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CHAOTIC DYNAMICS IN FOOD-LIMITED POPULATIONS: IMPLICATIONS FOR WILDLIFE MANAGEMENT

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Abstract. Analysis of simple, discrete mechanistic models of population growth suggests that chaotic dynamics are more likely to occur than predicted by previous analyses of simple logistic models. Three outcomes of the analysis are interesting: (1) adding predation may induce chaotic dynamics in food-limited prey that otherwise would not exhibit chaos, (2) chaos is more likely in more productive environments, and (3) if chaotic dynamics occur, most often they will result in local extinction of the population. These outcomes suggest that chaos can occur even in large vertebrate species with inherently low reproductive rates. In addition, wildlife populations may be more likely to exhibit chaos in eutrophic environments such as agricultural areas. Consequently, the potential for chaotic dynamics may be an important consideration in decisions about wildlife conservation and management.

INTRODUCTION

Chaotic population dynamics result if population trajectories vs. time diverge from slightly different initial conditions and do not repeat over time (Gleick 1987). These dynamics may appear random but are deterministic; i.e. they are produced by the specific properties of individuals within a population. Chaotic dynamics can also appear as "cycles" with variable amplitudes and periods. The most important characteristics of these dynamics are:

(1) Populations are unpredictable over long periods of time.
(2) Slightly different initial conditions lead to very different population trajectories over time.
(3) Populations can regularly "crash" to very low levels or go to extinction locally.
(4) Populations may exhibit periodic "irruptions" or "outbreaks".

The potential for animal populations to exhibit chaotic dynamics has been known since the mid-1970's (May 1974). However, wildlife population biologists have generally disregarded the importance of chaos for wildlife species because chaotic dynamics appeared to occur only in populations with a reproductive rate much higher than that achieved by most vertebrates (Berryman and Millstein 1989).

Most models in which chaotic population dynamics were studied were not mechanistic, i.e., did not represent reproduction as a function of physiological or behavioral variables (Lomnicki 1988), and did not consider the effects of interactions with other species (Gilpin 1979, Schaffer and Kot 1985). In this paper, I will show how mechanistic models of interacting species are more likely to produce chaotic population dynamics than most of the previously studied population growth models. I will also discuss how chaotic dynamics may affect management decisions and conservation plans.

MODELLING

Mechanistic models

Recently, Lomnicki (1988) derived the necessary conditions for chaos in a simple model of single species population growth over discrete time intervals for species with overlapping generations (the situation most likely to apply to wildlife species). His model assumed that the population was limited by resources, e.g. food, and explicitly incorporated the mechanisms by which food would limit population growth (i.e., was mechanistic). Population growth is given by

$$N_{t+1} - N_t = RN_t[(I/N_t) - M] \quad , \tag{1}$$

where N_t is the population size in the current time period, N_{t+1} is the population size in the next time period, R is the conversion efficiency of food into offspring, I is the amount of food available per time period, and M is an individual's food requirement for the current time period. Chaos will occur when,

$$R > 2 / M \ . \tag{2}$$

Using some approximate values of R and M from the literature, the likelihood of chaos for some wildlife species is evaluated in Table 1. In spite of the crudeness of these numbers, it is interesting to note that *Microtus pennsylvanicus* is the only species for which chaos is suggested to be likely, and is the only species that typically exhibits dynamics that resemble chaos (see EVIDENCE OF CHAOS below). In addition, the maximum intrinsic rate of increase for *M. pennsylvanicus* has been estimated as less than 1.5 (Blueweiss et al. 1978), well below the required level of 2.5 for chaos in previous models (May 1974). Consequently, population growth models in which the relationship between food and reproductive rate is explicitly modelled may be more likely to exhibit chaos. To the extent that mechanistic models are realistic, this conclusion suggests that chaos may be more likely than previously thought.

Table 1. Conversion efficiency of offspring production per unit energy, energy requirements per year, and likelihood of chaos for three mammal species.

