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Abstract: Some major ecological patterns indicate that the herbivore trophic level (as defined) is regulated in the long run by food. Three levels of factors of population control must be clearly distinguished and have different evolutionary consequences. The remarkably regular evolution of mammalian body size on islands needs study. A consideration of various possibilities does not clearly resolve the Enigma of Balance: How can it be that some species regulated even ultimately by food do not periodically greatly reduce their food supply by overeating?

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Introduction

The subject of this paper is one that is easy to gloss over. It has a remarkable propensity for encouraging superficial thought, and so is often regarded as trivial. Yet it is one of the most important well-defined problems in ecology. It has unexpectedly deep roots, and their ramifications underly apparently quite unrelated matters. Many answers seem plausible until they are put into a broader context. My argument is necessarily convoluted and branched; most of the notes are an integral part of the argument but are separated for ease of reading. I have found the problem intellectually more difficult than any other I have considered, including that of the preceding paper (Van Valen, 1973b).

In their well-known paper, Hairston, Smith and Slobodkin (1960; = HSS) proposed, among other points, that in terrestrial communities the dominant herbivores are predator-limited while dominant predators are food-limited. Murdoch (1966) and Ehrlich and Birch (1967) criticized HSS; most of their arguments were adequately met by Slobodkin, Smith, and Hairston (1967; = SSH). I will present evidence that seems more compelling than that of HSS, that leads to a reverse conclusion, but that does not destroy HSS's argument. The latter now appears as a paradox.

To avoid irrelevant wrangles we can define the "dominant herbivores" of a community as those herbivores that jointly use most of the energy or reduced carbon from plants that is used by all herbivores (cf. Van Valen, 1973a). HSS's conclusion can be rephrased as saying that, of the energy in living plant material that is eaten, most is eaten by species whose local populations are regulated by predation. The overlap of trophic levels can be partitioned in the same way. However, HSS's argument actually leads to a slightly different conclusion: that the rate of energy flow through the herbivore trophic level is regulated by predation. In other words, if the amount of predation on herbivores is changed and the system remains stable and biotically self-contained, the rate of energy flow from plants to all eaters of plants will change to a different equilibrium value. Removal of all predators would be an appropriate if difficult procedure.

SSH distinguished between seed-eaters and other herbivores. Janzen (1969) has pointed out that seeds are young plants and that their loss to herbivores can have an important effect on the plant population; I therefore provisionally include seed-eaters among herbivores (1). Predators include parasites here (2).

Janzen's point is important in a more general context. It is true that if herbivores ate the same proportion of the leaves of a plant as they do of its seeds, the effect would be much greater and usually lethal, thereby precluding future seed production as well. The existence of some level of seed-eating which strains the energy budget of the plant is all that is necessary to regard seed-eaters and leaf-eaters as comparable, though, with reference to a single plant species. The greater proportion of seeds than leaves that can be eaten without serious harm to the plant may explain, via food-limitation of herbivores, the observation that a greater proportion of seeds than leaves are in fact eaten. SSH used the latter pattern to support the unimportance of food-limitation for leaf-eaters, but it is consistent with either alternative. The mechanism poses a problem which I consider later.

HSS proposed predator regulation for herbivores for three reasons: green plants are usually not appreciably depleted by herbivores, weather is usually implausible as a regulator, and regulation by predators seemed the only widely applicable alternative. HSS proposed food regulation for predators simply because of consequences of the argument that the predators regulate their own food. SSH did not substantially modify any of these arguments. The last three arguments may be accepted in the form given and the first seems descriptively unexceptionable (3, 4)

"The world is green" (Slobodkin in Murdoch, 1966). This is the fact (if it is a fact) to be explained. A different way of looking at most of the same issues is to ask how it is that more than one monophagous species (often several) of herbivores coexist locally on a single species of plant. This is related to the nature of a resource (Haigh and Maynard Smith, 1972)(5).

Levels of Control

There are three levels of population control that must be clearly distinguished. The difference of levels is of fundamental importance in evolutionary ecology, and confusion among them seems to have been one of the major difficulties with theoretical ecology in the past decade or more (6). Dominant factors can be defined as those that cause the greatest amount of mortality, suppression of reproduction, and other effects that lower the actual rate of increase of a population below r_m (7). The other two levels operate in the regulation of population density. Proximally regulating factors are those that are density-dependent and sufficiently important to keep population density within some equilibrium range of values. The third level operates more or less on the evolutionary time scale and may be called that of ultimately regulating factors (8). These factors determine the density that can be supported indefinitely by the environment (i.e. how much of the resource space is used) and thereby the level at which proximally regulating factors act. They may operate only in very bad years.

An example where all three levels differ sharply would be a case where most mortality and variation in reproduction were caused over the whole population by weather, apart from the effect of any density-dependent refuges; the usual regulation of density was by rigid territoriality (or density-produced stress, etc); and the size of territories (or the density at which stress occurs) was determined genetically, the thresholds having been originally selected in relation to food supply. In the experimental populations of the weevil Calandra oryzae that Ehrlich and Birch (1967) used as an illustration, proximal regulation is by egg cannibalism and ultimate regulation is by food. Strix aluco, the tawny owl, seems to be a species where all three levels are separate (review by Lack, 1966).

