Original article

Time-course in attractiveness of pheromone lure on the smaller tea tortrix moth: a generalized additive mixed model approach

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Abstract

Long-term pest insect monitoring in agriculture and forestry has advanced population ecology. However, the discontinuation of research materials such as pheromone lure products jeopardizes data collection continuity, which constrains the utilization of the industrial datasets in ecology. Three pheromone lures against the smaller tea tortrix moth *Adoxophyes honmai* Yasuda (Lepidoptera; Tortricidae) were available but one was recently discontinued. Hence, a statistical method is required to convert data among records of moths captured with different lures. We developed several generalized additive mixed models (GAMM) separating temporal fluctuation in the background male density during trapping and attenuation of lure attractiveness due to aging or air exposure after settlement. We collected multisite trap data over four moth generations. The lures in each of these were unsealed at different times before trap settlement. We used cross-validation to select the model with the best generalization performance. The preferred GAMM had nonlinear density fluctuation terms and lure attractiveness decreased exponentially after unsealing. The attenuation rates varied among lures but there were no differences among moth generations (seasons). A light trap dataset near the pheromone traps was a candidate for a male density predictor. Nevertheless, there was only a weak correlation between trap yields, suggesting the difficulty of data conversion between the traps differing in attraction mechanisms.

Keywords: relative density estimation, historical data, nonlinear regression, data integration, state-space model

Introduction

An aim of population ecology is to clarify the dynamics driving the population of an organism. Long-term field monitoring of population fluctuations is a fundamental information source (Royama 1996; Yamamura et al. 2006; Reinke et al. 2019). Large scale- and time data have been collected for agriculture, fishery (Jorgensen et al. 2007), hunting (Elton and Nicholson 1942) and forestry (Klapwijk et al. 2013; Osada et al. 2018). Data sources in the industrial sectors have advocated and tested basic concepts in ecology and evolutionary and conservation biology. However, it has also been difficult to obtain census data with sufficient length and methodological consistency (Bonebrake et al. 2010). For insect pest species, data recycling has been constrained by temporal changes in chemical pesticides and cultivars (Osakabe 1985; Yamamura et al. 2006), suspension and/or site change during the census (Yamamura et al. 2006), and data crudeness and ordinal measurements (Osada et al. 2018; Sudo et al. 2019).

A census dataset may be inconsistent because of changes in equipment and materials or coexistence of multiple materials. The smaller tea tortrix *Adoxophyes honmai* Yasuda (Lepidoptera; Tortricidae) is a common tea pest insect in Japan. It is characterized by four (Honshu Island) or five (Southern Japan) discrete generations (Osakabe 1986; Nabeta et al. 2005; Sato et al. 2005; Ishijima et al. 2009) per season. Timing of insecticide application to the larvae is determined from the adult emergence of the previous generation. Field monitoring of *A. honmai* has been routinely performed by Japanese agricultural researchers since the end of World War II (Oba 1979; Osakabe 1985). Legacy data have been used in population ecology analyses (Yamanaka et al. 2012).

Since the 1960s, numerous female insect pest sex pheromones have been identified. Synthetic pheromone products have been deployed to monitor tools that control population density via mass trapping and/or mating disruption (Cardé 1976; Witzgall et al. 2010). Early *A. honmai* censuses relied solely on fluorescent light traps. The female *A. honmai* sex pheromone was first identified by Tamaki et al. (1971). It comprises (Z)-9-tetradecenyl acetate (Z9-14Ac) and (Z)-11-tetradecenyl acetate (Z11-14Ac) and causes sexual stimulation in males. (E)-11-tetradecenyl acetate (E11-14Ac) and 10-methyldodecyl acetate (10-Me-12Ac) were later isolated and deemed essential for male moth flight orientation. The mass ratio of the components in the female moths was 63:31:4:2 (Z9-14Ac:Z11-14Ac:E11-14Ac:10-Me-12Ac) (Tamaki et al. 1979).

Three synthetic pheromone products have since been dedicated to monitoring *A. honmai* (Oba 1979; Japan Plant Protection Association 2000). Each one has a unique mixing ratio, total component content, and pheromone dispenser substrate. The first was released from Ohtsuka Pharmaceutical Co. Ltd. (hereafter, OT). It has a 23:10:0.1:67 mixing ratio and its format is 9.1 mg per plastic capsule. The ratio of the fourth component was 100× greater than that occurring in living females. It was used in monitoring programs in several prefectures, but its production was discontinued in 2019. The product from Sumitomo Chemical Co. Ltd. (hereafter, SC; originally developed by the agrochemical division of Takeda Pharmaceutical) has a 15:8:1:9 mixing ratio and its format is 10 mg per rubber septum. The third product was commercialized by Shin-Etsu Chemical Co. Ltd. (hereafter, SE). Its unofficial mixing ratio is 65:35:5:200 and its format is 3.05 mg per rubber septum (Yoshioka and Sakaida 2008).

A statistical framework to estimate background population sizes using data derived from multiple research materials compares across time periods and regions. Here, we sought an appropriate statistical model structure to separate the effects of temporal fluctuations in population size and the pheromone lure attractiveness. To this end, we used a trap dataset over four adult *A. honmai* generations, three lure types, and daily light trap capture simultaneously. The model structure was decomposed to (1) the state of the system or temporal male population size fluctuation including daily changes in flight activity and (2) the observation process or lure attractiveness and trap capture. We could also assume a parametric formulation considering male population dynamics which ecologists recognize as a state-space model (Kéry and Schaub 2011; Fukaya 2016; Yamamura 2016). For the sake of simplicity, however, we adopted a nonlinear regression.

Along with lure product (OT, SC, and SE) chemical composition, attenuation of the volatile concentrations in each lure with air exposure time affects lure attractiveness (Butler and McDonough 1979; Tamaki and Noguchi 1983). This change is temporal as are population density and male activity. We must design the model so that it can divide these effects. We compared the yields from traps with different lure ages. This configuration was set up by unsealing some of the lures before the start of the session (Tamaki et al. 1980). Besides, as a way to trap insects independently of lure degradation, we also approximated the moth population size using the number of males captured by a light trap near the pheromone lures.

2. Methods

Experimental setup

The field survey was conducted in the experimental fields of Kanaya Tea Research Station, Shizuoka, Japan (34°48’26.6” N, 138°07’57.5” E, 202 m a.s.l.) (Figure 1A). The 0th, 1st, 2nd, and 3rd *A. honmai* generations usually occur annually in Kanaya (Ishijima et al. 2009). We captured the generations 1–3 of the 2017 season and the 0th (overwintering) generation of 2018 using traps equipped with pheromone lures.

