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The Importance of a Relative Shortage of Food in Animal Ecology

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Summary. It is proposed that for many if not most animals – both herbivore and carnivore, vertebrate and invertebrate – the single most important factor limiting their abundance is a relative shortage of nitrogenous food for the very young. Any component of the environment of a plant, by varying the amount of adequately nutritious plant tissue available to herbivores, may consequently affect the abundance of food through all subsequent trophic levels; in this regard weather may be important more often than is immediately obvious.

The hypothesis proposes that animals live in a variably inadequate environment wherein many are born but few survive, and leads to a concept of populations being "limited from below" rather than "controlled from above". And it may lead to a reappraisal of the role of predation, competition and social and territorial behaviour as factors likely to influence the *numbers* of animals in the environment, the response of "pests" to manipulation of populations of their food plants by Man, and the likely effectiveness of agents of biological control.

I. Introduction

Most ecologists would agree that the ultimate limit to the abundance of any species of organism must be set by the supply of some resource in the environment. If pressed in a theoretical argument, most would agree that, for animals, food is the most likely candidate for this limiting resource. But, in an empirical discussion, few would agree that the usual and immediate factor limiting the number of animals in nature is a shortage of food – that the natural world is a *passively* harsh and inhospitable place wherein survival of the individual depends not so much on the intensity of attack by other organisms as on the chance of finding enough suitable food.

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This paper extends and expands an earlier hypothesis relating to herbivorous insects (White, 1969, 1974, 1976) to include mammals and birds, and both herbivores and carnivores. The hypothesis is that the component of the environment which seems to exert the major influence on the abundance of animals is a relative shortage of food for the very young; that for most of the time there is an inadequate supply of too-thinly or too-patchily dispersed nitrogenous food in the environment, and most young animals cannot get enough of this food to maintain their very rapid growth. Occasionally, however, for some populations, and for varying lengths of time, the amount of this food available in the environment may be increased to the point where many or most of the young produced do get sufficient, and their numbers increase greatly. Variation in the weather (especially of the amount of rainfall) seems to be the major factor influencing the amount and nutritional quality of the food available for herbivores. Their predators and parasites – the carnivores – appear to have little influence on either increases or decreases in the abundance of their prey, being in turn limited largely by the supply of food available to them for the successful rearing of their young[1].

Having discussed evidence in some of the recent literature on populations of vertebrates which seems to support this hypothesis, the paper goes on to suggest how the hypothesis, if true, might clarify our understanding of some ecological mechanisms and modify interpretation of the significance of predation, competition and self regulating mechanisms as factors influencing the abundance of animals. It may also modify our understanding and use of predators as agents of biological control of pests of Man's crops.

II. The Concept of an Inadequate Environment

In a great deal of writing about population ecology the concepts of "regulation" and "control" are paramount, indicating an implicit belief that in an environment in which resources are apparently rarely if ever fully used, some factor or factors must actively operate to keep the numbers of animals within certain predetermined bounds, or to return them to some predetermined mean density. If not their numbers would soon swamp the world. This usual way of thinking about ecological mechanisms is well illustrated by the following paraphrased quotation from Harper and White (1970). "(One of) The major stimuli to the development of a study of the dynamics of ... populations ... was Darwin's emphasis and re-emphasis of the *struggle for existence that follows remorselessly from the capacity of organisms to increase their numbers exponentially.*" (my italics). Rather, the reverse view may be more useful, i.e. that *the capacity of organisms to increase their numbers exponentially follows remorselessly from the struggle for existence.* To survive on this earth is, and always has been – especially for the very young – a struggle, a very chancy business. So much so that to survive, organisms have had to evolve the capacity to produce many more

[1] In this paper I use the term predator as defined by Andrewartha (1970) to include all organisms using the host as food

offspring than are likely to survive to maturity and reproduce. I suggest that this capacity did not evolve to provide a struggle for existence as a vehicle for evolution, but rather it evolved because only in a population in which each female produced many offspring did sufficient individuals survive in each generation to enable the population to persist.

