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ALLEE EFFECT AND A CATASTROPHE MODEL OF POPULATION DYNAMICS

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Abstract. Some assumptions of Logistic Equation are frequently violated. We applied the Allee effect to the Logistic Equation so as to avoid these unrealistic assumptions. Following basic principles of Catastrophe theory, this new model is identical to a Fold catastrophe type model. An ecological interpretation of the results is provided.

1. Introduction. The original example of the Allee Effect was the observation that goldfish grew faster in water that had previously contained other goldfish than in water that had not[1]. Although the Allee Effect is well known nowadays, the concept has a range of meanings. In this paper "Allee Effect" strictly refers to inverse density dependence at low density. Several hypothetical mechanisms for the Allee Effect have been proposed, including difficulty in finding mates, reduced defenses against predators and decreased foraging efficiency at low population densities [2][3]. These mechanisms can be classified into three main categories. The first involves genetic inbreeding and loss of heterozygosity leading to decreased fitness. The second pertains to demographic stochasticity, as illustrated by the failure of many biological control programmes that released insufficient numbers of control insects. The third category concerns the reduction in cooperative interactions when there are fewer individuals. An example of the action of such mechanisms is provided by the Glanville fritillary butterfly which displays decreasing mating success with decreasing population density [4].(See Fig.1).Previous work by Ma and Ting [5] found similar evidence of increasing fecundity and decreasing egg mortality with increasing population density in low density populations of the Oriental Migratory Locust (See Fig. 2).

2. Catastrophe theory Catastrophe theory was introduced by the French mathematician R, Thom . Several papers dealing with the application of this theory to ecological modeling have been published[6]-[8]. Three axioms of observed behavior should be included in such applications: (1) there exists a stable equilibrium condition; (2) there is a threshold for a stimulating factor that triggers a fast departure from equilibrium; (3) there is a subsequent return to the original equilibrium. The major requirement for the system is the existence of some function$V(x;p)$. such that when p is held fixed,$V(x;p)$ is minimized as the system evolves. The effect of the minimization of $V(x;p)$ is that for any fixed p, the system will move to some equilibrium x^*. In terms of familiar differential equations, for fixed p the system evolves according to

$$dx/dt = f(x;p)$$

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to some state x^* when $f(x^*;p) = 0$. In many applications $f(x;p)$ can be equated with the negative of the gradient of$V(x;p)$ with respect to x. There are only seven elementary catastrophes for control variables less than or equal to 4 [9].

