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Chance Establishment for Sexual, Semelparous Species: Overcoming the Allee Effect

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ABSTRACT: We formalize the establishment process for a sexual, semelparous organism through the use of hierarchical probability modeling from parameters of survival, probability of being female, probability of being fertilized, and expected fecundity. We show how to calculate the expected per capita growth rate and probability of extinction. An Allee effect is observed if the expected population growth rate decreases as the initial population size decreases. The model can be further extended as a stochastic process to evaluate the probability of extinction in subsequent generations. One of the novel results is the formulation of an analytical probability distribution for the next generation population size. As case studies, we use the Chinese mitten crab (*Eriocheir sinensis*) and the apple snail (*Pomacea canaliculata*), both of which appear on the World Conservation Union's list of 100 worst invaders. We evaluate the strength of the Allee effect and conclude that apple snails experience a weak Allee effect and Chinese mitten crabs experience a strong Allee effect. We emphasize one scenario where the stochastic process reveals that invasion risk can be estimated by the probability of the survival of one fertilized female, because the expected fecundity for one surviving female overwhelms the system such that population persistence is almost certain.

Keywords: nonindigenous species, hierarchical modeling, establishment, demographic stochasticity, propagule pressure, Allee effect.

Introduction

Populations at low densities are potentially prone to declining or negative per capita growth rates as population density decreases (Allee effect; e.g., Allee 1938; Odum and Allee 1954; Dennis 1989). This effect has been invoked to explain why many repeatedly introduced nonindigenous species (NIS) fail to establish (Sakai et al. 2001; Lockwood et al. 2005). For some NIS such as zebra mussels (*Dreissena polymorpha*), there is evidence that the Allee effect is a plausible explanation for the frequency of unsuccessful invasions at locations receiving low levels of propagule pressure (Leung et al. 2004).

In the absence of an Allee effect, repeated introductions will eventually lead to successful establishment, although this may take considerable time to occur (Jerde and Lewis 2007). The only management action that will negate the risk of invasion is to eliminate all propagule pressure. However, because of the costs of searching for and eliminating the last few individuals in a population (Regan et al. 2006) or in the arrival pathway, the elimination of propagule pressure may be difficult or impossible (Simberloff 2003*a*). In contrast, the presence of Allee effects allows alternative management: if propagule pressure can be reduced below a threshold, then repeated introductions will continually fail to establish (Taylor and Hastings 2005; Drake and Lodge 2006). However, assessing and testing the strength of Allee effects generally requires collecting population data after a species establishes and while it spreads (Veit and Lewis 1996; Leung et al. 2004). This has led some to question the utility of population models for invasive-species risk assessment and proactive management (Simberloff 2003*b*).

Distinct from Allee effects, demographic stochasticity will also influence the persistence or extinction of a species (Goodman 1987). Demographic stochasticity arises from chance events that result from individual birth and death processes (Lande 1993) and through fluctuations in the sex ratio (Bessa-Gomes et al. 2004). At high population abundances, the variability due to demographic stochasticity becomes negligible (Engen et al. 1989), but at low population abundances, demographic stochasticity can be a dominant force that will determine the fate of a population (Lande 1993), which, in turn, will have conse-

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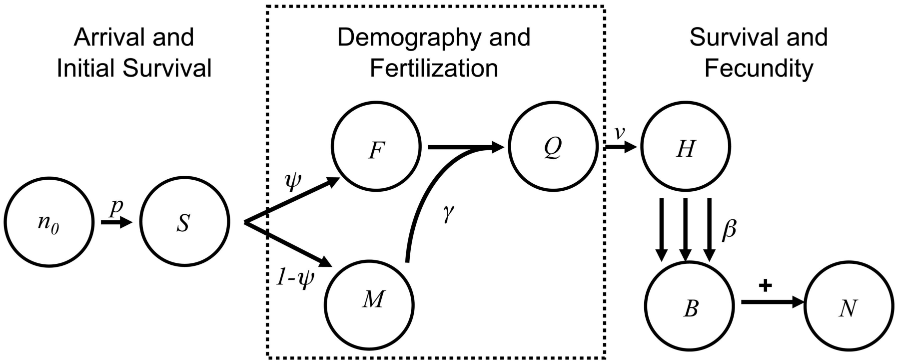

Figure 1: Flow diagram of the hierarchical population model. Random variables are defined in table 1, and parameters are defined in table 2. Plus sign indicates the summation of random variables.

quences on conservation management (Goodman 1987). Because NIS are often introduced at relatively low abundances (Lockwood et al. 2005), the influence of demographic stochasticity is an additional, critical consideration in evaluating risk and predicting invasions (Drake and Jerde 2009).

Using life-history traits to predict invasions has a mixed record of success, but some generalizations have been identified (Williamson 1999; Kolar and Lodge 2001). For example, Keller et al. (2007) found that fecundity of freshwater mollusks was a significant predictor of whether a species would cause ecological or economic damage. Similarly, statistics of life history, such as the net reproductive rate R_0, which is the lifetime production of offspring per female, can be estimated for a wide variety of life histories (de Camino Beck and Lewis 2007) and is related to the spread rate of invading organisms (Kot et al. 1996). But can life-history traits be used to predict the presence and strength of Allee effects?

We propose a stochastic model for the establishment of a semelparous, two-sex species that has an emerging Allee effect and demographic stochasticity. The model employs life-history parameters (survival, sex ratio, fertilization probability, and fecundity) from which it is possible to calculate the probability of extinction in the next generation, the expected net per capita growth rate, and the expected net population change for an initial population size introduced into a location. From the model, we identify whether a weak or a strong Allee effect is expected in the population, using independently estimated parameters from other locations or laboratory studies. Additionally, introduced populations have the potential to persist for a few generations and then become extinct as a result of the Allee effect and demographic stochasticity. Therefore, we show how the model can be formulated as a stochastic process and demonstrate the resulting temporal changes in the distribution of population abundance. This allows us to predict the persistence and extinction probabilities of newly arrived species, which is critical for assessing and managing invasion risk (Leung et al. 2002).

Two semelparous organisms, the apple snail and the Chinese mitten crab, are classified as two of the world's worst invaders by the World Conservation Union's Invasive Species Specialist Group (http://www.issg.org). After application of the model, we conclude that the apple snail has a weak Allee effect and the Chinese mitten crab has a strong Allee effect. However, because the expected fecundities of these two organisms are so large, the Allee effect, while present, does not significantly influence the probability of population establishment. Instead, the probability of at least one female becoming fertilized and surviving to give rise to the next generation is the critical consideration for predicting successful invasions and is a mechanistic justification for fecundity and net reproductive rate being used to identify species likely to become invasive (Keller et al. 2007; de Camino Beck and Lewis 2008).