The three levels do not, of course, have to have different factors; one factor (e.g. food limitation) may operate at each level. In fact, not all three levels need to occur in every case. Dominant factors must always occur, by definition and biological reality. Colonizing (or, with different emphases and referents, fugitive, nonequilibrium, r -selected, opportunistic) species may often, perhaps, have even no proximally regulatory factors, which is to say they may never reach densities where such factors would operate. The relative frequency of such species is unknown even beyond an order of magnitude and depends on the frequency of extinction of local populations (9). If local extinction is caused by trophic competition, as it normally is during succession, then regulatory factors must occur. Species or populations regulated proximally by predation (including parasitism) may have no ultimate regulation that acts specifically on them (10), although at some level of complexity the predator-prey systems of which they are members will be subject to ultimate regulation (cf. Van Valen and Sloan, 1966, and below).

Each level of population control has a different evolutionary significance. Dominant factors are of course those most important in natural selection, at least insofar as natural selection operates on the intrinsic rate of natural increase (11). This is not to say that natural selection can't operate importantly on other aspects of the life cycle, such as development rate or meiotic segregation, that are not directly factors of population control. (Development rate is an important part of the intrinsic rate of natural increase and so its determination could perhaps be considered an aspect of population control.)

Proximally regulating factors, on the other hand, are those most important for the K selection of MacArthur and Wilson (1967). I use the term in its original and useful sense, selection to increase the equilibrium density K . This selection operates near equilibrium density and concerns trophic efficiency and the like. Interference competition and defense against predation have a similar relation to proximal regulation but are related to other theoretical parameters. Because proximally regulating factors are those most important in keeping the population near equilibrium density, they will be most important in the selection based on this density.

Ultimately regulating factors are the basis for success or failure in trophic competition. Varley (1949) seems to have been the first to see this. They determine what part of the resource space a species uses. Trophic competition occurs only when two species use the same resource, normally an aspect of food or space in the broadest senses, and then only when this resource is at least ultimately regulatory for at least one of the species (12).

K selection is often regarded as the basis for success in trophic competition. I believe this is wrong in general, for the reasons given above, although it can be true when proximal and ultimately regulating factors are the same. In this case selection to improve competition [which by analogy could be called α selection (13)] would coincide with K selection. Furthermore, the same adaptations are undoubtedly sometimes effective for different proximal and ultimate factors. A larger body size may permit a longer period without food and also be useful in intimidation.

If ultimate regulation happens sufficiently rarely, there may be cyclic microevolution. As an example, mean territory size may decrease because individuals with smaller territories can get enough food, until there is an extreme food shortage, which would remove such individuals.

Even if each species of herbivore (or green plant) is proximally regulated by the next higher trophic level, it doesn't follow that the trophic level in question is so regulated, because the number of species could be ultimately regulated by food. Unused food permits immigration of species to use it, however these species are regulated (10). For this reason, and more

importantly because the level of regulation must itself be determined for the entire predator-prey system, as discussed below, the argument of HSS can lead to conclusions only about ultimate regulation although they state the argument partly in terms of proximal regulation. Predator and prey may each regulate the other proximally, but the joint equilibrium range requires ultimate regulation (14). The fact that the classical predator-prey equations are self-contained, at the level of proximal regulation, is an argument against their adequacy rather than against the biology.

For the sequel it is necessary to define a new parameter, trophic rate of increase (r_t). This is the rate of increase of a population at optimal density in any real habitat, but with competition and predation removed. The removal might be directly done experimentally but is probably more easily done indirectly by determining the effects of competition and predation. r_t obviously depends on the populations' phenotype and habitat, and could be generalized to depend on density. The effective environment here, the niche in a common usage, is the physical environment (including nonbiological interactions of all trophic levels), the trophic levels below that of the species considered, decomposers (for the environment of non-decomposer species), and any commensal or mutualistic effects. Like r_m , r_t must be positive to avoid extinction.

Patterns

The argument of HSS starts on the level of ultimate regulation, with an observation of an apparently under-used resource. There are, however, several observations of comparably general applicability that can be made on the same level and that lead to the reverse conclusion (Van Valen and Sloan, 1966). These observations are of major patterns of the distribution of species in the resource space, analogous to those of Elton (1927) and Jordan (1971), and may be listed as follows:

1. The maximum equilibrium density of large herbivores is much less per species than that for small ones. Compare deer, mice, and aphids in the same forest. This does not of course deny the possibility of rare small species. The same pattern occurs for obligate leaf-eaters.

2. The maximum number of sympatric species of large herbivores is much smaller than that for small ones. The same example applies. Observations 1 and 2 can be combined, as Elton (1927) did for entire communities rather than single trophic levels in his "pyramid of numbers." Such a combination is stronger than either observation separately and is what is directly related to the availability of resources.

