Running title: Season-long and peak abundance relationship

Linear relationship between peak and season-long abundances in insects

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1. **Abstract** An accurate quantitative relationship between key characteristics of an insect population, such as season-long and peak abundances, can be very useful in pest management programs. To the best of our knowledge, no such relationship has been established.
2. Here we establish a predictive linear relationship between insect count M_{pw} during the week of peak abundance, the length of seasonal flight period, F (number of weeks) and season-long cumulative abundance $A \approx 0.41 M_{pw}$. The derivation of the equation is based on several general assumptions, and does not involve fitting to experimental data, which implies generality of the result.
3. The equation was tested using extensive data collected on captures of male gypsy moth *Lymantria dispar* (L.) (Lepidoptera: Erebidae), in pheromone-baited traps during 15 years.
4. The model was also tested using trap catch data for two species of mosquitoes, *Culex pipiens* (L.) (Diptera: Culicidae) and *Aedes albopictus* (Skuse) (Diptera: Culicidae), in Gravid and BG-sentinel mosquito traps.
5. The simple, parameter-free equation approximates experimental data points with relative error of 13% and $R^2 = 0.997$, across all of the species tested.
6. For gypsy moth, we also related season-long and weekly trap catches to the daily trap catches during peak flight.
7. We describe several usage scenarios, in which the derived relationships are employed to help link results of the small-scale field study to the operational Slow the Spread of the gypsy moth program.

Key words: gypsy moth, mosquito, trap catches, flight period, sampling, pest management, mathematical model

Introduction

Surveys are crucial for monitoring insect activity, crop pest levels, local movement, long-range migration, feeding and reproduction, and are widely used in pest management programs. Various tools are used for insect surveys, including several types of traps, which are deployed extensively to detect and monitor insect population levels, presence of invading populations and phenological development, for purposes of both applied pest management and research (Abell et al., 2015; El-Sayed et al., 2006; Elkinton & Cardé, 1981; Liebhold & Tobin, 2008; Poland & McCullough, 2006; Sharov et al., 1995; Thorpe et al., 2006; Tobin et al., 2009; Wall & Perry, 1987; Witzgall et al., 2010; Witzgall et al., 2008). At least 20 million pheromone lures are produced for monitoring and mass trapping annually worldwide (Witzgall et al., 2010). In the United

States, over 100,000 pheromone-baited traps are deployed annually just to monitor gypsy moth (Roberts & Ziegler, 2007).

Insect surveys also play an important role in research on population dynamics, seasonal phenology, mating success and mating disruption in various species, including but not limited to gypsy moth, codling moth, light brown apple moth and oriental fruit moth (Casado et al., 2014; Epstein et al., 2006; Knight et al., 2015; Onufrieva et al., 2013; Onufrieva et al., 2008; Onufrieva et al., 2010; Pfeiffer, 1993; Sharov et al., 2002; Stelinski et al., 2013; Stelinski et al., 2004; Stelinski et al., 2010; Stelinski et al., 2007; Tcheslavskaia et al., 2005a; Tcheslavskaia et al., 2005b; Thorpe et al., 2006; Thorpe et al., 1999; Thorpe et al., 2007). Many of the studies are conducted using releases of laboratory reared insects rather than wild populations, which helps to ensure similar population densities among experimental plots and can provide a longer season of flight for data collection (Casado et al., 2014; Onufrieva et al., 2013; Onufrieva et al., 2008; Onufrieva et al., 2010; Stelinski et al., 2013; Tcheslavskaia et al., 2005a; Tcheslavskaia et al., 2005b). Due to logistics and experimental design, researchers often work with daily or weekly insect counts (Onufrieva et al., 2008; Onufrieva et al., 2010; Pfeiffer, 1993; Sharov et al., 2002; Tcheslavskaia et al., 2005b; Thorpe et al., 2006; Thorpe et al., 1999; Thorpe et al., 1993), while large-scale management programs normally have access to season-long counts only (Tobin & Blackburn, 2007). To the best of our knowledge, no method currently exists to relate daily or weekly counts to season-long counts. Relating daily and weekly counts to season-long counts as well as the converse problem of predicting maximum daily counts from the known season-long ones is important for interpretation of research results and their application in the management programs. Since collecting daily or weekly data in a large-scale management program is very costly and impractical, a model that relates daily and weekly population characteristics to the easy to obtain season-long counts should be of practical benefit.

