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A Discrete Time Stochastic Model of  
a Two prey, One Predator Species Interaction

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## Abstract

A stochastic discrete time model of a two prey, one predator interaction, an extension of one and two species models proposed by Leslie (1958) and Leslie and Gower (1958, 1960), is studied. Monte Carlo simulations and the stability properties of the analogous continuous time deterministic model suggest the following hypotheses: 1. The two prey, one predator interaction is in general unstable. The range of parameters allowing coexistence of all three species is small. 2. Deterministically the predator always survives. 3. If the parameters defining the effects of density on the rates of population growth are large, the simulations lead to the rapid extinction of all three species or all but one of the prey species even if the interaction is deterministically stable. 4. The outcome of this three species interaction is largely probabilistic over a wide range of parameters. 5. A prey species with a competitive advantage over a second prey species may still find it difficult to invade and displace the second prey species if the density of the second prey species is high. Increasing the density of the predator offsets this numerical advantage somewhat. 6. The introduction of a predator common to two non-competing species of prey usually leads to the extinction of one of the prey species. 7. In a stable two prey, one predator interaction the fluctuations of the two prey species are non-periodic and erratic. The fluctuations of the rarer prey species are damped relative to the commoner species and the fluctuations of the rarer prey species behave as if the series has no fixed mean abundance. The predator population fluctuates with a remarkably constant period. The relevance of these hypotheses to the problem of relating population stability and persistence with the number of species in a community is discussed.

## Introduction

In a series of papers Leslie (1958) and Leslie and Gower (1958, 1960) studied discrete time stochastic models of one and two species population interactions based on Kendall's (1949) discrete time birth-death process. In Kendall's model the expected population density at time  $t+1$  is

$$E(N_{t+1} | N_t) = e^{(b_t - d_t)N_t} \quad 1)$$

where  $N_t$  is the population density at time  $t$  and  $b_t$  and  $d_t$  are the intrinsic birth and death rates at time  $t$  respectively. If the birth and death rates are constants, Eq. 1 is easily recognized as a discrete time version of the familiar exponential growth function.

The variance of the density at time  $t+1$  is

$$\begin{aligned} \text{Var}(N_{t+1} | N_t) &= \left[ \frac{b_t + d_t}{b_t - d_t} \right] \left[ e^{(b_t - d_t)N_t} - 1 \right] \left[ e^{(b_t - d_t)N_t} \right] N_t && b_t \neq d_t \\ &= 2b_t N_t && b_t = d_t \end{aligned}$$

The growth of the population can be simulated with Monte Carlo techniques. By assuming that  $N_{t+1}$  is normally distributed the effect of chance can be incorporated by: 1) calculating  $E(N_{t+1} | N_t)$ , 2) calculating  $\text{Var}(N_{t+1} | N_t)$ , 3) taking the square root of the variance and multiplying it times a random normal deviate with zero mean and variance of one, and 4) adding this deviation to  $E(N_{t+1} | N_t)$ . The process is continued by using the quantity calculated in step four as  $N_t$ . The normality assumption is justified in a paper by Bartlett, Gower, and Leslie (1960). Although the distribution of densities at time  $t+1$  cannot be exactly normal, the normal approximation should be reasonably good provided the abundances of the species are not too small.

A logistic model can be written as

$$E(N_{t+1} | N_t) = \frac{\lambda N_t}{1 + \alpha N_t}$$

where the constant  $\alpha$  is  $(\lambda - 1)/K$  with  $\lambda$  the finite rate of increase and  $K$  the carrying capacity of the environment. Because the finite rate of increase  $\lambda$  is equal to  $e^r$ ,  $\ln \lambda_t = r_t$ . The quantity  $1 + \alpha N_t = q_t$  represents a linear functional dependence of the rate of increase on density so  $\lambda_t = \lambda/q_t$ . The variance of  $N_{t+1}$  can be found by assuming that either the birth rate or the death rate remains constant, i.e. is not affected by density. Leslie (1958) shows for a birth rate constant model

$$\begin{aligned} \text{Var}(N_{t+1} | N_t) &= \left[ \frac{2b}{r_t} - 1 \right] \left[ \lambda_t - 1 \right] E(N_{t+1} | N_t) && r_t \neq 0 \\ &= 2b E(N_{t+1} | N_t) && r_t = 0 \end{aligned}$$

For two competing species  $N_1$  and  $N_2$

$$\begin{aligned} E[N_1(t+1) | N_1(t), N_2(t)] &= \frac{\lambda_1 N_1(t)}{1 + \alpha_1 N_1(t) + \beta_1 N_2(t)} \\ E[N_2(t+1) | N_1(t), N_2(t)] &= \frac{\lambda_2 N_2(t)}{1 + \alpha_2 N_2(t) + \beta_2 N_1(t)} \end{aligned} \quad 2)$$

