Energy in Animal Ecology

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I. The Relevance of Energy Studies to Ecology

No single measurement is intrinsically significant. All measurements derive their interest from their context and the richness of predictive generalizations that can be produced from them. The fact that energy measurements have high intellectual prestige in chemistry and physics does not necessarily imply major ecological significance, any more than electron spin measurements as such have ecological significance.

Precise measurement of energetic parameters is almost impossible, and even rather crude measurements are time-consuming and expensive. It must, therefore, be initially established that such measurements are of sufficient ecological significance to be worth our trouble.

One demonstration of the relevance and interest of energetics to ecology has been presented by Hairston *et al.* (1960). Energy-rich organic sediments accumulate at a rate that is completely insignificant compared with the rate of energy fixation by green plants. This implies that the biosphere as a whole is energy limited, although individual decomposer populations may be temporarily limited by predators or other factors.

In some situations, particularly the free water of lakes and oceans, plants are depleted by herbivores so that the herbivores are obviously limited by energy. Occasionally, it can be directly demonstrated that herbivore population-size is dependent on the rate of energy fixation by food plants (Borecky, 1956). In terrestrial situations, living vege-

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tation is not usually depleted by the activities of herbivores. Situations in which terrestrial vegetation is eliminated often involve exotic herbivores. The success of exotic herbivores at plant destruction implies that climate does not usually regulate the size of herbivore populations, since the exotic herbivore cannot be expected to show higher adaptation to the weather than the native species. An exotic herbivore might however be immune to native predators.

It is tautological that if herbivores are usually predator limited, then predators are usually food limited. Except to the degree that water or some other chemical component of the food is in particularly short supply, food limitation is identical with energy limitation.

Another demonstration of relevance can be made from a combination of evolutionary theory and direct calorimetry data (Slobodkin and Richman, 1961; Slobodkin, 1961a). An assortment of whole animals was burned in a microbomb calorimeter. The observed calorific values are a skewed normal distribution with relatively low variance (Fig. 1).
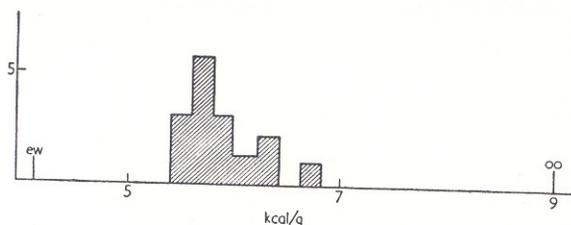

FIG. 1. The calories per ash-free gram in a collection, chosen at random, of seventeen species of animals representing five phyla. The line ew is that for carbohydrates and oo for olive oil. (From Slobodkin, 1961a.)

TABLE I

Variation in Calorific Value of Spitbugs (kcal/ash-free g)

Date 1960	♀	♂
27 June	5·625	5·575
14 July	6·110	6·003
2 August	6·015	5·952
16 August	6·114	5·76?
5 September	5·853	5·783
13 September	5·949	5·804
27 September	5·791	5·574
Eggs 6·529 kcal/ash-free g		

Data provided by R. Wiegert (personal communication, 1961). *Philaenus leucopthalus* collected at the old field, Edwin S. George Reserve, Pinckney, Michigan.

Within a single species there may be seasonal variations (Table I). Animals about to initiate a fast are generally high in calorific value. Analysis of calorific value in pre-pupal and newly emerged adult sarcophagid flies clearly demonstrate that on emergence the flies are again at the low modal value for calorific content. The pre-pupal larvae of *Sarcophaga bullata* had 5·914, 11 day pupae 5·399 and newly emerged adults 5·079 kcal/ash-free g.

Certain species have relatively high values. The three highest values in our initial survey were those for a *Tenebrio* larva about to pupate, *Artemia* nauplii that had just hatched and were still laden with yolk, and overfed laboratory-reared *Dugesia tigrina* fed on *Artemia* nauplii.

The specimens to be burned were initially chosen at random. A tentative explanation was developed after the data from the first seventeen species (cf. Slobodkin and Richman, 1961).

We might have expected any of three possible distributions *a priori*:

1. A normal distribution, implying that energetic content of organisms is determined by the overall biochemical similarities known to exist between almost all species.