An alternative hypothesis that is equally tenable is that for most, if not all species of animals (independent of their trophic level) during most, if not all, generations, they must struggle merely to persist in a passively hostile, inadequate environment, the quality of which is fluctuating, for most of the time, randomly with respect to the number of animals in the population.

Exponential increase in numbers does occur in nature, but for only very brief periods. And then it illustrates, very forcibly, that in an *adequate* environment in which most or all the progeny survive, the production of many offspring is a selective *dis*advantage, rapidly leading to destruction of some resource in that environment. In fact, all ecological studies – with some important exceptions that I will mention later (pp. 78 and 79) – are dealing with situations in which individual organisms are struggling to survive in an environment which is variably inadequate, especially for very young animals when they are first thrust out to fend for themselves.

But in what way is the environment inadequate? If we approach the interpretation of ecological interactions as Andrewartha (1970) does, by considering all the possible components of the environment that might influence an individual organisms's chance to survive and reproduce, it is clear that only some sort of resource can become inescapably and passively inadequate (as distinct from some factor in the environment actively killing individuals). And of all the resources in the environment of animals, food is the universal and essential one, and that most likely to be inadequate.

Half a century ago Elton (1927) wrote "Animals are not always struggling for existence, but when they do begin, they spend the greater part of their lives eating. Feeding is such a universal and commonplace business that we are inclined to forget its importance. The primary driving force of all animals is the necessity of finding the right type of food and enough of it. Food is the burning question in animal society, and the whole structure and activities of the community are dependent upon questions of food-supply".

I believe he was correct, both in emphasising the importance of food, and in warning of the dangers of overlooking its importance. Until quite recently most ecologists had largely ignored or overlooked food as a possible factor having any immediate influence on the abundance of animals. Today, however, there is growing evidence that food *is* in short supply for most animals. But I would suggest that it is "the right type of food" which is limiting. Specifically that which contains enough nitrogen. Animals have a ubiquitous need for nitrogen to maintain body weight. More importantly, breeding females and rapidly growing young animals need increased amounts to produce new body tissue. There is a great deal of nitrogen in the world, but most of it is in a form that is not available as food for animals. And what is available tends to be thinly spread in the environment – there is a relative rather than absolute shortage. By contrast, there would appear to be no shortage of carbohydrates. So it is not the amount of energy flowing through the ecosystem that is limiting the abundance of animals in the ecosystem, it is the amount of nitrogen readily available for incorporation into body protein.

III. Food for Herbivores

No shortage has been apparent. The idea that the supply of food could be limiting the numbers of animals that eat plants has largely been rejected by ecologists because rarely are herbivores seen to eat more than a small fraction of the plants available to be eaten. (And on the comparatively few occasions when they do, the hunt is on for the agent in the environment which has ceased to kill so many, allowing this to happen). The mistake has been to assume that demonstratably edible plant material is necessarily an adequate source of nutrition for the animals eating it. All herbivores – be they aphids or elephants – spend a great deal of their time eating, and "process" vast amounts of food through their alimentary tracts. Why? Because the ratio of nitrogen to fibre and carbohydrates in the food plants is low – often critically so.

Published studies of populations of many herbivores (both vertebrates and invertebrates) reveal that very many species exhibit the following similarities in their ecologies.

(1) Their food is low in nitrogen. At times so low as to be below the minimum level necessary for the individual animals to maintain body weight, let alone grow or nourish young, *when they are consuming the maximum amount of food of which they are capable.*

(2) Individual animals feed selectively. Not only on specific species of plants but on certain parts of plants. This selection is for the tissue *with the highest content of available nitrogen.*

(3) The greatest number of individuals dying in any generation do so as very young animals.

(4) The nutritional adequancy of the food is the major factor influencing survival of the very young – directly in insects; through maternal nutrition and/or feeding of the young in birds and mammals. Changes in the cause are nearly always reflected quickly in changes in the effect.

