A general mechanism affecting the overall growth rate of metapopulations

Ng I

Abstract

In a subdivided population or metapopulation, the overall population growth rate is the *weighted* average of the per capita population growth rate, R(N), in each subpopulation. Population densities in different subpopulations will not be identical at all times. Assuming negative density dependence in R(N), the variance between subpopulations often reduce the expected population growth rate for the metapopulation overall, relative to that of a comparable continuous population. The range of situations in which this is true is explored and found to be quite liberal. The distinction between population size and population density, and the shape of the function relating population growth rate (or per capita growth rate) and populations. The effect has implications for how we interpret and compare empirical data related to population growth rates of different populations, since this will depend on the patchiness of the landscape/habitat and the spatial distribution and dispersal abilities of the organism. It also has management implications for populations in patchy landscapes.

Tormod Vaaland Burkey Princeton University Department of Ecology and Evolutionary Biology Princeton, NJ 08544-1003 USA

Present address: University of Oslo Centre for Development and the Environment POBox 1116, Blindern N-0317 Oslo Norway

e-mail: tvburkey@phoenix.princeton.edu

Metapopulation growth rates

Introduction

Populations are spatially distributed in ways ranging from isolation in different habitat patches to continuous and panmictic populations uniformly distributed across the landscape. Landscapes may exhibit patchiness at several scales. Habitat patches will bound populations locally in different ways depending upon the nature of the boundary and the focal species. Bounded subpopulations will experience local density dependence and together they may be modeled as metapopulations. Here I present a mechanism by which local density dependence changes the overall per capita population growth rates in metapopulations, and discuss the implications of this mechanism for empirical population dynamic studies and for conservation biology.

Consider a population distributed across two (or more) identical patches, where the population in different patches can fluctuate independently of each other. That is not to say that the subpopulations have to be completely isolated from each other or that the population sizes cannot be highly correlated, just that population sizes sometimes may drift away from their deterministic expectation (for whatever reason) and differ between patches. In this paper, I investigate the effect of this variance on the expected overall growth rate of a metapopulation relative to a comparable continuous population where this variance is zero.

Model Analysis

To consider habitat patches of different areas, we must deal with absolute population sizes rather than population density. Let R(N) be the per capita population growth rate in a population of size N. Let $R_n(N)$ be the per capita population growth rate for a population in a habitat patch in a set of n patches — each $\frac{1}{n}$ the size of the single large patch. For a continuous population — i.e. a single large patch (n=1) — I will use $R_1(N)$ and R(N) interchangeably. Assume that the dynamics of a population can be described by the equation $N_{t+1} = R(N) N_t$. Assume negative density dependence, i.e. R'(N) < 0 for all N, which implies

Metapopulation growth rates

that there are no Allee effects (Allee 1949). Assume that there are no edge effects and that the habitat is equivalent in all patches. Define the area of a given habitat in terms of its carrying capacity, K, for the focal species, and define K as the population size for which the expectation of R(K)=1.

Take a single continuous population of size N, in an area of size K. The comparable situation for a fragmented population (assuming equal sized fragments) is a set of small populations in n areas each of size $\frac{K}{n}$. Since N is absolute population size and not density, R(N) must scale with the size of the patch. Barring edge effects, there is no *a priori* reason why, say, 50 individuals in a 1000 ha patch should face different conditions than would 100 individuals in a 2000 ha patch. That is, $R\left(\frac{N}{2}\right)$ in a reserve of size $\frac{K}{2}$ should be equal to R(N) in a reserve of size K, or $R_1(N) = R_n\left(\frac{N}{n}\right)$. As long as the N individuals are evenly distributed across n patches each of size $\frac{K}{n}$, their overall growth rate should be equal to the growth rate in a single large population of size N in an area of size K, and

$$n\frac{N}{n} R_n\left(\frac{N}{n}\right) = NR_I(N) \tag{1}$$

Comparing a single large patch with two half as large, $R_1(N) = R_2\left(\frac{N}{2}\right)$ so that

$$NR_{I}(N) = \frac{N}{2} R_{2}\left(\frac{N}{2}\right) + \frac{N}{2} R_{2}\left(\frac{N}{2}\right)$$
(2).

