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Generation Separation in Simple Structured Life Cycles: Models and 48 Years of Field Data on a Tea Tortrix Moth

Takehiko Yamanaka,^{1,*} William A. Nelson,² Koichiro Uchimura,³ and Ottar N. Bjørnstad⁴

1. Biodiversity Division, National Institute for Agro-Environmental Sciences, 3-1-3 Kannondai, Tsukuba, Ibaraki 305-8604, Japan; 2. Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada; 3. Kagoshima Tea Experiment Station, 3964 Nagasato Chiran-cho, Minami-Kyushu city, Kagoshima, 897-0303, Japan; 4. Departments of Entomology and Biology, 501 Agricultural Sciences and Industries Building, Pennsylvania State University, University Park, Pennsylvania 16802

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ABSTRACT: Population cycles have fascinated ecologists since the early nineteenth century, and the dynamics of insect populations have been central to understanding the intrinsic and extrinsic biological processes responsible for these cycles. We analyzed an extraordinary long-term data set (every 5 days for 48 years) of a tea tortrix moth (*Adoxophyes honmai*) that exhibits two dominant cycles: an annual cycle with a conspicuous pattern of four or five single-generation cycles superimposed on it. General theory offers several candidate mechanisms for generation cycles. To evaluate these, we construct and parameterize a series of temperature-dependent, stage-structured models that include intraspecific competition, parasitism, mate-finding Allee effects, and adult senescence, all in the context of a seasonal environment. By comparing the observed dynamics with predictions from the models, we find that even weak larval competition in the presence of seasonal temperature forcing predicts the two cycles accurately. None of the other mechanisms predicts the dynamics. Detailed dissection of the results shows that a short reproductive life span and differential winter mortality among stages are the additional life-cycle characteristics that permit the sustained cycles. Our general modeling approach is applicable to a wide range of organisms with temperature-dependent life histories and is likely to prove particularly useful in temperate systems where insect pest outbreaks are both density and temperature dependent.

Keywords: *Adoxophyes honmai*, delay differential equations, wavelet and periodogram analysis, generation separation, stage-structured models, Allee effects.

Introduction

Population cycles have fascinated ecologists since the early nineteenth century (Elton 1924), and dynamics of insect populations have been central to understanding the intrinsic and extrinsic biological processes responsible for these cycles (e.g., Andrewartha and Birch 1954; Nicholson

1954a). Various laboratory systems have been used to study the underlying mechanics of population cycles: famously, the single-generation cycles in the Indian meal moth (Gurney et al. 1983), the overcompensation (two-generation) cycles of Nicholson's blowflies (Nicholson 1954b; Gurney et al. 1980), and the cyclic and chaotic fluctuations in flour beetles (e.g., Costantino et al. 1997) and bruchid beetles (Shimada and Tuda 1996). Wild insects also provide prominent examples of cyclic dynamics, particularly among univoltine (single generation per year) foliage feeders such as the larch budmoth (Baltensweiler 1993), the spruce budworm (Royama et al. 2005), and the pine looper (Kendall et al. 2005). Interestingly, many of the classic cycles observed in natural populations are generated by interspecific interactions (e.g., consumer-resource interactions) rather than by the within- and among-stage intraspecific interactions found in many laboratory populations (Berryman 2002). One consequence is that the population cycles in natural systems tend to have a longer period (relative to their maturation time) than the cycles observed in the lab, as predicted by theory (Murdoch et al. 2002).

In this article, we analyze a long-term data set on intra-annual population cycles of a multivoltine (multiple generations per year) tortrix tea pest (*Adoxophyes honmai*) in the wild. The adults are small moths (15–22-mm wingspan) that commonly infest tea plantations from central to southern Japan. The larvae feed on tea leaves and make nests, webbing one or several young leaves together, which results in reduced productivity and commercial value (Tamaki 1991). The data are counts of adult moths at the Kagoshima Tea Experiment Station every 5 days for 48 years, and they show strong high-frequency cycles with a period close to the generation time (four or five cycles each year) superimposed on a slower annual cycle (fig. 1). We find these cycles particularly intriguing for two reasons. First, while single-generation cycles are common in ex-

* Corresponding author; e-mail: apple@affrc.go.jp.

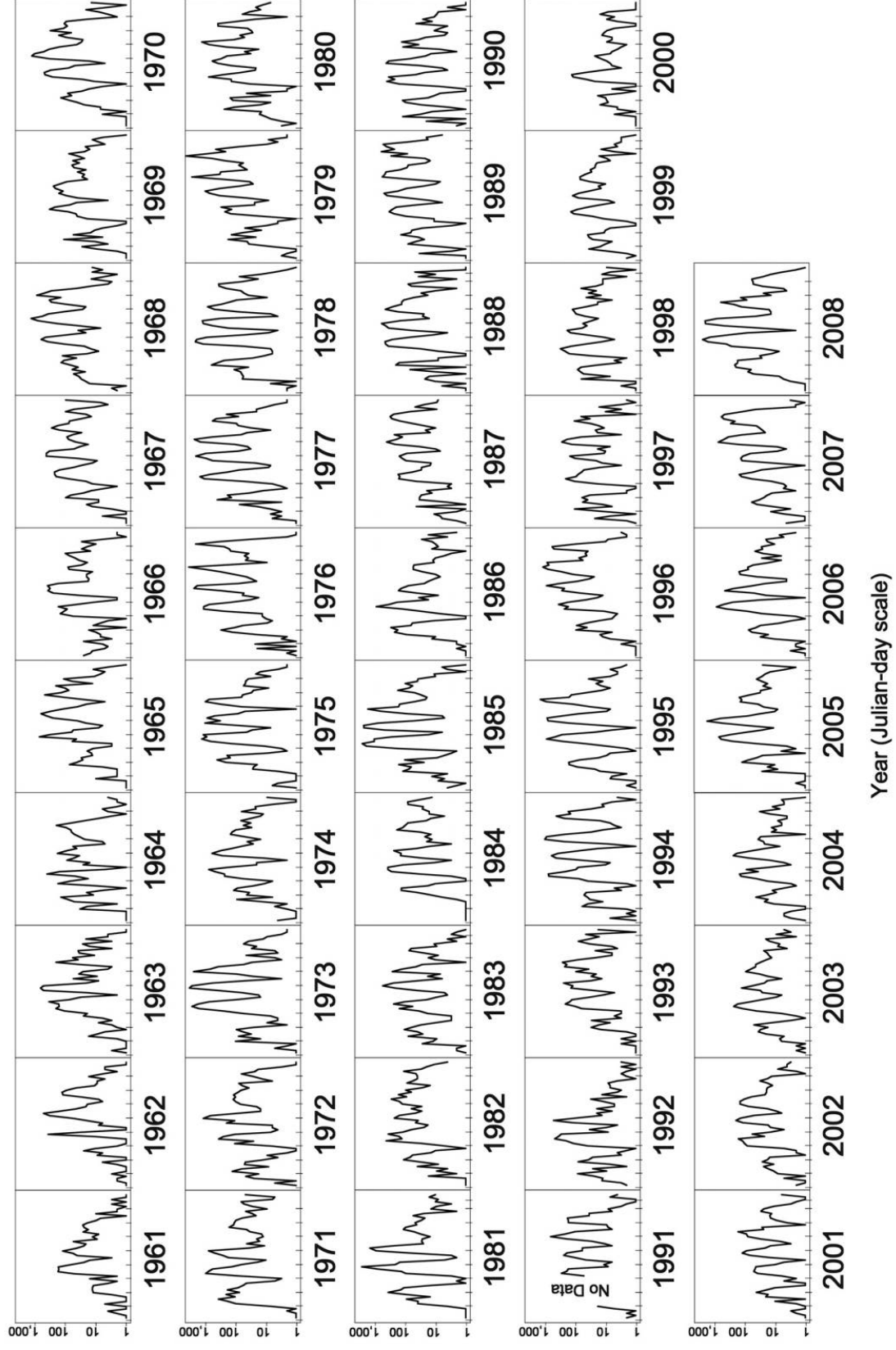


Figure 1: Light-trap census of adult tortrix moths (*Adoxophyes hommai*) over 48 years (from March 1 to November 30). Counts are log transformed, and the X-axis is measured in Julian days.

perimental populations in controlled laboratory environments (Utida 1967; Bellows 1982; Gurney et al. 1983; Bjørnstad et al. 1998), they have been less studied in wild populations (but see Godfray and Hassell 1987, 1989 and Nakamura et al. 2004 for some examples). Second, there is no apparent smearing of the generation cycles, even toward the end of each year. Intuitively, one might expect that environmental variability leading to variation in developmental period would lead to loss of generation separation toward the end of each year.