Each pheromone trap consisted of an adhesive (SE trap; Sankei Chemical Co. Ltd., Kagoshima, Japan) upon which the plastic capsule or the rubber septum of the pheromone lure was placed. The pheromone traps were set in the middle of the tea field hedges at the height of the plucking surface. To calibrate the lure attractiveness based on the number of moths captured per light trap per day, light trap data (Figure 1B: site “LT”) were added to some of the following analyses. Tea-pest monitoring at the light trap site has been conducted since 1947 (Osakabe 1986). The light trap consisted of a water pan (H 10 cm × W 100 cm × L 100 cm) to capture the insects and a suspended blue fluorescent lamp (20 W; FL20S-BL-K; Panasonic Corp., Osaka, Japan). The light was switched on every night between 19:00 and 7:00 and captured insects including *A. honmai* were counted during the daytime.

The trapping session for each generation was planned to start immediately after the appearance of adults in the field. The latter was confirmed using the light trap. The pheromone lures were set in the traps on the first day of the session (hereafter, Session Day = 0). Adult male *A. honmai* were

counted in the trap every morning from the next day (first day of counting; Session Day = 1). The sessions occurred from June 26, 2017 to July 10, 2017 for the first generation and counting started on June 27, 2017. The second-generation session ran from July 31, 2017 to August 21, 2017. The third-generation session was from September 11, 2017 to October 2, 2017. The zeroth-generation session was from April 28, 2018 to May 12, 2018 (Table 1). The weather at the research station was permanently monitored and meteorological data are available at https://www.naro.affrc.go.jp/org/vegetea/mms-kanaya/Menu.html.

To separate the temporal changes in the post-settlement lure attractiveness and the population density and activity, the pheromone lures were unsealed at five different times per moth generation. Lures were opened immediately before (Session Day = 0; hereafter, Minus0w) in addition to 7, 14, 21, and 28 days before trap settlement (Minus1w, Minus2w, Minus3w, and Minus4w). The capture session of each generation continued for two (0th and 1st) or three weeks (2nd and 3rd). Hence, the capture data covered 1–49 days after lure opening.

The experiment was conducted in four fields (sites A–D; Figures 1B and S1) over each of the four moth generations. Each replicate was a combination of pheromone traps distributed within a single tea field and comprised three lure types × five open timings (Supplementary Figure S1). The minimum distance between adjacent pheromone traps was 7.65 m; the attractiveness range for *A. honmai* is ~5 m (Kawasaki et al. 1979). Hence, interference might have occurred. Nevertheless, an earlier study compared spatiotemporal dynamics in tea tortrix moth lure attractiveness and reported a consensus of 5 m distance between traps (Kawasaki and Tamaki 1980).

Model

The model components include the daily male density at each trap site and the attractiveness of the pheromone lure.

Male density

Let $d_{g,i,\tau}$ be the density of active males of the gth insect generation at the ith trap site on the τth trap night. In the scope of the present study, daily male density is defined as the mixture reflecting population dynamics such as recruitment or survival and daily flight activity. It will be affected by weather conditions and male mating drive. To treat the internal population state as a black box, $d_{g,i,\tau}$ was defined as the natural logarithm of factors that synergistically influence the observed number of moths.

The mean regional-scale population density was determined first. Let $\overline{d_g}$ be the regional mean (log-) density of *A. honmai* adult males in the gth generation. Considering stochastic changes in male density in each tea field, the mean density at the ith site during the gth generation is:

$$\overline{d_{g,i}} = \overline{d_g} + \varepsilon_{g,i}, \quad \varepsilon_{g,i} \sim \mathrm{N}(0, \sigma^2_{\mathrm{GenSite}})$$

Eq. 1

Here, $\varepsilon_{g,i} \sim \mathrm{N}(0, \sigma^2_{\mathrm{GenSite}})$ is the random effect of generation × site. It follows a normal distribution with mean = 0 and variance = $\sigma^2_{\mathrm{GenSite}}$. When the trap session of the gth generation continues over T_g days, the site-specific male density of the τth day, $d_{g,i,\tau}$ ($\tau = 1,2,3,\ldots,T_g$), is expressed as:

$$d_{g,i,\tau} = \overline{d_{g,i}} + f_g(\tau), \quad \sum_{\tau=1}^{T_g} f_g(\tau) = 0$$

Eq. 2

The shape of the generation-specific smoothing function $f_g(\tau)$, signifies the temporal fluctuation in male density during the season. The function is centered about the mean (log-) generation density.

When the male density is approximated by the number captured in the light trap on the same day, the predictor should be defined as follows:

$$d_{g,i,\tau} = f_L\left(\ln\left(L_{g,\tau} + 0.5\right)\right) + \varepsilon_{g,i}, \quad \varepsilon_{g,i} \sim \mathrm{N}(0, \sigma^2_{\mathrm{GenSite}})$$

Eq. 3

The variable $L_{g,\tau}$ is the measured number of *A. honmai* males captured in the light trap on the same day. As this number may be zero, however, 0.5 is added to it and it is then converted to a logarithm to meet the homoscedasticity assumption (Yamamura 1999). The shape of the smoothing function f_L indicates the relationship between the numbers caught in the light traps and the pheromone traps. The shape of f_L may be linear or nonlinear and may differ with generation.

Lure attractiveness

Next, the lure attractiveness is modeled. As some of the pheromone lures were unsealed before the start of the session, each lure had an age of (pre-session opening period) + (days in the session). Let the lures with the kth treatment level (Minus0w, Minus1w, ...) age for m_k d at settlement in the fields (Session Day = 0). The lures aged $s_{k,\tau} = \tau + m_k$ days upon counting Session Day = τ. For instance, the first treatment level in the experiment was Minus0w; hence, $m_{k=1} = 0$ holds. When the males were counted in the trap for the first time, $s_{k=1,\tau=1} = 1$ holds as $\tau = 1$ was defined as the next morning of the trap settlement. If the treatment was Minus1w ($k = 2$), then $m_{k=2} = 7$ and $s_{k=2,\tau=1} = 8$.

The predictor of the number of males captured in each trap was defined. Let $\lambda_{g,i,j,k,\tau}$ be the expected number of unique individuals entering the trap sampling range (site i, type j, and treatment k) during the period from $\tau - 1$ to τ in the trap session of the gth generation. Note that $\lambda_{g,i,j,k,\tau}$ is on a linear scale. When $d_{g,i,\tau}$ gives the local male density, the captured number of males in the morning of Session Day = τ is denoted by $N_{g,i,j,k,\tau}$ and is expressed as

$$\ln(\lambda_{g,i,j,k,\tau}) = d_{g,i,\tau} + \psi_{g,j}(s_{k,\tau}),$$

$$N_{g,i,j,k,\tau} \sim \text{Poisson}(\lambda_{g,i,j,k,\tau}),$$

Eq. 4

where $P(N = k) = \lambda^k e^{-\lambda}/k!$ is the Poisson distribution of the parameter λ. The effect of the number of days since lure opening ($s_{k,\tau}$) on lure attractiveness is expressed using the continuous function $\psi_{g,j}$. Whether the effect of the exposure period is taken to be linear or nonlinear, the ψ_{gj} intercept in Eq. 4 must be fixed for model identifiability. When it is assumed that $\psi_{g,j}(s_{k,\tau})$ is a linear function, it may be conveniently fixed as $\psi_{g,j=1}(0) = 0$. The lure type reference class has relative attractiveness = 1 at the first sampling in the trap session. If it assumed that $\psi_{g,j}(s_{k,\tau})$ is nonlinear, then it should be centered for the entire session counting ($\tau = 1,2,3,\ldots,T_g$) as it was for $f_g(\tau)$.