Materials and Methods

Experimental design. We used data from standard USDA milk carton pheromone-baited traps (Webb, 1982) deployed in 2000, 2001, 2013 and 2014 in Goshen Wildlife Management Area, VA and in 2001, 2002, 2004 and 2006 in Appomattox-Buckingham and Cumberland State Forests, VA. In 2000 – 2006. At each location, 5 to 20 USDA pheromone-baited traps were deployed and checked weekly to monitor the flight period of wild gypsy moth populations as part of ongoing research experiments. Captures from all traps in a given location were averaged and considered a single observation. Since 2013, we began to monitor the traps on a daily basis: in 2013, traps were monitored from June 14 to August 4; in 2014, traps were monitored from June 30 to August 8. In both 2013 and 2014, 2 sentinel traps were deployed and

checked daily for 5 days each week. In 2016, a trap was placed in Blacksburg, VA and monitored every day from June 20 to August 10.

Season-long trap catch for gypsy moth. Season-long trap counts were highly variable, showing strong dependence of the season-long cumulative catch (abundance) A on both the length of the flight period F and the trap catch during the week of peak flight, M_{pw} (Figure 1).

[Figure 1]

A standard assumption often made by others (Hokyo & Kiritani, 1967; Robinet et al., 2007; Tobin et al., 2009) is that the distribution of trap captures as a function of time is Gaussian. We have verified this assumption explicitly for two randomly selected years (2006 and 2014) of gypsy moth trap catches, (Figure 2).

[Figure 2]

Robustness of the model to insect and trap type. To test robustness of our main result (Equation 1) to insect and trap type, we used mosquito trapping data collected by the Mosquito and Forest Pest Management program, Prince William County, VA in 2015. We used *Culex pipiens* catches in gravid traps (Irish et al., 2013) and *Aedes albopictus* catches in BG-Sentinel traps (Maciel-de-Freitas et al., 2006). The trap data were collected weekly from May 3 to October 23, 2015.

Daily trap catch for gypsy moth. Daily gypsy moth male trap catches were not available to us prior to 2013. Once daily trap catches became available in 2013, followed by 2014 and 2016, we also sought to relate maximum daily trap catch at peak flight to the season-long trap catch. For this relationship, we used daily trap catches collected in 2014 as a training set, and daily trap catches collected in 2013 and 2016 served as test sets. Unlike the weekly counts, in which day-to-day fluctuations of insect counts are automatically averaged out to produce a smooth distribution that deviates little from the expected Gaussian distribution (Figure 2), individual daily values are too variable for a single characteristic such as daily average to be useful in practice. Instead, here we seek to establish a predictive relationship for the range of the daily counts, that is its conservative upper and lower bounds. It is probably hopeless to try to derive the range from first principles; instead, we deduce it from our experimental data for gypsy moth, which we re-interpret as follows. Since the beginning of peak flight week assignment is arbitrary and depends on the day a trap was checked, we simulated different week assignments using a sliding window of 7 days to determine the week of peak flight, making sure that the maximum observed value of daily catch is always included in the “peak flight” week. In effect, the procedure simulates 7 different experimental outcomes. The analysis yielded a range of proportionality coefficients between trap catch during the peak flight week and the peak daily value.

Results

The model and its derivation. The model describes the relationship between insect counts M_{pw} during the week of peak activity, the flight period *F*, and season-long cumulative counts A, which is a direct measure of the insect abundance. It is known that pheromone traps achieve detection probability of nearly 100% even for relatively sparse populations (Larsson, 2016). It is therefore reasonable to assume high sensitivity of the traps. Specifically, we assume that traps are sensitive enough to start catching insects when their population reaches 1% of the maximum population, consistent with our own experiments, Figure 2. We also demonstrate below that the specific value of "trap sensitivity" is not very important for as long as it is high enough – the mathematical structure of the resulting equation is such that it is insensitive to the value of the "sensitivity threshold". For a symmetric distribution, the flight period F is defined as follows: the traps begin to catch insects at $t = t_p - F/2$, when the insect density rises above the 1% trap sensitivity threshold, and stop at $t = t_p + F/2$, once the insect density drops below this threshold, Figure 2. We model the distribution of insects caught as a function of time as a Gaussian function $M_{pw}e^{-(t-t_p)^2/2\sigma}$, centered around the peak flight time point t_p, Figure 2. Then, the cumulative catch (A)

$$A = \int_{-F/2}^{+F/2} M_{pw}e^{-(t-t_p)^2/2\sigma}dt \approx M_{pw}\int_{-\infty}^{+\infty} e^{-(t-t_p)^2/2\sigma}dt = M_{pw} \times \sigma\sqrt{2\pi}$$

The full width *F* of a Gaussian function at 1/100 (1%) of the maximum is related to σ via

$$F = 2\sigma\sqrt{2ln100}$$

Therefore,

$$A = \frac{2\pi}{2\sqrt{2ln100}}M_{pw}F \approx 0.41M_{pw}F \qquad \text{(Equation 1)}$$

which is the main result of this work. Its robustness to the assumptions is discussed below, and is demonstrated experimentally.