The parameters  $\alpha_1$  and  $\alpha_2$  represent the influence of the density of each species on its own rate of increase, and  $\beta_1$  and  $\beta_2$  the effect of the density of one species on the rate of increase of the second. The deterministic stationary point of the two competing species interaction is

$$L_1 = \frac{\alpha_2(\lambda_1 - 1) - \beta_1(\lambda_2 - 1)}{\alpha_1\alpha_2 - \beta_1\beta_2}$$

$$L_2 = \frac{\alpha_1(\lambda_2 - 1) - \beta_2(\lambda_1 - 1)}{\alpha_1\alpha_2 - \beta_1\beta_2}$$

If  $L_1, L_2 > 0$ , the interaction is stable, i.e. both species persist, provided

$$\alpha_1\alpha_2 - \beta_1\beta_2 > 0.$$

The Leslie-Gower model of a predator-prey interaction where  $N_1$  is the density of the prey species and  $N_2$  the density of the predator population is

$$E [N_1(t+1) | N_1(t), N_2(t)] = \frac{\lambda_1 N_1(t)}{1 + \alpha_1 N_1(t) + \gamma_1 N_2(t)}$$

3)

$$E [N_2(t+1) | N_1(t), N_2(t)] = \frac{\lambda_2 N_2(t)}{1 + \alpha_3 [N_2(t)/N_1(t)]}$$

where  $\gamma_1$  represents the effect of the predator density on the prey rate of increase and  $\alpha_3$  is a parameter denoting the influence of the density of the prey relative to the predator density on the rate of increase of the predator. The deterministic stationary point of this predator-prey model is

$$L_{\text{prey}} = \frac{\alpha_3(\lambda_1 - 1)}{\beta_1(\lambda_2 - 1) + \alpha_1\alpha_3}$$

4)

$$L_{\text{predator}} = \frac{(\lambda_2 - 1)L_{\text{prey}}}{\alpha_3}$$

This stationary point is a stable point provided  $\lambda_1, \lambda_2 > 1$  in contrast to the Lotka-Volterra model in which there is no damping of the fluctuations of the two populations to the equilibrium point.

The variances of  $N_{t+1}$  for each species in both two species interactions (Eqs. 2,3) for the  $i$ th species are

$$\begin{aligned} \text{Var} [N_i(t+1) | N_1(t), N_2(t)] &= \left[ \frac{2b_i}{r_i(t)} - 1 \right] \left[ \lambda_i(t) - 1 \right] \mathbb{E} [N_i(t+1)] && \lambda_i(t) \neq 1 \\ &= 2b_i \mathbb{E} [N_i(t+1)] && \lambda_i(t) = 1 \end{aligned}$$

where  $b_i$  is the constant birth rate of the  $i$ th species.

The properties of the two competing species model are discussed in Leslie and Gower (1958). The predator-prey system results usually in a pair of damped curves, but stochastic fluctuations are continually reasserting fluctuations in both the prey and the predator populations. As the predator pressure,  $\gamma_1$ , increases, the fluctuations relative to the mean density of each population become more intense and can lead to the extinction of the prey or the predator population even though the system is deterministically stable. Further properties of the model are discussed in Leslie and Gower (1960).

#### A One predator, two prey interaction: The deterministic model

The basic discrete time model can easily be extended to three species, a predator and two prey species. This system also corresponds to a one parasite, two host interaction. Representing the two prey species and the predator as  $N_1$ ,  $N_2$ , and  $N_3$  respectively

$$N_1(t+1) = \frac{\lambda_1 N_1(t)}{1 + \alpha_1 N_1(t) + \beta_1 N_2(t) + \gamma_1 N_3(t)}$$

$$N_2(t) = \frac{\lambda_2 N_2(t)}{1 + \alpha_2 N_2(t) + \beta_2 N_1(t) + \gamma_2 N_3(t)}$$

5)

$$N_3(t) = \frac{\lambda_3 N_3(t)}{1 + \alpha_3 [N_3(t)/N_1(t) + N_2(t)]}$$

The stationary points  $L_1$ ,  $L_2$ , and  $L_3$  of this system of equations are

$$L_1 = \frac{(\lambda_1 - 1) \left[ \alpha_2 + \frac{\gamma_2 (\lambda_3 - 1)}{\alpha_3} \right] - (\lambda_2 - 1) \left[ \beta_1 + \frac{\gamma_1 (\lambda_3 - 1)}{\alpha_3} \right]}{\alpha_1 \alpha_2 - \beta_1 \beta_2 + \frac{\gamma_1 (\lambda_3 - 1)}{\alpha_3} (\alpha_2 - \beta_2) + \frac{\gamma_2 (\lambda_3 - 1)}{\alpha_3} (\alpha_1 - \beta_1)}$$

$$L_2 = \frac{(\lambda_2 - 1) \left[ \alpha_1 + \frac{\gamma_1 (\lambda_3 - 1)}{\alpha_3} \right] - (\lambda_1 - 1) \left[ \beta_2 + \frac{\gamma_2 (\lambda_3 - 1)}{\alpha_3} \right]}{\alpha_1 \alpha_2 - \beta_1 \beta_2 + \frac{\gamma_1 (\lambda_3 - 1)}{\alpha_3} (\alpha_2 - \beta_2) + \frac{\gamma_2 (\lambda_3 - 1)}{\alpha_3} (\alpha_1 - \beta_1)}$$