Parameter estimation

The aforementioned model structure is a type of generalized additive mixed model. To estimate the parameter with the *A. honmai* data, R v. 3.6.1 (R Core Team 2019) and the R package "mgcv" v. 1.8-33 (Wood 2020) were used. To determine whether the shapes of smoothing terms such as $f_g(\tau)$ and $\psi_{g,j}(s_{k,\tau})$ should be approximated as linear or nonlinear functions, the following 16 candidate models were constructed and their generalization performances were compared by cross-validation.

Models using pheromone traps with different lure ages

A family of candidate models was constructed based on Eq. 2. The temporal change in lure attractiveness was evaluated using pheromone traps exposed to the air for different lengths of time. The standard models in the family were named models "s1" (one smoothing term on male density fluctuation) and "s2" (two smoothing terms on male density and attenuation of lure attractiveness) expressed in R-style formula notations as follows:

```
s1 <- gam(N ~ Generation + s(Site, bs="re") + s(SessionDay,
by=Generation) + Company * Since.open, data=data,
family=Poisson(log))
```

```
s2 <- gam(N ~ Generation + s(Site, bs="re") + s(SessionDay,
by=Generation) + Company + s(Since.open, by=Company), data=data,
family=Poisson(log))
```

The variables τ and $s_{k,\tau}$ are stored in the dataset as "SessionDay" and "Since.open." The terms s(Session Day) and s(Since.open) correspond to the smoothing terms $f_g(\tau)$ and $\psi_{g,j}(s_{k,\tau})$, respectively. Moth generation and lure manufacturer are stored as the data variables "Generation" and "Company", respectively. The difference between models s1 and s2 is the use of spline in the $s_{k,\tau}$ effect where the term "Company * Since.open" in s1 corresponds to "Company + s(Since.open, by=Company)." The companies were included as $s_{k,\tau}$ covariates denoted with the "by" argument of

the gam function. As any smoothing term in mgcv is centered to be mean = 0, the s2 model requires the separate "Company" term.

The mgcv package is a tool of R that fits the generalized additive model (GAM). The package also has the gamm() function that fits the GAMM parameter and random intercepts may be implemented with s(Variable, bs="re") where bs is the spline basis. The package developer also recommends gam() (Wood 2020). The default setting for the smoother terms of gam() is s(bs="tp") fitted by the penalized thin-plate spline. Spline smoothness is automatically optimized by generalized cross-validation (gcv).

It is appropriate to express the random effect by s(Generation, Site, bs="re") rather than by "Generation + s(Site, bs="re")" if $\varepsilon_{g,i} \sim \mathrm{N}\left(0, \sigma_g^2\right)$ is strictly implemented in Eq. 1 calculating the inter-site differences in male density per generation. Here, however, generation was treated as a fixed effect and permitted intuitive interpretation of the coefficient of population density per generation.

Models using light trap data as male density calibrator

Another model family was constructed to evaluate lure attenuation after air exposure by using light trap data as the calibrator of the male density of the day. They are distinguished from their counterparts by the suffix "*.LT" (Table 2). The variants of the s1 and s2 models are named s1.LT and s2.LT, respectively, and have the following formulae:

```
s1.LT <- gam(N ~ Generation + s(Site, bs="re") + s(Ltlog,
by=Generation) + Company * Since.open, data=data,
family=Poisson(log))
```

```
s2.LT <- gam(N ~ Generation + s(Site, bs="re") + s(Ltlog,
by=Generation) + Company + s(Since.open, by=Company), data=data,
family=Poisson(log))
```

The variable "Ltlog" corresponds to $\ln\left(L_{g,\tau} + 0.5\right)$ in Eq. 3.

Cross-validation of candidate models

Along with the aforementioned basic models, 16 candidate models were constructed and cross-validated. The generalization performance of the model was defined as the prediction accuracy for the daily capture in an unknown trap site. The model parameters were fitted using count data from three out of four sites (A–D), in which the data for four insect generations were combined. The remaining unused site then served as the test data source. The prediction accuracy was calculated as the probability of observing $N_{g,i,j,k,\tau}$ under a predictor of size $\lambda_{g,i,j,k,\tau}$ in Eq. 4. A maximum of four test cases may be deployed. Hence, by excluding A, B, C, or D in turn, the sum of the negative log-likelihood (NLL) of the four leave-one-out cross-validations could be obtained. The model structure with the highest generalization performance i.e., minimizing NLL, was selected.

The structures of all 16 candidate models are listed in Table 2. Lacking the site effect term, the error structures used in the validation processes were not strictly mixed models. The final model

parameters were fitted using full data from all four sites. The original dataset and the R code are provided as Supplementary Materials S1 and S2, respectively.

In the model family combining various lure exposures, the variants "sz" and "glm" were created in addition to s1 and s2. In the former variants, temporal fluctuation in the moth population density was fitted by a linear term where "glm" is implemented as a linear model because it no longer contains any smoother. Furthermore, "s1.GT" and "s2.GT" were designated the variants of s1 and s2, respectively, and represented the rates across generations at which the lures were attenuated after air exposure.

Other candidate models were also created using the light trap data wherein the effect of number of days since lure exposure was assumed to be either nonlinear (s1.LT and s2.LT) or linear (sz.LT and glm.LT) (Table 2). The variants glob.s1.LT, glob.s2.LT, glob.sz.LT, and glob.glm.LT were also assigned. For these models, no inter-generational differences were assumed for the relationship between pheromone and light trap yield. These variants were implemented by excluding the "Generation" term that was originally included as the "Ltlog" covariate. For instance, "Generation + s(Ltlog, by=Generation)" became "s(Ltlog)." It might also be the case, however, only the "Generation" intercept was adopted and the shape of the smoother term $\psi_{g,j}(s_{k,\tau})$ was common to all generations. Therefore, "s1p.LT" and "szp.LT" were designated variants of "s1.LT" and "sz.LT", respectively.

4. Results

During the 2017–2018 trap sessions, the temperature was lower for the 0th (overwintering) *A. honmai* generation emerging in April than it was for the other moth generations that occurs in Shizuoka prefecture from late June to August (Table 1). Every generation was subjected to heavy rainfall (> 10 mm/day). The trap sessions covered nearly all 2nd and 3rd generation adult emergence periods in 2017. Trap settlement was delayed in the 1st generation of 2017 and the 0th generation of 2018 because pre-settlement lure exposure had to be planned retroactively based on long-term weather forecasts.