However, most of the time, there will not be identical population densities across patches in a fragmented system. Considering the variance in population density between subpopulations, I will show that, if and only if the function NR(N) is concave down, we have

$$NR_1(N) > N_1R_2(N_1) + N_2R_2(N_2)$$
, (3)

where $N_1+N_2 = N$, $N_1 \neq N_2$; that is, the growth rate of the single population exceeds that of the fragmented ensemble when we allow for variation in population density between subpopulations.

(3) is equivalent to

$$2 N R(N) > (N+x) R(N+x) + (N-x)R(N-x) , \qquad (4)$$

where $x=N_1-N_2$ (see Appendix). Dividing by 2N on both sides we see that this is essentially a comparison between the per capita growth rate in an evenly distributed (or single large) population, R(N), and the *weighted* mean of the growth rates in a metapopulation with nonzero variance in population density between subpopulations — where each subpopulation is weighted by its size (cf. Fig. 2). Testing equation (3) is a simple matter of comparing R(N) with the weighted mean of R(N+x) and R(N-x).

Defining a new function G(N)=NR(N), (4) becomes

$$2G(N) > G(N+x) + G(N-x) \tag{5}$$

which is equivalent to

$$G(N+x) - G(N) < G(N) - G(N-x)$$

$$\tag{6}$$

(6) is true for all N and x if and only if G(N) is concave down. Since G(N) = NR(N) we have G''(N) = 2R'(N) + NR''(N), and (3) is true for all N and x if and only if

$$2R'(N) + NR''(N) < 0$$
⁽⁷⁾

More generally, it follows from Jensen's inequality (Råde and Westergren 1990) that a continuous population has a higher expected growth rate than a metapopulation if G(N) is concave down on [N-x, N+x]. Concavity is stronger than G''(N)<0, so Jensen's inequality makes a stronger argument for (3). Jensen's inequality also generalizes to a metapopulation consisting of *n* patches. G(N) is equivalent to the expected population size in the next time interval, $E[N_{t+1}]$. Hence, for the case n=2, we can quickly see which way the inequality in

(3) goes when we plot the expected N_{t+1} (i.e. G(N)) against N_t . If the line between two points on the graph is below the point on the graph half way between them, then (3) holds (see Fig. 3).

With a linear R(N), R'(N) is negative and R''(N) is zero. Therefore, (7) is satisfied and (3) holds for all N. From Fig. 2a it is also clear that the per capita metapopulation growth rate is always lower than in a single large population, when you consider that the largest subpopulation, which always has the lowest per capita growth rate, is weighted more the smaller populations with higher R(N).

In the concave down case we have R'(N) < 0 and R''(N) < 0. Therefore, (7) is satisfied and (3) holds for all N. From Fig. 2b it is also clear that the per capita metapopulation growth rate is always lower than in single large population, even without considering the different weighting of large and small subpopulations.

In the concave up case we have R'(N) < 0 and R''(N) > 0. If R'(N) grows fast enough (R(N) is curved enough) to counterbalance the greater weighting of the smaller R(N+x) relative to R(N-x), (3) will not be true. Below, I discuss the stringency of this requirement by analyzing one example of a concave up function.

Example: R(N) is a negative exponential.

Write $R(N) = R_0 e^{-kN}$. R''(N) = -kR'(N), so (7) reduces to

$$2R'(N) < kNR'(N)$$
(8)

or

$$\frac{2}{N} > k \tag{9}$$

Thus, G(N) is concave down for such functions R only for sufficiently small population sizes. The carrying capacity of a given area can be defined in terms of the population size at which the expected per capita growth rate R(N)=1. Hence, Tormod Vaaland Burkey

Metapopulation growth rates

$$R_0 e^{-kK} = 1 \tag{10}$$

or

$$k = \frac{\ln R_0}{K} \tag{11}.$$

Substituting (11) into (9), the conditions under which (3) is true is

$$\frac{\ln R_0}{K} < \frac{2}{N} \quad \text{or } N < \frac{2K}{\ln R_0} \tag{12}.$$

For N=K, (12) is equivalent to $ln R_0 < 2$, i.e. $R_0 < e^2 \approx 7.38$. Hence, (3) is true at N=K for negative exponential R(N) with $R_0 < 7.38$. At $N = \frac{K}{2}$, (3) is true for $R_0 < e^4 \approx 54.59$. That is, although the true mean R(N) of an unevenly distributed metapopulation is greater than R(N) in an evenly distributed (or single large) population, due to the curvature of R(N), the greater weighting of the largest subpopulation will counteract that if these conditions hold (Fig. 2c). Populations with very high values of R_0 , however, are more likely to overshoot carrying capacity and reach densities where G(N) is concave up. Even so, G(N) typically has a dominant hump that is concave down (cp. Fig. 3).

