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# Detection and monitoring of pink bollworm moths and invasive insects using pheromone traps and encounter rate models

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## Summary

**1.** The pink bollworm moth *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae) is one of the most destructive pests in agriculture. An ongoing eradication program using a combination of sex pheromone monitoring and mating disruption, irradiated sterile moth releases, genetically modified Bt cotton and local insecticide applications have all but exterminated the pink bollworm from the south-western USA and portions of northern Mexico. However, the continued threat of reinvasion from Mexico reinforces the need to improve pheromone-based monitoring. Invasions from other parts of the world such as India, where resistance to single-gene transgenic Bt cotton has evolved, further heightens the need for better monitoring strategies.

**2.** The mean flight height and standard deviation (SD) of the vertical flight distribution of pink bollworm males were estimated from catches on transparent sticky cylinder traps baited with synthetic pheromone at several heights above-ground. An effective attraction radius (EAR) of a standard pheromone lure was estimated from male moth catches on the pheromone-baited sticky traps and many similar blank traps. The circular $EAR_c$ was estimated from the spherical EAR and SD.

**3.** The EAR of a pheromone lure for pink bollworm was 1·03 m, and the $EAR_c$ was 2·61 m. The mean flight height of males was 0·82 m, and the vertical flight distribution SD was 0·26 m.

**4.** A computer program simulated male moth movement and capture on various numbers of traps of $EAR_c$ distributed over areas of 1–100 km$^2$. The simulated catch results were comparable to predictions using the $EAR_c$ with modified encounter rate equations of Royama and Rogers. The encounter rate equations were solved for initial populations of male moths in the regions, and Poisson statistics were used to calculate population confidence limits.

**5.** *Synthesis and applications*. Encounter rate models and Poisson methods can be used to determine levels of pheromone trap densities that are likely to detect and estimate low population levels of resident or invasive pink bollworms and many other pest insect species.

**Key-words:** computer simulation, effective attraction radius, integrated pest management, invasive species, moth pheromones, Poisson distribution, predator–prey encounter equations

## Introduction

Detection and monitoring of invasive species is becoming increasingly important due to globalization and climate change (Carruthers 2003; Hulme 2009; Paini *et al.* 2010; Ziska *et al.* 2011; Sanderson, McLaughlin & Antunes 2012). One of the most sensitive means of detecting invasive insects and monitoring their population levels is the use of traps baited with pheromones or other semiochemicals (Allen *et al.* 1986; Gage, Wirth & Simmons 1990; Asaro *et al.* 2004; Walton, Daane & Pringle 2004; El-Sayed *et al.* 2006). During dispersal and search for mates, insects usually fly in correlated random walks in all directions over large areas within a relatively shallow air layer (Reynolds *et al.* 2007; Byers 2012a). When encountering an elongated pheromone plume of ill-defined complexity, the insects attempt to orient upwind towards the source of the pheromone (Elkinton, Cardé & Mason 1984; Byers 2009). The insect response probabilities within a spatially and temporally dynamic odour plume are poorly known and difficult to model. These complex pro-

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cesses can instead be modelled using a sphere of interception, the size of which determines trap capture. Thus, the 'effective attraction radius' (EAR) of a pheromone source is defined as the radius of a theoretical sphere that would intercept the same number of insects over time as that caught by a trap releasing the pheromone (Fig. 1; Byers, Anderbrant & Löfqvist 1989; Byers 2008, 2009). The EAR is estimated by comparison of catches on a blank sticky trap of high-capture efficiency to another similar trap releasing pheromone. The EAR value depends on the attractant's release rate and ecological function for the species, but not on insect density.

Along with estimates of average flight speed and time (or distance searched), the circular equivalent of the EAR ($EAR_c$) can be used in stochastic computer simulations in two dimensions to explore the respective effects of different numbers of traps and insect population density on trap captures (Byers 1991, 1996, 2007, 2012a,b). These interactive simulations could be used to estimate the numbers of traps needed to detect invasive pests. However, such simulations are cumbersome to formulate and time consuming to run, and it may be possible to gain equivalent information by use of instantaneous encounter rate equations. The Holling type I functional response equation in two dimensions is an encounter rate model that calculates the number of prey at a constant density that would be encountered by a predator per unit time (Holling 1959). This predator–prey equation was modified to account for an exponential decline in prey density as they are eaten in a specific arena (Royama 1971; Rogers 1972).

The pink bollworm *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae) is considered one of the most destructive pests of cotton globally and is found in nearly all cotton growing regions of the world (Ballou 1920; Ingram 1994). The moth was first described in 1842 from cotton in India, thereafter invading many parts of the world during the early to mid 1900s. Cotton-growing areas of Mexico were the suspected source of pink bollworm moths that invaded Texas in 1917 and eventually spread to Arizona, California, New Mexico and other southern states in the USA (Spears 1968). The presence of a sex pheromone in the female pink bollworm was recognized as early as 1957 and was eventually identified as a two-component blend of *Z,Z*- and *Z,E*-(7,11)-hexadecadienyl acetate, commonly called *gossyplure* (Hummel *et al.* 1973). This sex pheromone has been used for mating disruption and for population monitoring to enable more effective control from insecticides and sterile male releases (Flint *et al.* 1976; Gaston *et al.* 1977; Baker, Staten & Flint 1990).

Beginning in 1968, a sterile moth release program was initiated to exclude pink bollworm from cotton in the Central Valley of California (Henneberry 1994). This program involved the rearing and sterilization (via gamma radiation) of hundreds of thousands of moths, released periodically from small airplanes over cotton fields, where they would then compete with native males. A female usually mates once (Flint & Merkle 1981), and thus, either a mating with an irradiated male prevents egg hatch or the offspring are sterile (Graham *et al.* 1972; Flint *et al.* 1973). Transgenic cotton producing the insecticidal Cry toxins of *Bacillus thuringiensis* (Bt) (Perlak *et al.* 1990; Flint, Henneberry & Wilson 1995) was first commercially grown in the USA in 1996 and has become a major tactic for management of pink bollworm in the south-western USA (Naranjo *et al.* 2008; Naranjo & Ellsworth 2010). The success of Bt cotton in reducing regional populations of the pest (Carrière *et al.* 2003), along with other proven technologies noted above, prompted initiation of a program in the early 2000s to eradicate the pink bollworm from Texas, New Mexico, Arizona, California and the northern states of Mexico (National Cotton Council 2001). The eradication program is now nearly complete but its maintenance will require constant vigilance against reinvasion from other portions of Mexico and South America as well as from regions like India where resistance to single-gene Bt cottons has recently evolved (Bagla 2010).