Using three pheromone traps, four sites, and 70 trap nights, we captured 8882, 9215, 17607, and 18728 *A. honmai* adults (median capture per trap per day = 4, 2, 7, and 8, respectively) in the 1st, 2nd, 3rd, and 0th generations, respectively (Figure 2). The "SE" lures captured 29931 adult males or 5218, 6520, 10347, and 7846 in the 1st, 2nd, 3rd, and 0th generations, respectively. The maximum and median captures per trap per day were 345 and 11, respectively. These rates were 1.8× and 3.8× larger than those obtained using the "SC" traps (16545 [2603, 1782, 4711, and 7449] individuals; daily maximum and median = 201 and 5, respectively) and "OT" traps (7956 [1061, 913, 2549, and 3433] individuals; daily maximum and median = 132 and 2, respectively).

Using the light trap, we captured 269, 1164, 6347, and 64 adult males (median capture per trap per day = 9, 35, 206, and 1, respectively) in the 1st, 2nd, 3rd, and 0th generations, respectively (Figure 2). Hence, the light trap captured more moths than the pheromone trap in the summertime but not during the earlier seasons for the 0th and 1st generations.

Cross validation of the candidate models

Leave-one-out cross validation of the four trap sites demonstrated that the strategy used to quantify pheromone lure attractiveness and with the most robust generalization performance on unknown sites was to combine lures with different opening timings and use them as an internal reference rather than an external calibrator such as a light trap. Among the 16 candidate models, "s1" had the highest generalization performance. Its sum NLL was 30794 and that for "s2" was 31333 (Table 2). The model family using light trap data as a population fluctuation predictor ("*.LT") performed poorly. The best model was s1.LT (NLL = 35143).

A comparison of s1 and s2 confirmed that linear regression is appropriate for lure degradation after air exposure while base population dynamics must be fitted with a nonlinear regression. For the best s1 model, temporal male population density fluctuation was smoothed by a spline whereas lure attractiveness was linearly attenuated on a log scale. For the second-best s2 model, pheromone attenuation was also approximated by spline regression. After we assumed linearity for the population density, the goodness-of-fit substantially declined (Table 2: s2 *versus* sz: ΔNLL = 8305; s1 *versus* glm: ΔNLL = 8812). There was no eminent effect of season on the rate of lure attractiveness attenuation after air exposure as the generalization performance of s1.GT and s2.GT slightly decreased relative to s1 and s2.

Models using pheromone traps with different lure ages

Based on the s1 and s2 structures, the final model parameters were fitted using data from all four sites (Table 3). The AIC of s1-based GAMM was 1113.2 greater than that of s2-based GAMM. The adjusted R^2 were 0.462 and 0.492 for s1 and s2, respectively. Thus, s2 fit slightly better than s1. However, the generalization performance was better for s1 (Figure 3B) than s2 (Figure 3C). Nonlinear regression of lure attenuation may have caused overfitting and background population fluctuation should be fitted nonlinearly (Figure 3A).

According to the s1 model, the initial lure attractiveness values and rates of temporal lure attenuation differed among lure types. The standard lure attractiveness for this model was defined as the expected capture rate using the "OT" lure immediately after opening. For the "SC" lure, the relative attractiveness was $e^{0.4367} = 154.8\%$ immediately after opening. For the "SE" lure, it was $e^{1.034} = 281.2\%$ (Table 3).

Attraction of all three lure types decreased with the number of days after opening (Figure 3B). The rate of attractiveness attenuation was the size of the "Since.open" effect term. It showed the largest decline in OT (−0.02814 ± 0.001048; estimated coefficient ± standard error). The estimates were −0.01315 and −0.01337, respectively, for the SC and SE lures. These values were calculated as the sums of Since.open and SC:Since.open or SE:Since.open. Hence, their interval estimates were not obtained. That is, the daily attractiveness decreased to 97.23% (OT), 98.69% (SC), and 98.67% (SE).

Although the s2 model may have been overfitting, the shape of attenuation after air exposure may differ among lure types. Attractiveness of the OT lures decreased linearly even by spline smoothing

(s2: Figure 3C). In contrast, attractiveness of the SC and SE lures remained at their initial levels for the first several weeks and rapidly decreased thereafter.

Models using light trap data as a male density calibrator

Although calibration using light trap data poorly fit pheromone trap capture on the same day, we analyzed to some extent the relationship between the yields for the two lure types. The relative attractiveness of the light trap was greater than that of the pheromone traps for the summertime but not in the springtime generations. The "s1.LT" followed by the "s2.LT" model showed the highest generalization performances (Table 4). The variants glob.s1.LT, glob.s2.LT, glob.sz.LT, and glob.glm.LT performed more poorly than s1.LT, s2.LT, sz.LT, and glm.LT—their counterparts with the assumption of heterogeneous effect of generation. Likewise, the s1p.LT and s2p.LT did not capture the data characteristics. These variants of s1.LT and s2.LT, respectively, lacked the generation-specific covariate of "Ltlog" (Table 2).

Taken together, no single regression curve (or line) can convert all light trap capture data to pheromone trap capture data or vice versa. Thus, the data must be individually converted for each generation using a nonlinear regression such as spline (Figure 4A; four regression curves corresponding to each generation). However, converting light trap data to pheromone data is not recommended as it creates a larger residual (Figure 4A) than calibration by pheromone traps with multiple lure ages (Figure 3A). The adjusted R^2 were 0.384 and 0.402 for s1.LT and s2.LT, respectively, and were ten points lower than those for s1 and s2.

The goodness-of-fit was substantially lower in the models using light trap data. However, the lure attenuation patterns estimated by s1.LT (Figure 4B) and s2.LT (Figure 4C) resembled those estimated by s1 (Figure 3B) and s2 (Figure 3C), respectively. Thus, our results for the pheromone attractiveness time courses seemed robust. If we adopted s1.LT as the final model, the initial attractiveness efficacies of the SC- and SE-type lures would be 153.6% and 279.7%, respectively, relative to OT. For the lure attenuation rate, the OT slope was −0.03304 ± 0.001053 (estimate ± SE), while the those for the SC and SE lures were −0.01768 and −0.01791, respectively. Hence, the daily attractiveness declined to 96.75% (OT), 98.25% (SC), and 98.22% (SE). These estimates were nearly the same as those for s1.

6. Discussion

Here, we quantified the temporal dynamics of tortrix moth pheromone lure attractiveness independently of fluctuations in insect population density. We combined lures with different opening (air exposure) timings as an internal reference. In the supported model, base dynamics were fitted with a nonlinear regression whereas linear regression was suitable to attenuate the lure ability after field settlement. The effects of season on lure attenuation rate were not supported.

Linearity of the s1 model means that the expected male moth capture decreases exponentially with lure age. If we allow the reduction in attractiveness to 90% of the initial value, the attenuation becomes non-negligible at 3.74, 8.12, and 7.88 days after settlement of the OT, SC, and SE lures,

respectively. Thus, the estimated male density is biased if we do not eliminate the lure attenuation effect.

This modeling approach enables us to utilize trap data for long periods as it calibrates heterogeneous trap records using various lure types and conditions. Pest insects are monitored over the long term to detect peak regional adult emergence timing or to evaluate local population abundance, including the detection of the species at regional scale. In either case, we start from obtaining some unbiased index of the regional male density at each time point.

