

**ELECTRONIC SUPPLEMENTARY MATERIAL – BJØRNSTAD, NELSON
AND TOBIN – DEVELOPMENTAL SYNCHRONY IN MULTIVOLTINE
INSECTS: GENERATION SEPARATION VERSUS SMEARING**

1. DERIVATION OF RENEWAL EQUATIONS

1.1. PDE model for a stage-structured population with temperature dependent rates. We developed a general temperature-dependent model based on the approach of renewal equations and motivated by the work of Breda et al. (2012). We begin by defining four life stages: egg, larva, pupa and adult. Since individuals in the population can transition between stages at any age, we create a PDE model to describe the dynamics within each stage and model the transitions among stages explicitly.

Let $e(t, x)$, $l(t, x)$, $p(t, x)$ and $a(t, x)$ be the density of animals in the egg, larval, pupal and adult stages, respectively at time t and at within-stage age x (i.e., individuals that enter a stage outside of initial conditions have age $x = 0$). We assume that reproduction is given by a per-capita adult birth rate $\beta(t)$ that depends on time-varying temperature $T(t)$, and mortality is given by a temperature-dependent per-capita rate $\delta_i(t)$ for stage i . The through-stage development rate is given by $\mu_i(t, x)$, which is both time- and age-dependent.

The dynamics and boundary conditions for each stage are

$$(1) \quad \frac{\partial e(t, x)}{\partial t} + \frac{\partial e(t, x)}{\partial x} = -\mu_E(t, x)e(t, x) - \delta_E(t)e(t, x)$$

$$e(t, 0) = \beta(t) \int_0^\infty a(t, \xi) d\xi$$

$$(2) \quad \frac{\partial l(t, x)}{\partial t} + \frac{\partial l(t, x)}{\partial x} = -\mu_L(t, x)l(t, x) - \delta_L(t)l(t, x)$$

$$l(t, 0) = \mu_E(t, x)e(t, x)$$

$$(3) \quad \frac{\partial p(t, x)}{\partial t} + \frac{\partial p(t, x)}{\partial x} = -\mu_P(t, x)p(t, x) - \delta_P(t)p(t, x)$$

$$p(t, 0) = \mu_L(t, x)l(t, x)$$

$$(4) \quad \frac{\partial a(t, x)}{\partial t} + \frac{\partial a(t, x)}{\partial x} = -\mu_A(t, x)a(t, x) - \delta_A(t)a(t, x)$$

$$a(t, 0) = \mu_P(t, x)p(t, x)$$

The development rates $\mu_i(t, x)$ are based on the probability $f_i(t, x)$ that an individual of age x will mature out of stage i at time t . For non-adult stages, movement among stages represents maturation. For the adult stage, movement out of the stage represents senescence. The birth, death and transition probabilities are defined below in the section *Temperature dependence in the vital rates*.

1.2. Converting to integro-differential equations. Define the total number of individuals in each stage as

$$(5) \quad E(t) = \int_0^\infty e(t, \xi) d\xi$$

$$(6) \quad L(t) = \int_0^\infty l(t, \xi) d\xi$$

$$(7) \quad P(t) = \int_0^\infty p(t, \xi) d\xi$$

$$(8) \quad A(t) = \int_0^\infty a(t, \xi) d\xi$$

Differentiating (5)-(8) by time yields

$$(9) \quad \frac{dE(t)}{dt} = \int_0^\infty \frac{d}{dt} e(t, \xi) d\xi = \int_0^\infty \left(\frac{\partial e(t, \xi)}{\partial t} + \frac{\partial e(t, \xi)}{\partial \xi} \right) d\xi$$

$$(10) \quad \frac{dL(t)}{dt} = \int_0^\infty \frac{d}{dt} l(t, \xi) d\xi = \int_0^\infty \left(\frac{\partial l(t, \xi)}{\partial t} + \frac{\partial l(t, \xi)}{\partial \xi} \right) d\xi$$

$$(11) \quad \frac{dP(t)}{dt} = \int_0^\infty \frac{d}{dt} p(t, \xi) d\xi = \int_0^\infty \left(\frac{\partial p(t, \xi)}{\partial t} + \frac{\partial p(t, \xi)}{\partial \xi} \right) d\xi$$

$$(12) \quad \frac{dA(t)}{dt} = \int_0^\infty \frac{d}{dt} a(t, \xi) d\xi = \int_0^\infty \left(\frac{\partial a(t, \xi)}{\partial t} + \frac{\partial a(t, \xi)}{\partial \xi} \right) d\xi$$

substituting the expressions for mortality and development in (1)-(4), and adding the recruitment term yields

$$(13) \quad \frac{dE(t)}{dt} = \int_0^\infty \beta(t) a(t, \xi) - \delta_E(t) e(t, \xi) - \mu_E(t, \xi) e(t, \xi) d\xi$$

$$(14) \quad \frac{dL(t)}{dt} = \int_0^\infty \mu_E(t, \xi) e(t, \xi) - \delta_L(t) l(t, \xi) - \mu_L(t, \xi) l(t, \xi) d\xi$$

$$(15) \quad \frac{dP(t)}{dt} = \int_0^\infty \mu_L(t, \xi) l(t, \xi) - \delta_P(t) p(t, \xi) - \mu_P(t, \xi) p(t, \xi) d\xi$$

$$(16) \quad \frac{dA(t)}{dt} = \int_0^\infty \mu_P(t, \xi)p(t, \xi) - \delta_A(t)a(t, \xi) - \mu_A(t, \xi)a(t, \xi)d\xi$$

substituting the definitions in (5)-(8) and simplifying yields

$$(17) \quad \frac{dE(t)}{dt} = \beta(t)A(t) - \int_0^\infty \mu_E(t, \xi)e(t, \xi)d\xi - \delta_E(t)E(t)$$

$$(18) \quad \frac{dL(t)}{dt} = \int_0^\infty \mu_E(t, \xi)e(t, \xi)d\xi - \int_0^\infty \mu_L(t, \xi)l(t, \xi)d\xi - \delta_L(t)L(t)$$

$$(19) \quad \frac{dP(t)}{dt} = \int_0^\infty \mu_L(t, \xi)l(t, \xi)d\xi - \int_0^\infty \mu_P(t, \xi)p(t, \xi)d\xi - \delta_P(t)P(t)$$

$$(20) \quad \frac{dA(t)}{dt} = \int_0^\infty \mu_P(t, \xi)p(t, \xi)d\xi - \int_0^\infty \mu_A(t, \xi)a(t, \xi)d\xi - \delta_A(t)A(t)$$

1.3. Temperature dependence in the vital rates. We illustrate the full range of population dynamics from generation synchrony to overlap using a temperature-dependent physiologically-structured population model developed for tortrix moths (Nelson et al. 2013). Motivated by life history experiments on the tortrix moth *Adoxophyes honmai*, temperature dependence in the birth rate is given by

$$(21) \quad \beta(t) = be^{cT(t)}$$

and temperature dependence in the mortality rates is given by

$$(22) \quad \delta_i(t) = d_i e^{cT(t)} + d_W e^{-c_W T(t)} \text{ for } i = E, P, A$$

$$(23) \quad \delta_L(t) = d_L e^{cT(t)} + d_W e^{-c_W T(t)} + d_C e^{c_L T(t)} L(t)$$

where $d_W e^{-c_W T(t)}$ is mortality due to cold temperatures common to all life stages, and $d_i e^{cT(t)}$ is stage-specific temperature-dependent mortality. The larval stage includes temperature-dependent density-dependent mortality.

