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Individual Size Variation and Population Stability in a Seasonal Environment: A Discrete-Time Model and Its Calibration Using Grasshoppers

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ABSTRACT: Much recent literature is concerned with how variation among individuals (e.g., variability in their traits and fates) translates into higher-level (i.e., population and community) dynamics. Although several theoretical frameworks have been devised to deal with the effects of individual variation on population dynamics, there are very few reports of empirically based estimates of the sign and magnitude of these effects. Here we describe an analytical model for size-dependent, seasonal life cycles and evaluate the effect of individual size variation on population dynamics and stability. We demonstrate that the effect of size variation on the population net reproductive rate varies in both magnitude and sign, depending on season length. We calibrate our model with field data on size- and density-dependent growth and survival of the generalist grasshopper *Melanoplus femurrubrum*. Under deterministic dynamics (fixed season length), size variation impairs population stability, given naturally occurring densities. However, in the stochastic case, where season length exhibits yearly fluctuations, size variation reduces the variance in population growth rates, thus enhancing stability. This occurs because the effect of size variation on net reproductive rate is dependent on season length. We discuss several limitations of the current model and outline possible routes for future model development.

Keywords: body size, individual variation, population stability, seasonal environment, univoltine lifecycle.

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Ecological entities are organized hierarchically into different levels of organization, such as the individual, the population, and the community (MacMahon et al. 1987; Allen and Hoekstra 1992; Pickett et al. 1994). The way in which these different organizational levels combine to influence the dynamics of natural systems remains a fundamental research topic in ecology (Lomnicki 1988; Nisbet et al. 1989; Abrams 1995; Levin et al. 1997; Schmitz 2001). Such research is motivated by the need to understand the level of mechanistic biological detail that must be included in ecological theory as well as how much can be safely abstracted while still achieving biologically faithful and quantitatively accurate descriptions of population and community dynamics.

In the past 30 years, ecologists have become increasingly interested in linking individual phenotypic variation (in behavior, morphology, physiology, and life history) to population and community dynamics (e.g., Lomnicki 1978; Metz and Diekmann 1986; Begon and Wall 1987; Ebenman and Persson 1988; Nisbet et al. 1989; Bjørnstad and Hansen 1994; Uchmanski 1999; Schmitz 2000; de Roos et al. 2003). Specifically, many theoretical studies have demonstrated how age, stage, and size structure; cohort effects; and other forms of individual variation (e.g., in developmental and growth rates or in competitive ability) have important consequences for population dynamics, stability, and persistence (e.g., Bellows 1986a, 1986b; Lomnicki 1988; Bjørnstad and Hansen 1994; de Roos 1997; Uchmanski 2000; Kendall and Fox 2001; Grimm and Uchmanski 2002; Lindström and Kokko 2002; Kendall and Fox 2003). For example, Persson et al. (1998) have shown how competitive interactions among different-sized cohorts may cause several types of population cycles. At the community level, Begon and Wall (1987) showed how variation in competitive ability within species facilitates coexistence.

Body size is a fundamental physiological trait that structures populations and influences all facets of an individual's function and performance, such as foraging (e.g.,

Belovsky 1997), growth rate (e.g., Pfister and Stevens 2002), and survival (e.g., Ovadia and Schmitz 2002). Invariably, besides variation linked to ontogenetic stage, phenotypic variation in body size exists within any natural population (e.g., Uchmanski 1985). This size variation translates into variation in survival and reproduction and may be both the cause and the consequence of differences in growth and competitive ability among individuals. For example, in a study of the dynamics of size variability in three distantly related organisms—a kelp, a whelk, and a sculpin—Pfister and Stevens (2002) showed marked variation in growth rates among individuals that often led to increasing size variability over time (i.e., growth depensation).

Wall and Begon (1987a) showed that there is substantial variation in size-related life-history traits (e.g., weight at maturity and time to maturity) within grasshopper populations. Such variation has important consequences for grasshopper population dynamics (Joern and Gaines 1990). Ovadia and Schmitz (2002) found that the survival rates of the grasshopper *Melanoplus femurrubrum* change as a function of body size. In addition, theoretical work at the community level showed that size variation markedly influences the strengths of trophic interactions as mediated through mean herbivore survival (Ovadia et al. 2007). Overall, both empirical studies and theoretical work emphasize that size variability is a fundamental property of natural populations, which has important ramifications for understanding the dynamics and stability of ecological systems.

Concerning population stability, Uchmanski (1999, 2000) and Grimm and Uchmanski (2002) investigated the effect of variability in body size on the stability and persistence of populations, using an individual-based model of consumer-resource dynamics. They demonstrated how variability in body size produces "imperfect regulation" that may enhance stability and persistence, that is, causes longer extinction times in comparison with homogenous populations. These results support earlier investigations that had already established the stabilizing consequences of individual variability on population dynamics (e.g., Lomnicki 1988). Bjørnstad and Hansen (1994), however, developed a general analytical framework for dealing with trait-related variation in vital rates. They have concluded that individual variation may have either a stabilizing or a destabilizing effect on population dynamics, depending on the form of trait dependence of survival and reproduction (i.e., either concave or convex). Similar conclusions have been reached by Lindström and Kokko (2002) in the context of cohort effects and by Kendall and Fox (2001, 2003) concerning demographic stochasticity.

In this study, we consider the effects of variation in individual size on population dynamics and stability of a generalist herbivore in a seasonal environment. A recent synthesis by Murdoch et al. (2002) has demonstrated that the dynamics of generalist consumers can be captured using single-species models rather than consumer-resource models. That is, the dynamics of the resource can be safely abstracted when considering generalist consumers. Therefore, we develop a single-species model using previous analytical formulations of seasonal life cycles (Sibly and Monk 1987; Grant et al. 1993; Willott and Hassal 1998). We incorporate size variation by using the theoretical framework of Bjørnstad and Hansen (1994) and explore how size variation affects the mean net reproductive rate, that is, the expected rate of population increase between seasons. A major issue in our study is the effect of size variation on the stability properties of population dynamics. We calibrate our analytical model with results of field observations and experiments on the generalist grasshopper *M. femurrubrum* inhabiting old fields in Connecticut (e.g., Schmitz et al. 1997; Schmitz and Suttle 2001; Ovadia and Schmitz 2002).

Our main theoretical conclusion is that the interaction between size variation and variability in season length among years determines both the sign and the magnitude of the effect of size variation on population stability. Size variation may either stabilize or destabilize population dynamics, depending on the range of possible season lengths and the functional forms of survival and time to maturity, with respect to initial size. For *M. femurrubrum*, we find that size variation should enhance population stability by decreasing the magnitude of relative fluctuations in density.

