



ACADEMIC  
PRESS

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

SCIENCE @ DIRECT®

Theoretical Population Biology 64 (2003) 201–209

**Theoretical  
Population  
Biology**

<http://www.elsevier.com/locate/ytptbi>

# Allee effects, extinctions, and chaotic transients in simple population models

Sebastian J. Schreiber\*

*Department of Mathematics, College of William and Mary, Williamsburg, VA 23187-8795, USA*

Received 17 October 2002; accepted 14 April 2003

## Abstract

Discrete time single species models with overcompensating density dependence and an Allee effect due to predator satiation and mating limitation are investigated. The models exhibit four behaviors: persistence for all initial population densities, bistability in which a population persists for intermediate initial densities and otherwise goes extinct, extinction for all initial densities, and essential extinction in which “almost every” initial density leads to extinction. For fast-growing populations, these models show populations can persist at high levels of predation even though lower levels of predation lead to essential extinction. Alternatively, increasing the predator’s handling time, the population’s carrying capacity, or the likelihood of mating success may lead to essential extinction. In each of these cases, the mechanism behind these disappearances are chaotic dynamics driving populations below a critical threshold determined by the Allee effect. These disappearances are preceded by chaotic transients that are proven to be approximately exponentially distributed in length and highly sensitive to initial population densities.

© 2003 Elsevier Inc. All rights reserved.

## 1. Introduction

The per-capita growth rate of a species can be broken down into negative density-dependent, density-independent, and positive density-dependent factors. Negative density-dependent factors include resource depletion due to competition (Tilman, 1982), environment modification (Jones et al., 1997), mutual interference (Arditi and Akcakaya, 1990) and cannibalism (Fox, 1975). Positive density-dependent factors include predator saturation, cooperative predation or resource defense, increased availability of mates, and conspecific enhancement of reproduction (Courchamp et al., 1999; Stephens and Sutherland, 1999; Stephens et al., 1999; Levitan and McGovern, in press). Since populations do not grow without bound, there is growing consensus due to mathematical and empirical advances that negative density-dependent factors operate at higher population densities (Wolda and Dennis, 1993; Turchin, 1995; Harrison and Cappuccino, 1995). At lower population densities, any of these factors can dominate. The Allee effect occurs when positive density-dependence dominates at low densities. When the Allee effect is

sufficiently strong, there is a critical threshold below which populations experience rapid extinction. Consequently, the importance of the Allee effect has been widely recognized in conservation biology (Dennis, 1989; Fowler and Baker, 1991; Courchamp et al., 1999; Stephens and Sutherland, 1999; Stephens et al., 1999; Lande et al., 2003).

Population with fluctuating dynamics and a strong Allee effect are especially vulnerable to extinction as the fluctuations may drive their densities below the critical threshold. For instance, these combined effects have been used to explain one of the most dramatic extinctions of modern times—that of the passenger pigeon *Ectopistes migratorius* (Stephens and Sutherland, 1999). One source of population fluctuations is a high intrinsic rate of growth coupled with overcompensating density dependence. Models of populations with discrete generations exhibiting these characteristics can exhibit complex dynamical patterns (May, 1975; Stone, 1993; Getz, 1996) that have been observed in insect populations (Turchin and Taylor, 1992; Costantino et al., 1997; Cushing et al., 1998), annual plant populations (Symonides et al., 1986), and vertebrate populations (Grenfell et al., 1992; Turchin and Taylor, 1992; Turchin, 1993).

In this article, we examine the interaction between the Allee effect and overcompensating density dependence

\*Tel.: 757-221-2002; fax: 757-221-2988.

E-mail address: [sjs@math.wm.edu](mailto:sjs@math.wm.edu).

in single species models with discrete generations. We determine under what conditions these combined effects result in extinction and how the times to extinction depend on initial conditions. More specifically, we discuss how the dynamics of these models can be classified into four types (extinction, bistability, persistence, and essential extinction) and prove that uncertainty in the initial population state can result in exponentially distributed extinction times. We apply these results to models that combine the Ricker equation (Ricker, 1954) with two forms of positive density dependence corresponding to predator saturation and mating limitation.

## 2. Results

The dynamics of populations with synchronized generations are described by difference equations of the form

$$N_{t+1} = N_t f(N_t), \quad (1)$$

where  $N_t$  is the population density at generation  $t$ , and  $f(N_t)$  represents the per-capita growth rate of the population. We consider models that are unimodal with a long tail (Ricker, 1954; May, 1975; Bellows, 1981; Getz, 1996). Namely, there is a unique positive density  $C$  that leads to the maximum population density  $M$  in the next generation, and extremely large population densities lead to extremely small population densities in the next generation. For models of this form, two facts are well-known:

**Persistence:** If  $f(0) > 1$  and  $f(N) > 0$  for all  $N > 0$ , then for all positive initial densities the population persists.

**Extinction:** If the per-capita growth rate is less than one for all densities, then extinction occurs for all initial population densities.

An *Allee effect* occurs when the per-capita growth rate increases at low densities (i.e.  $f'(N) > 0$  for  $N$  sufficiently small). A *strong Allee effect* occurs when there is a positive equilibrium density  $A$  such that the per-capita growth rate is less than one for lower densities (i.e.  $f(N) < 1$  for  $N < A$ ) and is greater than one for some densities greater than  $A$  (see Fig. 1). Whenever populations fall below this critical threshold, extinction occurs. Under the assumption that the function  $g(N) = Nf(N)$  has a negative Schwartzian derivative (i.e.  $\frac{g'''(x)}{g'(x)} - \frac{3}{2} \frac{g''(x)^2}{g'(x)^3} < 0$ ) on the interval  $[A, \infty)$  work of the author (Schreiber, 2001) can be extended to prove that the dynamics of (1) with a strong Allee effect fall generically into two categories:

**Bistability:** If a population initiated at the maximal density  $M$  exceeds the critical density  $A$  in

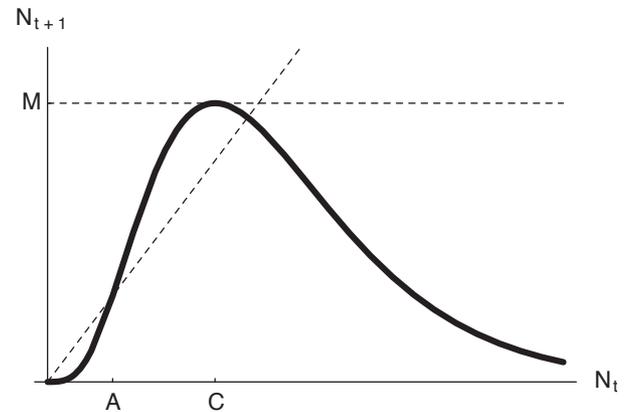


Fig. 1. Important quantities associated with (1).

the next generation (i.e.  $Mf(M) > A$ ), then there is an interval of initial population densities for which the population persists. For initial densities outside this interval, extinction occurs (see Figs. 2a–c).

**Essential extinction:** If a population initiated at  $M$  falls below  $A$  in the next generation (i.e.  $Mf(M) < A$  as illustrated in Fig. 2d), then for almost every initial population density extinction occurs (i.e. for a randomly chosen initial condition, extinction occurs with probability one).

In the case of essential extinction, the negative Schwartzian derivative hypothesis is necessary to ensure that almost every initial density goes to extinction. Without this condition, we are only assured that initial densities near  $C$  lead to extinction and other initial densities may lead to stable periodic points. In fact, a  $f(N)$  can be constructed by piecing together polynomials such that  $Nf(N)$  is unimodal and  $Mf(M) < A$ , but  $Nf(N)$  has a stable positive equilibrium (Schreiber, 2001). None the less, numerical and symbolic investigations of many population models (e.g. variants of Ricker, generalized Beverton-Holt, Logistic, and Hassel equations) suggest that they all satisfy the negative Schwartzian derivative hypothesis.

In the case of essential extinction, work of Gyllenberg et al. (1996) implies that the set of initial densities that do not lead to extinction define a chaotic repeller, and, consequently, extinction can be preceded by long-term chaotic transients. To quantify these transients, let  $\tau(N)$  equal the first generation in which a population initiated at density  $N$  falls below the critical Allee density  $A$  (i.e.  $\tau(N) = \inf\{t \geq 0 : g^t(N) < A\}$ ). Using the work of Pianigiani and Yorke (1979), the appendix proves that the distribution of extinction times  $\tau(N)$  is approximately exponential. More specifically, if  $p_t$  is the probability a population with a randomly chosen initial density from the interval  $[A, M]$  satisfies  $\tau(N) \leq t$ , then there exist

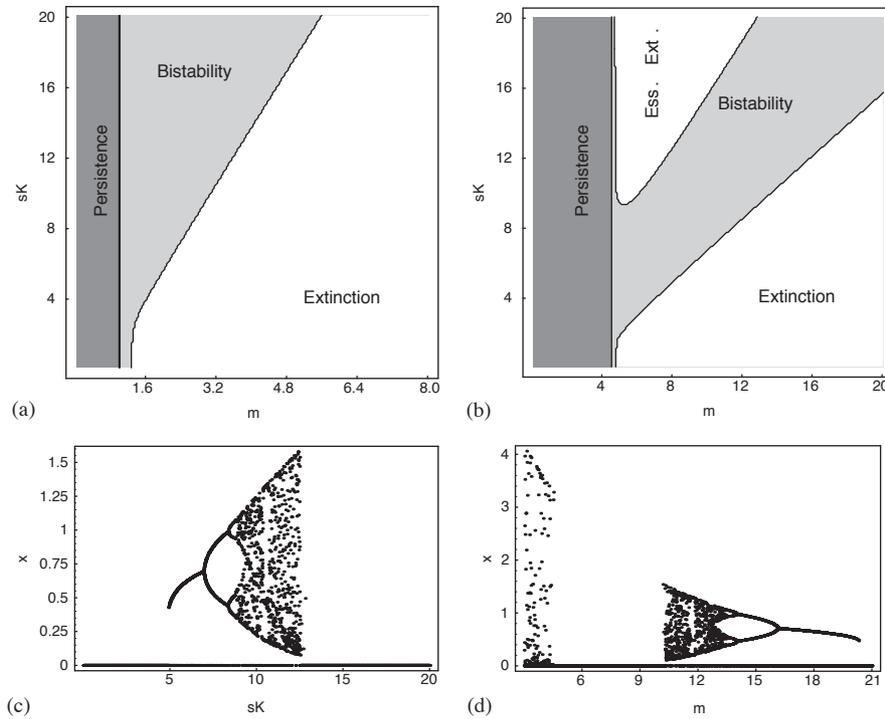


Fig. 2. Bifurcation diagrams for (3). In (a),  $r = 1.0$  and in (b),  $r = 4.5$ . In the orbital diagrams, a random initial condition  $x_0 \in [0, 1]$  for each parameter value is selected and  $x_{100}$  is plotted. In (c),  $r = 4.5$  and  $m = 8$ , and in (d),  $r = 4.5$  and  $sK = 16$ .

constants  $\alpha > 0$  and  $\kappa > 0$  independent of  $t$  such that  $\exp(-\alpha t) / \kappa \leq p_t \leq \kappa \exp(-\alpha t)$ .

To illustrate these results, we consider two models of the form

$$N_{t+1} = N_t \exp(r(1 - N_t/K))I(N_t), \tag{2}$$

where  $I(N)$  represents a positive density-dependent factor and  $\exp(r(1 - N/K))$  represents a negative density-dependent factor.  $r$  and  $K$  represent the intrinsic growth rate and the carrying capacity of the population in the absence of the positive density dependence (i.e.  $I(N_t) = 1$ ).