Hierarchical Allee Effect Model

We take the approach of modeling population dynamics with discrete probability events formulated in a hierarchy of processes (fig. 1). All random variables are defined in table 1, and all parameters are defined in table 2. First, a fixed number of individuals, n_0, are introduced into a new landscape. These individuals must then survive to reproductive maturity with a survival probability, denoted p. These surviving individuals, S, are then separated into females, F, and males, M, with the probability of being female denoted as ψ. A female is fertilized by any given male with probability γ. Assuming promiscuous mating and no mate choice, the probability of a female becoming fertilized

Table 1: Random variables of the hierarchical model

Random variable	Description	Support
S	Number of initially surviving individuals in the population	$(0, 1, 2, \ldots, n_0)$
F	Number of females in the population	$(0, 1, 2, \ldots, S)$
M	Number of males in the population	$(0, 1, 2, \ldots, S)$
D	Number of individuals that do not initially survive (see app. A)	$(0, 1, 2, \ldots, n_0)$
K	Success of one male attempting to fertilize one female (see app. A)	$(0, 1)$
Y	Number of males that successfully fertilize a female (see app. A)	$(0, 1, 2, \ldots, M)$
Q	Number of successfully fertilized females	$(0, 1, 2, \ldots, F)$
H	Number of successfully fertilized females that survive to reproduce	$(0, 1, 2, \ldots, Q)$
B	Fecundity	$(0, 1, 2, \ldots)$
N	Total number of offspring (next-generation population size)	$(0, 1, 2, \ldots)$
R	Geometric growth rate	$-1 < r < \infty$

increases monotonically, $1 - e^{-n_0 \gamma p(1-\psi)}$, with the number of males ($n_0 p(1-\psi)$). The mate-finding strategy of an organism is a known mechanism of the Allee effect (Courchamp et al. 2008), and alternative mate-finding strategies will result in a variety of female fertilization functions (Lee et al. 2008) beyond the promiscuous mating function used here. Each fertilized female has a probability ν of survival to reproduction. The model is of a semelparous organism, so the number of offspring B produced by each fertilized female H becomes the population at the next generation, N.

Hierarchical probability models are synonymous with conditional probability. If a distribution has a parameter that is a random variable, then it is a hierarchical or conditional process (Casella and Berger 2002). A common application of this approach is with Bayesian inference where a prior distribution formed from belief, data, or a mixture of the two is placed on the value of a parameter in order to account for parameter uncertainty. However, hierarchical models are not proprietary to Bayesian inference (e.g., Dennis and Lele 2009). The approach we have taken has a subtle distinction in that variability in the distribution of the next generation's population size arises from a series of chance death, reproduction, and birth processes that are linked through conditional probability. This variability is often referred to as process variability (Dennis et al. 2006) and is perceptibly, although not mathematically, different from parameter uncertainty. The consequences of parameter uncertainty are addressed after the case studies.

Reducing the model through conditional probability results in a compound Poisson process (CPP) that is conditional on the random variables that describe the number of fertilized females that survive to reproduction, H, and the number of offspring per surviving fertilized female, B:

$$N|H, B = \sum_{i=1}^{H} B_i, \qquad (1)$$

where $H \sim \text{Poisson}\{n_0 \nu p \psi[1 - e^{-n_0 \gamma p(1-\psi)}]\}$ and $B \sim \text{Poisson}(\beta)$. The random variable, N, is the population size of the next generation. The model formulation and details of the simplifications used to arrive at equation (1) are found in "Formulation of the Hierarchical Probability Model of Establishment" in appendix A in the online edition of the *American Naturalist*.

A number of mathematical and biological assumptions are used to reduce the hierarchical model to a CPP; these can be found in appendix A. However, one assumption is worth emphasizing here. We assume that Poisson approximations can be substituted for binomial probability distributions. For invasive species, the approximation is biologically reasonable when the probability of finding a surviving fertilized female, $\nu p \psi[1 - e^{-n_0 \gamma p(1-\psi)}]$, is small. If this probability is large, a population will readily establish, and evaluating the presence and strength of an Allee effect is unnecessary as a practical concern. However, exact probabilities when this assumption is questionable can be calculated using compound binomial processes, which will result in properties similar to those presented here (Leipus and Viano 2003). Implementing a compound binomial model will follow a similar procedure to that described in appendix A, but it will require separating the initial population size (n_0) from the Poisson distribution, resulting in binomial distributions (e.g., Taylor and Karlin 1998, p. 27).

Model Properties

Mean, Variance, and Probability-Generating Function of CPPs

CPP random variables do not have convenient marginal distributions from which to make predictions of the observed next-generation population size, N. Instead, we rely on the probability-generating function to describe the shape of a random variable's distribution. Probability-generating functions are useful mathematical constructs that

Table 2: Parameters of the hierarchical model and the parameter estimates, with source citations, used for the Chinese mitten crab (*Eriocheir sinensis*) and apple snail (*Pomacea canaliculata*) examples

	Model properties		*E. sinensis*		*P. canaliculata*	
Parameter	Description	Support	Value	Sources	Value	Sources
n_0	Initial population size	(1, 2, …)	…	…	…	…
p	Probability of surviving from introduction to mating	$0 \le p \le 1$	.01	Anger 1991	.8	Estebenet and Cazzaniga 1992; Estebenet and Martin 2002
ψ	Probability of being female	$0 \le \psi \le 1$	.5	Zhang et al. 2001	.5	Yusa 2007
γ	Probability of a male fertilizing a female	$0 \le \gamma \le 1$	.01	Herborg et al. 2006	~1	Albrecht et al. 1996
ν	Probability of surviving from mating to reproduction	$0 \le \nu \le 1$	~1	Anger 2006	.8	Estebenet and Cazzaniga 1992; Estebenet and Martin 2002
β	Expected number of offspring	$\beta > 0$	250,000	Kobayashi 2001	4,500	Estebenet and Martin 2002; Albrecht et al. 1996

capture the random variable's distributional form as a power series and allow for the calculation of the mean, variance, and probability mass.

The probability-generating function for the CPP is

$$G(t) = \mathrm{E}(t^N) = \sum_{n=0}^{\infty} \Pr(N = n)t^n$$
$$= \exp\left(\left[e^{(t-1)\beta} - 1\right]\left\{n_0 \nu p \psi\left[1 - e^{-n_0\gamma p(1-\psi)}\right]\right\}\right), \quad (2)$$

and it is used to calculate the mean and variance of N (e.g., Chatfield and Theobald 1973):

$$\mathrm{E}(N) = \beta\left\{n_0 \nu p \psi\left[1 - e^{-n_0\gamma p(1-\psi)}\right]\right\}, \quad (3)$$
$$\mathrm{Var}(N) = (\beta + \beta^2)\left\{n_0 \nu p \psi\left[1 - e^{-n_0\gamma p(1-\psi)}\right]\right\}$$
$$= (1 + \beta)\mathrm{E}(N). \quad (4)$$

The mean next generation size, $\mathrm{E}(N)$, is the product of the expected offspring per female, β, the number of females that survive to reproduction, $n_0 \nu p \psi$, and the discounting of the number of fertilized females that survive to reproduction due to mate-finding limitation, $1 - e^{-n_0\gamma p(1-\psi)}$. Although mathematically motivated, the expectation is biologically interpretable and shows that the nonlinearity, which is indicative of a mechanism leading to an Allee effect (Courchamp et al. 2008), emerges because of the mating function. This is a point we will return to in the formulation of the geometric growth rate.

The probability mass function (PMF) is recovered from the probability-generating function by

$$\Pr(N = n) = \frac{G^{(n)}(0)}{n!}. \quad (5)$$

This formulation of the PMF is computationally expensive because evaluating $\Pr(N = n)$ requires calculating the nth derivative of the generating function and evaluating the derivative at $t = 0$. Alternatively, it is possible to write the probability of $N = n$ recursively such that

$$\Pr(N = n) = \begin{cases} G(0) & \text{when } n = 0 \\ \dfrac{c(n_0)\beta^n}{n}\displaystyle\sum_{i=0}^{n-1}\frac{\Pr(N = i)}{\beta^i(n-1-i)!} & \text{when } n > 0 \end{cases}, \quad (6)$$

where $c(n_0) = n_0 p \nu \psi\left\{1 - e^{[-n_0\gamma p(1-\psi)]}\right\}e^{-\beta}$. This recursive formulation does not require the calculation of derivatives, thus easing the computational burden. Because this formulation is previously unreported, a derivation and a proof of the recursive formula are presented in appendix B in the online edition of the *American Naturalist*. For the purpose of predicting invasions, the hierarchical modeling approach leading to the CPP provides an analytical solution for the PMF that was previously studied with Monte Carlo simulation (Grevstad 1999).