(5) Predators that prevent substantial increases or cause substantial decreases in abundance of their herbivorous prey are the exception rather than the rule. But predators may often intensify and prolong a decline in abundance by "overriding" a decreasing population of their prey.

(6) To a large extent weather, and especially rainfall, is the dominant factor influencing the amount and nutritional quality of the food for herbivores.

I have previously discussed this pattern of similarities between populations of herbivorous insects (White, 1969 et. seq.). The following examples from the literature illustrate that the same would seem to be true for populations of many vertebrate herbivores.

Sinclair's (1973, 1974a, b, c) study of populations of buffalo in East Africa has demonstrated that the amount and quality of nitrogen in the food of these animals is the most important component of the environment limiting their abundance. And this in spite of their ability to select not only areas where food is most abundant and species of grass which are most nutritious, but particular parts of plants having the highest protein content. Further, his data show that the greatest mortality each year is of the very young, and that this is most probably the result of under-nutrition of pregnant females influencing the birth weight (and hence the viability) of calves. Predation is unimportant, acting, at best, only as a secondary agent "... hastening the response of the population to its environment ...". He points out (Sinclair, 1975) that only a small part of the apparently available food is ever consumed by all the herbivores combined (large and small mammals, and insects) living on these vast East African grasslands. The content of nitrogen in the plants drops to a level where it is no longer possible for the animals to extract sufficient nitrogen from the bulk of fibre consumed to maintain body wight, let alone grow. He concludes that "... all trophic levels of these terrestrial ecosystems are resource limited". I suggest that, more specifically, they are limited by a relative shortage of the right sort of food in the environment. Other studies (Phillipson, 1975; Coe et al., 1976) have demonstrated that the amount and quality of the food available to these herbivores is largely influenced by the amount and distribution of rainfall experienced.

Other ungulates are known to selectively feed on plants with a high content of nitrogen (Bell, 1970; Lauckhart, 1962) and a shortage of food (including under-nutrition of pregnant females) affecting survival in the first year of life is a major factor influencing their abundance (Caughley, 1970; Thorne et al., 1976; Wegge, 1975).

Similar stories revealing various combinations of a shortage of nitrogenous food, high mortality of the very young, the absence of any significant influence of predators, and the influence of weather, are found for populations of such diverse herbivores as rabbits and hares (Keith, 1974; Lindlof et al., 1974; Miller, 1968; Meslow and Keith, 1968; Myers and Poole, 1963; Snyder et al., 1976; Stoddart and Myers, 1966), squirrels (Kemp and Keith, 1970; Nixon et al., 1975), deer (Klein, 1970) and elephants (Hanks and McIntosh, 1973; Phillipson, 1975).

It would seem that even in populations of some farm animals starvation of the very young is a much more important cause of death than the commonly blamed predators (Houston, 1977; Rowley, 1970) and the ability to select plant tissue of high nitrogen content is not lost through domestication (Bath et al., 1956).

There is much indirect evidence (Lauckhart, 1957) and some more positive evidence (Keith, 1974) that changes in the nitrogen content of the food, induced by changes in the weather, may well hold the key to an explanation of cycles of mammals like the microtines and the snowshoe hare. The hypothesis is at least worth pursuing.

The story of the Red Grouse in Scotland is another example of food being the principal component of the environment influencing the abundance of a population of herbivorous animals. The Red Grouse is not strictly herbivorous, relying on insects for a considerable proportion of its nitrogenous food, especially at breeding time (Butterfield and Coulson, 1975). But apart from this it eats mostly heather, a plant with a low content of nitrogen and thus a nutritionally marginal food (Miller et al., 1966). It has been demonstrated that not only do these birds feed selectively upon the more nutritious growing tips of heather plants, but that they select those which are more nutritious than others – specifically those having a higher content of nitrogen and phosphorus (Moss, 1972; Moss et al., 1972). This preferential selection of food includes the ability to detect the heather plants with higher nitrogen content growing in spring (Moss, 1967) on fertilised plots (Miller, 1968; Miller et al., 1970) on richer soils (Miller et al., 1966) of different ages (Moss et al., 1972) and which have been stressed (Moss, pers. comm.).