Model Development

Basic Formulations

We consider univoltine, seasonal life cycles that are characteristic of many insects living in seasonal environments, for example, temperate (Howard and Harrison 1984; Monk 1985) and arid (Antoniou 1978; Whitman 1988). Specifically, we consider a typical grasshopper life cycle (e.g., Sibly and Monk 1987), in which eggs overwinter in a state of embryonic diapause; first instars emerge in early summer; and growth, maturation, and reproduction occur within a relatively short time, often terminated by the seasonal onset of frosts that kill the arthropod community and cause herbaceous plants to senesce. Thus, the between-year population growth can be described mathematically using a discrete-time model: $N(t + 1) = \lambda \times N(t)$ (where t is measured in years). The net reproductive rate λ may depend on time t, population density N, and population structure $f(z)$, which is a frequency distribution function describing variation in some trait z of the individuals mak-

ing up the population (i.e., $\lambda = \lambda[N, t, f(z)]$). Specifically, we refer here to variation in body size; therefore, z will represent individual size. (We note that $f(z)$ can describe the distribution of either continuous size or discrete size classes; see also "Model Calibration.")

First we examine a homogenous population in which all the individuals share the same size throughout the entire season. We also assume both here and below (when we consider size variation) that all individuals begin their life at the same time (i.e., at the beginning of the season). For a homogenous population, we obtain $\lambda = \lambda(N, t, z_0)$, where z_0 represents the initial size of individuals (e.g., hatchling size). Individuals reach maturity at size z_m, that is, adult size, after time T_m. The time to maturity depends on initial size z_0 and final size z_m; hence, $T_m = T_m(z_0, z_m)$. Additionally, since individuals may die before reaching maturity, survival to maturity is represented by $S_m(z_0, z_m)$, which decreases as either initial size z_0 decreases or size at maturity z_m increases.

After reaching maturity, a female starts laying clutches at regular time intervals until the end of the season at $t = T$ (i.e., season length is denoted by T). The length of these interclutch intervals, T_c, is the time required for producing a clutch once the females are mature. Consequently, the maximal number of clutches that a mature female can produce is the integer part of $(T - T_m)/T_c$, denoted by $\nu(T_m, T)$. In addition, adults suffer mortality at a rate given by μ_m, which may depend on adult size (i.e., $\mu_m = \mu_m(z_m)$).

Given standard life-table formulations (see appendix in the online edition of the *American Naturalist*), we can obtain the following expression for the net reproductive rate:

$$\lambda(z_0, z_m) = C \times S_m(z_0, z_m) \times \mathrm{RLS}(T_m, T), \quad (1)$$

where C is a constant (considered below), and RLS is the expected reproductive life span of mature females. The RLS is the expectancy of the duration of successful reproduction, evaluated at the time of maturation. It accounts for the fact that reproductive allocation between consecutive ovipositions may fail to be translated into actual (successful) reproduction, because the female may die during the interclutch interval (see appendix). Consequently, RLS depends on adult mortality μ_m and the duration of interclutch intervals T_c in the following manner (see appendix for derivation):

$$\mathrm{RLS}(T_m, T) = \mathrm{RLS}_{T=\infty} \times (1 - e^{-\mu_m T_c \times \nu(T_m, T)}), \quad (2a)$$

$$\mathrm{RLS}_{T=\infty} = T_c \times \frac{e^{-\mu_m T_c}}{1 - e^{-\mu_m T_c}}. \quad (2b)$$

In addition, equations (2) demonstrate how RLS depends on season termination, that is, on the maximal time available for reproduction: $T - T_m$. Overall, the RLS (eq. [2a]) decreases with adult mortality μ_m and time to maturity T_m and increases with season length T to an asymptote, given by $\mathrm{RLS}_{T=\infty}$ (eq. [2b]). The dependence of RLS on season length is presented in figure 1 for a set of parameter values estimated from data on *Melanoplus femurrubrum* (see "Model Calibration"). As expected, because of punctuated reproduction in discrete clutches, RLS increases in a steplike fashion with season length. The magnitude of each increment in the RLS decreases gradually as seasons become longer, representing the asymptotic approach to $\mathrm{RLS}_{T=\infty}$. This asymptote occurs at very long seasons, because adult life expectancy is then determined only by adult mortality, regardless of season length or time to maturity, and reproductive activity is terminated by individual death within the season and not by season end. Finally, the decrease in RLS with increasing time to maturity is evident in figure 1 on comparison of the three curves for small, average, and large initial sizes (for which time to maturity is long, intermediate, and short, respectively).

The constant parameter C in equation (1) encompasses the rate of egg production by mature females, egg mortality during overwintering, hatching success, sex ratio (representing the fact that only females produce eggs), and any additional vital rates that must be considered in the life cycle and are assumed to be independent of initial size z_0. Note that although fecundity is expected to change with size at maturity z_m (e.g., Roff 2002, pp. 198–199), it can be included in the constant C because z_m is a fixed parameter in the model expressed by equation (1). Additionally, when we consider variation in initial size z_0, size at maturity z_m remains a fixed parameter, and therefore, fecundity can still be incorporated through the parameter C. A similar argument holds for adult mortality; that is, because z_m is the same for all individuals, μ_m (which may depend on z_m) is also a fixed parameter. Finally, including a continuous rate of egg production may at first seem incompatible with the usual discontinuous mode of grasshopper reproduction, that is, a discrete number of clutches, each containing several eggs that are oviposited simultaneously. However, this element has already been accounted for in the RLS (see appendix).

Reproductive Life Span and Definition of Long and Short Seasons

We explore two variants of equation (2a) for two extreme cases of season length. A long season is characterized by a long postmaturation period and/or high adult mortality
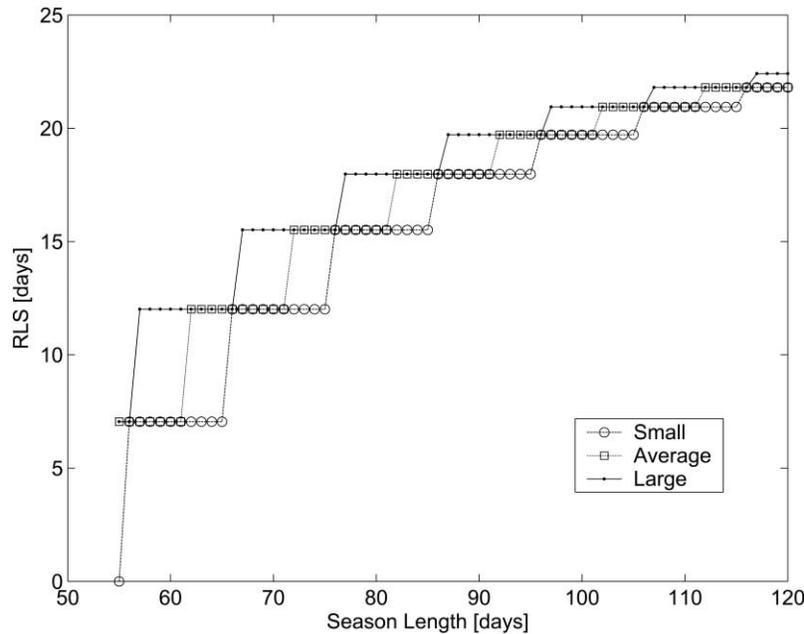
Figure 1: Reproductive life span (RLS) as a function of season length for three initial sizes (denoted "small," "average," and "large"). The specific curves displayed were obtained using parameter values for *Melanoplus femurrubrum*, as described in "Model Calibration." Notice that RLS increases discontinuously with season length because of the discontinuous mode of reproduction in clutches (one egg pod every 10 days). Steps occur whenever season length increases enough to allow yet another clutch to be produced before the end of the season (i.e., $\nu(T_m, T)$ increases by 1). In addition, the three RLS curves for the three size classes are, in fact, identical in form but are displaced along the season length (i.e., time) axis relative to one another. This is because of the differences in time to maturity between the three size classes. Finally, all curves asymptotically approach $\text{RLS}_{T=\infty}$ ($=23.86$ days) as season lengths increase.

