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STOCHASTICITY IN REPRODUCTIVE OPPORTUNITY AND THE EVOLUTION OF EGG LIMITATION IN INSECTS

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Is reproduction by adult female insects limited by the finite time available to locate hosts (time limitation) or by the finite supply of eggs (egg limitation)? An influential model predicted that stochasticity in reproductive opportunity favors elevated fecundity, rendering egg limitation sufficiently rare that its importance would be greatly diminished. Here, I use models to explore how stochasticity shapes fecundity, the likelihood of egg limitation, and the ecological importance of egg limitation. The models make three predictions. First, whereas spatially stochastic environments favor increased fecundity, temporally stochastic environments favor increases, decreases, or intermediate maxima in fecundity, depending on egg costs. Second, even when spatially or temporally stochastic environments favor life histories with less-frequent egg limitation, stochasticity still increases the proportion of all eggs laid in the population that is laid by females destined to become egg limited. This counterintuitive result is explained by noting that stochasticity concentrates reproduction in the hands of a few females that are likely to become egg limited. Third, spatially or temporally stochastic environments amplify the constraints imposed by time and eggs on total reproduction by the population. I conclude that both egg and time constraints are fundamental in shaping insect reproductive behavior and population dynamics in stochastic environments.

KEY WORDS: **Bet hedging, Liebig's Law, life-history evolution, limiting factors, oviposition behavior, time limitation.**

Insect herbivores and parasitoids have been used extensively as tractable models for the study of animal reproductive behavior and population dynamics. Nevertheless, a fundamental question concerning the reproductive success of these insects remains unresolved: is the realized lifetime reproductive success of adult females limited by the finite amount of time available to locate hosts that can serve as oviposition sites (time limitation) or by the finite supply of mature eggs (egg limitation)? For over 80 years, different researchers have answered this question differently. The result has been the creation of competing families of models for host–parasitoid population dynamics, one emphasizing time limitation (Lotka 1925; Nicholson and Bailey 1935; Hassell 1978, 2000; Murdoch et al. 2003) and another emphasizing egg limitation (Thompson 1924, Getz and Mills 1996; Shea et al. 1996; Heimpel et al. 2003; Schreiber 2006, 2007; Schreiber and Vejdani 2006; Kon and Schreiber 2009), and competing families of models of insect reproductive behavior, again one emphasizing time limitation (Charnov and Skinner 1985; Visser et al. 1992; Godfray 1994) and another emphasizing egg limitation (Iwasa et al. 1984; Mangel 1987; Mangel and Heimpel 1998). These different classes of models often make very different predictions (e.g., Mangel 1989), underscoring the importance of resolving the relative importance of time and egg limitation. Although it should be possible to achieve this resolution through the study of insects in nature, much of the empirical evidence is indirect or subject to divergent interpretations (reviewed in Rosenheim et al. 2008).

As a complement to the early empirical studies, I introduced a model that explored how insect fecundities and associated risks of egg limitation might evolve (Rosenheim 1996). The model's predictions emerged from the interplay of two factors: first, stochasticity in reproductive opportunity for females, and second, life-history trade-offs that involve fecundity (egg size vs. egg number, or egg number vs. female longevity). The model and subsequent elaborations (Rosenheim 1999a; Rosenheim et al. 2000) predicted that an evolutionary equilibrium cannot be reached without some fraction of the population being egg limited. The fraction of the population that is time limited (i.e., females dying with unlaid eggs remaining in the ovaries) creates directional selection for reduced fecundity, with resources in the "excess" eggs being redirected to making more richly provisioned eggs or to the soma to support extended longevity or enhanced searching ability. The fraction of the population that is egg limited (i.e., females completely exhausting their lifetime complement of eggs while they are still capable of locating hosts for oviposition) creates directional selection for increased fecundity. An equilibrium, then, can only be reached when these opposing sources of directional selection are balanced. I concluded, therefore, that models of insect reproduction and population dynamics should not exclude a role for egg limitation.

Sevenster et al. (1998) and Ellers et al. (2000) challenged this conclusion. Their models demonstrated that increasing the level of stochasticity (spatial) in reproductive opportunity to what they argued were realistically high levels led to an increase in reproductive investment and a decrease in egg limitation. Sevenster et al. (1998) concluded from this that egg limitation would be sufficiently rare that models that assumed strict time limitation were a sensible default (see also Begon and Parker 1986). The hypothesis that real-world levels of stochasticity increase allocation to reproduction has been invoked to explain several aspects of insect life-history evolution (Ellers and Jervis 2003, 2004; Jervis and Ferns 2004; Jervis et al. 2007, 2008). Godfray (1994) and van Baalen (2000) speculated that temporally stochastic environments might act similarly to spatially stochastic environments, again favoring a decrease in egg limitation. Jervis et al. (2005) sounded a cautionary note, however, suggesting that variation in opportunities to oviposit might favor increased allocations to reserves, allowing lifespan to be extended when reproductive opportunities were scarce, and noted that this prediction ran counter to the hypothesis advanced by Ellers et al. (2000).

Divergent views of the importance of egg limitation have therefore emerged from models of insect life-history evolution and now resided in the literature for some time. Many authors consider the question to be controversial (e.g., West and Rivero 2000; West and Cunningham 2002; Boggs 2003; Heimpel et al. 2003), and without a consensus view ongoing theoretical work continues to be built upon widely varying assumptions, with some authors adopting the assumption of strict time limitation (e.g., Tentelier et al. 2006; Wajnberg 2006; Haccou and van Alphen 2008) and others arguing for a central role for egg limitation (e.g., Bernstein and Jervis 2008). A growing number of authors have moved away from the poles of the debate, adopting more inclusive models that recognize the importance of both time and egg constraints for both behavior (Ellers et al. 2000; West and Cunningham 2002; Jervis et al. 2008, Gandon et al. 2009; Richard and Casas 2009; Roitberg et al. 2010) and population dynamics (Getz and Mills 1996; Hassell 2000; Murdoch et al. 2003). Additional work is, however, needed to help us choose among these different frameworks and to see if the more inclusive approach is supported.

My goal here is to build upon the insights presented in Sevenster et al. (1998) and Ellers et al. (2000) to explore further how stochastic environments influence the evolution of egg limitation in insects. I use an optimality model to ask: how does stochasticity in reproductive opportunity shape (1) the optimal investment in egg maturation, (2) the likelihood of egg limitation, and (3) the ecological importance of egg limitation? Questions (1) and (2) were addressed previously by Ellers et al. (2000) for the case of spatially stochastic environments; but, because spatially and temporally stochastic environments may have different effects on life-history evolution (Roff 2002), I expand their treatment here to include the temporal case as well.

Model

Dialogue between the earlier modeling studies (Rosenheim 1996; Sevenster et al. 1998) was facilitated by retaining the same basic model structure, and I will continue that here. The model examines lifetime reproductive success for a strictly proovigenic female (i.e., all eggs are matured prior to the emergence of the adult) that cannot resorb eggs; incorporating the potentially important effects of plasticity in egg maturation and resorption (Papaj 2000; Casas et al. 2009) is thus left for future work. The model asks how stochasticity in reproductive opportunity (i.e., unpredictability in the number of suitable hosts that will be discovered over a lifetime of foraging activity) shapes the optimal investment in reproduction versus expected lifespan.