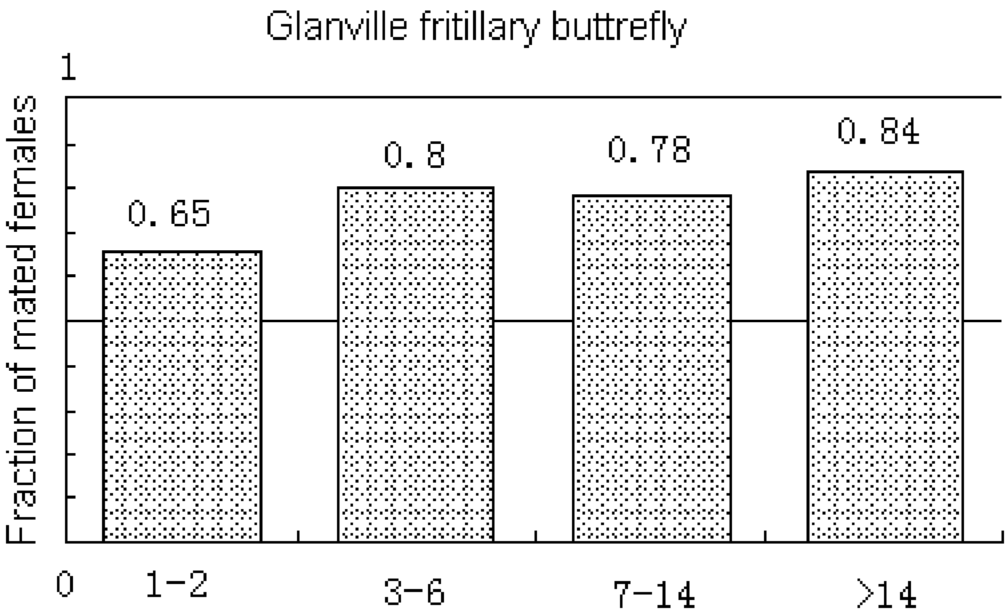

Fig1. Population size (larval group)
(Kuussaari, et al 1998)

3.Derivation of a catastrophe model of population dynamics with Allee Effect E. C. Pielou pointed out that some assumptions of the Logistic Equation are frequently false, for example (1) that population growth rates are density-dependent even at the lowest densities. It may be more reasonable to suppose that there is a threshold density below which individuals do not interfere with one another. (2) That females in a sexually reproducing population always find mates, even when the population density is low[10]. We should modify the model so as to avoid these two unrealistic assumptions. We start from the Logistic Equation

$$(1/N)dN/dt = (a - bN) = F(N)$$

Now suppose that by applying Taylor's theorem, $F(N)$ may be expanded as a power series in N so that

$$(1/N)dN/dt = a_0 + a_1N + a_2N^2 + - - -$$

If we incorporate the Allee Effect into the equation, the simplest formula for $F(N)$ to satisfy the condition is

$$F(N) = (1/N)dN/dt = -cN^2 + bN - a \quad (a, b, c > 0)$$

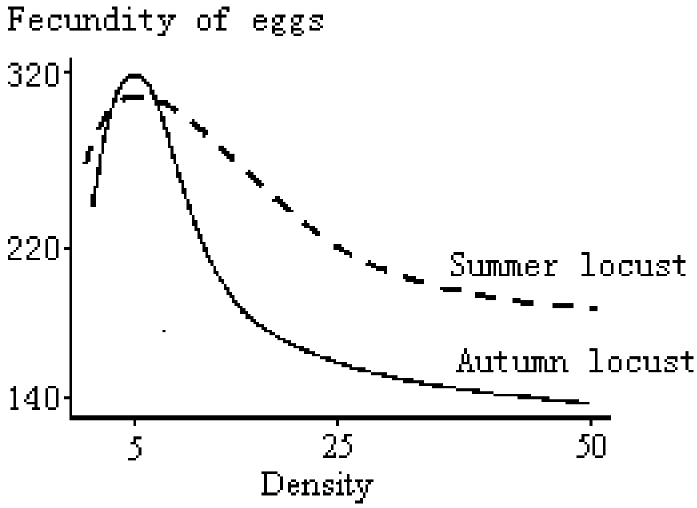

Figure 2.a The relation between fecundity and density (Ma and Ting 1965)

Figure 2.b The relation between egg mortality and density (Ma and Ting 1965)

The roots of $F(N)$ are $\frac{-b\pm\sqrt{b^2-4ac}}{-2c}$, b and c should satisfy the condition:

$$\frac{dF(N)}{dN} = b - 2cN > 0$$

when N is small. Actually, this mechanism is the Allee Effect. We follow the basic principle of Catastrophe theory

$$(1/N)dN/dt = F(N) = -cN^2 + bN - a \tag{1}$$

Then according to Table 1, $\bigtriangledown_x V(x,p) = -cN^2 + bN - a = 0$ then

$$(N - a_1)^2 - a_2 = 0, \tag{2}$$

$a_1 = \frac{b}{2c}$, $a_2 = \frac{b^2-4ac}{4c^2}$. If we consider N as behavior variable and a_2 as a control variable. This model is identical to Fold catastrophe type models (See Table 1).

