Appendix from I. Filin and O. Ovadia, "Individual Size Variation and Population Stability in a Seasonal Environment: A Discrete-Time Model and Its Calibration Using Grasshoppers"

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Supplemental Derivations and Explanations of the Model and Its Calibration

An Analytical Formulation of Seasonal Life Cycles

A fundamental life-table expression asserts that the net reproductive rate is given by

$$\lambda = \sum_x b_x S_x, \tag{A1}$$

where x represents age; b_x and S_x are age-dependent reproduction and survival, respectively; and the summation is carried over all ages for which there is nonzero reproduction. In our model, reproductive events occur at ages $x = T_m + T_c, T_m + 2T_c, T_m + 3T_c, \ldots, T_m + \nu T_c$, where $\nu = \nu(T_m, T)$ is the maximal number of clutches, given season length T and time to maturity T_m. Age-dependent survival is the product of survival from egg laying to maturity times survival from maturity to postmaturation age x. The former is incorporated in equation (1) through C and S_m (see "Model Development" and the next section). The latter is simply given by $\exp[-\mu_m \times (x - T_m)]$, because adult mortality μ_m is constant (i.e., in the context of this model, independent of initial size).

In addition, because we assume that egg production rate is constant, clutch size at all ages (i.e., b_x) is given by (egg production rate $\times T_c$), where egg production rate is also incorporated into the parameter C. Consequently, the life-table expression for net reproductive rate (eq. [A1]) is now given by

$$\lambda = C \times S_m \times T_c \times \sum_{j=1}^{\nu} \exp(-j \times \mu_m T_c). \tag{A2}$$

It is now straightforward to see that the summation term describes the sum of a geometric series, which, combined with T_c of the right-hand side of equation (A2), produces equations (2) for the reproductive life span (RLS; compare eq. [A2] to eq. [1]). In the rest of this section, we compare this model with previous formulations of seasonal life cycles.

Grant et al. (1993) presented the following expression for the finite rate of increase of an allele based on a model of grasshopper life cycles derived by Sibly and Monk (1987; see also Willott and Hassal 1998):

$$e^F = \frac{(1/2) \times n \times e^{-\mu_1 t_1 - M} \times (1 - e^{-m \times \mu_2 t_2})}{1 - e^{-\mu_2 t_2}}, \tag{A3}$$

where n = number of eggs in a single clutch; μ_1, μ_2 = juvenile and adult mortality rates, respectively; M = overall egg mortality; t_1 = time to first oviposition; t_2 = time interval between clutches; m = maximal number of clutches that can be laid during the season. In equation (A3), e^F is equivalent to our λ, but because we consider the rate of increase of the population and not of specific alleles, the factor (1/2) in the right-hand side of the equation is not included in our model (a factor of 1/2 nonetheless enters the formulation through sex ratio; see below).

Clearly, our T_c is equivalent to t_2 of Grant et al. (1993), and our μ_m is equivalent to their μ_2. Our $\nu(T_m, T)$ is represented by m in their model. The number of eggs per clutch, n, is given in our formulation by (egg production rate) $\times T_c$, that is, the rate of egg production multiplied by the interclutch interval. Subsequently, we incorporate the T_c of this latter product into the expression for RLS (eqq. [2]), and the egg production rate is

included in the parameter C. Time to first oviposition is the sum of time to maturity and time from maturity to first oviposition, that is, $t_1 = T_m + T_c$.

The expression of Grant et al. (1993) for survival to first oviposition, $\exp(-\mu_1 \times t_1)$, is represented in our model by $S_m \times \exp(-\mu_m T_c)$, where $\exp(-\mu_m T_c)$ is subsequently incorporated in equations (2) for the RLS. Our formulation using S_m is more general than that of Grant et al. because we do not assume that juvenile mortality is constant. Moreover, we assume that during the interval between maturity and first oviposition, individuals die according to the adult mortality rate and not the juvenile mortality rate, as in Grant et al. Finally, egg survival, $\exp(-M)$, is also incorporated in our model within the parameter C. The remaining terms of equation (A3) are incorporated in the expression for the RLS (eqq. [2]). These terms represent the sum of the geometric series of survivorships at each oviposition event, as given by equation (A2).