3. The density within comparable herbivorous species is usually less in habitats of low productivity than in habitats of high productivity. I know of no data specifically on this point for terrestrial herbivores beyond those reviewed by Lack (1954), but its truth is further supported by the great decrease in insect density in arid regions as one goes from a stream-border community to the dry divides that have little vegetation. How this decrease is partitioned between species diversity and single-species density is conjectural, but either suffices for the argument and I suspect both occur. The fact that here, as with other points, formal studies are inadequate doesn't detract from the value of a strong qualitative observation which is common knowledge and which I have personally observed. It is the qualitative observation itself which is relevant (15).

4. The number of sympatric species of comparable herbivores is usually less in habitats of low productivity than in habitats of high productivity. The evidence for this point is the same as for the previous one but the argument from species number is weaker, since terrestrial predictability and

perhaps habitat diversity are highly correlated with productivity and these may be the important variables (cf. Sanders, 1968, for benthic marine comparisons). Observations 3 and 4 can also be combined.

I submit that none of these patterns can be explained unless the density of the dominant herbivores in any habitat is regulated, at the ultimate level, by food. Proof of such a statement requires elimination of all conceivable alternatives and so is limited by our imagination. Possible alternative interpretations will be evaluated later. The patterns seem to be major structural features of the living world (16) and, like any natural patterns, need an explanation.

The Island Rule in Mammals

As I have remarked elsewhere (Van Valen, 1970) with another emphasis, the regular evolution of mammalian body size on islands is an extraordinary phenomenon which seems to have fewer exceptions than any other ecotypic rule in animals. Small herbivorous mammals increase in size, while carnivores and ungulates, and apparently also insectivores, become smaller. Adult elephants can be a meter tall. The cause of this pattern is unknown and even an adequate description of the pattern itself is unavailable.

Despite some progress, as by Rosenzweig (1968) for carnivores, we don't understand why mammals have the sizes they do. The island rule brings this into focus. Perhaps predation is a component that tends to make herbivores larger; it is commonly believed that this is true (Rensch, 1960). Removal of this vector on many islands would then lead to smaller size. But rodents and lagomorphs become larger. We might complicate the hypothesis by saying that predators prefer middle-sized mammals. This would help somewhat; it predicts the observation (Foster, 1965) that Peromyscus maniculatus is smaller on the two Queen Charlotte Islands that have carnivores (these islands are also the largest, though) than on the other islands. But insectivores then become embarrassing, and Microtus agrestis is as large on the Scottish islands with carnivores as on those without. It would also be desirable to accommodate the Shetland pony. Grant (1965) suggested plausibly that island birds and rodents tend to become larger in order to use a wider variety of food in an area with fewer competitors than on the mainland.

One class of explanations for the island rule involves different sorts of regulations of herbivores and predators. If on the mainland most herbivores are regulated proximally by predation and most predators by food, then removal of each group to islands will have different effects. If there are no carnivores on the islands, the herbivores will have to be regulated by something else, like food, at a perhaps higher density. Klein (1964) has an example of this, with appropriate phenotypic results, in island deer. For predators, on the other hand, food may well be scarcer or less predictable than on the mainland. Smaller individuals need to eat less and so might be selected for, although if food is proximally regulatory in both regions it is entirely unclear why such selection would operate more strongly on islands. Starvation is starvation at any density. If food is relatively scarcer for large herbivores than for small ones, the same implausible mechanism would apply to them as to predators. Thus the explanation is rather general and is limited only by its implausibility, the lack of evidence, and the troublesome application of the island rule to some herbivores on islands that have carnivores. Obviously, the phenomenon needs study.

Outline of the Major Argument

Some ubiquitous patterns apply to terrestrial herbivores as well as to other animals and strongly suggest that the ultimate regulation of this trophic level as a whole, like that of other trophic levels, is by resources, in this case food. The patterns are that there are more small animal individuals than large ones, and that communities with greater primary productivity have more animals. There should also be evolution to use available resources that aren't used. A moderate proportion of herbivores are even proximally regulated by food.

The general conclusion on regulation of herbivores then makes it paradoxical that the world is green. Several ways exist to escape from the paradox, but none seem especially plausible as a general resolution:

1. Perhaps the world isn't green. But it seems to be.
2. Perhaps predation is ultimately regulatory after all, with a reservoir of food in the more abundant decomposer trophic level. But not enough predators seem to act this way.
3. Perhaps predation is ultimately regulatory after all, with each predator-prey subsystem regulating itself. But other species should then immigrate to use the available food.
4. Perhaps the patterns don't require regulation by food. But alternatives are implausible, and the joint herbivore-predator system itself needs ultimate regulation.
5. Perhaps some aspect of space is regulatory. But there is so much space in a forest for animals, even of restricted kinds. We would then have the problem that the world is open.
6. Perhaps greenness persists because herbivores eat as much as the plants can tolerate. But a suitable mechanism is difficult to find; the herbivores don't know in advance that they are overeating.
7. Perhaps the trophic distinction between living and dead plants is arbitrary, so it doesn't matter to the argument if the world is green or brown. But eaters of live food get there first and shouldn't leave available morsels to the decomposers from the goodness of their hearts.
8. Perhaps much that is green is inedible. But every plant has its herbivores, each of which has a positive trophic rate of increase and must somehow be regulated below that rate.
9. Perhaps the degree of palatability depends on the density of the herbivore. But this seems implausible for vertebrate herbivores, whatever validity it may have for arthropods.
10. Perhaps.