4. Conclusion, interpretation and discussion Another modification of the Logistic Equation incorporating the Allee Effect has been presented (Courchamp et al 1999). This model is actually quite similar to the above equation (1). Because

$$\begin{aligned} F(N) = (1/N)dN/dt &= r(1 - N/K)(N/K_{\_} - 1) \\ &= r[-\frac{N^2}{KK_{\_}} + N/K_{\_} - (1 - N/K)] \\ &= r[-\frac{N^2}{KK_{\_}} + N(1/K_{\_} + 1/K) - 1]. \end{aligned}$$

Comparing this function with equation(1). Actually,

$$c = \frac{r}{KK_{\_}}, \quad b = r/K + r/K_{\_}, \quad and \quad a = r$$

Now we go back to the catastrophe model of equation (2). The control variable a_2, in this case, should be:

$$a_2 = \frac{b^2 - 4ac}{4c^2} = [(r/k_{\_} + r/K)^2 - 4r\frac{r}{KK_{\_}}]/[4(\frac{r}{KK_{\_}})^2] = \frac{(K - K_{\_})^2}{4}$$

$$a_1 = \frac{b}{2c} = \frac{r(1/K + 1/K_{\_})}{2\frac{r}{KK_{\_}}} = \frac{(K + K_{\_})}{2}$$

Referring to Zeeman [9], the manifold of this fold catastrophe model is shown in Fig. 3. When a population goes below $K_{\_}$, it will probably go to extinction. Lowered population growth rate with decreasing density, i.e. the Allee Effect, causes the population's extinction. A well documented example of the extinction of an isolated population in which the Allee Effect was involved is the disappearance of the middle-spotted woodpecker Dendrocopos medius from Sweden in 1982 [12].

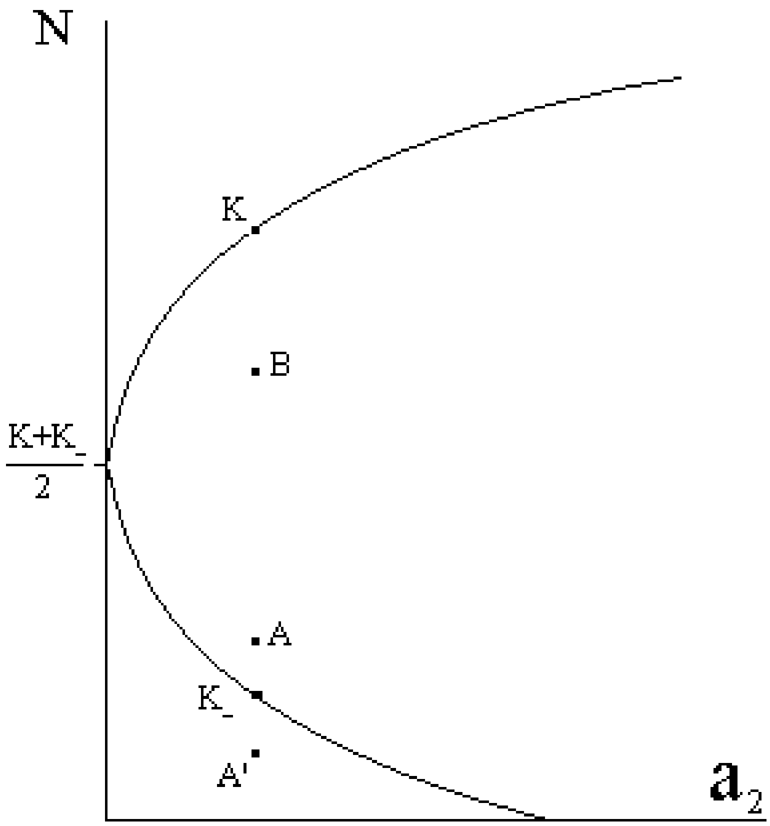

Fig.3: Manifold of the fold catastrophe model control variable $a_2 = (K - K\_)^2/4$ and its bifurcation set consists of a single point:$a_2 = 0, N = (K + K\_)/2$