rate, such that $\mu_m(T - T_m) \gg 1$. In that case, for the long-season scenario, equation (2a) reduces to

$$\text{RLS} \approx \text{RLS}_{T=\infty}. \tag{3}$$

Similarly, for short seasons, where $\mu_m(T - T_m) \ll 1$, that is, a short postmaturation period and/or low adult mortality, we obtain an equation for the short-season scenario:

$$\text{RLS} \approx \text{RLS}_{T=\infty} \times \mu_m T_c \times \nu(T_m, T). \tag{4}$$

Note that for long seasons, the RLS does not depend on season length or time to maturity. Rather, it depends only on adult mortality and the duration of the interclutch interval. All individuals mature, reproduce, and die during the course of the season, and they rarely survive to the end of the long season. Therefore, increasing season length will have no effect on the RLS. In contrast, when the season is short, most mature individuals die at the end of the season rather than during it. Therefore, an increase in season length translates into a significant increase in the RLS. Moreover, a decrease in the time to maturity also translates into an increase in the RLS (eq. [4]).

Substituting either equation (3) or equation (4) into the expression for the net reproductive rate (eq. [1]) shows that for long seasons, the initial size of individuals z_0 affects population dynamics only through survival to maturity, S_m. Conversely, for short seasons, initial size affects population dynamics via its effects on both survival to maturity and time to maturity (i.e., both S_m and T_m). In natural systems, season length will probably fluctuate between those two extremes, taking a range of intermediate values. Therefore, the sensitivity of population growth to variation in time to maturity may vary between years. Our general conclusion is therefore that season length may have important consequences for the effect of size variation on population dynamics, because λ may depend differently on initial size, depending on season length. This is the subject of the next subsection.

Incorporating Size Variation

Given variation in the initial size of individuals, that is, a distribution of initial sizes ($f(z_0)$), the population finite rate of increase becomes (Bjørnstad and Hansen 1994)

$$\lambda = C \times E[S_m(z_0) \times RLS(z_0)], \qquad (5)$$

where $E(\cdot)$ represents averaging over the initial size distribution (cf. eq. [1]). We note that in equation (5), only the dependence of S_m and RLS on z_0 is considered, because size at maturity z_m, adult mortality μ_m, interclutch duration T_c, and season length T are set as fixed parameters. We wish to describe how $E(S_m \times RLS)$ (i.e., the right-hand side of eq. [5]) changes with the mean $E(z_0)$ and variance ζ^2 of the initial size distribution.

Specifically, we wish to identify whether the population finite growth rate (λ; eq. [5]) increases or decreases when variation in initial size is introduced (i.e., as ζ increases) while holding the mean initial size ($E(z_0)$) fixed. As the variance in initial size increases, both individuals that are larger then average ($z_0 > E(z_0)$), and individuals that are smaller then average ($z_0 < E(z_0)$) increase in frequency. Because $S_m \times RLS$ is expected to increase with initial size (due to higher survival to maturity and shorter time to maturity), larger (than average) individuals will tend to increase the mean population growth rate (i.e., eq. [5]), while smaller individuals will tend to decrease it. Depending on the shape of $S_m \times RLS$ with respect to z_0 (i.e., convex, concave, or linear), the increase in λ due to larger individuals may overcompensate for, undercompensate for, or balance exactly the reduction due to smaller individuals. Therefore, λ may either increase, decrease, or remain unchanged as we increase the variance in initial size, ζ^2. This is the essence of Jensen's inequality, which states that the mean of a nonlinear function is not equal to the value of this function evaluated at the mean. (For additional explanations of Jensen's inequality, see Bjørnstad and Hansen 1994; Kendall and Fox 2001, 2003; Lindström and Kokko 2002; Ovadia et al. 2007.)

Therefore, the effect of size variation (ζ^2) on population growth depends on the shape of $S_m \times RLS$ with respect to z_0, along the relevant range of z_0 values. If $S_m \times RLS$ is a concave function of z_0 (i.e., concave down, as some authors prefer; e.g., Kendall and Fox 2001; i.e., negative second derivative), then increasing size variation (ζ^2) leads to a decrease in λ. If the relationship is convex (i.e., concave up; positive second derivative), then size variation raises λ. If the relationship is linear (i.e., zero second derivative), then variation has no effect on λ. Finally, it is also possible that $S_m \times RLS$ will be of a sigmoid form, where the relationship is convex over some range of initial sizes and concave over another. In that case, the relationship will be either concave or convex, depending on where the actual initial sizes of individuals cluster.

In order to establish how $S_m \times RLS$ varies with initial size z_0, we refer to the extreme cases of long and short seasons outlined above. For long seasons, $S_m \times RLS = S_m(z_0) \times RLS_{T=\infty}$ (eq. [3]); that is, the relationship be-

tween λ and initial size depends only on survival to maturity. Generally, survival to maturity monotonically increases with initial size; however, the form of the relationship, that is, either concave or convex, is not as easily determined. Based on empirical observations, we obtain a concave relationship (see "Model Calibration"), but in general, both options are feasible.

In terms of underlying biology, the form of the relationship $S_m(z_0)$ depends on the ratio $\mu(z_0)/g(z_0)$, that is, size-specific mortality over size-specific growth (Werner and Gilliam 1984; see appendix). Therefore, whether the form of $S_m(z_0)$ is convex, concave, or linear is determined by how growth and mortality are distributed among initial sizes. Roughly speaking, if at small initial sizes mortality is high and growth is slow, while at intermediate and large initial sizes mortality is low and growth is fast, the resulting curve $S_m(z_0)$ is likely concave. Similarly, if mortality is concentrated at large initial sizes and growth is fastest at small initial sizes, we obtain a convex form of $S_m(z_0)$. However, there are additional, more subtle points concerning the relationship between μ/g and the shape of $S_m(z_0)$. These are considered in the appendix.