Our objectives were to determine the EAR and $EAR_c$ of pink bollworm pheromone traps in the field and to develop computer simulation models to examine various

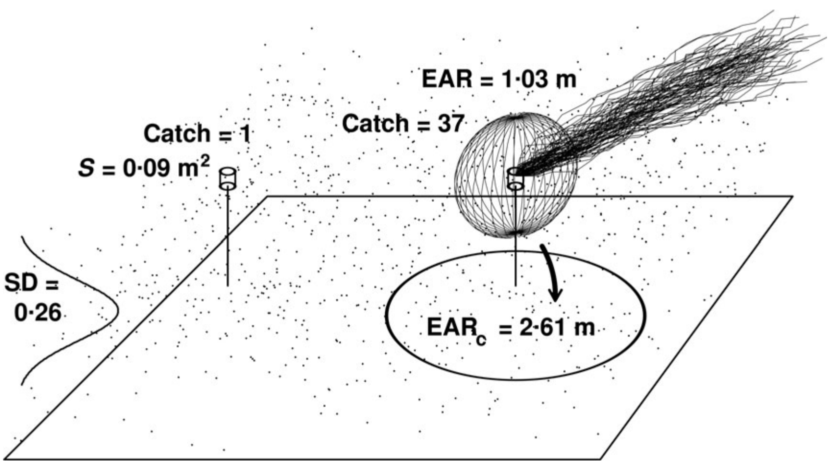


**Fig. 1.** Two cylindrical sticky traps, a blank catching one insect and a pheromone trap catching 37 insects, are each $0{\cdot}09\ m^2$ in silhouette area ($S$), giving a spherical EAR = 1·03 m that can be converted to a circular $EAR_c$ = 2·61 m (Byers 2008; equations in Methods). The black wavy lines represent a pheromone plume, while the small dots represent 1000 insects distributed vertically in a normal distribution (SD = 0·26 m).

moth and trap density scenarios. We then asked whether our simulation results could be accurately predicted by modified predator–prey encounter rate equations. We found that the modified Royama–Rogers equations gave results essentially identical to the mean catch of stochastic simulations of individual male pink bollworm moth flights in areas with pheromone traps. The equations were used with the Poisson distribution to estimate confidence ranges for adult populations. We suggest these methods should be applicable to detection and monitoring of many pest insects attracted to traps by means of olfaction or vision.

## Materials and Methods

Field studies were conducted on the University of Arizona, Maricopa Agricultural Center Farm, Maricopa, AZ, USA, where the eradication program was releasing sterile pink bollworm moths three times per week. Pink bollworm larvae reared for the program are fed diet with red dye (CAS 4477-79-6) causing the moths to become reddish pink. Moths were sterilized with gamma irradiation (20 krad). No adverse affects of irradiation on longevity or dispersal have been noted (Graham & Mangum 1971; Flint *et al.* 1973, 1975).

### VERTICAL FLIGHT DISTRIBUTION

In order to convert the spherical EAR of the pheromone trap to two dimensions ($\mathrm{EAR_c}$) for models, the SD of the vertical flight distribution of male *P. gossypiella* moths needs to be estimated from catches on a vertical array of pheromone traps on poles. Sticky traps were made of clear polyvinyl chloride (PVC) plastic sheets (0·25 mm thick, Graphix, Maple Heights, OH, USA) formed into a cylinder 18 cm high × 13 cm diameter covered with a sticky layer of polyethylene polymers (Pestek®, Phytotronics Inc., Earth City, MO, USA). Two brass binder pins fastened the cylinder to a pole (2·5-cm-diameter PVC pipe). On two 3-m poles, six sticky traps each baited with a pink bollworm pheromone lure were centred evenly at heights from 0·66 to 2·95 m above-ground to ensure that most of the vertical flight distribution was sampled (Byers 2011). A lure, consisting of grey-rubber septa impregnated with 2 mg each of (*Z,E*)- and (*Z,Z*)-7,11-hexadecadienyl acetate (Shin-Etsu Chemical Co., Tokyo, Japan), was placed in the centre of each trap. A third pole (2·1-m pole) held six traps evenly spaced from 0·18 to 1·96 m above the ground, while a fourth pole (4-m pole) held six traps evenly spaced from 0·81 to 3·86 m above-ground. The poles were placed about 30 m apart in barren lanes (~4 m wide) between plots of non-Bt cotton (27 July to 3 August 2011). Assuming flight height is directly related to catch height, the mean flight height and SD were estimated (Byers 2011).

### EFFECTIVE ATTRACTION RADIUS (EAR)

To obtain a circular $\mathrm{EAR_c}$ for use in two-dimensional models, the spherical EAR of a pheromone trap was estimated. The EAR of a pheromone-baited trap was determined using a 5 × 5 grid of cylindrical sticky traps identical to those described above. Rows and columns of the grid were separated by about 27 m, with traps positioned in the barren lanes (~4 m wide) between plots of cotton subjected to moth releases. In the first test (12–26 July 2011), four traps were baited with pheromone lures at (row, column): (2, 2), (2, 4), (4, 2) and (4, 4), while the other 21 positions were unbaited traps. Each sticky trap was centred at 1 m height and fastened to a 1·2-m long × 1-cm diameter wooden dowel. After 2–3 days, the traps and lures were collected and males (all dyed) were counted in the laboratory. A second test, identical to the first, was conducted from 17–19 August 2011.

The EAR was calculated using the equation:

$$\mathrm{EAR} = \sqrt{\frac{Ca \cdot S}{Cb \cdot \pi}} \qquad \text{eqn 1}$$

where $Ca$ is the mean catch of the pheromone traps, $Cb$ is the mean catch of the unbaited traps, and $S$ is the silhouette area (0·02336 $\mathrm{m^2}$) of the cylindrical trap (Byers, Anderbrant & Löfqvist 1989; Byers 2008). The *SD* of the vertical flight distribution was used to convert the spherical EAR to a circular $\mathrm{EAR_c}$ (Byers 2009, 2012a) for use in two-dimensional simulations with the following formula:

$$\mathrm{EAR_c} = \frac{\pi \cdot \mathrm{EAR}^2}{2 \cdot SD \cdot \sqrt{2 \cdot \pi}} \qquad \text{eqn 2}$$

### COMPUTER-SIMULATED MONITORING

Male moth flight and capture by traps were simulated in two dimensions within a square x- and y-coordinate system that was adjusted to obtain the desired area (e.g. 10000 × 10000 m = 100 $\mathrm{km^2}$). Simulated traps were placed in the system, either at random or in a grid, but with no overlap of $\mathrm{EAR_c}$ of adjacent traps (Fig. 2). Simulated male moths flew in the area according to a correlated random walk (CRW) as in earlier models (Byers 2001, 2008, 2009). Each insect was randomly assigned an initial position and direction. Thereafter, each insect followed a CRW made of a series of steps of 1 m distance each second, with each step calculated as a polar vector from the former position. The direction at each step was the former direction plus a turning angle chosen at random from a normal distribution of 6° standard deviation (Byers 2001). Insect encounters with any $\mathrm{EAR_c}$ were recorded as captures as determined using the algorithm reported by Byers (1991). Based on 14 h of cumulative flight of male pink bollworms in flight mill studies (Wu *et al.* 2006), each simulation represented a cumulative 10 h (36 000 steps) of male flight. Simulations were conducted at various values of $\mathrm{EAR_c}$ (2·61 m or 10 m), number of traps (1 or 16) and number of males (1–1000) in areas of 1 or 100 km².

