a lure to attract the target insect to the trap. Earlier, Byers et al. (1989) proposed that the EAR serves as a means to compare the effectiveness of various pheromone release rates among species of insects. The EAR is a spherical radius that would intercept the same number of insects as that actually caught by a semiochemical-baited trap. The EAR can be determined by the catch ratio on attractive (baited) and nonattractive (blank) sticky traps and the silhouette area of the trap (Fig. 1). In mass trapping, the most effective lure would be that with the largest EAR obtained by field-testing a series of increasing release rates of semiochemical (Byers 2007). The EAR is expressed as a radius that is always much less than the distance from the semiochemical source to the extremities of a plume's active space (Byers 2008, 2009).

In subsequent work, it was found that the circular EAR (termed EAR_c) used in the encounter-rate simulations in two-dimensions was not identical to the spherical EAR obtained from field tests (Byers 2008). A transformation of the EAR was necessary (Fig. 1) for more accurate simulations that required an estimation of the effective flight layer (F_L), which approximately represents a layer where the particular insect species flies in search of mates and host plants (Byers 2008, 2009). The equation for the F_L , presented subsequently, calculates the thickness of the flight layer that corresponds to the assumed normal distribution of the insect compressed into a uniform density equivalent to the density at the mean flight height. Because many insects fly in a vertical distribution described well by a Gaussian function that is asymptotic, the F_L limits this unbounded layer thickness to one of uniform density, but the F_L does not correspond to a real boundary layer. However, it would be expected that there is a characteristic F_L for each species that might vary somewhat because of habitat and season but

would otherwise be independent and possibly quite different from those of other species (Byers 2009). The F_L is based on the standard deviation (SD) of trap catches at various heights.

Thus, the first objective here was to investigate published work involving catches on at least three trap heights to determine the mean flight height and SD , and then use the SD to calculate F_L . Only those studies in which trap catches diminished with height were analyzed because they were considered to have sampled the vertical flight distribution adequately. Such data were analyzed for normality (skew and kurtosis) and fit to a hypothesized normal distribution with the calculated mean and SD . Because some studies only reported proportions of catch at several heights, these were converted to numbers amenable for calculating mean and SD . The effects of various conversion assumptions involving sample size were tested with iterative calculations. The previous studies were placed into three categories, those where the traps at three or more heights were 1) visually attractive, 2) olfactorily attractive, or 3) not attractive (blank traps). The last objective was to simulate flight of insects in three dimensions in which individuals can fly anywhere, but the population maintains a specified normal distribution of vertical flight heights (Byers 2009). During these simulated population flights of specified mean height and SD within a three-dimensional space, the catches on spherical traps at various heights and distributions were counted to study effects on the observed mean and SD . The simulation results should indicate how reliable the estimates of mean flight height and SD , based on previous reports of trap catches at various heights, might be.

Materials and Methods

Mean Catch Height (\bar{h}) \pm SD from Field Studies Reported in the Literature. The scientific literature was examined (BIOSIS Previews) for articles on flight heights of insects caught by traps to determine the mean height of flight and SD needed to estimate the effective flight layer F_L of search (presented subsequently). The mean catch height \bar{h} and standard deviation, SD , can be calculated, for example, from four traps at heights of 1, 2, 3, and 4 m that caught 30, 85, 50, and 12 insects, respectively, from the following iterative algorithms:

$$\bar{h} = \text{sum}x / n \tag{1}$$

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

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 (McCall 1970). Thus, $\bar{h} = 2.25 \text{ m}$ and $SD = 0.82 \text{ m}$ using the data above. The mean catch height and SD are assumed to sample the mean flight height and SD

accurately and thus will be used interchangeably hereafter.

In some cases, studies reported only the proportions of catch on traps but gave an overall n , thus allowing calculations, but in fewer cases only the proportions were given. In these, n was assumed to be 100 and apportioned appropriately to traps. This assumption was tested with n of 20, 100, and 2000 with catch proportions of 0.1, 0.3, 0.3, 0.2, and 0.1 at trap heights of 1, 2, 3, 4, and 5, respectively, to determine effects on the mean flight height and SD by using equations 1 and 2.

The Effective Flight Layer, F_L . The maximum height Y of the normal curve (McCall 1970) occurs at $x = \bar{h}$ (the mean height of flight), which reduces to:

$$Y = \frac{e^{-\frac{(x-\bar{h})^2}{2SD^2}}}{SD \cdot \sqrt{2 \cdot \pi}} = \frac{1}{SD \cdot \sqrt{2 \cdot \pi}} \quad [3]$$

where SD is the standard deviation of the flight distribution. The height of the normal curve at the mean, $1/(SD \cdot \sqrt{2 \cdot \pi})$, times the value in the denominator will give a value of 1, which is equal to the standardized area under the curve. The density distribution under the normal curve thus can be compressed into a flight layer, F_L , of uniform density equivalent to that at the mean height of flight, as given by:

$$F_L = SD \cdot \sqrt{2 \cdot \pi} \quad [4]$$

(Byers 2008, 2009). The normal equation that describes the catch or flight density with height (h), given the mean flight height (\bar{h}) and SD , was found from the following equation:

$$Catch = A \cdot (\exp - (h - \bar{h})^2 / (2 \cdot SD^2)) / (SD \cdot \sqrt{2 \cdot \pi}) \quad [5]$$

The best-fitting normal equation 5 was found by iteration of least squared differences of the observed catches on the trap heights with the corresponding theoretical values found from equation 5. Starting with a maximum A in equation 5 found by:

$$A = 2 \cdot Max / (1 / (SD \cdot \sqrt{2 \cdot \pi})) \quad [6]$$

where Max is the maximum trap catch at any height. The iteration proceeded by diminishing A by $A/10,000$ until A reached 0.01. The A where the sum of the squared differences was least was found during these iterations and was the best fitting A for \bar{h} and SD calculated for the trap catch data. Computing a squared product-moment correlation, r^2 , indicated the strength of the fit between the best-fitting normal equation and the observed catch data:

$$r^2 = \frac{\left[\sum (c_i - \bar{c}) \cdot (p_i - \bar{p}) / \sqrt{\sum (c_i - \bar{c})^2 \cdot \sum (p_i - \bar{p})^2} \right]^2}{\sum (c_i - \bar{c})^2 \cdot \sum (p_i - \bar{p})^2} \quad [7]$$

where c_i and p_i are the observed and predicted catch, respectively, at each trap level, and \bar{c} and \bar{p} are the

observed and predicted mean catch, respectively (Sokal and Rohlf 1995). In addition, the vertical catch distributions were analyzed for skew and kurtosis (Sokal and Rohlf 1995). Calculations and models (presented subsequently) were programmed in QuickBASIC 4.5 (Microsoft Corp., Redmond, WA) as well as Java 6.0 (Oracle, Redwood City, CA) for general demonstration on the Internet with a web browser (<http://www.chemical-ecology.net/java2/flt-3d.htm>).

