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Journal

The American Naturalist, 175(4)

ISSN

1537-5323

Authors

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Publication Date

2010-04-01

DOI

10.1086/650724

Supplemental Material

<https://escholarship.org/uc/item/39b938pf#supplemental>

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A Stochastic Model for Annual Reproductive Success

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Submitted July 3, 2009; Accepted November 19, 2009; Electronically published February 17, 2010

Online enhancement: appendix. Dryad data: <http://hdl.handle.net/10255/dryad.1087>.

ABSTRACT: Demographic stochasticity can have large effects on the dynamics of small populations as well as on the persistence of rare genotypes and lineages. Survival is sensibly modeled as a binomial process, but annual reproductive success (ARS) is more complex and general models for demographic stochasticity do not exist. Here we introduce a stochastic model framework for ARS and illustrate some of its properties. We model a sequence of stochastic events: nest completion, the number of eggs or neonates produced, nest predation, and the survival of individual offspring to independence. We also allow multiple nesting attempts within a breeding season. Most of these components can be described by Bernoulli or binomial processes; the exception is the distribution of offspring number. Using clutch and litter size distributions from 53 vertebrate species, we demonstrate that among-individual variability in offspring number can usually be described by the generalized Poisson distribution. Our model framework allows the demographic variance to be calculated from underlying biological processes and can easily be linked to models of environmental stochasticity or selection because of its parametric structure. In addition, it reveals that the distributions of ARS are often multimodal and skewed, with implications for extinction risk and evolution in small populations.

Keywords: clutch size distributions, demographic stochasticity, generalized Poisson distribution, litter size distributions, nesting success, reproductive success.

Introduction

Stochasticity in population growth rates is inevitable in real populations and arises from multiple sources including demographic stochasticity, environmental stochasticity, sex-ratio fluctuations, and demographic heterogeneity (Melbourne and Hastings 2008). This stochasticity often reduces the long-term population growth rate and increases extinction risk (Bartlett 1955) and may be selected against (Gillespie 1975, 1977; Lehmann and Balloux 2007; Shpak 2007). There are exceptions to this general pattern

(e.g., Doak et al. 2005), and stochasticity can, under appropriate circumstances, promote the coexistence of competing species (e.g., Chesson 2000).

Demographic stochasticity—the uncertainty in an individual’s demographic fate, given an environment and a set of phenotypic traits—is particularly important in determining a small population’s extinction risk (Melbourne and Hastings 2008) and is susceptible to selection under Gillespie’s (1975, 1977) model. In continuous time, this form of stochasticity can be modeled as a birth-death process (Bartlett 1960; MacArthur and Wilson 1967; Richter-Dyn and Goel 1972; Goodman 1987), although building in appropriate correlation structures can be challenging (Ferson et al. 1989). When considering organisms that have discrete breeding seasons, in contrast, we need stochastic processes that integrate survival across a year and that incorporate appropriate variation in annual reproductive success. Such processes should be biologically justified and parameterized in ways that can be linked to environmental stochasticity and demographic heterogeneity (Melbourne and Hastings 2008) as well as to environmental trends such as climate change (Morris et al. 2008).

Survival of an individual over a finite time interval is a Bernoulli process: the individual either lives or dies. This leads to a natural choice of the binomial probability distribution to model demographic stochasticity in survival at the population level (Renshaw 1990; Akçakaya 1991), which is well established in population biology. For some species, notably seabirds and many large mammals, a breeding pair can produce at most one offspring in a breeding season, in which case demographic stochasticity in reproductive success can also be modeled using a binomial distribution (Conner and White 1999). However, in general the number of offspring that become independent of their parents is the product of a number of stochastic processes, and the resulting probability distribution of reproductive success may be quite complex.

Demographic stochasticity has received particular attention in population viability analysis (PVA). The two major PVA software packages take very different ap-

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Am. Nat. 2010. Vol. 175, pp. 461–468. © 2010 by The University of Chicago. 0003-0147/2010/17504-51409\$15.00. All rights reserved.

DOI: 10.1086/650724

proaches to this problem. RAMAS (Akçakaya 2002) uses a Poisson distribution to describe demographic stochasticity in reproductive output (Akçakaya 1991, 2004); there is no subsequent mortality of offspring. In contrast, VORTEX (Lacy 1993; Miller and Lacy 2005) requires the analyst to specify an empirically derived nonparametric distribution of offspring numbers that is then sampled to obtain the realized number of offspring; these offspring then survive according to a binomial distribution. Most of the independently developed PVA models in the literature apply one of these approaches (e.g., Walters et al. 2002; Robert et al. 2003; Wiegand et al. 2004).