Perhaps the most common Allee effect occurs in species subject to predation by a generalist predator with a saturating functional response. Within such populations, an individual's risk of predation decreases as the population's density increases. The importance of this form of positive density dependence is evidenced by the fact that many prey species have evolved responses to it. Plants can satiate seed and fruit predators by the periodic synchronous production of large seed crops, so-called mast seeding or fruiting. For example, in field studies [Crawley and Long \(1995\)](#) found that per-capita rates of acorn loss of *Quercus robur* L. to invertebrate seed predators were greatest (as high as 90%) amongst low acorn crops and lower (as low as 30%) on large acorn crops. In field studies, [Williams et al. \(1993\)](#) found that birds generally consumed nearly 100% of the population as the density of adult cicadas declined in

June, but they consumed proportionately very little of the standing crop when cicada densities were greater than 24,000 individuals/ha. Furthermore, predation on bird eggs and nestlings often decreases with increasing colony size ([Wiklund and Andersson, 1994](#)) and some fish species form large schools to minimize vulnerability to predators ([Ehrlich, 1975](#)).

To study Allee effects due to predator saturation, let  $I(N) = \exp(-\frac{m}{1+sN})$  be the probability of escaping predation by a predator with a saturating functional response where  $m$  represents predation intensity and  $s$  is proportional to the handling time ([Hassell et al., 1976](#)). Non-dimensionalizing (2) by setting  $x_t = N_t/K$  gives

$$x_{t+1} = x_t \exp\left(r(1 - x_t) - \frac{m}{1 + sKx_t}\right) \tag{3}$$

whose dynamics depends exclusively on the quantities  $r$ ,  $sK$ , and  $m$ .

The per-capita growth for (3) at very low densities is given by  $\exp(r - m)$  (i.e.  $f(0) = \exp(r - m)$ ). Thus, if  $r > m$ , the populations persist for all initial densities. Alternatively, if  $r < m$ , then the zero equilibrium is stable. Solving for the non-zero equilibria of (3) results in

$$x = \frac{r(sK - 1) \pm \sqrt{r^2 - 4msKr + 2r^2sK + r^2sK^2}}{2rsK}.$$

From this expression, we can draw two conclusions. First, if  $m > \frac{r(sK+1)^2}{4sK}$ , or  $sK < 1$  and  $r < m$ , then there are

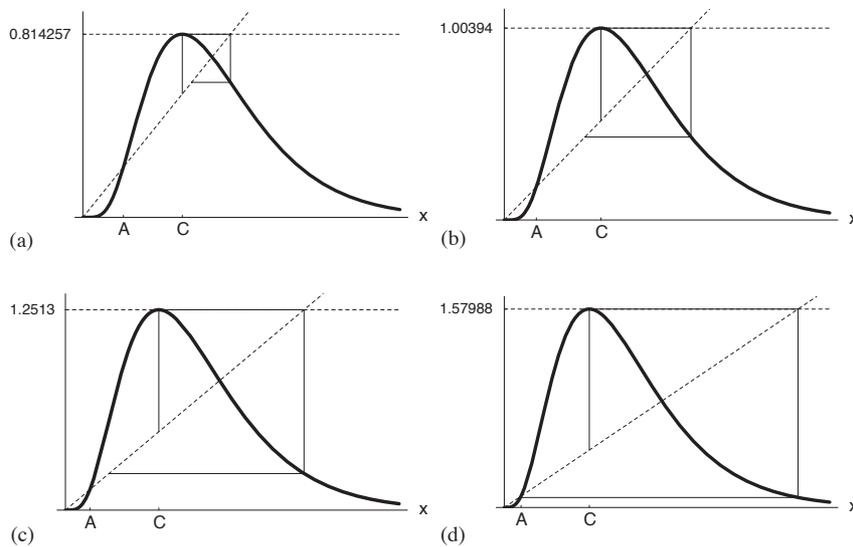


Fig. 3. Cobweb diagrams for (3). These cobweb diagrams illustrate the transition from bistability to essential extinction due to decreased predation intensity for (3) with  $r = 4.5$  and  $sK = 16$ . In (a), (b), (c), and (d),  $m = 16$ ,  $m = 14$ ,  $m = 12$ , and  $m = 10$ , respectively.

no positive equilibria and extinction occurs for all initial densities. Second, if  $r < m < \frac{r(sK+1)^2}{4sK}$  and  $sK > 1$ , there are two positive equilibria. Moreover, since the origin is stable, the per-capita growth rate for densities below the smaller equilibrium is less than one.

In the appendix, we show that (3) has a unique critical point  $C$ . To distinguish between the cases of bistability and essential extinction, we numerically compute bifurcation diagrams by determining the fate of the unique critical point  $C$  (see Figs. 3a and b). These diagrams show for slow growing populations, bistability occurs at intermediate values of  $m$ . Alternatively, for fast growing populations with either a large carrying capacity or a quickly satiating predator, there are transitions between bistability and essential extinction. These transitions are illustrated in the orbital bifurcation diagrams in Figs. 3c and d. Fig. 3c shows that increasing  $sK$  leads to period doubling cascades that increase demographic variability and culminate in essential extinction. Fig. 3d shows that populations can persist at relatively high predation intensities even though at lower predation intensities the population experiences extinction. This initially counter-intuitive transition occurs because decreasing predation intensity allows populations to achieve higher densities that result in more extreme population crashes (see Fig. 3).

In the case of essential extinction, extinction can either occur rapidly or be preceded by long-term chaotic transients (see Figs. 4a and b). These transients arise from the existence of a chaotic repeller which exhibits a fractal like structure and sensitive dependence on initial conditions. Fig. 4c illustrates that the times to extinction depend sensitively on initial conditions. As predicted by our theoretical results, Fig. 4d shows that the extinction

times are nearly exponentially distributed which is consistent with the observation that the standard deviation 13.83 and the mean 14.86 of the extinction times are approximately the same.