Simulation of Insect Flight Distributions and Catch on Spherical Traps in Three Dimensions. Insects were simulated in a three-dimensional (3D) area with x-axis (xa), y-axis (ya), and z-axis (za) of 20 by 20 by 10 m, respectively. Each insect was given a starting position (x, y, z) at random according to a specified normal distribution of SD . This was done by selecting a z-coordinate uniformly at random from 0 to za . Then, if a uniform random number (0–1) times the second part of equation 3 was less than the first part of equation 3, where $z = x$, then z was accepted as a coordinate, otherwise random selections were continued until the condition was met. The x- and y-coordinate values were selected at random with no constraints. Thereafter each insect followed a correlated random walk (CRW) in 3D comprised of a series of steps each of length 0.1 m. Spherical coordinates (Hearn and Baker 1994) were calculated at each insect step as a 3D vector from the former position (x_0, y_0, z_0) to the present position (x_1, y_1, z_1) where $x_1 = x_0 \cdot s \cdot \cos(\theta) \cdot \sin(\phi)$, $y_1 = y_0 \cdot s \cdot \sin(\theta) \cdot \sin(\phi)$, and $z_1 = z_0 \cdot s \cdot \cos(\phi)$ based on the former direction plus random angular changes (in radians) in the two directional angles (θ and ϕ). Thus, $\theta = \theta + \alpha$ (if $\theta > 2\pi$ then $\theta = \theta - 2\pi$, if $\theta < 0$ then $\theta = \theta + 2\pi$) and $\phi = \phi + \beta$ (if $\phi > \pi$ then $\phi = \phi - \pi$, if $\phi < 0$ then $\phi = \phi + \pi$), where α and β were chosen at random from a normal distribution with a 6° SDA (standard deviation of angular turns). This was done at each step for α (and β) by iteration: $\alpha = \alpha + \sqrt{-2 \cdot \ln(R_1) \cdot \cos(2 \cdot \pi \cdot R_2) \cdot SDA}$ where R_1 and R_2 were uniform random numbers between 0 and one (Byers 2001). Insects rebounded at random angles at the volume boundaries. The (x, y, z) coordinates of each insect step were additionally transformed to 3D perspective coordinates when viewing the simulations (Adams 1987). Insects flew within the volume such that the population had a mean height of $za/2$ and were distributed normally with a specified SD , as accomplished by the following simple algorithm. If the insect was above the mean ($za/2$) then $\phi = \phi - \omega$, while if it was below the mean then $\phi = \phi + \omega$, and then if $\phi > \pi$ then $\phi = \pi$ and if $\phi < 0$ then $\phi = 0$, where ω = an incremental turn angle in radians that depended on which step size, SD and SDA were used (Byers 2009). The flight model (Fig. 2) was used to simulate vertical flight distributions of $SD = 1.67$ m as set up by insect flight steps of 0.1 m each, $SDA = 6^\circ$ and using $\omega = 0.0715 SD^{-0.9327} = 0.0444$ radians (details in Byers 2009).

Either 2, 4, 6, 8, 10, or 12 spherical traps of 0.2-m radius (EAR) were placed at even spacing (e.g., at 3.3 and 6.6 m height for two traps, or every 0.714 m for 12

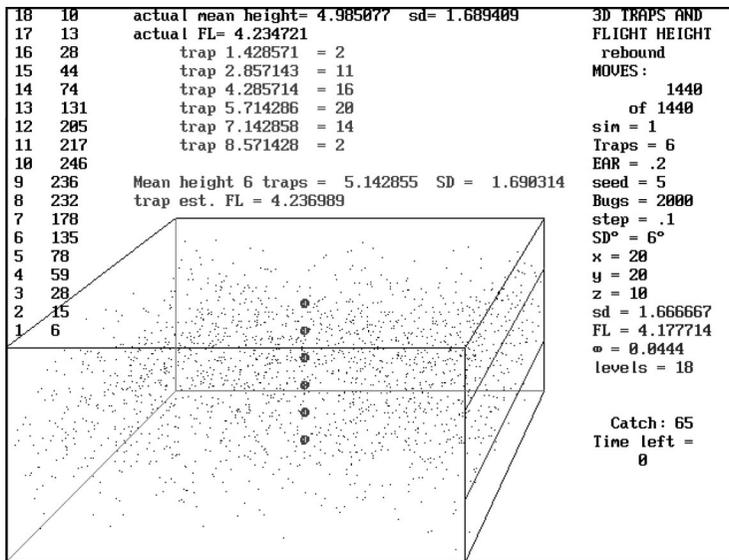


Fig. 2. Computer screen showing simulation of spherical traps (0.2 m radius) at six heights from 1.43 to 8.57 m in 1.42-m increments in a 20 by 20 by 10-m three-dimensional space in which individual insects (small points) can fly anywhere but the population distributes in a normal distribution of specified standard deviation (in this case SD = 1.67 m). Other flight parameters described in methods.

traps) within the 10-m high flight volume. This resulted in traps being evenly spaced above and below the mean flight height of 5 m. Two thousand insects were released in the volume and individuals were allowed to fly anywhere, but the populations always exhibited a normal distribution at any instant in time (Fig. 2) as accomplished by the individual-based movement algorithms described above. The numbers caught on the EAR trap spheres over a period of 1,440; 2,880; or more steps (as noted) were recorded and not replaced in the volume (eight simulations for each set of traps). The algorithm to determine whether insects entered or passed through the spherical EAR in 3D during a step from (x, y, z) to (p, q, r) , i.e., were caught, was modified from that in Byers (1991, his Fig. 3), for a circle in 2D. In the 2D algorithm, the EAR's (j, k) coordinates are compared with the insect's step from (x, y) to (p, q) coordinates in the x-y plane. Additionally, by repeating the algorithm for the x-z plane (from x, z to p, r) and the y-z plane (from y, z to q, r), then

any interception of a sphere by an insect during a 3D step can thus be determined.

Results

Calculating Flight Parameters and Effective Flight Layer from Field Studies Reported in the Literature. Over 100 articles were found on insect flight heights of which only some were suitable for estimating the flight layer of search, F_L (Tables 1–3). Insects attracted to colors or semiochemicals may have had their natural flight distributions altered (Tables 1 and 2), which is unlikely for species caught by nonattractive traps (sticky screens or window barriers, Table 3). Insects feeding on crops usually fly within a few meters above ground. For example, the minute western flower thrips [*Frankliniella occidentalis* (Pergande)] that feed on vegetable crops have a mean flight height of 1.14 ± 0.70 m ($\pm SD$) giving a F_L of 1.76 m (catch on yellow sticky cards), whereas another study reported a mean height of 2.26 ± 0.43 m and F_L of 1.08 m (Table 1). The important whitefly pest of numerous crops, *Bemisia tabaci*, distributed worldwide has a similar mean flight height of $\approx 1.16 \pm 1.86$ m and apparently wider F_L of 4.64 m (Table 1). In contrast, bark beetles that search for susceptible host trees of Norway spruce [*Picea abies* (L.) H. Karst.] and Scotch pine (*Pinus sylvestris* L.) have a higher mean flight height of 5–6 m and F_L of ≈ 7 m (Table 3).

The mean flight height can vary depending on the habitat. For example, over open areas of grass, mean flight heights were lower than when flying in orchard and wooded areas (Table 2, sap beetles, *G. fasciatus*: 1.63 and 2.52 m, respectively; Table 3, Diptera, *S. bedfordi*: 2.85 and 4.80 m, respectively). In many cases

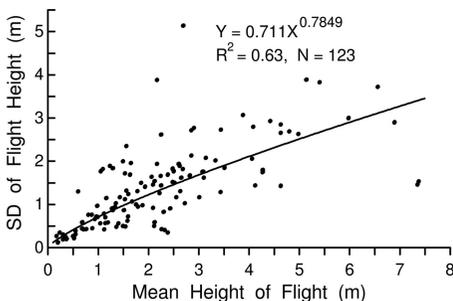


Fig. 3. Relationship between mean height of flight and SD (data from Tables 1–3).

Table 1. Analysis of mean height of catch (\bar{h}) \pm *SD* and effective flight layer (F_L) of insect species caught on visually attractive traps at various heights reported in the literature [best-fit normal equation: $A (\exp(-(h-\bar{h})^2/(2 \cdot SD^2)))/(SD \cdot 2 \cdot \pi)$, where h is ht in m]