We stress that the derivation of Eq. 1 did not involve any fitting to experimental data. The relationship is expected to hold as long as the following conditions are satisfied: (1) The seasonal change in the insect population as a function of time (weekly averages) can be reasonably approximated by a Gaussian function. (2) The trap method is sensitive enough to detect insects during most of the flight period. (3) Traps do not saturate. The importance of (1) and (2) for our model is self-evident. To understand the importance of the last assumption, consider a situation where it breaks

down completely: at very high population density during several weeks, high enough so the traps are completely saturated. Obviously, if this were the case, the weekly catch estimates would be flat around the peak, no longer representative of the true insect abundance, and the model that assumes a Gaussian distribution would fail.

Robustness of the model. Assumptions (2) and (3) essentially state that the catch method is, in some sense, "well designed". As long as this is the case, Equation 1 is not very sensitive to details. Indeed, consider a trap that faithfully represents the true population density in the following sense: catch = α*(true population), where the constant α stays the same within a given year and experiment, but may vary for different species and years. Now suppose a different trap is used, which changes the value of α by a factor of 2 for a different species/year. Both A and M_{pw} in Equation 1 will change by a factor of 2, without affecting the linear nature of the relationship. There will be a slight effect on the proportionality constant K in $A = K*M_{pw}*F$ due to the use of more/less sensitive trap (e.g. one that can sense 1/200 instead of 1/100 of the maximum population, which will affect the trap sensitivity threshold, Figure 2), but note that the functional dependence of K on the trap sensitivity threshold is extremely weak, $K \sim \sqrt{\log(1/threshold)}$. In the above example of the threshold changing from 1/100 to 1/200, the difference in the proportionality constant in Equation 1 is $\sqrt{2ln100}$ vs. $\sqrt{2ln\,200}$, or 3.03 vs. 3.25, which is small.

While assumption (1) is likely to hold for many species, it implies that the insects are short-lived relative to their entire developmental periods. Otherwise, even if the developmental period itself is normally distributed (which is approximately true even for humans), the abundance can reach a long plateau during the season, inconsistent with the Gaussian shape. However, as we shall see below, the simple and parameter-free model described by Equation 1 works surprisingly well for completely different insect species and trapping methods in the temperate climate zones. We note that tropical species may not have a distinct start and end of flight points, and so the model may not be applicable.

Experimental verification of the model. In our test data set, see "Methods", season-long male gypsy moth trap catches ranged from 7.3 to 462 males/trap/week; flight duration ranged from 3.7 to 7 weeks; and maximum trap catch during peak week ranged from 4.4 to 172 males/trap. Season-long trap catches of *C. pipiens* and *A. albopictus* ranged from 6.22 to 60.72 and from 0.12 to 31.12, respectively. Flight duration of both species was 24 weeks. The data strongly confirms the proposed functional dependence of season-long trap catch on flight duration and trap catch during peak flight (Figures 3 and 4).

[Figure 3]

The predicted season-long trap catches from trap catches during the week of peak flight correlate strongly with the actual, measured season-long trap catches for all three species tested ($R^2 = 0.9977$, SD = 0.13, Figure 4).

It is remarkable that the accuracy of Equation 1 is the same for all of the species tested, even though the biology, catch methods, and the geographical areas are different. Moreover, for the mosquito species the catch distributions (not shown) are not as close to idealized Gaussian as they are for the gypsy moth, Figure 2, although in all cases there is a clear peak, the beginning and the end of flight points. This observation suggests strong robustness of the proposed model, and its potential to work for other species as well.

