

EFFECT OF AGGREGATION ON THE REPRODUCTIVE RATE OF POPULATIONS

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INTRODUCTION

Insects often live in resource patches which distribute contagiously. Moreover, the number of insects in each resource patch may also vary widely, i.e., insect distribution per resource patch may be also contagious. Thus, three kinds of distributions can be considered: patch distribution, insect distribution per patch and the absolute distribution of insects which is the joint product of the former two. Among these three, insect distribution per resource patch seems to be the most important one, because the reproductive rate of insects is more likely to be determined by the interaction between the insects and their resource patches. Several theoretical models have been developed to analyze the effect of such a spatial distribution on population dynamics. DE JONG (1979), KUNO (1983) and IVES and MAY (1985) have clearly shown by applying difference equations using the negative binomial distribution that aggregation reduces the equilibrium density and enhances the stability of population dynamics. KUNO (1988) proposed a differential equation based on IWAO (1968)'s \bar{n} - m relationship or TAYLOR (1961)'s power law relationship which are more realistic spatial relations than the negative binomial distribution with common k . This model also shows the effects of aggregation on the reduction of the equilibrium density of a population. However, it remains to be determined whether this phenomenon is universal or specific to the assumptions put forward in these models. The purpose of this note is to provide more general explanations on the effect of aggregation using data based on the entomological literature.

MODEL

Model structure

I consider a population living in an environment which contains k resource patches. Generations are discrete. Each adult enters one of these patches for reproduction. Let n_i be the number of adults which reproduce in the i th patch and m be the average of n_i . The reproductive rate of these adults is assumed to be $f(n_i)$ as a function of n_i . Then the total reproductive rate of the population (abbreviated *TRR*) is:

$$TRR = \frac{\sum_{i=1}^k \{n_i f(n_i)\}}{\sum_{i=1}^k n_i} \tag{1}$$

The value of *TRR* depends not only on the average density *m* but also on the distribution of *n_i*.

Numerical example

First, I illustrate the problem by numerical examples. One example of *f(n)* is given by Fig. 1. If each patch is not too small, the reproductive rate has a maximum value when the density is low (range A in Fig. 1). Above this range, the reproductive rate will decrease and approach zero as the density increases (rangs B and C in Fig. 1).

Table 1 shows some examples of the combination of *n_i* and the *TRR* value. In the case 1 in Table 1, all *n_i*'s equal 2 and *TRR*=*f(m)*=8. In cases 2 and 3, *n_i* is variable with the avarage value of 2. In these cases, the values of *TRR* are smaller than those of *f(m)*. Similar results are obtained when *n_i* becomes variable with an average value of 4 (cases 4, 5 and 6). When *m*=6, however, opposite results are obtained. Under these conditions, the population becomes extinct when the distribution is uniform, because all the patches deteriorate (case 7). However, when the distribution is aggregated, a fraction of individuals are able to survive in some patches in which the density happens to be low. Thus, the value of *TRR* becomes larger than that of *f(m)* and the population can be maintained (cases 8 and 9).

General approximation

f(n) is a discrete function where *n* is a positive integer. When the spatial distribution is completely uniform, the value of *TRR* lies on the lines connecting (0, *f(1)*) and adjacent (*m*, *f(m)*)'s (*m*=1,2,...) which is illustrated in Fig. 1. If *f(n)* changes gradually

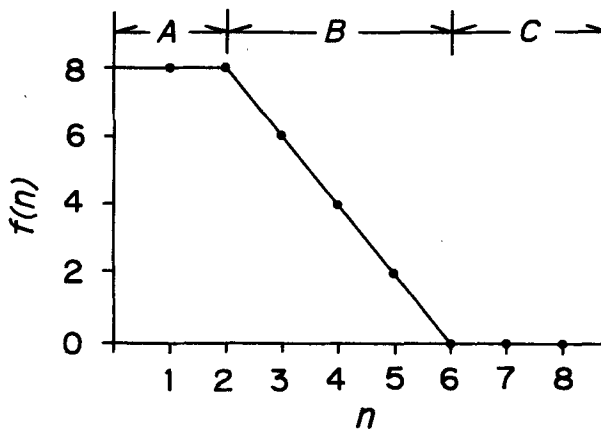


Fig. 1. A hypothetical example of the reproductive rate function *f(n)*.