Species	Trapping method ^a	Range of trap heights	Number of trap levels	Total catch ^b	Mean ht of catch \pm <i>SD</i> (m)	A of normal equation (r^2) ^c	Kurtosis ^d	Skewness (tailing) ^e	F_L (m)
Thysanoptera: Thripidae									
<i>Frankliniella occidentalis</i> (Pergande) ^f	Y-St-card	0.25–2.5	5	(1,000)	1.14 \pm 0.70	547 (0.51)	P (–0.94)**	R (0.21)**	1.76
<i>Frankliniella occidentalis</i> (Pergande) ^g	Blue-St-card	0.6–3	5	858	2.32 \pm 0.41	581 (0.89)	L (5.59)**	L (–1.79)**	1.03
<i>Frankliniella occidentalis</i> (Pergande) ^g	Y-St-card	0.6–3	5	711	2.26 \pm 0.43	484 (0.83)	L (5.29)**	L (–1.96)**	1.08
<i>Frankliniella occidentalis</i> (Pergande) ^g	W-St-card	0.6–3	5	537	2.38 \pm 0.35	351 (0.97)	L (7.30)**	L (–1.62)**	0.87
Hemiptera: Triozidae									
<i>Trioxa erytreae</i> (Del Guercio) ^h	Y-St-card	0.1–10	4	389	1.56 \pm 2.35	1,590 (0.85)	L (1.00)**	R (1.39)**	5.89
Hemiptera: Aleyrodidae									
<i>Parabemisia myricae</i> (Kuwana) ⁱ	Y-St-card	0.76–6.1	8	5445	1.93 \pm 1.41	4,544 (0.40)	L (1.05)**	R (1.34)**	3.55
<i>Bemisia tabaci</i> (Gennadius) males ^j	W-St-card	0.16–7.36	4	258	1.09 \pm 1.82	696 (0.61)	L (3.16)**	R (1.99)**	4.55
<i>Bemisia tabaci</i> (Gennadius) females ^j	W-St-card	0.16–7.36	4	265	1.23 \pm 1.89	700 (0.60)	L (2.52)**	R (1.80)**	4.73
<i>Bemisia tabaci</i> (Gennadius) ^k	Y-St-card	0.3–1.2	4	799	0.55 \pm 0.31	240 (0.26)	P (–0.44)*	R (0.93)**	0.77
<i>Alewoacanthus woglumi</i> Ashby ^l	Y-St-card	0.6–6	7	439	1.59 \pm 0.72	425 (0.95)	L (5.69)**	R (1.48)**	1.81
Hemiptera: Cicadellidae									
<i>Circulifer tenellus</i> (Baker) males ^m	Y-St-card	0.11–2.81	7	2,905	0.17 \pm 0.27	1,250 (0.69)	L (56.8)**	R (6.90)**	0.67
<i>Circulifer tenellus</i> (Baker) females ^m	Y-St-card	0.11–2.81	7	657	0.23 \pm 0.35	283 (0.53)	L (27.6)**	R (4.85)**	0.89
<i>Scaphytopius magdalenis</i> (Provancher) ⁿ	Y-St-card	0.12–1.82	8	(100)	0.30 \pm 0.19	25 (0.88)	0.06	R (0.82)**	0.48
Hemiptera: Miridae									
<i>Lygus lineolaris</i> (P. de Beauvois) males ^o	W-St-card	0.6–3.05	3	1,780	0.93 \pm 0.66	2,337 (0.90)	L (2.65)**	R (1.89)**	1.66
<i>Lygus lineolaris</i> (P. de Beauvois) females ^o	W-St-card	0.6–3.05	3	1,396	0.99 \pm 0.71	1,823 (0.80)	L (1.83)**	R (1.79)**	1.79
<i>Lygus lineolaris</i> (P. de Beauvois) ^p	W-St-card	0.5–3.5	7	561	1.11 \pm 0.79	311 (0.44)	L (1.40)**	R (1.47)**	1.97
<i>Lygocoris communis</i> (Knight) ^p	W-St-card	0.5–3.5	7	175	2.09 \pm 0.92	84 (0.28)	P (–0.99)**	–0.30	2.31
<i>Lygidea mendax</i> Reuter ^q	W-St-card	0.5–3.5	7	58	1.51 \pm 0.87	28 (0.34)	–0.96	0.41	2.18
<i>Campylomma verbasci</i> (Meyer) ^p	W-St-card	0.5–3.5	7	11,647	2.30 \pm 0.83	5,593 (0.75)	P (–0.95)**	L (–0.16)**	2.08
<i>Heterocodolmus malinus</i> Reuter ^q	W-St-card	0.5–3.5	7	63	1.27 \pm 0.91	32 (0.12)	–0.67	R (0.82)**	2.28
Diptera: Agromyzidae									
<i>Liriomyza trifolii</i> (Burgess) fall ^q	Y-St-card	0.3–1.5	5	(100)	0.55 \pm 0.39	34 (0.24)	0.94	R (1.50)**	0.99
<i>Liriomyza trifolii</i> (Burgess) spring ^q	Y-St-card	0.3–1.5	5	(100)	0.50 \pm 0.27	31 (0.62)	L (1.49)**	R (1.41)**	0.69
Diptera: Culicidae									
<i>Aedes cantator</i> (Coquillett) ^r	B/W-box	0.6–2.4	4	178	1.49 \pm 0.50	105 (0.75)	–0.49	R (0.40)*	1.25
<i>Aedes punctator</i> (Kirby) ^r	B/W-box	0.6–2.4	4	137	1.40 \pm 0.56	80 (0.98)	P (–0.84)*	0.16	1.40
<i>Mansonia perturbans</i> (Walker) ^r	B/W-box	0.6–2.4	4	1,043	1.54 \pm 0.49	613 (0.88)	P (–0.59)**	R (0.23)**	1.23
Diptera: Calliphoridae									
<i>Cochliomyia hominivorax</i> (Coquerel) ^s	Y-bucket	0.4–1.5	3	(100)	0.76 \pm 0.43	53 (0.27)	P (–1.10)*	R (0.66)**	1.08
Lepidoptera: Geometridae									
<i>Idaea squamipunctata</i> Warrant	R-light	1–30	3	529	18.0 \pm 11.1	7,281 (0.53)	P (–1.27)**	L (–0.28)**	27.90
<i>Hypomecis costaria</i> Guenée ^t	R-light	1–30	3	252	2.17 \pm 3.88	2,350 (0.99)	L (7.26)**	R (3.03)**	9.72
<i>Ornithospila avicularia</i> Guenée ^t	R-light	1–30	3	85	8.98 \pm 8.93	1,190 (0.89)	–0.30	R (0.72)**	22.38
<i>Codonella avicularia</i> Walker ^t	R-light	1–30	3	63	9.38 \pm 10.86	876 (0.33)	–0.60	R (0.90)**	27.23
<i>Hypomecis tetragonata</i> Walker ^t	R-light	1–30	3	37	10.54 \pm 8.94	516 (0.97)	–0.38	0.44	22.42
Lepidoptera: Pyralidae									
<i>Ostrinia nubilalis</i> (Hübner) ^u	Light-UV	1.5–4.6	3	7,172	2.55 \pm 1.17	10,431 (0.28)	P (–1.05)**	R (0.62)**	2.93
Coleoptera: Scarabaeidae									
<i>Phyllophaga crinita</i> Burmeister ^v	St-card-UV	0.15–2.29	15	3,250	0.68 \pm 0.59	534 (0.17)	0.13	R (1.09)**	1.49
Coleoptera: Chrysomelidae									
<i>Diabrotica virgifera</i> LeConte ^w	Y-St-box	3.05–7.62	4	4,528	4.12 \pm 1.44	7,035 (0.40)	0.09	R (1.12)**	3.60
<i>Trirhabda virgata</i> LeConte ^x	W-St-card	1–4	4	377	1.75 \pm 1.00	382 (0.28)	–0.19	R (1.05)**	2.51
<i>Phyllotreta cruciferae</i> (Goeze) ^y	Y-St-card	0.5–7	8	173	2.68 \pm 1.82	163 (0.72)	–0.48	R (0.59)**	4.57
Coleoptera: Elateridae									
<i>Ctenicera appropinquans</i> (Randall) ^z	Y-X-pane	0.8–14.3	10	115	5.40 \pm 3.83	174 (0.38)	–0.35	R (0.65)**	9.59
<i>Ctenicera pulchra</i> (LeConte) ^z	Y-X-pane	0.8–14.3	10	56	5.14 \pm 3.89	83 (0.17)	–0.94	0.49	9.74
<i>Ctenicera tarsalis</i> (Melsheimer) ^z	Y-X-pane	0.8–14.3	10	74	3.88 \pm 3.07	114 (0.48)	0.17	R (0.94)**	7.70
<i>Melanotus similis</i> (Kirby) ^z	Y-X-pane	0.8–14.3	10	97	2.50 \pm 1.77	155 (0.89)	L (2.94)**	R (1.41)**	4.43
<i>Sericus brunneus</i> (L.) ^z	Y-X-pane	0.8–14.3	10	118	6.56 \pm 3.72	172 (0.49)	–0.85	0.11	9.31
<i>Melanotus communis</i> (Gyllenhal) [#]	Light-UV	1–5	3	2,078	1.53 \pm 1.12	4,621 (0.86)	L (3.03)**	R (2.04)**	2.82

^a Y-St-card (yellow sticky card); Blue-St-card (blue sticky card); W-St-card (white sticky card); B/W-box (black and white box with funnel entrance); Y-bucket (yellow bucket trap); R-light (Rothamsted light trap); Light-UV (UV light trap); St-card-UV (sticky card with UV light); Y-St-box (yellow sticky box); Y-X-pane (yellow cross panes).