The age-specific development rate can be calculated from the probability $f_i(t, x)$ that an individual of age x matures from stage i at time t . The maturation probability is a function of age (x) with time varying (t) parameters. The development rate is given as

$$\mu_i(t, x) = \frac{f_i(t, x)}{1 - F_i(t, x)}$$

where $F_i(t, x)$ is the cumulative probability function over x for stage i . We leave the shape of the distribution general at this point, but define the expectation by the following integral

constraint that ensures the average individual has experienced enough heat to mature from a particular stage

$$(24) \quad \frac{1}{\alpha_i} = \int_{t-\tau_i(t)}^t e^{cT(\xi)} d\xi$$

where $\alpha_i \exp(cT(t))$ is the instantaneous temperature-dependent development rate, and $\tau_i(t)$ is the potentially time-varying stage duration.

Substituting the vital rate expressions into (17)-(20) yields

$$\begin{aligned} \frac{dE(t)}{dt} &= be^{cT(t)} A(t) - \int_0^\infty \mu_E(t, \xi) e(t, \xi) d\xi - \left(d_E e^{cT(t)} + d_W e^{-c_W T(t)} \right) E(t) \\ \frac{dL(t)}{dt} &= \int_0^\infty \left(\mu_E(t, \xi) e(t, \xi) - \mu_L(t, \xi) l(t, \xi) \right) d\xi - \left(d_L e^{cT(t)} + d_W e^{-c_W T(t)} + d_C e^{c_L T(t)} L(t) \right) L(t) \\ \frac{dP(t)}{dt} &= \int_0^\infty \left(\mu_L(t, \xi) l(t, \xi) - \mu_P(t, \xi) p(t, \xi) \right) d\xi - \left(d_P e^{cT(t)} + d_W e^{-c_W T(t)} \right) P(t) \\ \frac{dA(t)}{dt} &= \int_0^\infty \left(\mu_P(t, \xi) p(t, \xi) - \mu_A(t, \xi) a(t, \xi) \right) d\xi - \left(d_A e^{cT(t)} + d_W e^{-c_W T(t)} \right) A(t) \end{aligned}$$

1.4. Changing the integration scale. The model can be simplified by a change of variables from time t to a physiological cumulative heat scale $\phi(t) = \int_0^t \exp(cT(\xi)) d\xi$. Since ageing and time must progress at the same rate, we define a corresponding new age variable as $\nu(x) = \int_0^x \exp(cT(\xi)) d\xi$.

We begin by developing the phi-scale development rate function $h_i(\phi, \nu)$. Define $f_{i,\phi}(\phi, \nu)$ as the phi-scale function describing the probability of maturing from stage i (second subscript indicates scale), which has the inverse function $g(t) = \int_0^t \exp(cT(\xi)) d\xi$ that maps $t \rightarrow \phi$. The corresponding t-scale function is then given as

$$(25) \quad f_{i,t}(t, x) = f_{i,\phi}(g(t), g(x)) \frac{dg(t)}{dt} = f_{i,\phi}(g(t), g(x)) e^{cT(t)}$$

which allows us to write

$$(26) \quad f_{i,\phi}(g(t), g(x)) = f_{i,t}(t, x) e^{-cT(t)}$$

The cumulative probability function $F_{i,t}(t, x)$ across age x on the t-scale is given as

$$(27) \quad F_{i,t}(t, x) = \int_0^t f_{i,t}(t, \xi) d\xi = \int_0^t f_{i,\phi}(g(t), g(\xi)) \frac{dg(\xi)}{dt} d\xi$$

$$(28) \quad F_{i,t}(t, x) = \int_0^t f_{i,\phi}(g(t), u) du$$

where $u = g(x)$. Performing the integration and recognizing that $F_{i,\phi}(g(t), g(0)) = 0$ allows us to write

$$(29) \quad F_{i,t}(t, x) = F_{i,\phi}(g(t), g(x))$$

The phi-scale development rate function can now be expressed as

$$(30) \quad h_i(g(t), g(x)) = \frac{f_{i,\phi}(g(t), g(x))}{1 - F_{i,\phi}(g(t), g(x))} = \frac{f_{i,t}(t, x)e^{-cT(t)}}{1 - F_{i,t}(t, x)}$$

$$(31) \quad h_i(g(t), g(x)) = \mu_i(t, x)e^{-cT(t)}$$

$$(32) \quad h_i(\phi, \nu) = \mu_i(t, x)e^{-cT(t)}$$

Following Nelson et al. (2013), and using the expression in (32), the population model on the phi-scale becomes

$$(33) \quad \frac{dE(\phi)}{d\phi} \frac{d\phi}{dt} = be^{cT(z)}A(\phi) - e^{cT(z)} \int_0^\infty h_E(\phi, \omega)e(\phi, \omega)d\omega - \delta_E(\phi)E(\phi)$$

$$(34) \quad \frac{dL(\phi)}{d\phi} \frac{d\phi}{dt} = e^{cT(z)} \int_0^\infty \left(h_E(\phi, \omega)e(\phi, \omega) - h_L(\phi, \xi)l(\phi, \omega) \right) d\omega - \delta_L(\phi)L(\phi)$$

$$(35) \quad \frac{dP(\phi)}{d\phi} \frac{d\phi}{dt} = e^{cT(z)} \int_0^\infty \left(h_L(\phi, \omega)l(\phi, \omega) - h_P(\phi, \omega)p(\phi, \omega) \right) d\omega - \delta_P(\phi)P(\phi)$$

$$(36) \quad \frac{dA(\phi)}{d\phi} \frac{d\phi}{dt} = e^{cT(z)} \int_0^\infty \left(h_P(\phi, \omega)p(\phi, \omega) - h_A(\phi, \omega)a(\phi, \omega) \right) d\omega - \delta_A(\phi)A(\phi)$$

$$(37) \quad \delta_E(\phi) = d_E + d_W e^{-(c+c_W)T(z)}$$

$$(38) \quad \delta_L(\phi) = d_L + d_W e^{-(c+c_W)T(z)} + d_C e^{(c_L-c)T(z)} L(\phi)$$

$$(39) \quad \delta_P(\phi) = d_P + d_W e^{-(c+c_W)T(z)}$$

$$(40) \quad \delta_A(\phi) = d_A + d_W e^{-(c+c_W)T(z)}$$

where, for clarity, ω is introduced as the integration variable for ν and $z = z(\phi)$ is the value of t that corresponds to the current value of ϕ . There is no analytical expression for $z(\phi)$ under real-world temperature dynamics, which means the value will need to be calculated numerically.