For short seasons, the RLS depends strongly on time to maturity (eq. [4]). Therefore, λ is affected by size variation through both survival to maturity and time to maturity. The shape of $S_m \times RLS$ can again be either concave or convex, depending now on the shape of both $S_m(z_0)$ and $RLS(z_0)$, as determined by size-specific growth and mortality rates. Finally, for intermediate season length, that is, $\mu_m(T - T_m) \sim 1$, the RLS is given by equation (2a). As in short seasons, the relationship between λ and z_0 also depends on both survival to maturity and time to maturity. However, the sensitivity of the relationship to time to maturity is lower than that for the short-season scenario (eq. [4]), and it vanishes altogether as the long-season limit is approached (eq. [3]; fig. 1).

Therefore, it is expected that the effect of size variation on λ will vary among years, depending on season length. It is also conceivable that size variation may increase the net reproductive rate for some season lengths (i.e., for which $S_m \times RLS$ is convex) but decrease it for others (i.e., for which $S_m \times RLS$ is concave). Therefore, the effect of size variation on population growth depends on season length and may change in both magnitude and sign as season length fluctuates.

Incorporating Density Dependence

Finally, density dependence is incorporated into the model through density-dependent factors that multiply survival to maturity, time to maturity, or both. Therefore, we assume that the effects of initial size and initial density act multiplicatively (as Bjørnstad and Hansen 1994 did in their

example of variation in clutch size). In other words, the survival to maturity of individuals of all sizes is influenced by density in a similar manner, that is, through the same multiplicative factor. Although such an assumption may not hold in general, for example, under the influence of frequency-dependent effects, we do not know enough about how such effects function in our *M. femurrubrum* system. Therefore, we consider a simple and tractable model that nonetheless fits observed patterns (see "Model Calibration").

We use the Ricker model (e.g., Gurney and Nisbet 1998, p. 27) to describe the density dependence of survival to maturity:

$$S_m(z_0, N) = S_m(z_0, 0) \times \exp(-\alpha N). \quad (6)$$

Equation (6) shows that the survival to maturity of an individual with initial size z_0 at density N is given by its maximal survival at zero density multiplied by a factor that decreases as density increases, that is, $\exp(-\alpha N)$. The parameter α is a measure of the strength of density regulation. We demonstrate in the appendix that such a form of density dependence (i.e., eq. [6]) provides an excellent description of the survival data of figure 2 (see "Model Calibration").

A similar expression using a multiplicative density-dependent factor may also exist for time to maturity. How-ever, we show in the appendix (see "Model Calibration") that for our grasshopper species, density dependence of time to maturity is not observed. Therefore, in subsequent calculations, we consider only density dependence in survival.

Substituting expression (6) into equation (5) gives the density dependence relationship of the population growth rate λ. Note that because of the way density dependence is introduced, survival to maturity of all initial sizes increases or decreases by the same multiplicative density-dependent factor. As such, the density-dependent term can be written outside of the averaging term in equation (5), that is, outside the $E(\dots)$ term. Hence, it does not affect the form of $S_m \times$ RLS with respect to z_0 and therefore does not influence the way size variation affects λ.

Model Calibration Based on Data for *Melanoplus femurrubrum* in Northeastern Connecticut

We now quantify the components of the model, using results and observations from our reference system of *M. femurrubrum* in northeastern Connecticut. We first emphasize that the above model is formulated in terms of a distribution of any arbitrary initial size, which can be either a continuous distribution of continuous size, or a set of frequencies of discrete size classes. Therefore, users of the model may choose to work with either a continuous size
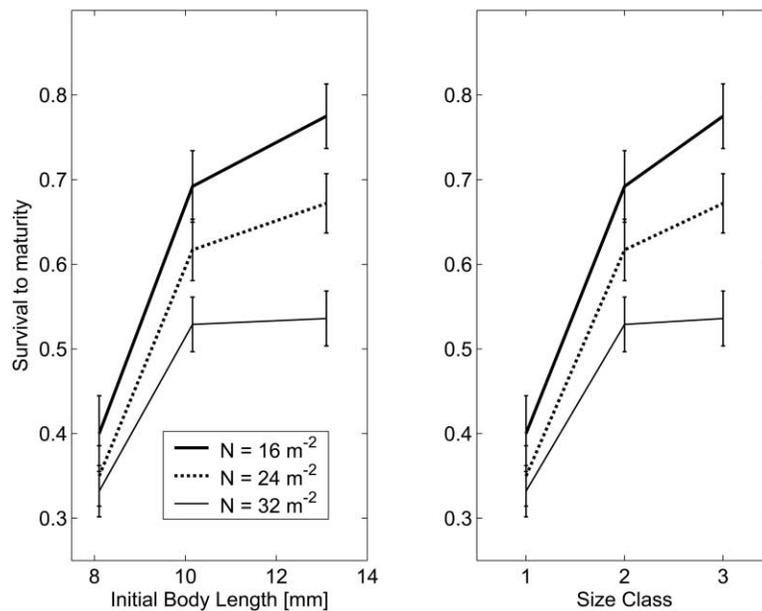
Figure 2: Size-dependent survival to maturity for *Melanoplus femurrubrum* second instars, based on field experiments (Ovadia and Schmitz 2002; O. Ovadia, unpublished data). Survival to maturity is given for three different initial nymphal densities. *Left*, survival to maturity as a function of initial body length (mm). *Right*, Survival to maturity as a function of size class (for a definition of size class values, see "Model Calibration" and the appendix in the online edition of the *American Naturalist*).

measure (e.g., body length/mass) or discrete size classes, depending on the nature of their experimental setup and available data. We choose here to use discrete size classes, based on the data available to us from experiments and observations in the *M. femurrubrum* field system.

We note that because survival to maturity is obtained for second instars (see next paragraph), the population dynamics model will refer to that stage; that is, N_t represents the density of second-instar nymphs. Similarly, "initial size" will refer to that of second instars and not to size at hatching. We consider three initial-size classes of second-instar nymphs based on body length (after Ova-

dia and Schmitz 2002), which are numerically denoted 1, 2, and 3 for initially small, average, and large individuals, respectively (see table 1 and the appendix for more details). Additionally, three different forms of initial-size distribution are considered, as described in table 1. We note that the mean size class value for all three distributions is 2, and only the variance in initial size varies. This allows us to study the effect of size variation alone, without the confounding effects of changes in mean initial size.