Using our GAMM approach, an intuitive index of male density is the quantity equivalent to $\overline{d_g} + f_g(\tau)$ (mean generation density + temporal fluctuation), as shown in Figure 3A. In biological sense, this quantity is the expected daily number of males captured using a trap equipped with a brand-new OT lure (note that this value is not an absolute density such as individuals/m^2). If we adhere to the R mgcv package, we first calculate the predicted values for the terms of the s1 model via the "predict(gam_object, type='terms')" command; then the estimate is given as the sum of the effects "Intercept + Generation + s(SessionDay, by = Generation)" (also see ESM S2).

Lure attractiveness is determined by the evaporation of the pheromone components from the lure dispenser. A classical first-order model has been used to explain the measured exponential decrease in evaporation rate (McDonough and Butler 1983; McDonough et al. 1992; Heuskin et al. 2011). In a first-order relationship, the release rates are proportional to the volatile content in the dispenser. Both the volatile content and the evaporation rates linearly decrease on a logarithmic scale. For tea tortricid moths, Tamaki and Noguchi (1983) used this assumption to estimate the rates of decline in the pheromone components for *A. honmai* and its co-occurring species *Homona magnanima* Diakonoff (Tortricidae). They prepared synthetic pheromone by mixing Z9-14Ac, Z11-14Ac, E11-14Ac, and 10-Me-12Ac at 70:30:10:200. This formulation resembled that of the OT lure. In the dispenser, its half-lives were ~10 and ~30 days when the volatiles were loaded onto a plastic cap or a rubber septum, respectively.

Tamaki and Noguchi (1983) also found that the half-life of the E11-14Ac content was nearly twice that of the major two components, Z9-14Ac and Z11-14Ac, whereas the half-life of 10-Me-12Ac was half that of the two especially when they were loaded on a rubber septum. However, the authors argued that the heterogeneous pheromone evaporation rates did not markedly affect lure attractiveness stability. The minor components had wider ranges at the optimal mixing ratios than the major two. Pheromonal activity persisted in *H. magnanima* as long as Z9-14Ac:Z11-14Ac was kept 3:1 (Noguchi et al. 1981). According to Tamaki and Noguchi (1983), the four components were kept for 30 days and 60 days within the optimal mixing ratio for *A. honmai* males on a plastic cap or a rubber septa, respectively. They concluded that the exhaust of the volatiles, rather than the deviation from the optimal mixing ratio, were responsible for the persistence.

Regarding OT lure trap data, attractiveness could be calibrated based on s1 as this pheromone lure decreases rapidly but shows strong linearity. In contrast, according to s2, the attractiveness of the SC and SE lures sightly decreased initially but rapidly declined thereafter (Figure 3C). Therefore, uncalibrated capture data could be used for SC and SE. In this case, we can truncate data

gathered > 1 month after the pheromone lure settlement dates just as survey guidelines have recommended (Tatara and Kodomari 2000).

The first-order assumption clearly explains the relationship between exposure time and pheromone evaporation rate (≈ dose). However, another assumption is required to explain our result that the *A. honmai* male captures decreased exponentially after unsealing the lures, especially the OT lures. Although there has been a long-standing debate how should we model the diffusion of pheromone plume in the ambient, studies have assumed the area of the attraction range (∝ expected capture if the males distribute uniformly) increases linearly first with the pheromone dose (Wall and Perry 1987; Turchin and Odendaal 1996; Branco et al. 2006). However, there seems a saturation at higher dose range; the cause has been considered the limit in the flyable distance of the male insects (Wall and Perry 1987; Östrand and Anderbrant 2003). Regarding *A. honmai*, table 7 of Tamaki et al. (1980) shows that male *A. honmai* capture is initially linearly correlated with synthetic pheromone dose (at a 63:31:4:200 mixing ratio) approximately on a log-log scale. Thence, capture reaches a plateau as the initial load increases beyond 10 mg/dispenser.

These properties of *A. honmai* pheromone could explain why the attenuation of SC/SE lure attractiveness was relatively slow and nonlinear. The threshold level reported by Tamaki et al. (1980) approached the initial loads of 9.1 for OT and 10 for SC. Therefore, the commercial lure yields may also fluctuate around the threshold immediately after lure settlement. Thereafter, the expected capture started to decline exponentially. For OT, the dispenser substrate was a plastic capsule whereas it was a rubber septum for SC and SE. The former provided a pheromone dose half-life that was threefold longer than those of the latter. Overall, the pheromone charge in the OT lure underwent exponential decrease very soon after opening whereas the SC and SE dose levels remained on a plateau for the first month after opening.

A few earlier studies used nonlinear regression methods including GAM to separate the trend in background insect population density from long-term insect population monitoring data (Benton et al. 2002; Klapwijk et al. 2013; Yamamura 2016). An advantage of GAM(M) is that its terms are biologically interpretable. In s1, $d_{g,i,\tau}$ corresponds to the fluctuation in regional male density while $\psi_{g,j}(s)$ corresponds to the time course of pheromone lure attractiveness. The estimated effect values (especially $d_{g,i,\tau}$) may then be used in subsequent ecological investigations as population density indices.

Caution is needed when interpreting the estimated parameter values using datasets for multiple trap sessions with different time periods. For s1, the intercept was ~408.3 (Table 3), which was not a plausible density range of insects. The mgcv::gam() function tried to centralize the smoother term 's(SessionDay)' for the entire [1, 21] domain over all four generations. Nevertheless, the actual data only covered [1, 14] for the 1st and 0th generations (Figure 3A) and extrapolation occurred.

Extrapolation may be avoided by running the models with probabilistic programming languages such as JAGS or Stan. However, the GAM(M) approach is reproducible and feasible for agricultural scientists and policymakers. In this case, the intercept shift was compensated by the terms Generation and s(SessionDay). We can nonetheless predict regional male density in GAMM using the sum of "intercept + Generation + s(SessionDay)." As it is expressed as the sum of multiple

terms, we may be unable to obtain interval estimates such as prediction intervals for male density. Though this problem persists with GAM(M), we may obtain interval estimates by sampling from posterior distributions when we use Monte Carlo methods.

Our model structure comparison demonstrated no universal correlation between pheromone and light trap records for the same day. The light trap was relatively more efficient in the summertime (generations with high population densities) but not during earlier seasons. Similar trends were reported for other lepidopteran (Campbell et al. 1992; Tanaka et al. 1995; Delisle et al. 1998) and hemipteran (Nakamura and Nishino 1999) pest species. The mechanism might entail interference between pheromone lure attractiveness and female moths and decrease lure attractiveness at higher densities. However, this theory has not yet been fully corroborated by field experiments (Campbell et al. 1992; Laurent and Frérot 2007).