Since $d\phi/dt = e^{cT(z)}$, the renewal equations simplify to

$$(41) \quad \frac{dE(\phi)}{d\phi} = bA(\phi) - \int_0^\infty h_E(\phi, \omega)e(\phi, \omega)d\omega - \delta_E(\phi)E(\phi)$$

$$(42) \quad \frac{dL(\phi)}{d\phi} = \int_0^\infty \left(h_E(\phi, \omega)e(\phi, \omega) - h_L(\phi, \omega)l(\phi, \omega) \right) d\omega - \delta_L(\phi)L(\phi)$$

$$(43) \quad \frac{dP(\phi)}{d\phi} = \int_0^\infty \left(h_L(\phi, \omega)l(\phi, \omega) - h_P(\phi, \omega)p(\phi, \omega) \right) d\omega - \delta_P(\phi)P(\phi)$$

$$(44) \quad \frac{dA(\phi)}{d\phi} = \int_0^\infty \left(h_P(\phi, \omega)p(\phi, \omega) - h_A(\phi, \omega)a(\phi, \omega) \right) d\omega - \delta_A(\phi)A(\phi)$$

$$(45) \quad \delta_E(\phi) = d_E + d_W e^{-(c+c_W)T(z)}$$

$$(46) \quad \delta_L(\phi) = d_L + d_W e^{-(c+c_W)T(z)} + d_C e^{(c_L-c)T(z)} L(\phi)$$

$$(47) \quad \delta_P(\phi) = d_P + d_W e^{-(c+c_W)T(z)}$$

$$(48) \quad \delta_A(\phi) = d_A + d_W e^{-(c+c_W)T(z)}$$

While further analysis requires defining the probability distribution for the development times, we can write the general recruitment condition on the phi-scale. Using the definition that $dt/d\phi = \exp(-cT(t))$, the stage transition condition is

$$(49) \quad \int_{t-\tau_i(t)}^t \exp(cT(\xi)) d\xi = \frac{1}{\alpha_i}$$

$$(50) \quad \int_{\phi(t-\tau_i(t))}^{\phi(t)} \exp(cT(\omega)) \frac{dt}{d\omega} d\omega = \frac{1}{\alpha_i}$$

$$(51) \quad \int_{\phi(t-\tau_i(t))}^{\phi(t)} d\xi = \frac{1}{\alpha_i}$$

$$(52) \quad \phi(t) - \phi(t - \tau_i(t)) = \frac{1}{\alpha_i}$$

$$(53) \quad \phi(\tau_i(t)) = \frac{1}{\alpha_i}$$

which is a constant value on the cumulative heat scale.

1.5. Model variants for different development time distributions. In the previous section we developed the model for a generic development time distribution with the only constraint being the expectation of the distribution. In this section we develop the final models for three development time distributions: Exponential, Gamma, and the Dirac delta function.

1.5.1. Exponential development time distribution. Exponential development time distributions describe a process where every individual in a stage has the same likelihood of maturing that is independent of age. From the expression in (32) we see that the function describing the probability of maturation is the same function on both scales. The only difference

is in the expectation of the distribution. The Exponential development time distribution on the phi-scale is $f_{i,\phi}(\phi, \nu) = \lambda e^{-\lambda\nu}$ with expectation λ^{-1} . Using the constraint that the expectation be $\phi(\tau_i(t)) = 1/\alpha_i$, the age-specific development rate is given as

$$(54) \quad h_i(\phi, \nu) = \frac{f_{i,\phi}(\phi, \nu)}{(1 - F_{i,\phi}(\phi, \nu))}$$

$$(55) \quad h_i(\phi, \nu) = \frac{\alpha_i e^{-\alpha_i \nu}}{1 - (1 - e^{-\alpha_i \nu})}$$

$$(56) \quad h_i(\phi, \nu) = \alpha_i$$

Since the development rates are age-independent, the development rate can be moved outside of the age integral.

The exponential variant of the population model then becomes

$$(57) \quad \frac{dE(\phi)}{d\phi} = bA(\phi) - \alpha_E \int_0^\infty e(\phi, \omega) d\omega - \delta_E(\phi)E(\phi)$$

$$(58) \quad \frac{dL(\phi)}{d\phi} = \alpha_E \int_0^\infty e(\phi, \omega) d\omega - \alpha_L \int_0^\infty l(\phi, \omega) d\omega - \delta_E(\phi)L(\phi)$$

$$(59) \quad \frac{dP(\phi)}{d\phi} = \alpha_L \int_0^\infty l(\phi, \omega) d\omega - \alpha_P \int_0^\infty p(\phi, \omega) d\omega - \delta_E(\phi)P(\phi)$$

$$(60) \quad \frac{dA(\phi)}{d\phi} = \alpha_P \int_0^\infty p(\phi, \omega) d\omega - \alpha_A \int_0^\infty a(\phi, \omega) d\omega - \delta_E(\phi)A(\phi)$$

$$(61) \quad \delta_E(\phi) = d_E + d_W e^{-(c+c_W)T(z)}$$

$$(62) \quad \delta_L(\phi) = d_L + d_W e^{-(c+c_W)T(z)} + d_C e^{(c_L-c)T(z)} L(\phi)$$

$$(63) \quad \delta_P(\phi) = d_P + d_W e^{-(c+c_W)T(z)}$$

$$(64) \quad \delta_A(\phi) = d_A + d_W e^{-(c+c_W)T(z)}$$

which simplifies to the following set of ODEs

$$(65) \quad \frac{dE(\phi)}{d\phi} = bA(\phi) - \alpha_E E(\phi) - \delta_E(\phi)E(\phi)$$

$$(66) \quad \frac{dL(\phi)}{d\phi} = \alpha_E E(\phi) - \alpha_L L(\phi) - \delta_L(\phi)L(\phi)$$

$$(67) \quad \frac{dP(\phi)}{d\phi} = \alpha_L L(\phi) - \alpha_P P(\phi) - \delta_P(\phi)P(\phi)$$

$$(68) \quad \frac{dA(\phi)}{d\phi} = \alpha_P P(\phi) - \alpha_A A(\phi) - \delta_A(\phi) A(\phi)$$

$$(69) \quad \delta_E(\phi) = d_E + d_W e^{-(c+c_W)T(z)}$$

$$(70) \quad \delta_L(\phi) = d_L + d_W e^{-(c+c_W)T(z)} + d_C e^{(c_L-c)T(z)} L(\phi)$$

$$(71) \quad \delta_P(\phi) = d_P + d_W e^{-(c+c_W)T(z)}$$

$$(72) \quad \delta_A(\phi) = d_A + d_W e^{-(c+c_W)T(z)}$$

1.5.2. *Erlang development time distribution.* The Erlang distribution is a special case of the Gamma distribution with an integer shape parameter k . The Erlang development time distribution on the phi-scale is

$$f_{i,\phi}(\phi, \nu) = \frac{\lambda^k \nu^{k-1} e^{-\lambda\nu}}{(k-1)!}$$

with expectation k/λ . If $k = 1$, the Erlang distribution is exponentially distributed. Using the constraint that the expectation be $\phi(\tau_i(t))$, the age-specific development rate is given as

$$(73) \quad h_i(\phi, \nu) = \frac{f_{i,\phi}(\phi, \nu)}{(1 - F_{i,\phi}(\phi, \nu))}$$

$$(74) \quad h_i(\phi, \nu) = \frac{\lambda^k \nu^{k-1} e^{-\lambda\nu}}{(k-1)! \sum_{n=0}^{k-1} \frac{1}{n!} (\lambda\nu)^n}$$

$$(75) \quad h_i(\phi, \nu) = \frac{1}{\nu(k-1)! \sum_{n=0}^{k-1} \frac{1}{n!} (\lambda\nu)^{n-k}} = \frac{1}{\sum_{n=0}^{k-1} \left(\frac{\nu(k-1)!}{n!} (k\alpha_i \nu)^{n-k} \right)}$$

Since the development rates are age-dependent, the development function must be jointly integrated with the density of individuals at each age, which doesn't help simplify the model at this stage. However, we can take advantage of the special nature of the Erlang distribution to create a much simpler chain of ODEs (MacDonald et al. 2008; Breda et al. 2012; de Valpine et al. 2014). The Erlang distribution is the probability distribution for the sum of k identical exponentially distributed waiting times. The expectation for the Erlang distribution is $k\lambda^{-1}$, and the expectation for each constituent Exponential distribution is λ^{-1} . Such a system can be setup by having individuals recruit through a set of k serial substages within each stage, with recruitment through each substage following an Exponential development time distribution. Using the constraint that the mean stage development time is $1/\alpha_i$, we can solve for the mean Exponential substage development time λ_i using the expectation of the Erlang distribution, which gives us $\lambda_i = k\alpha_i$.

