Fluctuations of Animal Populations and a Measure of Community Stability

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FLUCTUATIONS OF ANIMAL POPULATIONS, AND A MEASURE OF COMMUNITY STABILITY[1]

FLUCTUATIONS

Consider a food web as in Figure 1. This is interpreted to mean that S_1 eats S_2 and S_3, S_2 eats S_3 and S_4, and S_3 and S_4 rely upon a food supply, *i.e.* a source of energy, not shown.
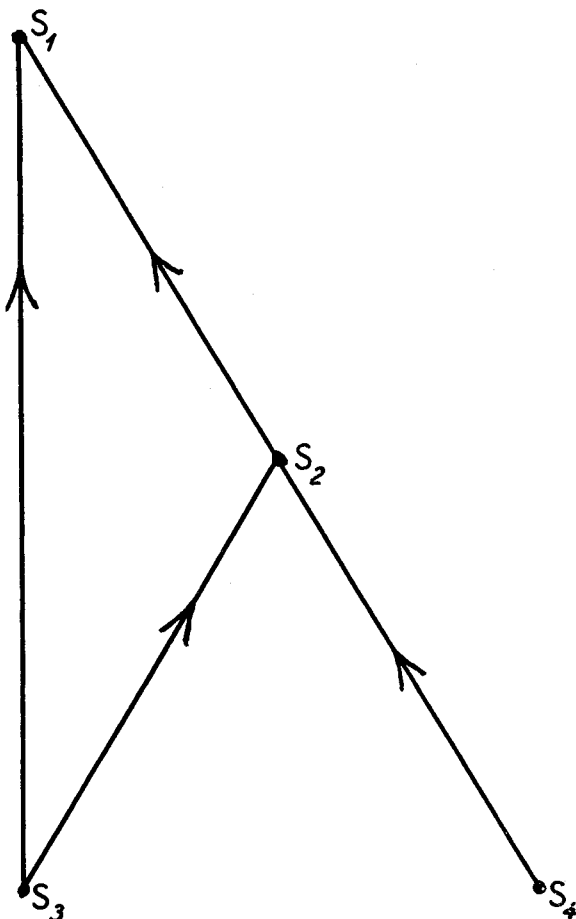

FIG. 1. A sample food web. S_1, S_2, S_3, S_4 are species, and arrows indicate direction in which energy flows.

[1] Contribution from the Osborn Zoological Laboratory, Yale University, New Haven, Connecticut.

Three assumptions will be made and a conclusion will be deduced from these. Since the conclusion is not always correct, it will be justifiable to conclude that one or more of the assumptions is responsible. First, temporarily assume that the amount of energy entering the community (at the lowest trophic level, of course) does not vary with time. Second, assume that the length of time that energy is retained by a species before being passed on to the next doesn't change from time to time. For example, if the animals die young in some year, this would violate the assumption. Third, assume that the population of each species varies directly with the food energy available. If a species first overeats and then starves (essentially a predator-prey reaction) or follows changes in available energy only after a time lag, then this assumption is violated.

These three assumptions imply that the population of each species tends to a specific constant, independent of the initial populations of the species. Proof: Since no species is perfectly efficient at transferring energy from its prey to its predators (Lindeman 1942), energy leaves the web from each species, and in view of the assumptions the amount of energy leaving equals that entering. This is then equivalent to saying that the energy leaving the community is the energy which reenters. That is, the consequences of this will be identical. This energy can now be entered on the food web of Figure 1 as S_5 and it now looks like Figure 2. Let p_{ij} be the proportion of the energy of S_i which goes to S_j. Since all of the energy transferences are shown.

$$\Sigma_j p_{ij} = 1.$$

This equation shows that the food web considered as an energy transformer is what is known in probability theory as a Markov chain (Feller 1950). Furthermore, if the number of links in a complete cycle of the energy is called the length of the cycle, the greatest common divisor of these lengths is 1 and so the conditions set forth in Shannon and Weaver (1949) for the Markov chain to be "ergodic" are satisfied. Therefore, as shown in Feller (1950), the amount of energy at each point tends toward a constant, independent of the initial conditions. In view of the assumptions, the species populations also approach constant values. This completes the proof.