As there is only a weak correlation between the light trap and pheromone trap capture records (Figure 4A), straightforward data conversion between them is improbable. As relative density estimates are saturated by method-specific constraints, we require an absolute density measurement to integrate heterogeneous monitoring data and investigate the dynamics of long-term population fluctuations. Absolute density estimation with pheromone traps has been conducted via marked insect release-recapture (Turchin and Odendaal 1996; Östrand and Anderbrant 2003; Arakaki et al. 2008; Adams et al. 2017). Going forward, our model structure will be updated to enable inference on the absolute density. Such an update includes a more full-fledged state-space model framework because the research design of release-recapture requires the implementation of intrinsic population dynamics such as adult emergence, survival, and possibly the frequency and distance of flight as well as the mating motivation, which may also vary during the lifespan of adult males.

Data availability

The data source used in this study is archived on figshare.com/****.

Author contribution

SY designed the field experiments and collected the pheromone trap data. SY and YH collected the light trap data. SM created the statistical framework and wrote the first draft. All authors wrote the final manuscript.

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Table and figure captions

Table 1. Weather conditions during the trap sessions were obtained from meteorological data generated by the Kanaya Tea Research Station. There were no observations between July 31, 2017 and August 6, 2018. Hence, data for the 2nd session covers August 7, 2017 to August 21, 2017.

Generation	1st	2nd	3rd	0th
Trap start (SessionDay = 0)	2017-06-26	2017-07-31	2017-09-11	2018-04-28
Trap end	2017-07-10	2017-08-21	2017-10-02	2018-05-12
Mean temperature (°C)	23.7	25.3	21.3	16.1
Min temperature (°C)	18.3	21.9	14.4	7.6
Max temperature (°C)	33.3	35.1	29.9	25.5
Precipitation (total) (mm)	39.5	78.0	123.5	270.5
Precipitation (daily max) (mm)	26.5	37.0	83.0	82.5
Mean wind velocity (m/s)	2.9	2.6	3.0	3.4
Max wind velocity (m/s)	8.2	6.6	8.6	10.3
Mean daylight hours (hour)	4.6	3.3	3.9	7.3
Mean daily irradiation (MJ/m^2)	13.1	10.4	10.6	14.8

Table 2. Cross validation of candidate models. Each model was fitted using a dataset for three of four sites such as A, B, and C. Prediction was then made for the excluded site such as D. This procedure were repeated for all four sites. Goodness-of-fit was the sum of the negative log likelihood (NLL) where the probability for each data point was defined as dpois(x=(observed number of males), lambda=(model prediction)). The models "s1.GT" and "s2.GT" are variants of s1 and s2, respectively, and assume dependence of the lure attenuation rate on moth generation.

Model	formula	N.L.L.
s1	`gam(N ~ Generation + s(SessionDay, by=Generation) + Company * Since.open)`	30794
s2	`gam(N ~ Generation + s(SessionDay, by=Generation) + Company + s(Since.open, by=Company))`	31333
(s1.GT)	`gam(N ~ Generation * Since.open + s(SessionDay, by=Generation) + Company * Since.open)`	30846
(s2.GT)	`gam(N ~ Generation * Since.open + s(SessionDay, by=Generation) + Company + s(Since.open, by=Company))`	31405
sz	`gam(N ~ SessionDay * Generation + Company + s(Since.open, by=Company))`	39638
glm	`glm(N ~ SessionDay * Generation + Company * Since.open)`	39606
s1.LT	`gam(N ~ Generation + s(Ltlog, by=Generation) + Company * Since.open)`	35143
s1p.LT	`gam(N ~ Generation + s(Ltlog) + Company * Since.open)`	39410
s2.LT	`gam(N ~ Generation + s(Ltlog, by=Generation) + Company + s(Since.open, by=Company))`	35859
sz.LT	`gam(N ~ Ltlog * Generation + Company + s(Since.open, by=Company))`	41017
szp.LT	`gam(N ~ Ltlog + Generation + Company + s(Since.open, by=Company))`	42532
glm.LT	`glm(N ~ Ltlog * Generation + Company * Since.open)`	40269
glob.s1.LT	`gam(N ~ s(Ltlog) + Company * Since.open)`	45310
glob.s2.LT	`gam(N ~ s(Ltlog) + Company + s(Since.open, by=Company))`	46004
glob.sz.LT	`gam(N ~ Ltlog + Company+ s(Since.open, by=Company))`	49250
glob.glm.LT	`glm(N ~ Ltlog + Company * Since.open)`	48648

Table 3. Summary table for GAMM (s1) assuming that lure attractiveness linearly decreases after air exposure ("Since.open"). The reference levels for the parametric coefficients are "OT" and "0" for lure type ("Company") and discrete moth generation per year ("Generation"), respectively. Smooth terms show daily fluctuations ("SessionDay") in population abundance during sampling of each generation.

Model variation	s1 (linear attenuation)	s2 (nonlinear attenuation)
Parametric coefficients	Estimate (SE)	
Intercept	408.3 (18.25)	406.2 (18.19)
Generation = 1	−155.8 (30.96)	−154.2 (30.93)
Generation = 2	–406.8 (18.25)	–405.4 (18.19)
Generation = 3	–406.2 (18.25)	–404.7 (18.19)
Company = SC	0.4367 (0.02771)	0.7676 (0.01498)
Company = SE	1.034 (0.02544)	1.367 (0.01385)
Since.open	−0.02814 (0.001048)	–
SC: Since.open	0.01499 (0.001243)	–
SE: Since.open	0.01477 (0.001152)	–
Smooth terms	edf (Chisq)	
s(Site)	2.995 (4284)	2.996 (4285.9)
s(SessionDay): Generation0	8.994 (9085)	8.988 (9457.6)
s(SessionDay): Generation1	8.986 (4687)	8.986 (4898.8)
s(SessionDay): Generation2	8.932 (4527)	8.934 (4295.9)
s(SessionDay): Generation3	8.988 (5415)	8.989 (5013.7)
s(Since.open): CompanyOT	–	8.346 (713.9)
s(Since.open): CompanySC	–	7.928 (512.4)
s(Since.open): CompanySE	–	8.800 (1386.9)
Deviance explained	63.3%	64.5%
AIC	49666.11	48552.94

Table 4. Summary table for model structure using light trap data as proxy for daily male population. The models s1.LT and s2.LT are counterparts of s1 and s2, respectively. Ltlog is the natural logarithm of the "capture with the light trap of the day + 0.5."