6)

$$L_3 = \frac{(\lambda_3 - 1)(L_1 + L_2)}{\alpha_3}$$

Define the following three quantities:

$$y_1 = \frac{(\lambda_2 - 1) \left[ \beta_1 + \frac{\gamma_1 (\lambda_3 - 1)}{\alpha_3} \right]}{(\lambda_1 - 1) \left[ \alpha_2 + \frac{\gamma_2 (\lambda_3 - 1)}{\alpha_3} \right]}, \quad y_2 = \frac{(\lambda_1 - 1) \left[ \beta_2 + \frac{\gamma_2 (\lambda_3 - 1)}{\alpha_3} \right]}{(\lambda_2 - 1) \left[ \alpha_1 + \frac{\gamma_1 (\lambda_3 - 1)}{\alpha_3} \right]}$$

and

$$x \equiv \alpha_1 \alpha_2 - \beta_1 \beta_2 + \frac{\gamma_1 (\lambda_3 - 1)}{\alpha_3} (\alpha_2 - \beta_2) + \frac{\gamma_2 (\lambda_3 - 1)}{\alpha_3} (\alpha_1 - \beta_1)$$

It is shown in Appendix I that there are four possible outcomes of this two prey, one predator interaction:

1.  $x > 0$ ;  $y_1, y_2 < 1$  Interaction stable, all three species survive
2.  $x < 0$ ;  $y_1 < 1, y_2 > 1$  Prey species one and the predator persist, prey species two becomes extinct
3.  $x < 0$ ;  $y_1 > 1, y_2 < 1$  Prey species two and the predator persist, prey species one becomes extinct
4.  $x < 0$ ;  $y_1, y_2 > 1$  Unstable stationary point, either prey species one or two becoming extinct depending on the initial densities of all three species

If the system is not stable, the stationary states for the remaining prey species and the predator or parasite are given by Eq. 4. Some specific examples of the deterministic model are given below.

No competition. -- The course of population growth in the three species with the parameters  $\alpha_1 = .0005$ ,  $\alpha_2 = .0007$ ,  $\beta_1 = \beta_2 = 0$ ,  $\gamma_1 = \gamma_2 = .002$ ,  $\lambda_1 = 1.2574$ ,  $\lambda_2 = 1.3378$ , and  $\lambda_3 = 1.1892$ , and  $\alpha_3 = .285$  and with initial densities  $N_1 = N_2 = N_3 = 10$  is illustrated in Fig. 1. The quantities  $x$ ,  $y_1$ , and  $y_2$  are  $x > 0$ ,  $y_1 = .8735$ , and  $y_2 = .9904$ . Because  $x > 0$  and both  $y_1$  and  $y_2$  are less than one the system is stable and all three



species persist with stationary states  $L_1=37.78$ ,  $L_2=141.85$ , and  $L_3=119.25$ . However, if the predator pressure on species two is decreased to  $Y_2=.001$ ,  $y_1=1.0568$  and  $y_2=.8928$ ; the first prey species will become extinct and only the second prey species will persist. Increasing the pressure on the second prey species to  $Y_2=.01$ ,  $y_1=.7823$  and  $y_2=1.7654$ . Therefore the second prey species will become extinct and the first persist. Therefore if two non-competing species occur together and a predator or parasite common to both is introduced, the model predicts that over a wide range of parameters one or the other of the prey species will become extinct. In field studies this unstable interaction might be mistakenly interpreted as competitive exclusion.

Stable state, competition present.-- If the parameters of the model are  $\alpha_1=.0005$ ,  $\alpha_2=.0007$ ,  $\beta_1=.0003$ ,  $\beta_2=.0005$ ,  $Y_1=.0020$ ,  $Y_2=.0035$ ,  $\alpha_3=.285$ ,  $\lambda_1=1.2574$ ,  $\lambda_2=1.3378$ ,  $\lambda_3=1.1892$ , then  $x > 0$ ,  $y_1 < 1$ ,  $y_2 < 1$ , and the system is stable with steady states  $L_1=72.13$ ,  $L_2=77.14$ , and  $L_3=99.10$ . In the absence of the predator this competitive interaction is also stable with steady states  $L_1=394.20$  and  $L_2=201.00$ . The presence of the predator has caused both species to reach equilibrium at much lower densities than if the predator were absent. If the predator pressures on both species are equal, i.e.  $Y_1=Y_2=.002$ ,  $x < 0$ ,  $y_1 > 1$ ,  $y_2 < 1$ , and only the second species of prey will persist even though the two species competitive interaction is stable. In fact in the vast majority of cases the three species system will be unstable even though the two prey competitive interaction may be deterministically stable.