2. Broad differences between taxonomic groups might have been expected since taxonomic groups differ in so many ways that it would not be too surprising if they differed in energetic content. This is compatible with the biochemical similarities when it is considered that a biochemical potentiality does not necessarily imply the realization of that potentiality.

3. A distribution skewed in one direction is the only remaining possibility.

The observed skewed distribution with a low modal value is explained on the assumption that in general, energy is limiting to almost all populations almost all of the time and that this limitation has been the case throughout evolutionary history. This explanation is supported by evolutionary considerations since selective advantage is defined by Fisher and others in terms of the intrinsic rate of increase (m in Fisher, 1958, r in most ecological literature). That is, there is a clear selective advantage to reproduction but no clear advantage to adiposity. Excess calories will, therefore, be converted to offspring throughout evolutionary history.

If energy were not limiting, a normal distribution of calorific value in organisms or taxonomic differences in energy content might be expected. The limitation of energy would imply that animals usually maintain the lowest possible set of biochemical components consonant with survival. The possible argument that the narrow range of calorific values is due to biochemical inability to maintain other higher values is refuted by the occurrence on occasion of energy-rich organisms.

Once the above hypothesis has been formulated it would be very difficult to avoid unconscious selection of material if further testing were done by continuing our survey of animals. Calorific determinations are continuing, however, with reference to special problems.

The highest calorific value for any whole animal was 7·432 kcal/ash-free g for *Calanus hyperboreus* collected in the field by Dr R. Conover of Woods Hole. Apparently this copepod feeds very heavily on oil-rich diatoms during the brief periods of phytoplankton blooms and subsists largely on its own fat between blooms. A remarkably similar value of 7·380 was reported for a male *C. finmarchicus* by Marshall and Orr demonstrating that at least high latitude copepods become very fat and also demonstrating that the gain in calorific value is not simply an adaptation to egg laying (Marshall and Orr, 1961, personal communication).

Extremely low values were found for a razor clam, *Ensis minor* (c. 3·5 kcal/ash-free g), and a polychaete worm, *Strenelais articulata* (c. 4·7 kcal/ash-free g). These low values may be due to the inclusion of scleratized protein and polysaccharide shells, skins, and scales which would burn, thereby being included in the ash-free fraction, but would have a low calorific value. This explanation of low values requires further test.

We received samples of dried Australian brush turkey (*Leipoa ocellata*) egg yolk and found that it was identical with that of chicken egg yolk. We, therefore, burned the yolk of ten species of birds (Table II). There was no significant difference between any two species. They are all essentially identical in calorific value. Pooling all determinations, bird yolk has 8·0 ± 0·1 kcal/ash-free g. Difference between birds in precocial properties of the young and incubation period are therefore not related to yolk chemistry but to either egg size, subtle differences in developmental chemistry or both. It is also apparent that birds have long ago established their energy storage mechanism for yolk and have not been able to make it any more perfect since.

TABLE II

List of Species of Birds used for Calorimetry of Egg Yolk

Agelaius phoeniceus	*Melospiza melodia*
Archilochus colubris	*Molothrus ater*
Colinus virginianus	*Passer domesticus*
Dendroica petechia	*Phasianus colchicus*
Gallus domesticus	*Rhea americana*
Leipoa ocellata	*Riparia riparia*

Frog eggs (*Rana pipiens*), newly fertilized, are not beyond the calorific range for whole organisms (6·0) and newly-hatched tadpoles (144 hours old), with yolk still present, are in the modal region (5·8). Salamander eggs (*Ambystoma punctatum*) are identical with those of frogs. We are left with the problem of the phylogeny of energy-rich eggs in the lower vertebrates. Skate (*Raja erinacea*) egg yolk has an intermediate value of 5·6. Reptilian egg yolks are intermediate between birds and amphibians (*Urosaurus ornatus*, 6·9 kcal/ash-free g, *Sceloporus undulatus*, 6·7, *Pseudemys scripta*, 6·7, *Chelydra serpentina*, 6·6).

The calorific data abundantly demonstrate the relevance of energy analysis in ecology and actually do stimulate the formulation of evolutionary theorems and questions.

II. THEORY OF ENERGY BUDGETS

The relation between energetics and the numerical properties of populations must be in terms of energy budget analysis in which the population is considered as a steady-state system through which potential energy passes. We restrict attention to steady states since seasonal differences in climate and physiology combined with essentially random meteorological or biological events in short-term data collections will permit so much variance as to obscure real constancies and differences.