Geometric Growth Rate and the Allee Effect

The presence and strength of the Allee effect are reflected in population growth as a function of population size (Dennis 1989). Because the model projects the population from n_0 to the random variable N in discrete time (with a time step of one generation), we use the geometric per capita growth rate, R, to assess population growth:

$$R = \frac{N}{n_0}. \quad (7)$$

The population at the next generation, N, is a random variable, so R is also a random variable, where $\mathrm{E}(R) = \mathrm{E}(N)/n_0$ and $\mathrm{Var}(R) = \mathrm{Var}(N)/n_0^2$. When n_0 becomes

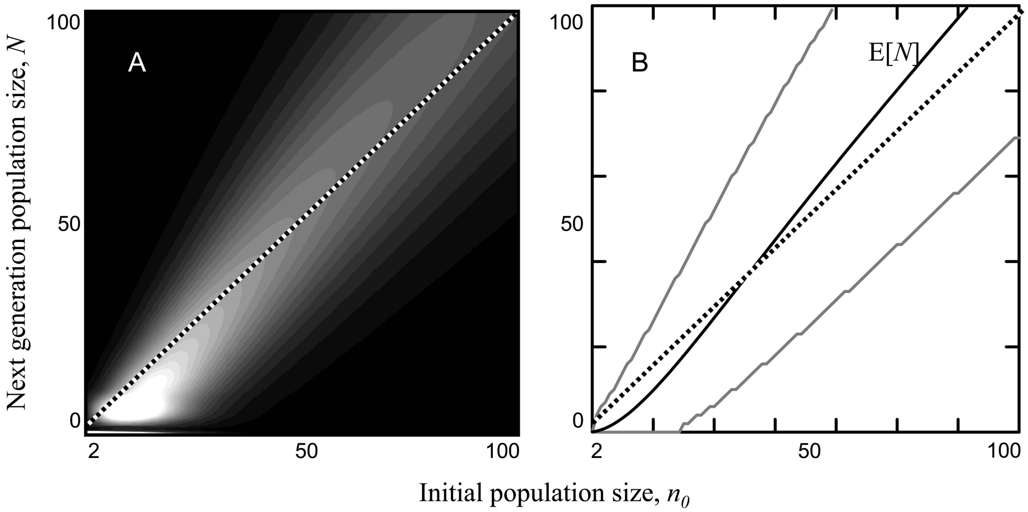

Figure 2: Interpolated probability surface of N (*A*) and expectation of N (*B*) with ~90% prediction intervals (*gray lines*) as a function of the initial population size, n_0, for $p = 0.8$, $\nu = 0.8$, $\psi = 0.3$, $\gamma = 0.1$, and $\beta = 6$. Dark shading in *A* indicates low probability, and light shading indicates higher probability. The dashed line in both *A* and *B* is a 1 : 1 line ($N = n_0$). For small values of n_0, there is a high probability of individuals being unable to replace themselves ($N < n_0$). However, as n_0 increases, the influence of the Allee effect is diminished, the expectation crosses the 1 : 1 line, and the probability that $N > n_0$ increases.

large, R converges to $p\nu\psi\beta$ where $\mathrm{Var}(R) \rightarrow 0$. A value of $R > 1$ indicates population growth, $R < 1$ indicates population decline, and $R = 1$ results in no change from the initial population size to the next-generation population size, $N = n_0$.

The asymptotic growth rate ($n_0 \rightarrow \infty$) is the product of survival ($p\nu$), the probability of being female (ψ), and fecundity (β). However, when the initial population size (n_0) is small, the expected geometric growth rate, $\mathrm{E}(R)$, is discounted by the probability of at least one male fertilizing a female, $1 - e^{[-n_0\gamma p(1-\psi)]}$. This is one mechanism that leads to Allee effects (e.g., Allee 1938; Boukal and Berec 2002; Hurford et al. 2006 and references therein). The mating function is the critical mechanism of the emerging Allee effect (Bessa-Gomes et al. 2004; Courchamp et al. 2008). Consequently, differences in mating behavior and success will change the strength of the Allee effect (e.g., Molnar et al. 2008), and tactical invasion risk assessments may require alternative mating functions beyond the one used here. For a general mating function approach, see Lee et al. (2008).

As discussed above, the Allee effect arises because individuals in the population, on average, cannot replace themselves. This effect may be a strong or a weak influence on the per capita growth rate (Wang and Kot 2001). A weak Allee effect is said to occur when the per capita growth rate is greater than 1 but decreases as the initial population size decreases. In contrast, a strong Allee effect is said to occur when the per capita growth rate or expected net population change becomes <1 for low population density. Only strong Allee effects induce an Allee threshold ($\mathrm{E}(R) = 1$). The expected net population change, where $\mathrm{E}(\Delta N) = \mathrm{E}(N) - n_0$, is another common function used to identify the presence and strength of Allee effects (Lewis and Kareiva 1993). The Allee threshold in this formulation occurs when $\mathrm{E}(\Delta N) = 0$, and it is consistent with a deterministic formulation of the Allee effect.

Demographic Stochasticity

The probability mass function for N (eq. [5]) allows for investigation of the influence of demographic stochasticity in the presence of the Allee effect. Figure 2 contains an interpolated surface of probability masses. The probability space can be separated into three distinct classes: the probability of extinction ($\Pr(N = 0)$; fig. 2*A*, *white area near the origin*), the probability of persisting with $N < n_0$ (fig. 2*A*, *below the dashed line*), and the probability that $N > n_0$ (fig. 2*A*, *above the dashed line*).

In deterministic settings with Allee effects, initial populations below an Allee threshold will become extinct while initial populations above the threshold will grow (Dennis 1989; Wang and Kot 2001). In contrast, stochastic models with Allee effects (Dennis 2002) assign a nonzero probability to population persistence due to chance events. As such, our model assigns a nonzero probability to population persistence in regions where deterministic models

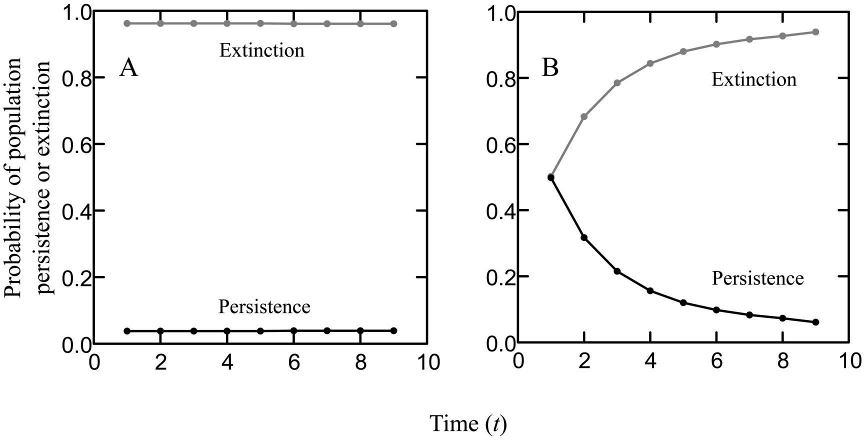

Figure 3: Two realizations of the stochastic process resulting from equation (8). The graph in *A* is parameterized using the life history of the Chinese mitten crab (table 2) and initialized at $n_0 = 400$. The graph in *B* (where $p = 0.8$, $\nu = 0.8$, $\psi = 0.3$, $\gamma = 0.1$, and $\beta = 6$), which is a random parameter set, was initialized at $n_0 = 15$, approximately half the value of the Allee threshold. For the mitten crab, the probability of establishing is very small ($\Pr(N_1 \neq 0) = 0.038$), but once established, the population persists. This is evident because the probability of the initial population persisting remains constant. In contrast, the population in *B* experiences an increased probability of extinction through time. Therefore, at each time step there is an increasing likelihood that the population has perished.

indicate extinction, which is consistent with previous results based on simulations (Grevstad 1999).