Unstable stationary state.-- If the parameters of the model are  $\alpha_1=.0004$ ,  $\alpha_2=.0005$ ,  $\beta_1=.0008$ ,  $\beta_2=.0007$ ,  $Y_1=.001$ ,  $Y_2=.002$ , and the finite rates of increase as before, then  $x < 0$ ,  $y_1=1.01$ , and  $y_2=1.11$ . Because both  $y_1$  and  $y_2$  are greater than one, the stationary state is not stable and one species of prey or the other will become extinct depending on the initial densities of both prey species and the predator.

If initially  $N_1=N_2=N_3=10$ , prey species two will become extinct. This interaction is shown in Fig. 2. The paths to extinction with different initial densities are quite complicated compared with paths to extinction for the non-stable stationary state in the two species competition model (e.g. see Barnett, 1962, fig. 1).

Competition with one prey species always persisting.-- If the parameters of the model are  $\alpha_1=.0003$ ,  $\alpha_2=.0005$ ,  $\beta_1=.0005$ ,  $\beta_2=.0007$ ,  $\gamma_1=\gamma_2=.002$ , and the finite rates of increase as before, then  $\bar{x} < 0$ ,  $y_1=1.06$ , and  $y_2=.99$ . Only prey species two will persist.

### The Stochastic Model

The expected densities of the three species in the stochastic model, i.e.  $E [N_i(t+1) | N_1(t), N_2(t), N_3(t)]$  are the same as the deterministic values given by Eq. 5. If the birth rates  $b_i$  remain constant the variance of the density of the  $i$ th species is

$$\begin{aligned} \text{Var} [N_i(t+1) | N_1(t), N_2(t), N_3(t)] &= \left[ \frac{2b_i}{r_i(t)} - 1 \right] \left[ \lambda_i(t) - 1 \right] E [N_i(t+1)] \\ & \qquad \qquad \qquad \lambda_i(t) \neq 1 \\ &= 2b_i E [N_i(t+1)] \qquad \qquad \qquad \lambda_i(t) = 1 \end{aligned}$$

In the simulations of the discrete time process that follow, pseudo-random normal deviates with a zero mean and unit variance were generated using the GAUSS subroutine of the IBM Scientific Subroutine Package, Version III (1970).

No competition and a stable stationary state.-- If the parameters of the model are  $\alpha_1=.0005$ ,  $\alpha_2=.0007$ ,  $\beta_1=\beta_2=0$ ,  $\gamma_1=\gamma_2=.002$ ,  $\lambda_1=1.2574$ ,  $\lambda_2=1.3378$ ,  $\lambda_3=1.1892$ ,  $\alpha_3=.285$ ,  $b_1=.2577$ ,  $b_2=.2783$ , and  $b_3=.2521$ , the deterministic steady states are  $\bar{L}_1=37.78$ ,  $\bar{L}_2=141.25$ , and  $\bar{L}_3=119.25$ . The system is deterministically stable.

A simulation using these parameters started with initial densities  $N_1=N_2=N_3=10$  is shown in Fig. 3 up to  $t=400$ . The densities of all three species fluctuate considerably about their equilibrium values. Because of the nature of the model consistent periodical fluctuations are not expected, i.e. fluctuations in the population densities should have at most variable periods and amplitudes. To check this supposition serial correlations  $r_s$  were estimated as

$$r_s = \frac{\sum_{t=1}^{n-s} X_t X_{t+s} - \frac{\sum_{t=1}^{n-s} X_t \sum_{t=s+1}^n X_{t+s}}{n-s}}{\left[ \sum_{t=1}^{n-s} X_t^2 - \left( \sum_{t=1}^{n-s} X_t \right)^2 / n-s \right]^{\frac{1}{2}} \left[ \sum_{t=s+1}^n X_{t+s}^2 - \left( \sum_{t=s+1}^n X_{t+s} \right)^2 / n-s \right]^{\frac{1}{2}}}$$

where  $X_t$  is the density of the population at time  $t$  and  $X_{t+s}$  the population density at time  $t+s$  where  $s$  is a lag of  $s$  time periods. The serial correlation  $r_s$  represents the correlation of the population density at time  $t$  with the population density at time  $t+s$ . Lag periods of  $s=1$  to 50 were used and the serial correlations estimated. The serial correlations are plotted as a correlogram in Fig. 4. The serial correlations were estimated with  $n=400$ , i.e. from  $t=100$  to  $t=500$  after the series representing the population densities of the three species had reached the stationary point.