### 2.1. Mating limitation

For many sexually reproducing organisms, finding mates becomes more difficult at low densities. For instance, pollination of plants by animal vectors becomes less effective when patches become too small because lower densities result in reduced visitation rates by pollinators (Groom, 1998). Alternatively, species with low dispersal rates are less likely to encounter mates at small population sizes. For instance, in a field experiment, Grevstad (unpublished data) found a significant difference in mating frequency in low- (42% mated) versus high-density treatments (95% mated) for a less mobile species *Galerucella pusilla* of chrysomelid beetle, and found no mating frequency difference in low- versus high-density treatments of the more mobile species *Galerucella calmariensis*. Fertilization by free spawning gametes of benthic invertebrates can become insufficient at low densities (Knowlton, 1992; Levitan et al., 1992; Levitan and McGovern, in press). For example, in a field experiment Levitan et al. (1992) found 0% of a small dispersed group of sea urchins *Strongylocentrotus franciscanus* were fertilized, while a 82.2% fertilization rate was reported in the center of a large aggregated group of sea urchins.

To model mate limitation, let  $I(N) = \frac{sN}{sN+1}$  be the probability of finding a mate where  $s$  is an individual's searching efficiency (Dennis, 1989; McCarthy, 1997; Scheuring, 1999). Non-dimensionalizing by setting

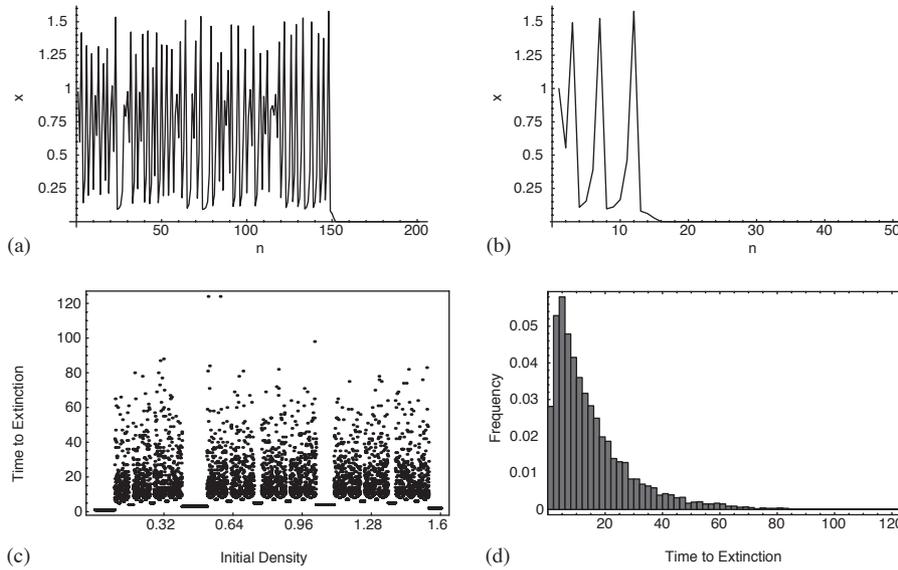


Fig. 4. Transients and extinction times for (3). In all figures,  $r = 4.5$ ,  $m = 10$ , and  $sK = 16$ . In (a) and (b), the time series  $x_t$  corresponding to the initial density  $x_0 = 0.9748$  and  $x_0 = 1.0$  are shown. In (c), the number of generations until the population density falls below the critical density as a function of the initial density is shown. In (d), the distribution of the extinction times for (c) are shown.

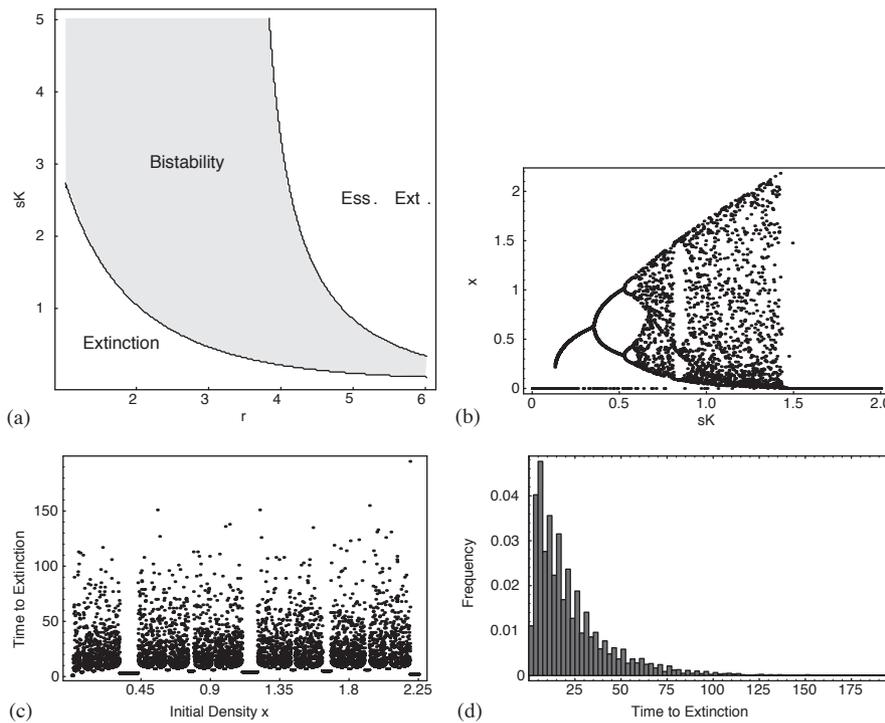


Fig. 5. Diagrams for (4): a bifurcation diagram in (a), an orbital bifurcation diagram with  $r = 4.5$  in (b), times to extinction as function of initial density in (c) for  $r = 4.5$  and  $sK = 1.5$ , and the distribution of extinction times for (c) in (d).