Considering previous theoretical and experimental works, generation separation and single-generation cycles in the tea tortrix may potentially be a consequence of several different ecological processes (reviewed in Knell 1998). There are two notable examples: asymmetrical competition among stages (Gurney et al. 1983; Gurney and Nisbet 1985; Nisbet and Onyiah 1994; Briggs et al. 2000; Nakamura et al. 2004) and host-parasitoid interactions with short parasitoid generation times (Godfray and Hassell 1987, 1989). Seasonality may also promote single-generation cycles if life stages tolerate changes in the environment differentially. For example, theoretical models predict generation synchronization if there is an unsuitable season in which only one particular life stage can survive (Gurney et al. 1994; Powell and Logan 2005). For temperate pest insects, this may also lead to predictable outbreaks whose timing depends only on the temperature or, in particular, on the accumulation of degree days (e.g., Morris and Bennett 1967; Kikukawa and Chippendale 1984; Porter 1995). However, in species with many generations per year, one would intuit that microgeographic variation in temperature should erode the generation separation as the season progresses.

In this study, we use the long-term tortrix data set to investigate the relative importance of regular disturbance from seasonal temperature changes (favored by the empirical entomological literature) and intra- or interspecific density-dependent interactions (favored by the theoretical literature) in generating intra-annual single-generation cycles and sustaining generation separation. We follow the now more-or-less standard protocol, in the study of population cycles, of combining mechanistic mathematical models with detailed time-series analysis (e.g., Ellner et al. 1998; Kendall et al. 1999; Bjørnstad and Grenfell 2001). We apply wavelet analysis to the time series to dissect the pattern of periodicity in the data. We then construct a stage-structured population model of a set of delay-differential equations to investigate the genesis of the single-generation cycles (Gurney et al. 1980, 1983; Nisbet and Gurney 1983) on the basis of temperature-dependent growth, birth, and death rates from laboratory life-cycle experiments. One challenge with this class of models is that simulating dynamics under fluctuating seasonal tem-

peratures means that development rates will vary through time, which introduces time dependence in the delays. To circumvent this challenge, we use a rescaling-of-time method (McCauley et al. 2008) to transform the time-dependent delay model into a fixed-delay model on a physiological timescale, which allows us to use standard methods to study stability and cyclicity.

Methods

Data

The number of adult smaller tea tortrix *Adoxophyes honmai* Yasuda (Lepidoptera: Tortricidae) caught by a light trap (equipped with a 20-W fluorescent lamp and a 1-m-diameter water pan) was counted every five or six days for 48 years from 1961 to 2008. This monitoring program is carried out by prefectural researchers to guide pesticide application on commercial farms. Sampling covered the full flight season of the moth, from March 1 to November 30 each year (fig. 1). The trap is located in a tea orchard of the Kagoshima Tea Experiment Station, Japan (Chiran township, 31°22'N, 130°26'E). The main tea cultivar planted there is Yabukita (*Camellia sinensis* L. var. Yabukita), although there are several other varieties present. Scheduled pest control was routinely conducted with generic organophosphorus insecticides such as fenitrothion (MEP; Sumitomo Chemical, Tokyo) since the 1960s or granulovirus application since the early 1990s (Nakai 2009). The daily mean temperature used in our study was recorded at the Kagoshima Tea Experiment Station.

Study System

Adoxophyes honmai is a leafroller and is one of the major tea pests in Japan. The species produces four to five generations per year. Although there are no reports of an obligatory diapause in winter, stages other than larval are rarely seen during the coldest months (Tamaki 1991). Egg, pupal, and adult stages suffer high mortality in this period. There are generally five or six larval instars. In our study, we aggregated these into two stages (young larvae and old larvae) when investigating asymmetric competition. Larvae inhabit and pupate in nest webs made of one or several young leaves spun together. Adult moths can live more than 2 weeks, but females ordinarily mate and oviposit only during the first half of their adult lives (Nabeta et al. 2005; see also app. A, available online). Mating behavior is typically observed at night. Male moths find their mates by using female-emitted sex pheromones as a sexual communication cue (Tamaki 1991). As with most insects, both developmental rates and vital rates are highly temperature dependent (app. A).

More than 20 parasitoids are reported to forage on eggs and larvae of *A. honmai*. *Ascogaster reticulata* (Braconidae) and *Apanteles adoxophyesi* (Braconidae) are the most two abundant wasps throughout Japan (Takagi 1974; Yukinari 1976; Nakai 2009). Roughly speaking, these wasps have life cycles of the same duration as that of the host (Takagi 1974; Yukinari 1976). For example, the females of *A. reticulata* oviposit on the egg mass of *A. honmai*, and only a single adult parasitoid emerges from each parasitized larva. The fully developed parasitoid larva emerges from the host to pupate outside the host (Kainoh and Tamaki 1982). Parasitized host larvae continue to feed on tea leaves (Nakai 2009), and wasp emergence is synchronous with host pupation, so we may assume that parasitized eggs and larvae have the same mortality rates as unparasitized hosts.

Statistical Analysis

We convert the data from a Julian-day timescale to a temperature-based physiological scale because the developmental rate of insects depends on temperature. A common approach in entomology is to scale development rate by cumulative degree-days so as to better predict the timing of pest outbreaks (e.g., Baskerville and Emin 1969; Yamanaka et al. 2008). Cumulative degree-days are often calculated by summing the daily temperature for days when the temperature is above the minimum required for development (Roltsch et al. 1999), which implies that development rate (1) is a linear function of temperature and (2) falls abruptly to 0 at a critical threshold. While cumulative degree-days represent a step toward scaling time to a more appropriate development-rate scale based on temperature, this measure does not fully incorporate the observed response of insect development to temperature. Here we use a transformation that explicitly includes the influence of temperature on development rates in *A. honmai*.

Temperature at time t ($D(t)$) is converted to the physiological scale of the insect with the following empirically motivated logistic development-rate function:

$$h_i(t) = \frac{\alpha_i}{1 + \exp(-\gamma_D(D(t) - h_D))}, \quad (1)$$

where h_D is the temperature at which the development-rate function reaches half the asymptotic value, α_i is a scaling coefficient specific to each stage (egg, larva, pupa, adult), and γ_D controls the steepness of the function (see app. A for full details). The development rate $h_i(t)$ indicates how fast individuals move through the i th stage. While alternative functions (e.g., exponential or quadratic) provide a similar fit to the data, we chose the logistic function because it approaches a finite level at high temperatures

and approaches 0 smoothly at low temperatures. The new physiological timescale $\phi(t)$ (hereafter referred to as the “phi scale”) is calculated by integrating the stage-independent (i.e., excluding α_i in eq. [1]) base function,

$$g(t) = \frac{1}{1 + \exp(-\gamma_D(D(t) - h_D))}, \quad (2)$$

according to

$$\phi(t) = \int_0^t g(x) dx. \quad (3)$$

The base function $g(t)$ has no direct biological interpretation but can be used to rescale Julian days into a developmental scale for all stages. Moreover, there is a direct connection between the rescaling used in the data analysis and the rescaling used in the model. Specifically, when $\phi(t_1) - \phi(t_2) = 1/\alpha_i$, then a cohort entering stage i at time t_1 will have completed the development through this stage at time t_2 (see apps. A, B for full details). It should be noted that we have only mean daily temperatures at the study site. Therefore, estimates of $\phi(t)$ from the field were calculated using the mean daily temperature.