[Figure 4]

Relationship to daily trap catch for gypsy moth. For reasons discussed in "Methods", here we seek to relate the range of daily trap catches during the peak flight week to the other measurable parameters such as the maximum weekly and the total catch, M_{pw} and A. Experimental daily trap catches ranged from 0 to 13.5 males/trap/day in 2013, from 0 to 10 males/trap/day in 2014, and from 0 to 15 in 2016. In an idealized scenario, without random day-to-day variation, trap catches during the peak week of flight period can be calculated as:

$$M_{pw} = \int_{t_p-3.5}^{t_p+3.5} M_{pd} \times e^{\frac{-(t-t_p)^2}{2\sigma^2}} \approx 7 \times M_{pd}$$

where M_{pd} is the daily peak, that is the absolute maximum of the distribution. In the idealized case this simple relationship holds because for the species discussed here, σ is considerably larger than 7 days, and so the integrand varies little over the integration range in the above expression. However, in reality, daily values fluctuate significantly around the predicted Gaussian peak, resulting in two effects. First, the proportionality coefficient *K* in $M_{pw} = KM_{pd}$ becomes less than 7, with daily peak values that deviate stronger from the Gaussian-based expectation resulting in lower *K*. Second, *K* will vary from year to year. In 2014, *K* ranged from 2.35 to 4.66. Below we estimate maximum and minimum bounds on *K*, based on the variation in daily trap catches inferred from our analysis of the experimental data on gypsy moth from 2014, see "Methods" for details. Our estimate is that $2.35M_{pd} < M_{pw} < 7M_{pd}$, or conversely, $0.14M_{pw} < M_{pd} < 0.43M_{pw}$. We use data points from 2013 and 2016 to validate the estimate (Figure 5). Clearly, the maximum daily catch during the week of peak flight is within the estimated lower and upper bounds.

[Figure 5]

Using our main result $A \approx 0.41 M_{pw} F$, we arrive at another useful relationship:

$$0.96 M_{pd} F < \mathrm{A} < 2.87 M_{pd} F \qquad \text{(Equation 2)}$$

Discussion

In this paper, we have established a predictive linear relationship between insect count M_{pw} during the week of peak abundance, the length of seasonal flight period, F (number of weeks) and season-long cumulative catch $A \approx 0.41 M_{pw} F$. This relationship was derived without any fitting to experiment, based on very general assumptions, which likely explains its remarkable accuracy and the fact that it works across the three tested species with very different biology, behavior, and trapping methods: *Lymantria dispar* (Lepidoptera: Lymantriidae), *Culex pipiens* (Diptera: Culicidae) and *Aedes albopictus* (Diptera: Culicidae). Although the model has only been validated using three species of insects, we expect the relationship, Equation 1, between maximum weekly counts and season-long counts to hold true for many other species, as long as their emergence is reasonably approximated by Gaussian distribution, and the collection method is sensitive and faithfully reflects variation in abundance. The expectation is based on the generality of the arguments used in the derivation, absence of fitting to a specific species or trap type, and the already established agreement with experiment across three species.

Two interrelated scenarios of the model use in practice are exemplified below:

Example Usage Scenario I.

The formula $A \approx 0.41 M_{pw} F$ is used to estimate the hard-to-measure peak abundance M_{pw} from the other two population parameters, *A*and *F,* which themselves do not require intense monitoring. Thus, data collected as part of monitoring in the pest management program can be analyzed using this formula and appropriate method of control can be chosen based on the maximum daily value. This is important in large-scale control/monitoring programs, in which a method of control depends on the population density. For example, currently, in the Slow The Spread of the gypsy moth program (STS), the low dosage (6 g AI/acre) of mating disruptant is recommended for use in low-density gypsy moth populations, in which trap catches do not exceed 30 males/trap/season (Thorpe et al., 2006). Ability to directly relate weekly trap catches from experimental plots to the season-long trap catches used by STS decision algorithm (Tobin & Sharov, 2007; Tobin et al., 2004) may allow us to improve the method of mating disruption used against gypsy moth by accurately estimating population densities during peak flight and using more appropriate control measures.

Example Usage Scenario II

In this situation, the unknown season-long trap catch for a model (artificially created) population used in a research study is estimated from the peak abundance of that model population, which in this scenario is easily available by experimental design. In most cases, researchers are not trying to simulate flight, they simply repeatedly release similar numbers of insects to assess treatment efficacy. Therefore, the total of all captured insects in an experimental plot cannot be interpreted as the true season-long catch, which, therefore, would be unknown. Instead, each trap catch can be treated as the catch during peak flight and a season-long trap catch can be estimated using the proposed formula. This approach allows to estimate the population density for which the treatment efficacy is assessed, to better interpret research results and to appropriately apply them in the management programs.

The data collected on gypsy moth phenology over the past 16 years allowed us to conduct a comprehensive analysis and relate season-long and weekly trap catches and flight duration to the daily trap catches. The data collectively indicate a significant variability in flight duration, which in turn causes significant variability in peak trap catches in populations with the same density as measured by male moth catches in pheromone-baited traps.