$x_t = N_t/K$ , (2) becomes

$$x_{t+1} = x_t \exp(r(1 - x_t)) \frac{sKx_t}{1 + sKx_t} \quad (4)$$

whose the dynamics are determined by the quantities  $r$  and  $sK$ . In the appendix, we show that (4) has a unique critical point  $C$  and negative Schwartzian derivative.

To distinguish between the cases of extinction, bistability, and essential extinction, we numerically computed bifurcation diagrams (see Figs. 5a and b). Extinction occurs whenever  $sK$  is too small (i.e. mate finding is difficult). Alternatively, when the intrinsic rate of growth is sufficiently high and  $sK$  sufficiently large, the population exhibits essential extinction. This result

asserts that fast-growing species with highly effective mate finding capabilities are more prone to extinction than fast-growing species with less effective mate finding capabilities. Figs. 5c and d show that the extinction times are sensitive to initial conditions and are approximately exponentially distributed.

### 3. Discussion

Examination of simple models of population dynamics reveal complex interactions between chaotic dynamics and Allee effects. Most notably, highly variable population dynamics coupled with an Allee effect can lead to extinctions with chaotic transients. The length of these transients are sensitive to initial conditions and nearly exponentially distributed.

#### 3.1. Disappearances due predation

The idea that prey population subject to saturating predation by a generalist predation can exhibit multiple stable states is not new. To better understand grazing systems, Noy-Meir (1975) performed a graphical analysis of a continuously reproducing prey population subject to predation by a predator population of approximately constant size with a saturating functional response. Noy-Meir found the dynamics of this system (excluding the cases allowing for an unconsumable prey reserve) exhibited three behaviors. At low predation levels, there is single stable equilibrium at which prey density is high though lower than the equilibrium density in the absence of predation. At high predation levels, extinction is inevitable regardless of initial population size. At intermediate predation levels, there are two stable equilibria (i.e. bistability), one corresponding to extinction and the other to persistence, separated by an unstable equilibrium. This model was also studied in a review article of May (1977) and in the context of Allee effects by Dennis (1989). These authors showed that increasing the maximal predation rate or decreasing the carrying capacity of the prey population can lead to population disappearances; there is a critical break point for these parameters beyond which the stable equilibrium corresponding intermediate prey densities suddenly vanishes.

Replacing continuous time with discrete time results in similar behaviors and also introduces two new mechanisms of extinction for fast-growing populations. First, lowering levels of predation can result in essential extinction despite the fact that at higher levels of predation the prey population can persist. Second, enriching the system can lead to essential extinction and, thereby, provides an alternative form of the paradox of enrichment (Rosenzweig, 1971). These two mechanisms have been observed in discrete time models

of populations subject to constant harvesting (Sinha and Parthasarathy, 1996; Vandermeer and Yodzis, 1999; Schreiber, 2001). An explanation for these disappearances is that these parameter changes increase the population's demographic variability. This variability results in lower minimum population densities that coupled with the Allee effect leads to extinction.

#### 3.2. Disappearances due to mating limitation

Previous work on the effects of mating limitation have shown that mate limitation can lead to population disappearances when the population's carrying capacity or mate finding abilities are pushed below a critical level (Dennis, 1989; Scheuring, 1999). In studying a broad class of one-dimensional difference equations including mate limitation, Scheuring (1999) found that the cost of rarity can stabilize population dynamics. This conclusion follows from the observation that as the population's carrying capacity or mate finding abilities decrease the dynamics exhibit a period-halving cascade (Stone, 1993). In contrast, our results show that for populations with a potential for rapid growth enriching the system or enhancing the population's mate finding abilities can lead to population disappearances that are preceded by chaotic transients.

#### 3.3. Chaotic transients and population viability

For species that exhibit inherently variable dynamics, our results suggest that an environmental shift from the dynamical regime of persistence to eventual extinction may go unnoticed for hundreds of generations before the population plunges unexpectedly to extinction without additional environmental perturbations. These shifts occur when the parameter changes result in the basin of attraction of the upper attractor (corresponding to the population persisting) colliding with the basin of attraction of the origin (extinction). Following this collision, the remnants of upper attractor form a chaotic repeller that lead to long-term chaotic transients. This mechanism for chaotic transients has been observed in various ecological models (Hastings and Higgins, 1994; McCann and Yodzis, 1994; Sinha and Parthasarathy, 1996; Gyllenberg et al., 1996; Vandermeer and Yodzis, 1999; Schreiber, 2001).

Our analysis shows that the time to extinction can be quite sensitive to initial conditions: small changes in initial conditions result in large changes in the time to extinction. Hence, even if ecological system were free from environmental and demographic stochasticity, just the slightest uncertainty about the current state of the ecological system limits our ability to make accurate predictions about how much time there is to act before a species vanishes. The times to extinction are proven to be approximately exponentially distributed.

Consequently, given the uncertainty about the actual state of a system, the most likely times to extinction are short- and long-term transients are rare. Interestingly, these predictions from these deterministic models coincide with the predictions of stochastic models used for population viability analysis (Goodman, 1987; Mangel and Tier, 1994). For stochastic models, extinction is inevitable due to demographic stochasticity, and the distribution of extinction times are often approximately exponentially distributed (Goodman, 1987; Mangel and Tier, 1994). Thus (Mangel and Tier, 1994, p. 611) “in an ‘ensemble world view’ the mean time to extinction” in deterministic models exhibiting essential extinction and stochastic models “is achieved by the average of lots of very rapid extinctions with some very long persistences.” These coinciding predictions are not coincidental. A common mathematical structure underlies these predictions; the existence of conditional invariant distributions (equivalently quasi-stationary distributions) for the deterministic and stochastic models. Ideally, future research in this area will lead to rules of thumb on how the shape of these distributions (e.g. the mean and more information about the left-hand side of the distribution) depend on the general form of the underlying non-linearities and demographic stochasticity of the population dynamics.

