

Experimental Studies of Extinction Dynamics

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Extinction of populations occurs naturally, but global extinction rates are accelerating, making understanding extinction a high priority for conservation. Extinction in experimental populations of brine shrimp (*Artemia franciscana*) was measured to assess hypothesized extinction processes. Greater initial population size, greater maximum population size supported by the environment, and lower variation in environmental conditions reduced the likelihood of extinction, as hypothesized. However, initial population size was less important, and maximum population size and environmental variation were more important than often hypothesized. Unexpectedly, deterministic oscillations in population size due to inherent nonlinear dynamics and overcrowding were as important or more important than hypothesized processes.

How populations naturally go extinct is not well understood, but such understanding is critical for appreciating the local periodic disappearance of species in ecological time and the global disappearance of species in the fossil record (1). The need to understand extinction processes has gained urgency as the number of species threatened with extinction increases throughout the world and conservationists combat this trend (2). Hypothesized extinction processes, however, have been applied in conservation planning without validation (3).

Several factors have been hypothesized to influence the likelihood of extinction: (i) small population size, (ii) deleterious environmental variations, (iii) periodic catastrophes, and (iv) migration. Small populations occur when a population is first established or is reduced to a low level and when the maximum population size sustainable by the environment (carrying capacity) is low (1, 4). The role of small population size is termed demographic stochasticity because random declines in survival and birth rates can produce extinction. Periodic deleterious environmental variations can reduce survival and birth rates, as well as carrying capacity (5). This initiates demographic stochasticity in large populations and has been termed environmental stochasticity. Periodic catastrophes, such as epidemics, can reduce populations to small size so that demographic stochasticity can operate (6). Finally, the above factors can be countered by migration of individuals from other populations (7). All of these factors are impor-

tant to the conservation of the world's fauna and flora because populations, carrying capacity, and migration are often reduced by human activities (2, 8).

To examine how demographic and environmental stochasticity affect extinction, we used laboratory populations of brine shrimp (*Artemia franciscana*) (9) in two experiments. One experiment examined extinction dynamics and the other examined population growth rates without extinction. The experiments were completed after four years when the last population went extinct.

Extinction experiments used sets of replicate populations established under different conditions [initial adult number, mean daily food supply rate, and coefficient of variation (CV_K) for randomly varying daily food supply rate (10) (Table 1)]. Populations were censused and numbers were expressed in adult equivalents (11) until extinction occurred (12). Food supply rates determined carrying capacity (K) (number of adult equivalents) (13). Likelihood of extinction was expressed as mean persistence time (MT) and its standard deviation for sets of replicate populations under the same conditions.

Population growth experiments were conducted at different constant food supply rates (Table 1), but extinction could not occur because a constant adult density (10 males and 10 females) was maintained. We replaced dead males and females and removed nauplii (hatchlings) and cysts (diapausing eggs) after censuses to maintain a constant adult density (12). Removed nauplii were used to initiate 10 replicate populations containing 20 individuals at different food levels to compute mortality (14). The density of populations initiated with nauplii was kept constant by replacing dead individuals and individuals that became adults with nauplii from the same food level after each census (12). Populations

were studied for 4 weeks (one generation), and population growth rate was measured [$r = \ln(\text{birth rate} - \text{death rate})/\text{generation time}$] (12).

With the extinction experiment (Fig. 1), we addressed the validity of hypothesized extinction processes. Demographic stochasticity should produce MTs for populations under the same conditions that increase as initial population number (I) and carrying capacity (K) increase and that decrease as environmental variability (CV_K) increases. Contrary to expectation, I had no effect on persistence and CV_K had mixed effects; however, K had the expected effect (15).

Instead of measuring CV_K , others (16) substitute population variability (CV_P) for it, assuming that environmental variability causes population variability. When CV_P was substituted for CV_K , mean persistence time was positively correlated with I and K and negatively correlated with CV_P as hypothesized (17). Initial population size is often assumed to be the most important determinant of MT, but we found that carrying capacity and population variability were much more important, accounting for 36 and 48% of explained variance, respectively. CV_P was not an individual population's coefficient of variation as commonly used (16), which is a biased estimator of population variability, but was the average coefficient of variation for all populations under the same conditions (18).