Survival data from field experiments provides a concave (i.e., concave down) relationship between survival to maturity and initial size of second instars, given three different

Table 1: Values used in calibrating the model to the *Melanoplus femurrubrum* system

	Values	Reference
Initial-size classes	1, 2, 3	Ovadia and Schmitz 2002; appendix
Initial-size distributions (i.e., levels of size variation; numbers denote size classes)		Appendix
None:	1: 0%	
	2: 100%	
	3: 0%	
Natural:	1: 15%	
	2: 70%	
	3: 15%	
Uniform:	1: 33.33%	
	2: 33.34%	
	3: 33.33%	
Survival to maturity	See figure 2	Ovadia and Schmitz 2002; O. Ovadia, unpublished data
Time to maturity (days; size classes 1–3)		Appendix
T_m estimate 1:	1: 44.1	
	2: 41.5	
	3: 41.5	
T_m estimate 2:	1: 45.4	
	2: 41.6	
	3: 36.2	
Interclutch interval (T_c, days)[a]	10	Beckerman 1999, 2002
No. of eggs per pod (clutch size)	20	Pfadt 1994
Daily rate of egg production	2	No. eggs per pod divided by the interclutch interval
Sex ratio (fraction of females among second instars)[b]	.5	Joern and Gaines 1990
Overwinter egg survival	.29	Appendix
Survival from hatching to second instar stage[c]	.29	Appendix
Fixed parameter C (day^{-1})	.084	Appendix (eq. [A4])
Coefficient of density dependence (α in eq. [6], m^2)	.0152	Appendix
Adult mortality (μ_m, day^{-1})	.035	Oedekoven and Joern 1998
Season length (T, days)	55–120	Beckerman 1999; Ovadia and Schmitz 2004*b*

Note: Additional information on model calibration is provided in the appendix in the online edition of the *American Naturalist*.

[a] Beckerman (1999, 2002) found that under favorable conditions, each female *M. femurrubrum* laid about four clutches during a 6-week period. Therefore, we set the interclutch period to be $T_c = 10$ days. This value is in agreement with the observed duration of the preoviposition period in this species (Pfadt 1994).

[b] Based on general observations in many grasshopper species.

[c] Beckerman (1999, 2002) reported on size-dependent survival of *M. femurrubrum* first instars from the same system of old fields in northeastern Connecticut. However, his results are based on experiments designed to study the effect of a pure grass diet on the survival of first instars. It is therefore difficult to transform the size-dependent mortality that Beckerman reports on to the naturally occurring situation in which herbs are also available for consumption.

initial densities (fig. 2; Ovadia and Schmitz 2002; O. Ovadia, unpublished data). Consequently, for long seasons, the net reproductive rate λ will decrease as variation in initial size increases.

Finally, the remaining components of the model are considered in table 1 and the appendix. The reader should note that there are two different estimates of size-dependent time to maturity (table 1). These are based on two different sources, as described in the appendix, and are termed "T_m estimate 1" and "T_m estimate 2." In the following, we present results for both of these estimates of time to maturity. (We note that for the small- and average-size classes, the two estimates give very close values. The main difference is in time to maturity of large individuals.)

Results

In figure 3, we present how time to maturity, reproductive life span, and size-specific reproductive rate ($\lambda(z_0)$; eq. [1]) change with initial-size class and season length, given the two estimates of time to maturity (table 1). Note that for the first estimate (fig. 3a–3c), time to maturity does not vary greatly among size classes (fig. 3a). As a result, for most values of season length, RLS is independent of initial size (fig. 3b), and if it does vary among size classes, it is always described by a concave relationship (fig. 3b; $T =$

63, 72). Such forms of RLS(z_0) are a direct consequence of the discontinuous mode of reproduction, that is, in discrete clutches. Coupled with the concave form of size-specific survival (fig. 2), we find that $\lambda(z_0)$ is concave for all season lengths (fig. 3c). This means that the population finite rate of increase (eq. [5]) always decreases when size variation is introduced (fig. 4a).

In contrast, considering the second estimate of time to maturity (fig. 3d–3f), convex forms of RLS may occur (fig. 3e) as a result of both the discontinuous mode of reproduction and the now larger differences in time to maturity among the three size classes (cf. fig. 3a, 3d). Consequently, we may obtain convex forms of $\lambda(z_0)$ when the season is short (fig. 3f; $T = 60$ days). This means that for some (short) season lengths, the population net reproductive rate (eq. [5]) may actually increase with size variation (fig. 4b).

These latter results support our theoretical expectation that the effect of size variation on the population growth rate may vary in both magnitude and sign, depending on season length (see "Model Development"). Next, we explore implications for population stability.

Population Stability: Deterministic Case

Given a time-invariant season length, the equilibrium density N^* is given by $\lambda(N^*) = 1$. The local stability of such
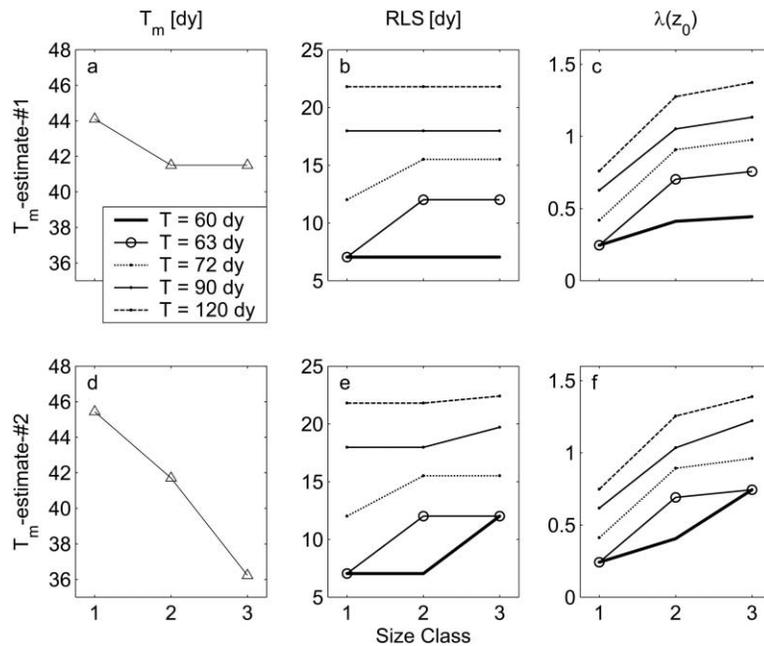
Figure 3: Time to maturity (T_m; *a, d*), reproductive life span (RLS; *b, e*), and size-specific net reproductive rate ($\lambda(z_0)$; *c, f*) as functions of initial-size class, for two estimates of time to maturity (top row vs. bottom row). Time to maturity and reproductive life span are given in days. Reproductive life span and size-specific reproductive rate are given for five different season lengths (key in *a*).
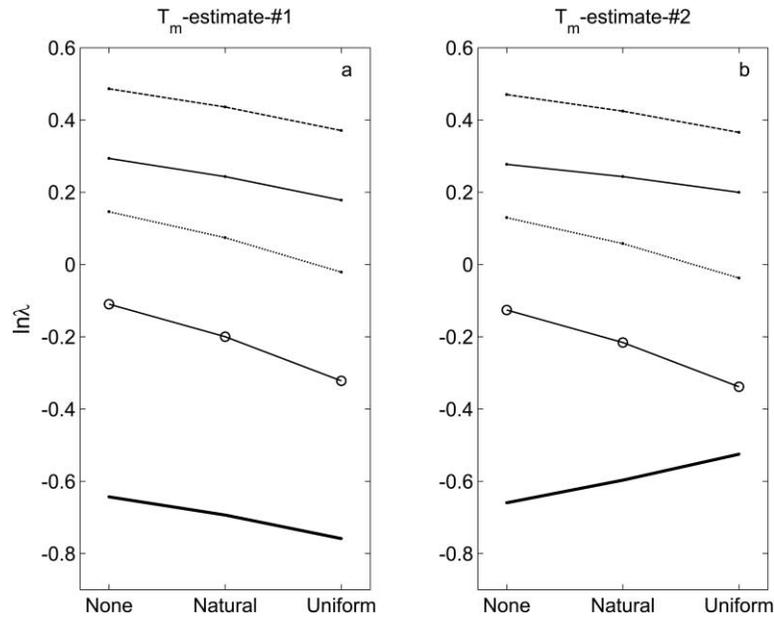
Figure 4: Natural logarithm of overall population net reproductive rate (λ; eq. [5]) as a function of size variation (none, naturally occurring, and uniform size distribution). Curves of $\ln \lambda$ versus size variation are given for two estimates of time to maturity (*a* vs. *b*) and for five different season lengths (see key in fig. 3*a*). Note that λ always decreases with size variation for T_m estimate 1 (*a*). In contrast, for T_m estimate 2 and when the season is short enough, λ can increase with size variation (*b*, *bottom curve*).