The concept of ecological steady states has been discussed by Odum (1957) and Slobodkin (1960) and both of these authors have indicated something of the theoretical importance of making energy measurements at or near steady-state conditions. An obvious point that neither of them mentions is the difference in meaning between the concept of steady state when applied to an entire community and when applied to a single population.

While a population may maintain its own standing crop in a steady state, no population of mortal animals can maintain a steady state in its immediate spatial environment since the process of population maintenance requires the production of a continuing stream of dead animals and, therefore, a new accumulation of potential energy in the physical environment of the populations.

To avoid confusion, let us establish units now. The population, itself, is measured in units of calories; energy income to the population or energy expenditure by the population is generally in calorie/time units. The term "cost" will be in units of calories per item, so that, for example, maintenance cost of a population will be in units of calories per calorie-days and replacement cost of an individual organism will be in units of calories per individual.

Efficiencies will always be dimensionless fractions. Only if the units

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of both numerator and denominator are the same can two efficiencies be legitimately compared.

There are three equations that have been commonly used to represent the energy budget of populations. They all meet the requirements of energy conservation but they differ seriously in emphasis and the translation between them might well be made explicit.

The simplest energy budget is derived by equating the energy income I, to the heat loss, R, a function of respiration, plus the yield from the population of potential energy in the form of dead animals and excretory products, Y. This has been used by many workers, including: H. T. Odum (1957), E. P. Odum and A. E. Smalley (1959), Richman (1958), and Teal (1957).

$$I = R + Y \tag{1}$$

This formulation ignores the standing crop of the population, and the composition of the yield. It is certainly adequate as a description but is relatively low in certain kinds of predictive power, since, although, yield and respiration are additive, if I should choose to remove an additional calorie per day of yield from a population, I could not reasonably expect that R would decrease by one calorie while everything else stayed constant. There would probably be changes in the size of the population, its age-structure and the availability of other kinds of yield. Up to certain limits which will be discussed below, I could actually increase yield by one calorie, with a compensatory decrease in heat production but the equation would not supply me with the technique for this.

If standing crop, P, is of primary interest, it is possible to write the following equation:

$$I = cP \tag{2}$$

in which c, the maintenance cost, is $\dfrac{R + Y}{P}$. Yield and respiration are obscured in this formulation but it has the advantage of permitting a solution from standing crop data and also permits some theoretical expansion that is not available to Eq. (1) alone. Maintenance cost has been evaluated using this equation for *Hydra* and *Daphnia* in the laboratory (Table III).

Either of these equations can be used to describe a community as well as a population. In communities, Eq. (1) becomes

$$I = \sum R_i + \sum Y_i \tag{1'}$$

where only the potential energy that leaves the community completely

TABLE III

	Daphnia pulex	*Hydra littoralis*
Maintenance cost (cal/4 cal-days)	1·68	0·79
Population efficiency		
adults	0·48	
young	0·04	0·06
eggs	0·06	

Values for maintenance cost and population efficiency calculated from Eq. (14) using laboratory data.

and not that which is eaten by another member of the community is counted as yield.

Equation (2) becomes

$$I = c_i P_i \qquad (2')$$

with no mention of yield. Yield production is a piece of maintenance cost from the standpoint of the species producing it and any consumption of yield from one species by another species in the community will be reflected in the maintenance cost of both species.

The expansion of Eq. (2) to the community level presents operational difficulties. Operationally, c can be evaluated from a situation in which I and P are both known for a particular species. If one is dealing with a mixed species system, it is possible to solve for the combined maintenance cost of all species in a corresponding way but the assignment of maintenance cost to each species requires at least as many different communities as there are species. There is reason to expect that any two communities with the same species composition will also have the same relative numbers of the various species unless physical conditions are different (Slobodkin, 1961b). We can also expect that change in physical conditions will alter c. We can, therefore, not evaluate the c values for each species in any particular community if the only available data are from communities with identical species lists. Solutions are possible by least squares analysis of standing crop data from communities which differ in species lists, but direct evaluation of c has not yet been made in any natural community.