All simulations were coded in Java 6 language (Oracle, Redwood Shores, CA, USA) and performed on a personal computer. A Java applet demonstration is available at http://www.chemical-ecology.net/java2/pbw-1.htm.

### PREDICTIONS FROM ENCOUNTER RATE EQUATIONS

Holling (1959) proposed a functional response equation that calculated the number of prey encountered by a predator per unit time where the prey density was considered essentially constant. Royama (1971) and Rogers (1972) independently modified the Holling equation in the random predator equation to account for exponential decay of prey densities as they are eaten over time:

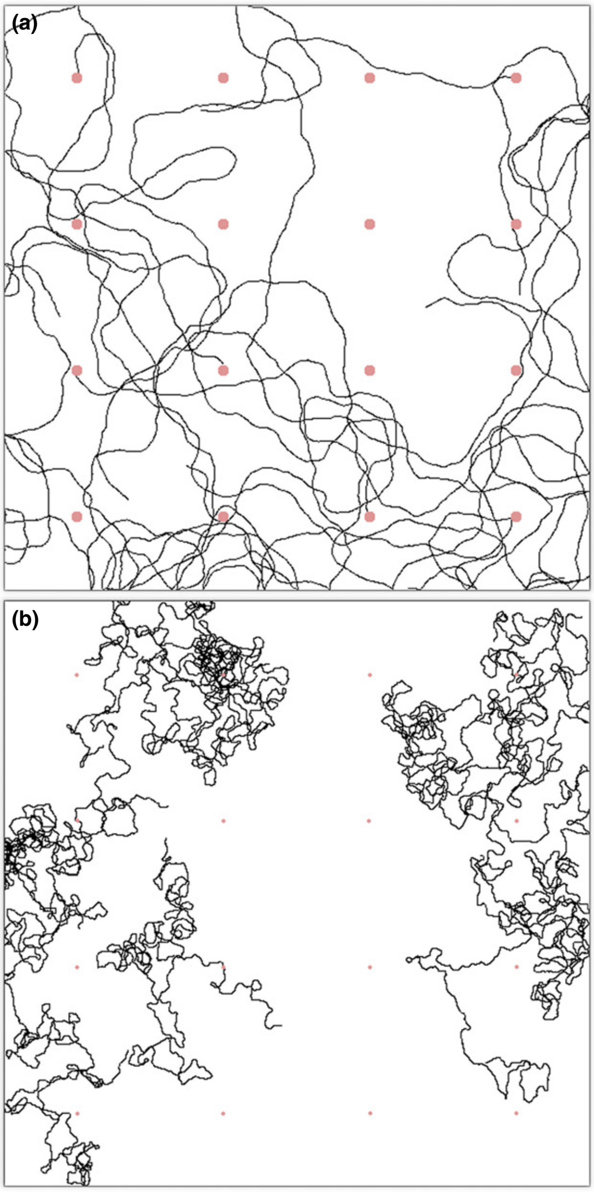


**Fig. 2.** (a) Tracks of 10 males in 1-km$^2$ area with 16 traps ($EAR_c$ = 10 m) evenly spaced in a grid as indicated; all males eventually were caught and total distance covered by males was 26 306 m. (b) Tracks of 10 males in 100-km$^2$ area with 16 traps ($EAR_c$ = 10 m) evenly spaced in a grid (tiny dots); only one male was caught and total distance covered by males was 352 006 m. All males flew with the same correlated random walk (see Methods) for 10 h (36 000 m) unless caught by a trap.

$$N_a = N \cdot (1 - \exp(-a \cdot P \cdot T)) \qquad \text{eqn 3}$$

where $N_a$ is the number of prey eaten, given an initial prey number $N$ during time $T$ at an attack coefficient $a$ (area searched per unit time) and predator density $P$. The attack coefficient in the encounter rate eqn 3 could be considered analogous to the male's speed times the trap's effective diameter (2 $EAR_c$). The prey density ($P$) is the number of males divided by area. The encounter rate catch of pheromone-baited traps can be predicted from the modified random predator equation:

$$\text{Catch} = M \cdot (1 - \exp(-2 \cdot \text{EAR}_c \cdot V \cdot T \cdot K/A)) \qquad \text{eqn 4}$$

where $M$ = initial number of males, $EAR_c$ is in m, $V$ = average ground speed of males in m s$^{-1}$, $T$ = flight time in s, $K$ = number of pheromone traps, and $A$ = area in m$^2$. Rearranging eqn 4, the number of traps ($K$) needed in the area to capture a given number of moths is given by:

$$K = \ln((M - \text{Catch})/M) \cdot A/(-2 \cdot \text{EAR}_c \cdot V \cdot T) \qquad \text{eqn 5}$$

Solving for $M$ (initial males in the area) gives:

$$M = \text{Catch}/(1 - \exp(-2 \cdot \text{EAR}_c \cdot V \cdot T \cdot K/A)) \qquad \text{eqn 6}$$

The surface equation best fitting the initial populations related to the number of traps (1–10) and catches (1–10) as determined by the modified eqn 6 was found using TableCurve 3D version 3.01 (Systat, San Jose, CA, USA).

### POISSON PROBABILITY OF MONITORING SUCCESS

Catch on one or more traps in nature, as in simulations, is a discrete integer event. Thus, the Poisson probability distribution (Sokal & Rohlf 1995) can be used to calculate probabilities of various numbers of catches that are more or less than the observed catch in the field or in simulations. This distribution describes the probability of a specific number of events ($k$) (here captures) based on a mean frequency of events ($\lambda$) from many experiments:

$$f(k; \lambda) = \lambda^k e^{-\lambda}/k! \qquad \text{eqn 7}$$

In eqn 7, when $k$ becomes large (e.g. >170), $k!$ cannot be calculated on most personal computers. To overcome this limitation, we used the laws of logarithms to derive the following formula from eqn 7:

$$f(k; \lambda) = \exp[k \cdot \ln(\lambda) - \lambda - \sum_{i=1}^{k} \ln(i)] \qquad \text{eqn 8}$$

The modified-Poisson formula (Eqn 8) was tested by simulating 16 traps in a grid and 100 males in a 100-km$^2$ area for 10 h as described above. Each simulation (equal to one experiment) was repeated 100 times, and the number of experiments with captures from 0 to 10 was categorized in a frequency distribution. These 100 simulations were repeated eight times, their results were averaged, and 95% confidence limits were calculated (McCall 1970). The expected catch per simulation with the 100 males using eqn 4 was $\lambda = 2{\cdot}96$, and this was used to calculated the Poisson expected probabilities of captures ($k$ = 0, 1, 2…10) per simulation using eqn 8.