It is when birds are growing or laying that their feeding preferences are most strongly correlated with the nitrogen and phosphorus content of the heather (Moss et al., 1972) and there is evidence that it is nitrogen not phosphorus which is critical when in short supply (Miller et al., 1970).

But in spite of the evolution of this preferential feeding these animals still experience a relative shortage of nitrogenous food. Changes in their breeding success from year to year are due largely to variations in the proportion of chicks which die a few days after hatching (Moss et al., 1975). This mortality is determined before the eggs are hatched – indeed before they are laid – by the level of nitrogen and phosphorus in the food eaten by the hens (Moss, 1972). Breeding male grouse are reported to prefer food which is high in carbohydrate (Gardarsson and Moss, 1970). Apparently their need at this time is for energy rather than body building!

The ability to select food with a high content of nitrogen, and the importance of this to survival of the young, has been demonstrated for populations of related species (Doerr et al., 1974; Gardarsson and Moss, 1970; Gurchinoff and Robinson, 1972; Pulliainen, 1970) including evidence that the availability of arthropods as a source of nitrogenous food for very young chicks may be more important than so far realised (Lance and Mahon, 1975; Pendergast and Boag, 1970).

There is a great deal of evidence, with David Lack as its chief proponent, demonstrating the importance of food influencing the survival of the young as the major influence on the abundance of herbivorous birds. Some other more recent examples are those for tits (Perrins, 1965, 1966), bullfinches (Newton, 1967) and redpolls (Eriksson, 1970; Hogstad, 1967). But few, if any, herbivorous birds are truly herbivorous. Most turn to insects as a source of protein at least to feed their young. For this reason correlations commonly found between, for example, size of seed crops and breeding success of seed-eating birds may not be as straight foreward as they seem. The same sort of weather which will stress plants sufficiently to induce a heavy crop of fruit will stress them sufficiently to enable many more herbivorous insects feeding on them to survive. The increased mobilisation of nitrogen that results from stress may well be the cause of both heavy fruiting and higher survival of insects (see especially Perrins (1966) and the next section of this paper for evidence supporting this suggestion).

It should be noted here that some ecologists studying the management of populations of wild animals that are hunted for sport, had seen more clearly than most the true picture of the limitation of numbers in nature. In particular the ideas of Lauckhart (1957, 1962) presage much of what is suggested in this paper.

IV. Plants as Food

Why is it that plants, by and large, are such a poor source of nitrogenous food for animals? Presumably any species of plant which was adequately nutritious and freely available to a herbivore throughout its life-cycle would soon be exterminated. Evolution of various physical and chemical means of defence can be (and mostly have been) successfully circumvented by complementary evolution of the herbivores. Under the selection pressure of continued attack by herbivores a species of plant could become so scattered and rare in the environment that the probability of any one plant being found by individual predators is so low that the species can persist. Increasingly efficient dispersal of increasing numbers of predators is the obvious (and observed – although only partially successful) counter to this strategy.

Another strategy by which plants might evade destruction by their predators would be to reduce the quality of their tissues as a source of food for the herbivores. There must be a minimum level of nutrition, especially for the growing young, at which an individual animal cannot possibly evolve "resistence" to further dilution of its food. A plant's tissues could become so dilute in one or more essential nutrients that the probability of any individual herbivore which feeds on these tissues getting enough to survive, is such that most would quickly die before causing any serious damage to the plant. Nitrogen would seem to have been the essential nutrient selected for diminution.

But plants, like animals, must have an increased input of nitrogen to grow new tissue – and growing plant tissue is the most nutritious form of food for herbivores. By restricting growth to a short period, and/or a small part of the plant (while the bulk of its tissues remained low in nitrogen) a plant could achieve new growth before herbivores could become sufficiently numerous to cause serious harm to the plant. Various combinations of this strategy (in combination with that of becoming rare in the environment) would have the effect of creating a relative shortage of food for herbivores, thus avoiding extinction, and at the same time providing a major (and unassailable) factor limiting the abundance of the herbivores.