The raw time series of moth abundance suggests that the tea pest populations cycle at more than one frequency. To decompose the frequency-specific dynamics and how they may change through time, we use wavelet analysis (Carmona et al. 1998; Torrence and Compo 1998; Grenfell et al. 2001; Keitt and Urban 2005). Specifically, we use the Morlet wavelet transformation, which is a complex exponential function with amplitude that is localized by a Gaussian window. The wavelet analysis was performed with the *Rwave* library in the R statistical environment (R Development Core Team 2009). Although insect abundance was estimated regularly on the Julian-day scale, transformation to the physiological scale results in temporally uneven data that cannot be used directly for wavelet analyses. To conduct the wavelet analysis, we therefore smoothed the abundance data on the phi scale and resampled it every $\phi = 1.62$ units, which corresponds to about 100 data points per year. Smoothing was conducted with a flexible cubic smoothing spline ($df = 60$) in the *mgcv* library of R. The global periodogram is shown as the wavelet averaged across time. We used a randomization test on the global periodogram to generate a 99% null envelope, under the assumption that the patterns in the time series represent random noise. Peaks in the observed periodogram that extend outside of this envelope represent statistically nonrandom patterns at the 1% level. We used 1,000 permutations for the randomization test.

Model Development

We consider six plausible ecological mechanisms to explain the strong generation cycle observed in the tortrix moth: (1) density dependence through symmetric intraspecific larval competition, (2) density dependence through asymmetric intraspecific larval competition, (3) adult senescence, (4) an Allee effect due to mate-finding limitation, (5) interaction with a parasitoid wasp, and (6) strong winter mortality on egg, pupal, and adult stages. As we expand on below, temperature influences all aspects of moth life history. The first five mechanisms are ecologically based and assume that all stages respond synchronously to natural variation in temperature. The last mechanism, winter mortality, introduces a more realistic temperature effect on mortality that is not synchronous across stages. Here we outline the general model (see app. B for full model development) and a series of model variants that incorporate different combinations of these six mechanisms (summarized here and fully developed in app. C, available online for a total of 12 models).

The general model is motivated by the tortrix moth life cycle, which has five morphologically distinct stages: eggs ($E(t)$), young larvae ($L_1(t)$), old larvae ($L_2(t)$), pupae ($P(t)$), and adults ($A(t)$). Since cohorts of individuals develop through the stages synchronously, the most appropriate modeling framework is delay-differential equations, which is similar in structure to many previous models of insect population dynamics (Gurney et al. 1983; Nisbet and Gurney 1983; Gurney and Nisbet 1985; Nisbet 1996). While there is some variation among individuals in development time in real populations, our conclusions are robust to the assumption of a fixed stage duration rather than exponentially or gamma-distributed stage durations (see app. D, available online).

Parasitism is modeled on the basis of the life cycle of the dominant parasitoid wasp of tortrix moths, *A. reticulata*. The number of parasitized moth larvae, young and old, and the number of adult wasps are denoted by $L_1^W(t)$, $L_2^W(t)$, and $W(t)$, respectively. We assume that the stage durations of the wasp match those of its host, such that they share the same developmental rates α_{L_1} , α_{L_2} , and α_A (α_p for pupa is also assumed implicitly in eq. [4]; see ‘‘Study System’’). We also assume that parasitism does not affect the mortality rates of the juvenile stages (i.e., δ_{L_1} , δ_{L_2} , and δ_p are used for parasitized hosts as well).

The development rate through each stage is temperature dependent (app. A), which means that stage durations, and thus the time-delays in the delay-differential equations, fluctuate through time. To make the models more amenable to analysis, we follow McCauley et al. (2008) and transform the model from the timescale where the delays are variable to a development-rate scale where the

delays are fixed (app. B). The procedure is analogous to the rescaling done in the statistical analysis of the field data. When $\phi(t)$ is defined as the new physiological scale (eq. [2]), the dynamics of egg ($E(\phi)$), larval ($L_1(\phi)$, $L_2(\phi)$), pupal ($P(\phi)$), adult ($A(\phi)$), parasitized larval ($L_1^W(\phi)$, $L_2^W(\phi)$), and wasp ($W(\phi)$) populations can be modeled in general by

$$\begin{aligned}
 \frac{dE(\phi)}{d\phi} &= \frac{\beta(\phi)}{m(\phi)} A(\phi) - \frac{\beta(\phi_E)}{m(\phi_E)} A(\phi_E) S_E(\phi) \\
 &\quad - \frac{\delta_E(\phi) + \rho_w(\phi)}{m(\phi)} E(\phi), \\
 \frac{dL_1(\phi)}{d\phi} &= \frac{\beta(\phi_E)}{m(\phi_E)} A(\phi_E) S_E(\phi) \\
 &\quad - \frac{\beta(\phi_{L_1})}{m(\phi_{L_1})} A(\phi_{L_1}) S_{L_1}(\phi) - \frac{\delta_{L_1}(\phi)}{m(\phi)} L_1(\phi), \\
 \frac{dL_2(\phi)}{d\phi} &= \frac{\beta(\phi_{L_1})}{m(\phi_{L_1})} A(\phi_{L_1}) S_{L_1}(\phi) \\
 &\quad - \frac{\beta(\phi_{L_2})}{m(\phi_{L_2})} A(\phi_{L_2}) S_{L_2}(\phi) - \frac{\delta_{L_2}(\phi)}{m(\phi)} L_2(\phi), \\
 \frac{dP(\phi)}{d\phi} &= \frac{\beta(\phi_{L_2})}{m(\phi_{L_2})} A(\phi_{L_2}) S_{L_2}(\phi) \\
 &\quad - \frac{\beta(\phi_p)}{m(\phi_p)} A(\phi_p) S_p(\phi) - \frac{\delta_p(\phi)}{m(\phi)} P(\phi), \quad (4) \\
 \frac{dA(\phi)}{d\phi} &= \frac{\beta(\phi_p)}{m(\phi_p)} A(\phi_p) S_p(\phi) - \sigma \frac{\beta(\phi_A)}{m(\phi_A)} A(\phi_A) S_A(\phi) \\
 &\quad - \frac{\delta_A(\phi)}{m(\phi)} A(\phi), \\
 \frac{dL_1^W(\phi)}{d\phi} &= \frac{\rho_w(\phi)}{m(\phi)} E(\phi) - \frac{\rho_w(\phi_{L_1})}{m(\phi_{L_1})} E(\phi_{L_1}) S_{L_1}^W(\phi) \\
 &\quad - \frac{\delta_{L_1}(\phi)}{m(\phi)} L_1^W(\phi), \\
 \frac{dL_2^W(\phi)}{d\phi} &= \frac{\rho_w(\phi_{L_1})}{m(\phi_{L_1})} E(\phi_{L_1}) S_{L_1}^W(\phi) \\
 &\quad - \frac{\rho_w(\phi_{L_2})}{m(\phi_{L_2})} E(\phi_{L_2}) S_{L_2}^W(\phi) - \frac{\delta_{L_2}(\phi)}{m(\phi)} L_2^W(\phi), \\
 \frac{dW(\phi)}{d\phi} &= \frac{\rho_w(\phi_p)}{m(\phi_p)} E(\phi_p) S_p^W(\phi) - \frac{\delta_w(\phi)}{m(\phi)} W(\phi),
 \end{aligned}$$

$$S_i(\phi) = \exp\left(-\sum_{x=E}^i \int_{\hat{\phi}_{x:i}}^{\hat{\phi}_{x+1:i}} \frac{\delta_x(\xi)}{m(\xi)} d\xi\right),$$

$$S_i^W(\phi) = \exp\left(-\sum_{x=L_1}^i \int_{\hat{\phi}_{x:i}}^{\hat{\phi}_{x+1:i}} \frac{\delta_x(\xi)}{m(\xi)} d\xi\right),$$

$$\phi_i = \phi - \sum_{x=E}^i \frac{1}{\alpha_x},$$

$$\hat{\phi}_{j:k} = \begin{cases} \phi - \sum_{x=j}^k \frac{1}{\alpha_x} & j \leq k \\ \phi & j > k \end{cases}.$$