The shape of population growth rates

Density dependence is highly prevalent in populations of animals and plants. Tanner (1966) detected significant negative density dependence in 47 of 71 time series from a wide variety of taxa. Woiwod and Hanski (1992) analysed 5715 time-series of annual abundance of 447 moth and aphid species and detected density dependence in 79% and 88% of the 778 time-series longer than 20 years (moths and aphids respectively). Unfortunately, no information about the shape of R(N) is given in these reviews. Tanner's estimates of density dependence were correlation coefficients (i.e. linear density dependence), and apparently no attempt was

made to look for higher order terms. Data on shapes of density dependence in individual life history parameters are a little easier to come by, but cannot easily be considered from the point of the present model. For instance, Grubb (1974) gives data for Soay sheep (*Ovis aries*) and Fowler (1986) for northern fur seal pups (*Callorhinus ursinus*) which yield a highly concave down probability of juvenile survival. Teer et al. (1965) show that embryos per doe in white-tailed deer (*Odocoileus virginianus*) is concave down with density. See Fowler (1987) and Tanner (1966) for reviews on the importance of density dependence.

I have conducted a survey of the ecological literature to find data sets from which the shape of R(N) as a function of N could be gleaned. R(N) was estimated by $\frac{N(t+1)}{N(t)}$ from published time series and plotted against N(t). The shape of R(N) was estimated by fitting linear, logarithmic and exponential functions to the data, and selecting the one which explained the highest proportion of the variance. Log transforms of N were tried if the curvature of R(N) seemed too great to be captured by logarithmic or exponential functions in N. Polynomial equations of N were also used, but were not used for the final regressions since they cannot be trusted to decline monotonically. Populations for which higher order time-lags were needed to describe the population dynamics were not used (except where the dynamics were explicitly characterized by the authors), although the proposed mechanism can be evaluated from the concavity of the population trajectory in a higher dimensional phase space. For this reason, and due to the paucity of long term studies on long-lived organisms, most of the data are from insect populations, protozoa, or crustaceans. The survey is by no means complete, and is only intended to illustrate what I believe to be a rather general mechanism. There were no indications of Allee effects in any of the data sets (but see Lamont et al. 1993).

Populations that follow the logistic or Monod equations always have concave down G(N). This is seen most easily by realizing that the continuous analog to G(N) is $\frac{dN}{dt}$. In the logistic equation $\frac{dN}{dt} = aN-bN^2$, where a = r and $b = \frac{r}{K}$; r being the intrinsic population

Metapopulation growth rates

growth rate. Hence, the per capita rate of change is linear and $\frac{dN}{dt}$ is concave down throughout. Hence, organisms whose growth is described by the logistic equation is expected to have higher instantaneous rates of change in continuous populations than in metapopulations.

Table 1 lists the data from which shapes of R(N) could be gleaned. Although many had R(N) which were concave up, none have corresponding G(N) that were concave up in any part of the range. Although I made a conscious effort to find data sets that might yield concave up G(N), none were found. Many data sets that I have characterized as having concave up R(N) may in fact be linear in large parts of the range. The concavity of the entire range may simply be due to the fact that R(N) cannot be negative, or populations may in fact tend to be bounded away from zero. Populations that are not bounded away from zero may yield only short time series which may not get published.

Not all R(N) and G(N) from the data in Table 1 can be reconstructed here, but the two most concave up examples are shown in Figs. 4 and 5. Berryman (1991) fits a model of population growth for pine loopers (*Bupalus piniarus*) to data from Klomp 1965. His model yields a concave up R(N), and a corresponding concave down G(N). I fitted concave up curves for R(N) with even greater curvature than Berryman's model, and obtained better fits (Fig. 4). My regressions also yield concave down G(N) over the entire range of population sizes in the time series. Fig. 4 shows the estimated R(N) and corresponding G(N) for the pine loopers. These regressions are entirely phenomenological, details in their curvature may acquire undue importance, and they should not be attributed too much weight. Hence, I show two different regression in Fig. 4 which yield different G(N). The "true" G(N) may be something in between Fig 4b and 4d. Fig. 5 shows estimated R(N) and corresponding G(N) for the azuki been weevils (*Callosobruchus chinensis* L.) estimated from data from Utida (1957). Both species are outbreak species with highly curved R(N), but their G(N) are concave down throughout.