There are shortcomings to both approaches. In general, there is neither biological nor theoretical justification for the use of the Poisson distribution, and survival (of either the offspring or their parents, depending on how the model is formulated) is a key component of the reproductive term in discrete-time population models (Morris and Doak 2002). In contrast, nonparametric distributions are adequate to the population at hand, but the lack of biological parameters makes it difficult to evaluate the effects of environmental stochasticity, management, or evolutionary change. In this article we consider the biological processes that underlie demographic stochasticity in animal annual reproductive success and use these to develop and analyze a general parametric model of this phenomenon.

The General Model

First, a comment on terminology. Very different vocabularies have developed to describe reproduction in oviparous and viviparous species. For simplicity, we primarily use oviparous terms and phrases such as “laying eggs,” “clutch size,” and “nest.” However, the models apply equally to mammals and other viviparous species; simply substitute appropriate terms such as “giving birth,” “litter size,” and “den.”

The Outcome of a Single Breeding Attempt

Consider a single breeding attempt. The number of independent offspring depends on (1) whether nest building and mating is completed; (2) the number of eggs laid or neonates birthed; (3) whether the nest is depredated, destroyed, or abandoned; and (4) the probability that each offspring survives from egg laying to independence (contingent on nest success).

The first step (egg laying), being binary, can be modeled as a Bernoulli process. The second step (clutch size) is quite a bit more challenging, as there is no conventionally accepted model for the probability distribution for the number of eggs or neonates produced in a breeding at-

tempt. We propose that the generalized Poisson distribution (Consul 1989) will often be appropriate; see “Clutch Size Distributions” for theoretical arguments and empirical evidence. The third stage (nest failure) can also be represented as a Bernoulli process (although from the point of view of the offspring, it represents correlated mortality). There are a number of options for the last item (offspring survival). Each individual’s survival might be independent of that of its broodmates; if the survival probabilities are equal, then the number of survivors follows a binomial distribution. However, if fates are not independent, the distribution might be different. For example, if the instantaneous survival probability is a declining function of the number of currently living broodmates (because of competition for parental provisions), then the number of deaths might be described by a generalized Poisson distribution (Consul 1989).

For the rest of the examples in this article we will assume that each offspring has an identical and independent survival probability. Given that, then the probability that a breeder has $i > 0$ independent offspring from a breeding attempt is

$$\begin{aligned}\phi(i) &= \Pr(f = i) \\ &= bs \sum_{n=i}^{\infty} g(n) \binom{n}{i} p^i (1-p)^{n-i},\end{aligned}\quad (1)$$

where b is the probability that the breeder actually lays eggs, s is the probability of nest survival, $g(n)$ is the probability of laying n eggs (contingent on egg laying), and p is the probability that an individual offspring survives to independence. The probability that the breeder produces no independent offspring is the sum of the probabilities that no eggs are laid, that eggs are laid but the nest is destroyed, and that the nest survives but none of the offspring do:

$$\begin{aligned}\phi(0) &= \Pr(f = 0) \\ &= (1-b) + b \left[(1-s) + s \sum_{n=1}^{\infty} g(n) (1-p)^n \right]\end{aligned}\quad (2)$$

$$= 1 - bs + bs \sum_{n=1}^{\infty} g(n) (1-p)^n.\quad (3)$$

An example of this probability distribution with clutch size being Poisson distributed is shown in figure 1. The distribution is bimodal, with one mode at 0 representing breeding failure and the other representing the most likely number of independent offspring from a successful breeding attempt.