If primary attention is focused on the yield from a particular population, the energy budget can be written as

$$I = \frac{Y_i}{E_i} \qquad (3)$$

where the Y_i are specific kinds of yield calories and each E_i is a growth

efficiency (or inverse of cost per calories of producing yield of the sort i).

E_i requires further elucidation. The energetic cost of producing an animal of age i is the total food energy consumed by that animal during its free life plus the energy expended by its parents on its behalf between the moment of its inception and its freedom. The first of these cost components is relatively simple to determine. The second is more difficult but has been done in at least one case (Armstrong, 1960) which will be discussed below. The growth efficiency up to any age is, therefore, the calories of standing crop represented by the body of an animal of that age divided by the energy expended in the animal's production (cf. Fig. 2).
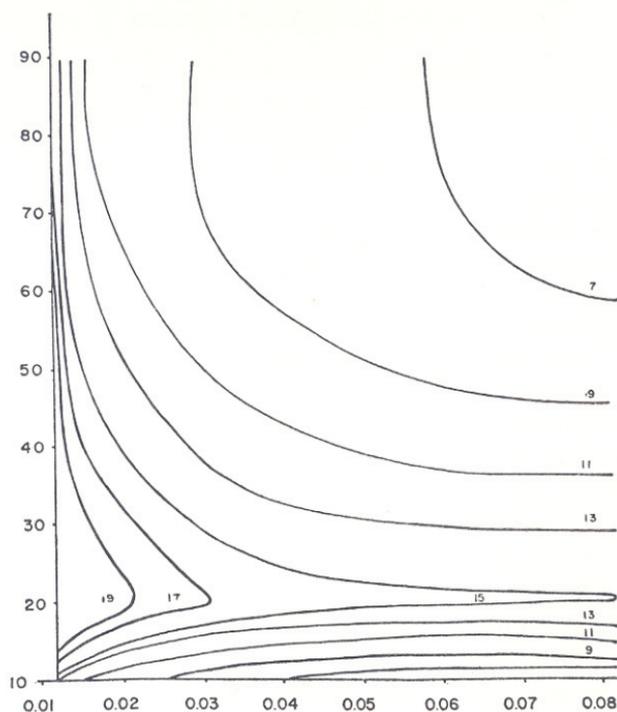

FIG. 2. Percent growth efficiency (E_i) of *Daphnia pulex* as a function of algal concentration in thousands of *Chloamydomonas* cells per ml (ordinate) and calories in the body of the *Daphnia* (abscissa). (From Slobodkin, 1960 using data of Armstrong, 1960.)

On the community level, Eq. (3) is only of significance if total yield from the community as a whole is of significance, that is, if the entire community is being treated as a device for producing potential energy.

In Eq. (3), for example, the Y_i may represent simply the dead animals produced by the population in the complete absence of pre-

dation. The total cost of this rain of dead animals is the same as the cost of replacing these dead animals with a new supply of dead.

The advantage of Eq. (3) is that, in combination with Eq. (2), it is most fruitful for the analysis of the effect of environmental change. Consider that some new source of mortality, either a predator, exploiter or disease appears. There will be a period of transition in the population and some new steady state will be achieved (except if the population is completely eliminated).

That is, assuming I constant, we will have from Eq. (2)

$$I = P'(c + \Delta c) \tag{4}$$

where Δc is the maintenance cost induced by the new mortality source. Let Y' represent the new distribution of potential energy in yield. It follows from Eqs. (2), (3) and (4) that

$$\Delta c = \frac{I}{P'} \sum \frac{Y'}{E_i} - \frac{I}{P} \sum \frac{Y_i}{E_i} \tag{5}$$

This is developed explicitly in Slobodkin (1960).

Let us consider that the change in environment involves a new predator as exploiting agent and let us assume that this exploiter is interested in proper conservation practices with reference to the population in question. He would like to know the degree to which his exploitation programme alters the standing crop of the exploited population, which is in a sense equivalent to knowing how much of the energy income to the exploited population is being diverted to the production of his yield, rather than to the production of the other sorts of potential energy-rich particles that are involved in population maintenance. He is also concerned with the energy per unit time of his yield.

He would, therefore, like an equation for the population's energy budget which will include both his yield and the standing crop, ignoring other possible yields.