^b Trap catch reported as proportions so catch in parentheses was assumed in order to calculate mean height of catch and variation.

^c Squared product-moment correlation indicating strength of fit by normal equation to observed data.

^d Kurtosis values denoting departure from theoretical normal distribution, with P = platykurtic and L = leptokurtic forms, * denotes significant departure at $P < 0.05$ and ** at $P < 0.01$.

^e Skewness values denoting departure from theoretical normal distribution, with R = right tailing and L = left tailing, * and ** as above.

^f Pearsall and Myers 2001, ^g Gillespie and Vernon 1990, ^h Van den Berg and Deacon 1989, ⁱ Meyerdirk and Moreno 1984, ^j Isaacs and Byrne 1998, ^k Diraviam and Uthamasamy 1992, ^l Meyerdirk et al. 1979, ^m Meyerdirk and Oldfield 1985, ⁿ Meyer and Colvin 1985, ^o Stewart and Gaylor 1991, ^p Boivin and Stewart 1984, ^q Chandler 1985, ^r Browne and Bennett 1981, ^s Peterson II 1982, ^t Intachat and Holloway 2000, ^u Ficht and Hinton 1941, ^v Stone 1986, ^w VanWoerkom et al. 1983, ^x Messina 1982, ^y Lamb 1983, ^z Boiteau et al. 2000, [#] Cherry and Hall 1986.

there was little difference between the mean height and *SD* of males and females (Table 1, whiteflies: *B. tabaci*, leafhoppers: *C. tenellus*, plant bugs: *L. lineolaris*; Table 2, scarabs: *P. horticola*; or Table 3, Bibionidae: *B. johannis*, bark beetles: *I. typographus*). However, in cases when the two sexes have different behaviors,

such as when males search for calling females or have male territories, then the mean flight height and *SD* were different between the sexes (Table 3: mosquitoes: *C. thalassius*; butterflies: *H. numata*). Of the insects that were caught on visually attractive traps (Table 1), 30 of 33 species fit normal distributions

Table 2. Analysis of mean height of catch \pm SD (m) and effective flight layer (F_L) of insect species caught on traps releasing attractive semiochemicals at various heights reported in the literature [best-fit normal equation: $A \exp(-(h-\bar{h})^2/(2 \cdot SD^2))/(SD \cdot 2 \cdot \pi)$], where h is height in m]

Species	Trapping method ^d	Range of trap heights	Number of trap levels	Total catch ^b	Mean ht of catch \pm SD	A of normal equation (r^2) ^c	Kurtosis ^d	Skewness ^e (tailing)	F_L (m)
Diptera: Culicidae									
<i>Culex tritaeniorhynchus</i> Giles ^f	UV-CO ₂	0.5-5	4	(100)	0.98 \pm 0.97	116 (0.90)	L (10.34)**	R (3.24)**	2.44
<i>Culex pipiens</i> L. ^f	UV-CO ₂	0.5-5	4	(100)	2.48 \pm 1.52	167 (0.83)	P (-1.06)**	0.29	3.81
<i>Anopheles sinensis</i> Wiedemann ^f	UV-CO ₂	0.5-5	4	(100)	1.16 \pm 1.15	128 (0.83)	L (4.42)**	R (2.27)**	2.89
<i>Aedes vexans nipponii</i> (Theobald) ^f	UV-CO ₂	0.5-5	4	(100)	1.60 \pm 1.24	140 (0.96)	0.10	R (1.05)**	3.10
Diptera: Tephritidae									
<i>Anastrepha ludens</i> (Loew) ^g	G-yeast	0.1-3	4	240	1.58 \pm 0.62	242 (0.96)	-0.20	L (-0.50)**	1.55
Lepidoptera: Tortricidae									
<i>Grapholitha molesta</i> (Busck) ^h	Delta-P	1-4	3	427	2.72 \pm 1.03	790 (0.93)	P (-1.60)**	R (0.33)**	2.58
<i>Platynota flavedana</i> Clemens ⁱ	Pherocon-P	0.3-3.9	5	850	1.79 \pm 0.95	737 (0.87)	P (-0.86)**	-0.06	2.38
<i>Platynota idaeusalis</i> (Walker) ⁱ	Pherocon-P	0.3-3.9	5	1817	1.88 \pm 0.98	1579 (0.93)	P (-0.80)**	0.05	2.45
Lepidoptera: Pyralidae									
<i>Diaphania nitidalis</i> (Stoll) males ^j	VF-bucket	0.3-1.8	4	188	1.12 \pm 0.42	117 (0.86)	P (-1.20)**	L (-0.36)*	1.06
<i>Coniesta ignefusalis</i> (Hampson) ^k	Water-P	0.1-2	4	392	0.30 \pm 0.30	176 (0.86)	L (5.33)**	R (2.05)**	0.76
Lepidoptera: Noctuidae									
<i>Busseola fusca</i> (Fuller) ^l	Funnel-P	0.5-2	4	102	1.36 \pm 0.48	50 (0.81)	-0.82	-0.33	1.21
Lepidoptera: Plutellidae									
<i>Plutella xylostella</i> (L.) ^m	Pherocon-P	0.3-1.5	3	170	0.37 \pm 0.20	82 (0.99)	L (7.60)**	R (2.84)**	0.51
Lepidoptera: Cossidae									
<i>Prionoxystus robiniae</i> Peck ⁿ	Bucket-P	1.5-9	4	160	4.42 \pm 2.93	387 (0.02)	P (-1.28)**	R (0.55)**	7.34
Lepidoptera: Sesiidae									
<i>Synanthedon exitiosa</i> (Say) ^o	Pherocon-P	0.1-5.6	4	124	2.09 \pm 1.46	223 (0.98)	-0.18	0.42	3.66
<i>Synanthedon pictipes</i> (Grote & Rob.) ^o	Pherocon-P	0.1-5.6	4	1,110	2.06 \pm 1.64	1960 (0.90)	P (-0.56)**	R (0.47)**	4.10
Coleoptera: Nitidulidae									
<i>Carpophilus humeralis</i> (F.) ^p	Funnel-P	0.3-3	4	131	0.80 \pm 0.76	110 (0.41)	L (1.22)**	R (1.48)**	1.92
<i>Glischrochilus quadrisignatus</i> (Say) ^q	Bucket-d	0.3-5	5	3,684	2.65 \pm 1.62	4,283 (0.69)	P (-1.28)**	L (-0.08)*	4.06
<i>G. fasciatus</i> (Olivier) apple trees ^q	Bucket-d	0.3-5	5	1,104	2.52 \pm 1.50	1,334 (0.77)	P (-1.08)**	0.04	3.77
<i>G. fasciatus</i> (Olivier) grass ^q	Bucket-d	0.3-5	5	52	1.63 \pm 1.69	69 (0.15)	-0.55	R (0.95)**	4.24
<i>Carpophilus lugubris</i> Murray ^q	Bucket-d	0.3-5	5	105	1.56 \pm 1.32	146 (0.83)	0.74	R (1.15)**	3.30
Coleoptera: Curculionidae									
<i>Anthonomus grandis</i> Boheman ^r	Y-St-X-pane-P	0-9.1	6	22,310	1.65 \pm 1.96	36,202 (0.64)	L (0.84)**	R (1.23)**	4.91
<i>Cylas formicarius</i> F. ^s	Funnel-P	0.09-0.85	7	3,892	0.20 \pm 0.12	387 (0.78)	L (4.43)**	R (1.86)**	0.31
Coleoptera: Scolytidae									
<i>Ips typographus</i> (L.) ^t	St-screen-P	0.7-11.5	10	740	1.53 \pm 1.72	1175 (0.53)	L (11.6)**	R (3.18)**	4.32
<i>Tomicus piniperda</i> (L.) ^t	St-screen-A	0.7-11.5	10	48	2.90 \pm 2.77	63 (0.27)	0.42	R (1.24)**	6.95
Coleoptera: Scarabaeidae									
<i>Hoplia equina</i> LeConte ^u	X-pane-P	0.2-1	3	852	0.35 \pm 0.25	362 (0.76)	L (0.95)**	R (1.45)**	0.62
<i>Phyllopertha horticola</i> L. males ^v	Y-X-vane-A	0.5-2	3	1,119	1.14 \pm 0.57	788 (0.70)	P (-1.22)**	R (0.26)**	1.43
<i>Phyllopertha horticola</i> L. females ^v	Y-X-vane-A	0.5-2	3	416	1.04 \pm 0.56	297 (0.51)	P (-1.04)**	R (0.52)**	1.40
<i>Popillia japonica</i> Newman ^w	Y-floral	0.28-0.84	3	17,175	0.52 \pm 0.22	4,495 (0.52)	P (-1.28)**	R (0.28)**	0.54
Coleoptera: Chrysomelidae									
<i>Diabrotica virgifera</i> LeConte ^x	Pherocon-F	0-2.4	5	2,235	0.96 \pm 0.72	1,296 (0.75)	P (-0.82)**	R (0.36)**	1.80