Here, $\beta(\phi)$ is the function describing the per capita birth rate, $\delta_i(\phi)$ is the function describing the instantaneous per capita mortality rate of stage i , and $\rho_w(\phi)$ is the per capita parasitoid attack rate at ϕ . The function $m(\phi)$ is the base development rate at the current (ϕ) or delayed (ϕ_i) physiological time, where ϕ_i is the fixed stage duration from the beginning of the egg stage to the end of stage i ($i \in \{E, L_1, L_2, P, A\}$). The function $S_i(\phi)$ is through-stage survivorship from the beginning of the egg stage at delayed physiological time (ϕ_i) to stage i at current physiological time (ϕ). The parameter σ is introduced to switch adult senescence on or off and takes a value of either 1 or 0. Although the transformed model appears more complex than the untransformed model (eqq. [B1]–[B6] in app. B), it has fixed delays and thus is amenable to analysis using standard mathematical tools to study equilibria and stability. Since the transformation influences only the time axis, stability and cycle amplitudes are identical for the two scales (phi and time), which allows us to study the timescale system dynamics using phi-scale models that are

easier to characterize. The model given by equations (4) is the general case for a hierarchy of simplified model variants, which we describe in the next section (and app. C). These models represent a series of plausible biological hypotheses to explain the cycles. Also, for a number of these model variants, the $m(\phi)$ function cancels out on the phi scale, which means that the qualitative dynamics of the system do not depend on temperature even though the life cycle is highly temperature dependent.

Each model variant is arrived at by specifying a particular form for the birth-, death-, and parasitism-rate functions, along with the accompanying parameters. Table 1 lays out the functions used for each of the biological mechanisms, table 2 shows the estimated parameter values, and table 3 shows the model variants studied. The next section details the model development for each biological mechanism, and the simplified equations are presented in appendix. C. Model dynamics were characterized through equilibrium stability analysis and numerical simulations. Numerical simulations were performed with the *PBSddesolve* library in R and run for $\phi = 1,616$ units (corresponding to roughly 10 years) to reach asymptotic dynamics. Cycle period was estimated from the last $\phi = 808$ units (corresponding to 5 years). All simulations were started with an adult inoculation that mimics the emergence of overwintering moths in early spring (Gaussian distribution with mean = 11.3 and SD = 2.2 on the phi scale).

Model Variants

The life-history data for tortrix moths suggest that, in the absence of larval density dependence, birth and death rates are strongly temperature dependent in a manner similar to the development rate (Nabeta et al. 2005; app. A). Therefore, we define the base birth- and mortality-rate functions as $\beta(\phi) = cm(\phi)$ and $\delta_i(\phi) = n_i m(\phi)$, respec-

Table 1: Function definition for proposed biological mechanisms

Mechanism ^a	$\beta(\phi)/m(\phi)$	$\delta_E(\phi)/m(\phi)$	$\delta_A(\phi)/m(\phi)$	$\rho_w(\phi)/m(\phi)$	$\delta_{L_1}(\phi)/m(\phi)$	$\delta_{L_2}(\phi)/m(\phi)$	$\delta_P(\phi)/m(\phi)$	σ
Base	c	n_E	n_A	0	n_L	n_L	n_P	0
SLDD	c	n_E	n_A	0	$n_L + n_c L(\phi)^b$	$n_L + n_c L(\phi)^b$	n_P	0
ALDD	c	n_E	n_A	0	$n_L + n_c(L_1(\phi) + \psi L_2(\phi))$	$n_L + n_c\left(\frac{L_1(\phi)}{\psi} + L_2(\phi)\right)$	n_P	0
Sen	c	n_E	n_A	0	$n_L + n_c L(\phi)^b$	$n_L + n_c L(\phi)^b$	n_P	1
Allee	$c(1 - \exp(\nu A(\phi)))$	n_E	n_A	0	$n_L + n_c L(\phi)^b$	$n_L + n_c L(\phi)^b$	n_P	0
W mort	c	$n_E + n_{q_1} \frac{\exp(-n_{q_1} m(\phi))}{m(\phi)}$	$n_A + n_{q_1} \frac{\exp(-n_{q_1} m(\phi))}{m(\phi)}$	0	$n_L + n_c L(\phi)^b$	$n_L + n_c L(\phi)^b$	$n_P + n_{q_1} \frac{\exp(-n_{q_1} m(\phi))}{m(\phi)}$	0
Para	c	n_E	n_A	$k \ln\left(1 - \frac{\nu W(\phi)}{k}\right)$	n_L	n_L	n_P	0

Note: Note that the birth and mortality rates are scaled by the base development function $m(\phi)$ to simplify notation.

^a Mechanism definitions: SLDD = density dependence through symmetric intraspecific larval competition; ALDD = density dependence through asymmetric intraspecific larval competition; Sen = adult senescence; Allee = Allee effect due to mate-finding limitation; W mort = strong winter mortality on egg, pupae, and adult stages; and Para = interaction with a parasitoid wasp.

^b $L(\phi) = L_1(\phi) + L_2(\phi)$.

Table 2: Model parameters

Symbol	Description	Value (range)	Source
γ_D	Steepness parameter in base physiological-scale function	.258	Appendix A
h_D	Half-saturation parameter in base physiological-scale function	18.6	Appendix A
α_E	Egg-stage development scalar	.184	Appendix A
$\alpha_{L_1}, \alpha_{L_2}$	Larval-stage development scalar	.148	Appendix A
α_P	Pupal-stage development scalar	.198	Appendix A
α_A	Adult-stage development scalar (i.e., senescence)	.149	Appendix A
n_E	Egg-stage mortality scalar	6.32×10^{-2}	Appendix A
n_{L_1}, n_{L_2}	Larval-stage mortality scalar	2.57×10^{-3}	Appendix A
n_P	Pupal-stage mortality scalar	2.02×10^{-2}	Appendix A
n_A	Adult-stage mortality scalar	8.07×10^{-2}	Appendix A
n_C	Density-dependent larval mortality scalar	1×10^{-6}	“Methods”
n_{q_1}	Temperature mortality scalar	20	“Methods”
n_{q_2}	Temperature mortality response	.45	“Methods”
c	Maximum per capita birth rate	21 (0–30)	“Methods”
ν	Strength of the Allee effect	.01 (.0001–1.0)	“Methods”
k	Wasp interference parameter in parasitoid attack-rate function	(0–30)	“Methods”
u	Wasp search efficiency in parasitoid attack-rate function	(0–1.0)	“Methods”
ψ	Asymmetry in larval competition	5.0 (0–100)	“Methods”

tively, where c is a constant birth-rate scalar and n_i is a stage-specific constant mortality-rate scalar. Stage-specific development-rate functions are given by $h_i(\phi) = \alpha_i m(\phi)$, where α_i is the stage-specific development-rate scalar. This base model is density independent and thus an unrealistic description for a system with a well-defined seasonal mean abundance. However, these functions describe the basic structured moth life history in the absence of the candidate density-dependent interactions and serve as the point of departure for a series of models.