Model variation	s1.LT (linear attenuation)	s2.LT (nonlinear attenuation)
Parametric coefficients	Estimate (SE)	
Intercept	293.6 (158.4)	299.9 (416.6)
Generation = 1	523.6 (270.9)	543.3 (470.3)
Generation = 2	–65.53 (158.7)	–75.07 (416.7)
Generation = 3	3953 (313.6)	3801 (496.7)
Company = SC	0.4295 (0.02797)	0.7684 (0.01497)
Company = SE	1.027 (0.02569)	1.368 (0.01383)
Since.open	−0.03304 (0.001053)	–
SC: Since.open	0.01536 (0.001259)	–
SE: Since.open	0.01513 (0.001167)	–
Smooth terms	edf (Chisq)	
s(Site)	2.995 (4285)	2.998 (4288.1)
s(Ltlog): Generation0	5.997 (3307)	6.000 (3684.5)
s(Ltlog): Generation1	8.964 (3998)	8.951 (3962.5)
s(Ltlog): Generation2	8.995 (4484)	8.997 (4343.5)
s(Ltlog): Generation3	8.995 (6253)	8.994 (5890.7)
s(Since.open): CompanyOT	–	7.929 (1064.8)
s(Since.open): CompanySC	–	8.563 (780.4)
s(Since.open): CompanySE	–	8.918 (1595.6)
Deviance explained	54.2%	55.1%
AIC	58594.59	57698.81

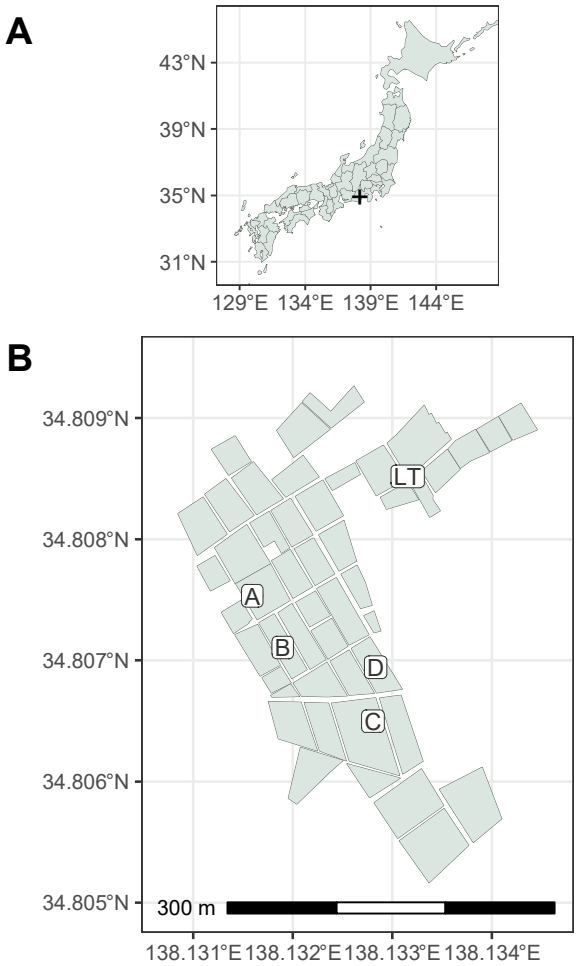

Figure 1. Research field map. Sites "A"–"D" in panel B show fields in Kanaya Tea Research Station wherein pheromone traps were settled. Each polygon signifies a tea field. "LT" is the permanent light trap site. Detailed spatial treatment arrangements in tea fields are shown in Supplementary Figure S1.

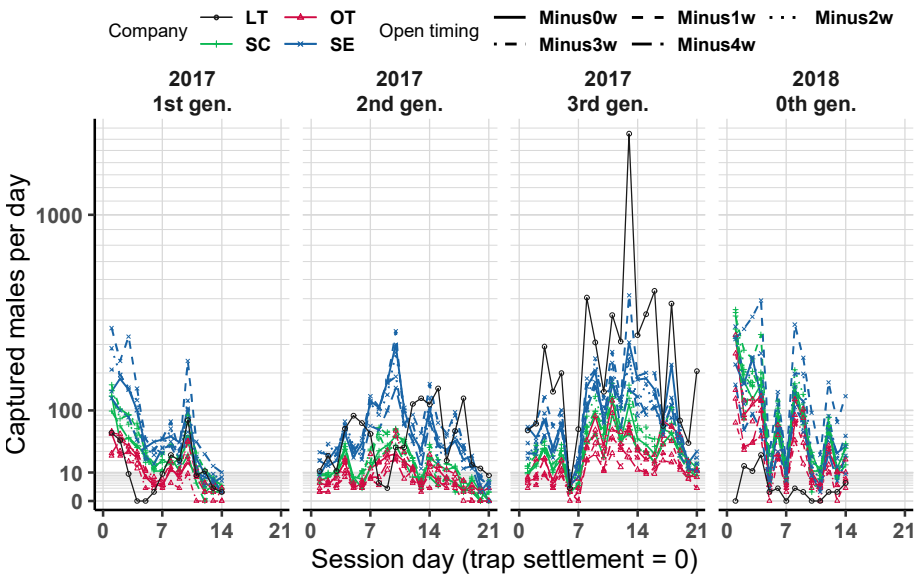

Figure 2. Raw capture during trap sessions. Numbers of captured males from four pheromone-trap sites are pooled.

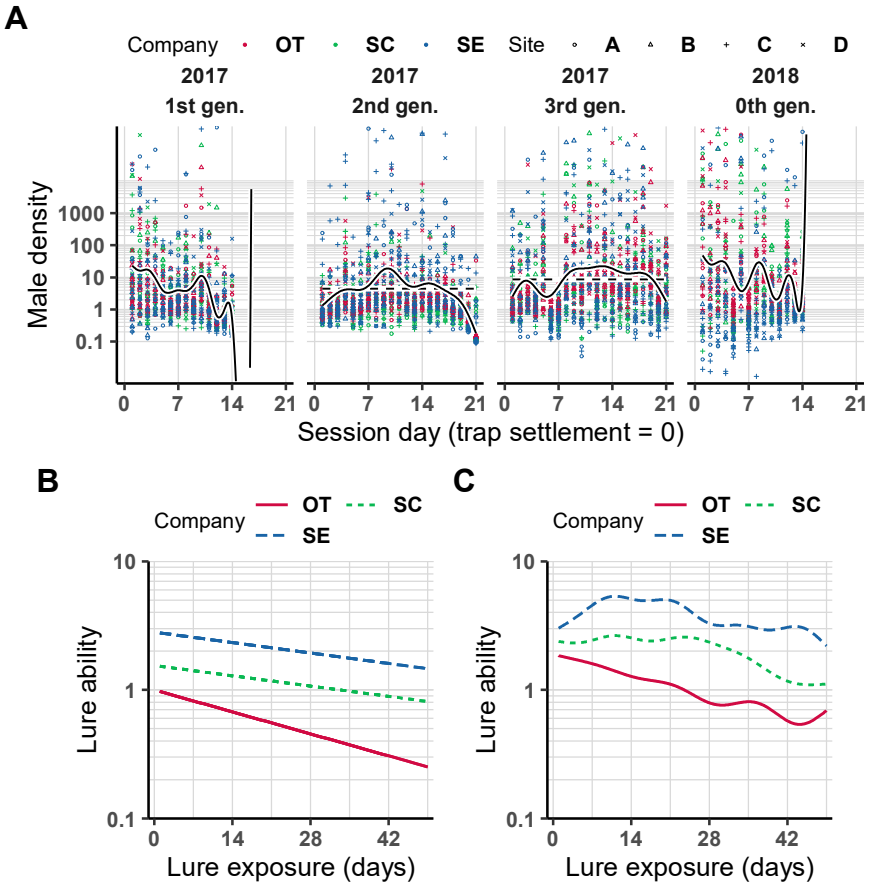

Figure 3. Graphical summary of GAMM s1 assuming exponential decrease in pheromone lure attractiveness and s2 assuming nonlinear decrease in pheromone lure attractiveness. A) Regional male density fluctuation estimated as sum of effect terms "intercept + Generation + s(SessionDay)." Points signify partial independence defined as "(working residual of the model) + (estimated size of the effect)" for each data point. Result for s1 is plotted here. However, s2 showed nearly the same result. Horizontal broken lines indicate size of "intercept" alone but are not shown within y-axis range for Generations 1 and 0. B) Fluctuations in attractiveness of three lure products predicted from s1 and corresponding to effect terms "intercept + Company*Since.open." C) Lure attractiveness predicted from s2 corresponding to "intercept + Company + s(Since.open, by=Company)."