^a UV-CO₂ (UV light and dry ice); G-yeast (green food color and yeast hydrolysate in bucket trap); Delta-P (Delta trap with synthetic pheromone); Pherocon-P (Pherocon 1C trap with synthetic pheromone); VF-bucket (4 virgin females in bucket trap); Water-P (water trap with synthetic pheromone); Funnel-P (2-funnel trap with synthetic pheromone); Bucket-P (sticky bucket with synthetic pheromone); Bucket-d (bucket trap with bread dough); Y-St-X-pane-P (yellow sticky cross panes with pheromone bait); St-screen-P (sticky screen with synthetic pheromone); St-screen-A (sticky screen with monoterpene attractants); X-pane-P (cross window panes with pheromone bait); Y-X-vane-A (yellow cross vanes with floral volatiles); Y-floral (yellow funnels with synthetic floral lure); Pherocon-F (Pherocon 1C trap with synthetic floral attractants).

^b Trap catch reported as proportions so catch in parentheses was assumed in order to calculate mean height of catch and variation.

^c Squared product-moment correlation indicating strength of fit by normal equation to observed data.

^d Kurtosis values denoting departure from theoretical normal distribution, with P = platykurtic and L = leptokurtic forms, * denotes significant departure at $P < 0.05$ and ** at $P < 0.01$.

^e Skewness values denoting departure from theoretical normal distribution, with R = right tailing and L = left tailing, * and ** as above.

^f Lee et al. 2006, ^g Robacker et al. 1990, ^h Rothschild and Minks 1977, ⁱ David and Horsburgh 1989, ^j Valles et al. 1991, ^k Youm and Beevor 1995, ^l Critchley et al. 1997, ^m Chisholm et al. 1979, ⁿ Dix et al. 1979, ^o Cottrell et al. 2010, ^p Bartelt et al. 1994, ^q Peng and Williams 1991, ^r Rummel et al. 1977, ^s Proshold et al. 1986, ^t Byers et al. 1989, ^u Weber et al. 2005, ^v Ruther 2004, ^w Ladd and Klein 1982, ^x Weissling and Meinke 1991.

reasonably well ($r^2 \geq 0.25$), whereas 27 of 28 species attracted to odors (Table 2) fit a normal distribution, and 44 of 53 species intercepted by blank traps (Table 3) fit a normal distribution.

There was no relation between the number of trap levels (X) in the field studies and the calculated mean flight height (Y) for either the visual or semiochemical traps (Tables 1 and 2), while there was an increase in mean flight height for the blank traps with an increasing number of trap levels ($Y = 0.97 +$

$0.273X$, $R^2 = 0.30$, $n = 54$, $P < 0.001$). The number of trap levels had little effect on how well the data fit a normal curve. In all three categories, however, there was a significant effect on increasing the SD when the mean flight height was larger, thus, all data were pooled. The SD of flight increased as a power function of mean height of flight (X), as $SD = 0.711X^{0.7849}$ ($R^2 = 0.63$, $n = 123$, $P < 0.001$; Fig. 3).

The studies reporting only proportions of catch with trap height were assumed to have caught $n = 100$

Table 3. Analysis of mean height of catch \pm SD (m) and effective flight layer (F_L) of insect species caught on non-attractive traps at various heights reported in the literature [best-fit normal equation: $A (\exp(-(h-h)^2/(2 \cdot SD^2)))/(SD \cdot 2 \cdot \pi)$, where h is ht in m]