Other Evidence

Control of most herbivores at the ultimate level by resources is also suggested by another argument, somewhat weaker but still important. If resource density is irrelevant to herbivore density, as would be true by HSS, then it is hard to understand why other species have not evolved to more or less fill up the interstices in the resource space. At one level the problem is easily resolved, because predator-limited species would evolve randomly with respect to resources and so some parts of the resource space would be empty, although accessible evolutionarily, at any time. The problem reappears, however, when we consider the total system of predators and prey (Van Valen and Sloan, 1966). This system is necessarily at or below the density set by ultimate regulation, and such a density would not exist if there were no ultimate regulation. We do not see very dense populations that literally fill the air, as would sometimes happen without ultimate regulation.

(There would then be a random walk of levels of proximal regulation, since there would be no counterbalance to any force changing any current level of proximal regulation. If the forces in each direction are more or less equal, but applied randomly, the expected density of surviving populations increases without limit.) As a related point, species seem to be packed without major gaps in the resource space; cf. MacArthur and Wilson (1967), Raven (1967), Cody (1968) and Culver (1970, 1972). It follows that there is evolutionary pressure to use unoccupied or under-occupied parts of the resource space (and to herbivory if HSS are right), insofar as these are evolutionarily accessible.

The distinction between living and dead organisms isn't always important. We could think that what herbivores don't eat, decomposers will, so it doesn't matter whether the world is green or brown. The distinction between these two trophic classes is probably best thought of in terms of the reproductive values (Fisher, 1930) of the food organisms, or an analogous parameter that has a constant maximum value until reproduction starts. Such parameters should be evaluated for the present purpose in the absence of predation and perhaps multiplied by the energy available in the prey. Then surplus or senescent individuals that would die anyway will be trophically equivalent to dead individuals, and predators or herbivores compete with scavengers and decomposers. However, any herbivores (and parasitic fungi are such herbivores) that eat potentially reproductive plants will have an advantage because they get there first; this part of the resource space is open to such organisms without interference by decomposers. Therefore the problem remains.

The evolution of plants in response (against palatability, etc) may well be unimportant to the argument although important to the plants and herbivores, because the existence of any positive trophic rate of increase can lead to any equilibrium density. Exceptions to this effect of a positive r_t exist and may be significant; Dixon and McKay (1970) found what can be interpreted as a chemical defense by a tree with an effect on an aphid that depends on the density of the aphid. We have here a model explanation of regulation by food that does not deplete the food. But how general this explanation is, especially for larger herbivores, may be questionable. It does give a causal path for the difference between leaf-eaters and seed-eaters, because seeds lack the power of responding to the intensity of predation on them after they are formed. It is crucial, but insufficient for a conclusion of the unimportance of allelopathy at this level, that, as SSH pointed out in another connection, every plant has its herbivores. This is because each herbivore must have a positive trophic rate of increase and must somehow be regulated below this level (17).

Some patterns similar to those in a previous section give further evidence on regulation by food; e.g., the deer-wolf system is less dense than the aphid-ladybeetle system (including or excluding the other components of both). Since predator-prey systems themselves therefore fall under ultimate regulation, there will be some amount of competition for resources in most habitats, at least occasionally.

If predators ultimately regulate herbivores and are ultimately regulated by them, it is difficult to see what regulates the joint system. HSS pointed out that "all organisms taken together are limited by the amount of energy fixed" and that decomposers (and also primary producers) are resource-limited. It follows by subtraction that the two remaining classes, herbivores and predators, are also resource-limited when considered as a single system or are ultimately regulated below this level. But why should ultimate regulation, if not itself due to relative scarcity of resources, have any relation whatever to the amount of resources? There are many communities on earth, of widely differing kinds, and if the level of regulation of their herbivore-carnivore systems were independent of resources we would expect

many or most of them to be proximally regulated, on occasion, above this level, and even many orders of magnitude above it. Of course such communities would soon experience more or less catastrophic declines, but since these declines would be due to resource scarcity it follows that ultimate regulation by resources occurs even for the hypothetically exempt communities. It therefore occurs for all communities. Because in a herbivore-carnivore system it is the herbivores which are trophically in contact with the rest of the community, the conclusion that ultimate regulation occurs for this system must also apply to the herbivores alone, especially since the large majority of the energy or reduced carbon in the system occurs in the herbivores.

If even every species at one trophic level is opportunistic or predator-controlled, the patterns of food availability would seem to indicate a control of species number by resources. Additional species would then immigrate to use the uneaten food. What is true for each may not be true for all jointly. But the size patterns seem more restrictive on the regulation of individual species.