Table 1. Numerical examples of the combination of n_i and the TRR value. $f(n)$ is assumed to take the values shown in Fig. 1.

case no.	m	n_i	TRR
1	2	2 2 2 2 2 2 2 2 2 2 2 2	8.0
2	2	1 2 3 1 2 3 1 2 3 1 2 3 2	7.1
3	2	1 3 1 3 1 3 1 3 1 3 1 3	6.5
4	4	4 4 4 4 4 4 4 4 4 4 4 4	4.0
5	4	3 4 5 3 4 5 3 4 5 3 4 5 4	3.7
6	4	3 5 3 5 3 5 3 5 3 5 3 5	3.5
7	6	6 6 6 6 6 6 6 6 6 6 6 6	0
8	6	5 6 7 5 6 7 5 6 7 5 6 7 6	0.5
9	6	5 7 5 7 5 7 5 7 5 7 5 7	0.83

as the density increases, we can approximate this discrete function by a smooth continuous function connecting the discrete values. To examine the effect of aggregation on TRR analytically, I adopt here such an approximate smooth function as $f(n)$. Then, we can approximate the equation (1) using TAYLOR's expansion with respect to m assuming that the function $f(n)$ is continuous and differentiable:

$$\begin{aligned}
 TRR &= \overline{f(m)} + \frac{1}{m} \text{cov}(n_i, f(n_i)) \\
 &\simeq f(m) + \frac{1}{2} \text{var}(n_i) f''(m) + \frac{1}{m} \text{var}(n_i) f'(m) \\
 &= f(m) + \text{var}(n_i) \left\{ \frac{1}{m} f'(m) + \frac{1}{2} f''(m) \right\}, \tag{2}
 \end{aligned}$$

where $\text{cov}(n_i, f(n_i))$ denotes the covariance between n_i and $f(n_i)$, $\text{var}(n_i)$ denotes the variance of n_i , $f'(m)$ and $f''(m)$ denote the differential coefficients of $f(n)$ of first and second order when $n=m$, respectively. Let $F(n)$ be the number of offspring in each patch, i.e., $nf(n)$. Then, we can approximate TRR by another formula:

$$TRR \simeq f(m) + \text{var}(n_i) \left\{ \frac{F''(m)}{2m} \right\}, \tag{3}$$

where $F''(m)$ denotes the differential coefficients of $F(n)$ of second order when $n=m$.

APPLICATIONS

BELLOWS (1981) compared the descriptive ability of several difference equations and concluded that the equation of MAYNARD SMITH and SLATKIN (1973) is most suitable:

$$f(n) = \frac{c}{1 + (an)^b}, \tag{4}$$

Table 2. Parameter values estimated by fitting equation (4) to the data of reproductive rate based on entomological experiment.

species	a	b	c	density range of experiment	n_{thr}	Authors
(a) <i>Trichogramma evanescens</i>	0.146	1.955	18.68	50	12	Salt (1936)
(b) <i>Callosobruchus chinensis</i>	0.0148	1.535	21.70	768	186	Utida (1941)
(c) <i>Heterospilus prosopidis</i>	0.1034	1.245	24.92	96	57	Utida (1944)
(d) <i>Trichogramma japonicum</i>	0.0525	1.847	4.920	128	37	Kuno (1962)
(e) <i>Cryptolestes</i>	0.0421	1.170	29.36	128	none	Varley et al. (1973)
(f) <i>Cathartus</i>	0.0834	1.125	47.78	128	none	Varley et al. (1973)

where a, b and c are constants. I applied this equation to the data of reproductive rate obtained by experiments reported in entomological literatures. Table 2 lists the parameters estimated by fitting $F(n)$ to the mean of replicates using the least square method. The number of female adults is used for parasitic wasps (a, c and d), while the total population size including both sexes is used for others (b, e and f). Fig. 2 shows two typical examples of fitted curves and the corresponding values of $F''(n)/(2n)$, i.e., the values of $f'(n)/n + f''(n)/2$. In the data of *C. chinensis*, there is the optimal density n_{max} which maximizes $F(n)$. This type of competition was called scramble-type competition by NICHOLSON (1954). In contrast, for *Cryptolestes*, $F(n)$ seems to increase monotonically approaching asymptotic maximum value as the density increases. This type of competition was called contest-type competition.