Equations (1) and (2) are very similar to expressions that Kozlowski and Wiegert (1986) derived for life span reproductive allocation in the context of a model for optimal size at maturity. Total life span reproductive allocation is represented by the instantaneous rate of reproductive allocation multiplied by the average duration of energy allocation to reproduction, as evaluated at birth (their eqq. [4], with $\alpha = 0$). This is equivalent to our equation (1): the first term in the product corresponds to our C (which, however, also includes mortality factors in our model); the second term corresponds to our $S_m \times$ RLS, because we consider reproductive life span as evaluated at maturity (and not at birth, as Kozlowski and Wiegert [1986] did). In fact, substituting equations (2) in the product $S_m \times$ RLS gives an expression almost identical to that of Kozlowski and Wiegert (1986) for their case of reproduction in clutches (their eq. [17]; the expressions are not identical, however, because Kozlowski and Wiegert [1986] did not account for the fact that the last clutch produced is often not laid because the season ends and the mother dies while still producing it).

Components of the Parameter C and Their Empirically Based Estimates

Survival to maturity, S_m, refers in our model to the survival from some initial juvenile stage (specifically, we consider the second instar stage to be the initial stage). Mortality at the adult stage is accounted for in the RLS (see eqq. [2]). Earlier mortality is incorporated in the parameter C. In addition, C includes both the per capita egg production rate of a female and a factor smaller than 1 that represents the sex ratio of the population, that is, the proportion of females in the population (representing the fact that only females produce and lay eggs). The parameter C is therefore the product of all these components:

$$C = \text{sex ratio} \times \text{egg production rate} \times \text{survival to hatching} \times \text{early juvenile survival}. \qquad \text{(A4)}$$

Given empirical estimates of sex ratio and the rate of egg production (table 1), the other two components in equation (A4) were estimated by setting $C = 0.084$ day^{-1}, to produce an equilibrium density of 16 m^{-2} (typical field densities of *Melanoplus femurrubrum* second instars; Ovadia and Schmitz 2002) when season length is 90 days (this procedure is described in the following section). In other words, (survival to hatching) = (early juvenile survival) = square root of $[0.084/(0.5 \times 2)] = 0.29$ (as given in table 1). This value is at the low end of the range of reported estimates for egg and first-instar survivorships (Joern and Gaines 1990; Grant et al. 1993; Beckerman 2002), and it may be because we overestimated egg production, which is expected to drop as the season progresses (e.g., Joern and Gaines [1990] present data for within-season reduction in egg production by a factor greater than 2). Another reason may be that there was no consideration to stochastic variation in season length in the calculation of C. But when this is corrected by considering a uniform distribution of season lengths between 60 and 120 days, the estimate rises only slightly to 0.3.

Survival and Time to Maturity as Determined by Size-Specific Mortality and Growth: Some Theoretical Considerations

In general, survival from initial time t_0 to some subsequent time t_m is related to instantaneous mortality through the expression

$$S(t_0, t_m) = \exp\left(-\int_{t_0}^{t_m} \mu(t)dt\right). \tag{A5}$$

Given that growth also occurs, one can rewrite equation (A5) in terms of size, rather than time:

$$S(z_0, z_m) = \exp\left(-\int_{z_0}^{z_m} \frac{\mu(z)}{g(z)}dz\right), \tag{A6}$$

where $\mu(z)$ and $g(z)$ are size-specific instantaneous mortality and growth rates, respectively (Werner and Gilliam 1984). Based on equation (A6), we find

$$\frac{d\ln S_m}{dz_0} = \frac{\mu(z_0)}{g(z_0)}, \tag{A7}$$

and, therefore, the way survival to maturity S_m varies with initial size z_0 depends on how the ratio μ/g changes with initial size.

We first note that the relationship $S_m(z_0)$ is predisposed to be convex (i.e., concave up) because of the exponent in equation (A6). That means that if μ/g is independent of size, then we obtain a convex (specifically, exponential) relationship, that is, $S_m(z_0) = \exp[-\mu/g \times (z_m - z_0)]$. Moreover, the relationship is also convex wherever μ/g increases with size. This may occur, for example, if mortality rate is constant and growth rate decreases with size.