HSS state that plants which are overgrazed would be replaced by others which are not. Clearly this occurs sometimes, as in the replacement of elephant-eaten trees by grass in East Africa (Wing and Buss, 1970). It does not always occur, however (Rood, 1970; Bartholomew, 1970), and the existence at ecological equilibrium of such cases of bare ground caused by overgrazing makes particularly acute the problem of why overgrazing is not more common. In the intertidal zone and oceanic plankton, algae are commonly more or less eliminated by herbivores (Sutherland, 1970; Beers and Stewart, 1971). Why not on land? Why is it that the grasses which replace the trees are not themselves overgrazed, by something other than elephants? Again it is important to note that every plant has its herbivores.

Small animals tend to have a larger trophic rate of increase (r_t) than do large animals, in a causal feedback with higher mortality, but this is irrelevant to average density for equilibrium species. For colonizers it would give the observed result, yet it is inadequate. Aphids are more numerous than voles, and both have some attributes of colonizers. Clearly, if aphids had as small an r_t as voles, expressed in units of absolute time, they would be much less numerous and perhaps extinct. We see, though, that if voles did become as numerous as aphids there would be a rapid depletion of suitable vegetation. r_t can evolve in part independently of body size. The amount of energy available sets a limit to the amount that can pass through herbivores, however the latter may be partitioned in body size and species. (Some preliminary results of mine indicate that the partitioning is variable but rather predictable.) Without ultimate regulation, ordinarily by food, there seems to be no reason why even each colonizing species should not often be, say, a million times more numerous than it is (18). In fact, if there were extreme colonizing species and so r_t and dispersal were all that ever mattered, a species with as low an r_t as a vole shouldn't exist. Species that do not sometimes experience regulation may therefore be rare.

Body size has other effects. A given environment tends to be of a larger grain size for small animals, i.e. their small size in itself helps them distinguish among aspects of the environment that would be more uniform to a larger animal. They should, therefore, often have a competitive advantage; cf. Levins (1968). This and other disadvantages of large size are often offset by advantages (Rensch, 1960). It is therefore unclear why grain size should have a different status from other adaptive aspects of body size. It is not an imposed constraint, as is resource availability. Perhaps there are more species of small animals because they can partition the environment more finely. This would be related to ultimate regulation

by resources because it is determined by trophic competition, so it does not affect the argument.

Large terrestrial species have fewer refuges from predation and so might be considered more susceptible to predation. This reverses the usual, and I believe well-founded, statement of the relationship. There are many small predators, and larger body size is a protection against them; large predators often eat much smaller prey (wolves eat mice, skunks eat insects, etc.) (19).

If leaf-eating herbivores compete for food they should, in appropriate cases, exemplify the common phenomena of character displacement and ecological release in feeding-related structures and behavior. This would then imply ultimate regulation by food. I know of no evidence on this point (20).

Darwin (1859, pp. 67-68), Paine (1966, 1971), and others have found that a predator often (not always: Harper, 1969) permits coexistence of more species than could coexist in its absence. This is commonly believed to indicate relative unimportance of resource partitioning in coexistence. The reverse, however, seems to be the case. When adequate analysis is made of such cases it is the competitively dominant species that is predominantly harmed by the predator. This reduces its competitive advantage in relatively marginal situations and forces it into a smaller niche, where it is still superior and from which it can overflow into other niches if predation decreases (Van Valen, in press).

Conclusion

I interpret the total argument above, in conjunction with HSS and SSH, to indicate that dominant herbivores, like green plants, decomposers, and carnivores, are ultimately regulated by food. This is a somewhat odd conclusion because it requires each trophic level to be regulated by the one below without in turn regulating it. The distinction between proximal and ultimate regulation may help, because the regulation from below can be ultimate while that from above cannot be. The large overlap in trophic levels may also help.

There seems to be evidence, therefore, that decomposers, green plants, herbivores, and predators all experience ultimate regulation of population density to an appreciable extent. What then are we to do with the observation of an apparently highly under-used food resource, palatable living leaves? "The world is green." If ultimate regulation occurs only very rarely, this would suffice, but known mechanisms seem to require it to happen too frequently to be invisible. Perhaps one of the observations (such as palatability) is wrong, although this would need to be shown. In areas dominated by annuals, perennial herbs that die down in the winter or dry season, and deciduous woody plants, the problem is not acute because herbivore regulation could be in the unfavorable season. Diapause often alleviates this seasonal severity, however, and the abundance of communities with leaves present throughout the year makes it irrelevant to the general problem. Many insects feed on flowers, which are only seasonally available for most species (Evans and Murdoch, 1968). Hughes and Gilbert (1968) suggest that there is not in fact much under-utilization of green plants, because they need their green parts to survive and may need about as much as is left to them by the herbivores. Raves (1970), Batzli and Pitelka (1970), Wing and Buss (1970) and others imply the same conclusion.