To account for this variability, the model provides a range for a daily peak value, to allow researches and managers to estimate best and worst case scenarios, predict efficacy of control tactic, and make decisions to ensure optimal results. In addition to the immediate application in gypsy moth management programs, this model may be utilized to predict mating success of gypsy moth females and likelihood of persistence of isolated low-density populations (Contarini et al., 2009; Sharov et al., 1995; Tobin et al., 2013).

Our main result – the uncovered linear relationship between insect counts during the week of peak abundance, length of activity period and season-long trap catches – has already been verified for three very different insect species. The fact that the relationship holds, quantitatively and accurately, for species with quite different biology, is indicative of the generality of the relationship. It may therefore not be surprising if future investigations identify other species for which the same relationship holds true.

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Figure 1: Season-long trap catches depend strongly both on trap catches during peak flight and flight duration. Conversely, trap catches during peak flight cannot be predicted from the flight period alone.

Figure 2: Weekly male gypsy moth catches in pheromone baited traps, 2006 (A) and 2014 (B) and list-square fit of experimental data points to a normal distribution. In both cases, the correlation $R^2 > 0.99$. Grey arrows indicate the time points where the insect population reaches the trap sensitivity threshold.

Figure 3: Season-long trap catches depend linearly on the product of trap catch during the peak flight week and the length of the flight period. The relationship holds true for several different insect species and catch methods.

Figure 4: Predicted (solid and checkered black columns for gypsy moth and mosquito data, respectively) and actual (solid and checkered grey columns for gypsy moth and mosquito data, respectively) season-long trap catches vs trap catches during peak flight and flight duration.

Figure 5: Daily gypsy moth male catches in pheromone-baited traps in Virginia, 2013 (A) and 2016 (B). Lines indicate estimated minimum and maximum possible daily values estimated from the maximum observed weekly peak value.

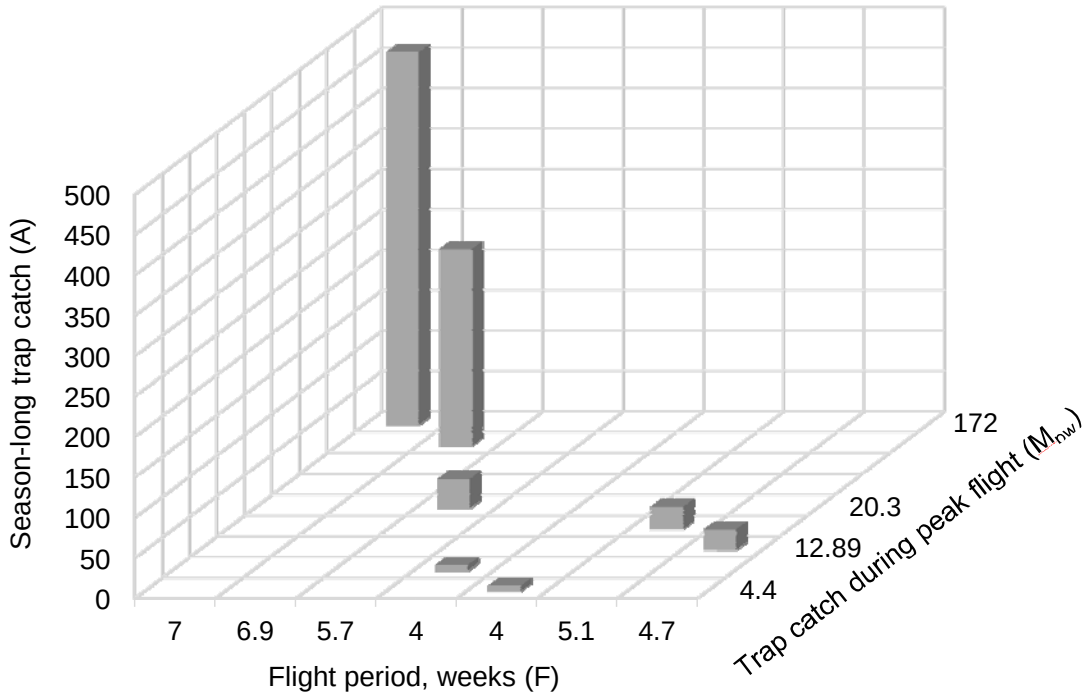
Season-long trap catch (A)
500
450
400
350
300
250
200
150
100
50
0
7
6.9
5.7
4
4
5.1
4.7
Flight period, weeks (F)
172
20.3
12.89
4.4
Trap catch during peak flight (M_now)