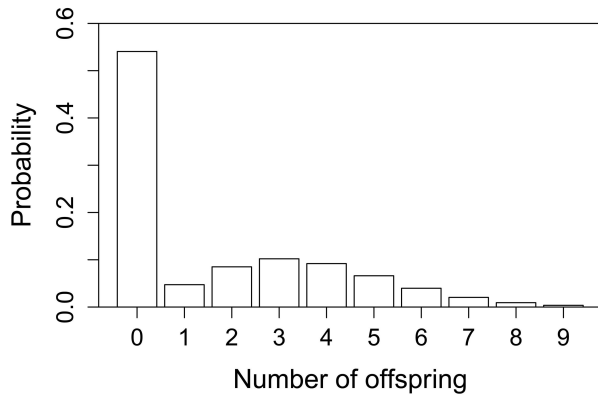


Figure 1: Probability distribution of reproductive outcomes from a single breeding attempt. Parameter values: nesting probability $b = 0.95$, nest survival probability $s = 0.5$, clutch size distribution $g(n) \sim \text{Poisson}(4.5)$, and nestling survival probability $p = 0.8$.

Rebreeding

Many animals can make multiple breeding attempts during a breeding season; often the probability of rebreeding depends on whether the previous breeding attempt succeeded or failed. For example, consider the situation where the breeder is capable of making two breeding attempts during the season, with rebreeding probabilities r_s and r_f , depending on whether the first breeding attempt was successful. Let $\phi_1(i)$ denote the probability of having i independent offspring in the first breeding attempt and $\phi_2(i)$ be the same for the second attempt (if it is made). Then the probability of reproductive failure over the season is

$$\Pr(F = 0) = \phi_1(0)(1 - r_f) + \phi_1(0)r_f\phi_2(0). \quad (4)$$

The first term represents a single breeding attempt and the second represents two breeding attempts (both failures). An outcome of $k = 1$ independent offspring can arise two ways (in either the first attempt or the second):

$$\Pr(F = 1) = \phi_1(1)(1 - r_s) + \phi_1(1)r_s\phi_2(0) + \phi_1(0)r_f\phi_2(1). \quad (5)$$

For $k > 1$, the distribution of reproductive success for the whole season is

$$\begin{aligned} \Pr(F = k) &= \phi_1(k)[(1 - r_s) + r_s\phi_2(0)] \\ &+ \phi_1(0)r_f\phi_2(k) \\ &+ \sum_{i=1}^{k-1} \phi_1(i)r_s\phi_2(k-i). \end{aligned} \quad (6)$$

The first term represents all the success coming from the first attempt, the second term represents all the success coming from the second attempt, and the third term represents success in both attempts.

Making the not-unreasonable assumption that the parameters of ϕ_1 and ϕ_2 are the same allows the equations to be simplified:

$$\Pr(F = 0) = (1 - r_f)\phi(0) + r_f\phi(0)^2, \quad (7)$$

$$\Pr(F = 1) = (1 - r_s)\phi(1) + (r_s + r_f)\phi(0)\phi(1), \quad (8)$$

$$\begin{aligned} \Pr(F = k > 1) &= (1 - r_s)\phi(k) + r_f\phi(0)\phi(k) \\ &+ r_s \sum_{i=1}^k \phi(i)\phi(k-i). \end{aligned} \quad (9)$$

An example is shown in figure 2; there is a third mode representing success in both attempts.

When considering species that rebreed multiple times, a decision must be made about r_i : does it apply whenever the previous breeding attempt fails or only when all prior breeding attempts have failed? This is a biological question; in the examples that follow, we choose the second definition, for simplicity.

Allowing up to two rebreeding attempts, and assuming that the parameters of all the breeding attempts are equal, the probability distribution for seasonal reproductive success is

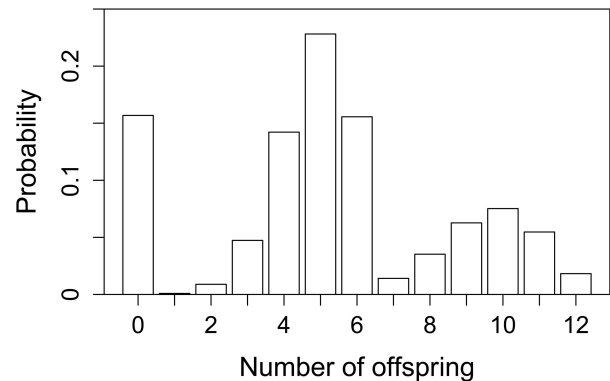


Figure 2: Probability distribution of reproductive outcomes from two breeding attempts. Parameter values: nesting probability $b = 0.95$, nest survival probability $s = 0.7$, all clutches are of size 6, and nestling survival probability $p = 0.8$. Rebreeding probabilities are $r_s = 0.6$ and $r_f = 0.8$.