Using the results from the above Exponential development time distribution, the model with a substage recruitment chain is given as

$$(76) \quad \frac{dE_j(\phi)}{d\phi} = \begin{cases} bA(\phi) - k\alpha_E E_1(\phi) - \delta_E(\phi)E_1(\phi) & \text{if } j = 1 \\ k\alpha_E (E_{j-1}(\phi) - E_j(\phi)) - \delta_E(\phi)E_j(\phi) & \text{if } j > 1 \end{cases}$$

$$(77) \quad \frac{dL_j(\phi)}{d\phi} = \begin{cases} k(\alpha_E E_k(\phi) - \alpha_L L_1(\phi)) - \delta_L(\phi)L_1(\phi) & \text{if } j = 1 \\ k\alpha_L (L_{j-1}(\phi) - L_j(\phi)) - \delta_L(\phi)L_j(\phi) & \text{if } j > 1 \end{cases}$$

$$(78) \quad \frac{dP_j(\phi)}{d\phi} = \begin{cases} k(\alpha_L L_k(\phi) - \alpha_P P_1(\phi)) - \delta_P(\phi)P_1(\phi) & \text{if } j = 1 \\ k\alpha_P (P_{j-1}(\phi) - P_j(\phi)) - \delta_P(\phi)P_j(\phi) & \text{if } j > 1 \end{cases}$$

$$(79) \quad \frac{dA_j(\phi)}{d\phi} = \begin{cases} k(\alpha_P P_k(\phi) - \alpha_A A_1(\phi)) - \delta_A(\phi)A_1(\phi) & \text{if } j = 1 \\ k\alpha_A (A_{j-1}(\phi) - A_j(\phi)) - \delta_A(\phi)A_j(\phi) & \text{if } j > 1 \end{cases}$$

$$(80) \quad \delta_E(\phi) = d_E + d_W e^{-(c+cw)T(z)}$$

$$(81) \quad \delta_L(\phi) = d_L + d_W e^{-(c+cw)T(z)} + d_C e^{(c_L-c)T(z)} L(\phi)$$

$$(82) \quad \delta_P(\phi) = d_P + d_W e^{-(c+cw)T(z)}$$

$$(83) \quad \delta_A(\phi) = d_A + d_W e^{-(c+cw)T(z)}$$

$$(84) \quad L(\phi) = \sum_{j=1}^k L_j(\phi)$$

$$(85) \quad A(\phi) = \sum_{j=1}^k A_j(\phi)$$

The chain of ODEs results a population with Erlang distributed development times.

1.5.3. *Dirac Delta development time distribution.* Delta development time distributions describe a situation where individuals require a fixed number of heat units before maturing. The Dirac Delta function on the phi-scale is

$$(86) \quad f_{i,\phi}(\phi, \nu) = \begin{cases} \infty & \text{if } \nu = \lambda \\ 0 & \text{otherwise} \end{cases}$$

with expectation λ . Using the constraint that the expectation be $\phi(\tau_i(t))$, the age-specific development rate is then given as

$$(87) \quad h_i(\phi, \nu) = \begin{cases} \infty & \text{if } \nu = \phi(\tau_i(t)) \\ 0 & \text{otherwise} \end{cases}$$

$$(88) \quad h_i(\phi, \nu) = \begin{cases} \infty & \text{if } \nu = \frac{1}{\alpha_i} \\ 0 & \text{otherwise} \end{cases}$$

With this definition, we can write the age-integral part of the model as

$$(89) \quad \int_0^\infty h_i(\phi, \omega) i(\phi, \omega) d\omega = i(\phi, 1/\alpha_i)$$

where $i(\phi, \nu)$ denotes the density of stage i . The density at age $\nu = 1/\alpha_i$ is the density at age $\nu = 0$ multiplied by the proportion surviving ($s_i(\phi, \nu)$).

$$(90) \quad i(\phi, 1/\alpha_i) = i(\phi - 1/\alpha_i, 0) s_i(\phi, 1/\alpha_i)$$

Since all individuals in stage i will mature at age $\nu = 1/\alpha_i$, we can shorten the survivorship notation to $s_i(\phi)$ and write

$$(91) \quad s_i(\phi) = \exp\left(-\int_{\phi - \frac{1}{\alpha_i}}^{\phi} \delta_i(\omega) d\omega\right)$$

All that remains is to determine the density of individuals of age $\nu = 0$ for each stage. Starting with the egg stage

$$(92) \quad e(\phi, 0) = bA(\phi)$$

Using the survivorship expression and letting $\phi_i = 1/\alpha_i$, the other stages are then given by

$$(93) \quad l(\phi, 0) = e(\phi - \phi_E, 0) s_E(\phi) = bA(\phi - \phi_E) s_E(\phi)$$

$$(94) \quad p(\phi, 0) = bA(\phi - \phi_E - \phi_L) s_E(\phi - \phi_L) s_L(\phi)$$

$$(95) \quad a(\phi, 0) = bA(\phi - \phi_P - \phi_L - \phi_E) s_E(\phi - \phi_P - \phi_L) s_L(\phi - \phi_P) s_P(\phi)$$

From equations (89) and (90), the Dirac Delta variant of the population model becomes

$$\begin{aligned} \frac{dE(\phi)}{d\phi} &= bA(\phi) - e(\phi - \phi_E, 0) s_E(\phi) - \delta_E(\phi) E(\phi) \\ \frac{dL(\phi)}{d\phi} &= e(\phi - \phi_E, 0) s_E(\phi) - l(\phi - \phi_L, 0) s_L(\phi) - \delta_L(\phi) L(\phi) \\ \frac{dP(\phi)}{d\phi} &= l(\phi - \phi_L, 0) s_L(\phi) - p(\phi - \phi_P, 0) s_P(\phi) - \delta_P(\phi) P(\phi) \\ \frac{dA(\phi)}{d\phi} &= p(\phi - \phi_P, 0) s_P(\phi) - a(\phi - \phi_A, 0) s_A(\phi) - \delta_A(\phi) A(\phi) \\ \delta_E(\phi) &= d_E + d_W e^{-(c+cw)T(z)} \\ \delta_L(\phi) &= d_L + d_W e^{-(c+cw)T(z)} + d_C e^{(c_L-c)T(z)} L(\phi) \\ \delta_P(\phi) &= d_P + d_W e^{-(c+cw)T(z)} \end{aligned}$$