Following Sevenster et al. (1998) I assume a linear trade-off between allocation from the total resource pool initially available, T, to reproduction, R, and expected longevity, m:

$$T = R + am, \tag{1}$$

where a is a conversion coefficient that describes the cost of sustaining foraging activity (units: resource units/hour; time units are arbitrary). If the cost of maturing one egg is s, then the total number of eggs matured will be R/s.

Stochasticity in lifetime reproductive opportunity can be introduced via either variation in longevity or variation in host abundance. Here, I use a stochastic survival distribution, but as with earlier models this is taken to incorporate all sources of

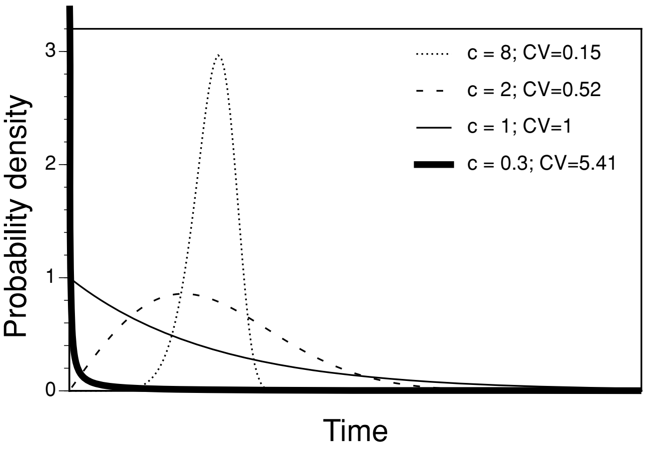

Figure 1. Probability density functions for the Weibull distribution with different shape parameters ($c = 0.3$–8) but with values of b chosen to maintain a constant mean longevity. Note that the coefficient of variation (CV) for longevity increases strongly as c decreases.

stochasticity in reproductive opportunity, including variation in host availability. (The model that is derived below is, with suitable redefinitions of variables, mathematically identical to a model that uses variation in the number of hosts encountered per unit time to produce stochasticity in lifetime reproductive opportunity.) Again following Sevenster et al. (1998), I use the Weibull distribution. Although previous formulations of this model have used the cumulative survival distributions (Rosenheim 1996; Sevenster et al. 1998; Ellers et al. 2000), here I frame the model in terms of the Weibull probability density function for mortality, because this facilitates the transition from spatial to temporal heterogeneity (see also van Baalen 2000; van Baalen and Hemerik 2008). Under the Weibull distribution, the probability of dying at age x is

$$P(x) = cb^{-c}x^{c-1}e^{-\left(\frac{x}{b}\right)^{c}}, \qquad (2)$$

where b is the scale parameter and c is the shape parameter. Together, b and c determine the mean life span, m as:

$$m = b \cdot \Gamma\left(\frac{c+1}{c}\right), \qquad (3)$$

where Γ is the gamma function. As c decreases, the amount of stochasticity introduced by the Weibull survival function increases (Fig. 1).

If the female encounters k hosts per hour, laying a single egg on each, then her lifetime supply of eggs will be exhausted at age $x = R/sk$. For the case of spatially stochastic environments, I follow the conventional approach of modeling female fitness, W_{spat}, as the arithmetic mean of the finite rate of increase, $\bar{\lambda}_A$(i.e., the expected number of offspring produced by a given individual)

$$W_{spat} = \bar{\lambda}_A = \int_0^{\frac{R}{sk}} P(x)kx\,dx + \int_{\frac{R}{sk}}^{\infty} P(x)\frac{R}{s}\,dx, \qquad (4)$$

where $P(x)$ is defined by equations (1–3). The first term on the right-hand side of equation (4) represents fitness returns from time-limited females; within the integral, we have the product of the probability of dying at age x, which is $P(x)$, and the lifetime reproduction of individuals who die at age x, which is kx (here, $x \leq R/sk$, so females do not exhaust their egg supply). The second term represents the fitness returns from egg-limited females; within the integral we have the product of the probability of dying at age x, which is $P(x)$, and the lifetime reproduction of individuals who die at age x, which is R/s (here $x > R/sk$, so females do exhaust their egg supply, and lifetime reproduction simply equals the total number of eggs matured). Note that by assuming that females always accept the host and produce the same clutch size, I avoid the complications that are introduced when phenotypic plasticity (variable oviposition behavior) interacts with the evolution of fecundity (e.g., Mangel and Heimpel 1998; Casas et al. 2000). W_{spat} is a heuristic fitness function that is suitable for populations with complete mixing and where selection can modify the proportional contribution of each location to the total offspring population.

Whereas spatially stochastic environments favor allocation strategies that do well in locations with abundant opportunities for reproduction, temporally stochastic environments may instead favor allocation strategies that avoid extremely low fitness during generations when opportunities for reproduction are poor (Roff 2002). More generally, temporally stochastic environments favor strategies that minimize year-to-year variation in reproductive success. To study life-history evolution in a temporally stochastic environment, I adopt the conventional approach of maximizing the geometric mean of the finite rate of increase, $\bar{\lambda}_G$, rather than the arithmetic mean, $\bar{\lambda}_A$(Haldane and Jayakar 1963, Cohen 1966, Lewontin and Cohen 1969, Gillespie 1973, Roff 2002, 2008).

The logic underlying the use of the geometric mean is clearest under the simple scenario of clonal selection (i.e., setting aside the complications of diploid genetics), no density dependence, and no age structure (i.e., discrete, nonoverlapping generations of fixed duration). We can then write: $N(t) = \lambda N(t-1)$, where $N(t)$ is the number of individuals in a particular clone during generation t, and λ is the finite rate of increase ($\lambda = e^{r}$). By extension,

$$N(t) = N(0)\lambda_1\lambda_2\lambda_3 \ldots \lambda_t = N(0)\prod_{i=1}^{t}\lambda_i. \qquad (5)$$

This equation recognizes the multiplicative nature of population growth across generations. Note that long-term clonal population growth is severely penalized by extremely low fitness during any generation, even if such generations are rare. For example, a single generation with $\lambda = 0$ results in the extinction of the clone, even if reproductive success during other generations is high. This is not true for spatial heterogeneity, where the reproductive failure of a clone in one location can be offset fully by success in another location.