$$\Pr(F = 0) = (1 - r_f)\phi(0) + r_f(1 - r_s)\phi(0)^2 + r_f^2\phi(0)^3, \tag{10}$$

$$\Pr(F = 1) = [1 - r_s + (1 - r_s)(r_s + r_f)\phi(0) + (r_s^2 + r_s r_f + r_f^2)\phi(0)^2]\phi(1), \tag{11}$$

$$\Pr(F = 2) = [1 - r_s + (1 - r_s)(r_s + r_f)\phi(0) + (r_s^2 + r_s r_f + r_f^2)\phi(0)^2]\phi(2) + [r_s(1 - r_s) + (r_s^2 + r_s r_f)\phi(0)]\phi(1)^2, \tag{12}$$

$$\Pr(F = k > 2) = [1 - r_s + (1 - r_s)(r_s + r_f)\phi(0) + (r_s^2 + r_s r_f + r_f^2)\phi(0)^2]\phi(k) + [r_s(1 - r_s) + (r_s^2 + r_s r_f)\phi(0)] \times \sum_{i=1}^{k-1} \phi(i)\phi(k-i) + r_s^2 \sum_{i=1}^{k-2} \sum_{j=1}^{k-i-1} \phi(i)\phi(j)\phi(k-i-j). \tag{13}$$

In principle, this can add a fourth mode to the distribution, but in practice, the effect of three successful attempts will usually appear as a long tail on the distribution (the exceptions are if r_s is close to 1 or the mean number of offspring per successful breeding attempt is large). The extension to four or more breeding attempts is straightforward (though tedious); since the additional modes will not be prominent, the primary reason for doing so is to obtain expressions for the mean and variance of reproductive success (see below).

Clutch Size Distributions

The Poisson distribution is strongly favored by ecologists when they want a multivalued, discrete, unimodal distribution. This probably stems from a combination of analytical tractability and the fact that it is a sensible model for measurement error in count data. Does it make sense for the among-individual distribution of clutch sizes? The underlying stochastic process is that an “event” (in this case, the laying of one egg) has a constant instantaneous probability of occurrence; the number of events over a given time interval is Poisson distributed. While this may be a good model for parasitoids searching for hosts in which to lay their eggs, it is not at all obvious that this is a good description of the physiological and energetic processes that underlie reproduction in other animals, especially terrestrial vertebrates. Furthermore, the Poisson distribution is strongly constrained, with the variance exactly

equaling the mean, a feature that is violated by many empirical clutch size distributions.

One modification of the Poisson process that might capture some of the energetic constraints and physiological feedbacks that animals face would be to have the instantaneous probability of the next egg be a declining function of the number of eggs already laid. A stochastic process very much like this is described by the “generalized Poisson distribution” (Consul and Jain 1973; Consul 1989).

The probability mass function for the generalized Poisson distribution is

$$P_x(\theta, \lambda) = \frac{\theta(\theta + x\lambda)^{x-1} e^{-(\theta+x\lambda)}}{x!}. \tag{14}$$

This distribution has two parameters, and in contrast to the Poisson distribution, the mean and variance need not be equal. If $\lambda < 1$, then the mean is $\theta/(1 - \lambda)$, and the variance is $\theta/(1 - \lambda)^3$. Notice that when $\lambda = 0$, this is simply a Poisson distribution with mean θ . Unfortunately, the name has also been applied to a variety of other distributions, including a “corrupted” Poisson distribution in which some ones are incorrectly recorded as zeros (Johnson and Kotz 1969).

This model approximates the biological intuition given above if $\lambda < 0$. Under this condition, the variance is always less than the mean. In addition, the probability distribution has an upper bound: nonzero probability is possible only for values of x that satisfy $0 \leq x < -\theta/\lambda$. This upper bound is a desirable feature for species, such as most birds and mammals, that have a physiological or morphological upper limit to clutch or litter size. Furthermore, as λ gets more negative, the mode of the distribution approaches the maximum value (Consul 1989), a feature often seen in clutch size distributions with small maximum clutch sizes.

Thus, we hypothesize that the generalized Poisson distribution will provide a good statistical description of clutch size distributions in many animals. To test this, we compiled data on clutch (or litter) size distributions from a wide variety of birds, mammals, and reptiles and attempted to fit them with the generalized Poisson distribution as well as a variety of other discrete probability distributions.