The problem nevertheless remains. With unused food in the plants, however necessary to the plant population, there should be intraspecific selection in herbivores for use of this food if the population is proximally self-regulated. Greater use might eliminate the food plant (Wiegert and

Owen, 1971), but the herbivore doesn't know this before it happens. Immediate effects of overuse will often be distributed among the entire herbivore population, not just one family, so kin selection for self-regulation seems implausible as a general mechanism. Group selection is too weak to offset individual selection (Maynard Smith, 1964), a conclusion which also applies to selection among ecosystems. This statement is not contradicted by recent use of group selection in special contexts (Levins, 1971; Van Valen, 1971) (21). Wynne-Edwards (1962) has discussed the general subject from a different viewpoint. Interference competition, such as territoriality or allelopathy, is relevant only to proximal regulation, since its level is determined by ultimate regulation.

An alternative explanation for the strong relationship between insect abundance and plant density in dry areas is that the plants provide a suitable microclimate, especially in relation to conservation of moisture. Then plant productivity controls insect abundance but by a component of space rather than of food. This seems plausible, although I know of no studies that distinguish the alternatives other than proximally. It apparently doesn't explain the regulation of insect abundance in moist areas, even river valleys in arid regions. There may be a correlation between productivity and the abundance and diversity of refuges from climate and predation. Satisfactory refuges differ extremely among different kinds of species, though, and it must be shown that these vary together or that one kind is predominantly important. Plant material also can provide cover from predators, so its density may be directly related to susceptibility of an animal to predation. Ultimate regulation, however, would explain why the predator-prey system is at its actual level rather than at some very different level, and unless there is a sufficient reservoir of prey in the decomposer trophic level (22) it is clear that predation cannot ultimately regulate the system. If predators survived by eating plant material when animal prey was insufficient, their ultimate regulation would then be by the abundance of plant material for food, which would thereby regulate the system.

Space is ultimately regulatory for many motile as well as sessile species, and it may be that this somehow provides a way around the dilemma. However, the difference between seed-eaters and leaf-eaters is then unexplained; the path is still foggy and the light may be an ignis fatuus. Moreover, many species seem to lack restrictive space requirements and should immigrate or evolve to use the available food.

Regulation of terrestrial herbivores by plants, and probably ultimate regulation by food, can be seen in the fertilization experiment of Hurd, Mellinger, Wolf, and McNaughton (1971), which was done for another purpose but in which arthropod herbivores consistently increased in the fertilized areas with more plant productivity. Vertebrate herbivores, however, were not considered. Elaboration of this approach and those of microclimate and density-dependent allelopathy, consideration of rarity of a plant relative to the dispersal of its specialized herbivores, measurement of the effect of removal of appropriate predators from natural communities, and study of simpler natural systems that are trophically more or less self-contained, may be the best means of attack.

The egestion of sugars by sap-feeding insects suggests that energy availability is not directly limiting to them even ultimately, but if ultimate regulation is by, say, nitrogen availability the effect on the plant is the same because the sugars are lost whether used by the aphid, an ant, or a decomposer. If proximal regulation of herbivores is usually by predation, suitable space, or other external means, this regulation limits the scope of selection for use of more food but does not eliminate the problem because another species could then immigrate and use the remaining food. This

species is presumably in fact absent because it is outcompeted by the species already present, but competition for food requires ultimate regulation by food and therefore a relative shortage. In extreme environments which only a few species can tolerate, immigration may be unimportant unless the environment lasts long enough for evolution to occur in other species, but such environments are rather rare and so do not affect the problem.

The problem is sufficiently acute that I give it a name, the Enigma of Balance: How can it be that some species regulated even ultimately by food do not periodically greatly reduce their food by overeating?

Acknowledgments

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Notes

- (1). Seed-eaters may never affect the total amount of plant material in an area, or more precisely may never affect the total primary productivity. If leaf-eaters often do (and they do sometimes, as discussed later), then it might seem that seed-eaters are irrelevant to the problem after all. SSH agree that seed-eaters are regulated by food. For the purposes of the present paper, it doesn't matter whether one considers seed-eaters to be herbivores; the arguments apply to both cases.
- (2). The usual depiction of a food pyramid is incomplete; it should end with the highest level of parasites, not the highest level of predators, when these are (as usual) distinguished. Lions are food for fleas.
- (3). Pulliam, Odum, and Barrett (1968) and Perkins (1970) think that the higher equitability they found for predaceous insects and fish than for herbivorous ones supports resource limitation for the predators and not for the herbivores, but the work of Cohen (1967, 1968) and Sanders (1968) in different ways makes this argument suspect in that equitability can have diverse causes. This does not, of course, affect the argument of HSS.
- (4). It has been suggested that a mathematical treatment of the subject would be preferable. I am hardly anti-mathematical (I teach a short course in biometrics), but I don't see how at present a useful mathematical version could be either more rigorous or anywhere nearly as general. Its persuasiveness would be spurious because the mathematical context is inadequate. The common prejudice against non-mathematical theory is curious for a subject like ecology whose mathematical foundations are of shifting sand.
- (5). If a predator has alternate food, it can regulate an indefinite number of preferred prey species. Man in fact does so, partly by this mechanism. Such verbal (and trivially quantifiable) counter-examples to a mathematical theory require getting outside the theory to think of them or even consider their validity.
- (6). The first person to distinguish between proximal and ultimate regulation seems to have been Baker (1938). Lack (1954) followed him in this, and Van Valen and Sloan (1966) made the same distinction with different