The energy diverted from standing crop maintenance is $\Delta c P'$. His yield is Y_i. We define

$$E_{pi} = \frac{Y_i}{P' \Delta c} \tag{6}$$

We will call E_{pi} population efficiency. Arranging his exploitation programme so as to maximize E_{pi} will give the exploiter his most appropriate exploitation procedure since he will then be getting the maximum yield per unit depletion of standing crop. The energy budget which is of primary interest to him is

$$I = P'c + \frac{Y}{E_p} \tag{7}$$

or, if he also takes yields of the sorts $j, k, l \ldots$

$$I = P'c + \sum \frac{Y_i}{E_{pi}} \tag{8}$$

where E_{pi} (population efficiency) is given by

$$E_{pi} = \frac{P_i}{P'(c + \Delta c) - \frac{cP'}{P}} \tag{9}$$

Equation (8) represents a particularly interesting energy-budget equation for a single species since it combines certain properties of all three energy-budget equations. Since yield is consumed within a community, Eq. (8) reduces to Eq. (2'), for complete communities.

In summary, the various equations that have been utilized for energy studies in ecology can be intertranslated in a straightforward manner. They differ primarily in the kind of data used and in emphasis.

III. Entropy and Information in Ecology

A review of energy relations in ecology can be written with suitable incorporation of all relevant data, without ever mentioning either entropy or information in their rigorous meanings. Several recent authors have, nevertheless, felt it of value to discuss ecological energetics in terms of entropy and information. Since the theory of information has been developed, specifically, to deal with communication problems, such as determining which of a particular set of messages was actually transmitted through a communications channel which was not perfect, it is immediately adaptable to situations in which the investigator's concern is with the distribution, organization, number or arrangement of entities in an imperfectly understood situation about which he has some partial knowledge.

Margalef (1958), Hairston (1959), MacArthur (1960), and MacArthur and MacArthur (1961) have used communication theory in this way to great profit. The significance of their work has been discussed at some length by Hutchinson (1959) and Slobodkin (1961a,b).

Occasionally, information theory has been used as an analogy to suggest models that might be of ecological interest (MacArthur, 1955).

There exists a certain formal correspondence between the rigorously defined concept of information and the rigorously defined concept of entropy.

In particular

$$H = \sum_{0}^{n} P_i \log P_i \tag{10}$$

represents the information H in a set of n independent messages, each with a probability P_i of being transmitted.

An expression of the same form is used in the definition of the statistical mechanical concept of entropy.

The statistical mechanical concept of entropy is in principle equivalent to the thermodynamic concept of entropy and changes in entropy are measurable for chemical systems at known pressures and temperatures by using the relation.

$$\Delta F = \Delta E - T \ \Delta S + P \ \Delta V \tag{11}$$

in which P is pressure, T absolute temperature, ΔV and ΔF are changes in volume and free energy, ΔF is the change in energy level of the system, defined as $Q - W$ where Q is the heat evolved during a transformation and W is the work done.

ΔS is defined as $\frac{Q}{T}$ or entropy change. The system is assumed to be thermodynamically isolated.

It would be very nice if we could, by suitable measurements, measure the various terms in Eq. (11) and, thereby, utilize the full theoretical power of thermodynamics in our analysis of ecological systems. The second law of thermodynamics, which can be verbalized as follows, "In an isolated system, the internal entropy is maximum when the system is in thermodynamic equilibrium", must be considered applicable in some sense to ecological communities. Apart from other theoretical and operational difficulties, which we will discuss below, an immediate problem arises from the fact that an ecological community cannot in any sense be considered as thermodynamically isolated, nor can any system containing a living organism be considered in thermodynamic equilibrium.

The equivalent law for a non-isolated steady state system is Prigogine's theorem which has been stated as follows by Foster *et al.* (1957): "In an open system, the rate of internal entropy production, which is always positive, is minimized when the system is in a steady state." An open system is defined by these authors as one which exchanges both energy and matter with the ambient universe. They, then, made a theoretical analysis which is immediately germane to the problem of the relation between thermodynamics and ecology.

They considered an electronic circuit in which internal entropy production is simply and directly proportional to the heat production or power dissipation by the resistance and is directly calculable from Kirchhoff's Laws. They find that for certain simple circuits the open system second law of thermodynamics actually does hold.