an equilibrium point is determined by the eigenvalue ε, which depends on the derivative of λ with respect to density (Bjørnstad and Hansen 1994). The closer to zero that the absolute value of ε (denoted as $|\varepsilon|$) is, the faster the population density returns to its equilibrium value following a perturbation.

Table 2 presents values of ε for the three types of within-population variation and for three values of season length. Additionally, we consider three different equilibrium field densities (achieved by modifying the value of C in eq. [5]; table 2; appendix). An inspection of table 2 reveals that rates of convergence to equilibrium density differ among cases. Specifically, considering the effect of size variation, we observe that for low field density (e.g., the naturally occurring density 16 m^{-2}), the general trend is for $|\varepsilon|$ to grow with increasing size variation. The trend is reversed, however, for medium and high field densities (95 and 130 m^{-2}; see fig. 5). Therefore, when population density is low, stability decreases with size variation, while for higher densities, stability increases as size variation is introduced into the population (fig. 5).

Additionally, we observe that when population density is high, it is possible to obtain nonconverging periodic oscillations (i.e., $\varepsilon < -1$) when the population is homogenous (no size variation) but converging oscillations (i.e., $-1 < \varepsilon < 0$) for a population with individual size variation (table 2: $N^* = 130$ m^{-2}, $T = 90$ days; fig. 5*c*). Therefore,

the stability properties of the population may also vary qualitatively as size variation changes.

We conclude this subsection by reinforcing the general expectation of Bjørnstad and Hansen (1994) that individual variation does not necessarily enhance population stability. As we showed here, under naturally occurring conditions ($N^* = 16$ m^{-2}), size variation is expected to impair population stability and cause longer return times to equilibrium density following a perturbation. This result, however, has been obtained using classical stability concepts of deterministic population models (as in Bjørnstad and Hansen 1994). Because stochastic environmental variability is especially important in seasonal environments, we consider next population stability when season length varies randomly among years.

Population Stability: Stochastic Case

The stability of population dynamics when the environment varies stochastically is not adequately described by ε. Stochastically varying environments cause random fluctuations in population density; hence, a useful measure of population stability may be the magnitude of relative fluctuations in density. Either the root mean square of relative fluctuations (e.g., May 1973) or the variance of log (density) (e.g., Lande et al. 2003) may be used as measures of stability (or rather, instability) in the stochastic

Table 2: Eigenvalue ε for three different season lengths (T), three forms of within-population variation in initial size, and three different equilibrium densities

Equilibrium density[a]	$T = 60$ days	$T = 90$ days	$T = 120$ days
16 m^{-2}:			
None	…[b]	.723	.530
Natural	…[b]	.757	.575
Uniform	…[b]	.800	.634
95 m^{-2}:			
None	.458 (.442)[c]	−.478	−.671
Natural	.396 (.493)[c]	−.444	−.625
Uniform	.324 (.558)[c]	−.401	−.567
130 m^{-2}:			
None	−.073 (−.090)[c]	−1.010[d]	−1.203[d]
Natural	−.136 (−.040)[c]	−.976	−1.157[d]
Uniform	−.208 (.026)[c]	−.933	−1.099[d]

Note: The ε values in the table are given for T_m estimate 2 (see footnotes).

[a] The different equilibrium densities were obtained by varying the value of the parameter C such that the specified density was achieved for naturally occurring size variation when season is 90 days long (appendix).

[b] In such a deterministic model, the short-season case ($T = 60$ days) for an equilibrium density of 16 m^{-2} shows a monotonic decay of population density to 0, that is, population extinction, regardless of the type of size variation.

[c] Values in parentheses are ε values for T_m estimate 1, given the same combination of season length, equilibrium density, and size variation. We note that for short seasons (the $T = 60$ column), there are pronounced differences in the ε values between the two estimates of time to maturity. In addition, we find opposite stability trends, that is, an increase in $|\varepsilon|$ with size variation for one estimate of time to maturity and a decrease for the other. These differences arise because of the opposite effects of size variation on population growth for the two estimates of time to maturity when seasons are short (cf. $T = 60$ days in fig. 4a, 4b). For long seasons ($T = 90$ or 120 days), there are very slight differences in the value of ε between the two estimates of time to maturity (not shown), because for long seasons, size variation affects population growth mainly though survival to maturity.

[d] In these cases, $\varepsilon < -1$; therefore, the population exhibits nonconverging periodic oscillations around the equilibrium density.

case. Regardless of the specific measure used, the magnitude of relative fluctuations in density increases with increasing environmental variance, represented by the variance of the density-independent part of $\ln \lambda$ (for brevity, we will refer to it as the variance of $\ln \lambda$).

When season length fluctuates among years, the range of values of $\ln \lambda$ either increases or decreases with size variation, depending on the estimate of time to maturity used (cf. fig. 4a, 4b). Similarly, if we assume that season length varies uniformly among the five different values of figure 4, then the variance of $\ln \lambda$ increases with size variation for T_m estimate 1 (fig. 4a) but decreases for T_m estimate 2 (fig. 4b; table 3). In other words, for our second estimate of size-dependent time to maturity, the magnitude of fluctuations in population density decreases as variation in initial size is introduced into the population. Hence, stability is enhanced by size variation.