Why do CV_P and CV_K produce dissimilar results, given that environmental variability is hypothesized to cause population variability (16)? The answer is that environmental variability does not solely cause population variability. From the population growth rate experiment, we used the mean food supply rate to estimate each population's maximum growth rate in the extinction experiment (19). Maximum growth rates were sufficiently large to generate nonlinear population dynamics, which cause populations to intrinsically oscillate (20). Nonlinear dynamics emerge when competition among population members causes the population to overshoot or undershoot K (20). Depending on maximum growth rate, oscillations about K can decrease until K is reached (damped oscillations), can continue with regular periodicity (limit cycles), or can continue with no apparent cyclicity (chaos). Oscillations are initially amplified if a population is started above K because competition is more intense.

The role of nonlinear dynamics in population variability (CV_P) was estimated (19), as was the initial amplification of oscillations when initial population number exceeds K (I/K). When the coefficient of variation in population numbers (CV_P) was compared with CV_P , I/K , and environmental variability (CV_K) (Fig. 2) (21), all three factors increased

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CV_p as expected. However, nonlinear dynamics (CV_r and I/K) were more important than environmental variability, accounting for 74% of the explained variance in CV_p .

How important are demographic and environmental stochasticity? Nonlinear dynamics (CV_r and I/K) are deterministic and account for 38% of the variation in population numbers (CV_K). Environmental sto-

chasticity accounts for 14% of variation in population numbers, which means that demographic stochasticity (plus experimental error, which is minimal owing to controlled conditions and precise censuses) accounts for 48%. Of the 48% of population variation due to demographic stochasticity, K accounts for 32% and I accounts for 16%. Our results do not quantitatively portray

field populations of brine shrimp or other species but do provide qualitative insights into extinction for many species. For example, like many populations, our experimental populations were restricted to sexual production of live young, and their maximum population growth rates may be typical of many species.

Demographic and environmental stochas-

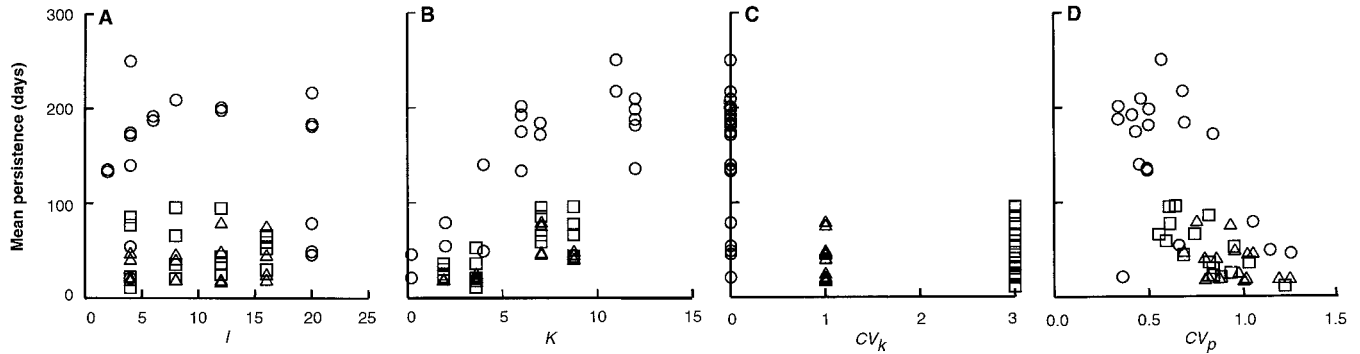


Fig. 1. MTs compared with experimental conditions. (A) Initial population size; (B) carrying capacity; (C) environmental variability; and (D) population variability. Circles indicate no environmental variability ($CV_K = 0$), triangles indicate intermediate variability ($CV_K = 1$), and squares indicate high variability ($CV_K = 3$). Results are for 51 sets of replicated populations (Table 1).

Fig. 2. Total population variability (CV_p) compared with its components (A) environmental variability, (B) variability due to nonlinear dynamics, and (C) initial overcrowding (Fig. 1).