However, if feedback occurs within the circuit, Prigogine's theorem does not necessarily hold. If the system is characterized by the presence of interlocking feedback loops, the theorem only holds if arbitrary

restrictions are introduced. Even for the case of uncrossed or non-interlocking feedback loops, the theorem is only valid if the power source for the feedback loop is contained within the system.

The degree to which an ecological community can be analogized to an electronic circuit is arguable (see Slobodkin, 1960), but it is clear that ecological communities are feedback systems of high complexity in which the power source for the feedback components, even if they could be physically distinguished in the way an electronic feedback component can, is almost certainly external to the system. For ecological communities, it is, therefore, impossible to make any unequivocal statement at all about the relation between steady state conditions and the rate of entropy production. Obviously net cosmic entropy is increased by the activity of ecological communities, but this is not a particularly surprising or heuristic conclusion.

Foster, *et al.*, continue with a general analysis of the limits of applicability of Prigogine's theorem but this is not of immediate ecological concern except to note that they were unable to find any other thermodynamic property that could be theoretically demonstrated to reach either a maximum or minimum when any complex feedback system comes to a steady state.

It might be noted concurrently that if the mass of an open system stayed constant, and if the rate of entropy production came to a minimum, the total entropy of the open system must also come to a minimum. While ecological communities may meet the first condition, we have no reason to believe they meet the second. The often repeated statement that evolution tends to lower the entropy of living organisms is not clearly demonstrated and is of problematic value.

Therefore, the most interesting theorems of thermodynamics don't seem to apply to ecological systems in any direct way. The interest of translating directly measurable ecological parameters into the language of thermodynamics is not obvious. Nevertheless, several authors have attempted this translation and have produced conclusions which might at first glance be mistaken for empirical generalizations. The two major recent expositions of the application of thermodynamic theory to ecology are those of Patten (1959), and Odum and Pinkerton (1955).

Patten quotes the aphorism of Schrodinger (1946): "What an organism feeds upon is negative entropy. Or, to put it less paradoxically, the essential thing in metabolism is that the organism succeeds in freeing itself from all the entropy it cannot help producing while alive."

Schrodinger points out, in support of the notion that negative entropy is what is consumed by organisms, the apparent lack of logic in metabolism. That is, "Any atom of nitrogen, oxygen, sulphur, etc., is as good as any other of its kind. What would be gained by exchanging

them?" and also, "For an adult organism, the energy content is as stationary as the material content since, surely, any calorie is worth as much as any other calorie. One cannot see how a mere exchange could help" (Schrodinger, 1946).

This is not merely a jocular or trivial point. It is possible to conceive a world in which organism-like entities do actually require only enough food to make good entropic gain and do not replace existing biomass. It is equally possible to imagine an astronomical world in which planets follow the eminently logical paths of epicycles. The reason for an organism requiring energy may be obvious, but after Schrodinger's question, it may deserve restatement. Organisms are not exchanging one calorie for another nor are they only maintaining body heat and performing the other energy-utilizing operations of normal physiology. When the first animal ate its first plant, the animal was not exchanging, it was gaining. To meet the conditions set by natural selection, the plant had to increase its rate of incorporation of energy to make good the loss to the animal or it would have disappeared in the process of evolution. Animals need energy to make good their loss of energy to other animals. We're not simply dealing with a steady state system sucking in negative entropy to maintain itself against the laws of thermodynamics, but we have a whole set of such systems, each one acquiring energy and matter at the expense of other organisms to make good its losses to yet other systems. The only reason for this state of affairs is that the systems or organisms which behaved in a rational way, as if they understood Schrodinger, have long since been eliminated by natural selection.

The energy losses of an organism in a population are not simply heat. Corpses, faeces, exudates are all necessary by-products of evolutionary success. The rate of energy passage through an organism or population can, in fact, be altered by altering the predation rate, and this is different from increasing the population's heat production. If a closed system including a living organism is considered, the metabolic activities of the organism in maintaining itself in an unchanged condition result in an entropy increase in the closed system. If it were possible in principle to measure the entropy of the isolated organism itself, this would have been found to be unchanged. Therefore, the organism is acting to increase the entropy of the world around it.