Tormod Vaaland Burkey

Metapopulation growth rates

Discussion

I have presented a general mechanism affecting subdivided populations with variance in population density between habitat patches, and explored the conditions under which these will have lower growth rates overall than their unfragmented, continuous, counterparts. The overall population growth rate for a metapopulation is the mean growth rate for its subpopulations, weighted by their population sizes. Since the larger subpopulations have lower per capita population growth rates and are weighted most heavily, while smaller subpopulations are weighted less, metapopulations frequently have lower overall population growth rates than comparable continuous populations. Subpopulations that have relatively high population sizes will be near carrying capacity and not growing very rapidly, and those that are at low population sizes will be growing slowly because their "capital" is small (Fig. 1).

This analysis has made simplifying assumptions, notably the absence of Allee effects, which can be relaxed for a more thorough understanding. Generally, Allee effects are considered to affect fragmented populations more than large continuous populations (e.g. Lamont et al. 1993). The extent to which (3) holds true can be explored graphically by drawing different versions of G(N) versus N (see Fig. 3). (3) is true wherever the line between two point on the graph passes below the point on the graph half way between them on the N axis. Varying N and x it seems that the average difference between G(N) and the line between G(N+x) and G(N-x) tends to be positive in natural populations. Readers can explore the validity of this claim themselves, perhaps by drawing biologically realistic G(N), cobwebbing population trajectories and picking x at random for each time step. Situations that represent temporary exceptions are those where Allee effects or values of N far beyond carrying capacity cause G(N) to be concave up, and x is relatively small. In most population trajectories these negative values will be overwhelmed by more common and larger positive values.

Even in the case of highly curved, concave up R(N) with Allee effects, G(N) typically has a highly dominant concave down hump which overwhelms local concave up regions. For small values of x, any function is approximately linear and the effect will be slight. The prevalence and importance of Allee effects in wild populations is not yet known and requires much more study. However, it seems likely that the range of population sizes at which Allee effects are important is relatively narrow compared to the full range of realized population sizes. The influence of Allee effects will also depend on whether specific Allee effects depend on low population *densities* or absolute population *size*.

Dealing with organisms that exhibits high level of patchiness or clumping, one must be extra cautious with interpretation of data on population growth rates. Empirical studies that detect differences in growth rates between populations may find that the discrepancy is due to one being more patchily distributed than the other. Spatial clumping and local processes, while altering growth rates at larger scales, may also alter the overall pattern of population fluctuations at those scales (De Jong 1979, May 1986, Bjørnstad and Hansen 1994). The reduction in growth rates at regional scales and fluctuations partially out of phase at local scales may for instance cause a reduction in the regional coefficient of variation in abundance, and alter the regional dynamics from regular fluctuations to relative stasis. The dynamic signals of smaller-scale regions (local interactions and processes may disappear at larger scales (see also May 1986, de Roos et al. 1991). The mechanism also affects dynamics of predator-prey intreractions and parasite-host interactions due to the aggregative response of predators on their host (see the large literature on aggregative responses, clumping, and the effects of individual behavior on population dynamics, notably in insect populations; e.g. Hassell and May 1974, 1985, De Jong 1979, Hassell 1980, Pearman and Wilbur 1990).

Although cast in a deterministic framework, this mechanism does not ignore the importance of stochastic events on population size, growth and viability. In fact, it depends on them for the non-uniform distribution of individuals to arise. The mechanism is simply an argument to show that the deck is stacked against either the metapopulation or the continuous population, depending on the shape of R(N). Around this biased expectation there is

stochasticity, but *on average* a population with a stochastic component to its dynamics will follow that bias (see also Bjørnstad and Hansen (1994) for a general treatment of the role of variation in population dynamic processes).

Application to anthropogenic patchiness and habitat fragmentation

The mechanism described above may be applied to man-made patches of previously continuous habitats. Anthropogenic limits on dispersal imposes a level of patchiness on top of whatever structure the resident populations exhibited beforehand. The new spatial boundaries imposed by human habitat alteration impose additional density dependence at the level of subpopulations, and consequences that are seen in simulation models exploring the effect of habitat subdivision on extinction risk (Wright and Hubbell 1983, Burkey 1989, 1995). Habitat that is patchy to the focal organism will support metapopulations which, overall, spend a greater proportion of their time with low overall population growth rates and consequently more time at low population sizes, than continuous, homogenous habitat. This should tend to make metapopulations more vulnerable to overall population extinction than continuous population of the same size (see Burkey 1989, 1995). The importance of spatial variability in density on population dynamics has been recognized by De Jong (1979), Chesson (1981), Bjørnstad and Hansen (1994) and others. Here, I have applied the mechanism to populations in fragmented landscapes, explored the consequence of different shapes of the density dependence, explored the shape of the density dependence in actual populations and observed a seemingly general pattern.