The exact 95% Poisson confidence limits for catch ($Y_L$ = lower, $Y_U$ = upper) can be calculated using the chi-square ($\chi^2$) distribution:

$$Y_L = \chi^2(\text{d.f.} = 2x, 1 - \alpha/2)/2 \text{ and } Y_U = \chi^2(\text{d.f.} = 2x + 2, \alpha/2)/2 \qquad \text{eqn 9}$$

where d.f. = degrees of freedom, $x$ = number of occurrences (catch), and $\alpha = 0{\cdot}05$ (Ulm 1990).

Because the chi-square distribution is difficult to calculate, a formula attributed to Pearson gives nearly the same confidence limits: $Y_L = x + a/b - a^{0{\cdot}5}(x + a/4)^{0{\cdot}5}$ and $Y_U = x + a/2 + a^{0{\cdot}5} \cdot (x + a/4)^{0{\cdot}5}$ where $a = \chi^2(\text{d.f.} = 1, \alpha = 0 \cdot 05) = 3{\cdot}8415$ (McCall 1970) and $b$ = 2 (however, we obtained a closer approximation for

$Y_L$ with $b = 3{\cdot}2$). The Poisson confidence limits for catch are then used in the encounter rate eqn 6 to calculate lower and upper estimates of the initial insect population.

## Results

### VERTICAL FLIGHT DISTRIBUTION

The average mean flight height based on catch of male pink bollworm moths was 0·82 m with a SD of 0·26 m for the vertical height distribution (average of 3-m poles, Table 1). The mean flight height obtained from the 4-m pole was similar to that of the 3-m poles (0·84 m), while the 2·1-m pole had a lower mean height of 0·53 m. The 3-m poles and 2·1-m pole had similar SD, while the 4-m pole had the smallest SD of 0·12 m, probably due to a larger vertical spacing between traps and no catches on the three highest traps. The flight height distributions were either leptokurtic (kurtosis greater than a normal distribution) or not significantly different from a normal curve, while their skewness was generally right tailing due to unbounded higher flight (Table 1).

### EFFECTIVE ATTRACTION RADIUS (EAR)

The EAR calculated from the mean catches of 21 blank traps and four pheromone traps was 1·03 m (Table 2). The corresponding $EAR_c$ for use in two-dimensional simulations using 0·26 m for the SD of the vertical flight distribution (Table 1, Eqn 2) was estimated as 2·61 m (Table 2).

### COMPUTER-SIMULATED MONITORING

Examples of movements of 10 simulated males within 1- and 100-km$^2$ areas are illustrated in Fig. 2. Each male flew for up to 10 h or until caught by one of 16 traps each with a hypothetical 10 m $EAR_c$ (Fig. 2). In the simulations of 1-km$^2$ areas, all males were caught during the 10-h flight period, and they covered a total distance of 26 306 m. In the 100-km$^2$ areas, only one male was caught in 10 h and the distance covered by all males was 352 006 m (13·4 times greater than males in the 1-km$^2$ area). Simulations in a 100-km$^2$ area with a pink bollworm trap $EAR_c$ of 2·61 m indicated trap captures increased with increasing numbers of traps and increasing moth population density (Table 3). Simulations using a single trap within the 100-km$^2$ arena rarely 'detected' the presence of moths when the initial number of males was <1000. In contrast, 16 traps simulated in the same arena generally detected the presence of moths at male population levels as low as 100. Simulated captures for traps placed at random were similar to those for traps placed in

**Table 1.** Analysis of mean height of catch ($\bar{h}$ ) ± SD (standard deviation of vertical flight distribution) of pink bollworm males, *Pectinophora gossypiella*, caught on pheromone-baited sticky traps at various heights on poles

| Experiment | Range of trap heights (m) | Number of trap levels† | Total catch | Mean height of catch ± *SD* (m) | *A* of normal equation‡ ($r^2$)§ | Kurtosis¶ | Skewness (tailing)†† |
|---|---|---|---|---|---|---|---|
| 3-m pole #1 | 0·66–2·95 | 6 | 207 | 0·83 ± 0·27 | 101 (0·92) | L (3·09)* | R (1·66)* |
| 3-m pole #2 | 0·66–2·95 | 6 | 125 | 0·80 ± 0·23 | 60 (0·99) | 0·33 | R (1·21)* |
| Both poles above | 0·66–2·95 | 6 | 332 | 0·82 ± 0·26 | 162 (0·95) | L (2·64)* | R (1·57)* |
| 2·1-m pole | 0·18–1·96 | 8 | 59 | 0·53 ± 0·30 | 14·7 (0·71) | −0·58 | 0·48 |
| 4-m pole | 0·81–3·86 | 6 | 135 | 0·84 ± 0·12 | 38 (0·99) | L (22·9)* | R (4·96)* |

†Transparent plastic cylinders (18 cm high × 13 cm diam.; 0·02336 m$^2$ silhouette area) covered on outside with sticky adhesive and placed in cotton field from 27 July to 3 August 2011.
‡Best-fit normal equation: $A \cdot (\exp(-(h-\bar{h})^2/(2\cdot \mathrm{SD}^2))/(\mathrm{SD}\cdot\sqrt{2\cdot\pi}))$, where $h$ is height in m.
§Squared product-moment correlation indicating strength of fit by normal equation to observed data.
¶Kurtosis values denoting departure from theoretical normal distribution, with P, platykurtic and L, leptokurtic forms; *denotes significant departure at $P < 0{\cdot}05$.
††Skewness values denoting departure from theoretical normal distribution, with R, right tailing and L, left tailing, *as above.

**Table 2.** Estimation of EAR and $EAR_c$ from catch of male pink bollworm, *Pectinophora gossypiella*, on transparent sticky cylinder traps baited with synthetic pheromone lures or left unbaited (blank) in cotton fields (July–August 2011, Maricopa, AZ)

| Experiment | Number pheromone traps* | Mean pheromone catch/trap | Number blank traps* | Mean blank catch/trap | EAR (m) | SD (m) | $EAR_c$ (m)† |
|---|---|---|---|---|---|---|---|
| 12–26 July | 4 | 7·75 | 21 | 0·0476 | 1·10 | 0·26 | 2·97 |
| 17–19 August | 4 | 19·5 | 21 | 0·1429 | 1·01 | 0·26 | 2·49 |
| Total | 4 | 27·25 | 21 | 0·1905 | 1·03 | 0·26 | 2·61 |

*Transparent plastic cylinders (18 cm high × 13 cm diam.; 0·02336 m$^2$ silhouette area) covered on outside with sticky adhesive.
†$EAR_c$ (in two dimensions) is calculated from EAR (in three dimensions) and SD (equations in Methods).

a grid at all combinations of trap numbers and male population levels (Table 3).