Most sorts of herbivores have become adapted to feeding only on the highly nutritious "flush" tissue produced by plants during periods of fast growth. (Either the whole plant as an annual or seedling, or specific tissues such as shoots and leaves, especially from perennials). As they mature, these tissues become fibrous and less nutritious; the supply of good food is temporary. But there are other herbivores just as specifically adapted to feed only on tissue which has fully expanded and is either mature or senescing (White, 1971, 1976). Both sorts of animals tend to be rare in their habitat for most of the time. They can persist only where there is *some* plant tissue with sufficient nitrogen (or if they have evolved some adaptation to tide them over periods when there is none). To increase in abundance both must have access, over one or more generations, to an increased amount of tissue with a high nitrogen content. And both sorts *do* sometimes increase enormously in abundance.

With the "flush feeders" such increases may either be fairly regular – annual "outbreaks", as with aphids multiplying on the flush of a rosebush – or more infrequent and spasmodic irruptions like those of the European rabbit in Australia on new grass following rain in arid areas.

Of the "mature/senescence feeders" many apparently never change very much in abundance, remaining permanently comparatively rare. Others, although "stable" at low levels for most of the time, may suddenly and irregularly become enormously abundant, often completely destroying their food plants.

Observed increases of "flush feeders" have usually been readily recognised by ecologists as a response to the increased supply of food in the rapidly growing tissues of the food plant. With "mature/senescence feeders" the response has *not* been so readily understood; no visible change takes place in plants which at one moment are hardly at all eaten, and in the next are almost completely devoured. With both sorts of feeders the ecological explanation would seem to be the same – a relative shortage of food, caused by the dilution of nitrogen in the plants, has been alleviated – by an increased *inflow* of high-nitrogen sap to the new growth, by an increased *outflow* of high-nitrogen sap from senescing tissue. I have discussed elsewhere (White, 1969, et seq.) some of the likely ways in which mature and senescing tissues may become a richer source of nitrogen for herbivores. Essentially the hypothesis is that when plants are stressed (by whatever means) their tissues become a richer source of available nitrogen for young animals feeding on those tissues. Whereas for most of the time herbivores feeding on mature or senescent tissues must rely on odd "refuges" of damaged or otherwise stressed plants on which to persist, occasionally more general and widespread stress (usually through rainfall influencing soil moisture) may stress many plants over wide areas thus allowing many to survive and an outbreak to develop.

The other strategy of combating herbivores, namely that of a plant becoming rare and scattered in the environment, will similarly produce a relative shortage of food for the herbivores, resulting in most young that are produced dying before they find food. And this "dilution in space" is only different from the situation where the young herbivore dies because it is feeding on tissue too dilute in nitrogen, in that the activity of the animals may influence the extent of the relative shortage. In the case of dilution of the tissues they have no such influence.

There are many examples in nature of scattered and rare food plants, but it is the man-made reversal of such cases that best illustrates the importance of this strategy as a factor reducing the numbers of herbivores that survive in nature. They are also important because many hypotheses about the abundance of animals in nature are based on studies of insects feeding on Man's crops. The observed response of such animals (and their predators) *cannot* be used to interpret the ecology of animals in nature – at least not until there is a clear understanding of what Man, by his manipulations, has done to the original evolved relationships. I think many ecologists have lost sight of this important reservation.

When Man domesticates a species of plant he selects a few individuals from which to propogate each generation (when it is a food plant this includes selection for greater nutritive value – greater protein content) and he propogates many individuals in dense aggregations where before there were only a few widely scattered plants. What is the likely response of herbivores with physiology and behaviour evolved to increase their chances of surviving on scattered food plants of inadequate (or at best, marginal) nutritive value? They rapidly increase in abundance. Man has thus created a series of permanent "outbreaks" of such animals by providing an abundance of food where before there was a relative shortage (equally is this true for pests of stored products). Prolonging the time during which plants put on new growth (by irrigation or the application of fertilisers) often further improves life for "flush feeders", as does planting species out of their normal range and in other stressful situations for "mature/senescence feeders".