Species	Conversion Efficiency (offspr/kJ)	Maintenance Requirement (kJ)	Chaos Likely?	Reference
Odocoileus virginianus	1.48×10^{-7}	4.04×10^{6}	No	Verme (1969)
Spermophilus columbianus	4.20×10^{-5}	4.32×10^{4}	No	Ritchie (1990)
Microtus pennsylvanicus	6.25×10^{-4}	2.59×10^{4}	Yes	Wiegert (1961)

In real environments, single species populations rarely exist, since there are usually other species that may interact with a given species. Consequently, it is crucial to understand the effect of species interactions on chaotic population dynamics. In general, increasing the number of species interacting in a system increases the likelihood of chaos (Hochberg et al. 1990, Hastings and Powell 1991). To examine this question properly, however, I added species interactions to Lomnicki's model (Equation 1) for population growth of a single species, for which the condition for chaotic population growth in the absence of interactions is already known (Equation 2).

Adding a predator

To add a predator, I assume that the predator has a linear functional response (consumption rate vs. prey density). Consequently, predator growth is given by

$$P_{t+1} - P_t = R_p P_t [aN_t - M_p] \quad , \tag{3}$$

where P_t is predator population size in time period t, R_p is the predator's conversion efficiency of a prey individual into predator offspring, a is the rate of increase in prey consumption per increase in prey density for an individual predator, and M_p is the maintenance requirement of prey per time period. The population growth of the prey becomes

$$N_{t+1} - N_t = RN_t[(I/N_t) - M] \; - \; aN_t P_{yt} \; . \tag{4}$$

Chaos and limit cycles will occur only if the predator-prey equilibrium is non-attractive; i.e. if the predator and prey populations are displaced from equilibrium, they do not return. Conditions under which non-attraction occurs is determined with a standard stability analysis (May 1973): the eigenvalues of the Jacobian matrix for the system must lie outside a circle in real and imaginary coordinates centered on (-1,0) and with radius 1. Applying this technique to the above predator-prey system reveals the condition under which limit cycles or chaos will occur:

$$R > 2/\{M[1 + 1/M_p(aI - MM_p)(2/M_p - aR_p)]\} \quad . \qquad (5)$$

Repeated simulations suggest that chaos results for most of the situations in which this inequality is true.

Adding a competitor

For a competitor, I add a second species sharing the same food resource as the first species. Consequently, I consider the effect of pure exploitative competition on the likelihood of chaos. Other mechanisms of competition, such as interference competition, are likely to have the same qualitative effects (Berryman and Millstein 1989) but will not be considered here.

The dynamics of the two competing species can be expressed as

$$N_{1,t+1} - N_{1,t} = R_1 N_{1,t}[I/(N_{1,t} + zN_{2,t}) - M_1] \qquad (6a)$$

and

$$N_{2,t+1} - N_{2,t} = R_2 N_{2,t}[zI/(N_{1,t} + zN_{2,t}) - M_2] \quad . \qquad (6b)$$

where the subscripts 1 and 2 denote species 1 and 2 and the constant z is the ratio of the consumption rate of food by species 2 to the consumption rate by species 1.

Because both species completely overlap in food resources, this system has no stable equilibrium where both species coexist (Schoener 1976). Consequently, the conditions under which chaos might occur cannot be determined with a standard stability analysis. However, the potential for chaos in each difference equation can be evaluated by a less rigorous technique that examines the change in N_{t+1} per unit change in N_t (this applies for either species) (May 1973, Lomnicki 1988). Limit cycles or chaos will result if:

$$N_{t+1}/N_t < -1 \quad . \qquad (7)$$

Species 1 will exhibit limit cycles or chaos if:

$$R_1 > [2 + zN_{2,t}/(N_{1,t} + zN_{2,t})^2]/M_1 \quad , \qquad (8a)$$

and species 2 will exhibit limit cycles or chaos if:

$$R_2 > [2 + N_{1,t}/(N_{1,t} + zN_{2,t})^2]/M_2 \qquad (8b)$$

for any positive values of $N_{1,t}$ and $N_{2,t}$.