Figure 1

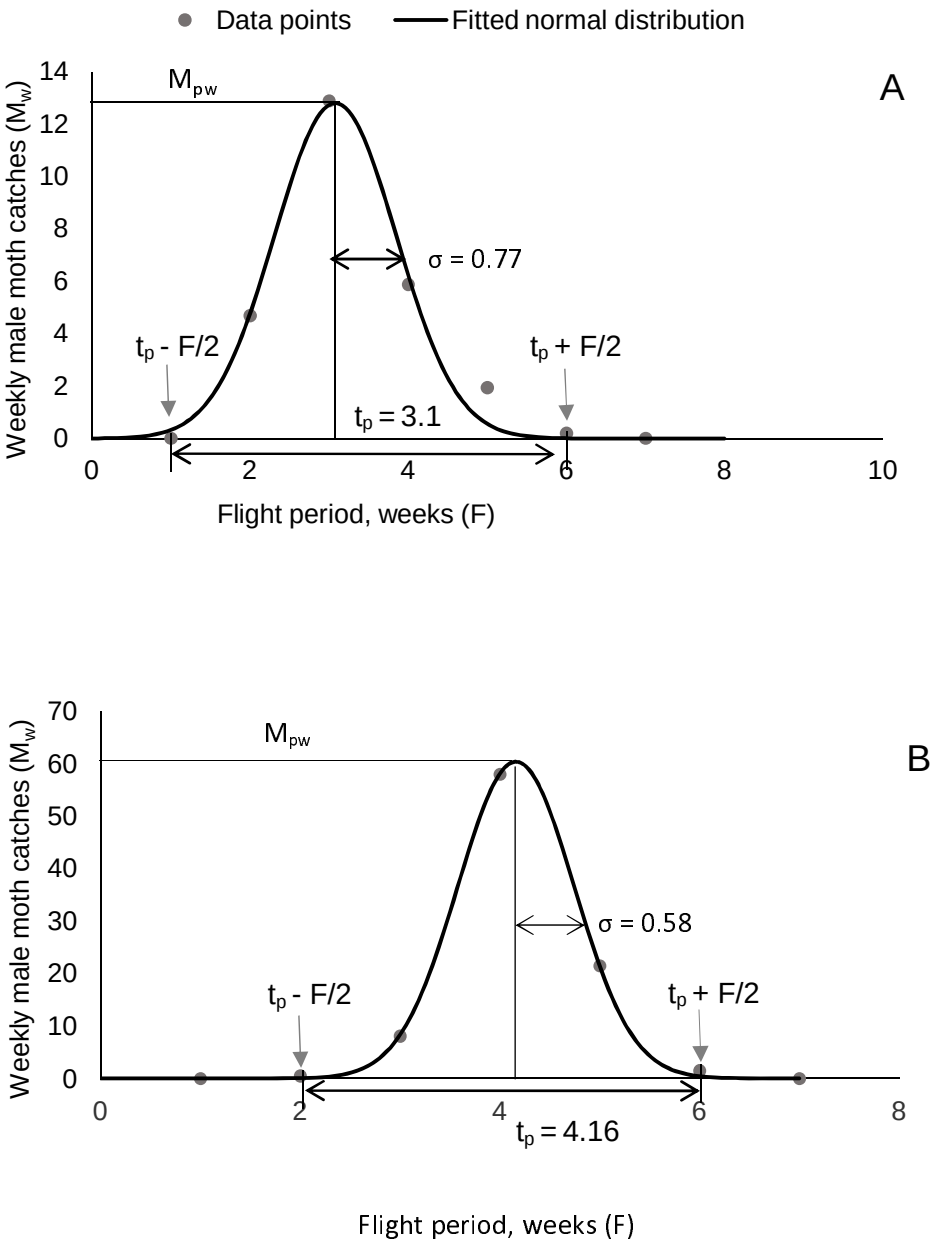
Data points
Fitted normal distribution
A
Weekly male moth catches (M_w)
M_{pw}
σ = 0.77
t_p - F/2
t_p + F/2
t_p = 3.1
Flight period, weeks (F)
B
Weekly male moth catches (M_w)
M_{pw}
σ = 0.58
t_p - F/2
t_p + F/2
t_p = 4.16
Flight period, weeks (F)