All such "outbreaks" will persist unless Man kills most of the herbivores in each generation, or until most of the food plants are destroyed and again become scattered and rare, with selection again favouring the least nutritious plants.

Similar caution must be used when considering populations of animals which Man manages so that he many hunt them. The modification of the environment of the Red Grouse is a good case in point. Without the extensive and controlled burning of the heather there would be much less food for grouse, and many fewer grouse to shoot.

V. Food for Carnivores

The food of carnivores, unlike that of herbivores, provides a highly concentrated source of nitrogen, but as with herbivores it would seem that it is a relative shortage of food which largely influences the abundance of predators. Generally there has been a much more ready acceptance by ecologists of the idea that the major factor affecting the abundance of predators is their food supply. It can be seen that prey are scarce, hard to catch, or have a variety of behavioural and physiological adaptations with which to protect themselves. And many predators are not themselves preyed upon or obviously harmed by other factors in the environment, so what else is there to control them? Most ecologists see this, however, in terms of a negative feedback "regulation" of the predator's own food supply – because it is assumed that the prey are *not* limited by their food supply. But if the concept of an inadequate environment, an environment in which *all* organisms are struggling to persist, is accepted, then it is easier to understand that predators too, are chasing a relative shortage of food. There is abundant evidence in the literature illustrating how their numbers, like those of their herbivorous prey, quickly respond to increases in their own food supply (the prey). There is also evidence that, as with populations of herbivores, the influence of a changing abundance of food is manifest mainly through changes in survival of the very young. Where predation occurs it seems to have little influence on the number of young surviving.

Keith (1974) in reviewing the population dynamics of a range of mammalian carnivores, and in some more recent papers (Nellis and Keith, 1976; Brand et al., 1976) illustrates these points very well. Other workers (Jordan et al., 1967) have found a similar pattern as have many studying carnivorous birds, ranging from puffins (Harris, 1969) and pelicans (Brown and Urban, 1969) to owls and hawks (Clough, 1965; Southern, 1970) sandpipers (Holmes, 1970) gulls (Carrick and Murray, 1964; Fordham, 1970) and skuas (Andersson, 1976).

Even the observed predation of young lambs of domestic sheep by foxes and crows, which is usually blamed for the death of the young, is apparently another example of carnivores obtaining what they can of a scarce food resource. They are only able to overpower those lambs already starving and doomed. Vigorous, non-starving lambs are secure from attack (Houston, 1977; Rowley, 1970).

VI. Discussion and Conclusions

What then, does all this mean? Van Valen (1973) has, I think, pinpointed the difficulties that many ecologists have. He asks how do we resolve the paradox of herbivores being limited by their food in a green world – in a world where the food is apparently greatly under-used? And how, alternatively, if the abundance of all populations at all trophic levels is determined by a shortage of food, is the system kept in balance? The answers lie in the fact that survival in nature is an exercise in probability – each individual must try its luck in a hostile environment, the adequacy of which fluctuates randomly from season to season.

The "green world" is not a paradox; neither is the activity of predators of the third trophic level sufficient or necessary to explain it. All that is green is not always good food for herbivores because, although palatable, its nitrogen content is often too low to provide a young herbivore with its minimum requirement for protein: the young will eat it, but will not survive on it. And this in turn removes the problem of how the system is kept in balance. Balance is an unnecessary idea when we are thinking about natural populations. This usual and variable shortage of food provides an alternative explanation. The tacit assumption in the balance of nature is that all species of organisms tend to produce an abundance of progeny that would survive to reproduce and lead to ever increasing numbers unless controlled by negative feedback mechanisms. As a consequence the mean observable density over a number of generations is seen as an optimum or equilibrium density – the further the numbers depart from this mean the greater will be the density/dependent pressures in the system pressing them back towards this mean (Huffaker and Messenger, 1964). But a mean population has no reality in nature. It is merely a statistic derived from a series of samples of the numbers in a population in which numbers are continually changing. And these changes result from the members of the population struggling to exploit the opportunities afforded by the inadequate environment. Nor is there an optimum or equilibrium density of a population in nature – only the maximum number that can survive each generation in a population that is pressing hard against the variable but limited supply of resources in its environment.