The situation becomes more complex if μ/g decreases with size. This is also the most biologically realistic case, because not only does survival increase with initial size, mortality is expected to decrease as initial size increases. Moreover, for the initial phase of growth (i.e., for the size range encompassed by initial sizes), growth rate is expected to increase with size. When μ/g decreases with size, we can obtain concave, convex, linear, or sigmoid relationships between survival to maturity and initial size.

The following simple example will serve to demonstrate that it is not straightforward to determine the shape of $S_m(z_0)$ just from the functional form of size-specific mortality and growth. Given constant juvenile mortality μ_j, and size-specific growth rates that are proportional to size $g(z) = g_0 \times z$ (resulting in exponential growth), we obtain

$$S_m(z_0) = \left(\frac{z_0}{z_m}\right)^{(\mu_j/g_0)}. \tag{A8}$$

This relationship can be convex, concave, or linear, depending on whether the ratio μ_j/g_0 is greater than, less than, or equal to 1 (respectively). Therefore, in order to determine the shape of $S_m(z_0)$, it is not enough to know the general functional form of μ/g with respect to size; the specific value of this ratio is also important.

Another example is that when growth rate is constant ($g = $ constant) and mortality decreases linearly with size, $\mu(z) = \mu_m + \mu_0 \times (z_m - z)$, one obtains a Gaussian (i.e., sigmoid) form of survival. Therefore, $S_m(z_0)$ is either concave or convex, depending on where actual initial sizes of individuals cluster.

Time to maturity can be found through the expression

$$T_m(z_0) = \int_{z_0}^{z_m} \frac{dz}{g(z)}, \tag{A9}$$

which for the scenario described by equation (A8) becomes

$$T_{\mathrm{m}}(z_0) = \frac{1}{g_0}\ln\left(\frac{z_{\mathrm{m}}}{z_0}\right), \tag{A10}$$

or, given equations (2),

$$\mathrm{RLS}(z_0) = \mathrm{RLS}_{T=\infty} \times \left[1 - e^{-\mu_{\mathrm{m}}T} \times \left(\frac{z_0}{z_{\mathrm{m}}}\right)^{(\mu_{\mathrm{m}}/g_0)}\right], \tag{A11}$$

when reproduction is continuous (T_{c} goes to zero). Again, equation (A11) can describe either a concave or a convex relationship, depending this time on the ratio of adult mortality to relative growth rate μ_{m}/g_0. (Recall that for this scenario survival to maturity depends on the ratio of juvenile mortality to relative growth rate, μ_{j}/g_0, rather than adult mortality; eq. [A8].)

Description of Size Classes and Size Variation in the *Melanoplus femurrubrum* System

Initial size refers to that of second instars ("Model Calibration") and not to size at hatching. We consider three initial-size classes of second-instar nymphs (after Ovadia and Schmitz 2002): small (body length < 9 mm; mean size ± SE: 8.106 ± 0.123 mm), average (9–12 mm; 10.157 ± 0.085 mm), and large (>12 mm; 13.1 ± 0.45 mm). Additionally, we numerically denote the three size classes as 1, 2, and 3. Survival to maturity and time to maturity (S_{m} and T_{m}, respectively), reproductive life span, and the product $S_{\mathrm{m}} \times \mathrm{RLS}$ (eq. [5]) will all be described as functions of size class, rather than of size per se (i.e., body length). In other words, values on a body-size axis will be 1, 2, or 3 and not body lengths in millimeters.

   The naturally occurring frequency distribution of these size classes is 15%, 70%, and 15%, for small, average and large, respectively (Ovadia and Schmitz 2002). We will additionally consider two hypothetical distributions in order to demonstrate how size variation may affect population dynamics. The first describes a homogenous population, in which all members are average (i.e., 0%, 100%, 0%). The second is a uniform distribution, with equal representation of all three size classes (i.e., 33.33%, 33.34%, 33.33%). A homogenous population describes the extreme case of no size variation in the population, while a uniform distribution describes the extreme case of maximal variation. (A bimodal distribution with many small and large and a few average individuals may describe a higher level of variation, but given the observed unimodality of the distribution in the field, we limit ourselves to uniform variation as the case of maximal variation.). Finally, we note that the mean size class value for all three distributions is 2. By choosing such frequency distributions, therefore, we keep the mean of the distribution fixed, while changing only the variance. This allows us to study the effect of size variation alone, without the confounding effects of changes in mean initial size.