### PREDICTIONS FROM ENCOUNTER RATE EQUATIONS

Equation 4 allows prediction of captures based on an initial population. For example, if 10 males fly a total of 10 km during the experiment in a 10 × 10 km area with 10 traps ($EAR_c$ = 2·61 m), then only 0·186 males should be caught. This is equivalent to catching a single male in one of five such experiments. Equation 5 predicts that 56 traps would be needed in this area to capture one moth. If instead three males were caught, then eqn 6 predicts that 161 males were initially in the area at the start of trapping. The equations give specific values that are comparable to the means of the stochastic simulations (which have confidence limits, Table 3). The expected initial populations of pink bollworm males flying in a 100-km$^2$ area based on catches on different numbers of traps (Fig. 3) were calculated using eqn 6. The surface equation, $\ln(Z) = 6{\cdot}2777 + \ln(X) - 0{\cdot}9975\ln(Y)$, obtained by regression, where $Z$ is the initial population, $X$ is catch, and $Y$ is number of traps fit the data of Fig. 3 perfectly ($R^2$ = 1). Thus, $Z = \exp[6{\cdot}2777 + \ln(X) - 0{\cdot}9975\ln(Y)]$.

### POISSON PROBABILITY OF MONITORING SUCCESS

Catches in the simulation model were random and fit a Poisson distribution with a mean of 2·96. The mean percentages of simulations with 0–9 catches had 95% confidence limits that encompassed the expected Poisson distribution (Fig. 4). The Poisson confidence limits (Eqn 9) applied to the modified Royama–Rogers Equation 6 using an $EAR_c$ = 2·61 m can be used to estimate male population levels based on any area with a known number of traps and total catch. Assuming males fly up to 10 km over the trapping period in a 100-km$^2$ area with 100 traps, and if 15 males are caught on the traps, then 95% Poisson limits predict that the catch could have ranged from 8·4 to 24·7 in repeated experiments. These captures with the encounter rate equation predict an initial male population of 88, which could range from 49 to 144 considering 95% Poisson limits.

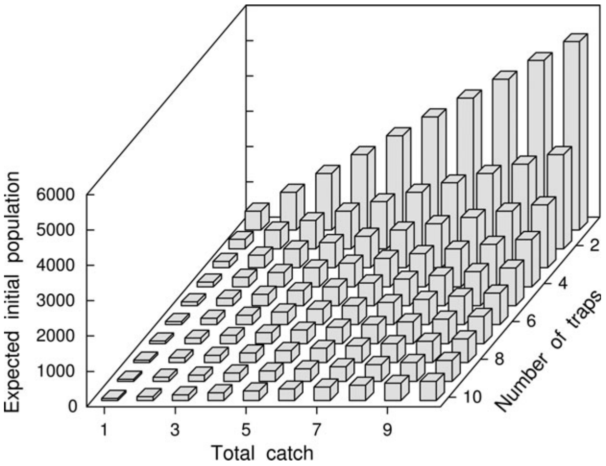


**Fig. 3.** Expected initial population of male pink bollworms flying at 1 m s$^{-1}$ for up to 10 h in a 100-km$^2$ area as related to the number of traps (2·61 m $EAR_c$) and the total catch on these traps (data generated from eqn 6).

**Table 3.** Comparison of simulation results with encounter rate eqn 4 in a 100-km$^2$ area in which male moths fly up to 10 h at 1 m s$^{-1}$ and traps have an $EAR_c$ of 2·61 m

| Trap placement | Number of traps | Number of males | Simulated catch ± 95% CL ($N$ = 8) | Encounter rate catch |
|---|---|---|---|---|
| Grid | 1 | 1 | 0 | 0·002 |
| | 1 | 10 | 0 | 0·02 |
| | 1 | 100 | 0·25 ± 0·39 | 0·19 |
| | 1 | 1000 | 2·12 ± 0·54 | 1·88 |
| | 16 | 1 | 0 | 0·03 |
| | 16 | 10 | 0·13 ± 0·30 | 0·30 |
| | 16 | 100 | 3·38 ± 1·73 | 2·96 |
| | 16 | 1000 | 27·00 ± 4·05 | 29·62 |
| Random | 1 | 1 | 0 | 0·002 |
| | 1 | 10 | 0 | 0·02 |
| | 1 | 100 | 0 | 0·19 |
| | 1 | 1000 | 2·00 ± 1·00 | 1·88 |
| | 16 | 1 | 0·13 ± 0·30 | 0·03 |
| | 16 | 10 | 0·63 ± 0·62 | 0·30 |
| | 16 | 100 | 3·25 ± 1·47 | 2·96 |
| | 16 | 1000 | 31·13 ± 4·08 | 29·62 |

## Discussion

Eradication of pink bollworm has been attempted over large areas many times since the invasion and reinvasion of this pest into North America (Spears 1968; Henneberry & Naranjo 1998). The current eradication program uses a

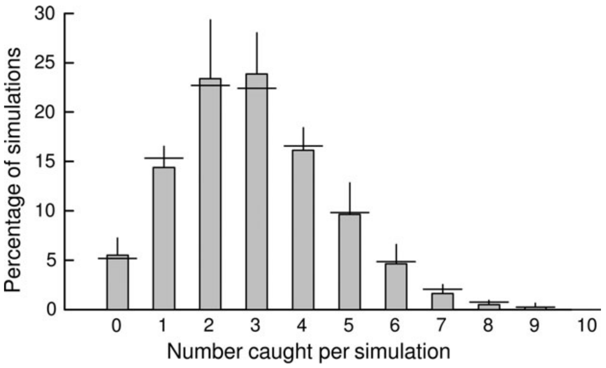


**Fig. 4.** Number of male moths caught per simulation (16 traps in grid, $EAR_c$ = 2·61 m, 100 males, 100-km$^2$ area, speed 1 m s$^{-1}$ for 10 h). Eight simulation sets of 100 each ($N$ = 800 simulations) were obtained, and means represented as bars with vertical error lines being upper 95% CL. The expected catch per simulation was 2·96 (Table 3) according to the modified encounter rate equation (Eqn 4), and the expected percentages of occurrences (0, 1, 2…) were calculated as a Poisson probability distribution (Eqn 8) and represented as horizontal lines across each bar.

high level of Bt cotton deployment that greatly reduces pink bollworm populations (Carrière *et al.* 2003; Tabashnik *et al.* 2010). This improved the effectiveness of other tactics, such as sterile insect release and mating disruption, that function best at low pest population densities. Despite the apparent success of the current program (Tabashnik *et al.* 2010), the pink bollworm is a known long-range migrant (McDonald & Loftin 1935; Bariola *et al.* 1973; Van Steenwyk *et al.* 1978; Stern 1979). Therefore, the constant threat of re-invasion necessitates long-term monitoring for re-infestation. It will thus be critical that monitoring programs be efficient at detecting re-invaders at a reasonable cost.