In the light of the hypothesis put forward in this paper the usual concept of control of populations from above might better be replaced by a concept of limitation of populations from below – from flows from one trophic level to the next. The conceptual system reduces thereby to a variety of interactions between animals and plants in which the numbers of herbivores initially are limited by a shortage of suitable food. The numbers of predators are then limited by the number of herbivores. Predators can "overtake" their prey and significantly influence their abundance, only if they can increase and disperse more rapidly and efficiently than the prey. It would seem that many predators have lower potential fecundity and powers of dispersal than their prey, and can thus generate a negative feedback interaction with their prey (and are often recorded doing so) *only* when the prey's own power of increase is below that of the predator (p. 298, White, 1974). Add to this the fact that prey animals have (like the plants) evolved various ways of being relatively inaccessible as a source of food for their predators, and it is not difficult to see why predators (like herbivores) are not often seen to use all the apparently available food – but do increase rapidly when the prey does.

Competition is often invoked as an important factor limiting the abundance of animals. Competition can occur only when two or more animals seek to use a resource of which there is not enough for all. We can imagine two populations of the same species of a hypothetical animal living in adjacent but different habitats. One has an acute shortage of nesting sites but abundant food, and the other abundant nesting sites but little food. In both, competition will occur between individuals once the numbers seeking to use either resource exceeds the supply of that resource – once there is an absolute shortage. And in both only a fraction of the total population can then survive and reproduce. But *how many* survive is decided in each case by two quite different variables in the environment – a shortage of nesting sites or food – *not* by the competition, which occurs *as a result of the shortage* in each case. Where competition is so important is as an evolutionary force. It decides *which ones* survive.

Without shortage there can be no competition. But there can be shortage without competition. Food may be in relatively short supply – so thinly spread through the environment that most individuals, although feeding continuously, and *whether or not other animals are seeking to use the same food*, do not get enough to survive. In such a situation selection will favour any individual with a trait that improves its chance of getting enough to survive *without* the need for it to compete with other individuals.

Other ecologists (e.g. Chitty, 1960; Wynne-Edwards, 1962) having found evidence that predators are not able to limit the abundance of their prey, and having seen no evidence of any shortage of food or other resource for the prey, nor of any other factor in the environment limiting their increase, have concluded that intrinsic behavioural or genetic "self regulating" mechanisms may be responsible for limiting the numbers of animals. But these hypotheses are not necessary if, indeed, there *is* a shortage of food for most young animals.

Territorial and other forms of social dominance behaviour do have the effect of restricting successful breeding to a selected few individuals in a population, and thus reducing the possible number of young produced. But the selective advantage of these mechanisms is not, as proposed by Wynne-Edwards, to reduce the size of the population in the next generation, but rather to *increase* it. In an environment that is inadequate such behavioural adaptations allow more effective use of a resource in short supply. Selectively preventing the birth or hastening the early death of the many, when linked with the ability to concentrate or sequester a limited resource, increases the probability of a favoured few rather than a chance few – or worse still, none at all – obtaining enough of the limited resource. This is a clear advance over the simpler strategy of producing as many young as possible and "spraying" them at random into the environment. But it still produces more young than the environment can maintain. These "surplus" young are thrust out from the territory or social unit in which they were raised into the surrounding world. If this world is inadequate they perish. If it is adequate they may survive and breed. In this way, then, social mechanisms have increased the *efficiency* with which a limited resource is used, while at the same time maintaining constant "pressure" on the environment so that any improvement – any increase in the amount or availability of a resource – is quickly used to increase the numbers in the population. And this is exactly what the more primitive scattering of large numbers of young achieves – but less economically in terms of energy expended. Some more spectacular examples of the latter are the dramatic changes in numbers of many insects in response to the changes in the quality of their food (White, 1974, 1976); of the former the equally dramatic changes in populations of animals like the European rabbit in Australia in response to changes in the amount of green food (Stoddart and Myers, 1966). In both they are responding to changes in the abundance of nitrogenous food available in their environment.