The correlograms of the three species are strikingly different. The correlogram of prey species two appears to damp down fairly rapidly, and the deviations of the correlogram around  $r_s=0$  are not consistent or larger than would be expected from sample fluctuations. However the correlogram of prey species one is surprising. The correlogram has not reached  $r_s=0$  even after a lag of 50 time intervals. This behavior can possibly be interpreted as an exceedingly long period

to each fluctuation of the density of prey species one or perhaps over 50 time intervals. In contrast the fluctuations of prey species two and the predator have fluctuations covering on the average only 10 to 15 time intervals. An alternative and possibly more reasonable interpretation of the first prey species is that the fluctuations are symptomatic of a stochastic process non-stationary in its mean. In fact the failure of the correlogram to decline to zero is characteristic of stochastic processes behaving as if they did not have a mean (Box and Jenkins, 1970). Therefore, if the fluctuations of prey species one are truly non-stationary in the mean, prey species one will fluctuate in abundance without any fixed mean value in spite of the stable stationary point predicted by the deterministic model. Also, if the fluctuations of prey species one are non-stationary, the drift of the series should eventually insure the extinction of the first prey species even though the system is deterministically stable. In the simulation, however, extinction had not occurred by  $t=400$  although the species approached extinction at least once. Perhaps in a stable one predator, two prey species system the influence of the commoner prey species and the predator population tends to damp fluctuations in the rarer prey species and cause the rarer prey species to behave as if it had no fixed mean abundance. In a natural situation this tendency would cause the rarer species of prey to have a much more stable population density, but possibly it would also insure the eventual extinction of the rarer prey species.

The correlogram of the predator is also interesting. Although the deterministic model does not predict a periodical fluctuation of the predator population, the correlogram of the simulation of the predator population shows a clear tendency for a periodical fluctuation of about 16 time intervals. Up to a lag of 50 time intervals there does not appear to be any tendency for the correlogram to damp down. To investigate lags of longer than 50 time intervals a spectral analysis of the population densities from  $t=100$  to  $t=500$  was carried out using methods described in Bartlett (1966). The spectrums of each of the three species are measures of the density of fluctuations of frequency  $f$  and period  $1/f$ . A sharp peak in the spectrum

is indicative of a true periodical component to the series while more rounded peaks indicate a periodical tendency of variable frequency or period, the variability of the period increasing as the width of the peak increases. Neither of the prey species populations showed any tendency for periodical fluctuations up to a period of 200 time intervals. Two hundred time intervals was the longest interval that could be investigated, i.e. it is the Nyquist folding frequency with 400 observations and time intervals equal to one. The predator population's spectrum, however, showed a strong sharp peak at a spectral frequency equivalent to 16 time intervals. If the model accurately represents a one predator, two prey interaction, both prey species should show irregular fluctuations and the fluctuations of the rarer species should be longer, more damped, and without a constant mean value than the fluctuations of the commoner prey species. In contrast the predator population should undergo regular fluctuations of a fairly constant period.

In the simulation in Fig. 3 prey species one approaches extinction at  $t=350$  to 400. In fact because of stochastic fluctuations the time to extinction of one of the prey species is always finite even though the deterministic model predicts that all three species will persist indefinitely. This is true even disregarding the apparent non-stationarity of the prey species one series. In this case the average time to extinction may be very long. However if  $\gamma_1=.007$ ,  $\gamma_2=.009$ , and the other parameters as above, the steady state stable densities are  $L_1=22.50$ ,  $L_2=6.86$ , and  $L_3=19.49$ . The probability of the rapid extinction of one prey species or the other is now relatively great. In 50 simulations carried to  $t=200$  both prey species persisted in only 20 of the simulations. The probability of extinction of one prey species or the other also depends on the initial densities of all three species even though the interaction is deterministically stable. In Table I the probabilities of prey species one surviving in those replicates out of 50 in which one prey species

or the other became extinct for different initial densities of the two prey species are listed. The population density of the predator population was initially always 10. Ninety-five percent confidence intervals for the probabilities are listed in parentheses following the probabilities. Because of the relatively small sample sizes, the confidence limits are rather wide, but the general trend is clear. In Table II the number of replicates out of 50 in which both prey species persisted until  $t=200$  are given. There is much heterogeneity in the table, but apparently both species survived until  $t=200$  most often if both species were started with equal densities.

Unstable steady state.-- If  $y_1$  and  $y_2 > 1$ , the deterministic model predicts that one prey species or the other will become extinct depending on the initial densities of the three species. In contrast the stochastic model associates a probability of survival with each prey species for each initial combination of densities of the three species. If  $\alpha_1 = .0004$ ,  $\alpha_2 = .0005$ ,  $\alpha_3 = .285$ ,  $\beta_1 = .0008$ ,  $\beta_2 = .0007$ ,  $\gamma_1 = .001$ ,  $\gamma_2 = .002$ ,  $\lambda_1 = 1.2574$ ,  $\lambda_2 = 1.3378$ ,  $\lambda_3 = 1.1892$ ,  $b_1 = .2577$ ,  $b_2 = .2783$ , and  $b_3 = .2521$ , then  $x < 0$ ,  $y_1 = 1.0105$ ,  $y_2 = 1.1142$ , and there is an unstable stationary point. If the initial predator density is 10, the probabilities of prey species one persisting based on 50 replicate simulations for several initial density combinations of the two prey species are listed in Table III. Because of the cost of the simulations each replicate was terminated at  $t=200$  if one prey or the other had not become extinct by then. In those replicates where both prey species had survived to  $t=200$  the species most likely to become extinct was listed as extinct. In most cases one prey species or the other was at such a low level by  $t=200$  that no great error should result from this truncation of the simulations. Also listed in Table III in parentheses are the observed mean times to extinction of one species or the other. These mean times to extinction are strongly biased because of the truncation of the simulations. This bias is particularly true of the density combinations where the number of persistences of both species is highest.