$$\delta_A(\phi) = d_A + d_W e^{-(c+c_W)T(z)}$$

Using (92)-(95), the model simplifies to

$$\frac{dE(\phi)}{d\phi} = b(A(\phi) - A(\phi_1)s_E(\phi)) - \delta_E(\phi)E(\phi)$$

$$\frac{dL(\phi)}{d\phi} = b(A(\phi_1)s_E(\phi) - A(\phi_3)s_L(\phi)) - \delta_L(\phi)L(\phi)$$

$$\frac{dP(\phi)}{d\phi} = b(A(\phi_3)s_L(\phi) - A(\phi_6)s_P(\phi)) - \delta_P(\phi)P(\phi)$$

$$\frac{dA(\phi)}{d\phi} = b(A(\phi_6)s_P(\phi) - bA(\phi_{10})s_A(\phi)) - \delta_A(\phi)A(\phi)$$

$$\delta_E(\phi) = d_E + d_W e^{-(c+c_W)T(z)}$$

$$\delta_L(\phi) = d_L + d_W e^{-(c+c_W)T(z)} + d_C e^{(c_L-c)T(z)} L(\phi)$$

$$\delta_P(\phi) = d_P + d_W e^{-(c+c_W)T(z)}$$

$$\delta_A(\phi) = d_A + d_W e^{-(c+c_W)T(z)}$$

$$s_E(\phi) = \exp\left(-\int_{\phi_1}^{\phi} \delta_E(\omega) d\omega\right)$$

$$s_L(\phi) = \exp\left(-\int_{\phi_3}^{\phi_2} \delta_E(\omega) d\omega - \int_{\phi_2}^{\phi} \delta_L(\omega) d\omega\right)$$

$$s_P(\phi) = \exp\left(-\int_{\phi_6}^{\phi_5} \delta_E(\omega) d\omega - \int_{\phi_5}^{\phi_4} \delta_L(\omega) d\omega - \int_{\phi_4}^{\phi} \delta_P(\omega) d\omega\right)$$

$$s_A(\phi) = \exp\left(-\int_{\phi_{10}}^{\phi_9} \delta_E(\omega) d\omega - \int_{\phi_9}^{\phi_8} \delta_L(\omega) d\omega - \int_{\phi_8}^{\phi_7} \delta_P(\omega) d\omega - \int_{\phi_7}^{\phi} \delta_A(\omega) d\omega\right)$$

$$\phi_1 = \phi - \phi_E$$

$$\phi_2 = \phi - \phi_L$$

$$\phi_3 = \phi - \phi_L - \phi_E$$

$$\phi_4 = \phi - \phi_P$$

$$\phi_5 = \phi - \phi_P - \phi_L$$

$$\phi_6 = \phi - \phi_P - \phi_L - \phi_E$$

$$\phi_7 = \phi - \phi_A$$

$$\phi_8 = \phi - \phi_A - \phi_P$$

$$\phi_9 = \phi - \phi_A - \phi_P - \phi_L$$

$$\phi_{10} = \phi - \phi_A - \phi_P - \phi_L - \phi_E$$

Since the model dynamics are independent of the number of individuals in either the egg ($E(\phi)$) or pupal ($P(\phi)$) stage, the model can be further simplified by dropping these two equations, resulting in a set of delay-differential equations (DDEs).

For each of the three distributions of development time looked at here, the general renewal equations reduce to a set of ODEs or DDEs. However, if the biology of the insect suggested other distributions of development time, or age-dependency in the vital rates, the resulting equations are likely to be partial differential equations or the equivalent integral equations.

2. MODEL FOR THE TORTRICID CASE STUDIES

2.1. Model Development. We illustrate the full range of population dynamics from generation synchrony to generation overlap using a general physiologically-structured population model developed for tortrix moths (Nelson et al. 2013). The model used for the simulations is a distributed-delay version (Fig. 2) of the point-delay model in Nelson et al. (2013) using $n=400$ sub-stages. The large number of sub-stages generates results with the same dynamics as the point-delay model, but allows for easy illustration of the change in distribution of development indices through time (Figs. 3 and 4). Following Yamanaka et al. (2012), the model is given as

$$(96) \quad \frac{dC_{i,j}(\phi)}{d\phi} = \begin{cases} b_o - (n\alpha_i + \Omega_i(\phi))C_{i,j}(\phi) & \text{if } i = 1 \text{ and } j = 1 \\ n\alpha_{i-1}C_{i-1,n}(\phi) - (n\alpha_i + \Omega_i(\phi))C_{i,j}(\phi) & \text{if } i \geq 1 \text{ and } j = 1 \\ n\alpha_i(C_{i,j-1}(\phi) - C_{i,j}(\phi)) - \Omega_i(\phi)C_{i,j}(\phi) & \text{otherwise} \end{cases}$$

where $C_{i,j}(\phi)$ is the density of individuals in sub-stage j of stage i . The stage-specific developmental rates on a physiological scale are given by α_i , the per-capita birth rate is given by b_o , and the per-capita mortality rates are given by

$$(97) \quad \Omega_E(\phi) = d_E + d_W e^{(c_W - c)D(t(\phi))}$$

$$(98) \quad \Omega_L(\phi) = d_L + d_C e^{(\gamma_C - c)D(t(\phi))} d_W e^{(c_W - c)D(t(\phi))}$$

$$(99) \quad \Omega_P(\phi) = d_P + d_W e^{(c_W - c)D(t(\phi))}$$

$$(100) \quad \Omega_A(\phi) = d_A + d_W e^{(c_W - c)D(t(\phi))}$$

where $D(t(\phi))$ is the potentially variable temperature ($^{\circ}\text{C}$) at time t corresponding to physiological time ϕ . Parameters in the mortality rate functions are described below and summarized in Table S1.

2.2. Parameter Estimation. Following Nelson et al. (2013), we estimated the model parameters for temperature-dependent birth and developmental rates for three species of tortrix moths: the smaller tea tortrix (TT), *Adoxophya honmai*; the grape berry moth (GBM), *Paralobesia viteana*; and the light brown apple moth (LBAM), *Epiphyas postvittana*. These species collectively represent a range of developmental synchrony, from generation separation to generation overlap. The data are from published experiments that follow individual life-history traits at different temperatures (Table S1), and all are fit assuming exponential temperature dependence over the temperature span of the simulations (Figs S1 and S2). Note that for LBAM, the assumption of exponential temperature dependence in the birth rate breaks down above 30°C . However, since we were interested in evaluating

TABLE S1. Parameter estimates based on laboratory data for three species of tortrix moths. Estimates are given for the tea tortrix (TT), grape berry moth (GBM) and the light brown apple moth (LBAM).