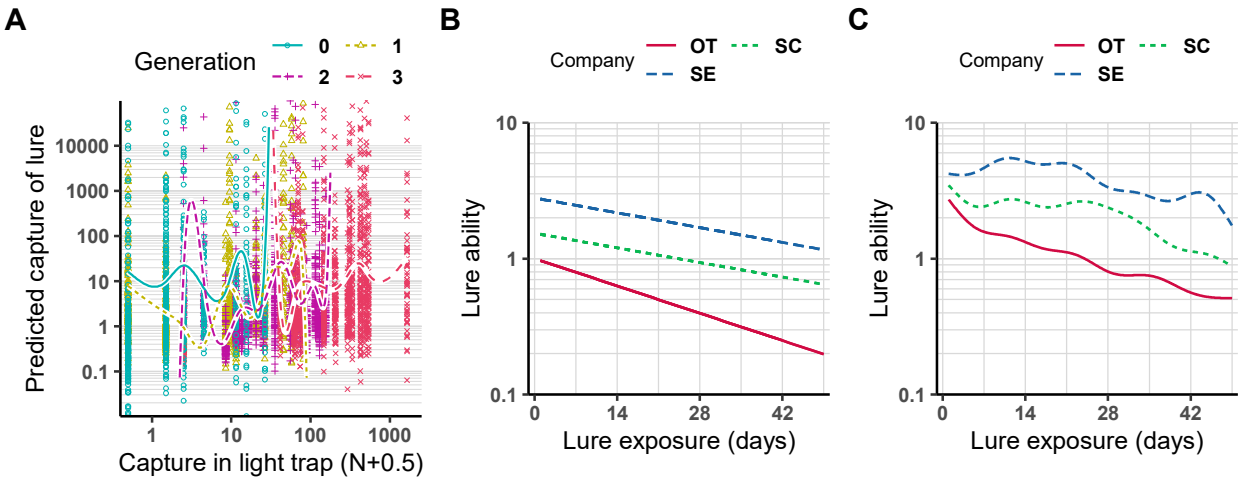

Figure 4. Graphical summary of GAMM structures using light trap data. A) Performance of light trap data (Ltlog: x-axis) as predictor of capture with pheromone lure on same day (y-axis). Regression curves are defined as sum of effect terms "intercept + s(Generation) + s(Ltlog)." Points signify partial independence. Though plots only show result of s1.LT assuming exponential decrease in pheromone lure attractiveness, s2.LT assuming nonlinear decrease in pheromone lure attractiveness had nearly same result. B) Fluctuations in attractiveness of three lure products predicted from s1.LT and C) s2.LT. Both are defined in same way as s1 and s2.

Supplementary Materials S1

Dataset: captured males

Supplementary Materials S2

R source code

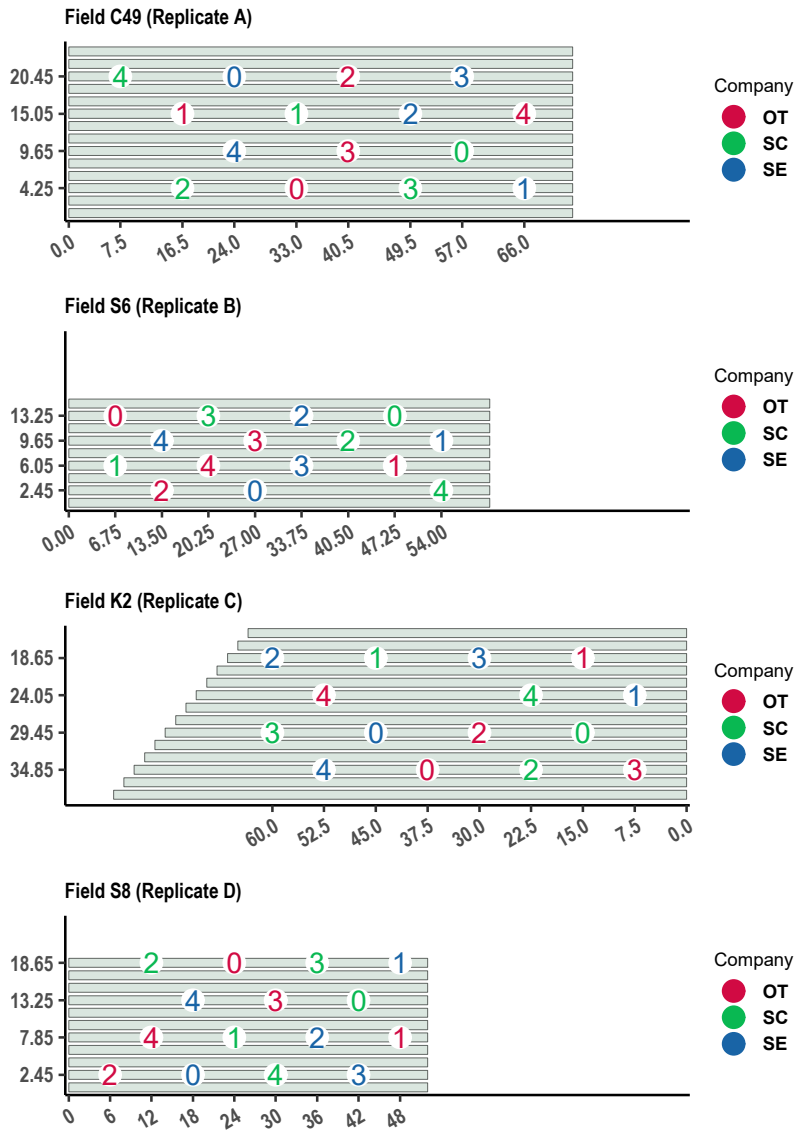

Figure S1. Location of traps in each tea field shown in Figure 1. Right direction points north. Scale represents distance from ends of tea hedges. Each is 1.3 m wide and furrow is 50 cm wide. Numbers on plot signify lengths of pre-settlement lure exposure periods (weeks).