Species	Trapping method ^a	Range of trap heights	Number of trap levels	Total catch ^b	Mean ht of catch \pm SD	A of normal equation (r^2) ^c	Kurtosis ^d	Skewness ^e (tailing)	F_L (m)
Hemiptera: Miridae									
<i>Lygus lineolaris</i> (P. de Beauvois) ^f	Window	1-4	4	300	2.12 \pm 1.39	n.a.	n.a.	n.a.	3.48
Hemiptera: Coreidae									
<i>Euthochtha galeator</i> (F.) ^g	Window	1-4	4	52	1.60 \pm 1.15	n.a.	n.a.	n.a.	2.88
Hemiptera: Alydidae									
<i>Alydus evarius</i> (Say) ^h	Window	1-7	7	145	1.35 \pm 1.03	197 (0.54)	L (14.3)**	R (3.64)**	2.58
<i>Alydus pilosulus</i> (Herrich-Schaeffer) ^h	Window	1-7	7	44	1.43 \pm 1.17	58 (0.38)	L (6.76)**	R (2.73)**	2.93
Hemiptera: Reduviidae									
<i>Sinea diadema</i> (F.) ⁱ	Window	1-7	7	45	1.29 \pm 0.87	60 (0.63)	L (10.4)**	R (3.30)**	2.18
<i>Sinea spinipes</i> (Herrich-Schaeffer) ⁱ	Window	1-7	7	33	4.06 \pm 2.06	31 (0.01)	-1.42	-0.20	5.17
Hemiptera: Nabidae									
<i>Nabis americanoferus</i> Carayon ^j	Window	1-7	7	58	2.48 \pm 1.83	60 (0.14)	-0.30	R (0.99)**	4.58
<i>Nabis roseipennis</i> Reuter ^j	Window	1-7	7	123	3.07 \pm 1.76	119 (0.26)	P (-0.88)*	0.36	4.41
Hemiptera: Anthocoridae									
<i>Oritus insidiosus</i> (Say) ^j	Window	1-7	7	5,187	3.45 \pm 1.81	5,026 (0.57)	P (-0.88)**	R (0.37)**	4.53
Hemiptera: Lygaeidae									
<i>Antilocoris pilosulus</i> (St ^{al}) ^k	Window	1-7	7	310	4.27 \pm 1.80	300 (0.82)	P (-0.93)**	-0.16	4.52
<i>Crophilus disconotus</i> (Say) ^k	Window	1-7	7	79	3.09 \pm 1.76	79 (0.55)	-0.33	R (0.73)**	4.42
<i>Geocoris punctipes</i> (Say) ^k	Window	1-7	7	78	2.37 \pm 1.74	82 (0.19)	-0.22	R (1.05)**	4.37
Hemiptera: Tingidae									
<i>Corythucha ciliata</i> (Say) ^l	Window	1-7	7	70	4.27 \pm 1.75	68 (0.74)	-0.90	-0.03	4.39
<i>Gargaphia solani</i> Heidemann ^l	Window	1-7	7	91	1.85 \pm 1.50	107 (0.28)	L (2.15)**	R (1.77)**	3.75
Hemiptera: Cydnidae									
<i>Amnestus basidentatus</i> Froeschner ^m	Window	1-7	7	609	4.63 \pm 1.43	604 (0.96)	-0.35	L (-0.25)*	3.60
<i>Amnestus pallidus</i> Zimmer ^m	Window	1-7	7	103	3.51 \pm 1.85	99 (0.26)	P (-1.06)*	0.21	4.64
<i>Amnestus spinifrons</i> (Say) ^m	Window	1-7	7	78	3.33 \pm 2.02	75 (0.01)	P (-1.15)*	0.34	5.07
Hemiptera: Pentatomidae									
<i>Brochymena quadripustulata</i> (F.) ^m	Window	1-7	7	514	3.01 \pm 1.17	525 (0.96)	L (0.67)**	R (0.59)**	2.94
<i>Euschistus servus</i> (Say) ^m	Window	1-7	7	143	2.12 \pm 1.54	159 (0.39)	L (1.59)**	R (1.50)**	3.85
Diptera: Culicidae									
<i>Anopheles melas</i> Theobald males ⁿ	Suction	0.1-7.9	7	54	1.49 \pm 2.00	50 (0.49)	L (3.95)**	R (2.05)**	5.00
<i>Anopheles melas</i> Theobald females ⁿ	Suction	0.1-7.9	7	24	1.05 \pm 1.77	21 (0.20)	L (9.85)**	R (2.92)**	4.43
<i>Aedes albocephalus</i> (Theobald) ⁿ	Suction	0.1-7.9	7	44	0.60 \pm 1.30	33 (0.50)	L (24.3)**	R (4.69)**	3.26
<i>Culex thalassius</i> Theobald males ⁿ	Suction	0.1-7.9	7	55	2.25 \pm 2.62	63 (0.01)	0.57	R (1.39)**	6.56
<i>Culex thalassius</i> Theobald females ⁿ	Suction	0.1-7.9	7	91	1.29 \pm 1.84	80 (0.50)	L (5.27)**	R (2.31)**	4.62
<i>Leptoconops noei</i> Clastrier et Coluzzi ^o	W-St-card	2-6	3	1,401	2.11 \pm 0.50	1,726 (0.99)	L (28.1)**	R (5.11)**	1.26
<i>Leptoconops irritans</i> (Noé) ^o	W-St-card	2-6	3	341	2.12 \pm 0.59	492 (0.99)	L (28.0)**	R (5.20)**	1.48
Diptera: Bibionidae									
<i>Biblio johannis</i> (L.) males ^p	St-cylinder	0.4-1.6	3	4,112	0.71 \pm 0.42	2,501 (0.50)	-0.12	R (1.12)**	1.05
<i>Biblio johannis</i> (L.) females ^p	St-cylinder	0.4-1.6	3	365	0.88 \pm 0.45	207 (0.56)	P (-1.13)**	R (0.42)**	1.13
Diptera: Psychodidae									
<i>Sergentomyia bedfordi</i> Newstead in open ^q	St-window	0.5-8.5	9	48	2.85 \pm 2.13	48 (0.24)	-0.23	R (0.85)*	5.34
Above in wooded area ^q	St-window	0.5-10.5	11	267	4.80 \pm 2.69	259 (0.37)	P (-0.79)**	R (0.35)*	6.75
<i>Sergentomyia antennatus</i> New. in open ^q	St-window	0.5-8.5	9	46	2.17 \pm 1.94	46 (0.18)	-1.03	0.69	4.87
Above in wooded area ^q	St-window	0.5-10.5	11	144	2.85 \pm 2.72	154 (0.12)	-0.11	R (1.17)**	6.83
Lepidoptera: Nymphalidae									
<i>Heliconius numata</i> Cramer males ^r	B-fly-net	-	-	90	2.30 \pm 0.95	n.a.	n.a.	n.a.	2.38
<i>Heliconius numata</i> Cramer females ^r	B-fly-net	-	-	34	1.09 \pm 0.64	n.a.	n.a.	n.a.	1.61
Coleoptera: Scarabaeidae									
<i>Hoplia spectabilis</i> Medvedev ^s	B-window	0.2-2.5	4	6,138	0.87 \pm 0.76	4,614 (0.89)	P (-0.29)**	R (1.00)**	1.90
Coleoptera: Scolytidae									
<i>Hylurgops palliatus</i> (Gryllenhal) ^t	St-screen	0.7-11.5	10	86	4.98 \pm 2.63	104 (0.64)	-0.07	R (0.77)**	6.60
<i>Ips typographus</i> (L.) males ^t	St-screen	0.7-11.5	10	48	4.63 \pm 2.66	59 (0.66)	0.41	R (0.84)*	6.68
<i>Ips typographus</i> (L.) females ^t	St-screen	0.7-11.5	10	55	4.63 \pm 2.85	64 (0.17)	-0.90	R (0.65)*	7.15
<i>Tomicus piniperda</i> (L.) ^t	St-screen	0.7-11.5	10	10	5.98 \pm 3.00	12 (0.15)	-0.21	0.23	7.53
<i>Trypodendron domesticum</i> (L.) ^t	St-screen	0.7-11.5	10	17	2.82 \pm 1.67	20 (0.34)	-1.14	0.63	4.19
<i>Cryphalus abietus</i> (Ratz.) ^t	St-screen	0.7-11.5	10	242	3.44 \pm 2.73	316 (0.58)	L (1.38)**	R (1.34)**	6.84
<i>Pityogenes bidentatus</i> (Herbst) ^t	St-screen	0.7-11.5	10	23	3.10 \pm 1.62	28 (0.65)	0.30	0.97	4.06
<i>Pityogenes chalcographus</i> (L.) ^t	St-screen	0.7-11.5	10	84	6.89 \pm 2.90	97 (0.41)	-0.93	-0.20	7.27
<i>Pityogenes quadridens</i> (Hartig) ^t	St-screen	0.7-11.5	10	50	4.08 \pm 2.80	61 (0.40)	0.14	R (0.98)**	7.03
<i>Ips calligraphus</i> (Germar) ^u	X-pane	1-5	3	(100)	2.63 \pm 1.31	187 (0.98)	-0.68	0.21	3.28
<i>Ips grandicollis</i> (Eichh.) ^u	X-pane	1-5	3	(100)	3.43 \pm 1.29	179 (0.98)	-0.64	-0.23	3.22
<i>Hylastes tenuis</i> Eichh. ^u	X-pane	1-5	3	(100)	2.43 \pm 0.91	191 (0.99)	P (-1.08)*	L (-0.97)**	2.27
<i>Xyleborus affinis</i> (Eichh.) ^u	X-pane	1-5	3	(100)	1.33 \pm 0.94	210 (0.97)	L (8.07)**	R (2.96)**	2.35
<i>Xyleborinus saxesini</i> (Ratz.) ^u	X-pane	1-5	3	(100)	2.25 \pm 1.44	181 (0.56)	-0.76	R (0.71)**	3.61
<i>Ambrosiodermus lecontei</i> Hopk. ^u	X-pane	1-5	3	(100)	2.38 \pm 1.69	183 (0.01)	P (-1.30)**	R (0.64)**	4.24
<i>Xylosandrus compactus</i> (Eichh.) ^u	X-pane	1-5	3	(100)	1.78 \pm 1.31	205 (0.64)	0.81	R (1.44)**	3.28
<i>Ips paraconfusus</i> Lanier ^v	Rotary net	1-30	4	660	2.69 \pm 5.14	7,099 (0.91)	L (14.4)**	R (3.67)**	12.88
<i>Dryocoetes autographus</i> (Ratz.) ^w	Window	1.5-7.5	3	(100)	2.60 \pm 1.94	325 (0.65)	L (1.07)*	R (1.52)**	4.86
<i>Dryocoetes betulae</i> Hopkins ^w	Window	1.5-7.5	3	(100)	3.14 \pm 2.08	302 (0.65)	-0.52	R (0.85)**	5.20

Continued on following page

Table 3. Continued

Species	Trapping method ^a	Range of trap heights	Number of trap levels	Total catch ^b	Mean ht of catch ± SD	A of normal equation (r ²) ^c	Kurtosis ^d	Skewness ^e (tailing)	F _L (m)
<i>Trypodendron bivittatum</i> Kirby ^o	Window	1.5–7.5	3	(100)	2.62 ± 1.89	323 (0.70)	L (0.95)*	R (1.45)**	4.75
Coleoptera: Curculionidae									
<i>Balanogastis kolae</i> (Desbr.) ^x	B-St-card	0.4–2.2	4	701	0.68 ± 0.44	439 (0.63)	L (0.97)**	R (1.40)**	1.11
<i>Hylobius pales</i> (Herbst.) ^y	X-pane	1–5	3	(100)	2.24 ± 1.66	188 (0.04)	P (–1.06)*	R (0.81)**	4.17
Coleoptera: Platypodidae									
<i>Platypus compositus</i> Say ^u	X-pane	1–5	3	(100)	1.67 ± 1.07	203 (0.95)	0.85	R (1.33)**	2.69
Hymenoptera: Ichneumonidae									
<i>Glypta fumiferanae</i> (Viereck) females ^q	Malaise	4.5–10	48	1,477	7.37 ± 1.53	161 (0.20)	P (–2.03)**	0.03	3.83
Hymenoptera: Braconidae									
<i>Apanteles fumiferanae</i> (Viereck) females ^q	Malaise	4.5–10	46	1455	7.35 ± 1.46	177 (0.32)	P (–1.91)**	0.03	3.67
Hymenoptera: Agaonidae									
<i>Elisabethiella bajnathi</i> Wiebes ^z	St-cylinder	0.5–2	3	(100)	1.19 ± 0.58	75 (0.75)	P (–s1.33)**	0.44	1.47
<i>Phagoblastus barbarus</i> Grandi ^c	St-cylinder	0.1–4.5	9	(200)	2.22 ± 1.26	114 (0.42)	P (–0.90)**	R (0.36)*	3.17

^a Window (transparent window); Suction (suction trap); W-St-card (white sticky card); St-cylinder (sticky plastic-cylinder); St-window (sticky window); B-fly-net (butterfly net pole); B-window (black window); St-screen (sticky screen); X-pane (cross window panes); Rotary net (rotating butterfly nets); B-St-card (brown sticky card); Malaise trap.