Figure 2

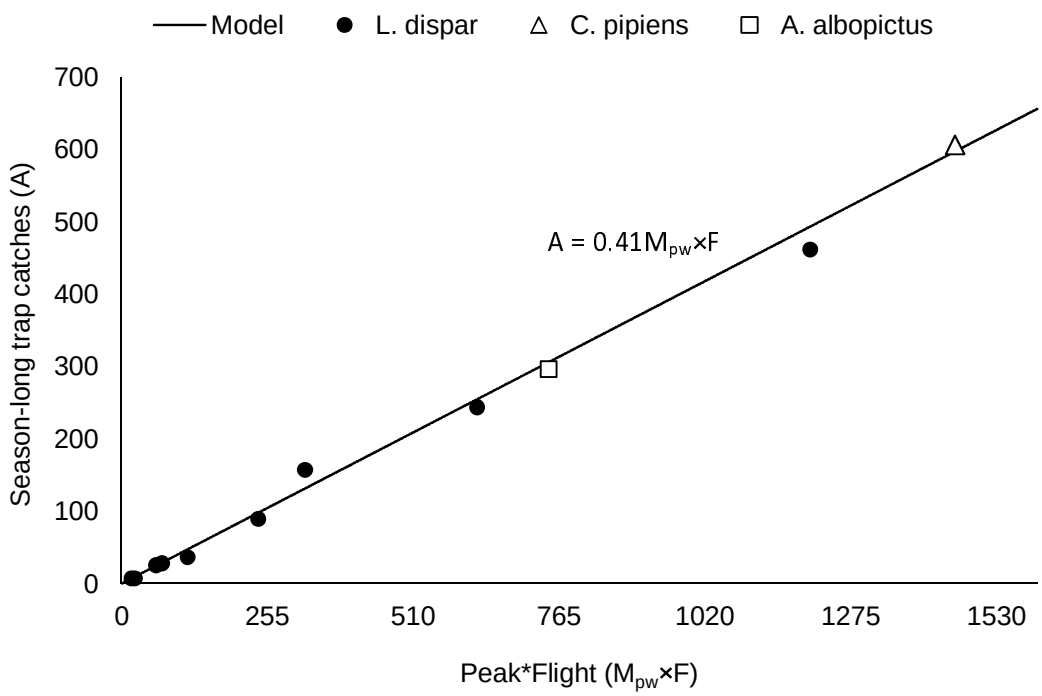
Model
L. dispar
C. pipiens
A. albopictus
Season-long trap catches (A)
700
600
500
400
300
200
100
0
A = 0.41M$_{pw}$×F
0
255
510
765
1020
1275
1530
Peak*Flight (M$_{pw}$×F)

Figure 3

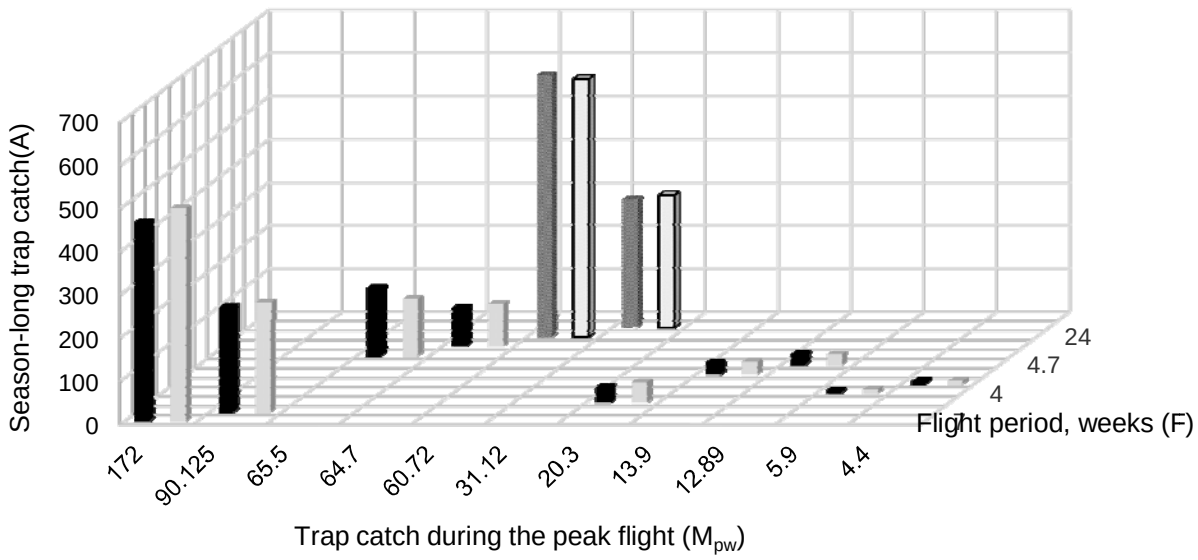
Season-long trap catch(A)
700
600
500
400
300
200
100
0
172
90.125
65.5
64.7
60.72
31.12
20.3
13.9
12.89
5.9
4.4
24
4.7
4
Flight period, weeks (F)
Trap catch during the peak flight (M_{pw})