In the insect life-history model considered here, it is longevity, x, that varies unpredictably across generations. In this case, assuming that $x_1, x_2, x_3, \ldots$ is a sequence of independent and identically distributed variables, and taking natural logarithms of equation (5) we obtain

$$\ln N(t) = \sum_{i=1}^{t} \ln \lambda(x_i) + \ln N_0. \tag{6}$$

Dividing both sides of equation (6) by t we obtain

$$\frac{\ln N(t)}{t} = \frac{\sum_{i=1}^{t} \ln \lambda(x_i)}{t} + \frac{\ln N_0}{t}. \tag{7}$$

Now taking the limit as $t \to \infty$, the second term on the right-hand side of equation (7) $\to 0$, and by the law of large numbers we obtain

$$\ln \overline{\lambda}_G = \mathbf{E}\left[\ln \lambda\left(x_i\right)\right], \tag{8}$$

where **E** denotes expectation. Assuming longevity is a continuous random variable with density $P(x)$, the right-hand side of equation (8) is, by definition, equal to $\int P(x) \ln \lambda\,(x) dx$. We thus arrive at an expression for expected mean fitness over many generations in a temporally stochastic environment, W_{temp}:

$$W_{temp} = \ln \overline{\lambda}_{\mathrm{G}} = \int P\,(x) \ln \lambda\,(x) dx. \tag{9}$$

Finally, returning to the particular case of insect reproduction, and decomposing fitness into contributions from time- and egg-limited individuals as was done for the spatial case (eq. 4), we have

$$W_{temp} = \ln \overline{\lambda}_{\mathrm{G}} = \int_{0}^{\frac{R}{sk}} P(x) \ln(kx) dx + \int_{\frac{R}{sk}}^{\infty} P(x) \ln\left(\frac{R}{s}\right) dx. \tag{10}$$

As reviewed by Roff (2002), the geometric mean of the finite rate of increase has been shown to be a useful heuristic under many conditions (e.g., diploid genetics, age structured populations). Lewontin and Cohen (1969), MacArthur (1972, pp. 165–168), and Roff (2002, pp. 69–75) also carefully explain why, if we wish to measure fitness for a single population experiencing a temporally unpredictable environment, it is inappropriate to try to create a fitness metric by taking the expected value of equation (5) across many different possible sequences of environmental conditions, because doing so will effectively, although inadvertently, re-introduce spatial heterogeneity into the considered scenario.

The optimal allocations to egg maturation in spatially stochastic environments, R^*_{spat}, or temporally stochastic environments, R^*_{temp}, were found by numerically maximizing equations (4) or (10), respectively, and results were confirmed with simulations (Matlab codes for the numerical solutions and the simulations are available from the author). The proportion of females expected to become egg limited was then calculated as the proportion of individuals living to reach age $\frac{R^*_{spat}}{sk}$ for the spatial case or $\frac{R^*_{temp}}{sk}$ for the temporal case.

The optimal allocation to egg maturation and the associated probabilities of egg and time limitation are important descriptors of insect life histories. I now introduce two new measures of the ecological importance of egg and time limitation that complement these metrics. First, we may be interested in how egg or time limitation shapes reproductive behavior (e.g., decisions regarding host acceptance, clutch size, host feeding, or sex allocation). We can think of female behavior being influenced by the risk of egg or time limitation in a way that falls along a spectrum. At one end of the spectrum, analyzed by Rosenheim (1999b), each female in the population adopts the same expected risk of egg- and time-limitation, and uses these expectations to weigh the relative contributions of eggs and time to the overall cost of oviposition. I will return to this scenario in the discussion. At the other end of the spectrum, we can imagine that females obtain information while they forage that allows them to adjust their personal expectations of risk from egg- versus time-limitation; in the extreme, we can imagine that females can correctly project their eventual fate (to die with unlaid eggs remaining, versus to exhaust their egg supply before dying). In this case, a well-established theoretical result (Iwasa et al. 1984; Mangel 1987, 1989) with substantial empirical support (Minkenberg et al. 1992; Roitberg et al. 1993; West and Rivero 2000; Babendreier and Hoffmeister 2002; Javois and Tammaru 2004; Jervis et al. 2008) is that females should adjust their reproductive behavior in response to their projected fate: females who expect to become egg limited should move toward behavior that maximizes fitness returns per egg laid, whereas females who expect to become time limited should move toward behavior that maximizes fitness returns per unit time. As shown in Figure 2, one measure of the ecological importance of egg limitation is therefore the proportion of all eggs laid in the population that is laid by females destined to become egg-limited. Reproduction by females destined to become egg limited is proportional to the area of Region II in Figure 2, computed as:

$$\text{Area (Region II)} = \phi\left(\frac{R^*_{\bullet}}{sk}\right) \cdot \frac{R^*_{\bullet}}{sk}, \tag{11}$$

where $\phi(x)$ is the proportion of individuals surviving to reach age x:

$$\phi(x) = e^{-\left(\frac{x}{b}\right)^{c}}, \tag{12}$$

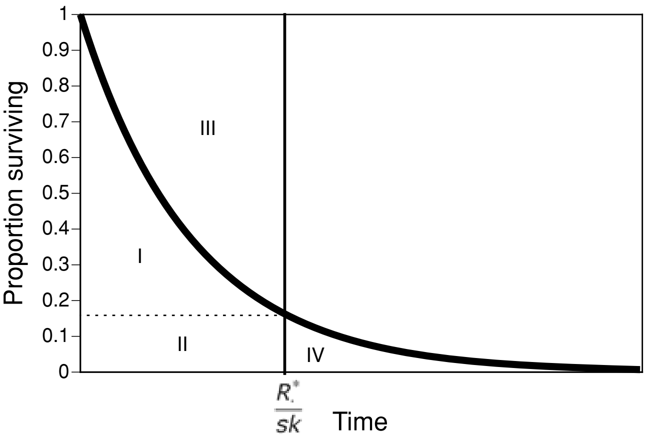

Figure 2. **Reproduction realized by female insects, as well as reproduction foregone due to the constraints imposed by a finite longevity and a finite fecundity. The longevity constraint is shown with the Weibull survival function (heavy curve; here, $c = 1$). Females exhaust their lifetime supply of eggs, and thus become egg limited, if they live to reach age $\frac{R_\bullet^*}{sk}$; thus, the fecundity constraint is shown with the vertical line at age $\frac{R_\bullet^*}{sk}$. A cohort of females that was free of longevity or fecundity constraints would exhibit infinite reproduction. For a cohort that was subject to only a longevity constraint (i.e., if longevity was finite, but fecundity was infinite), realized reproduction would be calculated as the area under the heavy curve (i.e., the sum of Regions I, II, and IV). For a cohort that was subject to only a fecundity constraint (i.e., if fecundity was finite, but longevity was infinite), realized reproduction would be calculated as the area of the rectangle containing Regions I, II, and III. The models developed here suggest that insect life histories evolve such that both longevity and fecundity constraints are important; thus, for a cohort subject to both constraints, realized reproduction is calculated as the area below the survival curve, but to the left of $\frac{R_\bullet^*}{sk}$ (i.e., the sum or Regions I and II). Reproduction by females destined for time limitation is calculated as the area of Region I; for this subcohort, the longevity constraint is encountered before the fecundity constraint (females die before reaching age $\frac{R_\bullet^*}{sk}$, and thus before they run out of eggs). Reproduction by females destined for egg limitation is calculated as the area of Region II; for this subcohort, the fecundity constraint is encountered before the longevity constraint (females are still alive at age $\frac{R_\bullet^*}{sk}$, and thus they exhaust their egg supply before they die). Reproduction foregone by virtue of time limitation can then be calculated as the area of Region III, and reproduction foregone by virtue of egg limitation can be calculated as the area of Region IV.**