^b Trap catch reported as proportions so catch in parentheses was assumed in order to calculate mean height of catch and variation.

^c Squared product-moment correlation indicating strength of fit by normal equation to observed data.

^d Kurtosis values denoting departure from theoretical normal distribution, with P = platykurtic and L = leptokurtic forms, * denotes significant departure at P < 0.05 and ** at P < 0.01.

^e Skewness values denoting departure from theoretical normal distribution, with R = right tailing and L = left tailing, * and ** as above.

^f McPherson et al. 1993, ^g McPherson and Weber 1990, ^h McPherson and Weber 1981a, ⁱ b, ^j c, ^k d, ^l e, ^m 1980, ⁿ Snow 1982, ^o Carrieri et al. 2007, ^p D'Arcy-Burt and Blackshaw 1987, ^q Basimike et al. 1989, ^r Joron 2005, ^s Zhang et al. 2011, ^t Byers et al. 1989, ^u Atkinson et al. 1988, ^v Gara 1963, ^w Hosking and Knight 1975, ^x Ivbijaro and Daramola 1977, ^y Elliott et al. 1986, ^z Ware and Compton 1994.

to calculate mean flight height and SD. However, this assumption of n appears to have little effect on the estimated parameters. For example, the same mean height of catch (2.9 m) and similar SD (1.165, 1.142, or 1.136) were obtained using n = 20, 100, or 2,000 (respectively) and proportions of 0.1, 0.3, 0.3, 0.2, and 0.1 at trap heights of 1, 2, 3, 4, and 5 m, respectively.

Simulation of Insect Flight Distributions and Catch on Spherical Traps in Three Dimensions. Results from the eight simulations at each set of parameters showed that an average of 28–105 insects were caught on from two to 10 traps of 0.2-m radius placed evenly within the 10-m-high flight volume (Fig. 4). The population was initially 2,000 insects that maintained a mean flight height of 5 m and SD = 1.67 while taking up to 1,440 steps. Alternatively, the mean and SD of the flight distribution can also be estimated using the stochastic trap catch at various levels and equations 1 and 2. The mean height and SD were very similar to the expected in all trap arrangements that were symmetrical about the mean height, for example, all 95% CL included the expected mean and SD (Fig. 4; Table 4). In the next set of trap arrangements with five trap levels (Fig. 5), the trap levels that were placed below the mean flight height (experiments 1 and 2) had a lower than expected mean height as well as a lower than expected SD (Table 4). Moderate to slight asymmetry of placement (experiments 3 and 4) were acceptably close to expected (Fig. 5), whereas smaller spacing of traps about the mean (experiment 5) produced a similar mean but the SD was less than expected (Table 4). In the arrangements with three trap levels (Fig. 6) that were symmetrical but widely spaced (experiment 1), the mean was as expected but the SD was smaller. In these experiments, insects were given more steps to compensate for less trap levels and to increase catches.

When two of the three levels were below the mean flight height, the calculated mean was below the expected (experiments 2, 4, and 6). Smaller vertical spacing of traps caused smaller SD than expected (experiment 5, Fig. 6). In one arrangement that was asymmetrical and sampled the lower ends of the normal distribution (experiment 4), the SD of 3.13 m was almost double the expected 1.67 m (Fig. 6). This wide SD could have resulted from inadequate catch because relatively low average catch (16, Fig. 6) occurred. Thus, simulations were performed in which the insects took many more steps to determine if the

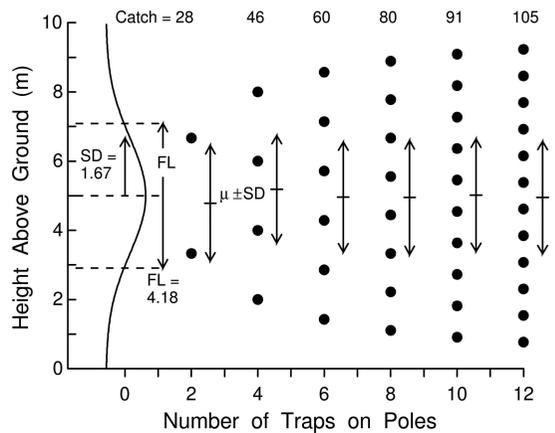


Fig. 4. Mean and SD of observed flight height (n = 8 simulations per trap arrangement) based on catch of insects on two to 12 spherical traps placed at various heights. Insects flew freely in the volume for 1,440 steps per simulation in the volume but were maintained in a normal distribution with mean height of 5 m and SD of 1.67 m. Catch represents that on all traps and was the average of eight simulations.

Table 4. Variation in mean flight height and SD based on catch at trap heights (as shown in Figures 4–6), and variation in mean catch on all traps in each simulation exp ($\pm 95\%$ Confidence Limits, $n = 8$)

Experiment	Number traps	Mean ht \pm 95% CL	SD \pm 95% CL	Catch \pm 95% CL
Figure 4^a				
	2	4.78 \pm 0.17	1.67 \pm 0.03	28.38 \pm 3.71
	4	5.19 \pm 0.15	1.55 \pm 0.20	46.00 \pm 6.06
	6	4.96 \pm 0.23	1.59 \pm 0.12	59.88 \pm 4.11
	8	4.95 \pm 0.19	1.65 \pm 0.03	79.50 \pm 9.78
	10	5.02 \pm 0.15	1.63 \pm 0.10	91.13 \pm 9.56
	12	4.95 \pm 0.11	1.63 \pm 0.05	104.99 \pm 8.95
Figure 5^a				
1	5	3.10 \pm 0.13	0.79 \pm 0.13	33.25 \pm 3.65
2	5	3.87 \pm 0.08	1.10 \pm 0.07	47.75 \pm 5.79
3	5	4.77 \pm 0.29	1.45 \pm 0.11	51.38 \pm 5.76
4	5	5.00 \pm 0.24	1.66 \pm 0.20	40.50 \pm 6.64
5	5	5.00 \pm 0.12	1.23 \pm 0.07	78.38 \pm 8.09
6	5	4.99 \pm 0.17	1.64 \pm 0.13	44.50 \pm 4.36
Figure 6^b				
1	3	4.98 \pm 0.14	1.17 \pm 0.24	49.75 \pm 6.52
2	3	4.34 \pm 0.23	1.70 \pm 0.12	55.38 \pm 7.92
3	3	5.33 \pm 0.20	1.44 \pm 0.10	74.00 \pm 6.14
4	3	4.22 \pm 0.50	3.13 \pm 0.18	15.88 \pm 2.07
5	3	5.48 \pm 0.11	1.22 \pm 0.05	96.00 \pm 4.60
6	3	4.45 \pm 0.17	1.64 \pm 0.05	66.88 \pm 4.39

^a Each of 2,000 insects took 1,440 steps, 0.1 m each, in volume.
^b Each of 2,000 insects took 2,880 steps, 0.1 m each, in volume.