Here, we developed a spatial model to simulate capture of male pink bollworm moths attracted to pheromone-baited traps and then showed that a simpler approach based on an encounter rate equation could substitute for time-consuming simulations in predicting the dynamics of trap capture. As with any model, assumptions are made that could be critical to the predictive accuracy and utility of the results. The first major assumption is that mean flight distance of males is known reasonably well. Using flight mills, Wu *et al.* (2006) found that 1-day-old females flew a mean distance of 41·2 km (23·9-h flight duration) compared with males that flew a mean of 23·5 km (14·1 h). Male flight speed was initially about 0·69 m $s^{-1}$ and declined to about 0·42 m $s^{-1}$ after 72 h. Female flight speeds declined similarly with age (Wu *et al.* 2006). The distance flown during the life of a male is a product of ground speed and time flying and would likely be composed of a series of flights over the life of the male. Flint and Merkle (1981) reported that males in the field may live up to 9 days based on the longest period they observed between release of fluorescent-dyed males and recapture in pheromone traps. Mild wind speeds will increase the ground speed and total distance covered if insects, including the pink bollworm (McDonald & Loftin 1935; Flint & Merkle 1981), fly in all directions regardless of wind direction (as in Fig. 2; Reynolds *et al.* 2007; equation 7 in Byers 2012a). However, periods of higher wind speeds that preclude upwind orientation flight to pheromone would not contribute to the male distance travelled because the traps would not catch males during this displacement. Thus, the flight parameters used in the simulations are reasonable, but predictions could be refined as we obtain more precise knowledge about male behaviour in the field.

Given that our experimental studies utilized mass-released sterile moths, another major assumption of the model is that lab-reared and irradiated males are similar to native males in flight ability and responsiveness to sex pheromone. Flint *et al.* (1975) released 6480 laboratory-reared males labelled with $^{32}P$ in the field and light traps caught 1110 males of which 1% were labelled. On traps baited with hexalure (a pheromone isomer mimic), 269 males were caught and 3% were labelled males. Similarly, about 2·7% of mated females caught in light traps had been mated by labelled males. The higher percentage of labelled males attracted to hexalure than to light traps indicates that labelled males were at least as well attracted to pheromone as were native males. The sterile moths were also marked with Calco Oil Red N-1700® dye. Graham and Mangum (1971) found no effects of this dye at 0·01% w/v on larval development time, pupal weight or adult longevity. Female pink bollworms reared on synthetic diets and irradiated with doses up to 25 krad were as attractive to native males as unirradiated females in the field, and adult longevity was unaffected by up to 25 krad of radiation (Flint *et al.* 1973). Flint *et al.* also released labelled males that were irradiated by 20 krad gamma rays (2300 males) or untreated (2300 males), and there was no apparent affect of irradiation on the ratios of catch on hexalure or light traps. It would thus appear that mass-reared sterile moths can serve as a reasonable proxy for native moths in the field.

The simulation models and modified encounter rate equations could be used to inform pest managers about the density of traps needed to effectively monitor suspected low-level populations. Managers could input different numbers of traps and moths in a large region and then balance trap and deployment/monitoring costs with increased accuracy in estimating invasive population levels. For example, given a large area of 400 $km^2$ containing 100 males, how many pheromone traps of 2·61 m $EAR_c$ are needed to have at least a 50% chance of detecting the presence of this population? Using the modified encounter rate equations with these parameters (Eqn 5), about 21 traps are needed to catch 1 individual (in other words, a Poisson probability of 63% for catching one or more males based on a mean of 1 using eqn 8). The size of the $EAR_c$ of traps could be manipulated in models consistent with the constraints of orientation behaviour of males and dispenser technology.

Managers also could use the models to estimate population levels based on trap captures because female and male densities are expected to be equivalent (McDonald & Loftin 1935). A density above a threshold level indicates that population suppression is warranted. For example, Toscano and Sevacherian (1980) suggested that if 12 males were caught per night on one pheromone trap per 20 acres (80 937 $m^2$) this should trigger control actions. Thus, assuming males fly at 1 m $s^{-1}$ for 2 h (7200 m) with 12 caught on a trap of 2·61 m $EAR_c$, then eqn 6 shows that this trap capture is equivalent to 32·3 males initially in this 20-acre area (4·0 males/ha). Using the same threshold for treatment, if instead 10 traps were used in a 100-ha area and 113 males were caught in total, then eqn 6 gives 360·7 males in the area (3·61 males $ha^{-1}$), which is below the threshold. Earlier studies have found strong linear correlations between numbers of male pink bollworm moths caught in pheromone traps and larval infestations of cotton bolls (Henneberry & Clayton 1982; Qureshi, Ahmad & Hussain 1993). Significant positive correlations between pheromone catches and crop damage have usually been found in pest insects (Zhang *et al.* 1998; Blackshaw & Vernon 2008; Rosell *et al.* 2008; Fernandes *et al.* 2011). These reports lend credibility to the application of our model for estimating indigenous pest populations. The adult densities estimated by our methods may also be input into temperature-driven growth models in order to predict future pest abundance and crop damage (Régnière & Sharov 1998; Parajulee *et al.* 2004; Spear-O'Mara & Allen 2007).

We show that the predator–prey encounter equations developed in the early 1970s may be used with pheromone-baited traps to provide practical information on how to develop and implement a monitoring program for the pink bollworm, be that management of extant populations or the detection of new invasions. The Poisson probabilities indicate the range of population levels that may exist based on trap catch, and whether more intense trapping is necessary to insure detection of the pest. Our methods can be applied to detect low-density populations of many other insect pests that utilize attractive semiochemicals.

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## References

Allen, D.C., Abrahamson, L.P., Eggen, D.A., Lanier, G.N., Swier, S.R., Kelley, R.S. & Auger, M. (1986) Monitoring spruce budworm (Lepidoptera: Tortricidae) populations with pheromone-baited traps. *Environmental Entomology*, **15**, 152–165.

Asaro, C., Cameron, R.S., Nowak, J.T., Grosman, D.M., Seckinger, J.O. & Berisford, C.W. (2004) Efficacy of wing versus delta traps for predicting infestation levels of four generations of the Nantucket pine tip moth (Lepidoptera: Tortricidae) in the Southern United States. *Environmental Entomology*, **33**, 397–404.