Symmetric Intraspecific Larval Competition. Direct competition might be only among larval stages in this insect, because this is the only stage that feeds. In this model variant (model A), larval mortality is uniformly density dependent because young and old larvae are assumed to be interchangeable in their mutual competitive reduction of survivorship. The intensity of competition, whether through increased feeding or metabolic rates, is assumed to be temperature dependent. We further assume a Lotka-Volterra formulation for competition (according to Briggs et al. 2000) that scales with temperature, which results in a larval mortality rate given by $\delta_{L_1} = \delta_{L_2} = (n_L + n_C L(\phi))m(\phi)$, where $L(\phi) = L_1(\phi) + L_2(\phi)$, n_L is the base density-independent mortality rate, and n_C controls the increase in mortality due to larval density dependence. To study how the strength of larval density dependence alters the system dynamics, we simulate dynamics over a range of birth rates from $c = 0$ to $c = 30$. It should be noted that changes in c influence the strength of density dependence through changes in the density of larvae, while changing the density-dependent scalar n_C has no influence

on model dynamics. We use $n_C = 1 \times 10^{-6}$ for the simulations, which generates cycles with amplitude similar to the observed dynamics.

Asymmetrical Intraspecific Larval Competition. Previous theoretical work has shown that asymmetrical larval density dependence (through either competition or cannibalism) can generate generation cycles in other insects (e.g., Gurney et al. 1983; Briggs et al. 2000), although there is no particular empirical evidence for this in tortrix moths. We investigate this mechanism by assuming that the larval stage can be divided into young ($L_1(\phi)$) and old larval stages ($L_2(\phi)$) at the midpoint, that the development

Table 3: Model variants

Model	SLDD ^a	ALDD ^a	Sen	Allee	Para ^a	W mort	GCP (ϕ)
A	X						31–40
B	X		X				32
C	X			X			50
D	X				X		240
E		X					14
F		X	X				14
G		X		X			14
H		X			X		240
I					X		240
J	X					X	40
K	X		X			X	32
L	X			X		X	40

Note: SLDD = symmetric larval density dependence; ALDD = asymmetrical larval density dependence; Sen = adult senescence; Allee = Allee effect due to mate-finding limitation; Para = interaction with a parasitoid wasp; W mort = strong winter mortality; GCP = generational cycle period.

^a Biological mechanisms with negative density dependence.

rate is the same for both stages, and that the total larval development time (α_i) remains unchanged (i.e., $1/\alpha_{L_1} = 1/\alpha_{L_2}$). We define the strength of asymmetry (ψ) as the competitive effect of old larvae on young larvae. Assuming that the competitive effect of young on old larvae is the inverse of ψ , we can write the larval-mortality functions as $\delta_{L_1} = [n_L + n_C(L_1(\phi) + \psi L_2(\phi))]m(\phi)$ and $\delta_{L_2} = \{n_L + n_C[(L_1(\phi)/\psi) + L_2(\phi)]\}m(\phi)$, respectively.

Adult Senescence. The life-history experiments provide strong evidence for senescence in reproductive females (Nabeta et al. 2005; see also app. A), which we incorporate by assuming a fixed duration of the adult life span (using the same fixed-delay structure as for recruitment through the immature stages). In equations (4), this is done by setting $\sigma = 1$. Since this mechanism is density independent, if it is not combined with some other density-dependent factor, it will never prevent population from experiencing an unrealistic growth explosion or abrupt extinction. Thus, we incorporate this in combination with some form of larval density dependence.

Mate-Finding Allee Effect. While there is no empirical evidence for an Allee effect in tortrix moths, it provides a possible explanation for sustaining cycles and generation separation (Srinivasa and Muralimohan 2008). A mate-finding Allee effect is common in many other lepidopteran pests (Yamanaka and Liebhold 2009). We incorporate this into the model by using the structure described by Dennis (1989). Specifically, the probability of a female finding a male searching in area μ is $1 - \exp(-\nu A(\phi))$, which yields a new birth-rate function $\beta(\phi) = c(1 - \exp(-\nu A(\phi)))m(\phi)$. To evaluate the impact of an Allee effect on the predicted dynamics, we consider values of ν from 0.0001 to 1.0. As with senescence, this mechanism is not negatively density dependent; we thus consider it only in combination with a form of larval density dependence.

Interaction with Parasitoid Wasps. Previous theoretical models have shown that parasitism can result in single-generation cycles (Knell 1998). We base our parasitoid model on the life history of the common solitary endoparasitoid *A. reticulata*. As outlined in "Study System," the wasp stage durations were assumed to be the same as those of *A. honmai*. One adult wasp of *A. reticulata* is produced per parasitized host. We assumed that the parasitized larvae and pupae have the same stage duration and also experience the same mortality as unparasitized ones. We define the foraging function of the female wasp as $\rho_w(\phi) = k \ln(1 - (uW(\phi)/k))m(\phi)$, which assumes a negative binomial encounter rate that scales with temperature. The key parameters are k and u , which are the effects of wasp interference and search efficiency, respectively (Godfray

and Hassell 1989; Bonsall and Eber 2001). Since we do not have any data to parameterize k and u , we consider the range explored by Bonsall and Eber (2001), which is $u = 0-1$ and $k = 0-30$.

Winter Mortality. The above five mechanisms assume that all life-history rates (i.e., birth, development, and death) respond in a proportional manner to temperature. However, field researchers have hypothesized that the strong single-generation cycles in the tortrix tea pest could be the result of asymmetrical winter survival among stages, in that only larvae appear to survive the winter (e.g., Furuno 1972; Kuroki and Izumi 1984). Such asymmetric winter survival is known to synchronize age structure in a number of theoretical models of univoltine (one year for each generation) or semivoltine (multiple years for each generation) insects (e.g., Crowley et al. 1987; Gurney et al. 1992; Powell and Logan 2005). Therefore, we evaluate the influence of differential winter survivorship on the system dynamics under a realistic temperature regime. Any functional form of mortality that increases with decreasing temperature will work for our purpose, so long as it kills a substantial number of individuals in the nonlarval stages over the winter. We define the additional winter mortality rate as $n_{q_1} \exp(-n_{q_2}m(\phi))$, where n_{q_1} is the maximum additional winter mortality rate and n_{q_2} controls the decrease in the additional mortality with increasing temperature. Combining the winter mortality with background mortality yields a stage-specific mortality rate of

$$\delta_i(\phi) = \left(n_i + n_{q_1} \frac{\exp(-n_{q_2}m(\phi))}{m(\phi)} \right) m(\phi).$$

Since we do not have any data to estimate n_{q_1} and n_{q_2} , we arbitrarily define them so that winter temperatures kill a sufficient proportion of the nonlarval stages in winter (mean total survival rates for December–February were set at 3.0×10^{-19} , 3.8×10^{-19} , and 2.7×10^{-19} for egg, pupal, and adult cohorts, respectively) but do not affect the survival rate from March to November. The new mortality function does not scale proportionally with the physiological-scale transformation, and the phi-scale equations retain periodic temperature-dependent terms (i.e., $m(\phi)$). Thus, to simulate dynamics with this level of biological mechanism, it is necessary to force the system with an explicit seasonal temperature driver. We use the smoothed daily mean temperature from meteorological records from the Chiran township. Smoothing was conducted with a cubic smoothing spline ($df = 1,000$).

Results

Periodogram of Tortrix Moth Dynamics

Wavelet analysis of 48 years of data revealed that there were two major cycle frequencies in the *Adoxophyes honmai* system. One is observed around a period of $\phi = 160$, which corresponds to an annual cycle on the physiological timescale ($\phi = 161.6$) calculated directly from the temperature record (fig. 2). The other and more dominant one is located at $\phi = 32.5$, which is a little longer than, but nearly concordant with, the physiological time from the egg stage to adult senescence ($\phi = 30.8$) estimated from laboratory data (see app. A). Both the annual and the single-generation cycles were highly significant in a randomization test (fig. 2). Note that a third intermediate period (around $\phi = 75$) is much less important but still significant. In the following sections, we compare the predicted periodicity from the six mechanisms with this wavelet analysis to assess the extent to which a laboratory-based life cycle and idealized forms of larval density dependence, winter mortality, and parasitism can explain the observed dynamics.