I have been unable to think of any way to demonstrate the effect of the mechanism described here because I see no way to separate it from the effects of demographic stochasticity under a regime of density dependence in demographic rates. Metapopulations tend to have reduced growth rates at the same population size, but since they also will tend to be more often at low population sizes (especially as they near extinction) differences in

÷

population growth rates over time would be difficult to detect in a population trajectory over time.

As analyzed here, the mechanism favors continuous populations over subdivided populations in all cases with R(N) linear or concave down, and under quite liberal constraints in the example given of a concave up R(N). I consider these constraints liberal enough to conclude that the proposed mechanism tends to reduce metapopulation growth rates in the dominant part of biologically realistic parameter space — especially for the kind of species for which conservation efforts are needed. An endangered species is not likely to have per capita population growth rates greater than 7 (see above), and certainly not greater than 50. Species with relatively low maximal growth rates are not likely to vastly overshoot their carrying capacity, either. These are the species most in need of protection and for which reserves are needed. For some threatened species, the reduction in population growth rate following habitat fragmentation may be enough to cause deterministic extinction. By affecting overall population growth rates, habitat subdivision may stabilize the dynamics of species with extremely high population growth rates at the landscape level, and this too may affect threatened and endangered species.

The above analysis can easily be expanded to more highly curved concave up functions (e.g. $R(N) = R_0 e^{-kN^2}$), to further explore the parameter space for which (3) does and does not hold true. No data were found for which fragmented populations would have greater overall growth rates than continuous populations, even though data from invertebrate species with high maximal growth rates and high curvature of R(N) were studied.

In its present state, this treatment seems to apply best to animals that are free to move around within the patch/reserve, spreading out in space so as to reduce the competitive effects of high local density (patchiness) at a smaller spatial scale. Density dependent dispersal between patches would tend to smooth out differences in the density of individuals among patches, reducing the effect of the proposed mechanism. Along with the "rescue effect" (Brown and Kodric-Brown 1977), this suggests a role for inter-patch dispersal in reducing the probability of extinction in fragmented landscapes. Habitat corridors (Harris 1984), may to some extent alleviate the effects of this mechanism by making otherwise isolated patches effectively contiguous. The effect may be reduced by regional environmental variability which could make subpopulations more correlated with each other. The mechanism is most likely to negatively impact subdivided populations of species with low to moderately high maximum population growth rates, which are the species most likely to be of concern to conservation biologists.

Acknowledgments— I thank Thomas Hansen, Simon Levin, Ben Bolker and Henry Horn for many constructive comments and insightful discussions.

References

- Allee, W. C. 1949. Group survival value for Philodina roseola, a rotifer. Ecology 30:395-397.
- Berryman, A. A. 1991. Stabilization or regulation: what it all means! Oecologia 86:140-143.
- Bitancourt, A. A. 1941. Expressao matematica do crescimento de formigueiros de "*Atta sexdens rubropilosa*" representado pelo augento do numero de olheiros. Arch Inst. Biol. 12: 229-236.

Bjørnstad, O. N. and Hansen, T. F. 1994. Individual variation and population dynamics. Oikos 69: 167-171.

Bodenheimer, F. S. 1937. Population Problems of Social Insects. Biol. Rev. 12:393-430.