and $R_\bullet^*$ is either R_{spat}^* or R_{temp}^*. Because females must take some time to adjust their projected estimates of egg versus time limitation, allocating all of Region II to oviposition events shaped by egg limitation includes some error. But, because an extensive early literature on insect oviposition behavior shows that female insects do adjust their estimates of host availability very quickly, often after just two to three rapid successive host encounters (reviewed in Rosenheim and Rosen 1991), I suggest that this error will be modest. More complex cases are addressed in the discussion. Reproduction by females destined to become time-limited is proportional to the area of Region I in Figure 2:

$$\text{Area(Region I)} = \int_0^{\frac{R_\bullet^*}{sk}} e^{-\left(\frac{x}{b}\right)^c} dx - \phi\left(\frac{R_\bullet^*}{sk}\right) \cdot \frac{R_\bullet^*}{sk}. \quad (13)$$

Finally, the proportion of all eggs laid in the population that is laid by females destined to become egg limited, ρ_e, is computed as:

$$\rho_e = \frac{\text{Area(Region II)}}{\text{Area(Region I)} + \text{Area(Region II)}}. \quad (14)$$

ρ_e tells us what sort of reproductive behavior we expect to see if we view all oviposition events within the population as one collective pool. Large values of ρ_e (i.e., ρ_e approaching 1.0) tell us that whereas high-quality hosts encountered by females with eggs remaining will be accepted, many lower quality hosts encountered by females will be rejected, and furthermore that clutch sizes observed will be smaller, such that fitness returns per egg will be relatively high. In contrast, small values of ρ_e (i.e., ρ_e approaching 0.0) tell us that both high-quality hosts and many lower quality hosts will be accepted for oviposition, and that clutch sizes will be larger, such that fitness returns per egg will be relatively low. The proportion of all eggs laid in the population that is laid by females destined to become time limited, ρ_t, is simply 1 - ρ_e; thus, any increase in ρ_e as a measure of how strongly egg limitation will influence reproductive behavior observed across the population implies a corresponding drop in the influence of time limitation.

Second, we may be interested in how egg or time limitation constrains overall reproductive recruitment by the population, important for studies of population dynamics. In principle, a female whose reproduction is constrained by neither time nor eggs may be expected to enjoy infinite reproduction; boundaries on this infinite reproduction can be imposed by either the finite supply of eggs (the vertical line at $x = \frac{R_\bullet^*}{sk}$ in Fig. 2) or a finite longevity (the declining survival function shown in Fig. 2). If we take finite longevity as a given, then reproduction that is foregone because of egg limitation is proportional to the area of Region IV in Figure 2:

$$\text{Area(Region IV)} = \int_{\frac{R_\bullet^*}{sk}}^{\infty} e^{-\left(\frac{x}{b}\right)^c} dx. \quad (15)$$

The proportion of all potential reproduction that is foregone due to egg limitation (i.e., suitable hosts are located, but oviposition is prevented by a lack of eggs), ω_e, can then be computed as:

$$\omega_e = \frac{\text{Area(Region IV)}}{\text{Area(Region I)} + \text{Area(Region II)} + \text{Area(Region IV)}}. \tag{16}$$

Analogously, if we take the finite egg supply as a given, then reproduction that is foregone because of time limitation is proportional to the area of Region III in Figure 2:

$$\text{Area(Region III)} = \int_0^{\frac{R^*_\bullet}{sk}} \left(1 - e^{-\left(\frac{x}{b}\right)^c}\right) dx. \tag{17}$$

The proportion of all potential reproduction that is foregone due to time limitation (i.e., mature eggs are available, but the female dies before finding hosts on which to lay them), ω_t, can then be computed as:

$$\omega_t = \frac{\text{Area(Region III)}}{\text{Area(Region I)} + \text{Area(Region II)} + \text{Area(Region III)}}. \tag{18}$$

It is important to note that ω_e and ω_t, unlike ρ_e and ρ_t, do not sum to 1.0; thus, ω_e and ω_t need not vary inversely.

For the numerical results presented below, the following parameter values were used: $T = 100$ resource units; $a = 1$ resource unit/hour; $k = 1$ host/hour; s was varied from 0.001 to 2.0 resource units; and c was varied from 0.3 to 8. The cost of an egg, s, was varied, because previous analyses have established that optimal fecundity varies strongly with s (Rosenheim 1996, Ellers et al. 2000).

Results

SPATIALLY STOCHASTIC ENVIRONMENTS

The model predicts that increasing spatial heterogeneity in reproductive opportunity increases the optimal investment in reproduction, R, any time when the cost of maturing an egg is less than the cost of living long enough to find a host (here, $s < 1$; Fig. 3A). When egg costs are higher than the cost of locating a host ($s = 2$), increasing stochasticity favors a decreased investment in reproduction. Nevertheless, for all parameter values explored, the level of egg limitation associated with the optimal life history decreases as spatial heterogeneity increases (Fig. 3B). Thus, the current analysis confirms the primary finding of Sevenster et al. (1998) and Ellers et al. (2000) that spatially stochastic environments are expected to decrease the prevalence of egg limitation. Note, however, that spatial heterogeneity and egg cost interact in their effects on egg limitation: spatial heterogeneity produces smaller drops in egg limitation when eggs are less expensive (e.g., Fig. 3B).

The decreased incidence of egg limitation associated with increasing spatial heterogeneity does not, however, translate into a decrease in the ecological importance of egg limitation. Instead, both of the measures of the ecological importance of egg limitation introduced here show strong increases in response to increasing spatial heterogeneity. First, the proportion of eggs laid by females destined to become egg limited (ρ_e) increases with increasing spatial heterogeneity whenever egg costs are not extremely high (Fig. 3C), with a concomitant drop in the proportion of eggs laid by females destined to become time limited (ρ_t; Fig. 3D). Second, the proportion of all potential reproduction by the population foregone because of egg limitation also increases strongly with increasing spatial heterogeneity (ω_e; Fig. 3E); importantly, in this case, this increase occurs with a parallel increase in reproduction foregone because of time limitation (ω_t; Fig. 3F), suggesting that stochasticity simultaneously amplifies the ecological impacts of both constraints.

TEMPORALLY STOCHASTIC ENVIRONMENTS

The model predicts that temporally stochastic environments generate very different effects on optimal reproductive allocations and egg limitation than do spatially stochastic environments (compare Fig. 3A,B with Fig. 4A,B). Increased temporal heterogeneity increases optimal investment in reproduction, R, when eggs are least expensive (e.g., $s = 0.001$–0.01), decreases optimal investment in reproduction when eggs are most expensive (e.g., $s = 0.6$–2), and produces peaks in reproductive allocations for intermediate levels of temporal heterogeneity when egg costs are intermediate (e.g., $s = 0.05$–0.4; Fig. 4A). This complexity is exactly mirrored in the predicted incidence of egg limitation: decreases, increases, or intermediate maxima are observed, depending on egg cost (Fig. 4B).