Since the value of $F(n)$ must approach zero for quite large n , the value of $F'(n)$ must be nearly zero for quite large n . In the scramble-type competition, however, the value of $F'(n)$ is negative for n a bit greater than n_{max} . In some density range greater than n_{max} , therefore, $F'(n)$ must increase to approach zero as the density increases and

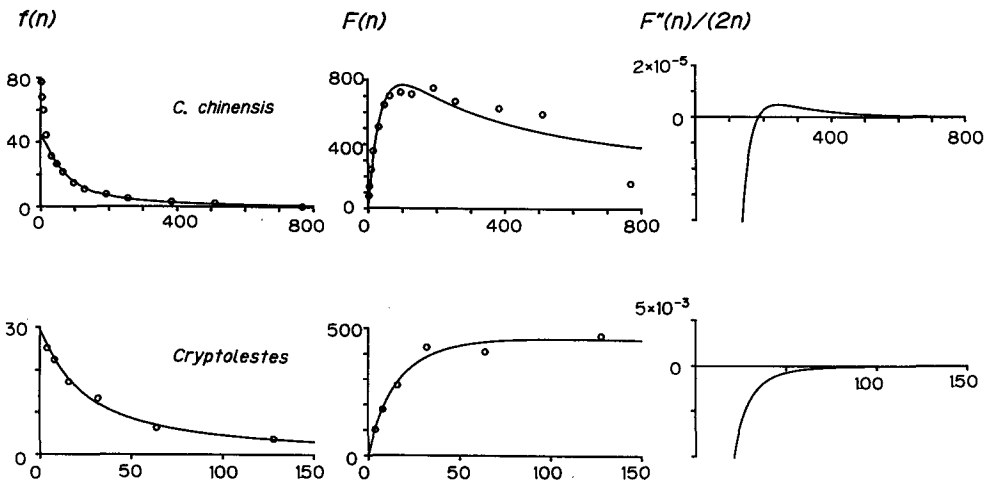


Fig. 2. Two typical examples of the effects of aggregation on the density dependency in reproduction.

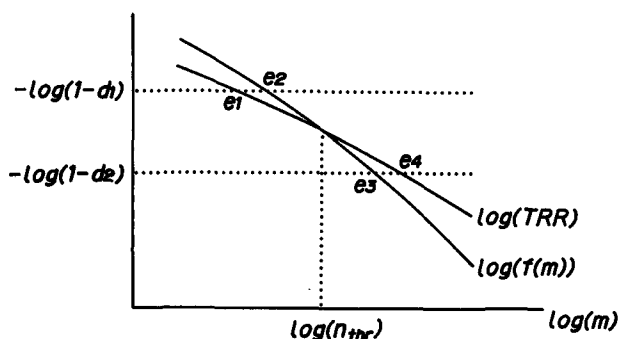


Fig. 3. Illustrated relationship between total reproductive rate TTR and $f(m)$ when $f(n)$ shows a scramble-type competition. Horizontal axis corresponds to the logarithm of mean population per patch. Vertical axis corresponds to the logarithm of reproductive rate. When there is additional density independent mortality d_1 , the new equilibrium density can be obtained at the point where the reproductive rate curve intersects horizontal line of $-\log(1-d_1)$.