SD would change. However, the calculated mean flight height and SD remained similar with 11,520 steps (4.48 \pm 0.26 and 3.13 \pm 0.05 m, respectively) as well as with 23,040 steps (4.56 \pm 0.15 and 3.11 \pm 0.02 m, respectively). The catch increased because of the higher number of steps as expected (68.99 \pm 5.18 and 149.13 \pm 8.06 catches with 11,520 and 23,040 steps, respectively). The simulation results show that as long as the traps are placed evenly across the flight distribution, the catches can be used to calculate mean height and SD of flight quite accurately. Almost all the field trap studies spaced traps evenly and attempted to

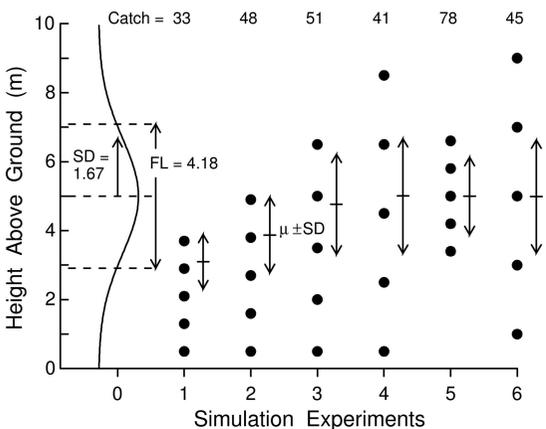


Fig. 5. Mean and SD of observed flight height ($n = 8$ simulations per trap arrangement) based on catches of insects on five spherical traps at various heights. Insects flew freely in the volume for 1,440 steps per simulation but were maintained in a normal distribution with mean height of 5 m and SD of 1.67 m. Catch represents that on all traps and was the average of eight simulations.

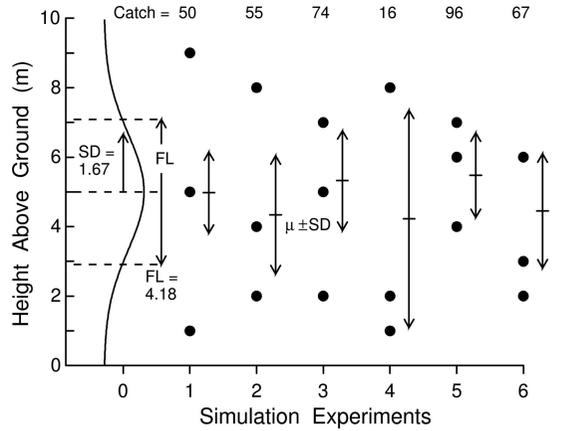


Fig. 6. Mean and SD of observed flight height ($n = 8$ simulations per trap arrangement) based on catches of insects on three spherical traps at various heights. Insects flew freely in the volume for 2,880 steps per simulation but were maintained in a normal distribution with mean height of 5 m and SD of 1.67 m. Catch represents that on all traps and was the average of eight simulations.

place them above and below the height that the investigators believed was the mean flight height—which would lead to accurate estimations of the mean height and SD with the iterative equations as indicated by the simulation results.

Discussion

Many studies have determined the catch of insects on traps placed at different heights to find the best height to place traps for monitoring or control. It is interesting from an ecological perspective to know at what height a particular species flies when searching for mates and hosts, as well as the nature of the distribution. A normal distribution is usually assumed, which can be described with a mean and SD. It is thus surprising that most previous studies did not determine the mean height of flight using equation 1 or calculate the SD of flight distribution using equation 2. McPherson and Weber (1980; 1981a,b,c,d,e; 1990) did report the mean height and SD, but no raw data were given to confirm the accuracy of the parameters. These authors, however, give values that seem reasonable and in line with the analyses here. In ≈ 60 studies with data sets showing that trap catches at several heights decreased with height, the majority fit a normal distribution (Tables 1–3) regardless of the trap type, number of levels of three or more, or whether the traps were attractive or not. The relationship of mean flight height and SD increased as a power function with slope 0.78 (Fig. 3) or linearly with slope 0.41 ($R^2 = 0.45$, $P < 0.001$). This is reasonable because at low mean flight height the flight is constrained by the ground, whereas at higher mean flight there is room for insects to fly in a wider range of heights, whether they use the room or not (i.e., the insect could still have a small SD at any mean flight height).

There were many types of traps used in the previous studies. Some traps may not catch as many insects as other types of traps. For example, window traps made of solid surfaces such as plastic or glass can cause insects in air to be buffeted around the trap, whereas screen traps that allow air to pass through do not appear to have this problem. Colored traps are often attractive but some colors could be repellent, although this is usually not tested; whereas traps releasing semiochemicals can affect flight behavior in unexpected ways. An example of this would be *Ips typographus* bark beetles that were caught in much higher numbers on the lower traps of a series of ten traps releasing aggregation pheromone than when the traps were not baited (Tables 2 and 3). The beetles attracted to aggregation pheromone sources may have expected a standing tree-sized trunk to appear and when this was not seen (a thin metal pole with nearly invisible sticky traps) the beetles flew downward in search of a fallen tree and thus were caught on the lower traps (Byers et al. 1989). Therefore, the data from blank (unattractive) traps may reflect the natural flight heights better than when using attractive traps.

Even though some traps may be more efficient in catching insects than other types, as long as the traps are the same type within the study, then the relative catches at the various heights are accurate and the calculations for mean height and *SD* are unaffected by trap efficiency. Calculation of a mean height and *SD* of flight for a species serves as a means to compare species, gives precise spatial information about the flight distribution, and allows placement of traps at the optimal height for monitoring and control with mass trapping or mating disruption. Models of these require an EAR_c , which is derived from the effective flight layer, F_L that uses the *SD* above by analyzing trap catches with height.

As mentioned earlier, the spherical EAR can be calculated from a ratio of catch between the blank and attractive traps as well as the interception area of the trap, S , as seen from one horizontal direction (Fig. 1). This is done best using sticky traps of larger mesh but that do not allow the insects of interest to pass through. Unfortunately, most studies have not reported catches on blank sticky traps, so an EAR is not possible to calculate and similarly no conversion to EAR_c is possible. However, Byers (2009) calculated a few EAR from trap catches reported in the literature: the bark beetle *I. typographus* had an $EAR = 1.55$ m ($EAR_c = 0.546$ m, $F_L = 6.9$ m) for a strong dose of synthetic pheromone; the pine shoot beetle *T. piniperda* had an $EAR = 0.84$ m ($EAR_c = 0.146$ m, $F_L = 7.53$ m) for a host log releasing attractive monoterpenes; and the California five spined ips (*I. paraconfusus* Lanier) had an $EAR = 3.18$ m ($EAR_c = 1.233$ m, $F_L = 12.88$ m) for a log infested with 50 males producing pheromone. The western flower thrips *F. occidentalis* had an $EAR = 0.18$ m ($EAR_c = 0.051$ m, $F_L = 0.99$ m) for a blue sticky card (Byers 2009).

The trap interception area S (Fig. 1) for sticky-screen cylinders is simply the diameter \times height,

which does not change depending on the angle of insect approach. However, for flat panel traps commonly used in studies, the width \times height varies in interception area depending on the angle of approach and thus must be an average of all possible angles (x):

$$S = height \cdot width \cdot \int_0^{\frac{\pi}{2}} \frac{2 \cdot \cos(x)}{\pi} dx$$

$$= height \cdot width \cdot 0.637 \tag{8}$$

(Byers et al. 1989). Cross-vane traps are also widely used in studies and have an average trap interception area of:

$$S = height \cdot width \cdot \int_0^{\frac{\pi}{4}} \frac{4 \cdot \cos(x)}{\pi} dx$$

$$= height \cdot width \cdot 0.9 \tag{9}$$

Neither the population density nor the length of the test period should significantly affect the EAR , assuming catch occurs on both types of traps, because of the catch ratio on control and treatment. The S area of the blank trap is used in the calculation of EAR and thus would seem to affect the size of the EAR , but in fact this is not the case. This is because a larger blank is expected to intercept proportionately more insects, thus compensating for the larger size in the calculation and having no effect on the EAR . Therefore, the EAR is a reliable estimate that only depends on the semiochemical blend and release rate as well as the sensitivity of the responding individuals of that species.

Future studies on trapping insects at various trap heights should use equations 1 and 2 to determine mean flight height and *SD* simply to better understand the flight ecology of a species. Additionally from a practical view, these equations allow more precise knowledge of the mean flight height and *SD* for optimal placement of lures or baited traps in control programs. The *SD* is also used to calculate F_L that converts the spherical EAR of attractive lures in traps for pest species into a circular EAR_c for use in computer models. EAR_c can alternatively be manipulated in models (Byers 2007) to determine a size that predicts sufficient control, and then this value is converted back to:

$$EAR = \sqrt{(2 \cdot F_L \cdot EAR_c) / \pi} \tag{10}$$

Field tests are then done with dosages of pheromone to achieve the same EAR for traps used in a control program. Both EAR_c and EAR can thus be used with computer models to aid in the development of more effective monitoring, mass trapping, or mating disruption methods in integrated pest management (IPM).

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