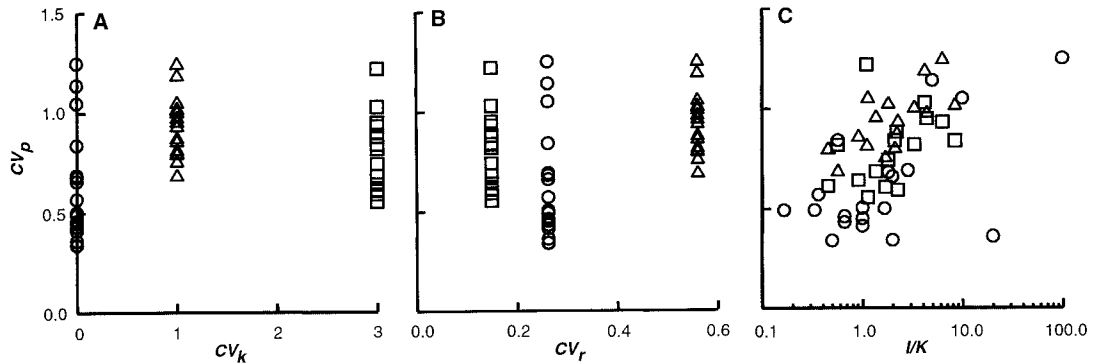


Table 1. The experimental design, showing the numbers of replicate populations.

Population (no. of individuals)	Food supply rate (mg of dry yeast/day)												
	0.00 (only algae + bacteria in water)	0.20	0.25	0.40	0.5	0.67	0.80	1.0	1.25	1.33	1.50	2.50	3.75
<i>Extinction experiment (51 sets for a total of 560 populations)</i>													
No environmental variability ($CV_K = 0$)													
2						20				20			
4	8		4		4	20		4		20		4	
6						20				20			
8						20				20			
12						20				20			
20			4		4			4		20		4	
Environmental variability ($CV_K = 1$ or 3)													
4		10		10			10	10					
8		10		10			10	10					
12		10		10			10	10					
16		10		10			10	10					
<i>Population growth experiment (total of 100 populations)</i>													
Constant density*		10				10			10			10	10

*10 adult females and 10 adult males or 20 nauplii.

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ticity produce a likelihood of extinction at a given time, which means that MT is one aspect of a probability distribution. A standard deviation (SD) of MT is another aspect. Based on hypothesized extinction dynamics, the probability distribution of persistence times under identical conditions should be a negative exponential function (22), which means that MT equals its SD. We found SD to be an approximate one-half multiple of MT ($r^2 = 0.81$, $n = 51$, $P < 0.00001$), which indicates a gamma probability distribution but not its special case of the negative exponential. This discrepancy is expected because the negative exponential emerges when demographic and environmental stochasticity are assumed to account for all of the variation in population numbers. However, our experiment found that these stochastic factors account for only 62% of the variation; the remaining variation is due to deterministic nonlinear dynamics. Therefore, SD in MT should be less than hypothesized, assuming that all variation is due to stochastic factors.

Although our experiments qualitatively support many hypothesized patterns in extinction dynamics, they do not necessarily support the hypothesized relative importance of each. Small initial population size (I) is least important to extinction because most populations can rapidly increase from a few individuals if they have sufficiently large K , which explains why we found K to be more important than I . Consequently, a few individuals colonizing a new area, representing the evolution of a new species or reintroduction of a species for conservation, may not be as prone to extinction as first hypothesized. Temporal variation in population numbers was most important to extinction. However, population variability due to environmental variation was less important than inherent oscillations due to nonlinear population dynamics and overcrowding. Environmental variation can intensify overcrowding when periodic beneficial conditions increase populations and temporarily produce overcrowding in subsequent less beneficial times. Therefore, nonlinear dynamics increase the likelihood of extinction, but greater likelihood of extinction does not mean that oscillating populations will not be observed (23).

What does this mean for conservation planning? First, conservationists need to preserve areas that either provide a species with as large a K as possible or enhance an area's K by management actions. Second, although conservationists can do little to influence environmental variability, they should consider its impact on population variability; but this is not enough. They should also consider population oscillations created by nonlinear dynamics. Nonlinear dynamics are deterministic influences on

extinction, which are seldom considered, and differ from deterministic reductions in survival and birth rates caused by pollution and harvesting that conservationists usually do consider (24). Third, overcrowding enhances population oscillations, which increases the likelihood of extinction. Overcrowding may be an underappreciated transient extinction threat as habitats are destroyed and as individuals populating destroyed areas migrate into remaining habitat fragments and increase population densities there. This overcrowding scenario was observed in birds during logging of Amazonian rainforest (25). Finally, the probability distribution of persistence times is not as broad as hypothesized, which means that many more populations will persist for periods approaching the mean than originally thought. Although MT for similar populations may be as pessimistic an indicator as conservationists fear, this observed narrower probability distribution provides some hope.