If the odds on survival of one prey species or the other are about even, the distribution of the observed times to extinction is approximately normal. If one species will almost always persist over the other, the distribution is piled up toward the 0 to 100 time intervals part of the frequency distribution. However, if the probabilities of extinction are in the neighborhood of 15 and 85 percent, the distribution is bimodal. In these simulations the species with the smaller probability of survival becomes extinct relatively fast in some of the replications, but in other replicates the species at the disadvantage will reach a density relative to the other species and the predator making the probabilities much more even and greatly lengthening the time to extinction for one prey species or the other. In field situation sets of observations on the same interaction may yield two different sets of observations and lead one to believe that two different competitive situations were occurring even though all of the interactions were generated by the same biological parameters.

One species always persists.-- If the parameters of the interaction are  $\alpha_1 = .0007$ ,  $\alpha_2 = .0005$ ,  $\beta_1 = .0005$ ,  $\beta_2 = .0008$ ,  $\gamma_1 = \gamma_2 = .002$ ,  $\alpha_3 = .285$ , and the finite rates of increase and birth rates the same as above, then  $y_1 = 1.0639$  and  $y_2 = .9494$ . The deterministic model predicts that prey species one should always become extinct and prey species two survive. However because of stochastic fluctuation prey species one does have a positive probability of survival greater than zero for any combination of initial densities, although for some combinations this probability may be exceedingly small. In Table IV these probabilities are listed for combinations of densities of the two prey species between 10 and 100. In Table IV the mean times to extinction for one prey species or the other are also listed.

In the density combinations investigated the probabilities of prey species one persisting are rather small, the probabilities increasing as the numerical advantage of the first prey species over the second increases. However, if the competitive interaction between the two prey species is made closer by using the

parameters  $\alpha_1 = .0003$ ,  $\alpha_2 = .0005$ ,  $\beta_1 = .0005$ ,  $\beta_2 = .0007$ , and the other parameters as above, then  $y_1 = 1.0639$ ,  $y_2 = .9872$ . Given these parameters the outcome of the interaction becomes much more unpredictable. If  $N_1 = N_2 = N_3 = 10$ , the estimated probability of prey species one surviving is zero based on 50 replicate simulations. If  $N_1 = 100$ ,  $N_2 = N_3 = 10$ , prey species two becomes extinct in 74 percent of the replicates. However, if  $N_1 = 100$ ,  $N_2 = 10$ , and  $N_3 = 50$ , prey species one will survive in only 42 percent of the replicates in contrast with 74 percent survival if  $N_3 = 10$ . In this particular situation the increase in the predator density appears to work against the first prey species. Finally if  $N_1 = 500$ ,  $N_2 = 10$ , and  $N_3 = 150$ , the probability of prey species one surviving is 88 percent. Therefore if two species compete and one species has a competitive advantage over the other, the superior species may still find it difficult to displace the other if its initial density is small compared to the established population of the first species. The addition of the predator to the system tends to compensate to some extent for the numerical advantage of the competitively inferior species. Therefore the higher the population density of the predator or parasite the greater the probability that the superior competitive species will displace the less competitive one.

Probability of the extinction of the predator first.-- In the deterministic model the predator will always survive provided it has a finite rate of increase greater than or equal to one. In the stochastic model there is a finite probability of the predator becoming extinct first, but in all of the cases so far discussed the probability has been exceedingly small. However, if the mean time to extinction of one of the three species is short, the probability of the extinction of the predator first may be relatively large. Simulations were run using the parameters  $\lambda_1 = 1.2574$ ,  $\lambda_2 = 1.3378$ ,  $\lambda_3 = 1.1892$ ,  $\alpha_1 = .010$ ,  $\alpha_2 = .012$ ,  $\beta_1 = .050$ ,  $\beta_2 = .060$ ,  $\alpha_3 = .285$ ,  $\gamma_1 = .070$ ,  $\gamma_2 = .080$ ,  $b_1 = .2577$ ,  $b_2 = .2783$ , and  $b_3 = .2521$ . The probabilities of the extinction first of all three species for different densities as determined from 50 replicates are listed in Table V. The initial density of the predator



population was always 10. Unlike the other cases studied stochastic fluctuations have caused the extinction of the predator first to be a significant possibility. The probability of the extinction of the predator first is largest if the two prey species are in approximately equal densities. The mean time to extinction of one of the three species in the interaction is very short (Table V). If one of the prey species is eliminated, the remaining predator-prey interaction is still stochastically quite unstable, although deterministically stable, and one would expect the relatively rapid extinction of either the predator or the prey population. Therefore an interaction defined by parameters similar to those above would exhibit either the rapid extinction of all three species or the elimination of the predator and one of the prey species.