As just described, spatially and temporally stochastic environments differ in their predicted effects on reproductive allocations and expected egg limitation. Nevertheless, just as was seen for spatial heterogeneity, increasing temporal heterogeneity is predicted to favor strong increases in both the proportion of eggs laid by females destined to become egg limited (ρ_e; Fig. 4C) and the proportion of all potential reproduction foregone because of egg limitation (ω_e; Fig. 4E) and time limitation (ω_t; Fig. 4E).

Discussion

The main results of the model analysis are as follows. First, I was able to repeat the primary result from Sevenster et al. (1998) and Ellers et al. (2000): spatially stochastic environments favor an increased allocation to reproduction and a decrease in the expected incidence of egg limitation. Second, spatially and temporally stochastic environments do not have equivalent effects on the evolution of egg limitation. Instead of producing consistent increases in reproductive allocation and decreases in egg limitation, increasing temporal heterogeneity was predicted to

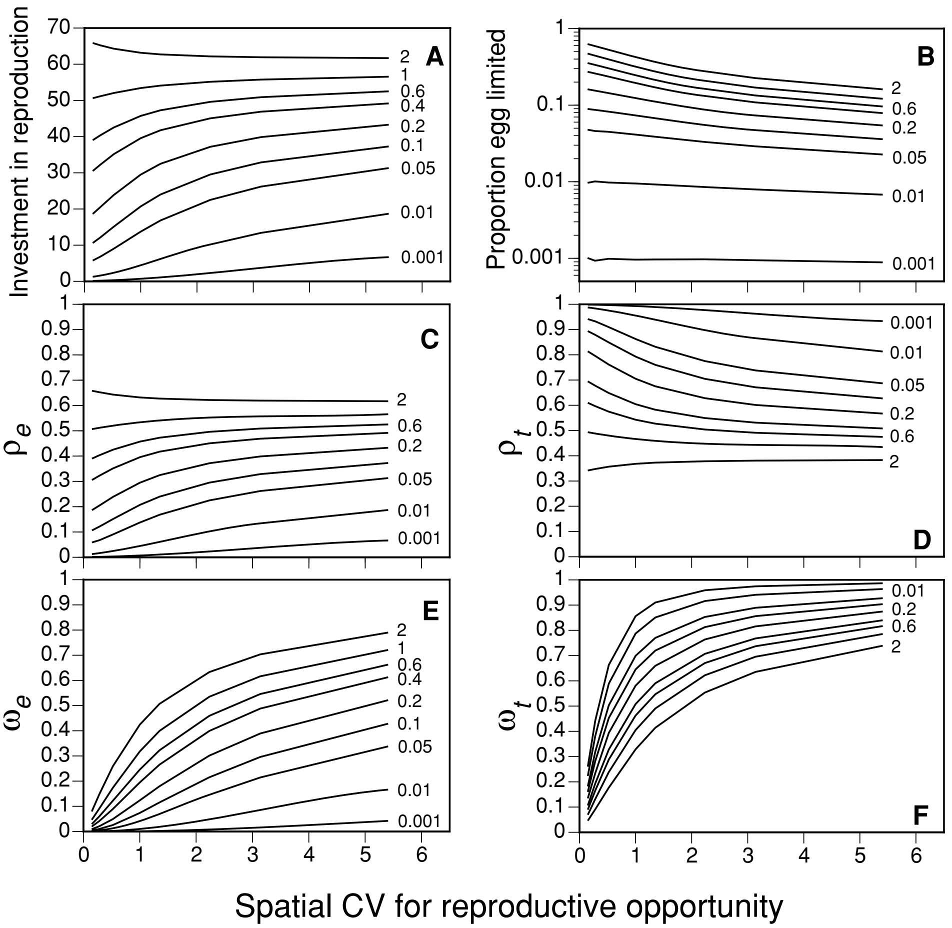

Figure 3. **Evolution of egg and time limitation in a spatially stochastic environment. Shown, for different values of egg costs (0.001 ≤ s ≤ 2.0), is the influence of increasing the coefficient of variation for reproductive opportunity (i.e., the number of hosts encountered during the lifetime of foraging activity) on (A) the optimal investment in egg maturation (resource units, out of a total of 100 units available for reproduction and longevity), obtained by numerically maximizing equation (4); (B) the proportion of females expected to become egg limited (i.e., females exhausting their lifetime supply of eggs before dying); (C) ρ_e, the proportion of all eggs laid by the population that is laid by females destined to become egg limited; (D) ρ_t, the proportion of all eggs laid by the population that is laid by females destined to become time limited; (E) ω_e, the proportion of total potential reproduction by the population (in this case, the total number of hosts encountered) that is foregone because the females had previously exhausted their egg supply; and (F) ω_t, the proportion of total potential reproduction by the population (in this case, the total number of eggs matured) that is foregone because the females did not live long enough to find hosts on which to deposit those eggs. Panel (B) shows that increasing spatial heterogeneity causes the incidence of egg limitation within the population to decline; but panels (C) and (E) show nevertheless that two measures of the ecological importance of egg limitation both increase strongly with increasing spatial heterogeneity.**

increase, decrease, or produce intermediate maxima in reproductive allocations and expected levels of egg limitation, depending on egg costs. Third, and most important, the models predict that two measures of the ecological importance of egg limitation increased strongly as heterogeneity (spatial or temporal) increased, even when the associated levels of egg limitation were predicted to decline.

The conclusion that spatial and temporal forms of stochasticity have different effects on the evolution of insect fecundity and associated risks of egg limitation is not surprising when viewed in the broader context of life-history evolution under uncertainty (Hopper 1999; Roff 2002; Orr 2007). For limiting factors problems that involve essential resources or essential components for reproductive success (e.g., in the case analyzed here, reproduction requires both a host and an egg), both spatially and temporally stochastic environments can favor over-allocation, relative to the deterministic case, in the less-expensive component of reproductive success (Cohen and Dukas 1990; Alexander 1997; Ellers et al. 2000; Rosenheim et al. 2010). Thus, increasing spatial heterogeneity favors larger investment in egg maturation any time the cost of an egg is less than the cost of extending longevity enough to encounter another host (i.e., $s < 1$). Spatially stochastic