Data Sources

We searched the literature for data on clutch or litter size distributions, restricting ourselves to unmanipulated populations and surveys that were either exhaustive or random and that reported data reflecting a single breeding attempt for each breeder. We sought information recorded in a single year at a given site, which we designated a “pop-

ulation.” We discarded data consisting of fewer than 20 records. In some cases, reported data were combinations of multiple years or sites; we used these only if the 20-record minimum applied to all site-year combinations and the authors reported a statistical test that failed to reject the null hypothesis that all the populations followed the same distributions. We also corresponded with authors who published summaries, but not distributions, of clutch size distributions; several of these generously shared the original data for us to analyze.

Records were used for a total of 182 populations of birds, mammals, and reptiles for which annual reproductive success data could be extracted from published and unpublished literature and data sets. There are 28 unique bird species represented by 123 populations, 14 mammal species represented by 17 populations, and 11 reptile species represented by 42 populations. These are listed in tables A1–A3 in the online edition of the *American Naturalist*. Only three studies counted clutches with zero eggs or litters with zero newborns, and such counts might be biased (e.g., nests without incubating parents might be more difficult to find; the pair might rebreed before the nest is found), so we discarded these zero counts.

Discrete Probability Distributions

We fitted various discrete probability distributions to the clutch size data for each population to identify parametric distributions that have empirical support. In addition to the generalized Poisson distribution, we fitted the Poisson, binomial, negative binomial, and hypergeometric distributions to the data. Three compound distributions (see “Compound Distributions” in the online edition of the *American Naturalist*) were also tested: Neyman’s type A (Poisson-Poisson), Poisson-rectangular, and the Poisson-binomial. Other distributions tested included the Beta-Pascal, Zipf, Borel, and Poisson-logseries, but these did not fit any of the data and we do not consider them further here. Because we did not have data on clutch sizes of zero, we used “zero-truncated” distributions: the zero event is removed, and the probability mass of the rest of the distribution rescaled so that the total probability sums to 1.

Fitting Methods

For each population, maximum likelihood parameter estimates (MLEs) were generated for each of the discrete models described above. Analytic expressions for MLEs do not exist with zero truncation, so we used numerical fitting with a multinomial likelihood function. We calculated the Akaike Information Criterion (AIC) for each model and evaluated the overall goodness-of-fit of each fitted distribution with a Pearson’s χ^2 test. Distributions with an AIC

within two units of the best-fitting model and for which $P > .05$ in the χ^2 test were considered plausible models for the data. Data sets for which all of the distribution had $P < .05$ in the χ^2 test were classified as “no fit.”

Results

The generalized Poisson distribution fitted the greatest number of populations (133 of 152) that were fitted by at least one of the distributions considered in this study. In all cases the second parameter was negative, which truncates the distribution. The hypergeometric and binomial distributions fitted fewer populations than did the generalized Poisson but performed much better than did the Poisson and negative binomial functions, which fitted 14 and 3 populations, respectively. Of the compound distributions, the Neyman’s type A provided a good fit for 16 populations, the Poisson-rectangular fitted 5 populations, and the Poisson-binomial fitted 3. In only 4 populations (all reptiles) did the compound functions offer a better fit than any of the five noncompounded functions. Thirty populations were not fitted well by any of the models (these had either bimodal distributions, complete or near invariance in clutch size, or approximately triangular distributions). “Results of Clutch Size Analysis” in the appendix details these findings for each species.

Model Analysis

It is straightforward (see “Derivation of Means and Variances” in the appendix) to show that the expected number of independent offspring from a single breeding attempt is

$$\bar{f} = bsp\bar{c}, \quad (15)$$

where \bar{c} is the mean of the clutch size distribution. This is a pleasantly intuitive result. However, the formula for the variance in reproductive success from a single attempt is quite complex:

$$\text{Var}(f) = bsp[(1-p)\bar{c} + p(1-bs)\bar{c}^2 + p\text{Var}(c)], \quad (16)$$

where $\text{Var}(c)$ is the variance of the clutch size distribution.