Estimating Density Dependence of Survival and Time to Maturity

We used data on the survival and growth of second instars in field cages, given three different initial-density treatments (16, 24, and 32 m^{-2}), three different initial-size treatments (described in the text), and two predator treatments (presence/absence; Ovadia and Schmitz 2002; O. Ovadia, unpublished data). A three-way ANOVA showed that the mean relative growth rate of grasshoppers (log[final size/initial size] divided by 26 days) varied significantly only by initial-size class ($F = 146.0$, df $= 2, 168$, $P < .001$). All other main and interaction effects were nonsignificant. Therefore, we did not incorporate density dependence into time to maturity. Tukey-Kramer multiple comparisons showed that the mean growth rate differed significantly among all size classes.

   A three-way ANOVA of log (survival) showed a significant effect of initial size ($F = 137.4$, df $= 2, 248$, $P < .001$) and of initial density ($F = 12.9$, df $= 2, 248$, $P < .001$). The effect of predator treatment and all interaction effects were nonsignificant. This result suggests that the form of density dependence described by equation (6) is appropriate in our case (specifically, because of no size × density interaction). Moreover, Tukey-Kramer multiple comparisons showed that mean survival to maturity was significantly different among all density treatments, closely following a linear relationship (as in the log of eq. [6]). Yet such multiple comparisons also demonstrated that mean survival to maturity of the small-size class differed significantly from that of the average- and large-size classes but did not differ between the latter two. Therefore, the effect of initial size on survival is nonlinear (as is indeed apparent in fig. 2).

Given these results for survival, we used multiple regression of log (survival) on density, initial body length, and the square of initial body length, based on the data of figure 2 ($R = 0.986$, df $= 2$, $P < .001$). The estimated coefficient of density is identified as α in equation (6) and was found to be 0.0152 m^2 (95% confidence interval: [0.0130, 0.0174]). Additionally, as expected from the nonlinear effect of initial-size class, both the linear and the quadratic terms of body length possessed coefficients significantly different from zero, further suggesting that no overfitting of the data was done and that the fitted model (based on eq. [6]) is an appropriate description of the survival data.

Season Length and Adult Mortality

First instars begin to emerge during either mid-June or early July (e.g., Ovadia and Schmitz 2004b). Adult-killing frosts may occur as early as mid-September or as late as the end of October and early November (Beckerman 1999). Therefore, we assert that season length for *M. femurrubrum* varies between 55 and 120 days. This range of season lengths lies below that reported for British grasshoppers. Grant et al. (1993) referred to 120 days as the minimum season length in southern England and to 70 days as unrealistically short (they consider season lengths of up to 190 days). They criticized a previous study by Sibly and Monk (1987), who considered much shorter season lengths, well within the range of 55–120 days considered here. Their disagreement mainly concerned the importance of season length in the evolution of grasshopper life cycles.

As discussed in the main text, the population growth rate λ (equivalent to fitness in Sibly and Monk 1987; Grant et al. 1993) becomes less sensitive to season length as seasons become longer. The relevant quantity here is $\mu_m(T - T_m)$ (see eqq. [2]–[4]), and therefore, the importance of season length to life-history evolution, as well as to population dynamics, must be considered with regard to both adult mortality and time to maturity. Adult mortality μ_m for British grasshoppers typically lies between 0.03 and 0.14 day^{-1} (Sibly and Monk 1987; Grant et al. 1993). Additionally, mortality rates may substantially vary between years (Belovsky and Joern 1995; Beckerman 2002; Ovadia and Schmitz 2004b). In this study, we are concerned mainly with variation in the initial size of individuals and in season length. Thus, we consider a fixed adult mortality of 0.035 day^{-1} (based on the results of Oedekoven and Joern [1998] for *Melanoplus sanguinipes*; see also Willott and Hassal 1998), who used 0.04 day^{-1} in order to obtain fitness estimates of four British grasshoppers].