Bagla, P. (2010) Hardy cotton-munching pests are latest blow to GM crops. *Science*, **327**, 1439.

Baker, T., Staten, R. & Flint, H. (1990) Use of pink bollworm pheromone in the Southwestern United States. *Behavior-Modifying Chemicals for Insect Management: Applications of Pheromones and Other Attractants* (eds R.L. Ridgway, R.M. Silverstein & M.N. Inscoe), pp. 417–436. Marcel Dekker, NY.

Ballou, H.A. (1920) *The Pink Boll Worm (Gelechia Gossypiella, Saunders) in Egypt in 1916–1917*. Ministry of Agriculture, Cairo, Egypt, 120 pp.

Bariola, L.A., Keller, J.C., Turley, D.L. & Farris, J.R. (1973) Migration and population studies of the pink bollworm in the arid west. *Environmental Entomology*, **2**, 205–208.

Blackshaw, R.P. & Vernon, R.S. (2008) Spatial relationships between two Agriotes click-beetle species and wireworms in agricultural fields. *Agricultural and Forest Entomology*, **10**, 1–11.

Byers, J.A. (1991) Simulation of mate-finding behaviour of pine shoot beetles, *Tomicus piniperda*. *Animal Behaviour*, **41**, 649–660.

Byers, J.A. (1996) An encounter rate model of bark beetle populations searching at random for susceptible host trees. *Ecological Modelling*, **91**, 57–66.

Byers, J.A. (2001) Correlated random walk equations of animal dispersal resolved by simulation. *Ecology*, **82**, 1680–1690.

Byers, J.A. (2007) Simulation of mating disruption and mass trapping with competitive attraction and camouflage. *Environmental Entomology*, **36**, 1328–1338.

Byers, J.A. (2008) Active space of pheromone plume and its relationship to effective attraction radius in applied models. *Journal of Chemical Ecology*, **34**, 1134–1145.

Byers, J.A. (2009) Modeling distributions of flying insects: effective attraction radius of pheromone in two and three dimensions. *Journal of Theoretical Biology*, **256**, 81–89.

Byers, J.A. (2011) Analysis of vertical distributions and effective flight layers of insects: three-dimensional simulation of flying insects and catch at trap heights. *Environmental Entomology*, **40**, 1210–1222.

Byers, J.A. (2012a) Estimating insect flight densities from attractive trap catches and flight height distributions. *Journal of Chemical Ecology*, **38**, 592–601.

Byers, J.A. (2012b) Modelling female mating success during mass trapping and natural competitive attraction of searching males or females. *Entomologia Experimentalis et Applicata*, **145**, 228–237.

Byers, J.A., Anderbrant, O. & Löfqvist, J. (1989) Effective attraction radius: a method for comparing species attractants and determining densities of flying insects. *Journal of Chemical Ecology*, **15**, 749–765.

Carrière, Y., Ellers Kirk, C., Sisterson, M., Antilla, L., Whitlow, M., Dennehy, T.J. & Tabashnik, B.E. (2003) Long-term regional suppression of pink bollworm by *Bacillus thuringiensis* cotton. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 1519–1523.

Carruthers, R.I. (2003) Invasive species research in the United States Department of Agriculture – Agricultural Research Service. *Pest Management Science*, **59**, 827–834.

Elkinton, J.S., Cardé, R.T. & Mason, C.J. (1984) Evaluation of time-averaged dispersion models for estimating pheromone concentration in a deciduous forest. *Journal of Chemical Ecology*, **10**, 1081–1108.

El-Sayed, A.M., Suckling, D.M., Wearing, C.H. & Byers, J.A. (2006) Potential of mass trapping for long-term pest management and eradication of invasive species. *Journal of Economic Entomology*, **99**, 1550–1564.

Fernandes, F.L., Picanço, M.C., Campos, S.O., Bastos, C.S., Chediak, M., Guedes, R.N.C. & Da Silva, R.S. (2011) Economic injury level for the coffee berry borer (Coleoptera: Curculionidae: Scolytinae) using attractive traps in Brazilian coffee fields. *Journal of Economic Entomology*, **104**, 1090–1917.

Flint, H.M., Henneberry, T.J. & Wilson, F.D. (1995) The effects of transgenic cotton, *Gossypium hirsutum* L., containing *Bacillus thuringiensis* toxin genes for the control of the pink bollworm (Saunders) and other arthropods. *Southwestern Entomologist*, **20**, 281–292.

Flint, H.M. & Merkle, J.R. (1981) Early-seacon movements of pink bollworm male moths between selected habitats. *Journal of Economic Entomology*, **74**, 366–371.

Flint, H.M., Staten, R.T., Bariola, L.A. & Palmer, D.L. (1973) Gamma-irradiated pink bollworms: attractiveness, mating, and longevity of females. *Environmental Entomology*, **2**, 97–100.

Flint, H.M., Wright, B.S., Sallam, H.A. & Horn, B. (1975) Dispersal and mating in the field by male pink bollworm, *Pectinophora gossypiella*, labeled with $^{32}$P. *Entomologia Experimentalis et Applicata*, **18**, 451–456.

Flint, H.M., Smith, R.L., Bariola, L.A., Horn, B.R., Forey, D.E. & Kuhn, S.J. (1976) Pink bollworm: trap tests with gossyplure. *Journal of Economic Entomology*, **69**, 535–538.

Gage, S.H., Wirth, T.M. & Simmons, G.A. (1990) Predicting regional gypsy moth (Lymantriidae) population trends in an expanding population using pheromone trap catch and spatial analysis. *Environmental Entomology*, **19**, 370–377.

Gaston, L.K., Kaae, R.S., Shorey, H.H. & Sellers, D. (1977) Controlling the pink bollworm by disrupting sex pheromone communication between adult moths. *Science*, **196**, 904–905.

Graham, H.M. & Mangum, C.L. (1971) Larval diets containing dyes for tagging pink bollworm moths internally. *Journal of Economic Entomology*, **64**, 376–379.

Graham, H.M., Ouye, M.T., Garcia, R.D. & De La Rosa, H.H. (1972) Dosages of gamma irradiation for full and inherited sterility in adult pink bollworms. *Journal of Economic Entomology*, **65**, 645–650.

Henneberry, T.J. (1994) Pink bollworm sterile moth releases: Suppression of established infestations and exclusion from noninfested areas. *Fruit Flies and the Sterile Insect Techniques* (ed. C.O. Calkins, W. Klassen & P. Liedo), pp. 181–207. CRC Press, Inc., Boca Raton, FL.