References and Notes

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9. Brine shrimp were hatched from commercial cysts and reared to adults in 40-liter aquaria containing aerated hypersaline water (90 parts per thousand). Shrimp were fed an aqueous suspension of dry baker's yeast (100 mg per aquarium per day). Sexes were separated as individuals became adults to prevent reproduction. The shrimp only sexually reproduce. Experimental populations were kept in 500-ml Nalgene bottles containing 400 ml of aerated hypersaline water and were kept in environmental chambers (25° to 27°C, 12 hours light:12 hours dark). Half of a bottle's solution was replaced and sediments were removed twice a week, and bottle walls were wiped with a sponge once a week to limit algae and bacteria as additional food and to reduce variation in pH.
10. A random number generator (normal distribution) provided each population's daily food ration. If a daily ration was negative, no food was supplied; this produces a more log-normal distribution.
11. Every 3 days, individuals in a bottle were counted, identified as to developmental stage, and sexed if adult. Three developmental stages were used [H. Heath, *J. Morphol.* **38**, 453 (1924)]; nauplii (≤ 5 mm), juveniles (> 5 and ≤ 9 mm), and adults (> 9 mm), and population size was expressed in adult equivalents based on body mass (nauplius = 0.13 adult; juvenile = 0.63 adult). Population dynamics were restricted to live births by removal of cysts, which ensured short generation time.
12. Population extinction occurred when (i) all individuals disappeared and (ii) all individuals were adults of a single sex. However, when adult females remained, observations continued until all females died in order to make sure that they were not gravid. If all individuals in a population were nauplii or juveniles, then observations continued until sexes could be assessed and condition (ii) was met.
13. $K = -0.29 + 6.93$ food supply rate ($r^2 = 0.81$, $n = 40$, $P < 0.001$).
14. Nauplii received the same food level as their maternal population (Table 1) except the two highest maternal levels, which were reduced to 1.88 and 2.5 mg/day, because unused food increased pH to a lethal level.
15. Analysis of covariance (ANCOVA) for MT was done as follows: I (continuous variable: $F = 0.24$; $df = 1$, 46; $P < 0.88$); K (continuous variable: $F = 63.03$; $df = 1$, 46; $P < 0.0001$); CV_K (categorical variable: $F = 49.95$; $df = 2$, 46; $P < 0.0001$); $r^2 = 0.82$.
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17. Multiple regression for MT was done as follows: I ($t = 1.74$, $df = 47$, $P < 0.08$); K ($t = 3.59$, $df = 47$, $P < 0.00001$); CV_K ($t = -4.45$, $df = 47$, $P < 0.00001$); $r^2 = 0.61$.
18. Coefficients of variation in population numbers (CV_p) over time for all replicate populations under the same conditions were averaged; this eliminates statistical biases for individual population values [P. A. Van Zandt, thesis, Utah State University, Logan, UT (1997)].
19. Based on mean food level, maximum population growth rate was estimated as 1.96 females produced per female per generation (\varnothing/\varnothing /generation) with no environmental variation, 2.22 \varnothing/\varnothing /generation for intermediate environmental variation ($CV_K = 1$), and 1.45 \varnothing/\varnothing /generation for high environmental variation ($CV_K = 3$). Using these growth rates and an initial population of 4 in the discrete logistic model of population growth (20), oscillations due to nonlinear dynamics were estimated as the coefficient of variation in population numbers over 50 time periods (CV_p); no environmental variation, $CV_p = 0.15$; intermediate environmental variation, $CV_p = 0.53$; high environmental variation, $CV_p = 0.08$.
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21. ANCOVA for CV_p was done as follows: CV_K (categorical variable: $F = 14.07$; $df = 1$, 47; $P < 0.0005$); CV_I (continuous variable: $F = 22.59$; $df = 1$, 47; $P = 0.00002$); $\log I/K$ (continuous variable: $F = 16.52$; $df = 1$, 47; $P < 0.0002$); $r^2 = 0.52$).
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