**Acknowledgments**

The author thanks Ted Case, Jim Cushing, Joseph Travis, and anonymous referees for their constructive suggestions on earlier drafts of this article. This work was partially supported by National Science Foundation Grant DMS 00-77986.

**Appendix**

In this appendix, we indicate how previous mathematical work (Pianigiani and Yorke, 1979; Gyllenberg et al., 1996; Schreiber, 2001) apply to the models being considered, prove that extinction times are approximately exponentially distributed, partially verify the technical conditions for the predator satiation model, and fully verify the technical conditions for the mating model.

Let  $g : [0, \infty) \rightarrow [0, \infty)$  be a three times continuous differentiable function.  $g(x)$  corresponds to  $xf(x)$  in (1). Assume that  $g$  has a unique positive critical point  $C$  (i.e.  $g'(C) = 0$ ) and that there exists an interval  $[a, b]$  with  $b > a > 0$  such that

- $g(x) > 0$  for all  $x \in [a, b]$ ,
- $\lim_{n \rightarrow \infty} g^n(x) = 0$  for all  $x \notin [a, b]$ ,

- the Schwartzian derivative of  $g$  on  $[a, b]$  is negative:

$$\frac{D^3g(x)}{Dg(x)} - \frac{3}{2} \left( \frac{D^2g(x)}{Dg(x)} \right)^2 < 0$$

for all  $x \in [a, b]$ .

- There is an  $A \in (a, b)$  such that  $g(A) = A$  and  $g(x) \neq x$  for all  $x \in (0, A)$ .

Define  $A^* = \max\{g^{-1}(A)\}$  and  $M = g(C)$ . Under these assumptions, prior work of the author (Schreiber, 2001) can be easily modified to prove the following:

- *Bistability*: If  $g(M) > A$ , then  $g^n(x) \geq A$  for all  $n \geq 0$ ,  $x \in [A, A^*]$  and  $\lim_{n \rightarrow \infty} g^n(x) = 0$  for all  $x \notin [A, A^*]$ .
- *Essential extinction*: If  $g(M) < A$ , then  $\lim_{n \rightarrow \infty} g^n(x) = 0$  for Lebesgue almost every  $x$ .
- *Chaotic semistability*: If  $g(M) = A$ , then the dynamics of  $g$  restricted to  $[A, A^*]$  are chaotic (e.g. the Lyapunov exponent for Lebesgue almost every point in  $[A, A^*]$  is positive) and  $\lim_{n \rightarrow \infty} g^n(x) = 0$  for all  $x \notin [A, A^*]$ .

To see why the “times to extinction” are approximately exponentially distributed, assume that  $g(M) < A$  and define  $\Lambda = \{x \geq 0 : \tau(x) = +\infty\}$ , the set of initial conditions that do not lead to extinction. Work of Schreiber (2001) implies that  $g$  is *expanding* near  $\Lambda$ ; there exist an open neighborhood  $V$  of  $\Lambda$  and constants  $\lambda > 1$  and  $c > 0$  such that

$$|Dg^n(x)| \geq c\lambda^n$$

whenever  $x, g(x), \dots, g^n(x) \in V$ . Let  $U$  be the union of the connected components of  $V$  that intersect  $\Lambda$ . By compactness of  $\Lambda$ , there exist a finite number of these connected components, call them  $U_1, \dots, U_k$ . Proposition 3.9 of Gyllenberg et al. (1996) implies that dynamics of  $g$  restricted to  $\Lambda$  are *transitive*; there exists an  $x \in \Lambda$  such that  $\{g^n(x)\}_{n \geq 1}$  is dense in  $\Lambda$ . It follows that for all  $1 \leq i, j \leq k$  there exists  $n$  such that  $g^n(U_i) \cap U_j \neq \emptyset$ . Theorem 2 of Pianigiani and Yorke (1979) implies there exists a unique continuous function  $\rho : U \rightarrow [0, \infty)$  and a constant  $L > 0$  such that

- $\int_U \rho(x) dx = 1$ ,
- $1/L \leq \rho(x) \leq L$  for all  $x \in U$ , and
- for all Borel subsets  $E$  of  $U$ ,

$$\int_E \rho(x) dx = \frac{\int_{g^{-1}(E) \cap U} \rho(x) dx}{\int_{g^{-1}(U) \cap U} \rho(x) dx} \tag{A.1}$$

Eq. (A.1) implies that  $\rho(x)$  is the density of a *conditionally invariant measure* for  $g$ . Define  $U(0) = U$  and  $U(n) = g^{-1}(U(n-1)) \cap U$  for all  $n \geq 1$ . Equivalently,

$$U(n) = \{x \in U : g(x), \dots, g^n(x) \in U\}.$$

$U(n)$  corresponds to the set of points in  $U$  that remain in  $U$  for at least  $n$  generations. Define

$$\alpha = -\ln \int_{U(1)} \rho(x) dx$$

which is positive as  $\int_{U(1)} \rho(x) dx < 1$ . Eq. (A.1) and the definition of  $U(n)$  implies that  $\int_{U(n+1)} \rho(x) dx = \exp(-\alpha) \int_{U(n)} \rho(x) dx$ . Hence  $\int_{U(n)} \rho(x) dx = \exp(-n\alpha)$  for all  $n \geq 0$ . Since  $1/L \leq \rho(x) \leq L$  for all  $x \in U$ , it follows that

$$\int_{U(n)} \frac{dx}{L} \leq \exp(-n\alpha) = \int_{U(n)} \rho(x) dx \leq \int_{U(n)} L dx$$

for all  $n \geq 1$ . Therefore,

$$\exp(-n\alpha)/L \leq \int_{U(n)} dx \leq L \exp(-n\alpha)$$

for all  $n \geq 1$ . Since  $[0, M] \setminus U$  is compact and all orbits starting in  $[0, M] \setminus U$  eventually enter  $[0, A]$ , continuity of  $g$  implies there is an integer  $i \geq 1$  such that  $g^i(x) \in [0, A]$  for all  $x \in [0, M] \setminus U$ . Choosing  $\kappa$  sufficiently large implies that for all  $n$  the probability  $p_n$  that a randomly chosen initial condition from  $[A, M]$  enters  $[0, A]$  in more than  $n$  generations is bounded above by  $\kappa \exp(-n\alpha)$  and bounded below by  $\exp(-n\alpha)/\kappa$ .