Equations (8*a*, *b*) suggest that competition will reduce the likelihood for chaos, i.e. R must be larger to produce chaos than in the absence of a competitor (see Equation 2).

MODEL PREDICTIONS

Analysis of these modelling results produces the following predictions.

(1) Chaos is more likely for a single species when maintenance costs are high relative to the conversion efficiency of food (or resources) into offspring.

(2) Adding a predator makes chaos more likely.

(3) Increasing environmental productivity makes chaos much more likely in predator-prey systems, but does not affect the likelihood of chaos for a single species population or for two competitors.

(4) In predator-prey systems, low conversion efficiency of food into offspring by the predator may make chaos *more* likely (Equation 5 is more easily satisfied). This counters the idea that chaos is possible only for organisms with high reproductive rates.

(5) Interspecific competition will make chaos less likely, i.e., adding a competitor may dampen the fluctuations of a population that exhibits chaos in the absence of a competitor.

These predictions suggest that chaos can occur in many animal species for which chaos has been assumed to be unlikely (Berryman and Millstein 1989). Virtually all animals are involved in predator-prey systems because they either eat other species, or are eaten *by* other species themselves. In addition, these predictions suggest that the environment, through its effects on maintenance requirements and food availability, can elicit chaotic dynamics. In particular, chaotic dynamics may be likely in eutrophic environments such as agricultural areas. Consequently, wildlife biologists and managers cannot ignore the possibility of chaotic dynamics in wildlife populations.

EVIDENCE OF CHAOS

Although the theoretical analysis above suggests that chaotic dynamics may be more likely than previously thought, debate remains about whether chaotic dynamics actually exist in terrestrial vertebrate populations. In addition to arguments about reproductive rates, some ecologists suggest that chaos should not be observed in natural populations because they are virtually guaranteed to go extinct within a few generations under most conditions in which chaos occurs (Thomas et al. 1980, Berryman and Millstein 1989). However, this argument ignores the possibility that *local* populations may exhibit chaos and go *locally* extinct, but dispersing individuals from neighboring populations (which may be chaotic but not yet extinct) may colonize the site, preventing permanent extinction. In this scenario, a mosaic of local populations exhibit chaotic dynamics, repeated crashes, and repeated recolonization from neighboring populations. It is unlikely that all local populations will go extinct simultaneously because (1) heterogeneity in the environment and random dispersal events are likely to produce different initial population densities in each local population following crashes, and (2) different initial densities will lead to different population trajectories over time, and consequently different times until extinction.

Fig. 1 demonstrates a simulation of predator densities over time, using the predator-prey model (Equations 3 and 4), where the predator population would ordinarily

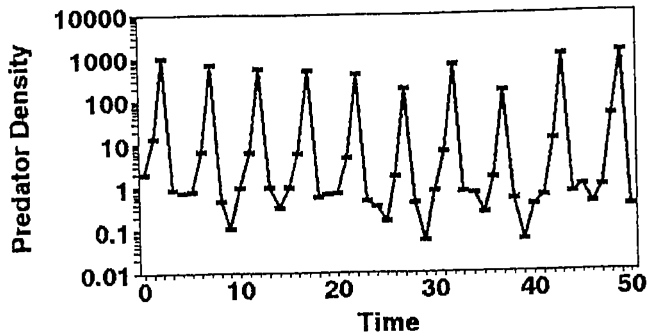

Fig. 1. Example of a simulated predator population that inevitably goes extinct but is always recolonized by a small number of emigrants.

go extinct except for the arrival of a low number of colonists from outside the population. The dynamics appear qualitatively similar to those of many "cyclic" wildlife populations.