Parameter	TT* Esti- mate	GBM† Esti- mate	LBAM‡ Esti- mate	Description
$c[1]$	0.0755	0.0876	0.0764	Temperature exponent in development and birth rate functions
$\alpha_E[1]$	0.0120	0.0226	0.0182	Scalar in egg development rate function
$\alpha_L[1]$	0.0073	0.0074	0.0064	Scalar in larval development rate function
$\alpha_P[1]$	0.0217	0.008	0.0173	Scalar in pupal development rate function
$\alpha_A[1]$	0.0129	0.0094	0.0142	Scalar in adult development rate function
$d_E[2]$		0.0050		Scalar in egg mortality rate function
$d_L[2]$		0.0012		Scalar in larval mortality rate function
$d_P[2]$		0.0043		Scalar in pupal mortality rate function
$d_A[2]$		0.0134		Scalar in adult mortality rate function
$b_o[1]$	5.688	0.441	4.597	Scalar in birth rate function
$c_W[2]$		0.2646		Temperature exponent in winter mortality function
$d_W[2]$		0.5614		Temperature scalar in winter mortality function for larval stage
$d_C[3]$		1e-6		Scalar for larval density dependence
$\gamma_C[3]$		0.04		Temperature exponent in larval competition rate function

*Data from Nabeta et al. (2005) and Kodomari et al. (2003). † Data from Luciani (1987), Tobin et al. (2001).‡ Data from Danthararayana (1975), Danthararayana et al. (1995). [1] Parameters estimated for each species using the data indicated by symbols in each column. [2] Parameters are estimated for *A. honmai*, but used for all species in the simulations. [3] Insufficient data to estimate these parameters, but they do not have a qualitative impact on dynamics (Nelson et al. 2013).

the predicted dynamics at temperatures below the upper threshold, these two data points were removed when estimating the coefficients. We leave the important in-depth analysis of non-exponential temperature dependence for future work. Sufficient state-specific data for temperature dependent mortality were only available for the smaller tea tortrix (Nelson et al 2013). For the purposes of illustrating the possible range in dynamics, we use these estimates for all species.

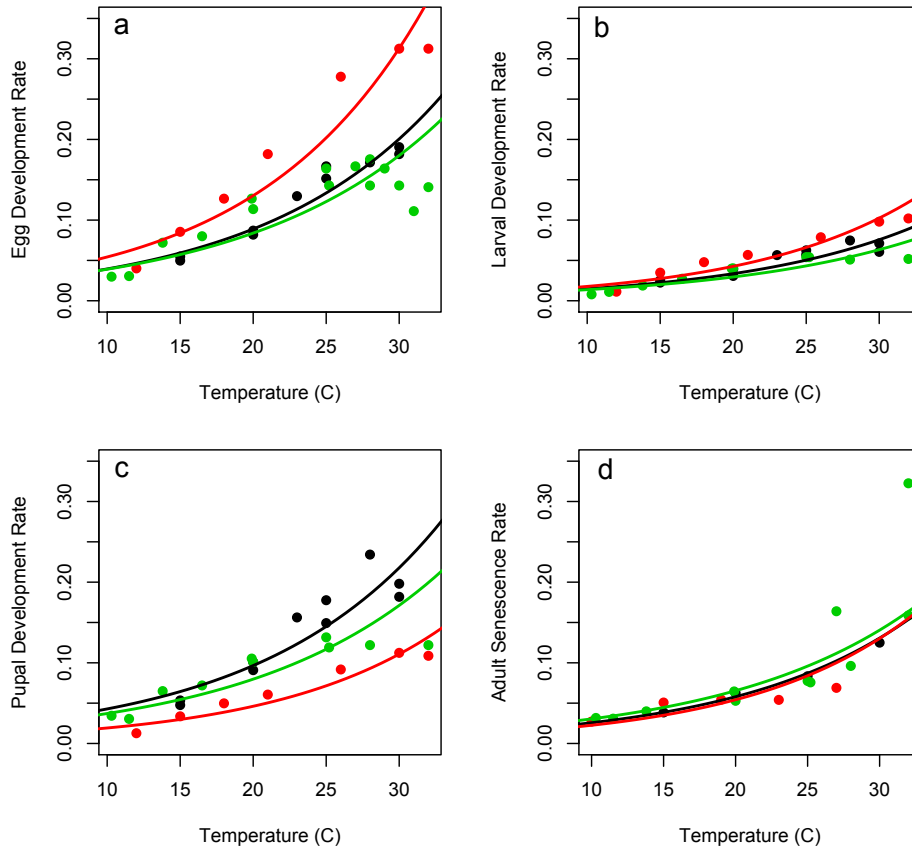


FIGURE S1. Stage-specific development rates for each species of tortrix moth: *Adoxophyes honmai* (black circles), *Paralobesia viteana* (red circles) and *Epiphyas postvittana* (green circles). Lines show fit of $y = \alpha_i \exp(cx)$, where y is development rate, x is temperature, and c is a species-specific temperature parameter shared across life-history traits. a) Egg development rate, b) Larval development rate, c) Pupal development rate, d) Adult senescent rate.

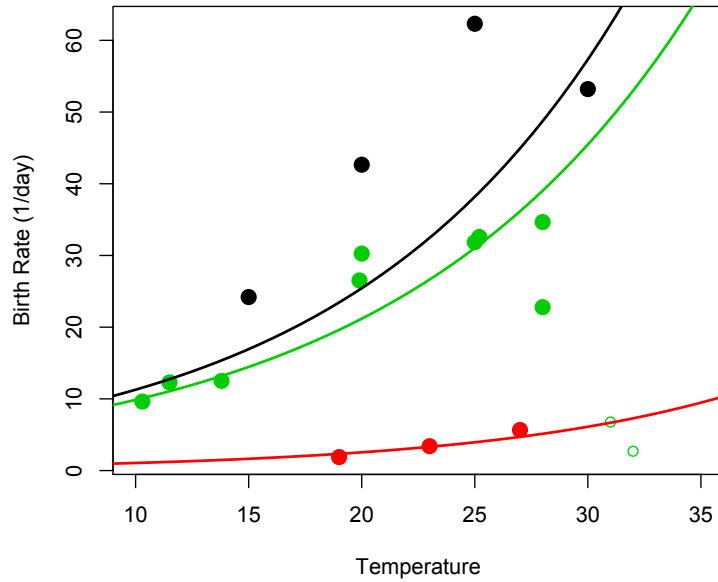


FIGURE S2. Birth rates for each species of tortrix moth: *Adoxophyes honmai* (black circles), *Paralobesia viteana* (red circles) and *Epiphyas postvittana* (green circles). Lines show fit of $y = b_0 \exp(cx)$, where y is the birth rate, x is temperature, c is a species-specific temperature parameter shared across life-history traits, and b_0 is the birth rate scalar. Open circles indicate data excluded when fitting the coefficients.