The variance in breeding success increases with both the mean and the variance of clutch size. It depends quadratically on both b and s , with negative second derivatives; it is maximized at

$$bs = \frac{1}{2} \left[1 + \frac{1-p}{p\bar{c}} + \text{CV}(c)^2 \right], \quad (17)$$

where CV is the coefficient of variation. The variance in breeding success also depends quadratically on p , the offspring survival probability, but the sign of the second derivative depends on the other parameter values. It is negative if

$$\text{Var}(c) < \bar{c} - (1 - bs)\bar{c}^2, \quad (18)$$

which is possible only if mean clutch size is small and bs is close to 1. If this condition holds, then the variance is maximized when

$$p = \frac{\bar{c}}{2[\bar{c} - (1 - bs)\bar{c}^2 - \text{Var}(c)]}. \quad (19)$$

Inequality (18) also provides the condition for $\text{Var}(f) < \bar{f}$, or underdispersion relative to a Poisson distribution.

The CV in breeding success is

$$\text{CV}(f) = \sqrt{\frac{1-p}{bsp\bar{c}} + \frac{1 + \text{CV}(c)^2}{bs} - 1}, \quad (20)$$

which decreases with b , s , p , and the mean clutch size and increases with the CV in clutch size.

For the rebreeding model with two attempts, the expected reproductive success for the breeding season is

$$\bar{F} = [1 + r_s + r_t\phi(0)]\bar{f}. \quad (21)$$

The variance in reproductive success is

$$\begin{aligned} \text{Var}(F) = & [1 + r_s + r_t\phi(0)] \text{Var}(f) \\ & - \{[r_s + r_t\phi(0)]^2 + r_t\phi(0)\}\bar{f}^2. \end{aligned} \quad (22)$$

This increases with the variance in success from an individual breeding attempt but decreases with the expected outcome of an individual attempt. The coefficient of variation is

$$\text{CV}(F) = \sqrt{\frac{\text{CV}(f)^2 - [r_s + r_t\phi(0)]}{1 + r_s + r_t\phi(0)} + \frac{r_s}{[1 + r_s + r_t\phi(0)]^2}}. \quad (23)$$

Discussion

Existing models of demographic stochasticity in annual reproductive success often lack biological justification or do not have parametric forms. Here we have developed a general model framework describing demographic sto-

chasticity in annual reproductive success, with the parameters of the underlying stochastic processes having ready biological interpretation. Furthermore, we have demonstrated that the generalized Poisson distribution may often be a sound model with which to describe variation in clutch or litter sizes in birds, mammals, and reptiles.

This work represents three important advances. First is the separation of the variance from the mean, which is impossible in the Poisson model. This “demographic variance” (Engen et al. 1998) has a large influence on the risk of extinction due to demographic stochasticity: all else being equal, a higher variance leads to higher extinction risk (e.g., Bartlett 1955). Furthermore, in small populations, natural selection will tend to reduce the demographic variance if this can be done without reducing the mean fitness (Gillespie 1975, 1977; although initially developed for small, unstructured populations, this model has recently been expanded to spatially structured and age-structured populations [Lehmann and Balloux 2007; Shpak 2007]). In both applications it is important to have a model that does not unnecessarily constrain the relationship between the variance and the mean of reproductive success.

Second, parametric distributions (in contrast to purely empirical distributions) are valuable, especially if the parameters can be clearly related to the biology of the organism and its interaction with its environment. These parameters create the link between potentially heritable traits and the mean and variance of fitness, allowing the Gillespie model to be applied with biologically realistic evolutionary constraints. Furthermore, these parameters allow environmental stochasticity to be integrated with demographic stochasticity in population models for PVA by allowing the parameters to vary from year to year. In addition, the framework allows explicit analysis of the effects of demographic heterogeneity in various components of reproduction. This phenomenon can be explicitly incorporated into population dynamic models through simulation (e.g., Conner and White 1999), and in many cases it may be possible to find analytic approximations of the effects of heterogeneity on the demographic variance (Fox and Kendall 2002; Kendall and Fox 2003).