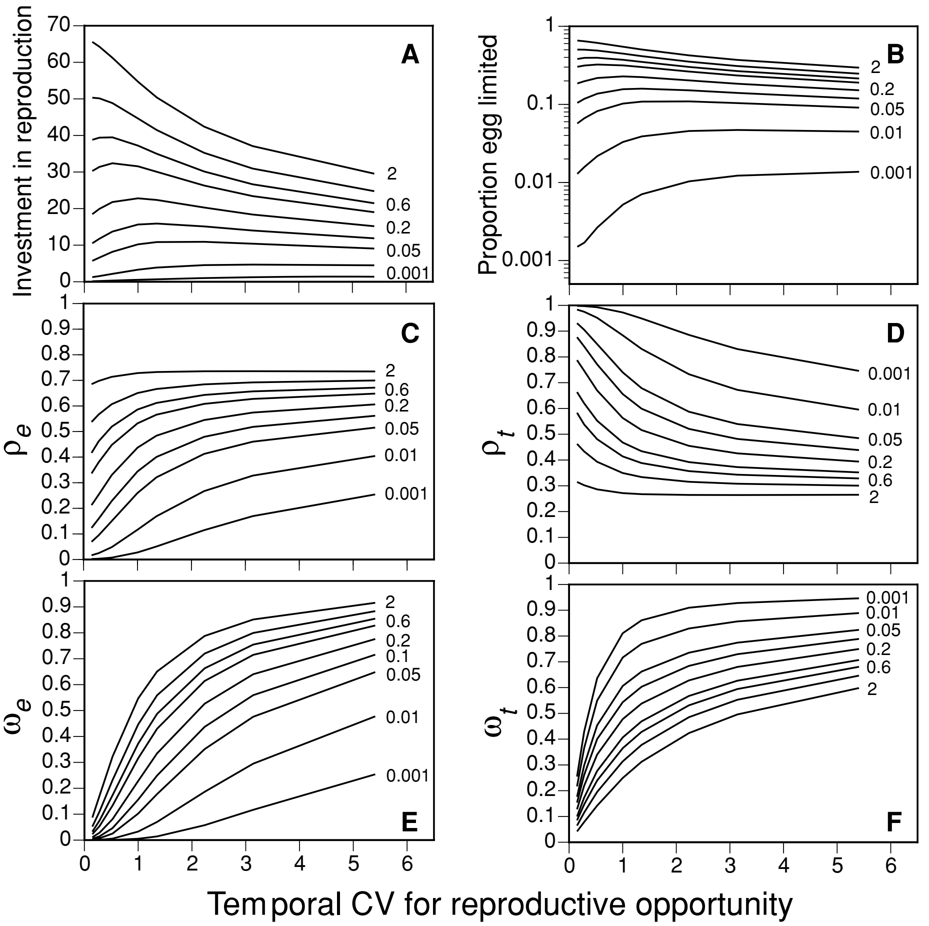

Figure 4. Evolution of egg and time limitation in a temporally stochastic environment. Shown, for different values of egg costs ($0.001 \leq s \leq 2.0$), is the influence of increasing the coefficient of variation for reproductive opportunity on (A) the optimal investment in egg maturation (resource units, out of a total of 100 units available for reproduction and longevity), obtained by numerically maximizing equation (10); (B) the proportion of females expected to become egg limited; (C) ρ_e, the proportion of all eggs laid by the population that is laid by females destined to become egg limited; (D) ρ_t, the proportion of all eggs laid by the population that is laid by females destined to become time limited; (E) ω_e, the proportion of total potential reproduction by the population (in this case, the total number of hosts encountered) that is foregone because the females had previously exhausted their egg supply; and (F) ω_t, the proportion of total potential reproduction by the population (in this case, the total number of eggs matured) that is foregone because the females did not live long enough to find hosts on which to deposit those eggs. Whereas panel (B) shows that increasing temporal heterogeneity can cause either decreases or increases in the incidence of egg limitation depending on the costliness of eggs, panels (C) and (D) show nevertheless that two measures of the ecological importance of egg limitation both increase strongly with increasing temporal heterogeneity.

environments favor allocation strategies that perform best in locations where opportunities for reproduction are high, because these locations make disproportionately large contributions to the pool of offspring; in the case examined here, this translates to host-rich habitat patches, where a higher fecundity and a shorter longevity are optimal. In temporally stochastic environments, however, a second process also shapes optimal life histories: temporal heterogeneity imposes particularly stiff penalties on strategies that perform very poorly during generations when opportunities for reproduction are unusually rare; in the case examined here, this translates to generations when suitable hosts are very scarce (the models do not incorporate any stochasticity in egg production). To avoid catastrophic reproductive failure during generations of host scarcity, the optimal life history is one that supports an extended longevity, allowing for greatly extended search for rare hosts, at the expense of producing fewer eggs (Jervis et al. 2005). The complex pattern of optimal fecundity observed for insects in a temporally stochastic environment (Fig. 4A) thus represents the interplay of these two opposing processes, with selection for greater fecundity predominating only when egg costs are low and the magnitude of stochasticity not too great.

Of course, real environments will generally exhibit some combination of spatial and temporal heterogeneity, and the relative contributions of the two to overall variation in reproductive opportunity is likely to vary widely across different systems. In the absence of quantitative data on the relative magnitudes of spatial and temporal heterogeneity, formal analysis is necessarily speculative; however, simulations of environments with equal coefficients of variation for spatial and temporal heterogeneity predict optimal investment in egg maturation and associated levels of egg limitation that are intermediate between the pure spatial and temporal cases (J. A. Rosenheim, unpubl. data).

The conclusion that spatially and temporally stochastic environments can have very different effects on how organisms cope with different limiting factors is consistent with the analysis of plant reproduction (flower to fruit ratios) presented by Cohen and Dukas (1990). They show that whereas spatially stochastic environments favor increases in allocations to flowers (the early, and less-expensive stage of reproduction, and therefore analogous to the allocations to egg production analyzed here), temporally stochastic environments may instead favor decreased allocation to flowers (see also Sakai 1996). Other forms of bet hedging in response to temporal unpredictability in the importance of different limiting factors, including the possibility of “mixed’ strategies, have not yet been explored, but could also be important (Roff 2002; Olofsson et al. 2009).

But how can we understand the seemingly counterintuitive result that declines in the proportion of egg-limited females can occur simultaneously with increases in the ecological importance of egg limitation? Two processes are at play here. First, the paradox of a declining incidence of egg limitation being combined with an increasing proportion of eggs laid by females who are destined for egg limitation can be resolved by noting that increasing stochasticity in reproductive opportunity acts to concentrate reproduction in the “hands” of a small fraction of the individuals within the population. It is within this small fraction of individuals that egg limitation emerges. Thus, egg-limited females make disproportionately large contributions to total reproduction by the population, thereby amplifying the ecological importance of egg limitation beyond what one might expect from simply asking what proportion of females are egg limited. This explanation echoes the point made by van Baalen (2000), who argued that the “jackpot effect” that occurs when females encounter super-abundant reproductive opportunities is expected to have significant influences on the evolution of insect fecundity.