3. WAVELET AND CIRCULAR DISPERSION STATISTICS

3.1. Wavelet Analysis. The wavelet transformation can be used to estimate the amplitude of population cycles (spectral power) at different frequencies through time. Following Torrence and Compo (1998), the wavelet transformation $W_t(a)$ of observations y_t at regularly spaced time points x_t is given by

$$(101) \quad W_t(a) = \sum_{i=1}^N y_i \sqrt{\frac{d}{a}} \Psi_0 \left(\frac{x_i - x_t}{a} \right)$$

where d is the time between observations, a is the cycle period of interest at time t , and N is the number of observations. The wavelet base function is denoted by $\Psi_0(z)$. While there are many basis functions from which to choose, here we use the Morlet wavelet base function, which is the product of a Gaussian function and a complex plane wave

$$(102) \quad \Psi_0(z) = \frac{1}{\sqrt[4]{\pi}} e^{i\omega_o z} e^{-z^2/2}$$

where ω_o defines the number of oscillations inside the Gaussian window. The wavelet transformation goes in both directions, which means that we can recreate the full time-series, or any subset thereof, using the wavelet coefficients. This later aspect is particularly useful for identifying synchrony versus overlap because we can disentangle the dynamics associated with generation cycles from other signals, such as a response to seasonal drivers (e.g., Nelson, 2013). Essentially, we are using the wavelet as a frequency filter to extract the generation cycle dynamics. The equation for reconstructing the time series (\hat{y}_t) from a Morlet wavelet is

$$(103) \quad \hat{y}_t = \frac{0.6\sqrt[4]{\pi}\sqrt{d}}{0.776} \sum_{j=A_0}^{A_1} \frac{\Re(W_t(a_j))}{\sqrt{a_j}}$$

where d is the time interval between observations, a_j is the period of the j th frequency scale, and \Re denotes the real part of the wavelet transform $W_t(a_j)$ at time t . The range of frequencies to consider is given by A_0 (lower index) and A_1 (upper index). To reconstruct the full time series, $A_0 = 1$ and $A_1 = J$ where J is the maximum index on the frequency scale used in the wavelet transform. The minimum and maximum frequency is determined by the frequency of observations and duration of the dataset, and the resolution between these bounds determines the quality of the reconstruction. To reconstruct the dynamics of just the generation cycle, A_0 and A_1 are modified to be the lower and upper indices, respectively, that bracket the generation cycle frequencies.

To quantify the dynamics at which population cycles exhibit synchrony or overlap, we can evaluate the change in the amplitude of the generation cycle. The generation cycle amplitude

g_t is calculated from the wavelet as

$$(104) \quad \hat{g}_t = 2 \frac{0.6 \sqrt[4]{\pi} \sqrt{d}}{0.776} \sum_{j=A_0}^{A_1} \frac{\|W_t(a_j)\|}{\sqrt{a_j}}$$

where $\|\dots\|$ denotes the vector norm of the complex number (modulus). The time-series of the generation cycle amplitude can be treated as any regular time series and evaluated for changes through time, such as through auto-regressive models, or for relationships with environmental variables. The main steps in using wavelets to determine if cycles are sustained or transient are:

- (1) Use linear interpolation to project observed dynamics onto an equally spaced time axis. The total number of projected observations should be the same as the raw data.
- (2) Carryout the wavelet transformation using a high-resolution frequency scale. In practice, this may require dividing the frequency scale into hundreds or thousands of intervals to achieve a quality reconstruction.
- (3) Reconstruct the full time-series using Equation 3 and compare the reconstructed time-series with raw data to ensure quality reconstruction.
- (4) Define the frequency range of the generation cycle. In practice, we have used 5% of the dominant generation cycle period, but this will likely depend on the system.
- (5) Extract the generation cycle dynamics using Equation 3 with modified frequency limits.
- (6) Calculate the change in amplitude of the generation cycle using Equation 4.
- (7) Evaluate the change in generation cycle amplitude against time or environmental variables.

An example R script is given below.

```
library(Rwave)
#x is a vector of evenly spaced time units
#y is a vector of population abundance at each x

#establish upper and lower band thresholds
#here they are centered on phi=65
SA.L=65*0.95;SA.U=65*1.05

#establish wavelet frequencies
```

```

no=15;nv=2^9;a=2^seq(1, no+1-1/nv, by=1/nv)

#estimating the wavelet
wfit=cwt(y,no,nv,plot=F)
wspec=Mod(wfit) #calculate the wavelet modulus

#select specific frequencies within the wavelet
ind=(a*diff(x)[1]<SA.U & a*diff(x)[1]>SA.L)

#calculate wavelet amplitude
wavelet.AMP=2*0.6*sqrt(diff(x)[1])*Mod(apply(wfit[,ind]/sqrt(a[
ind]),1,sum))/(0.776*(pi^(-1/4)))

```

3.2. Circular Dispersion Analysis. Circular variance (V) is calculated as $V = 1 - R$ (Fisher 1993), where R is known as the order parameter (also referred to as the resultant length). The order parameter is the average vector length among individuals when they are all placed on a circle based on their development index. It is given by

$$(105) \quad R = \frac{1}{n} \sqrt{\left(\sum_{i=1}^n \cos \theta_i\right)^2 + \left(\sum_{i=1}^n \sin \theta_i\right)^2}$$

where θ_i is the development index in radians for individual i and n is the total number of individuals. This calculation for circular variance assumes that the development index for each individual is known. However, in many instances we will only know the specific stage of an individual (e.g., larvae, pupae), which means that the individual could be anywhere within a range of development indices. Circular variance for stage-structured data can be calculated by assuming that the density of individuals in a stage is evenly distributed over the interval of development indices for that stage. Equation (105) can be modified by integrating over the interval of development indices for each stage. Specifically,

$$(106) \quad R_L = \frac{1}{\sum_{i=1}^k y_i} \sqrt{\left(\sum_{i=1}^k h_i \int_{\theta_{i-1}}^{\theta_i} \cos x dx\right)^2 + \left(\sum_{i=1}^k h_i \int_{\theta_{i-1}}^{\theta_i} \sin x dx\right)^2}$$

where i denotes the stage with development indices in the range θ_{i-1} to θ_i , and h_i is the mean density per unit development index

$$(107) \quad h_i = \frac{y_i}{\theta_i - \theta_{i-1}}$$

Taking the integrals, this simplifies to

$$(108) \quad R_L = \frac{1}{\sum_{i=1}^k y_i} \sqrt{\left(\sum_{i=1}^k h_i(\sin \theta_i - \sin \theta_{i-1})\right)^2 + \left(\sum_{i=1}^k h_i(\cos \theta_{i-1} - \cos \theta_i)\right)^2}$$

In cases where it is not possible to collect data on all stages, we must take care with the calculation of circular variance because missing data has the same effect as having zero abundance, which causes a bias in the estimate of circular variance. If the observed stages are spaced relatively even around the development circle (e.g., measures of larval and adult density, but not egg or pupal density), then some bias can be removed by redistributing the development indices over the full 2π unit circle. Specifically, if ϕ_{i-1} and ϕ_i define the radian limits for stage i when there are missing stages, the normalized angles are given by

$$(109) \quad \theta_i = \begin{cases} 0 & \text{if } i = 0 \\ \theta_{i-1} + 2\pi \frac{\theta_i - \theta_{i-1}}{\sum_{j=1}^k (\theta_j - \theta_{j-1})} & \text{if } 0 < i < k \\ 2\pi & \text{if } i = k \end{cases}$$