terms. Nevertheless, the distinction is almost universally ignored, perhaps in part because it has never been incorporated into the mathematical theory. Such incorporation can be done directly but is on the next level of abstraction from the received theory. A danger in mathematical theory in biology is that the assumptions tend to demarcate the development of subject. This is particularly serious when, as with ecology, the assumptions are known to be wrong although useful. They are simplifications rather than idealizations in that the results are sometimes importantly wrong too.

- (7). By r_m I mean the maximum rate of increase of a population with a stable age distribution; the conditions under which it occurs define the optimal environment and density of the population.
- (8). Ultimate regulation can itself have more than one level. For instance, the amount of food may be ultimately regulating but a greater range of food might permit a greater control of energy. Then the second level of ultimate regulation is whatever it is that keeps such a greater range of food from being achieved. A recent fascinating account by Isaev and Khlebopros (1973) of the beetle *Monochamus urussovi*, differs in that a great expansion of diet occurs regularly at high densities. Presumably the added kinds of food are suboptimal and contribute to proximal regulation, but this is not clear from the report.
- (9). It may be possible to estimate the maximum frequency of such species in animals most easily, although very roughly, by seeing what proportion of species can be included in a set to which the patterns described in the next section do not apply. For plants, at least easily visible ones, and for similarly immobile animals, direct observation is possible and should be attempted, although for perennials a very long time is clearly necessary. For some species historical records may be appropriate, although these are most likely to be available in disturbed areas, and for some cladocerans (cf. Deevey, 1969) and perhaps a few other cases the fossil record may be directly applicable.
- (10). It is appropriate here to note Janzen's theory of the promotion of tree diversity in tropical forests by the action of species-specific seed predators that eat every seed that falls near the parent (Janzen, 1970). This produces an entirely self-contained system and there would be much bare ground if only one tree-herbivore pair existed. Of course others then immigrate, so the mechanism isn't directly relevant to the regulation of the herbivore trophic level. Haldane (1949) had proposed a structurally similar regulation based on disease.
- (11). The symbol r has several related meanings, at least two of which are often confused (cf. MacArthur and Wilson, 1967, pp. 78 and 149): the intrinsic rate of increase and the rate of change in actual population size. Andrewartha and Birch (1954) and others have used separate symbols. Because of the apparently unresolvable ambiguity of the symbol r , I propose that the actual rate of change of a population's size or density be called r_a .
- (12). There can of course be no competition for a resource that is always superabundant relative to the needs of both species and that they have no difficulty finding, like oxygen for air-breathers, and competition does not exist when the limiting resource is everywhere reduced by an extraneous cause that has a much greater effect than the organisms, as for oxygen in a reducing hypolimnion. The latter effect is equivalent to that of other harsh habitats but is often regarded as trophic competition.
- (13). In the received theory α refers to both trophic (and other resource) and interference competition, which affect different levels of regulation.

It would be useful to separate these two processes.

- (14). It is impossible for a population to be regulated proximally at any one time by more than one factor, whether these factors are at one or more trophic levels, unless the weaker factor increases the sensitivity of the population to the stronger factor. This happens, in other words, if (for resources) an increase in either lets the organism survive on a smaller amount of the other per individual. More precisely, a given strengthening of a factor A (decrease if a resource, increase if a physical stress or predation) without change in factor B decreases equilibrium population density in a given environment from a level $\underline{u}$ by some proportion $\underline{x}$, which provides a comparative measurement scale. A given strengthening of factor B without change in factor A decreases equilibrium density from $\underline{u}$ by some factor $\underline{y} \leq \underline{x}$. The same strengthening as before of both factors simultaneously, decreases equilibrium density from $\underline{u}$ by a proportion $\underline{ax}$. The value of $\underline{a}$, which may be a function of the changes in A and B, measures the interaction. If and only if $\underline{a} > 1$ can the population be said to be regulated proximally by both factors simultaneously. This occurred, for example, in an experiment with *Daphnia* (Slobodkin, 1961), seems to be common for photosynthesis, and was perhaps first noticed by Darwin (1859, pp. 67-68). Proximal regulation at appreciably different times or places by any set of different factors is of course not excluded. The regulation is of one parameter (we can think of it as density or $\underline{r}_a$); separation into two parameters, as is sometimes done to give an appearance of double regulation, is therefore misleading even though double regulation does sometimes exist.
- (15). Fautin (1949-1957) has given data on cricetid mice (largely herbivorous; *Onychomys* is absent) for altitudinally separated communities in Wyoming, but the productivity of these communities is unknown. I have included only 3-day standard censuses and used unweighted means of all years for each locality; most localities were sampled for several years. For seven localities in the drier and lower habitats, sagebrush and grassland, the mean number of mice per year per locality was 11 and the mean number of species was 1.6. For 3 localities of mountain mahogany chaparral, the values were 53 and 2.4. For 4 localities of coniferous forest, the values were 18 and 3.2. The only, or the only other, value apparently odd is from 3 localities in aspen, which had values of 8 and 1.6. All comparisons except aspen and grassland are pairwise significant. Most of the mice are largely granivores rather than herbivores in the sense of SSH. The example is weak. Rosenzweig and Winakur (1969) compared numbers of species and individuals of largely herbivorous mice on 11 to 15 plots in arid regions of Arizona in 2 successive years. They have a measure of total foliage for each plot, which is here presumably related but far from identical to productivity. Their data give correlations between foliage and number of species of 0.10 and 0.72 (only the latter significant) and correlations between foliage and number of individuals of -0.16 and 0.54 (neither significant). For the ocean, Blackburn (1966) and previous workers whom he cites have found a positive correlation, among stations, between the density of herbivores (zooplankton) and plants (phytoplankton). Wynne-Edwards (1962, pp. 2-3) reviewed similar data for marine birds and phytoplankton, as did Lack (1954) for other aquatic birds. The seasonal correlation of abundance of edible plants and herbivores, reviewed by Hutchinson (1966) for the limnoplankton, may also be relevant.
- (16). The ambiguity of the word "biosphere" is amusingly evident from the September, 1970, issue of Scientific American, which had this word as its theme.