As with competition, so with different forms of social organisation, because they decide which few of the many survive they are powerful evolutionary mechanisms. But they do not determine *how many* of the animals can survive in a given environment – that is done by the level of adequacy of the environment – by the relative shortage or abundance of the food resource in that environment.

The hypothesis that changes in the proportion of genotypes in a population may determine the abundance of that population similarly does not stand up when approached from the basic thesis of a variably inadequate environment. Truly, at times when the numbers in a population increase, the range of genotypes surviving will increase, and vice versa. But it is wrong to think of these additionally surviving genotypes as "inferior", and in further assuming that an increase in the proportion of them in the population will cause numbers to decline. Rather it is the reverse. Numbers will increase when the environment becomes more favourable, allowing more individuals to survive. The lessened harshness of the environment means that selection pressures are less and so not just more individuals, but a wider range of genotypes will survive. When the environment again becomes harsher fewer individuals will survive. At the same time a lesser range of genotypes (but not necessarily the original range) is likely to be adaptive. So *changes in the environment* cause both changes in the number of individuals and the range of genotypes in a population. It is misleading to emphasise inferior and superior genotypes in this context; it is better to think of different genotypes being more or less well adapted at different times because the environment is changing all the time. Nor, I repeat, is the number of individuals increasing or decreasing *because* the range of genotypes is changing. *Both* are changing *because the favourability of the environment is changing.*

As discussed earlier (pp. 78 and 79), the relationship of herbivores to food plants which are cultivated by Man can be used to interpret herbivore-plant relationships found in nature only when there is a full realisation of how cultivation has altered the original, evolved relationships. Similarly when contemplating the selection of predators of herbivores as potential agents of biological control, if a correct selection is to be made it is necessary to understand the likely consequential "flow on" of Man's manipulations. Failure to understand that most predators are incapable of keeping pace with the increase of their prey *so long as the prey is provided with an abundance of food* has probably been one of the main reasons why so many attempts at biological control have been unsuccessful. Only if the predator can increase in abundance faster than its prey, and where, in addition, it is a facultative predator having alternative but *less preferred* prey available in the same environment, is it likely to be an efficient agent of biological control.

The only way in which "less efficient" predators may be used to effectively control pests is by artifically breeding and releasing them in large numbers. And this must be done for each new generation of the pest.

Finally, in widening the scope of the hypothesis that was put forward in earlier papers (White, 1969, et seq.), I am fully aware that I have generalised and simplified – perhaps oversimplified. There are exceptions where it can be shown that something other than food for the young is the major factor limiting the abundance of a population. But the number of examples supporting the hypothesis is growing. And there are many published reports where the indications are there, but the investigator had his eyes firmly fixed on some other hypothesis to explain his findings, and did not pursue the obvious!

My hypothesis depends on the assertion that juvenile death rates are usually high and highly variable and therefore of chief importance in causing fluctuations in the size of the population. Juvenile death rates are high because juveniles require a diet rich in nitrogenous food; and they are highly variable because plants usually make such food available to their "predators" in a highly erratic and temporary way.

Many will counter my hypothesis by arguing that in a population with a very high death rate among juveniles in each generation, what happens to the mature animals will be more important in determining the average size of the population if the juvenile death rate is invariable, or varies only a little. But the evidence suggests that *if survival of the very young increases*, then predators that have a major influence on the death rate of mature animals seem powerless to prevent increases in abundance of the population. Similarly, populations appear to decline because more young fail to survive, not because predators are able to kill more mature animals.

Consequently, when outbreaks occur in natural populations, or where animals become pests on Man's cultivated plants and stored products, then I believe the explanation for these phenomena – and attempts to manipulate or modify them – should be sought in terms of changes in the survival of the very young – specifically in changes in a relative shortage of their food.

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