Henneberry, T.J. & Clayton, T.E. (1982) Pink bollworm of cotton (*Pectinophora gossypiella* (Saunders)): male moth catches in gossyplure-baited traps and relationships to oviposition, boll infestation and moth emergence. *Crop Protection*, **1**, 497–504.

Henneberry, T.J. & Naranjo, S.E. (1998) Integrated management approaches for pink bollworm in the southwestern United States. *Integrated Pest Management and Review*, **3**, 31–52.

Holling, C.S. (1959) Some characteristics of simple types of predation and parasitism. *Canadian Entomologist*, **91**, 385–398.

Hulme, P.E. (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, **46**, 10–18.

Hummel, H.E., Gaston, L.K., Shorey, H.H., Kaae, R.S., Byrne, K.J. & Silverstein, R.M. (1973) Clarification of the chemical status of the pink bollworm sex pheromone. *Science*, **181**, 873–875.

Ingram, W.R. (1994) Pectinophora (Lepidoptera: Gelechiidae). *Insect Pests of Cotton* (eds G.A. Matthews & J.P. Tunstall), pp. 107–149. CAB International, Wallingford.

McCall, R.B. (1970) *Fundamental Statistics for Psychology*. Harcourt, Brace and World Inc., New York.

McDonald, R.E. & Loftin, U.C. (1935) Dispersal of the pink bollworm by flight or wind carriage of the moths. *Journal of Economic Entomology*, **28**, 745–755.

Naranjo, S.E. & Ellsworth, P.C. (2010) Fourteen years of *Bt* cotton advances IPM in Arizona. *Southwestern Entomologist*, **35**, 437–444.

Naranjo, S.E., Ruberson, J.R., Sharma, H.C., Wilson, L. & Wu, K.M. (2008) The present and future role of insect-resistant genetically modified cotton in IPM. *Intergration of Insect-Resistant Genetically Modified Crops With IPM Systems* (ed. J. Romeis, A.M. Shelton & G.G. Kennedy), pp. 159–194. Springer, Berlin, Germany.

National Cotton Council (2001) *Pink Bollworm Eradication*. National Cotton Council, Memphis, TN.

Paini, D.R., Worner, S.P., Cook, D.C., De Barro, P.J. & Thomas, M.B. (2010) Using a self-organizing map to predict invasive species: sensitivity to data errors and a comparison with expert opinion. *Journal of Applied Ecology*, **47**, 290–298.

Parajulee, M.N., Rummel, D.R., Arnold, M.D. & Carroll, S.C. (2004) Long-term seasonal abundance patterns of *Heliocoverpa zea* and *Heliothis virescens* (Lepidoptera: Noctuidae) in the Texas high plains. *Journal of Economic Entomology*, **97**, 668–677.

Perlak, F.J., Deaton, R.W., Armstrong, T.A., Fuchs, R.L., Sims, S.R., Greenplate, R.J. & Fischoff, D.A. (1990) Insect resistant cotton plants. *Biotechnology*, **8**, 939–943.

Qureshi, Z.A., Ahmad, N. & Hussain, T. (1993) Pheromone trap catches as a means of predicting damage by pink bollworm larvae in cotton. *Crop Protection*, **12**, 597–600.

Régnière, J. & Sharov, A. (1998) Phenology of Lymantria dispar (Lepidoptera: Lymantriidae), male flight and the effect of moth dispersal in heterogeneous landscapes. *International Journal of Biometerology*, **41**, 161–168.

Reynolds, A.M., Reynolds, D.R., Smith, A.D., Svensson, G.P. & Löfstedt, C. (2007) Appetitive flight patterns of male *Agrotis segetum* moths over landscape scales. *Journal of Theoretical Biology*, **245**, 141–149.

Rogers, D. (1972) Random search and insect population models. *Journal of Animal Ecology*, **41**, 369–383.

Rosell, G., Quero, C., Coll, J. & Guerrero, A. (2008) Biorational insecticides in pest management. *Journal of Pesticide Science*, **33**, 103–121.

Royama, T. (1971) A comparative study of models for predation and parasitism. *Researches on Population Ecology*, **1** (Suppl.), 1–99.

Sanderson, L.A., McLaughlin, J.A. & Antunes, P.M. (2012) The last great forest: a review of the status of invasive species in the North American boreal forest. *Forestry*, **85**, 329–339.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*. WH Freeman and Company, NY, USA.

Spear-O'Mara, J. & Allen, D.C. (2007) Monitoring populations of saddled prominent (Lepidoptera: Notodontidae) with pheromone-baited traps. *Journal of Economic Entomology*, **100**, 335–342.

Spears, J.F. (1968) The westward movement of the pink bollworm. *Bulletin of the Entomological Society of America*, **14**, 118–119.

Stern, V.M. (1979) Long and short range dispersal of the pink bollworm *Pectinophora gossypiella* over southern California. *Environmental Entomology*, **8**, 524–527.

Tabashnik, B.E., Sisterson, M.S., Ellsworth, P.C., Dennehy, T.J., Antilla, L., Liesner, L. *et al*. (2010) Suppressing resistance to Bt cotton with sterile insect releases. *Nature Biotechnology*, **28**, 1304–1307.

Toscano, N.C. & Sevacherian, V. (1980) Pink bollworm monitoring methods. *Pink Bollworm Control in the Western United States* (ed. H.M. Graham), pp. 40–45. US Department of Agriculture, Science and Education Administration, ARM-W-16, Washington, DC.

Ulm, K. (1990) A simple method to calculate the confidence interval of a standardized mortality ratio (SMR). *American Journal of Epidemiology*, **131**, 373–375.

Van Steenwyk, R.A., Ballmer, G.R., Page, A.L., Ganje, T.J. & Reynolds, H.T. (1978) Dispersal of rubidium-marked pink bollworm. *Environmental Entomology*, **7**, 608–613.

Walton, V.M., Daane, K.M. & Pringle, K.L. (2004) Monitoring *Planococcus ficus* in South African vineyards with sex pheromone-baited traps. *Crop Protection*, **23**, 1089–1096.

Wu, H., Wu, K., Wang, D. & Guo, Y. (2006) Flight potential of pink bollworm, *Pectinophora gossypiella* Saunders (Lepidoptera: Gelechiidae). *Environmental Entomology*, **35**, 887–893.

Zhang, Q.H., Schlyter, F., Chu, D., Ma, X.Y. & Ninomiya, Y. (1998) Diurnal and seasonal flight activity of males and population dynamics of fall webworm moth, *Hyphantria cunea*, (Drury)(Lep., Arctiidae) monitored by pheromone traps. *Journal of Applied Entomology*, **122**, 523–532.

Ziska, L.H., Blumenthal, D.M., Runion, G.B., Hunt, E.R. Jr & Diaz-Soltero, H. (2011) Invasive species and climate change: an agronomic perspective. *Climate Change*, **105**, 13–42.

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