Second, the paradox of a declining incidence of egg limitation being combined with a growing constraint imposed by egg limitation on total population reproduction can be resolved by noting that increasing stochasticity produces the potential for ever-larger mismatches between allocations to fecundity and longevity. When the environment is highly predictable, life histories are expected to evolve toward the perfectly balanced allocation to egg maturation and lifetime number of suitable hosts discovered, under which the female dies immediately upon laying her final egg. In this case, $\omega_e \approx \omega_t \approx 0$, and a population dynamics model that incorporated either egg or time constraints would accurately project total population reproduction, because the two constraints are essentially redundant—females are simultaneously limited by both factors at the perfectly balanced life history (Rosenheim et al. 2010). As the environment becomes increasingly unpredictable, however, more and more females find themselves in a condition of grossly unbalanced allocations: at times or places with abundant hosts, females have many more oviposition opportunities than they have eggs; at times or places with scarce hosts, females have many more eggs than they have oviposition opportunities. Thus, stochasticity produces strong and simultaneous increases in the importance of both egg and time constraints (ω_e and ω_t). In this case, a population dynamics model that incorporated either egg constraints or time constraints alone, or a population dynamics model that examined mean environmental quality rather than considering the variability in reproductive opportunity (e.g., Kean et al. 2003), would perform poorly, generating large overestimates of reproductive recruitment (Figs. 3E,F and 4E,F); egg and time constraints are no longer redundant, and thus models must include both kinds of constraints and the real spatial or temporal heterogeneity when environmental quality is unpredictable.

A thought experiment can perhaps help to clarify how high levels of stochasticity in reproductive opportunity act to amplify both measures of the ecological importance of egg limitation, even while creating a very low incidence of egg limitation. Imagine an insect parasitoid that exploits hosts living in discrete habitat patches and which matures 100 eggs over her lifetime. Imagine further that one parasitoid spends her entire life searching within a single patch, chosen randomly (i.e., independently of host density). Assume that the parasitoid excludes other parasitoids from the patch and eventually finds all hosts present. Assume that mean host density per patch = 10, which is low relative to parasitoid fecundity. Imagine now a scenario with extremely high spatial heterogeneity in reproductive opportunity: 99% of the patches harbor zero hosts, and 1% of the patches harbors 1000 hosts. The incidence of egg limitation will be very low: only 1% of females (the females that are found in patches with 1000 hosts) will exhaust their lifetime supply of hosts, with the remaining 99% of females experiencing time limitation. Nevertheless, in this case we would not want to conclude that time limitation was a sensible default for models of insect reproductive behavior or models of host–parasitoid population dynamics. Females destined to become egg limited would be responsible for 100% of the eggs laid within this population ($\rho_e = 1.0$), and thus we would expect all reproductive behavior expressed within the population to be shaped by the large opportunity costs of laying eggs (e.g., females should reject low-quality hosts and produce clutch sizes that maximize fitness returns per egg laid). Similarly, parasitoids would be unable to exploit 90% of discovered hosts because of egg limitation ($\omega_e = 0.9$), and simultaneously 99% of the eggs matured by the parasitoid population would never be laid (i.e., all eggs matured by parasitoids that are searching in patches devoid of hosts; $\omega_t = 0.99$). Thus, we would not want to adopt a model of host–parasitoid population dynamics that assumed that parasitoid recruitment is defined by host encounters alone or by egg maturation alone. Figure 5 shows how this crude caricature plays out within the framework of the model analyzed here; in the displayed example, increasing spatial heterogeneity in reproductive opportunity produces a 3.5-fold increase in optimal allocation to reproduction (R^*_{spat}) and a 60% drop in the expected incidence of egg limitation, but simultaneously produces a 3.5-fold increase in ρ_e, a 100.5-fold increase in ω_e, and a 5.6-fold increase in ω_t.

AN ALTERNATE MEASURE OF THE ECOLOGICAL IMPORTANCE OF EGG LIMITATION

ρ_e is an index of the ecological importance of egg limitation for females that can project whether their reproduction will be constrained by eggs or hosts, and adjust their reproductive behavior accordingly. It is also useful to consider the case where females do not adjust their personal estimates of the risks of egg/time limitation. In this case, even when egg limitation is a minority condition in the population, egg costs often make the dominant contribution to the cost of oviposition, and therefore egg costs are predicted to shape reproductive behavior (Rosenheim 1999b). Egg costs are usually generated by a small risk (the small probability of being egg limited) of incurring a large cost (the lost opportunity to oviposit on a potentially high-quality host to be encountered in the future), whereas time costs are usually generated by a large risk (the large probability of being time limited) of incurring a small cost (the lost opportunity for reproduction due to the use of time to deposit an egg on the current host). Time costs associated with oviposition are usually small, because most insects lay their eggs relatively quickly, whereas searching for hosts is a lengthy process; in a sample of 11 parasitoid species, the median ratio of oviposition time to search time was 0.02 (Rosenheim 1999b). In depositing a single egg on a current host, a time-limited parasitoid therefore can expect to forfeit reproductive returns from 0.02 hosts in the future. Thus, the potential loss of future reproduction under egg limitation (1.0 host) is 50 times as great as the potential loss of future reproduction under time limitation (0.02 hosts). Because of this, egg costs are exactly balanced with time costs when egg limitation is quite rare (for the median case, the balance occurs when ≈2% of the population is egg limited), and egg limitation must be very rare indeed (often <1%) before its influence on the cost of oviposition will be small enough to be safely ignored.

Such low levels of egg limitation (<1%) are predicted by optimality models only when the costs of eggs are very small relative to the cost of locating hosts (Rosenheim 1996, Sevenster et al. 1998, Ellers et al. 2000). How will increasing stochasticity in reproductive opportunity influence ρ_e in this case? Under increasing spatial heterogeneity, the expected incidence of egg limitation (and its contribution to the cost of oviposition) declines only modestly when egg costs are low; for example, when