Models without Additional Winter Mortality

Each of the biological mechanisms was able to generate cycles over some range of the parameter space explored (figs. 3, 4; table 3; app. C). Symmetric larval density dependence (model A; fig. 3a) generates cycles when both the birth rate and adult mortality are high. The cycles occur at a period between $\phi = 31$ and $\phi = 40$, which changes across mortality and at the lower end is similar to the period of the generation cycle observed in the empirical data. The shorter-period cycle is found under high birth rate (c) and a high adult mortality rate (n_A). Asymmetrical larval density dependence (model E; fig. 3b) generates cycles with a period shorter, at $\phi = 14$, than that found under symmetric larval density dependence. In the presence of symmetric larval density dependence, senescence (model B; fig. 3c) generated, over a wide range of birth rates, cycles with a consistent period of $\phi = 32$, which is concordant with the empirical data. Overall, the birth rate c had the greatest influence on the strength of competition by affecting larval density, while the intensity of larval dependence (n_C) did not affect the dynamics.

Allee effects, again in the presence of symmetric larval density dependence (model C; fig. 3d), generated cycles over only a very small range of parameters and with a

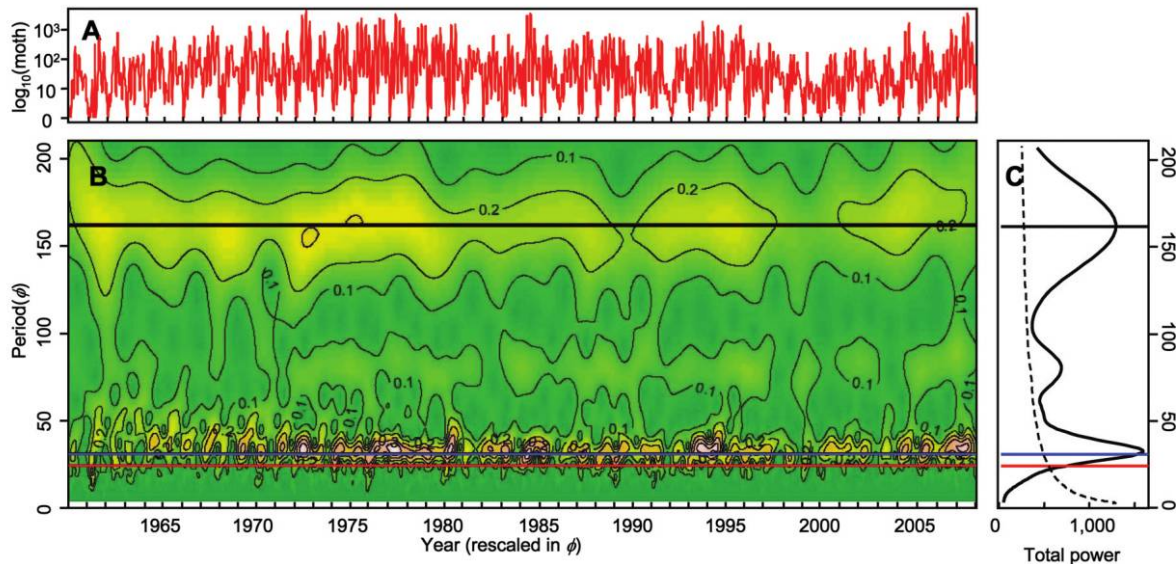


Figure 2: Wavelet analysis of moth dynamics. A, Smoothed dynamics of moth counts on the physiological scale, ϕ . B, Wavelet analysis, using the Morlet wavelet with eight octaves and 16 scales. C, Global spectrum of the dynamics across the sum of the local wavelets across years. The dashed line shows the 99% confidence limits of the global spectrum based on 1,000 bootstrap resamples of the original data. Horizontal lines denote the physiological time units required from egg to adult (red line, $\phi = 24.1$), from egg to adult senescence (blue line, $\phi = 30.8$), and for the annual cycle (black line, $\phi = 161.6$).