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because decomposers and herbivores are for the most part sufficiently different that different predator species specialize on each class.

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- (17). There can sometimes (Zomnicki, MS) be a regulated balance between herbivores and a polymorphism for palatability in the plant. The extent of conditions that will give such a balance is unknown but seems, on its face, to be rather narrow and so inapplicable to the general problem of the trophic level.
- (18). Horn and MacArthur (1972) have recently discussed a problem equivalent to the ultimate regulation of fugitive species.
- (19). It may be that an average species of large animal has a greater probability of extinction than an average small animal. For mammals this is not true but for foraminiferans it is (Van Valen, submitted); however, even rats are much larger than most herbivorous animals. Although phyletic size increase is more common than a decrease, the large majority of large animal species are derived from other large species. Therefore, if they become extinct more readily, they must also speciate more readily, for there to be an approximate steady state. So this approach does not help in explaining the relative abundance of large and small animals.
- (20). There is, as a subsidiary point, direct evidence for even the proximal regulation of some individual species of green plants by herbivores under natural conditions, and of herbivores by their food. Some species of Acacia grow only when the major herbivores are removed or discouraged by specialized ants (Janzen, 1966, 1967a,b). Undoubtedly there is also a resource limitation for these species of Acacia, but it is not known whether they approach it. An interaction in regulation of Acacia is of course also possible. Other references to the phenomenon among terrestrial herbivores are for a mite (Watson, 1964); various insects (Huffaker, 1957); a moth (Cactoblastis; review by Nicholson, 1958); aphids (Sluss, 1967; Way, 1968, with additional references; and Hughes and Gilbert, 1969); a pigeon (Murton, Westwood and Isaacson, 1964); mice (including voles) (Ashby, 1959; Pitelka, 1959; Bendell, 1959; Findley and Jones, 1962; Cameron, 1963, 1965; Raun and Wilks, 1964; Caldwell, 1964; Whitaker, 1967; Tast, 1968; and Koplin and Hoffmann, 1968); rabbits (Williams and Caskey, 1965); deer (Robinette, Julander, Gashwiler, and Smith, 1952; and Teer, Thomas and Walker, 1965); and antelope and other African ungulates (Vesey-FitzGerald, 1960; Talbot, 1962, 1963; Talbot and Talbot, 1963; Lamprey, 1963; Gwynne and Bell, 1968; Bell, 1970; Stewart and Stewart, 1970; Jarman, 1971; but not Van Zyl, 1965).
- (21). There may be a similar situation, on the next trophic level, for the tsetse fly, which Glasgow (1963) has claimed takes about as much blood from its ungulate hosts as they can stand. There is, however, a density-dependent defensive response by the ungulates, which react more strongly when there is a greater ratio of tsetse to ungulate. This may well remove Glasgow's mystery here, for the ungulates determine their own reaction and could govern it, proximally or ultimately, by their loss of blood.
- (22). On land 80 or 90 per cent of the energy in green plants, sometimes even more, goes to decomposers, not herbivores (Odum, 1971). Because little reduced carbon is buried (probably less than 10 per cent of net primary productivity even in peat bogs: Reader and Stewart, 1972), it follows deductively that at equilibrium much more energy goes through decomposers than through herbivores. Much of this energy is available to predators, so we might think that predators could retreat to decomposers when herbivores became too scarce and thereby give an ultimate regulation of the herbivore trophic level. Any herbivore that reappeared would be snapped up. Obviously this doesn't happen, presumably