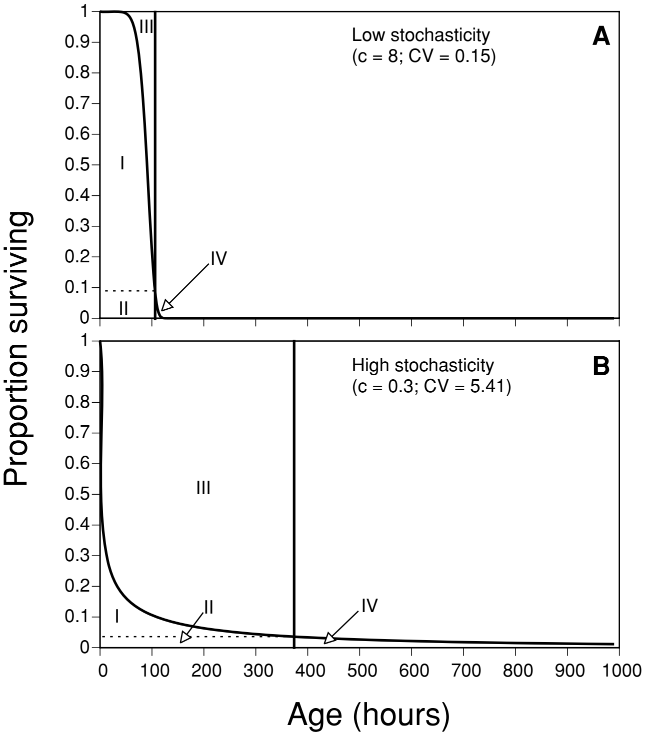

Figure 5. Influence of a spatially stochastic environment on the ecological importance of egg and time limitation. In this example, egg costs are modest ($s = 0.1$). (A) With low stochasticity in reproductive opportunity ($c = 8$; CV = 0.15), investment in reproduction is relatively low ($R^*_{spat} = 10.6$) and thus females exhaust their lifetime supply of eggs at a relatively early age ($\frac{R^*_{spat}}{sk} = 106$h). In this case, the proportion of females living long enough to exhaust their lifetime supply of eggs is relatively high (0.089), but the proportion of all eggs laid in the population that is laid by females destined to become egg limited, is modest ($\rho_e = 0.106$). Almost no reproduction by the population is foregone because of egg limitation ($\omega_e = 0.0043$), and only a modest amount of reproduction by the population is foregone because of time limitation ($\omega_t = 0.160$). (B) In contrast, with high stochasticity in reproductive opportunity ($c = 0.3$; CV = 5.41), investment in reproduction is relatively high ($R^*_{spat} = 37.3$) and thus females do not exhaust their lifetime supply of eggs until a relatively late age ($\frac{R^*_{spat}}{sk} = 372.8$h). In this case, the proportion of females living long enough to exhaust their lifetime supply of eggs is relatively low (0.036). Nevertheless, the proportion of all eggs laid in the population that is laid by females destined to become egg limited, is relatively large ($\rho_e = 0.373$, a 3.5-fold increase over the low stochasticity case). Furthermore, both egg and time limitation now impose very strong constraints on reproduction by the population: $\omega_e = 0.428$, a 100.5-fold increase over the low stochasticity case, and $\omega_t = 0.904$, a 5.6-fold increase over the low stochasticity case.

$s = 0.01$, even a very large increase in the CV of reproductive opportunity (from 0.15 to 5.41) decreases the expected incidence of egg limitation by only 30% (from 0.97% to 0.68%; see Fig. 3B). The corresponding response to increasing temporal heterogeneity is instead a 3.5-fold increase in the incidence of egg limitation (from 1.3% to 4.5%; see Fig. 4B). Thus, under the alternate measure of the ecological importance of egg limitation discussed in Rosenheim (1999b), increasing stochasticity in reproductive opportunity is unlikely to shift a system from a condition where egg costs are important to a condition where egg costs can safely be ignored.

This analysis also suggests that ρ_e may often underestimate the proportion of all oviposition behavior expressed within a population that is shaped predominantly by egg costs. When females are faced with substantial uncertainty regarding whether their fitness will eventually be constrained by eggs versus time (i.e., when the personal estimates of these two events are roughly similar in magnitude), egg costs will dominate the overall cost of oviposition, and consequently females will be expected to move toward behavior that maximizes fitness returns per egg. Thus, oviposition behavior expressed by individuals occupying portions of Region I may also be shaped by risks of egg limitation, even if that fate is not eventually realized. Additional work is needed to explore the behavior expressed by female insects that have incomplete knowledge of their eventual fate, rather than perfect knowledge (as explored here) or only an evolutionarily tuned mean expectation, uninformed by current conditions (as explored in Rosenheim 1999b).

INSIGHTS FROM THE BROADER LITERATURE ON LIMITING FACTORS

Limiting factors problems that emerge in entirely different settings may also provide important insights into the influence of stochastic environments on life-history evolution. Elsewhere my colleagues and I have argued that several seemingly disparate debates regarding limiting factors in the evolutionary ecology literature that involve essential resources or essential components of reproductive effort (e.g., evolution of senescence, physical wear of an organism's key structural elements, ecological stoichiometry, ovule packaging, pollen limitation, and egg versus time limitation in insects) are different expressions of a common problem that can be analyzed with an evolutionary application of Liebig's Law of the Minimum (Rosenheim et al. 2010). This broader literature is relevant to the current discussion in at least two ways.

First, the broader literature provides support for the metrics of the ecological importance of egg limitation that I have employed (eqs. 14, 16). Analysis of a generic model of a Liebigian limiting factor problem in a spatially stochastic environment suggests that within an optimized life history, the optimal allocation made to the harvest of an essential resource (Resource A) is equal to the fraction of the total reproductive output of the population contributed by individuals whose fitness is limited by Resource A; in our model this is measured by ρ_e. This equality can be seen by noting that the plots in Figure 3A,C are identical. Thus, the metric ρ_e is flagged by evolution as a biologically important quantity, suggesting that we are on firm footing in our use of this metric. Our second measure of the ecological importance of egg limitation, ω_e has, in the context of plant ecology, been the subject of an extensive research program examining pollen limitation (Ashman et al. 2004; Knight et al. 2006). Pollen supplementation experiments, which have now been conducted on hundreds of plant species, provide a direct quantification of foregone reproduction due to pollen limitation (the increase in reproduction is analogous to the area of Region III in Figure 2, which is the numerator of ω_e). Nutrient supplementation experiments in ecological stoichiometry are, similarly, quantifying metrics that are directly analogous to ω_e.

Second, the broader literature provides empirical support for the prediction made by Sevenster et al. (1998) and reaffirmed here (Fig. 3A), namely that increasing spatial heterogeneity will favor increased allocation to the less-expensive component of reproduction. Burd et al. (2009; see also Ashman et al. 2004) have demonstrated convincingly that plant species faced with greater spatial unpredictability in pollen receipt, measured as the variance in pollen grains received per stigma, have responded evolutionarily by producing a larger number of ovules per flower. To my knowledge, this is the first demonstration that the magnitude of environmental heterogeneity in the availability of potentially limiting factors does indeed elicit evolutionary responses in real organisms, as predicted by simple models of life-history evolution.

CONCLUSIONS

Stochasticity in reproductive opportunity plays a central role in shaping insect life histories. Previous analyses have focused exclusively on spatially stochastic environments, which favor increased allocation to reproduction and a decreased risk of egg limitation. Temporally stochastic environments may, however, favor either increases or decreases in allocation to reproduction; decreased allocation to reproduction hedges against the risk of extremely low reproduction during years when reproductive opportunities are extremely scarce. Most importantly, both forms of stochasticity increase the ecological importance of egg limitation, even when the associated risk of egg limitation is decreased. Stochasticity in reproductive opportunity amplifies the ecological importance of egg limitation by concentrating reproduction in the hands of a few members of the population whose risk of egg limitation is greatly elevated and by magnifying the opportunities for large mismatches between allocations to eggs versus longevity. These conclusions underscore the importance of building models of insect reproduction and population dynamics that incorporate the constraints imposed by both time limitation and egg limitation, rather than just one constraint or the other (e.g., Hassell 2000; West and Cunningham 2002; Murdoch et al. 2003; Gandon et al. 2009; Richard and Casas 2009; Roitberg et al. 2010). Life histories evolve to place insects on the "knife edge" between time and egg limitation, setting the stage for plastic oviposition behavior and shifting constraints on reproduction that are crucial in shaping insect reproduction and population dynamics.

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