Extending the System as a Stochastic Process

We have previously assumed the initial population size to be fixed and known; hence, in equation (6), n_0 appears as a parameter. Projecting the distribution of subsequent generations of the population requires that we account for n_0 arising as a random variable. This is a stochastic process for the population size, indexed by time (t), and it forms the basis for predicting the persistence and establishment of new NIS introductions (Drake and Jerde 2009). The probability model can be written as a dynamical system by formulating the distribution of the next generation through chains of conditional probability:

$$\Pr(N_{t+1} = n_{t+1}) = \sum_{n_t=0}^{\infty} \Pr(N_{t+1} = n_{t+1} | N_t = n_t) \Pr(N_t = n_t). \tag{8}$$

The distribution of the next generation can be projected using a linear process:

$$\overrightarrow{\Pr(N_{t+1})} = \mathbf{A} \overrightarrow{\Pr(N_t)}. \tag{9}$$

In this linear process, the jth element of the vector $\overrightarrow{\Pr(N_t)}$ is the probability of observing $N_t = j - 1$. The vector of probabilities for N_1 is calculated using equation (5) for the initial population size, n_0. The length of this vector is set to $n_{\max} + 1$ to account for extinction, $n = 0$. The matrix **A** comprises $i = 1 \ldots n_{\max} + 1$ column vectors of conditional probability (eq. [7]). Because we are projecting the population dynamics of a sexual species, columns $i = 1$ and $i = 2$ are absorbing states, meaning that the probability of being extinct in the next time step is 1 if there are 0 or one individuals in the population (Taylor and Karlin 1998). For the remaining $i = 3 \ldots n_{\max} + 1$ columns, the elements, $a_{j,i}$, are calculated using equation (6), where $n = j - 1$ and $n_0 = i - 1$, resulting in

$$a_{j,i} = \begin{cases} G(0) & \text{when } j = 1 \\ \dfrac{c(i-1)\beta^{j-1}}{j-1} \displaystyle\sum_{k=0}^{j-2} \dfrac{\Pr(N = j-2)}{\beta^k (j-2-k)!} & \text{when } j > 1 \end{cases}. \tag{10}$$

The resulting conditional probability matrix is

$$\mathbf{A} = \begin{bmatrix} 1 & 1 & a_{1,3} & \cdots & a_{1,n_{\max}+1} \\ 0 & 0 & a_{2,3} & \cdots & a_{2,n_{\max}+1} \\ 0 & 0 & a_{3,3} & \cdots & a_{3,n_{\max}+1} \\ 0 & 0 & a_{4,3} & \cdots & a_{4,n_{\max}+1} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & a_{n_{\max}+1,3} & \cdots & a_{n_{\max}+1,n_{\max}+1} \end{bmatrix}. \tag{11}$$

The distribution of any future population at time t can be obtained by iterating equation (8). In figure 3, we provide two examples with different dynamics where population persistence can be evaluated at each time step t. In figure 3*A*, population persistence is determined by the dynamics at the first time step. With 400 individuals introduced initially, it is very likely that the population will be extinct in the next time step. However, there is a 0.038 chance the population will be nonzero and escape the influence of the Allee effect and demographic stochasticity. The fact that this probability changes very little after the first time step indicates population persistence. In contrast, the dynamics of figure 3*B* show an increasing probability of extinction through time. The low expected fecundity β, in concert with the other life-history parameters, does not allow the population to quickly escape the clutches of the Allee effect and demographic stochasticity. Mechanistically, this is one explanation of why fecundity is a significant predictor of successful invasion (Keller et al. 2007).

Examples

The Chinese mitten crab and the apple snail are two aquatic invertebrates listed on the World Conservation Union's (IUCN's) "100 of the World's Worst" list of invasive species (http://www.issg.org). These species have invaded large regions of the world but continue to invade new locations and are of concern in North America. Both species, which are semelparous and sexually reproducing, have received attention because of their ecological and economical impacts (Carlsson et al. 2004; Ruiz et al. 2006) and because there is a mixture of observational and laboratory research from which to obtain life-history parameters.

*Chinese Mitten Crab (*Eriocheir sinensis*)*

The Chinese mitten crab, which is native to eastern and southern Asia, has successfully invaded parts of Europe, Japan, and the San Francisco and Chesapeake bays of the United States (Rudnick et al. 2005; Herborg et al. 2006; Ruiz et al. 2006). Mitten crabs are imported as a food source, but live imports into the United States have been banned since 1989, before their invasion of North America (Ruiz et al. 2006). The most likely introduction pathway is through the ballast water transport of larvae into estuaries (Herborg et al. 2007). Like other aquatic invaders, mitten crabs have changed estuary and stream food web dynamics, but the most noticeable ecological impact is erosion of stream banks by mitten crab burrows, which results in sedimentation into rivers and increased economic costs due to maintaining the structural integrity of levees (Rudnick et al. 2005).

Mitten crabs have a semelparous life history, where the larvae are released in the brackish water of estuaries (Rudnick et al. 2005). The temperature and salinity of the water in which the larvae are released appear to be key determinants of survival (Anger 1991) and can result in juvenile survival of <0.01 across variable salinity and temperature. For our analysis, we use the probability of survival to the megalopa stage under conditions of 12°C and salinity of 25% (table 2). After this stage, the individuals then migrate to freshwater streams, where they remain until sexual maturity. Adults return to the estuaries and mate. In the estuary, mate finding can be difficult at low densities because mate recognition occurs by physical contact, as opposed to by release of a pheromone into the water to attract males (Herborg et al. 2006). This would imply a very small probability of at least one male fertilizing a female, γ, for low population abundances, but probability would almost certainly be determined by the geography of the estuary. We use $\gamma = 0.01$ for the analysis, assuming that, at low densities, males are unlikely to find a mate. Male mitten crabs die shortly after reproduction. However, females can brood the egg cluster for 1–2 months before release of the larvae, after which the female dies (Rudnick et al. 2005). The sex ratio appears to be 1 : 1 (Zhang et al. 2001), and the fecundity of Chinese mitten crabs is thought to be similar to that of the Japanese mitten crab, with between 250,000 and 1 million eggs produced per female (Kobayashi 2001). A generation for the Chinese mitten crab is between 2 and 3 years (Rudnick et al. 2005). The point estimates used for the model are provided in table 2, along with the sources of information. Survival between mating and reproduction is assumed to be approximately 1 because of the short time period (1–2 months) and the absence of information for this parameter value. The consequences of parameter uncertainty for assessing Allee effects and predicting invasions are addressed in "Parameter Uncertainty and the Geometric Growth Rate."

The parameter estimates for the Chinese mitten crab reveal a strong Allee effect (fig. 4*B*; $\mathrm{E}(\Delta N) = 0$ occurs when $n_0 \approx 16$, an Allee threshold). Maybe even more surprising is the range in initial population sizes (n_0) that result in high probabilities of the population becoming extinct in the next generation (fig. 4*A*), a point we discuss further in an application of the stochastic process.

Chinese mitten crabs have an interesting detection history. Individuals have been observed in some United States ports, but only the San Francisco and Chesapeake bays have established, persistent populations (Ruiz et al. 2006). Although there have been individuals reported in several harbors, the possibility of Allee effects influencing the detection and establishment of mitten crabs has not been raised. The results from our model formulation indicate that the Allee effect may be a reasonable explanation for these observations.