Extinction induced by low population density is a particularly worrying threat for species with highly evolved sociality. Besides, individual development and physiology involve random factors, such as the sex of offspring. Hence there is a finite probability that all individuals in a population may die in the same unit of time. This probability of a population's extinction mainly depends on the current population size (small populations are most vulnerable), mean survival rate, and the variance in the survival rate among individuals. This demographic stochasticity poses a significant threat to the survival of very small populations.In different environmental conditions, logistical growth model will cause complex results [13]. Probabilities of birth and death in natural populations are typically affected by environmental factors with more or less correlated effects on many individuals. Such correlated stochasticity, or environmental stochasticity, will increase the variance in survival rate between individuals. This has the same effect as reducing population size and therefore also reduces a population's probability of survival. If both of these stochastic factors drive the population from A to A', (see Fig. 3), then the population will become extinct. Catastrophe theory deals with shifts in equilibrium or attractor points on the system level, and there is much evidence that such shifts take place in ecosystems that are exposed to gradual changes in climate, nutrient loading, habitat fragmentation or biotic exploitation. Studies on lakes, coral reefs, oceans, forests and arid lands have shown that smooth change can be interrupted by sudden drastic switches to a contrasting state. Recent studies show that a loss of resilience paves the way for a switch to alternative states [8]. In this paper, K and K_- actually represent environmental factors. When the control variable a_2 goes to zero, then $K_- = K$, the equation becomes

$$(1/N)dN/dt = -r(1 - N/K)^2,$$

which has only one equilibrium point $N = K$.The population will go to extinction eventually. The system have no resilience at all.

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REFERENCES

[1] Allee. W. C., *Animal aggregations.*, A Study in general sociobiology.Univ. of Chicago Press, Chicago (1931.).

[2] Saether, B. E., Ringsby, T. H. and Rϕskaft, E., *Life history variation, population processes and priorities in species conservation: towards a reunion of research pazadigms.*, OIKOS **77** (1996), 217-226.

[3] Fowler, C. W. and Baker, J. D. Rept., *A review of animal population dynamics at extremely reduced population levels.*, Int. Whaling Comm. **41** (1991), 545-554.

[4] Kuussaari, M. Saccheri, I., Camara, M and Hanski, I., *Allee effect and population dynamics in the Glanville fritillary butterfly.*, OIKOS **82** (1998), 384-392.

[5] Ma, Shihchun and Ting, Yanchin, *The regulatory mechanism in population fluctuations of the oriental migratory locust*, Acta Zoologica Sinica **17** (1965), 276-281.

[6] Kempf, J., *Multiple steady states and catastrophe in ecological models*, ISEM Journal **2** (1980), 55-80.

[7] Jones, D. D., *New directions in the analysis of ecological systems.*, In Simulation councils proceedings series. The application of catastrophe theory to ecological systems. **2** (1975).

[8] M. Scheffer, S. Carpenter, J. A. Foley, C. Folke & B. Walker, *Catastrophic shifts in ecosystems*, Nature **413** (2002), 11.

[9] Zeeman, E. C, *Catastrophe theory*, Scientific American **234** (1976), 65-83.

[10] Pielou, E. C., *Mathematical ecology*, John Wiley & Sons. Inc. (1977).

[11] Courchamp, F., Clutton-Brock, T. and Grenfell, B., *Inverse density dependence and the Allee effect*, TREE **14** (1999), 405-410.

[12] Petersson, B., *Extinction on an isolated population of the middle-spotted woodpecker Dendrocopus medius in Sweden and its relation to genome theories on extinctions*, Biological Conservation **32** (1985), 335-353.

[13] Tang X.H. and Zou X., *A 3/2 stability result for a regulated logistic growth model.*, Discrete and Continuous Dynamical Systems:B **2** (2002), 265-278.

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