Since populations of species often fluctuate in nature, it can be concluded that one or more of the three assumptions is failing to hold. Furthermore, it is clear from the theorem that the structure of the food web cannot
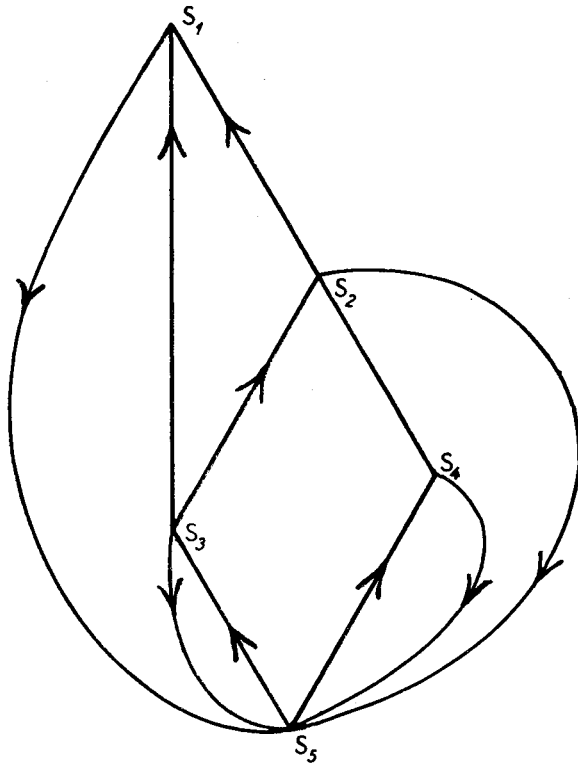
Fig. 2. The food web of Figure 1 modified to include lost energy.

be responsible for fluctuations. Therefore, an explanation of the fluctuations must lie in predator-prey relations, time lag phenomena, or other violations of assumption three; in environmental variations in available energy, violating assumption one; or in variations in age at death, violating assumption two.

COMMUNITY STABILITY

In some communities the abundance of species tends to stay quite constant, while in others the abundances vary greatly. We are inclined to call the first stable and the second unstable. This concept can be made more precise, however. Suppose, for some reason, that one species has an abnormal abundance. Then we shall say the community is unstable if the other species change markedly in abundance as a result of the first. The less effect this abnormal abundance has on the other species, the more stable the community.

This stability can arise in two ways. First, it can be due to patterns of interaction between the species forming the community; second, it can be intrinsic to the individual species. While the second is a problem requiring knowledge of the physiology of the particular species, the first can be at least partially understood in the general case. Only this kind of stability will be considered here.

The interactions between species are represented graphically in a "food web" of the community, in which "*a* eats *b*" is represented by

$$a$$
$$|$$
$$b$$

with the predator above the prey. Energy goes from b to a in this process. More generally it passes from the sun to the lowest trophic level and thence up through the web to the highest level of carnivore. A qualitative condition for stability can now be stated. The amount of choice which the energy has in following the paths up through the food web is a measure of the stability of the community (Odum 1953). To see this, consider first a community in which one species is abnormally common. For this to have a small effect upon the rest of the community there should be a large number of predators among which to distribute the excess energy, and there should be a large number of prey species of the given species in order that none should be reduced too much in population. To sum up, a large number of paths through each species is necessary to reduce the effect of overpopulation of one species. Second, suppose one species is abnormally uncommon. For this to have minimum effect upon the rest of the community, each predator of the species should have a large number of alternate foods to reduce the pressure on the scarce species and yet maintain their own abundance at very nearly the original level. There is good evidence for this in Lack (1954). We see that in either case the amount of choice of the energy in going through the web measures the stability.

A difficulty arises in making this definition quantitative, because our intuition of what stability means is ambiguous. For the concept "effect upon the other species of the community" required in the definition can be interpreted in many different ways. It could be the average (over all species) maximum change in abundance, or the relative changes, or mean square changes, or different species could be weighted differently, etc. The intuitive requirements seem to be that if each species has just one predator and one prey the stability should be minimum, say zero, and that as the number of links in the food web increases the stability should increase.