$F''(n)$ must be a positive value. On the other hand, $F''(n)$ is a negative value in the density range near n_{max} . So, there must be a threshold density $n_{thr}(n_{thr} > n_{max})$ where $F''(n)$ changes from a negative to a positive value. TTR crosses $f(m)$ at n_{thr} which is illustrated in Fig. 3. If there is additional density independent mortality d_1 , the reproductive rate becomes $TTR(1-d_1)$, and the equilibrium density is calculated by $TTR(1-d_1)=1$. This can be rewritten as $\log TTR = -\log(1-d_1)$. Thus, the new equilibrium density can be obtained as m of the intersection of $\log TTR$ and the horizontal line of $-\log(1-d_1)$. The equilibrium density corresponds to the e_2 point in Fig. 3 when the spatial distribution is completely uniform, but to the e_1 point when the distribution is aggregated. Therefore, if the equilibrium point lies in the range smaller than n_{thr} when the spatial distribution is uniform, aggregation reduces the equilibrium density. On the other hand, if the equilibrium density is larger than n_{thr} when the

Table 3. Parameter values estimated by fitting equation (5) to the data of survival rate based on entomological experiment.

species	a	b	c'	density range of experiment	n_{thr}	Authors
(g) <i>Rhizopertha dominica</i>	0.792	1.197	1.496	20	9.5	Crombie (1944)
(h) <i>Sitotroga cerealella</i>	0.848	1.160	1.463	20	11.2	Crombie (1944)
(i) <i>Plodia interpunctella</i>	0.00896	4.427	0.732	250	124	Snyman (1949)
(j) <i>Lucilia cuprina</i>	0.0274	3.203	0.808	240	45	Nicholson (1954)
(k) <i>Musca domestica</i>	0.000643	4.977	0.678	2560	1687	Sullivan & Sokal (1963)
(l) <i>Drosophila melanogaster</i>	0.00646	3.037	0.845	300	194	Miller (1964)
(m) <i>Drosophila simulans</i>	0.00717	6.799	0.728	300	146	Miller (1964)
(n) <i>Stegobium paneceum</i>	0.110	0.950	0.711	512	none	Bellows (1981)
(o) <i>Lasioderma serricorne</i>	0.0114	7.53	0.806	1024	91	Bellows (1981)
(p) <i>Tribolium confusum</i>	0.0116	3.12	0.610	130	107	Bellows (1981)
(q) <i>Tribolium castaneum</i>	0.0149	4.21	0.800	130	75	Bellows (1981)

distribution is uniform, aggregation leads to the increase of equilibrium density. For example, if additional weak density-independent mortality d_2 occurs, the equilibrium density corresponds to the e_3 point when the distribution is uniform, but to the e_4 point when the distribution is aggregated.

On the other hand, as $F''(n)$ is always negative in contest-type competition, the reproductive rate always decreases and the equilibrium density always decreases as the spatial distribution per experimental unit becomes aggregated in this case.

We can also use the density dependent survival rate $s(n)$ to analyze the effect of aggregation, assuming that the number of (female) eggs per female is constant and the survival rate in other stages is constant irrespective of the density. To illustrate, the following equation was fitted to the data of the survival rate in entomological literatures:

$$s(n) = \frac{c'}{1 + (an)^b} \quad (5)$$

Parameter values listed in Table 3 were estimated using the least square method except for the cases of (n), (o), (p), and (q) where the parameters were taken from the report of BELLOWS (1981). In many cases, the curve of the survival rate shows a scramble-type competition and, therefore, TRR is expected to cross $s(m)$.

DISCUSSION

Equation (1) is a general expression for the reproductive rate of a population in a patchy environment. DEJONG (1979) and KUNO (1983) analyzed mainly special cases of this expression where $f(n) = be^{-an}$ in the former and $f(n) = ba^{n-1}/n$ in the latter (a and b are constants). In this paper, to examine the effects of spatial distribution without assuming a simple form of $f(n)$ nor special distribution pattern, an approximate equation was applied to the data of reproductive rate and survival rate. This equation does not predict the effects of aggregation on the stability of population dynamics precisely. However, if $F(n)$ shows scramble-type competition as reported in the entomological literature, there is a threshold density n_{thr} where TRR crosses $f(m)$. The differential coefficient of TRR in a logarithmic scale (i.e., $d \log TRR / d \log m$) is larger than that of $f(m)$ at least at the density n_{thr} (see Fig. 3). Generally, local stability is clearly related to the differential coefficient of TRR in a logarithmic scale. If the value of $d \log TRR / d \log m$ near the equilibrium density lies between -1 and 0 , the population monotonically approaches the equilibrium density after a small disturbance in the equilibrium state. If it lies between -2 and -1 , the population shows damping oscillations. If it lies below -2 , the equilibrium point is locally unstable. So, we can expect that the local stability is enhanced at least at the density n_{thr} when the completely uniform distribution turns into a slightly aggregated distribution.