Estimating Time to Maturity

Despite criticism by Grant et al. (1993), various studies (e.g., Sibly and Monk 1987; Wall and Begon 1987a; review in Joern and Gaines 1990) suggest that smaller individuals take longer to develop. In fact, the insertion of an additional instar stage during development, which Grant et al. (1993) suggested as a way to compensate for small size at hatching (see also Willott and Hassal 1998), may itself cause a relationship between initial size and time to maturity. We obtained two possible estimates of time to maturity as a function of initial size, based on two independent sources. First, Vickery et al. (1981) reported the length of nymphal periods for five- and six-instar life cycles of *M. femurrubrum*. If individuals of our smallest size class go through a six-instar life cycle to compensate for their small initial size, we obtain (based on Vickery et al. 1981) nymphal periods of 44.1 and 41.5 days for our small- and average/large-size classes, respectively. These values are termed "T_m estimate 1."

A second estimate of time to maturity was obtained using growth data of second instars in field cages (Ovadia and Schmitz 2002, 2004a; O. Ovadia, unpublished data). These data give the following estimate of size-dependent time to maturity: 45.4 days for the small-size class, 41.6 days for the average class, and 36.2 days for the large class. These values are termed "T_m estimate 2."

In order to estimate time to maturity from field cage data, we used body length measurements of individual grasshoppers in field cages through the course of the season (O. Ovadia and O. J. Schmitz, unpublished data). We fitted a Gompertz growth curve to the data, using nonlinear regression and obtained the growth equation coefficients. Time to maturity was then estimated using 22 mm as the adult body length (this is a typical adult size in the old-field system that was studied; Schmitz and Suttle 2001; Ovadia and Schmitz 2002). Finally, because in using these data we could only estimate the time between second-instar and adult stages, we added 12.5 days based on Vickery et al. (1981; first-instar duration + half of the second-instar duration).

Modifying the Parameter *C* to Account for Different Equilibrium Densities

In our Ricker model of density dependence (eq. [6]), the equilibrium density is given by

$$N^* = \frac{\ln\{E[S_m(z_0, 0) \times \text{RLS}]\} + \ln C}{\alpha}. \tag{A12}$$

Given equation (A12), we note that equilibrium density depends on the parameter C and on the population mean $S_m \times \text{RLS}$, given some distribution of initial sizes. In addition, we can modify the parameter C to obtain different equilibrium densities. The different equilibrium densities considered in the subsection on population stability in the deterministic case were obtained by modifying C, where the mean $S_m \times \text{RLS}$ is given for normal size variation. This is most readily interpreted as variation in egg and/or first-instar survival (eq. [A4]). For example, if $N^* = 16$ m^{-2}, then we obtain egg and juvenile survival of 0.29 each (as in table 1; giving $C = 0.084$ day^{-1}). To obtain an equilibrium density of $N^* = 130$ m^{-2}, these two survival rates both increase to 0.69 (giving $C = 0.47$ day^{-1}). (This latter value of egg/first-instar survivorship is at the high end of the range of values reported for grasshoppers; Joern and Gaines 1990; Grant et al. 1993; Beckerman 2002.)

Continuous vs. Discontinuous Reproduction

We substitute $T_c = 1$ (day) in the expression for RLS (eqq. [2]). Consequently, RLS increases in a more continuous manner with season length (fig. A1; cf. fig. 1), and as a result, $\ln \lambda$ also changes continuously with season length (as opposed to the few discrete values presented in fig. 6).