- Brown, J. H. and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. Ecology 58:445-449.
- Burkey, T. V. 1989. Extinction in nature reserves: The effect of fragmentation and the importance of migration between reserve fragments. Oikos 55:75-81.
- Burkey, T. V. 1995. Extinction in fragmented landscapes: demographic mechanisms and predator-prey interactions. Ph.D. thesis. Princeton University.
- Chesson, P. L. 1981. Models for spatially distributed populations: the effect of within-patch variability. Theor. Pop. Biol. 19: 288-325.
- Davidson, J. 1938a. On the ecology of the growth of the sheep population in South Australia. Tr. Roy. Soc. S. Australia 62:141-148.
- Davidson, J. 1938b. On the growth of the sheep population in Tasmania. Tr. Roy. Soc. S. Australia 62: 342-346.
- 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.
- De Roos, A. M., McCauley, E. and Wilson, W. G. 1991. Mobility versus density-limited predator-prey dynamics on different spatial scales. Proc. R. Soc. Lond. B 246: 117-122.
- Edgerly, J. S. and Livdahl, T. P. 1992. Density-dependent interactions within a complex life cycle: the role of cohort structure and mode of recruitment. J. Anim. Ecol. 61:139-150.
- Fowler, C. W. 1986. Density dependence in northern fur seals (*Callorhinus ursinus*). Proceedings of a Conference on Fur Seals of the World, Cambridge England, April 1984.

- Fowler, C. W. 1987. A review of density dependence in populations of large mammals. In: Genoways, H. H. (ed.), Current Mammalogy. Plenum Press New York, pp. 401-441.
- Gause, G. F. 1931. The influence of Ecological Factors on the Size of Population. Am. Nat. 65:70-76.
- Gause, G. F. 1934. The Struggle for Existence. Williams and Wilkins, Baltimore.
- Grubb, P. 1974. Population dynamics of the Soay sheep. In: Jewell, P. A., Milner, C., and Boyd, J. M. (eds.), Island Survivors: The Ecology of Soay Sheep of St. Kilda. Athlone Press, London, pp. 242-272.
- Harris, L. D. 1984. The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity. University of Chicago Press, Chicago.
- Hassell, M. P. and May, R. M. 1974. Aggregation of predators and insect parasites and its effect on stability. J. Anim. Ecol. 43: 567-594.
- Hassell, M. P. and May, R. M. 1985. From individual behavior to population dynamics. In: Sibly, R. M. and Smith, R. H. (eds.), Behavioural Ecology — Ecological Consequences of Adaptive Behavior. Blackwell Scientific Publications, Oxford, pp. 3-32.
- Hochberg, M. E., Thomas, J. A. and Elmes, G. W. 1992. A model study of the population dynamics of a large blue butterfly, *Maculinea rebeli*, a parasite of red ant nests. J. Anim. Ecol. 61:397-409.
- Lamont, B. B., Klinkhamer, P. G. L. and Witkowski, E. T. F. 1993. Population fragmentation may reduce fertility to zero in *Banksia goodii* a demonstration of the Allee effect. Oikos 94:446-450.
- May, R. M. 1986. When two and two do not make four: nonlinear phenomena in ecology. Proc. R. Soc. Lond. B 228: 241-266.
- Park, T., Gregg, E. V. and Lutherman, C. Z. 1941. Studies in population physiology. X. Interspecific competition in populations of granary beetles. Physiological Zöology 14:395-430.
- Pearl, R. 1930. The Biology of Population Growth. Klopf, New York.
- Pearman, P. B. and Wilbur, H. M. 1990. Changes in population dynamics resulting from oviposition in a subdivided habitat. Am. Nat. 135: 708-723.
- Pimentel, D., Nigel, W. and Madden, J. 1963. Space-time structure of the environment and the survival of hostparasite systems. Am. Nat. 97:141-166.
- Råde, L. and Westergren, B. 1990. Beta β Mathematics Handbook. Second Edition. Chartwell-Bratt.
- Tanner, J. T. 1966. Effects of population density on growth rates of animal populations. Ecology 47:733-745.
- Teer, J. G., Thomas, J. W., and Walker, E. A. 1965. Ecology and management of white-tailed deer in the Llano Basin of Texas. Wildl. Monogr. 15:62.
- Terao, A. and Tanaka, T. 1928. Population growth of the Water-Flea, *Moina macrocopa* Strauss. Proc. Imper. Acad. (Japan) 4:550-552.
- Utida, S. 1957. Population fluctuation, an experimental and theoretical approach. Cold Spring Harb. Symp. Quant. Biol. 22:139-151.
- Woiwod, I. P. and Hanski, I. 1992. Patterns of density dependence in moths and aphids. J. Anim. Ecol. 61:619-629.
- Wright, J. P. and Hubbell, S. P. 1983. Stochastic extinction and reserve size: a focal species approach. Oikos 41: 466-476.