### A.1. The predator saturation model

In this section, we verify all the technical criteria outlined in the previous section except the negative Schwartzian hypothesis. Numerical simulations and partial analysis, however, suggest that the negative Schwartzian hypothesis is satisfied. Let  $g(x) = x \exp(r(1-x) - m/(1+sKx))$ .

As discussed in the main text, a strong Allee effect occurs if and only if  $r < m < \frac{r(sK+1)^2}{4sK}$  and  $sK > 1$  in which case there are two positive equilibria and the per-capita growth rate for densities below the smaller equilibrium is less than one. Let  $A$  equal the lower positive equilibrium. To verify that  $g(x)$  has a unique positive critical point, a computation of  $g'(x)$  shows that it is of the form  $p(x)q(x)$  where  $p(x) > 0$  for all  $x \geq 0$  and  $q(x) = 1 + (sKm - r + 2sK)x + sK(sK - 2r)x^2 - r(sK)^2x^3$ . The roots of  $q(x)$  correspond to the critical points of  $g(x)$ . Since  $sK > 1$  and  $m > r$ ,  $q'(0) = sKm - r + 2sK > 0$ . Since  $q(x)$  is a cubic with a negative leading coefficient,  $q(0) > 0$ , and  $q'(0) > 0$ , it follows  $q(x)$  has exactly one positive real root. Consequently,  $g(x)$  has a unique positive critical point. To apply the results of the previous section, choose  $a > 0$  to be any number less than  $A$  and  $b = \max\{g^{-1}(a)\}$ . Unimodality of  $g$  implies that  $\lim_{n \rightarrow \infty} g^n(x) = 0$  for all  $x \notin [a, b]$ .

### A.2. The mating model

In this section, we verify all the technical criteria for (4) outlined in the first section of the appendix. Let  $g(x) = xe^{r(1-x)\frac{x}{\beta+x}}$  where  $\beta = \frac{1}{sK}$ . The non-negative critical points of  $g(x)$  occur at  $x = 0$  and  $x = \frac{1-\beta r + \sqrt{1+6\beta r + \beta^2 r^2}}{2r}$ . Assume  $r$  and  $\beta$  are such that  $g(x) > x$  for some  $x > 0$ . Since  $x = 0$  is a critical point and a fixed point, it is superstable and there is a constant  $A > 0$  such that  $g(A) = A$  and  $g(x) < x$  for all  $x \in (0, A)$ . Choose any  $a \in (0, A)$ . Since  $g(x)$  approaches 0 as  $x$  approaches  $\infty$  and  $g(x)$  has a unique positive critical point, there exists a unique  $b > a$  such that  $g(b) = a$ . Furthermore,  $g(x) \in [0, A]$  for all  $x \in [b, \infty)$ . Hence,  $\lim_{n \rightarrow \infty} g^n(x) = 0$  for all  $x \in [b, \infty)$ . Finally, we verify that  $g$  has a negative Schwartzian derivative on the interval  $[a, b]$ . Taking the Schwartzian derivative and simplifying, we get

$$Sg(x) = -\frac{2\beta^2 r^2 x^3 q_1(x) + r^2 x^4 q_2(x) + \beta^2 q_3(x)}{2x^2(rx^2 + (\beta r - 1)x - 2\beta)^2},$$

where  $q_1(x) = r^2 x^2 - 6rx + 12$ ,  $q_2(x) = 6 - 4rx + r^2 x^2$ , and  $q_3(x) = 12 - 24rx + 24r^2 x^2 - 8r^3 x^3 + r^4 x^4$ . Since  $q_1(0) = 12 > 0$  and  $q_1$ 's discriminant equals  $-12r^2 < 0$ ,  $q_1(x) > 0$  for all  $x$ . A similar argument implies that  $q_2(x) > 0$  for all  $x$ . Taking the first and second derivative of  $q_3(x)$ , we find that  $q_3(x)$  has a global minimum of  $6(2 - 2^{1/3})$  at  $x = \frac{2-2^{1/3}}{r}$ . Hence  $q_3(x) > 0$  for all  $x$ . It follows that  $g$  has negative Schwartzian derivative.

### References

- Arditi, R., Akcakaya, H.R., 1990. Underestimation of mutual interference of predators. *Oecologia* 83, 358–361.
- Bellows, T.S., 1981. The descriptive properties of some models for density dependence. *J. Anim. Ecol.* 50, 139–156.
- Costantino, R.H., Desharnais, R.A., Cushing, J.M., Dennis, B., 1997. Chaotic dynamics in an insect population. *Science* 275, 389–391.
- Courchamp, F., Clutton-Brock, T., Grenfell, B., 1999. Inverse density dependence and the Allee effect. *TREE* 14, 405–410.
- Crawley, M.J., Long, C.R., 1995. Alternate bearing, predator saturation and seedling recruitment in *Quercus robur* L. *J. Ecol.* 83, 683–696.
- Cushing, J.M., Constantino, R.F., Dennis, B., Desharnais, R.A., Henson, S.M., 1998. Nonlinear population dynamics: models, experiments, and data. *J. Theor. Biol.* 194, 1–9.
- Dennis, B., 1989. Allee effects: population growth, critical density, and the chance of extinction. *Nat. Res. Model.* 3, 481–538.
- Ehrlich, P.R., 1975. The population biology of coral reef fishes. *Annu. Rev. Ecol. Sys.* 6, 211–247.
- Fowler, C.W., Baker, J.D., 1991. A review of animal population dynamics at extremely reduced population levels. *Rep. Int. Whal. Comm.* 41, 545–554.
- Fox, L.R., 1975. Cannibalism in natural populations. *Annu. Rev. Ecol. Syst.* 6, 87–106.
- Getz, W.M., 1996. A hypothesis regarding the abruptness of density dependence and the growth rate of populations. *Ecology* 77, 2014–2026.