One further (arbitrary) requirement will specify the function, however. For proof, see Shannon and Weaver (1949). The most convenient requirement is that the stability of two webs such as in Figure 3 and Figure 4 should be equal. Here the ½'s between ab and ae signify that each of b and e is an equally possible food of a (i.e. $\frac{1}{2} + \frac{1}{2} = 1$). Now energy has complete freedom of choice to go to a from section bcd or from section efg. Hence if $S(abe)$ refers to the stability of abe considered as a separate community, etc., it is reasonable to define the stability of the whole web in Figure 3 as $S(abe) + \frac{1}{2} S(bcd) + \frac{1}{2} S(efg)$. If we say that this should be equal to $S(a'c'd'f'g')$ in Figure 4, the appropriate stability function is

$$S = -\Sigma \, p_i \, log \, p_i$$

where the p_i are the numbers in Figure 4. (*E.g.*, for either the web of Figure 3 or of Figure 4 the stability is $-4(\frac{1}{4} \, log \, \frac{1}{4}) = log \, 4$). To find the stability of any web, construct an equivalent one by making a separate line from top to bottom for each different path the energy can take. The p_i in the definition are the products of the q_i of the original web along each path. It may be significant that this is identical in form to the functions measuring entropy in Maxwell-Boltzmann statistics and information in information theory (Shannon & Weaver 1949). Entropy is also analogous in the sense that maximum entropy is the condition for chemical equilibrium while maximum stability may be a condition for community equilibrium (Hinshelwood 1951). It should be pointed out that choice among various functions to define stability precisely rests only upon usefulness of the definition (provided of course that the intuitive conditions mentioned above are satisfied).
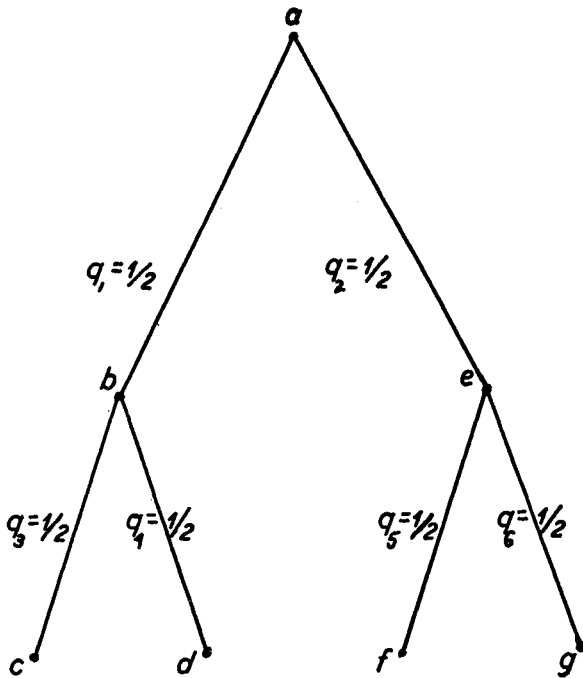
FIG. 3. A food web. a, b, c, d, e, f and g are species, and q on the line joining predator and prey signifies that fraction of the total number of prey species formed by the prey species in consideration.
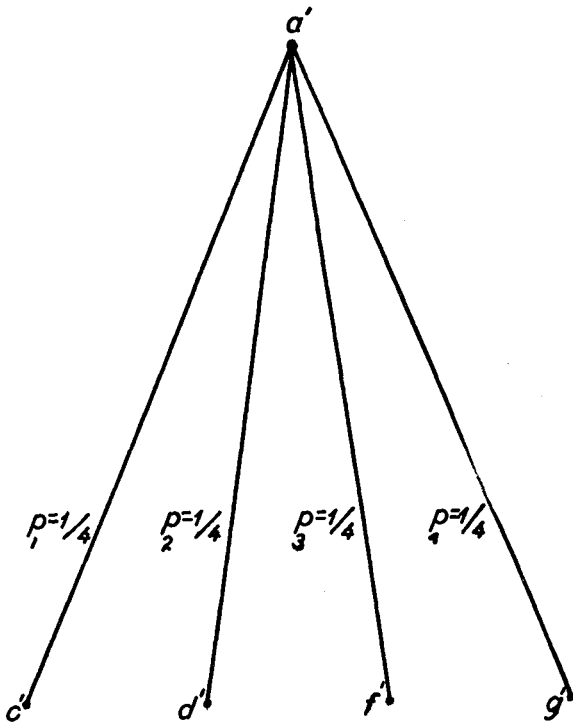