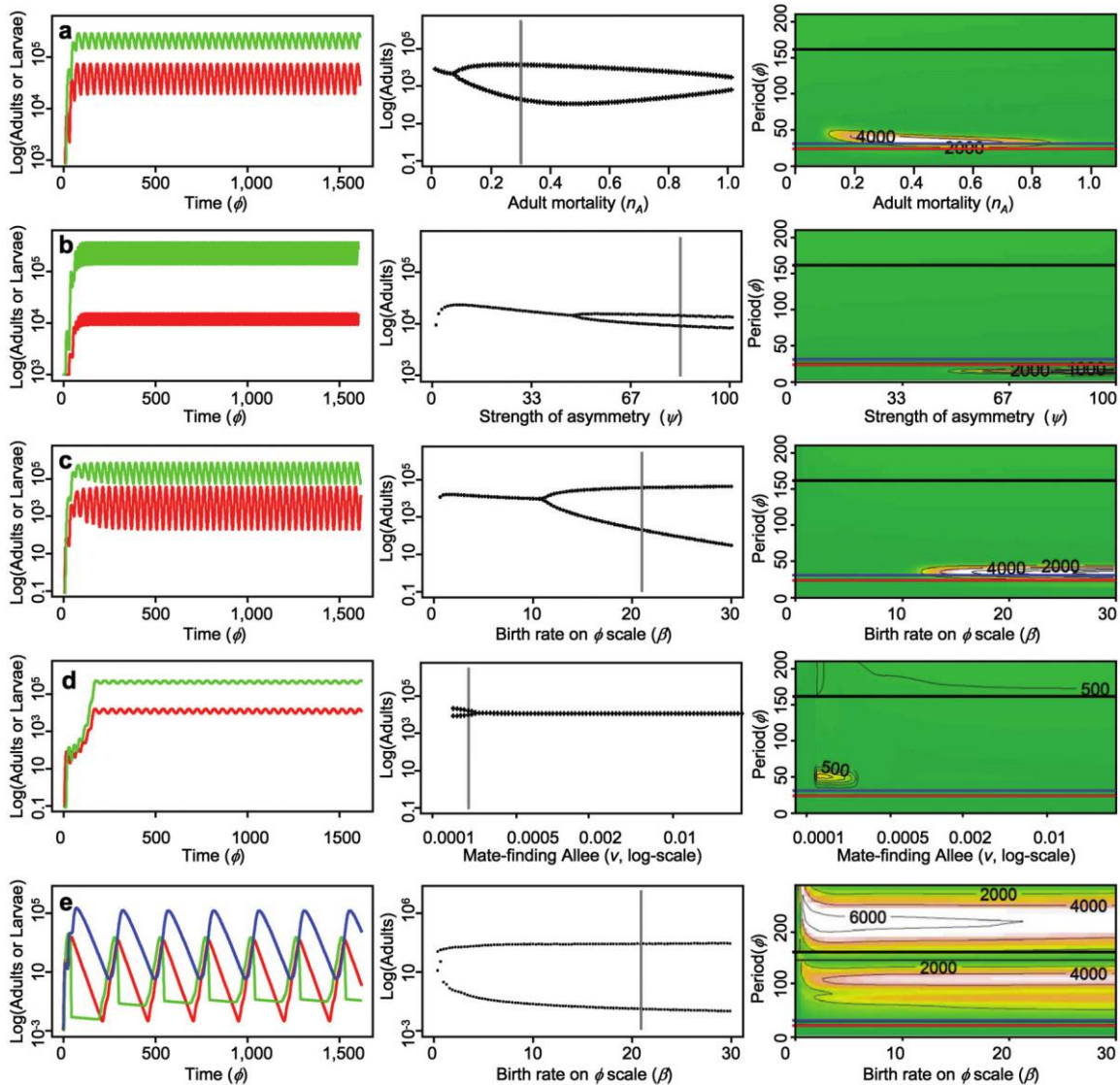
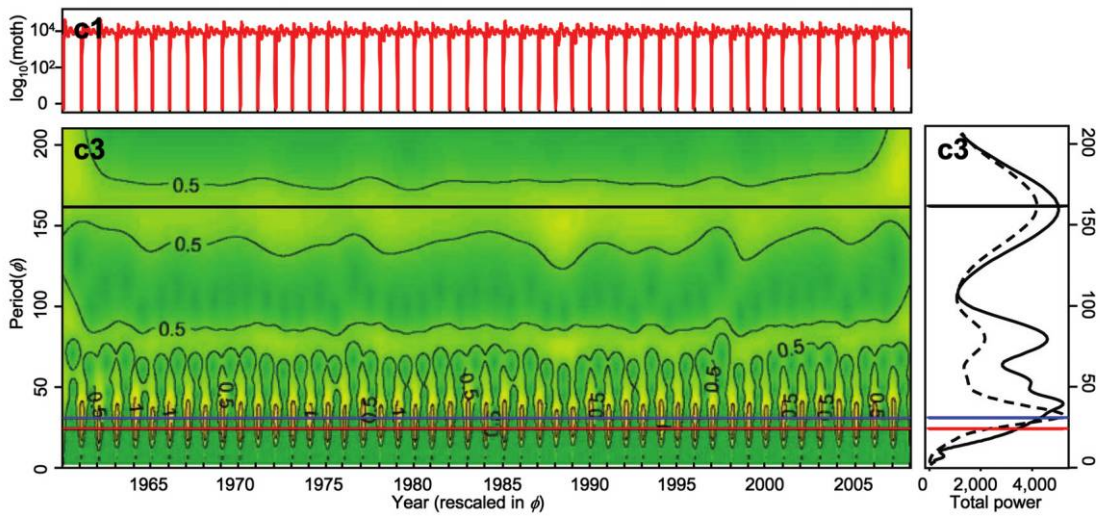
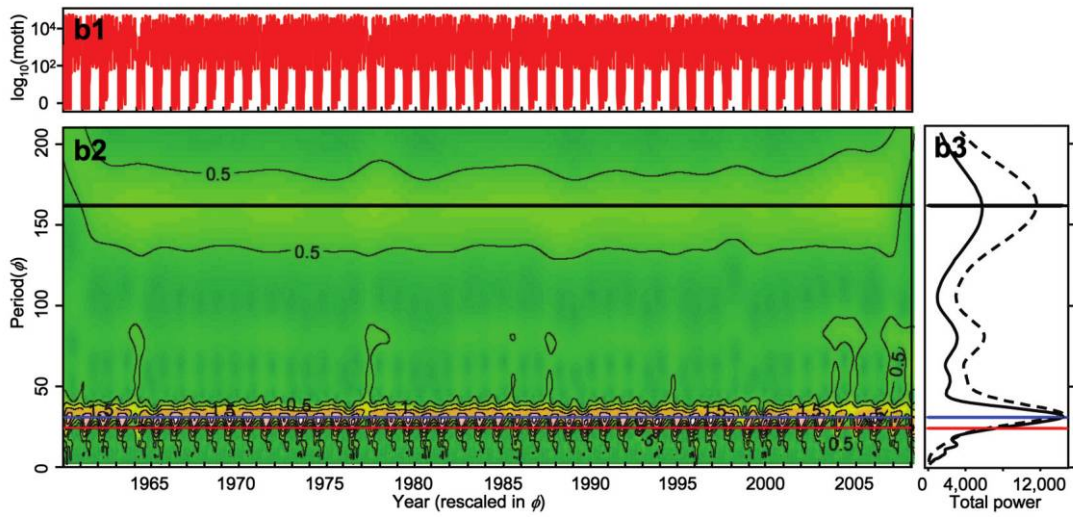
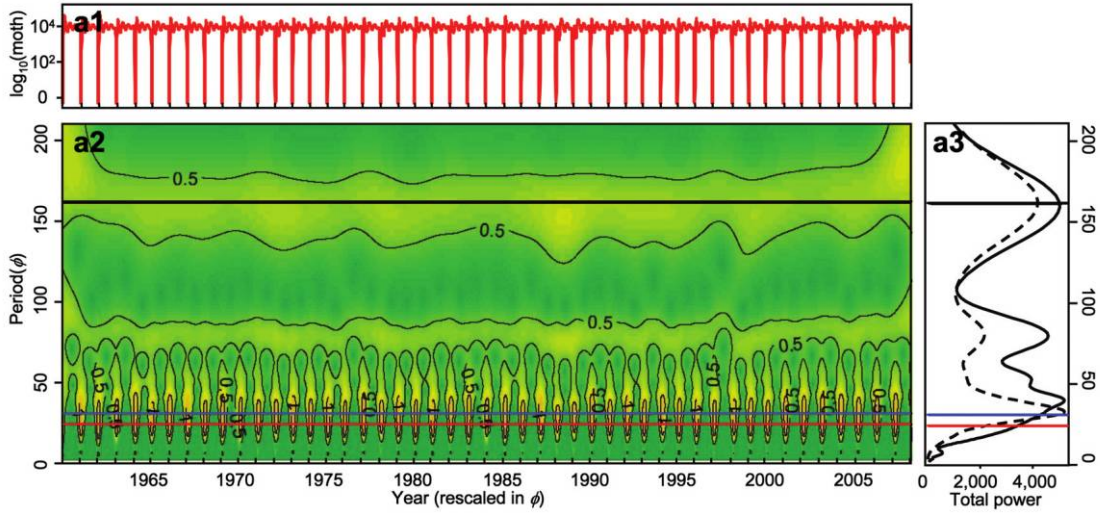


Figure 3: Illustrative model dynamics for each mechanism. The left-hand panel shows adult (red) and larval (green) dynamics; in the middle panel is the bifurcation plot showing the maximum and minimum of adult abundance as a function of a model parameter; and the right-hand panel shows a color map of the corresponding periodogram. The vertical gray line in the middle panel indicates parameter location for the simulation in the left-hand panel. Horizontal lines on the periodogram are the reference lines from figure 2. *a*, Symmetric larval competition (model A); *b*, asymmetric larval competition (model E); *c*, adult senescence (model B); *d*, mate-finding Allee effect (model C); *e*, interaction with parasitoid wasps (model I); the blue line in the left-hand panel represents adult-wasp dynamics. Parameters are as in table 2, with the exception of $c = 40$ for model A (*a*), $\psi = 80$ for model E (*b*), and $\nu = 0.002$ for model C (*d*).

period longer than that for larval density dependence in isolation at $\phi = 50$. The addition of parasitoids had a strong effect on the tendency of the system to cycle (model I; fig. 3*e*), but with a very long (multigenerational) period around $\phi = 240$.

When in combination, the different mechanisms produced results similar to those they produced in isolation, but with some of the mechanisms having a more dominant

influence on the dynamics (table 3). Parasitism always generated slow cycles with a period of $\phi = 240$, regardless of the other mechanisms present. In the absence of parasitism, asymmetrical larval competition always generated fast cycles with a period of $\phi = 14$ when the degree of asymmetry (ψ) was strong; otherwise, it had a stabilizing effect. The dynamics under symmetric larval competition changed, depending on the mechanism it was paired with.



Symmetric competition in isolation generated cycles with a period from $\phi = 31$ to $\phi = 40$. In the presence of an Allee effect, the period was $\phi = 50$, and the combination of symmetrical larval competition and adult senescence generated cycles with a period of $\phi = 32$, which is similar to the period found in the empirical data.