Appendix

Eq. (3) is equivalent to N R₁(N) > $\left(\frac{N}{2} + x\right) R_2\left(\frac{N}{2} + x\right) + \left(\frac{N}{2} - x\right) R_2\left(\frac{N}{2} - x\right)$. R₁(N) = R₂ $\left(\frac{N}{2}\right)$, yields R₂ $\left(\frac{N}{2} + x\right) = R_1(N + 2x)$ and R₂ $\left(\frac{N}{2} - x\right) = R_1(N - 2x)$. Hence (3) implies N R₁(N) > $\left(\frac{N}{2} + x\right) R_1(N + 2x) + \left(\frac{N}{2} - x\right) R_1(N - 2x)$ (A1).

Multiplying both sides by 2 and writing R instead of R_1 , we have

$$2N R(N) > (N + 2x) R(N + 2x) + (N - 2x) R(N - 2x)$$
(A2).

Writing x instead of 2x, we have

$$2N R(N) > (N + x) R(N + x) + (N - x) R(N - x)$$
(A3)

QED

Table 1. Studies considered where the qualitative shape of R(N) could be determined: reference, taxon, and shape of R(N). Population trajectories described by the author(s) as "logistic" have been listed as such. These will always have a concave down G(N) throughout the range of population sizes. Some authors may have sampled on a frequency somewhat different from the generation time of the organism.

Study	Taxon	Shape of R(N)
Klomp 1965	pine loopers, Bupalus piniarus	Concave up
Bodenheimer 1937	honey bee, Apis mellifera	Logistic
Edgerley and Livdahl 1992	treehole mosquito, Aedes triseriatus	Linear
Gause 1934 Gause 1931	flour beetle (f.b.), Tribolium confusum	Logistic Logistic
Park et al. 1941 Park et al. 1941	Trogoderma versicolor (a dermesid beetle)	Concave up Linear
Pearl 1930 Pearl 1930	yeast	Logistic
Davidson 1938a	sheep (South Australia)	Logistic Logistic
Davidson 1938b Pimentel et al. 1963	sheep (Tasmania) house fly pupae, <i>Musca domestica</i>	Logistic Concave up
Utida 1957	house fly adults, Musca domestica azuki been weevil, Callosobruchus chinensis a)	Linear Concave up
Utida 1957	azuki been weevil, Callosobruchus chinensis b)	Concave up



Figure 1. Twenty individuals (dots), in a) a single large reserve and b) unevenly distributed across two small reserves (squares); with corresponding locations (circles) on a logistic growth curve. Whenever the distribution of individuals in a subdivided reserve is non-uniform, the overall growth rate is lower than that in a continuous reserve. The critical factor is the slope of the growth curve $\left(\frac{dN}{dt}\right)$ inside the little circles, which follows from the function R(N) weighted by the population size at the same points. $\frac{dN}{dt}$ is greater in the single large reserve than in the two small reserves together.



Figure 2. Linear, concave down and concave up per capita growth functions. Compare the *weighted* mean of R(N-x) and R(N+x), with the magnitude of R(N). a) Linear: the mean is identical, but the weighted mean is less than R(N). b) both the mean and the weighted mean is less than R(N). c) the mean is greater, but the weighted mean is still less than R(N) in a large portion of parameter space.



Figure 3. Hypothetical map of N onto G(N), corresponding to a concave up R(N) — figure 2c. The dotted line indicates the mean of G(N-x) and G(N+x). The distance from the dotted line between any two points on G(N) and the point on G(N) halfway between them is the advantage to a continuous population over a metapopulation in that particular realization — or disadvantage if G(N) is concave up between G(N-x) and G(N+x).

ه. د

Figure 4. a) R(N) as a function of N, for pine loopers (*Bupalus piniarus*) (data from Klomp 1965). Curve is $R(N) = 99.64 \times 10^{-0.9 \times Log N}$ b) G(N) = R(N) N, calculated from the regression in a). c) Alternative R(N) for pine loopers ($R(N) = 10.6-25.1 \times Log(LogN)$) has greater R^2 -value but attains negative values for large N. d) G(N) based on the regression in c). Although R(N) is concave up with great curvature, G(N) is still concave down throughout the range of population sizes exhibited in the time series.





population sizes exhibited in the time series. **Figure 5.** a) R(N) as a function of N, for azuki been weevils (*Callosobruchus chinensis*) (data from Utida 1957). $R(N)=75.74\times10^{-0.85\times LogN}$. b) G(N) = R(N) N, calculated from the regression in a). Although R(N) is concave up with great curvature, G(N) is still concave down throughout the range of

٠