Figure 4

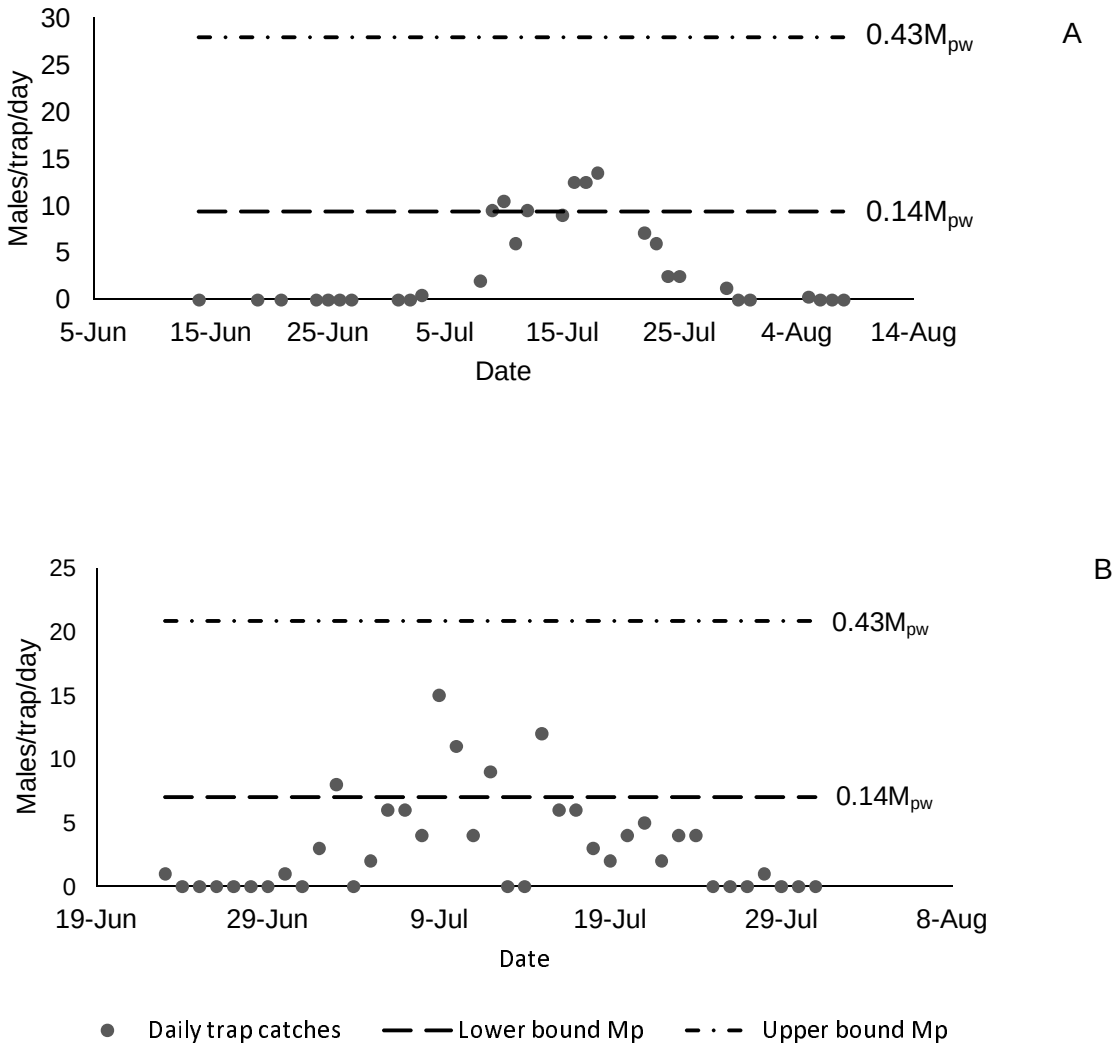
A
30
25
20
15
10
5
0
Males/trap/day
0.43Mpw
0.14Mpw
5-Jun
15-Jun
25-Jun
5-Jul
15-Jul
25-Jul
4-Aug
14-Aug
Date
B
25
20
15
10
5
0
Males/trap/day
0.43Mpw
0.14Mpw
19-Jun
29-Jun
9-Jul
19-Jul
29-Jul
8-Aug
Date
Daily trap catches
Lower bound Mp
Upper bound Mp

Figure 5