The parameter estimate of survival from birth to reproductive maturity (p) that is used for this analysis comes from laboratory experiments and is likely much lower in

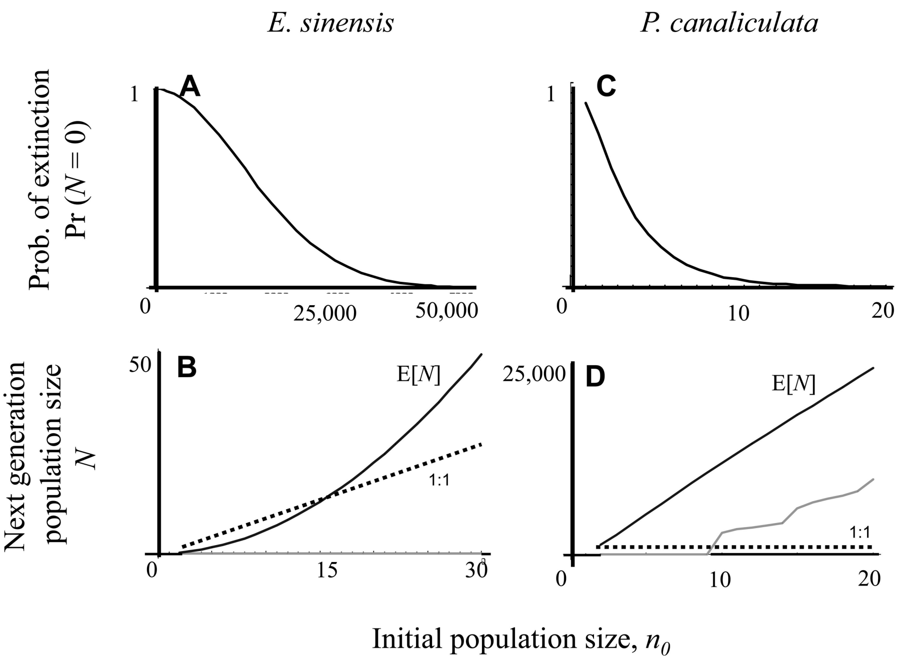

Figure 4: Probability of extinction for the mitten crab (*A*) is much greater than it is for the apple snail (*C*) at low abundances. With $n_0 < 10{,}000$, mitten crabs are likely to become extinct ($\Pr(N = 0)$). In contrast, with $n_0 > 10$, apple snails are almost certain to have population persistence. For small initial population sizes, mitten crabs are unable to replace themselves, on average, in the population, thus indicating a strong Allee effect (*B*). For apple snails at a low initial population size (*D*), the population is able, on average, to replace themselves. The solid gray lines in *B* and *D* are the lower 95% prediction boundaries (in *B*, the solid gray line visually overlaps the *X*-axis). The dashed line indicates the 1 : 1 line above which the population is able to replace itself in the next generation.

natural systems. As $p \rightarrow 0$, the Allee threshold increases. Of the parameters used in the analysis, the estimate of the probability of at least one male fertilizing a female, γ, is the most tenuous. Although Herborg et al. (2006) provided a detailed study of the biology of mitten crab mating, little is known about the factors affecting this probability.

*Apple Snail (*Pomacea canaliculata*)*

The apple snail is native to South America and has established invasive populations in southern Asia, Japan, and the southern United States. Many of these establishments occurred because the snail was intentionally introduced to rice fields as a secondary crop for the escargot industry. However, apple snails are voracious herbivores, causing substantial loss in rice yield and changes in the state and function of freshwater lakes. In some freshwater systems, the native vegetation is completely extirpated, resulting in lakes that had clear water and food webs regulated by macrophytes changing states to become turbid lakes dominated by phytoplankton (see Carlsson et al. 2004 and references therein).

In the United States, apple snails were introduced in some locations as a biological control of invasive plants. However, many of the introductions are thought to be a result of the aquarium trade, wherein apple snails were released haphazardly into the wild. Although the aquarium industry has stopped the import and sale of apple snails, many small populations persist in private aquariums, and sightings of apple snails, such as in Lake Wawasee, Indiana, where three individuals were found, are attributed to persons emptying private aquariums in lakes and streams (Anonymous 2005).

Apple snails have a variable life history that includes both semelparous and iteroparous strategies. Semelparous life histories are typically associated with the relatively constant temperatures in tropical and subtropical environments, taking approximately 1 year for a generation (Estebenet and Cazzaniga 1992). Apple snails are sexual organisms with equal proportions of males and females in the population, although there appears to be a large amount of variability in the sex ratio that can be attributed to genetic relatedness of populations (Yusa 2007). In laboratory experiments, survival from egg to sexual maturity and from sexual maturity to reproduction is approximately 0.8 for each stage (Estebenet and Cazzaniga 1992). In natural populations, the survival in both stages is likely to be substantially lower because snails are a common prey species for a wide array of predators, but snail egg masses are thought to be unpalatable, resulting in naturally high survival until the juveniles enter the water. Egg masses can vary from 100 to >1,000 eggs, with multiple egg masses being produced in a single reproductive bout. In one study, the average fecundity was 4,506 eggs, and it ranged from 1,136 to 10,869 eggs (Estebenet and Martin 2002).

Apple snails are promiscuous, with females able to store sperm, resulting in a probability of fertilization that is very close to 1 (Estebenet and Martin 2002). It has been reported that males are able to find females at long distances, at low density, and in the dark, suggesting a possible chemotactic mechanism. At experimentally controlled low densities, almost all females are fertilized (Albrecht et al. 1996). Although the values for all parameters are not available for a single study site, the estimates for survival, fecundity, sex ratio, and probability of being fertilized appear to be fairly consistent across studies. Table 2 contains the point estimates used to parameterize the model.

The probability of extinction (fig. 4*C*) and the population size (fig. 4*D*) are plotted as functions of the initial population size, n_0, using the parameters found in table 2. For as few as 20 individuals released into a location, the probability of the population becoming extinct in the next generation is approximately 0. For all n_0, the expected growth rate is positive and thus indicates weak Allee effects (see geometric growth rate [R] formulation).

For introductions of >10 individuals, it is almost a certainty that establishment of an apple snail population will occur. This observation is of particular concern, given the introduction pathway of private aquariums being exposed to freshwater lakes, and it likely explains the disparate observations in the locations where apple snails have successfully established. These systems were simply overwhelmed by propagule pressure (Von Holle and Simberloff 2005).

Of the parameter estimates used, the probabilities of survival are likely to be the most susceptible to changes because of biotic interactions (predation). Reducing the probabilities of survival to $p = 0.1$ and $\nu = 0.1$ results in the same weak Allee effect. However, the probability of extinction in the next time step is large (>0.8) for values of $n_0 \leq 446$. These results indicate that natural system and predation studies of apple snails are critical for assessing invasion risk. This has been noted previously (Estebenet and Martin 2002).

Parameter Uncertainty and the Geometric Growth Rate

For any modeling approach, uncertainty in the parameter estimates arising from a variety of mechanisms (Regan et al. 2002) will lead to uncertainty in model predictions. Here we have reported and used point estimates for inferences on the presence and strength of Allee effects. Admittedly, the parameters used for both examples (table 2) come from experiments conducted in a laboratory setting and in-field experiments where the invasive species is already well established. Alternatively, some estimates, such as the probability of being fertilized, are from noted observations reported in the literature but are void of reported parameter values. Parameter uncertainty is always problematic, but it is exaggerated for invasive species when little is known about how the species will interact in a new environment.