- Goodman, D., 1987. The demography of chance extinction. In: Soulé, M.E. (Ed.), *Viable Populations for Conservation*. Cambridge University Press, Cambridge, Great Britain, pp. 11–34.
- Grenfell, B.T., Price, O.F., Albon, S.D., Clutton-Brock, T.H., 1992. Overcompensation and population cycles in an ungulate. *Nature* 355, 823–826.
- Groom, M.J., 1998. Allee effects limit population viability of an annual plant. *Am. Nat.* 151, 487–496.
- Gyllenberg, M., Osipov, A.V., Söderbacka, G., 1996. Bifurcation analysis of a metapopulation model with sources and sinks. *J. Nonlinear Sci.* 6, 329–366.
- Harrison, S., Cappuccino, N., 1995. Using density-manipulation experiments to study population regulation. In: Cappuccino, N., Price, P.W. (Eds.), *Population Dynamics: New Approaches and Synthesis*. Academic Press, San Diego, CA, pp. 131–147.
- Hassell, M.P., Lawton, J.H., Beddington, J.R., 1976. The components of arthropod predation: I. The prey death-rate. *J. Anim. Ecol.* 45, 135–164.
- Hastings, A., Higgins, K., 1994. Persistence of transients in spatially structured ecological models. *Science* 263, 1133–1136.
- Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78, 1946–1957.
- Knowlton, N., 1992. Thresholds and multiple steady states in coral reef community dynamics. *Am. Zool.* 32, 674–682.
- Lande, R., Engen, S., Sæther, B.E., 2003. *Stochastic population dynamics in ecology and conservation*. Oxford University Press, Oxford.
- Levitan, D.R., McGovern, T.M., in press. The Allee effect in the sea. In: Norse, E.A., Crowder, L.B. (Eds.), *Marine Conservation Biology. The Science of Maintaining the Seas Biodiversity*. Island Press, Washington, DC.
- Levitan, D.R., Sewell, M.A., Chia, F., 1992. How distribution and abundance influence fertilization success in the sea urchin *Strongylocentotus franciscanus*. *Ecology* 73, 248–254.
- Mangel, M., Tier, C., 1994. Four facts every conservation biologist should know about persistence. *Ecology* 75, 607–614.
- May, R.M., 1975. *Stability and Complexity in Model Ecosystems*, 2nd Edition. Princeton University Press, Princeton, NJ.
- May, R.M., 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269, 471–477.
- McCann, K., Yodzis, P., 1994. Nonlinear dynamics and population disappearances. *Amer. Nat.* 144, 873–879.
- McCarthy, M.A., 1997. The Allee effect, finding mates and theoretical models. *Ecol. Model.* 103, 99–102.
- Noy-Meir, I., 1975. Stability of grazing systems: an application of predator-prey graphs. *J. Ecol.* 63, 459–481.
- Pianigiani, G., Yorke, J.A., 1979. Expanding maps on sets which are almost invariant. Decay and chaos. *Trans. Amer. Math. Soc.* 252, 351–366.
- Ricker, W.E., 1954. Stock and recruitment. *J. Fish. Res. Board. Can.* 11, 559–623.
- Rosenzweig, M.L., 1971. Paradox of enrichment: destabilization of paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171, 385–387.
- Scheuring, I., 1999. Allee effect increases dynamical stability in populations. *J. Theor. Biol.* 199, 407–414.
- Schreiber, S.J., 2001. Chaos and sudden extinction in simple ecological models. *J. Math. Biol.* 42, 239–260.
- Sinha, S., Parthasarathy, S., 1996. Unusual dynamics of extinction in a simple ecological model. *Proc. Natl. Acad. Sci. USA* 93, 1504–1508.
- Stephens, P.A., Sutherland, W.J., 1999. Consequences of the Allee effect for behavior, ecology, and conservation. *TREE* 14, 401–405.
- Stephens, P.A., Sutherland, W.J., Freckleton, R.P., 1999. What is the Allee effect? *Oikos* 87, 185–190.
- Stone, L., 1993. Period-doubling reversals and chaos in simple ecological models. *Nature* 365, 617–620.
- Symonides, E., Silvertown, J., Andreasen, V., 1986. Population cycles caused by overcompensating density-dependence in an annual plant. *Oecologia* 71, 156–158.
- Tilman, D., 1982. *Resource Competition and Community Structure*. Monographs in Population Biology, Vol. 17. Princeton University Press, Princeton, NJ.
- Turchin, P., 1993. Chaos and stability in rodent population dynamics: evidence from nonlinear time-series analysis. *Oikos* 68, 289–305.
- Turchin, P., 1995. Population regulation: old arguments, new synthesis. In: Cappuccino, N., Price, P.W. (Eds.), *Population Dynamics: New Approaches and Synthesis*. Academic Press, San Diego, CA, pp. 19–40.
- Turchin, P., Taylor, A.D., 1992. Complex dynamics in ecological time series. *Ecology* 73, 289–305.
- Vandermeer, J., Yodzis, P., 1999. Basin boundary collision as a model of discontinuous change in ecosystems. *Ecology* 80, 1817–1827.
- Wiklund, C.G., Andersson, M., 1994. Natural selection on colony size on a passerine bird. *J. Anim. Ecol.* 63, 765–774.
- Williams, K.S., Smith, K.G., Stephen, F.M., 1993. Emergence of 13 year periodical cicadas (Cicadae: Magicada): phenology, mortality, and predator saturation. *Ecology* 74, 1143–1152.
- Wolda, H., Dennis, B., 1993. Density dependence tests, are they? *Oecologia* 95, 581–591.