#### Discussion

The primary purpose of this simplified model of a one predator, two prey species interaction is to generate hypotheses which hopefully may be tested. Some of these hypotheses are:

1. The two prey, one predator species interaction can be stable or unstable depending on the biological parameters defining the interaction. However, the interaction is generally unstable. The range of parameters allowing coexistence of all three species is small.
2. Deterministically the predator will always survive provided its finite rate of increase is greater than or equal to one.
3. If the parameters defining the effect of density on the rate of population growth are relatively large, the system breaks down exceedingly rapidly leading to the extinction of all three species or all but one of the prey species.

Therefore if the carrying capacity of the environment for each of the two prey species is low, the interaction will rapidly degenerate leaving only a single prey species or none at all.

4. The end result of this three species interaction is largely probabilistic over a wide range of parameters.
5. A prey species with a competitive advantage over a second species may still find it difficult to invade and displace the second prey species if the density of the second prey species is high. Increasing the density of the predator population tends to offset this effect.
6. If a stable two prey, one predator species interaction does exist, the fluctuations of the two prey species will be erratic. The fluctuations of the rarer prey species will be considerably more damped than those of the commoner species and apparently the fluctuations of the rarer prey species behave as if the series of abundances had no fixed mean. The predator population, in contrast, should fluctuate periodically, not erratically.
7. The introduction of a predator or parasite common to two non-competing species can, and perhaps usually does, lead to the extinction of one of the prey species even though both prey species would persist in the absence of the predator.

The parameter values used in the simulations were chosen to illustrate the possible outcomes of this three species interaction. Of course if we wish to compare the model and the predictions of the model to a real biological two prey, one predator interaction, we should know what parameter values are biologically reasonable. Unfortunately little experimental work has been done on this type of three species interaction. Hairston et al. (1968) carried out experiments utilizing two species of Paramecium and one or two predator species of the genera Woodruffia and Didinium. In all cases the breakdown of the three species interaction was rapid and only 13 of 50 replicates contained any Protozoa 13 days after the introduction of the predator or predators. In all of these 13 replicates one prey and

the predator had become extinct leaving a single prey species surviving in the replicates. Although these results are in general agreement with hypothesis three above, alternative models based on different assumptions could lead to the same conclusions. Only if it were possible to estimate the parameters of the model from the data gathered by Hairston et al. (1968) and to compare the experimental results with simulations generated by the model, could the validity of the model be tested. Utida (1953) created a three species experiment utilizing Callosobruchus chinensis and C. quadrimaculatus as the two prey species and Neocatolaccus mamezophagus as the parasite. Unfortunately he was unable to carry the experiment past the sixth generation and the results are inconclusive. The reality of the model could be increased by including the effect of time lags to changes in population density. However, the addition of time lags would make the estimation of the parameters considerably more complex not to mention of the analytical difficulty of working with the model. In addition provision might be made for protecting a proportion of the population of each of the prey species from predation. In a predator-prey interaction protecting a proportion of the prey population from predation tends to increase the stability of the system and undoubtedly this is also true of the two prey, one predator interaction.

The most important hypothesis generated by this study, however, is that in general the two prey, one predator interaction is not a stable one, although some parameter combinations do lead to the persistence of all three species. This hypothesis is interesting because Paine (1966) in a study of the diversity of an intertidal zone in Washington found that the removal of the top predator, a starfish, from the community lead to a rapid and marked decrease in the number of species in the community. Paine's observation, if formulated as a principle, would predict that the introduction of a predator into a community might allow the coexistence of two competing prey species in situations where one species would exclude the other if the predator were absent. Parrish and Salla (1970) formulated a deterministic continuous time model of a two prey, one predator interaction in an

attempt to illustrate this stabilizing effect. Unfortunately, however, the range of parameter values allowing persistence of both prey species in Parrish and Salla's model is no greater than the parameter range of the simple two competing species interaction (Cramer and May, 1972). The same conclusion is true of the three species and two species models studied in this paper, although the Parrish and Salla model and the model of this paper are not directly comparable because of differences in the specification of the predator portion of the system of equations. The predictions of the three species model of this paper are in agreement with the conclusions of May (1971) who postulates that increasing the number of species and interactions between species in a community does not in general increase stability and in fact usually decreases the stability of the system in terms of the persistence of species.

One can wonder then why Paine (1966) observed that the presence of a dominant predator increases the number of species that can survive in a community. There are at least two possible explanations of the differences between Paine's observation and the hypotheses of the models. Firstly the simple multi-species models may have little biological reality. These models are only approximations ignoring the environmental fluctuations of the ecosystem, the dispersion patterns of the species, and the intrinsic biological characteristics unique to each species. The second possible explanation is the problem of observability. If multiple species interactions are generally unstable, the only interactions we will observe in established communities will be the stable ones, the unstable interactions having dissolved long ago. Undoubtedly both factors are to some extent responsible for the discrepancy between theory and observation.