However, figure 4 presents only a partial view of how size variation interacts with season length and other pa-

rameters to affect the population rate of increase. For example, considering figure 4b, if season length does not get as short as 60 days, we do not obtain an increase in $\ln \lambda$ with increased variation in size (fig. 4b, $T = 60$ days). Consequently, the variance of $\ln \lambda$ will not necessarily decrease with size variation, and therefore, variation in size might not enhance stability.

In figure 6a, we present curves of population growth rate versus size variation (as in fig. 4) for all values of season length between 55 and 120 days (in 1-day increments). Figure 6b–6d presents the same information, but the minimum season length is gradually increased from 55 (fig. 6a) to 69 (fig. 6d) days. The most important conclusion, illustrated by figure 6, is that the total range of population growth rates ($\ln \lambda$) may either increase (fig. 6a, 6c) or decrease (fig. 6b, 6d) with size variation, depending on the range of possible season lengths. As discussed above, this may have important consequences for population stability when season length fluctuates randomly
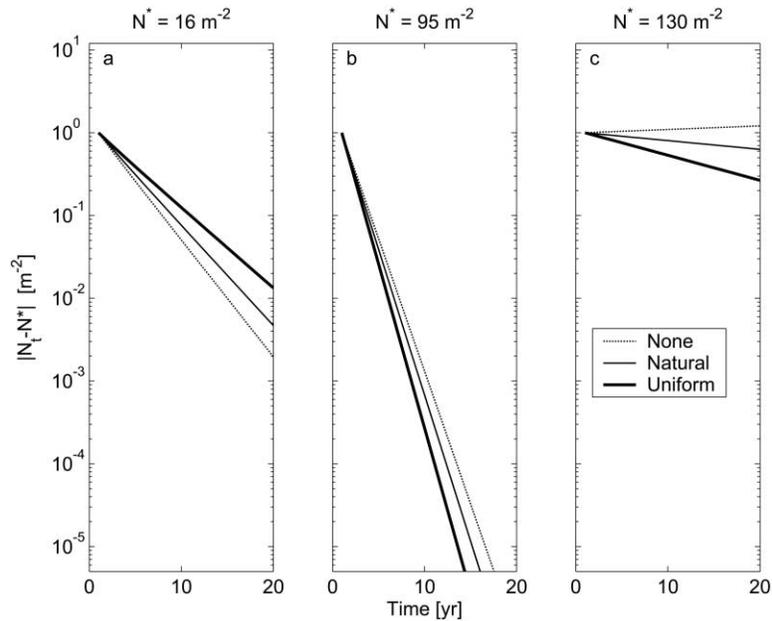
Figure 5: Magnitude of deviation from equilibrium density as a function of time, given an initial perturbation. Magnitude of deviation is given by the absolute value of $(N_t - N^*)$. The initial perturbation to population density is obtained by setting $N(t = 0) = N^* + 1(\mathrm{m}^{-2})$, that is, via an increase in population density by 1 (m^{-2}) above the equilibrium level. Curves are given for three different equilibrium densities (*a–c*) and for the three forms of size variation (refer to key in *c*). Note the logarithmic scale of the *Y*-axis. When equilibrium density is low (*a*), the perturbation decays faster as size variation is decreased; that is, size variation causes density perturbations to persist for longer times. The opposite is true for high equilibrium densities (*b*, *c*). Curves are based on T_m estimate 1.

between years. Yet the variance in $\ln \lambda$ decreases with size variation for all four cases of season-length variability (table 4), despite the increase in the range of $\ln \lambda$ values for two of these cases (fig. 6*a*, 6*c*). Therefore, size variation enhances population stability regardless of the range of season lengths (but the effect varies in magnitude among cases; see table 4).

Discussion

We developed an analytical model aiming to investigate the effect of body size variation on population dynamics and stability in a seasonal environment. We calibrated the model based on field observations and experiments performed in an old-field system, in which the generalist grasshopper *Melanoplus femurrubrum* is a dominant consumer (e.g., Schmitz et al. 1997; Schmitz and Suttle 2001). Using data on density- and size-dependent survival and growth (Beckerman 2000, 2002; Ovadia and Schmitz 2002; appendix) we quantified the effects of size variation on *M. femurrubrum* population dynamics. We found that in the case of deterministic dynamics (i.e., a fixed season length), size variation tends to destabilize population dynamics, that is, causes slower return to equilibrium density after a perturbation (fig. 5*a*). In the stochastic case, how-

ever, size variation interacts with stochastic variation in season length and through that tends to stabilize population dynamics in all cases considered.

From a theoretical perspective, our main conclusion is that the effect of size variation on the net reproductive rate can change in both magnitude and sign as season length changes. For long seasons, population dynamics are relatively insensitive to time to maturity. Consequently, the primary influence of size variation on population growth is via size-dependent survival to maturity. In this study, variation in initial size caused a decrease in mean survival because of the concave form of size-dependent survival (fig. 2). In contrast, when the season is short, population dynamics are strongly affected by both survival

Table 3: Environmental standard deviations of $\ln \lambda$ ($SD_{\ln \lambda}$; i.e., square root of the variance in $\ln \lambda$), based on figure 4

	T_m estimate 1		T_m estimate 2	
None	.4369	99.48%	.4369	108.91%
Natural	.4392	100.00%	.4012	100.00%
Uniform	.4437	101.04%	.3683	91.81%

Note: Values are presented for each of the two estimates of time to maturity. Additionally, values are also presented in the form of percentages normalized to $SD_{\ln \lambda}$ of the naturally occurring size variation, a form of presentation that demonstrates better the relative effect of size variation on population stability.
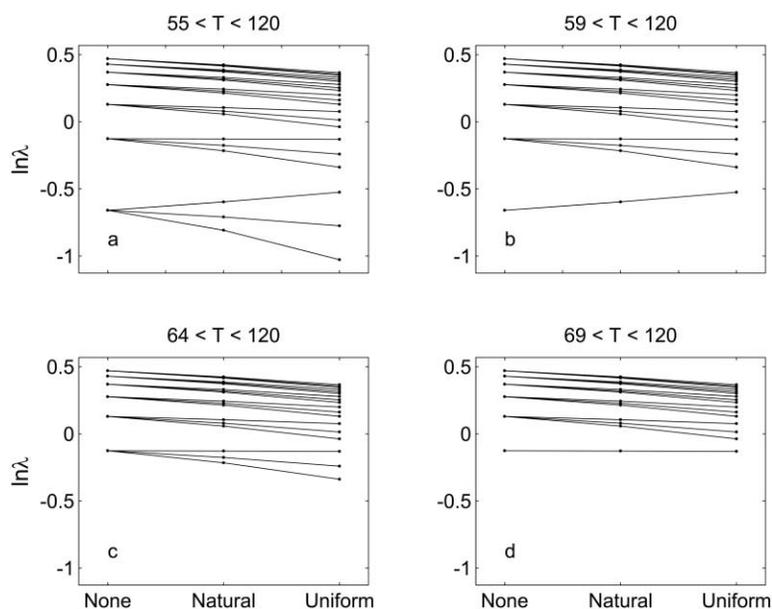
Figure 6: Logarithm of overall population net reproductive rate (λ) as a function of size variation for four different ranges of season length. In each case, all possible curves of $\ln \lambda$ versus size variation are presented, given that season length is varied in 1-day increments within the specified range. Season lengths are given in days. Only T_m estimate 2 was used in these graphs. Note that the number of different curves of $\ln \lambda$ versus size variation is much smaller than the total number of season lengths considered. For example, in *a*, we consider 66 different values of season length, which result in only 21 different curves. This is a direct consequence of the discontinuous mode of reproduction in clutches. In addition, for each value of $\ln \lambda$ in a homogenous population (*None*), there are up to three corresponding different values when size variation is not zero (*Natural* or *Uniform*). For example, based on *a*, when there is no size variation (*None*), $\ln \lambda$ has only seven different values, depending on season length. However, under the influence of size variation, $\ln \lambda$ takes on 21 different values because of differences in survival and time to maturity among the different size classes.