FIG. 4. A food web with stability equal to that of the food web in Figure 3.

There are several properties of this stability which are interesting.

1. Stability increases as the number of links increases.

2. If the number of prey species for each species remains constant, an increase in number of species in the community will increase the stability.

3. Combining 1 and 2, it follows that a given stability can be achieved either by large number of species each with a fairly restricted diet, or by a smaller number of species each eating a wide variety of other species.

4. The maximum stability possible for m species would arise when there are m trophic levels with one species on each, eating all species below. Similarly, the minimum stability would arise with one species eating all the others—these others being all on the same trophic level. (These are plotted in Figure 5.)
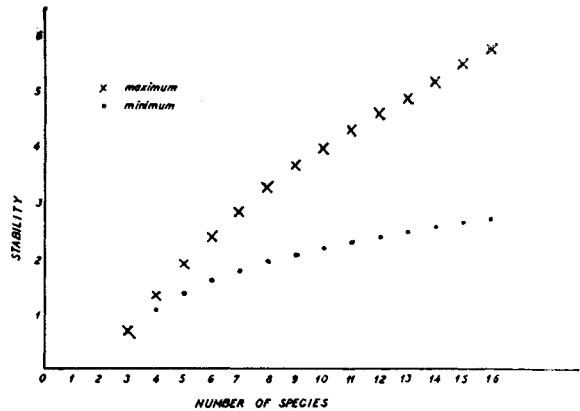

FIG. 5. Maximum and minimum stabilities for a given number of species. All communities must have stabilities within these limits.

Some interesting conclusions may be drawn from these properties. First, (1) implies that restricted diet lowers stability. But restricted diet is what is essential for efficiency. Furthermore, efficiency and stability are the two features required for survival under natural selection. Efficiency enables individual animals to outcompete others, but stability allows individual communities to outsurvive less stable ones. From this it seems reasonable that natural selection operates for maximum efficiency subject to a certain necessary stability. Combining this with the properties listed above the following seem plausible.

A. Where there is a small number of species (*e.g.* in arctic regions) the stability condition is hard or impossible to achieve; species have to eat a wide diet and a large number of trophic levels (compared to number of species) is expected. If the number of species is too small, even this will not assure stability, and, as in the Arctic, populations will vary considerably.

B. Where there is a large number of species (*e.g.* in tropical regions) the required stability can be achieved along with a fairly restricted diet; species can specialize along particular lines and a relatively small number of trophic levels (compared to number of species) is possible. (The possibility that the large number of species in tropical communities may be a result of, rather than the cause of, the restricted diets would not alter the above argument.)

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STUDIES FROM THE AUTOTREPHON, IV.
REARING MASS CULTURES OF ORYZAEPHILUS

The autotrephon (Stanley 1951) requires very large cultures of insects, from which eggs are obtained for seeding the replicated samples. This is so because all the eggs used for a run, perhaps 2,500 of each species, must be obtained within a period of not more than say 2 hr. This presents no problem with *Tribolium* as very large cultures of this insect can easily be maintained in flour. In the cases of *Oryzaephilus surinamensis* and *mercator*, this is not so easily done. These insects do not tunnel to any extent. They use only the superficial layers of flour, and crowding occurs, with reduction of egg-production.