In the absence of uncertainty estimates in life-history parameters, qualitative insights for the examples may be gained by decomposing the geometric growth rate into the asymptotic contribution ($p\nu\psi\beta$) and the discounted contribution due to the Allee effect ($1 - e^{n_0\gamma p(1-\psi)}$). The asymptotic growth rate, as mentioned above, is composed of the survival probability ($p\nu$), the probability of being female (ψ), and fecundity (β). Uncertainty in these parameter estimates reflects a larger question of whether the species is capable of establishing and growing a population in a new environment. With a sensitivity analysis, if a range of possible outcomes indicates growth rate values that are all <1, then assessing the influence of the Allee effect is of diminished concern. However, if the range of outcomes includes 1 or is largely greater than 1, we may ask whether the Allee effect is a critical mechanism for predicting invasions. The asymptotic growth rates for the mitten crab and the apple snail are 1,250 and 1,440, respectively. This is due to the large fecundity relative to survival. There is uncertainty in the estimate of mitten crab initial survival, and for both survival probabilities in the apple snail there is an absence of predator influence. Yet, for the growth rate to be reduced to 1, the mitten crab's survival probability would have to be $p = 8 \times 10^{-6}$ and the apple snail's survival would be reduced to $p \times \nu = 4.5 \times 10^{-4}$. Whether environmental or predator effects are sufficient to reduce survival probabilities to these levels is unknown.

The influence of the Allee effect is relative to the asymptotic growth rate. Using the mitten crab as an example, with an asymptotic growth rate of 1,250, the Allee effect must discount the asymptotic growth rate below $1/1{,}250 = 0.0008$ to cause an Allee threshold. Assessing changes in the Allee threshold due to variability in the initial population size, fertilization rate, initial survival, and the probability of being male would be a valuable sensitivity analysis.

For the apple snail, no Allee threshold exists because of the weak Allee effect. However, an Allee threshold has been demonstrated with the point estimates of the mitten crab. From the Allee function, the product of the parameters ($\gamma p(1 - \psi)$) is a probability and can range from 0 to 1. Each of these probability parameters influences the Allee function similarly. Figure 5 shows the Allee function ($1 - e^{n_0\gamma p(1-\psi)}$) across the parameter space of the product of probabilities ($\gamma p(1-\psi)$) and the initial population size (n_0). Because of the assumed large geometric growth rate (1,250), the Allee function ($1 - e^{n_0\gamma p(1-\psi)}$) must be <0.0008 for there to be an Allee threshold. In figure 5, this region parallels the *X*-axis. The contours come very close together as the initial population size increases, which indicates that if $\gamma p(1-\psi)$ is small, then parameter uncertainty could dramatically change the inferences regarding the existence and strength of an Allee effect. However, if we can be reasonably assured that the product of these probabilities is not near 0, we can also conclude that the Allee effect is unlikely to influence invasion risk.

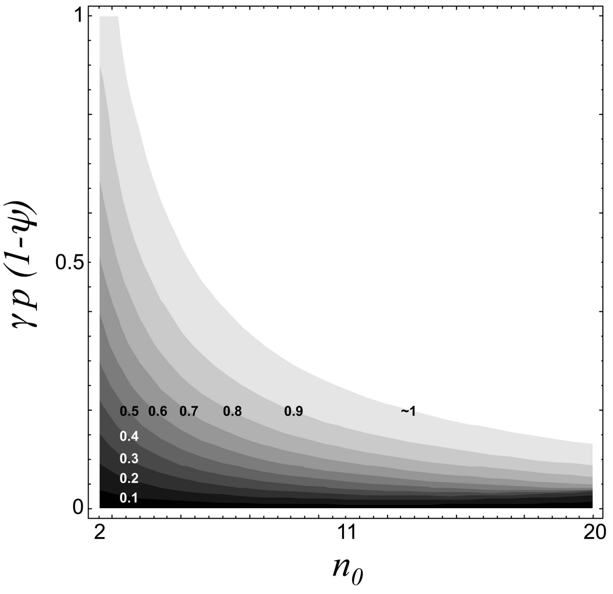

Figure 5: Parameter space of the Allee effect contribution to the geometric growth rate. The 0.1-interval contours show the regions of the Allee effect multiplier of the asymptotic geometric growth rate ($1 - e^{n_0\gamma p(1-\psi)}$). For the mitten crab, an Allee threshold occurs for values of less than 1/1,250 = 0.0008. This region is within the area with the very darkest shading. Consequently, the Allee effect is a concern for only a small portion of the overall parameter space, and small changes, especially in $\gamma p(1-\psi)$, will cause large changes in the influence of the Allee effect.

Evaluating Persistence

There is an apparent contradiction between a positive expected growth rate (fig. 4*B*) after the Allee threshold ($n_0 = 16$) and such a large probability of being extinct in the next time step (fig. 4*A*). With the presence of a weak or a strong Allee effect, the successful establishment of populations has been shown to largely depend on population dynamics that occur after the initial introduction (Drake et al. 2005). This appears not to be so for either the apple snail or the Chinese mitten crab, as can be observed in the stochastic process (eq. [7]) and resulting probability distributions of future generations (eq. [8]).

For illustration, consider an initial population size for the Chinese mitten crab of $n_0 = 400$ and a probability of being extinct in the next generation, $\Pr(N_1 = 0)$, of 0.962. For N_2–N_9, this probability remains essentially unchanged (fig. 3). That is to say, there is a probability $1 - \Pr(N_1 = 0)$ that the population will persist at $t = 1, \dots, 9$ that is approximately constant after the introduction. This "boom or bust" population dynamic occurs because of the small probability at n_0 of a surviving fertilized female, *H*, and the very large expected fecundity, β, where the number of offspring becoming the next generation overwhelms the system such that the probability of the N_2 generation being extinct is approximately equal to 0. This same dynamic is observed in the apple snail.

More generally, some NIS may have lower fecundities, resulting in Allee effects that contribute to the probability of being extinct in future generations. For these situations, the probability distributions resulting from the stochastic process (eq. [8]) are useful for estimating the probability of the population becoming extinct within some time *t*. This analysis is equivalent to performing population viability analysis, which is common in conservation biology (e.g., Brook et al. 2000), and it will likely have the same predictive shortcomings (Ellner et al. 2002). It may be possible to reconcile population viability theory for conservation biology to invasion theory for nonindigenous species (e.g., Drake and Bossenbroek 2004). Although management goals are different (preventing extinction vs. preventing invasion), the underlying dynamics are closely related. Consequently, further development of population viability theory from the perspective of reducing invasion success is likely to be a fertile avenue of future research.

For many pathways of invasion, there are repeated introductions that contribute to the increased probability of successful invasion (Carlton 1996; Cohen and Carlton 1998; Drury et al. 2007). Even though apple snails and Chinese mitten crabs have weak and strong Allee effects, respectively, the boom-bust dynamics of establishment fit well into the invasion waiting-time formulation of invasion risk (Jerde and Lewis 2007). The invasion waiting-time formulation assumes that each introduction event is independent of previous introduction events and has the same propagule pressure (n_0), leading to identically distributed probabilities of establishment, $1 - \Pr(N = 0)$, where $\Pr(N = 0) = G(0)|n_0$ (from eq. [5]) and n_0 is the propagule pressure. This implies that, at each time step, n_0 individuals are introduced to a location. For a specified, regularly recurring propagule pressure, the probability of an invasion by time *t* is

$$\Pr(T = t) = 1 - (1 - G(0)|n_0)^t \qquad (12)$$

(Jerde and Lewis 2007).