Finally, the model introduced here produces a distribution of reproductive success that is often skewed and multimodal, including a strong peak at 0. For some purposes this may not matter much. The central limit theorem tells us that if the population is large enough, then the demographic variation in the total number of offspring can be approximated by a normal distribution; numerical simulations suggest that this works well with as few as 10 breeding pairs. Thus, PVAs that set a quasi-extinction threshold high enough can use such a distribution in simulations once the appropriate variance has been deter-

mined (although ensuring that a truncated, discretized normal distribution actually has the appropriate variance is not trivial). However, if the population is followed all the way down to true extinction, then the shape of the distribution becomes important. For example, if we assume that adult survival is independent of age, then we can construct a simple branching process model to calculate the probability of extinction due to demographic stochasticity in the absence of density dependence (Harris 1963). Simulations suggest that when using the skewed annual reproductive success distributions produced by our model, a common approximation by Bartlett (1955) based only on the mean and variance of reproduction and survival tends to overestimate the extinction risk. For example, using the reproductive success distribution from figure 1 together with an annual survival probability of 0.45, Bartlett's approximation overestimates the extinction risk by about 7%. In other words, the positive skew makes the population less extinction-prone than would be predicted merely from the mean fitness and demographic variance. Likewise, strong skewness in lifetime reproductive success (which is likely if longevity is short and there is a good chance that any given breeding season results in failure) may influence the selection against demographic variance: Gillespie (1975, 1977) used a second-order truncation of a series expansion in his derivation.

In this analysis, we have focused on species in which the number of eggs or neonates is relatively small (fewer than 30) and the siblings from a particular breeding attempt experience a shared environment (reflecting both parental care and threats to the nest). These criteria apply to most birds, mammals, and reptiles (although there are notable exceptions, such as nest-parasitic cuckoos). In contrast, the reproductive success of most fish, invertebrates, and plants will not be well described by our model in its current form. For example, there is no particular reason to believe that the generalized Poisson distribution will describe broods with mean egg or larval numbers of hundreds or thousands, and in marine and aquatic environments, posthatching survival can be highly variable among individuals (e.g., Thorson 1950; Olafsson et al. 1994; Graham et al. 2008). Nevertheless, the principle we have adopted in our model construction—breaking reproductive success into its constituent components and asking what sorts of stochastic process best describes each component—could be applied to these other taxa.

The model has many parameters; can they be estimated from data? Yes, if we focus on the components of the model rather than the final distribution. If nests can be easily observed, then many model components (nest initiation, clutch size, nest failure, chick survival, rebreeding rates, etc.) can be quantified directly and transformed into parameter estimates for that portion of the model. The un-

certainities associated with each of these estimates would be largely uncorrelated, making their assembly into a final parameterized model straightforward. In contrast, trying to fit the complete model to a final distribution of reproductive success (such as the one shown in fig. 2) would be challenging at best (in particular, we expect that it would be very difficult to statistically disentangle the joint effects of p , \bar{c} , and $\text{Var}(c)$, especially with a clutch size distribution model that is as flexible as the generalized Poisson). Perhaps having just the detailed information on the clutch size distribution would be sufficient to constrain the remaining parameters when fitting the reproductive success distribution—this would be a topic for further research. In addition, environmental conditions or parental phenotypes might be more strongly related to particular components of reproductive success than to the final outcome. If so, then analyzing these components in the context of the full model would help reveal the potential impact of environmental variability or selection, especially if there are counteracting effects at different stages of the reproductive process.

This stochastic model of reproductive success, both in the particular form analyzed here and with extensions to relax our assumptions of independence of fates and identity of parameters between breeding attempts, provides a biologically motivated parametric model of demographic stochasticity in reproductive success. As such, it can be easily integrated with models of environmental stochasticity and demographic heterogeneity, as has already been done for survival (e.g., Kendall 1998; Fox et al. 2006), facilitating the rigorous development of integrated models (Melbourne and Hastings 2008). The model can also be integrated with recent advances in life-history dynamics (Tuljapurkar et al. 2009) to more rigorously evaluate how patterns of variation in reproductive success affect evolutionary demography.

Acknowledgments

We thank A. C. Berkley, K. Keith, S. Lieberman, and H. Tiwari for help in compiling the clutch and litter size data and P. Tingiris for database development. E. Cooch, M. Fujiwara, R. Gomulkiewicz, P. Lundburg, and, particularly, G. Fox provided valuable insights and discussion, and two anonymous reviewers provided feedback that improved the paper. R. Barclay, J. Iverson, F. Janzen, K. Larsen, J. Rodgers, D. Scott, S. Trauth, and J. Tucker kindly shared unpublished clutch size data. This work was supported by grant R82908801 from the STAR Program of the U.S. Environmental Protection Agency's National Center for Environmental Research and by National Science Foundation grant 615024.

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