Patten carries the paradoxical part of Schrodinger's statement further by stating that living organisms feed upon negative entropy to compensate for information losses attending the life process (Patten, 1959). Here the formal similarity between information and the statistical mechanical concept of entropy is taken to demonstrate identity between information and negative entropy. However, information in

communication theory does not have temperature as a significant parameter nor can the complete array of states be specified so as to permit a statistical mechanical definition of entropy to be operationally evaluated in any biological system. In short, while certain analogies between parts of ecological energetics and parts of thermodynamics can be verbalized, there is no evidence whatsoever that these are necessary or even fruitful for the advance of ecological comprehension.

Not only are thermodynamic analogies current in the literature but circuit diagrams and hydrostatic flow diagrams are also taken as analogies. All of these violate common sense. Note the statement by H. T. Odum (1960) in discussing an analogy between electric circuits and ecological communities: "The validity of this application may be recognized when one breaks away from the habit of thinking that a fish or bear, etc. takes food and thinks instead that accumulated food by its concentration practically forces food through the consumers." To my knowledge this sort of analogy has produced neither suggestions for practical experiments nor significant syntheses.

IV. Lindeman's Theoretical Formulation

The classical initial study of energy-passage through a natural community is that of Lindeman (1942).

The framework into which Lindeman fitted his data was essentially the following. Assume all organisms in a natural community to belong to one and only one of the trophic levels designated by $A_1, A_2, A_3 \ldots A_n$ such that any organism at trophic level $A_{i>1}$ is nourished by eating organisms of trophic level A_{i-1}. Trophic level A_1 consists of autotrophs deriving their energy from the sun. The energy passed per unit time from trophic level A_1 to trophic level A_{i+1} is designated as λ_i and is referred to as the productivity of level A_{i+1}. A problem has risen in the literature about whether the food consumption or the protoplasm synthesis of A_{i+1} should be called its production but this problem is not of fundamental importance for our immediate purpose. I'll try to keep the concepts clear as we proceed. A_i is a standing crop with a dimension of calories, λ_i has a dimension of calories per time and both are calculated per cm² of surface.

There is a relation between the concept of trophic levels and that of food chains but the two concepts are not identical, the first being a simplifying assumption while the second is purely descriptive. If a diagram of the passage of all high-energy molecules through an ecological community is made, it will be found that the potential energy of any given molecule will either have dissipated as heat in or near the body of some organism or been transferred to some other organism. The individual organisms can be arranged by drawing arrows to a point

representing any organism from the points representing all other organisms from which it has at any time received a high-energy molecule. The resultant network of arrows is a food chain. Since objective taxonomic criteria of specific discreteness exist, it is possible to superimpose all points representing organisms of the same species, which considerably simplifies the diagram. The concept of trophic level is based on the assumption that in any food-chain (or food-web) diagram there exist classes of points, each class being defined by a constant number of arrows intervening between any point in the class and some initial point characterized by the absence of arrows directed towards it (i.e. an autotroph). This also carries the implication that there is always a fixed number of arrows, or food-chain links, in the passage from an autotroph to any particular species, regardless of the route chosen. If this assumption is met, then all points characterized by a constant number of arrows (i) between them and an autotroph can be collapsed into a single point. The mean standing crop of all species represented by this single point is called Λ_{i+1} since autotrophs are Λ_1. All arrows leading to this point can be collapsed into a single arrow and the total energy flow represented by this arrow (in cal/time) is referred to as λ_i.

Several questions are raised by this formulation and the attempt to answer these questions empirically and theoretically has occupied most of the workers in the field of ecological energetics ever since Lindeman's paper appeared.

1. Is there any maximum number of possible links in a food chain? In a stronger form, we could ask, is there any characteristic number of links in a food chain.

2. Is there any characteristic ratio between standing crops of species at different locations in a food chain? In the terminology of trophic levels does knowledge of the indices i and j of two trophic levels predict in any sense the ratio $\Lambda_i : \Lambda_j$.

3. Are there any constancies in the ratios of the productivities of a species and the predators feeding on it? That is, is $\dfrac{\Lambda_j}{\Lambda_i}$ a constant? This ratio has been called either food-chain efficiency or ecological efficiency by other authors (Slobodkin, 1959, 1960; Englemann, 1961).

4. Are all or any of these questions interdependent? For example, could the existence of a characteristic number of links in a food chain permit prediction of the answer to the other questions.

These questions are independent of the simplifying assumptions made by Lindeman and also independent of the criticism of Lindeman's work which will be stated below.