Equation (12) is the cumulative mass function of a geometric waiting-time distribution. The probability of Chinese mitten crab establishment when $n_0 = 400$ is $1 - 0.962 = 0.038$. Therefore, the establishment probability of a population after $t = 5$, 10, and 100 generations is 0.18, 0.32, and 0.98, respectively. Consequently, the semelparous life-history strategy with overwhelming fecundity further supports the performance of ecological risk assessment that is based on propagule pressure (Lockwood et al. 2005) and proactive risk management, even in the absence of well-understood population dynamics (Simberloff 2003*b*).

Discussion

Demographic stochasticity and the Allee effect are known to decrease the chance of population persistence at low density (Shaffer 1981; Grevstad 1999; Dennis 2002), be the populations managed, endangered, or invasive species. The presence of an Allee effect and demographic stochasticity have been shown to change management actions, optimal control decisions, and risk assessments (Liebhold and Bascompte 2003; Taylor and Hastings 2005; Drake and Lodge 2006). Yet, assessment of the presence and strength of an Allee effect, particularly for invasive species, has been conducted only after the species has successfully become established in multiple locations under different propagule pressures (Leung et al. 2004) or by using population data of established invasive species (Veit and Lewis 1996; Courchamp et al. 2008). As a consequence, risk assessment and management of invasive species are commonly practiced without considering the influence of the Allee effect and demographic stochasticity (Simberloff 2003*b*; Taylor and Hastings 2005).

We have offered a life history–based approach for assessing and predicting the influences of Allee effects and demographic stochasticity on invasion risk. Although it is similar to Monte Carlo models for species persistence and establishment (Grevstad 1999), we developed a novel approach for finding an analytical form of the next-generation population distribution; thus, we do not rely on simulations for predicting the fate of introduced populations. Thus, the model connects the expectation of the next-generation population size and the geometric growth rate to the more studied deterministic models for Allee effects (Courchamp et al. 2008), and it allows for the evaluation of weak and strong Allee effects (Wang and Kot 2001). The stochastic process, following from the analytic PMFs, allows for the finding of probabilities of population persistence that were previously subject to Monte Carlo error.

The mating function—that is, the mathematics describing mating success (Molnar et al. 2008)—is crucial for assessing and predicting Allee effects. This is evident from comparisons of the expected growth rate with the asymptotic growth rate, where at low population abundance the expected growth rate is discounted by $1 - e^{[-n_0\gamma p(1-\psi)]}$. Although propagule pressure and survival of invasive species in similar habitats (Jerde and Lewis 2007; Leung and Mandrak 2007) are good predictors of invasions, at least equally critical is the underlying behavior needed to find mates. Thus, the generality of emerging Allee effects for semelparous organisms is contingent on including variable mating strategies, in a probabilistic framework (Lee et al. 2008), in the proposed life-history probability model.

Chinese mitten crabs and apple snails expose both the novelty of the approach and the limits of predicting invasions with limited life history. As both species are successful invaders throughout the world, it is unsurprising that the growth rates for similar regions were asymptotically positive. However, the Allee effect was evident in both through the mating function. With apple snails, the growth rate was always >1, indicating a weak Allee effect, but Chinese mitten crabs, with growth rates <1, have the potential for a strong Allee effect. This insight may explain the repeated observation of crabs in locations that do not have established populations (Ruiz et al. 2006). However, there are two limitations to the Allee effect being a significant contributor to the repeatedly failed establishment of mitten crabs that surfaced during this study, one related to the parameter space over which an Allee effect is capable of emerging and the other related to the contribution of fecundity to the size of the next population.

Ideally, a sensitivity analysis would be performed to evaluate the influence of parameter uncertainty on the emergence of the Allee effect. However, even for well-studied invasive species, the parameters and, most importantly, the variability in the estimates are often not available. While we were unable to conduct such an analysis for either species, evaluating the parameter space led to one critical insight: if the asymptotic growth rate is very large, then overcoming the Allee effect is likely, provided that the product of the initial survival probability (p), the fertilization probability (γ), and the probability of being a male ($1 - \psi$) is relatively large. Small increases in any of these parameters will lead to a diminished influence of the Allee effect.

High fecundity contributes to a high asymptotic growth rate and increased variability in the distribution of the next-generation population size (eq. [2]). As a consequence of high fecundity, any influence of the Allee effect on the next-generation population size or persistence of a population is diminished. This may explain why fecundity is positively correlated with invasiveness for some species (Keller et al. 2007). In the mitten crab, with a fecundity of 250,000 or more individuals, the risk of invasion even at low propagule pressure can be estimated by the probability of observing a fertilized female. There are simply so many offspring produced by one female that they are able to overwhelm a system and escape the Allee effect and demographic stochasticity. This is also true, although not as critical, for the apple snail, and it points to the risk of introducing fertilized females of any species with large fecundity.

We were largely motivated by a desire to expose the contribution of Allee effects to the invasion risk of semelparous, sexual species. Indeed, using life-history traits and mating functions has a large potential to uncover mechanisms leading to successful invasions. However, the novelty of the mathematical modeling results is overshadowed by the somewhat unexpected biological significance of some life-history traits being able to overcome the influence of the Allee effect. While there are justifiable reasons to question the need for detailed population biology studies to perform predictive risk assessments and manage invasive species (Simberloff 2003*b*), this study shows how theoretical evaluation of the life history can justify simplifications for identifying and predicting future invasions.

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Literature Cited

Albrecht, E., N. Carreno, and A. Castro-Vazquez. 1996. A quantitative study of copulation and spawning in the South American apple-snail *Pomacea canaliculata* Lamarck (Prosobranchia, Ampullariidae). Veliger 39:142–147.

Allee, W. 1938. The social life of animals. Norton, New York.

Anger, K. 1991. Effects of temperature and salinity on the larval development of the Chinese mitten crab *Eriocheir sinensis* (Decapoda: Grapsoidea). Marine Ecology Progress Series 72:103–110.

———. 2006. Contributions of larval biology to crustacean research: a review. Invertebrate Reproduction and Development 49:175–205.

Anonymous. 2005. Aquatic invasive species: channeled apple snail. Indiana Department of Natural Resources, Indianapolis.

Bessa-Gomes, C., S. Legendre, and J. Clobert. 2004. Allee effects, mating systems and the extinction risk in populations with two sexes. Ecology Letters 7:802–812.

Boukal, D., and L. Berec. 2002. Single-species models of the Allee effect: extinction boundaries, sex ratios, and mate encounters. Journal of Theoretical Biology 218:375–394.

Brook, B., J. O'Grady, A. Chapman, M. A. H. Burgman, and R. Frankham. 2000. Predictive accuracy of population viability analysis in conservation biology. Nature 404:385–387.

Carlsson, N., C. Bronmark, and L. Hansson. 2004. Invading herbivory: the golden apple snail alters ecosystem functioning in Asian wetlands. Ecology 85:1575–1580.

Carlton, J. 1996. Pattern, process, and prediction in marine invasion ecology. Biological Conservation 78:97–106.

Casella, G., and R. Berger. 2002. Statistical inference. 2nd ed. Duxbury, Pacific Grove, CA.

Chatfield, C., and C. Theobald. 1973. Mixtures and random sums. Statistician 22:281–287.

Cohen, A., and J. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279:555–558.

Courchamp, R., L. Berec, and J. Gascoigne. 2008. Allee effects in ecology and conservation. Oxford University Press, New York.

de Camino Beck, T., and M. Lewis. 2007. A new method for calculating net reproductive rate from graph reduction with applications to the control of invasive species. Bulletin of Mathematical Biology 69:1341–1354.

———. 2008. On net reproductive rate and the timing of reproductive output. American Naturalist 172:128–139.

Dennis, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. Natural Resource Modeling 3:481–538.