to maturity and time to maturity. The size dependence of time to maturity can then counter the negative effect of size variation on survival to the extent that the population growth rate can increase with size variation (figs. 3*d*–3*f*, 4). Such season-length-dependent effects of size variation have important consequences for stability. Collectively, they constitute the mechanism behind the trends of enhanced stability with increasing size variation evident in the stochastic case (i.e., when season length fluctuates among years; tables 3, 4).

In general, however, size variation can either stabilize or destabilize population dynamics, depending on how the shape of the relationship between net reproductive rate and initial size (i.e., $\lambda(z_0)$) changes with season length. Specifically, net reproductive rate always increases with season length, regardless of initial size (as longer seasons provide more opportunities for reproduction). When $\lambda(z_0)$ of long seasons is concave but that of short seasons is convex, size variation reduces the high population growth rates of long seasons while increasing the low growth rates of short seasons. Therefore, size variation is likely to enhance population stability in this case, because it decreases the between-year variability in population growth rates. If

the opposite occurs (i.e., $\lambda(z_0)$ is convex for long seasons but concave for short seasons), size variation will tend to destabilize population dynamics.

In the above analyses, we argued that specific results are consequences of the discontinuous mode of reproduction in clutches (e.g., figs. 3, 4). Therefore, our conclusions regarding the effect of size variation on stability may change if reproduction becomes more continuous. Substituting $T_c = 1$ (day) in the expression for RLS (eqq. [2]; instead of 10 days as in table 1), we found that size variation still enhances population stability (by decreasing the variance in $\ln \lambda$; see appendix). However, the effect was weaker for continuous reproduction, compared with the effect for reproduction in clutches (cf. table 4 with table A1 in the online edition of the *American Naturalist*). That is, the discontinuous mode of grasshopper reproduction magnifies the stabilizing effect of size variation.

In our model, all individuals begin their life at the same time, and their development (i.e., time to maturity) is determined only by their initial size. Previous studies considered the demographic consequences of developmental variance, that is, of differences among individuals in rates of growth and maturation, such as variation in instar durations

Table 4: Environmental standard deviations of ln λ (SD$_{\ln \lambda}$; i.e., square root of the variance in ln λ), based on figure 6 (discontinuous reproduction), assuming that all season lengths within a given range occur with equal probability

	$55 < T < 120$		$59 < T < 120$		$64 < T < 120$		$69 < T < 120$	
None	.3441	104.84%	.2820	106.51%	.1967	102.60%	.1606	105.00%
Natural	.3282	100.00%	.2648	100.00%	.1917	100.00%	.1529	100.00%
Uniform	.3166	96.46%	.2486	93.91%	.1889	98.55%	.1456	95.23%

Note: Season lengths (T) are given in days.

in insects (Nisbet and Gurney 1983; Bellows 1986*a*, 1986*b*). Moreover, high variability in hatching date is commonly observed in insects with seasonal life cycles (e.g., Pickford 1960; Joern and Gaines 1990). We predict that such variation, superimposed on the variation in initial size, will cause a situation similar to continuous reproduction (previous paragraph), because there will be variation in time to maturity, not only between size classes but also within each size class. As a result, the effect of size variation on population dynamics may become weaker.

In addition, we assumed that all individuals mature at the same size and perform similarly as adults. Additional sources of individual variation may be related to differences in size at maturity and adult performance (i.e., adult mortality or fecundity). Such differences in performance can be caused by changes in resource quality and availability or in the duration of the daily thermal window, as the season progresses (e.g., Stauffer and Whitman 1997 and references therein). For instance, several studies on grasshoppers have documented monotonic reductions in plant food quality and quantity during the growing season (e.g., Joern and Gaines 1990; Belovsky and Slade 1995; Oedekoven and Joern 2000). Consequently, the reproductive capacity of individuals that mature late in the season decreases not only owing to shorter reproductive life span but also because of poorer conditions (Wall and Begon 1987*b*; Joern and Gaines 1990; Stauffer and Whitman 1997). Such additional sources of variation will inflate differences in reproductive capacity among size classes. However, it remains to be seen how they modulate the effect of size variation on population dynamics and stability.

We directly introduced density dependence via a factor that modifies size-dependent survival, assuming that density influences all size classes similarly (eq. [6]). In that sense, it is a model of "perfect" regulation (sensu Uchmanski 2000) that overlooks lower-level details (e.g., interactions among individuals). As we demonstrate, however, this simplified form of density dependence can be readily estimated using field and experimental data, and in the case of *M. femurrubrum*, it provides an adequate description of survival in the field. Nonetheless, such phenomenological density dependence is caused by within-season interactions, which influence individual growth and survival. Specifically, the indirect effects of resource exploitation (e.g., Grimm and Uchmanski 2002) is the likely mechanism driving density regulation (e.g., causing asymmetric competition, which also influences the within-season body size distribution; Grimm and Uchmanski 2002). Indeed, empirical observations examining density-dependent effects in grasshoppers found no evidence of direct interference (e.g., Belovsky and Slade 1995; Branson 2003). Therefore, the explicit formulation of within-season dynamics represents a profitable extension of the basic model we described in this study.

In conclusion, our model captures and quantifies the effect of size variation on population dynamics and stability, based on an appropriate formulation of the organismal life cycle. The components of the model that determine the dynamics at the population level are all individual-level traits (*i*-state variables) that can be readily measured in the field. A fully factorial experiment testing for the effects of body size and density on the survival and growth of individuals should enable the calibration of this model, which will aid in predicting the dynamics of many other organisms with seasonal life cycles. In this way, quantitative predictions regarding population stability can be generated. The next logical step would be to extend the current model to account for additional sources of individual variation, as well as to add an explicit description of within-season demographic dynamics and the subsequent effects on resources. We suggest that developing and applying such analytical models will enable us to arrive at a more tractable understanding of how trait variation affects population and community dynamics.

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