Since food-chain efficiency is clearly less than one, the greater the

number of links in the food chain the lower the energy income per cm² of earth surface per time of the organisms high in the chain. If food-chain efficiency is constant (say E), the energy income of any species will be proportional to E^i where i is the mean number of food-chain links between that species and the autotrophs.

A species high in the food chain (j) might have an abundance equal to that of a species low in the food chain (i) if the ratio $\frac{c_j}{c_i}$ is equal to $\frac{c_i}{c_j}$ or greater than $E^{(j-i)}$ where E is the constant food-chain efficiency and c is maintenance cost. Since a large part of the maintenance cost of any species is respiration, and since there is no reason to expect a hunter to do less work than its prey, we would not expect species high in the food chain to be as abundant per unit area as those low in the food chain. Should maintenance cost of species be constant, we would expect the abundance of species at levels j and i to be proportional to $E^{(j-i)}$. The classical Eltonian pyramid depends on the fact that typically there is a correlation between body size and trophic level. Reversal or inverted Eltonian pyramids occasionally occur either as a temporary distortion of the normal steady state (Evans and Lanham, 1960) or as a consequence of extremely heavy predation and rapid growth in the lower levels of the food chain (Odum and Odum, 1955).

The maximum number of possible links in the food chain is dependent on relative abundance as a function of food-chain position. Since λ is expressed as cal/area, the food for an animal sufficiently high in the food chain is so dilute as to place it in the position of the sheep which must run, not walk, between grass blades lest it starve to death. The questions raised by the Lindeman formulation are, therefore, intimately interrelated.

There is, however, a serious logical error in Lindeman's study which effectively invalidates all his estimates of productivity and efficiency. This is not simply a matter of slight differences in definition or of high variance in the initial estimates. Since his procedure has been followed by other authors (Dineen, 1953) and his estimates have been quoted in various contexts (Slobodkin, 1960; Patten, 1959; and others) it is of importance to prevent further reliance on these data.

As already indicated, the energy budget for a trophic level can be written as

$$I = \text{Respiration} + \text{Yield}$$

Yield consists of all potential energy leaving the trophic level, including that consumed by predators and decomposers.

Lindeman, however constructed the following energy budget

$$I = \text{Respiration} + \text{Yield} + (\text{Turnover time} \times \text{Standing crop})$$

The final term is superfluous, regardless of the definition of turnover time.

It is not safe to salvage any of the values from Lindeman's data due to his sequential procedure of evaluation. The same remarks apply to the data of Dineen (1953) and to Lindeman's analysis of the data of Juday (1940).

It is of interest that Clarke (1946) does not commit the error of Lindeman but does not point it out explicitly.

The questions raised by Lindeman remain valid and to a large degree unanswered.

V. Daphnia Energetics

Perhaps the most complete study of ecological energetics has been made with *Daphnia* populations in the laboratory. Pratt (1943) demonstrated that *Daphnia magna* populations in the laboratory will fluctuate in even a constant environment. Slobodkin (1954) confirmed this result of Pratt's and showed that size of *Daphnia obtusa* populations in the laboratory is linearly dependent on food supply. The population fluctuations were considered to arise because of age and size-specific differences between the individual *Daphnia* composing the population. A population composed primarily of small, young animals will have a lower feeding rate than a population of the same number of large animals. Growth and reproduction in *Daphnia* are closely dependent on food supply. Under starvation conditions reproduction and growth effectively cease. Mortality is not severely altered by changes in nutrition (Frank, 1960). Given appropriate age and size distribution, mortality reduces competition for food just sufficiently to enhance the reproductive and growth rates of the survivors and this permits the population to return to its initial age structure. It can be shown in theory (Slobodkin, 1961b) that for a species with an essentially rectangular survivorship curve the number of animals of a given age in this stable age-structure is proportional to the inverse of the growth rate at that age. Age-structure change combined with the maintenance of severe starvation and the fact that different sized animals have different food consumption rates requires numerical fluctuations in the population even if the environment is kept as constant as possible.

If animals are removed from *Daphnia* populations by the experimenter at some fixed rate, the size of the residual population is reduced while the linear dependence on food supply persists. When small animals are preferentially removed (see Fig. 3) the relation between population size P_f and removal rate F (expressed as number of animals removed per unit time divided by the births during that time) is given by the simple equation