———. 2002. Allee effects in stochastic populations. Oikos 96:389–401.

Dennis, B., and S. Lele. 2009. Bayesian methods for hierarchical models: are ecologists making a Faustian bargain? Ecological Applications 19:581–584.

Dennis, B., J. Ponciano, S. Lele, M. Taper, and D. Staples. 2006. Estimating density dependence, process noise, and observation error. Ecological Monographs 76:323–341.

Drake, J., and J. Bossenbroek. 2004. The potential distribution of zebra mussels in the US. BioScience 54:931–941.

Drake, J., and C. Jerde. 2009. Stochastic models of propagule pressure and establishment. Pages 83–102 *in* R. P. Keller, D. M. Lodge, M. A. Lewis, and J. F. Shogren, eds. Bioeconomics of invasive species: integrating ecology, economics, policy, and management. Oxford University Press, Oxford.

Drake, J., and D. Lodge. 2006. Allee effects, propagule pressure and the probability of establishment: risk analysis for biological invasions. Biological Invasions 8:365–375.

Drake, J., P. Baggenstos, and D. Lodge. 2005. Propagule pressure and persistence in experimental populations. Biology Letters 1:480–483.

Drury, K., J. Drake, D. Lodge, and G. Dwyer. 2007. Immigration events dispersed in space and time: factors affecting invasion success. Ecological Modelling 206:63–78.

Ellner, S., J. Fieberg, D. Ludwig, and C. Wilcox. 2002. Precision of population viability analysis. Conservation Biology 16:258–261.

Engen, S., O. Bakke, and A. Islam. 1989. Demographic and environmental stochasticity: concepts and definitions. Biometrics 54: 840–846.

Estebenet, A., and N. Cazzaniga. 1992. Growth and demography of

Pomacea canaliculata (Gastropoda: Ampullariidae) under laboratory conditions. Malacological Review 25:1–12.

Estebenet, A., and P. Martin. 2002. *Pomacea canaliculata* (Gastropoda: Ampullariidae): life-history traits and their plasticity. Biocell 26: 83–89.

Goodman, D. 1987. Considerations of stochastic demography in the design and management of reserves. Natural Resource Modeling 1:205–234.

Grevstad, F. 1999. Factors influencing the chance of population establishment: implications for release strategies in biocontrol. Ecological Applications 9:1439–1447.

Herborg, L., M. Bentley, A. Clare, and K. Last. 2006. Mating behavior and chemical communication in the invasive Chinese mitten crab *Eriocheir sinensis*. Journal of Experimental Marine Biology and Ecology 329:1–10.

Herborg, L., C. Jerde, D. Lodge, G. Ruiz, and H. MacIsaac. 2007. Predicting the North American distribution of Chinese mitten crabs *(Eriocheir sinensis)* using measures of propagule pressure and environmental niche models. Ecological Applications 17:663–674.

Hurford, A., M. Hebblewhite, and M. Lewis. 2006. A spatially explicit model for an Allee effect: why wolves recolonize so slowly in Greater Yellowstone. Theoretical Population Biology 70:244–254.

Jerde, C., and M. Lewis. 2007. Waiting for invasions: a framework for the arrival of nonindigenous species. American Naturalist 170: 1–9.

Keller, R., L. Drake, and D. Lodge. 2007. Fecundity as a basis for risk assessment of nonindigenous freshwater molluscs. Conservation Biology 21:191–200.

Kobayashi, S. 2001. Fecundity of the Japanese mitten crab *Eriocheir japonica* (De Haan). Benthos Research 56:1–7.

Kolar, C., and D. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution 16:199–204.

Kot, M., M. Lewis, and P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. Ecology 77:2027–2042.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142:911–927.

Lee, A., S. Engen, and B. Sæther. 2008. Understanding mating systems: a mathematical model of the pair formation process. Theoretical Population Biology 73:112–124.

Leipus, R., and M. Viano. 2003. Long memory and stochastic trend. Statistics and Probability Letters 61:177–190.

Leung, B., and N. Mandrak. 2007. The risk of establishment of aquatic invasive species: joining invasibility and propagule pressure. Proceedings of the Royal Society B: Biological Sciences 274:2603–2609.

Leung, B., D. Lodge, D. Finnoff, J. Shogren, M. Lewis, and G. Lamberti. 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proceedings of the Royal Society B: Biological Sciences 269:2407–2413.

Leung, B., J. Drake, and D. Lodge. 2004. Predicting invasions: propagule pressure and the gravity of Allee effects. Ecology 85:1651–1660.

Lewis, M., and P. Kareiva. 1993. Allee dynamics and the spread of invading organisms. Theoretical Population Biology 43:141–158.

Liebhold, A., and J. Bascompte. 2003. The Allee effect, stochastic dynamics and the eradication of alien species. Ecology Letters 6: 133–140.

Lockwood, J., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20:223–228.

Molnar P., A. Derocher, M. Lewis, and M. Taylor. 2008. Modelling the mating system of polar bears: a mechanistic approach to the Allee effect. Proceedings of the Royal Society B: Biological Sciences 275:217–226.

Odum, H., and W. Allee. 1954. A note on the stable point of populations showing both intraspecific cooperation and disoperation. Ecology 35:95–97.

Regan, H., M. Colyvan, and M. Burgman. 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. Ecological Applications 12:618–628.

Regan, T., M. McCarthy, P. Baxter, R. Panetta, and H. Possingham. 2006. Optimal eradication: when to stop looking for an invasive plant. Ecology Letters 9:759–766.

Rudnick, D., T. Veldhuizen, R. Tullis, C. Culver, K. Hieb, and B. Tsukimura. 2005. A life history model for the San Francisco estuary population of the Chinese mitten crab, *Eriocheir sinensis* (Decapoda: Grapsoidea). Biological Invasions 7:333–350.

Ruiz, G., L. Fegley, P. Fofonoff, Y. Cheng, and R. Lemaitre. 2006. First records of *Eriocheir sinensis* H. Milne Edwards, 1853 (Crustacea: Brachyura: Varunidae) for Chesapeake Bay and the mid-Atlantic coast of North America. Aquatic Invasions 1:137–142.

Sakai, A., F. Allendorf, J. Holt, D. Lodge, J. Molofsky, K. With, S. Baughman, et al. 2001. The population biology of invasive species. Annual Reviews of Ecology and Systematics 32:305–332.

Shaffer, M. 1981. Minimum population sizes for species conservation. BioScience 31:131–134.

Simberloff, D. 2003*a*. Eradication: preventing invasions at the outset. Weed Science 51:247–253.

———. 2003*b*. How much information on population biology is needed to manage introduced species? Conservation Biology 17: 83–92.

Taylor, C., and A. Hastings. 2005. Allee effects in biological invasions. Ecology Letters 8:895–908.

Taylor, H., and S. Karlin. 1998. An introduction to stochastic modeling. 3rd ed. Academic Press, San Diego, CA.

Veit, R., and M. Lewis. 1996. Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. American Naturalist 148:255–274.

Von Holle, B., and D. Simberloff. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology 86: 3212–3218.

Wang, M., and M. Kot. 2001. Speeds of invasion in a model with strong and weak Allee effects. Mathematical Biosciences 171:83–97.

Williamson, M. 1999. Invasions. Ecography 22:5–12.

Yusa, Y. 2007. Nuclear sex-determining genes cause large sex-ratio variation in the apple snail, *Pomacea canaliculata*. Genetics 175: 179–184.

Zhang, T., Z. Li, and Y. Cui. 2001. Survival, growth, sex ratio, and maturity of the Chinese mitten crab *(Eriocheir sinensis)* reared in a Chinese pond. Journal of Freshwater Ecology 16:633–640.

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