The writers have found that these insects can be grown in enormous numbers in ordinary rolled oats if precautions are taken to cope with the large quantities of metabolic water produced. Referring to Figure 1, the culture is set up in a 1-gallon glass jar with a 3-in. disc of 40-mesh stainless steel cloth set in the lid for ventilation. A cardboard washer, ¼ in. wide with a 3 in. hole is used to seal the lid (Fig. 2). About 2 in. of soft-wood shavings are poured into the jar, and another 2 in. of rolled oats poured on top. A suitable temperature is 30°C., but the relative humidity should not be above 60%, or water will collect on the sides and run down into the oats. Extreme moulding will then occur. The life-history requires about 650 hr. for *surinamensis* and about 700 hr. for *mercator*, and the culture lasts without serious moulding for much longer than this.

In Figure 1, the apparent dark layer on top is merely the shadow of the lights (which show as reflections on the shavings). A faint gray line marked "frass" is a mixture of frass and larval smearing, indicating the original level of the oats. The shavings are clogged with frass which has fallen into them. Numerous larvae can be seen trying to climb the glass at the top of the oats.
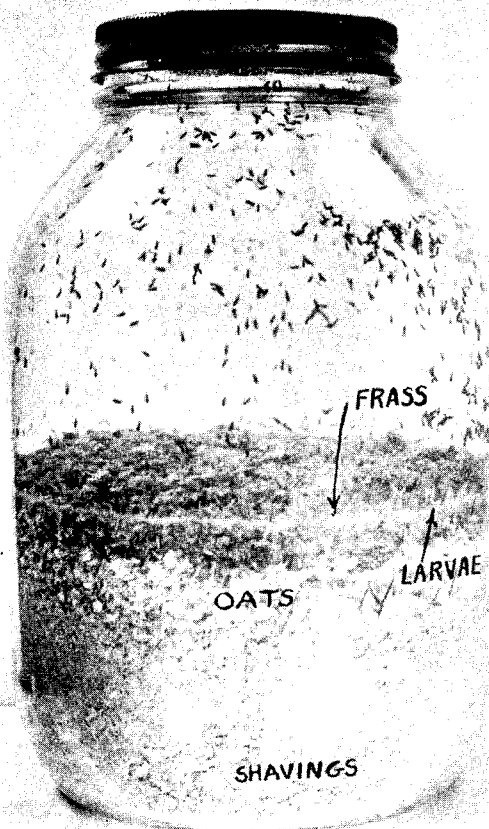

FIG. 1. A culture of *O. surinamensis*, with shavings at the bottom, rolled oats above this. Adults are climbing the glass, and larvae are trying to.
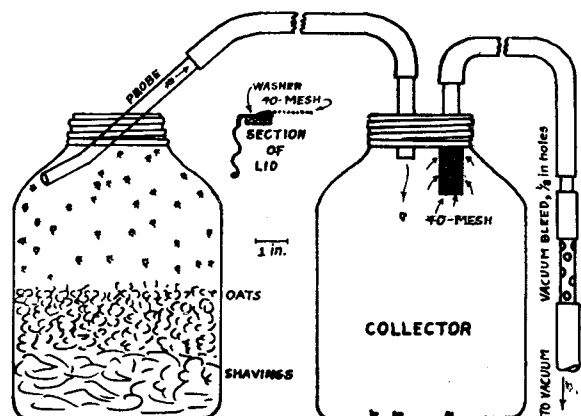

FIG. 2. Suction apparatus for removing *O. surinamensis* adults from a culture.

When disturbed, *O. surinamensis* climbs the glass in swarms, but *O. mercator* does not. It has been observed in this laboratory that if one considers a pair of similar kinds of insects, say *O. surinamensis* versus *O. mercator* or *Tribolium castaneum* versus *T. confusum* or even the red strain of *Tribolium* versus a black mutation (for either *castaneum* or *confusum*), the insect with the shorter life-history is always the more active. The first member of each pair above has the shorter history, climbs or flies more, and is more active and difficult to handle. The meaning of this is not clear, unless both characteristics be tied to higher basal metabolism.

A special technique is needed to get *O. surinamensis* into flour (siftable) for egg production. The writers