Figure A2 is equivalent to figure 6 but for continuous reproduction. It presents the curves of population growth rate versus size variation for all season lengths within a given range. A comparison with figure 6 highlights several differences between continuous and discontinuous reproduction: (1) for continuous reproduction, there are as many $\ln \lambda$ curves as there are different values of season length; (2) $\ln \lambda$ always decreases with size variation, unlike in the discontinuous case; (3) the range of values of $\ln \lambda$ always decreases with size variation (compare with fig. 6a, 6c). Nonetheless, size variation enhances population stability by decreasing the variance of $\ln \lambda$ in all cases (table A1), although this effect is weaker for the continuous than for the discontinuous case (cf. percentages in tables 4, A1).
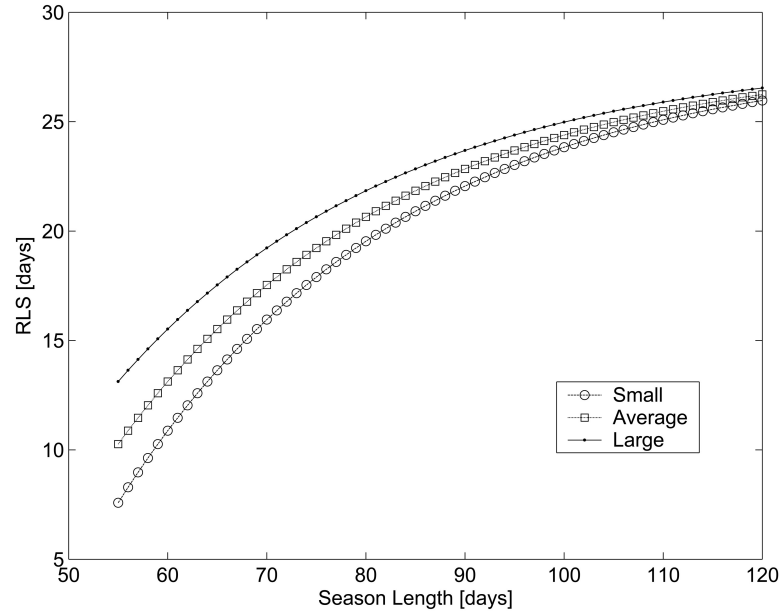
Figure A1: Reproductive life span (RLS) as a function of season length for three initial size classes (denoted *small*, *average*, and *large*). In this case, reproduction is continuous, and the interclutch period, T_c, is set at 1 (day); consequently, $\mathrm{RLS}_{T=\infty} = 28.07$ days (cf. fig. 1).
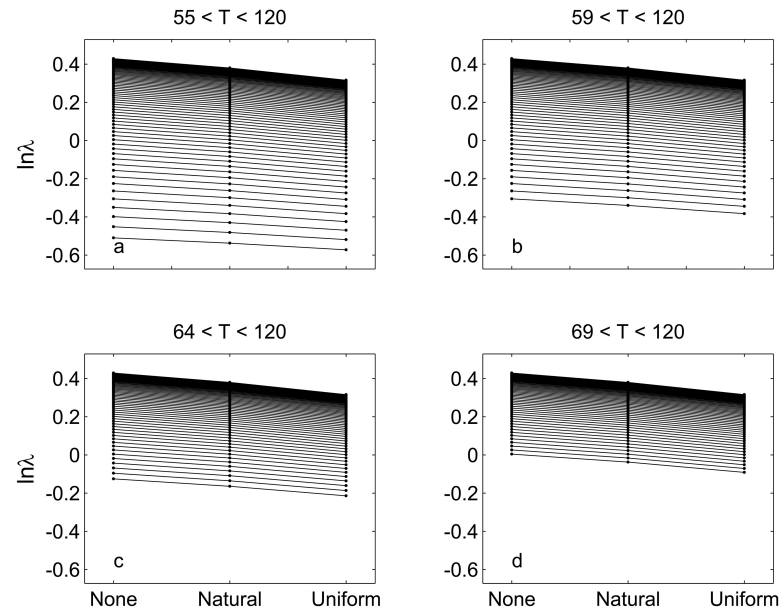

Figure A2: Curves of $\ln \lambda$ versus size variation, when reproduction is continuous (as opposed to discontinuous; cf. fig. 6).

Table A1

Environmental standard deviations of $\ln \lambda$ ($SD_{\ln \lambda}$; i.e., square root of the variance in $\ln \lambda$), based on figure A2 (continuous reproduction)

	$55 < T < 120$		$59 < T < 120$		$64 < T < 120$		$69 < T < 120$	
None	.2485	102.15%	.1997	101.97%	.1544	101.82%	.1205	101.72%
Natural	.2432	100.00%	.1958	100.00%	.1516	100.00%	.1185	100.00%
Uniform	.2362	97.11%	.1906	97.34%	.1479	97.53%	.1157	97.66%

Note: Season lengths are given in days. All season lengths within a given range occur with equal probability.