Models with Additional Winter Mortality

While the birth, development, and mortality functions are strongly temperature dependent, they have a proportional dependence that makes them cancel out on the physiological scale. As a result, the stability and amplitude of the cycles observed on the physiological scale hold true for all temperature dynamics. Differential winter mortality, however, does not have this property of proportional temperature dependence, so the dynamics, even on the physiological scale, depend on the exact patterns of fluctuations in temperature (rather than just the total annual degree-days). Under the local temperature regime, the models with symmetric larval density dependence generated frequency spectra with two dominant peaks, which is very similar to what was observed in data (fig. 4). The primary distinction among the three model variants is in the period of the generation cycle, which is $\phi = 40$ for asymmetrical larval density dependence with (model L) or without (model J) an Allee effect and $\phi = 32$ for symmetric larval density dependence with senescence (model K). Moreover, model K even has a close match to the small but significant third intermediate peak in the power spectrum at $\phi = 75$.

Differences among the models can also be seen in the overall character of the dynamics. In models L and J, the predicted moth abundance fluctuated a little at the beginning of each year but soon converged to the fixed point and crashed at the end of each year (fig. 4*a*, 4*c*). On the other hand, the population dynamics of the model variant with adult senescence (model K) produced sustained cycles throughout the year with a striking similarity to those from the field data (fig. 4*b*). To quantify the agreement between these model variants and the field data, we calculate the proportion of variation explained by each model variant. The coefficient of determination for symmetric larval density dependence with or without Allee effects was $R^2 = 0.18$, whereas the coefficient of determination for symmetric larval density dependence with senescence was the highest, at $R^2 = 0.32$. Therefore, we conclude that the field

data support the effect of adult senescence on its sustainable cycles.

Discussion

The smaller tea tortrix (*Adoxophyes honmai*) in Japan exhibits four or five regular outbreaks a year resulting from strong generation separation and violent single-generation cycles. Many field researchers had presumed that this pattern is the natural consequence of seasonality (e.g., Furuno 1972; Kuroki and Izumi 1984). Only larvae survive to the end of the winter, with the result that a synchronized cohort restarts spring growth. The generation cycles observed even after the second generation might have been merely a transient dampened oscillation (Taylor 1979). However, our series of models revealed that the combination of symmetric larval density dependence and rapid adult senescence is the most plausible explanation and predicts the strong and persistent generation cycles. The models without this set of mechanisms showed cycles of the wrong length or only rapidly dampening transients. Although previous mathematical models for laboratory (Gurney et al. 1983; Gurney and Nisbet 1985; Nisbet and Onyiah 1994; Briggs et al. 2000; Nakamura et al. 2004) or free-living populations (Godfray and Hassell 1987, 1989) have shown that several different mechanisms can create generation cycles, neither asymmetrical competition among stages nor host-parasitoid interactions can account for the system behavior when the detailed life histories of the moth and its natural enemies are considered.

Qualitatively speaking, our conclusion is in broad agreement with that of Gurney and Nisbet (1985). They predicted that self-organized single-generation cycles in structured models are rapidly established when instantaneous competition is combined with high adult fecundity and short reproductive duration. In our model, removal of adult senescence had a stabilizing effect on the system, and the population shows a brief damped oscillation with convergence on a fixed point (app. C). Although certain parameter combinations still permitted persistent cycles, they typically had a period that was too long (table 3). Gurney and Nisbet (1985) similarly showed that prolonged reproductive life span stabilizes dynamics. Generally speaking, a short reproductive life span can be achieved by either senescence (which results in a truncated age distribution of reproducing adults) or severe adult mortality (which results in a steeply declining exponential age distribution). When investigating this difference in modeling mortality,

Figure 4: Simulated dynamics of three models under realistic temperature regime. *a*, Symmetric larval competition without adult senescence (model J). *b*, Symmetric larval competition with adult senescence (model K). *c*, Symmetric larval competition with an Allee effect (model L). See figure 2 for panel descriptions.

we found that both adult senescence and severe adult mortality can create generation cycles. Since the laboratory data support the existence of adult senescence and adult mortality in nature would certainly have to be much higher than that seen in the laboratory to generate cycles with the correct frequency, we conclude that adult senescence is a parsimonious ingredient.

The three other broad mechanisms that have been invoked to explain single-generation cycles in insects (asymmetric competition, mate-finding Allee effects, and host-parasitoid interactions) do not appear to be causing cycles in the tortrix system. Asymmetric larval competition, with or without adult senescence (models E and F, respectively), showed either no cycles with the most plausible parameters or cycles that were much too fast (nearly half the generation length). Similar conclusions were reached by Briggs et al. (2000) in their model of the generation cycle in the Indian meal moth (*Plodia interpunctella*). In that case, additional egg cannibalism was required to generate the generation cycle. The smaller tea tortrix is a strict herbivore for which cannibalism has never been reported. Srinivasa and Muralimohan (2008) suggested mate-finding Allee effects as an alternative mechanism for generating single-generation cycles. Our models show that this is an unlikely cause in our system; a weak mate-finding Allee effect generally did not change the system behavior in the model variants. When the Allee effect is severe (for which there is no biological evidence), a cycle appears with a period of $\phi = 50$, which is much slower than that observed in nature ($\phi = 32.5$).

Finally, all model variants involving interactions with parasitoids exhibited a slow, multigenerational cycle (around $\phi = 240$) that would take longer than a year to complete. Murdoch et al. (2002) established that consumer-resource interactions often generate multigenerational cycles with a period 4–6 times the generation length. However, parasitoids are known to generate sustained generation cycles if the parasitoid generation time is different from that of the host (e.g., 0.5 or 1.5 times the length of the host's cycle; Godfray and Hassell 1987, 1989; see also Knell 1998; Bjørnstad et al. 2001). The two dominant parasitoid wasps of *A. honmai*, *Ascogaster reticulata* and *Apanteles adoxophyesi*, have life cycles that are synchronized with and of similar length to that of the host (Takagi 1974; Yukinari 1976; Nakai 2009). There is no major wasp with a shorter generation time than its host in the tea pest system. Consequently, none of the models involving parasitoids can account for the observed cycles.

Anthropogenic interventions, such as plucking of tea leaves and pesticide application, may provide an alternative explanation for the cycle. Because the light-trap census had been utilized to decide the timing of pesticide applications, it is conceivable that strictly periodic management

could induce apparent cycles. However, *A. honmai* is capable of flying more than 5 km per night (Shirai and Kosugi 2000), and there are many tea orchards with different management schedules around our station. So while we cannot eliminate the possibility of a human effect, the hypothesis of a seasonally forced life history with larval competition and adult senescence is a parsimonious explanation.

In this study, we explored a series of plausible mechanisms that could account for a sustained generation cycle observed in a multivoltine pest insect in a temperate zone. We combined time-series analysis with a mechanistic modeling approach by using a suite of delayed differential equations defined on a physiological timescale to incorporate realistic temperature dependence. We showed that the most parsimonious explanation for the observed dynamics is a surprisingly simple seasonally forced model involving larval competition and rapid adult senescence. Interaction with parasitoid wasps (Godfray and Hassell 1989) and/or asymmetrical larval density dependence (Briggs et al. 2000), which can account for single-generation cycles in other systems, predicts cycles with the wrong period in this tortrix tea pest system. We believe that our general approach is applicable to a wide range of organisms with temperature-dependent life histories and may prove particularly useful in temperate systems where insect pest outbreaks are both density and temperature dependent.

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Top, extended tea orchards in Kagoshima prefecture. The smaller tea tortrix moth (*Adoxophyes honmai*) is one of the serious pests in tea orchards all over Japan. Bottom, a larva (left) and a female moth (right). Photographs by Hiroshi Suenaga.