Evidence for chaotic dynamics must come ultimately from the analysis of time series of real populations. Schaffer and Kot (1985) provide several arguments for chaotic dynamics in lynx and snowshoe hares in Canada. In a separate paper (Ritchie, *submitted manuscript*), I have analyzed long-term population data from the literature for the existence of chaos by estimating Lyapunov exponents (the degree to which population trajectories diverge from similar initial conditions, Wolf 1986) and using non-linear forecasting (Sugihara and May 1990). These techniques are capable of distinguishing chaos from random population fluctuations, cycles, and cycles with noise. Out of 20 different mammal and bird species I analyzed, chaos appeared to be present in populations of both small mammals: *Microtus pennsylvanicus* (as predicted in Table 1), *Microtus californicus*, *Sigmodon hispidus*, *Apodemus flavicollis*, and *Lemmus sibiricus*; and birds: northern harrier (*Circus cyaneus*), Brent geese (*Branta bernicla*), grasshopper warbler (*Locustella naevia*), and two shorebirds (*Charadrius hiaticula* and *Calidris ferruginea*). These results suggest that many of the wildlife species thought to be "cyclic," "quasi-cyclic," or to exhibit "fluctuations" may actually exhibit chaotic dynamics.

MANAGEMENT IMPLICATIONS

If wildlife populations exhibit chaotic dynamics, then management plans should take these chaotic dynamics into account. I will briefly discuss a few prominent management problems: defining population carrying capacity, determining harvest levels, and conserving viable populations.

Establishing carrying capacity

Most wildlife population management is based on the assumption that there is some density at which a species will come into equilibrium with its food supply, predators, diseases, etc. (Robinson and Bolen 1989), i.e., "carrying capacity." Specifically, managers often estimate carrying capacity to indicate how many animals should occupy a given environment.

If population growth is chaotic, the concept of carrying capacity has little utility for management. Chaotic dynamics in even their simplest form resemble "cycles" with unpredictable periods and amplitudes. Furthermore, population density of a chaotic species will never remain at a single equilibrium. A better approach would be to specify the range or "boundaries" of densities that can be expected. In addition, managers must accept the fact that they will be uncertain of population densities in future times, although predictions over short time periods may be possible (Sugihara and May 1990).

Harvesting populations

To decide how many animals to harvest, managers must know how different magnitudes of harvest will affect future population dynamics. There are numerous harvest strategies designed to produce an equilibrium between population growth rate and harvest rate (Getz and Haight 1989). If population dynamics are chaotic, harvesting may produce various results: (1) an otherwise fluctuating population may stabilize at an equilibrium, (2) a persistent but fluctuating population may be driven to extinction, or (3) a population may continue to fluctuate but with different periods and amplitudes. Slightly different magnitudes of harvest or population densities at first harvest can potentially produce very different population trajectories over time, and potentially different chances for population extinction. The response of chaotic populations to harvesting is virtually unstudied, but preliminary indications (Hochberg et al. 1990) suggest that managers must depend on species-specific population growth models to determine appropriate harvest levels.

Conservation of viable populations

For a majority of wildlife species, a manager's goal is to maintain viable populations. The extensive literature on the subject (e.g. Soulé 1987) suggests that small populations are much more likely to go extinct than large ones, so management goals should provide for a sufficiently large population to greatly reduce the chances of accidental extinction. Populations with chaotic dynamics pose a special problem in this context. Over most of the ecological conditions under which chaos is likely, populations will either routinely reach low enough densities to risk accidental extinction or drive themselves to extinction (May 1974, Berryman and Millstein 1989). Consequently, the maximum or average *size* of a population with chaotic growth probably will not predict that population's chance of extinction.

Some ecologists argue that this characteristic makes chaotically growing populations unmanageable, i.e., there is little a manager can do to prevent extinction. However, the potential for local populations to be re-colonized suggests that maintenance of viable populations with chaotic dynamics requires: (1) a mosaic of local populations that potentially can provide colonizers to each other, and (2) a heterogeneous environment to help desynchronize the dynamics of the local populations. Rather than minimum viable population size, a more appropriate measure for conservation of chaotic species might be minimum viable number of local populations.

CONCLUSION

Chaotic dynamics in wildlife populations appear to be more likely than previously thought. Predator-prey systems, especially in eutrophic environments, show strong potential for chaotic dynamics. Evidence of chaos in real populations exists but is not overwhelming. Nevertheless, managers at least should consider that wildlife population dynamics may be chaotic and be prepared to use non-traditional conceptual approaches in the management of these populations.

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