An example R script is given below.

```
#the following function calculates circular dispersion

CircVar=function(y,theta.start,theta.end){
#y is an array where rows are time and columns are stages, but
  with no time index.
#Theta.start is the start developmental index (DI) for each
  stage, and theta.end is the end DI for each stage

p=(theta.end-theta.start)/sum(theta.end-theta.start)

#normalize theta for missing stages
theta.start=c(0,2*pi*cumsum(p[-length(p)]))
theta.end=2*pi*cumsum(p) #normalize theta for missing stages

if(length(dim(y))==0){y=matrix(y,nrow=1,ncol=length(y))}
diff.theta=matrix(theta.end-theta.start,nrow=dim(y)[1],ncol=dim
  (y)[2],byrow=T)
cos.theta1=matrix(cos(theta.start),nrow=dim(y)[1],ncol=dim(y)
  [2],byrow=T)
```

```
cos.theta2=matrix(cos(theta.end),nrow=dim(y)[1],ncol=dim(y)[2],
  byrow=T)
sin.theta1=matrix(sin(theta.start),nrow=dim(y)[1],ncol=dim(y)
  [2],byrow=T)
sin.theta2=matrix(sin(theta.end),nrow=dim(y)[1],ncol=dim(y)[2],
  byrow=T)
R=sqrt(rowSums((y/diff.theta)*(sin.theta2-sin.theta1))^2+
  rowSums((y/diff.theta)*(cos.theta1-cos.theta2))^2)/rowSums(y
  )
return(1-R)
}
```

4. DISENTANGLING GENERATION SEPARATION FROM DEVELOPMENTAL SYNCHRONY

Generation separation and developmental synchrony are often used synonymously in the literature. However, as we illustrate here through simulations, they are not necessarily linked. Consider a cohort of individuals in a population with stable population dynamics. Owing to variation in larval development times (Fig. 2) and reproduction over a the adult reproductive period, the subsequent generation will be distributed over a wider range of times (e.g., blue line in Fig. S3). If we follow the generation mapping for some time, we find that the generations are represented by an increasingly wide distribution of times (Nisbet et al. 1989). If the population started with a single cohort, the generations would begin to overlap rather quickly. Coincidental with generation overlap, the population will also have individuals at multiple developmental stages giving rise to increasing developmental asynchrony.

Now consider a cohort of individuals in a population with unstable population dynamics. To illustrate, we assume that density dependence is in mortality, but not the birth or development rates (ESM 2). Since the birth and development rates are the same as the stable population dynamics, subsequent generations of the initial cohort will still be distributed over a wider range of times (e.g., orange line in Fig. S3). Despite the fact that the population cycles cause temporal variation in mortality, the generations will start to overlap through time. Unstable dynamics, however, can have a disproportionate effect on stage-specific mortality, which means that the distribution of developmental stages is resynchronized each cycle. The net result is that while cyclic dynamics generate strong developmental synchrony compared to stable dynamics, the generations do not remain distinct.

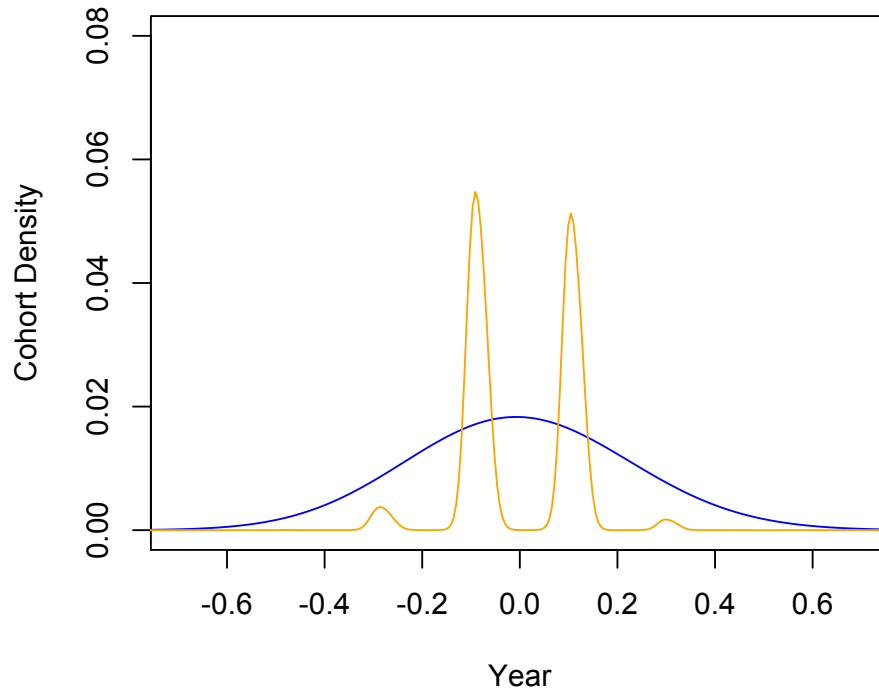


FIGURE S3. Distribution of the 90th generation under stable (blue line) and cyclic (orange line) dynamics. The model is as given in Fig. 6. The x-axis shows the year relative to the mean age of the 90th generation.

REFERENCES

- Breda D, Diekmann O, Graaf WD, Pugliese A, Vermiglio R (2012) On the formulation of epidemic models (an appraisal of Kermack and McKendrick). *J Biol Dyn* 6:103-117
- Danthanarayana W (1975) Factors determining variation in fecundity of the light brown apple moth, *Epiphyas postvittana* (Walker) (Tortricidae). *Aust J Zool* 23:439-451
- Danthanarayana W, Gu H, Ashley S (1995) Population growth potential of *Epiphyas postvittana*, the Lightbrown Apple Moth (Lepidoptera, Tortricidae) in relation to diet, temperature and climate. *Aust J Zool* 43:381-394
- de Valpine P, Scranton K, Knape J, Ram K, Mills NJ (2014) The importance of individual developmental variation in stage-structured population models. *Ecol Lett* 17:1026-1038
- Fisher NI (1993) *Statistical Analysis of Circular Data*. Cambridge University Press, Cambridge
- Kodomari S, Tatara A, Kosugi Y, Nishijima, T (2003) *Visual guide of the tea pests and pathogens*. Chamber of Tea Association of Shizuoka Prefecture, Shizuoka (in Japanese)
- Luciani MA (1987) The biology of the grape berry moth, *Endopiza viteana*, Clemens (Lepidoptera: Tortricidae) in Southern Ontario. University of Guelph, Guelph, Ontario
- MacDonald N, MacDonald N, Cannings C, Hoppensteadt FC (2008) *Biological delay systems: linear stability theory*. Cambridge University Press, Cambridge
- Nabeta FH, Nakai M, Kunimi Y (2005) Effects of temperature and photoperiod on the development and reproduction of *Adoxophyes honmai* (Lepidoptera: Tortricidae). *Appl Ent Zool* 40: 231-238
- Nelson WA, Bjørnstad ON, Yamanaka T (2013) Recurrent insect outbreaks caused by temperature-driven changes in system stability. *Science* 341:796-799
- Nisbet RM, Gurney WSC Metz, J. A. J. (1989). Stage structure models applied in evolutionary ecology. In: Levin SA, Hallam TG, Gross LJ (eds) *Applied Mathematical Ecology*. Springer-Verlag, Berlin, pp 428-449
- Tobin PC, Nagarkatti S, Saunders MC (2003) Phenology of grape berry moth (Lepidoptera: Tortricidae) in cultivated grape at selected geographic locations. *Environ Entomol* 32:340-346
- Torrence C, Compo GP (1998) A practical guide to wavelet analysis. *B Am Meteorol Soc* 79:61-78
- Yamanaka T, Nelson WA, Uchimura K, Bjørnstad ON (2012) Generation separation in simple structured life cycles: models and 48 years of field data on a tea tortrix moth. *Am Nat* 179:95-109