SUMMARY

The effect of spatial distribution on the reproductive rate of a population was examined by applying an approximate equation to several data based on the entomological literature. This study suggests that aggregation generally reduces the equilibrium level of the population density if the population density is not very high.

ACKNOWLEDGMENTS: I wish to express my sincere thanks to Prof. E. KUNO of Kyoto University and Drs. M. SHIYOMI and E. YANO of National Institute of Agro-Environmental Sciences for their invaluable comments on the manuscript.

REFERENCES

- BELLOWS, T. S. (1981) The descriptive properties of some models for density dependence. *J. Anim. Ecol.* **50**: 139–156.
- CROMBIE, A. C. (1944) On intraspecific and interspecific competition in larvae of graminivorous insects. *J. Exp. Biol.* **20**: 135–151.
- DE JONG, G. (1979) The influence of the distribution of juveniles over patches of food on the dynamics of a population. *Neth. J. Zool.* **29**: 33–51.
- IVES, A. R. and R. M. MAY (1985) Competition within and between species in a patchy environment: Relations between microscopic and macroscopic models. *J. Theor. Biol.* **115**: 65–92.
- IWAO, S. (1968) A new regression method for analyzing the aggregation pattern of animal populations. *Res. Popul. Ecol.* **10**: 1–20.
- KUNO, E. (1962) The effect of population density on the reproduction of *Trichogramma japonicum* ASHMEAD (Hymenoptera: Trichogrammatidae). *Res. Popul. Ecol.* **9**: 47–59.
- KUNO, E. (1983) Factors governing dynamical behaviour of insect populations: a theoretical inquiry. *Res. Popul. Ecol. Suppl.* **3**: 27–45.
- KUNO, E. (1988) Aggregation pattern of individuals and the outcomes of competition within and between species: Differential equation models. *Res. Popul. Ecol.* **30**: 69–82.
- MAYNARD SMITH, J. and M. SLATKIN (1973) The stability of predator-prey system. *Ecology* **54**: 384–391.
- MILLER, S. S. (1964) Larval competition in *Drosophila melanogaster* and *D. simulans*. *Ecology* **45**: 142–148.
- NICHOLSON, A. J. (1954) An outline of the dynamics of animal populations. *Aust. J. Zool.* **2**: 9–65.
- SALT, G. (1936) Experimental studies in insect parasitism. IV. The effect of superparasitism on populations of *Trichogramma evanescens*. *J. Exp. Biol.* **13**: 363–375.
- SNYMAN, A. (1949) The influence of population densities on the development and oviposition of *Plodia interpunctella* HÜBN. (Lepidoptera). *J. Ent. Soc. S. Africa* **12**: 137–171.
- SULLIVAN, R. L. and R. R. SOKAL (1963) The effect of larval density on several strains of housefly. *Ecology* **44**: 120–130.
- TAYLOR, L. R. (1961) Aggregation, variance and the mean. *Nature* **189**: 732–735.
- UTIDA, S. (1941) Studies on experimental population of the azuki, bean weevil, *Callosobruchus chinensis* (L.) II. The effect of population density on progeny populations under different conditions of atmospheric moisture. *Mem. Coll. Agr., Kyoto Imp. Univ.* **49**: 1–20.
- UTIDA, S. (1944) Host parasite interaction in the experimental population of the azuki bean weevil, *Callosobruchus chinensis* (L.). 2. The effect of density of parasite population on the growth of the host

population and also of the parasite population (2). *J. Appl. Zool* **15**: 1-18.
VARLEY, G. C., G. R. GRADWELL and M. P. HASSELL (1973) *Insect Population Ecology*. Blackwell, Oxford.

分布集中性が個体群の増殖率に与える影響について

山 村 光 司

近似式を過去のいくつかの実験データに適用することにより、分布集中性が個体群増殖率に与える影響を評価した。この結果、個体群密度が高すぎない場合には、分布集中性は一般に個体群の増殖率および平衡密度レベルを低下させることが示された。