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## Appendix I

The stability properties of the two prey, one predator model are slightly more complex than those of either the one prey, one predator or the two competing species models. In order to study the stability properties of this particular three species system of equations consider the analogous system of differential equations:

$$\frac{dN_1}{dt} = (r_1 - a_1 N_1 - b_1 N_2 - c_1 N_3) N_1$$

$$\frac{dN_2}{dt} = (r_2 - a_2 N_2 - b_2 N_1 - c_2 N_3) N_2$$

$$\frac{dN_3}{dt} = \left( r_3 - a_3 \frac{N_3}{N_1 + N_2} \right) N_3$$

A stationary point where  $\frac{dN_1}{dt} = \frac{dN_2}{dt} = \frac{dN_3}{dt} = 0$  is:

$$L_1 = \frac{r_1 \left( a_2 + \frac{c_2 r_3}{a_3} \right) - r_2 \left( b_1 + \frac{c_1 r_3}{a_3} \right)}{a_1 a_2 - b_1 b_2 + \frac{c_1 r_3}{a_3} (a_2 - b_2) + \frac{c_2 r_3}{a_3} (a_1 - b_1)}$$

$$L_2 = \frac{r_2 \left( a_1 + \frac{c_1 r_3}{a_3} \right) - r_1 \left( b_2 + \frac{c_2 r_3}{a_3} \right)}{a_1 a_2 - b_1 b_2 + \frac{c_1 r_3}{a_3} (a_2 - b_2) + \frac{c_2 r_3}{a_3} (a_1 - b_1)}$$

$$L_3 = \frac{r_3 (L_1 + L_2)}{a_3}$$

Let  $N_1 = L_1(1+u_1)$ ,  $N_2 = L_2(1+u_2)$ , and  $N_3 = L_3(1+u_3)$ . For  $u_1$ ,  $u_2$ , and  $u_3$  all sufficiently small a linear approximation of the system of equations in the deviations is

$$Du_1 = -a_1 L_1 u_1 - b_1 L_2 u_2 - c_1 L_3 u_3$$

$$Du_2 = -a_2 L_2 u_2 - b_2 L_1 u_1 - c_2 L_3 u_3$$

$$Du_3(L_1 + L_2) = r_3 L_1 u_1 + r_3 L_2 u_2 - a_3 L_3 u_3$$

where  $D$  is the operator  $d/dt$ . The auxiliary equation of this linear system is

$$\begin{vmatrix} D+a_1 L_1 & b_1 L_2 & c_1 L_3 \\ b_2 L_1 & D+a_2 L_2 & c_2 L_3 \\ -r_3 L_1 & -r_3 L_2 & (L_1+L_2)D+a_3 L_3 \end{vmatrix}$$

or

$$D^3 + D^2 \left[ r_3 + a_1 L_1 + a_2 L_2 \right] + D \left[ r_3 (a_1 L_1 + a_2 L_2) + \frac{r_3^2}{a_3} (c_1 L_1 + c_2 L_2) + L_1 L_2 (a_1 a_2 - b_1 b_2) \right] + a_3 L_1 L_2 L_3 \left[ a_1 a_2 - b_1 b_2 + \frac{r_3 c_1}{a_3} (a_2 - b_2) + \frac{r_3 c_2}{a_3} (a_1 - b_1) \right] = 0$$

If the system is to be stable, the auxiliary equation must have three real negative roots or one real negative root and a pair of complex conjugate roots with negative real parts. In this case all of the coefficients of the polynomial will be positive and the roots therefore all negative only if the expression

$$x = a_1 a_2 - b_1 b_2 + \frac{r_3 c_1}{a_3} (a_2 - b_2) + \frac{r_3 c_2}{a_3} (a_1 - b_1) > 0$$

is true. This expression is the denominator for the steady state expressions of

prey species one and two. Theoretically some constraints are also necessary on the third coefficient of the auxiliary equation, but within the reasonable ranges of  $a_1, a_2, b_1, b_2$  the third coefficient is always positive.

Define the following quantities:

$$y_1 = \frac{r_2(b_1 + \frac{c_1 r_3}{a_3})}{r_1(a_2 + \frac{c_2 r_3}{a_3})}, \quad y_2 = \frac{r_1(b_2 + \frac{c_2 r_3}{a_3})}{r_2(a_1 + \frac{c_1 r_3}{a_3})}$$

There are four possible outcomes of this three species interaction:

- |                              |  |
|------------------------------|--|
| 1. $x > 0; y_1, y_2 < 1$     | Interaction stable, all three species persisting   |
| 2. $x < 0; y_1 < 1, y_2 > 1$ | Prey species one persists and prey species two becomes extinct   |
| 3. $x < 0; y_1 > 1, y_2 < 1$ | Prey species two persists and prey species one becomes extinct   |
| 4. $x < 0; y_1 > 1, y_2 > 1$ | Unstable stationary point, either prey species one or two becoming extinct depending on the initial densities of the three species |

The stability conditions for the discrete time model are the same as those of the continuous model with appropriate parameter substitutions.



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