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POPULATION STUDIES: ANIMAL ECOLOGY AND DEMOGRAPHY*

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This concluding survey of the problems considered in the Symposium naturally falls into three sections. In the first brief section certain of the areas in which there is considerable difference in outlook are discussed with a view to ascertaining the nature of the differences in the points of view of workers in different parts of the field; no aspect of the Symposium has been more important than the reduction of areas of dispute. In the second section a rather detailed analysis of one particular problem is given, partly because the question, namely, the nature of the ecological niche and the validity of the principle of niche specificity has raised and continues to raise difficulties, and partly because discussion of this problem gives an opportunity to refer to new work of potential importance not otherwise considered in the Symposium. The third section deals with possible directions for future research.

1. The Demographic Symposium as a Heterogeneous Unstable Population. In the majority of cases the time taken to establish the general form of the curve of growth of a population from initial small numbers to a period of stability or of decline is equivalent to a number of generations. If, as in the case of man, the demographer is himself a member of one such generation, his attitude regarding the nature of the growth is certain to be different from that of an investigator studying, for instance, bacteria, where the whole process may unfold in a few days, or insects, where a few months are required for several cycles of growth and decline. This difference is apparent when Hajnal's remarks about the uselessness of the logistic are compared with the almost universal practice of animal demographers to start thinking by making some suitable, if almost unconscious, modification of this much abused function.

The human demographer by virtue of his position as a slow breeding participant observer, and also because he is usually called on to predict for practical purposes what will happen in the immediate future, is inevitably interested in what may be called the microdemography of man. The significant quantities are mainly second and third derivatives, rates of change of natality and mortality and the rates of change of such rates. These latter to the animal demographer might appear as random fluctuations which he can hardly hope to analyze in his experiments. What the animal demographer is mainly

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concerned with is the macrodemographic problem of the integral curve and its first derivative. He is accustomed to dealing with innumerable cases where the latter is negative, a situation that is so rare in human populations that it seems to be definitely pathological to the human demographer. Only when anthropology and archaeology enter the field of human demography does something comparable to animal demography, with its broad, if sometimes insufficiently supported generalizations, and its fascinating problems of purely intellectual interest, emerge. From this point of view the papers of Birdsell and Braidwood are likely to appeal most strongly to the zoologist, who may want to compare the rate of spread of man with that considered by Kurtén (1957) for the hyena.

It is quite likely that the difference that has just been pointed out is by no means trivial. The environmental variables that affect fast growing and slow growing populations are likely to be much the same, but their effect is qualitatively different. Famine and pestilence may reduce human populations greatly but they rarely decimate them in the strict sense of the word. Variations, due to climatic factors, of insect populations are no doubt often proportionately vastly greater. A long life and a long generation period confer a certain homeostatic property on the organisms that possess them, though they prove disadvantageous when a new and powerful predator appears. The elephant and the rhinoceros no longer provide models of human populations, but in the early Pleistocene both may have done so. The rapid evolution of all three groups in the face of a long generation time is at least suggestive.

It is evident that a difference in interest may underlie some of the arguments which have enlivened, or at times disgraced, discussions of this subject. Some of the most significant modern work has arisen from an interest in extending the concepts of the struggle for existence put forward as an evolutionary mechanism by Darwin practically a century ago. Such work, of which Lack's (1947a,b; 1954) recent contributions provide a distinguished example, tends to concentrate on relatively stable interacting populations in as undisturbed communition as possible. Another fertile field of research has been provided by the sudden increases in numbers of destructive animals, often after introduction or disturbance of natural environments. Here more than one point of view has been apparent. Where emphasis has been on biological control, that is, a conscious rebuilding of a complex biological association, a view point not unlike that of the evolutionist has emerged—where emphasis has been placed on the actual events leading to a very striking increase or decrease in abundance, given the immediate ecological conditions, the latter have appeared to be the most significant variables. Laboratory workers have moreover tended to keep all but a few factors constant, and to vary these few systematically. Field workers have tended to emphasize the ever changing nature of the environment. It is abundantly clear that all these points of view

are necessary to obtain a complete picture. It is also very likely that the differences in initial point of view are often responsible for the differences in the interpretation of the data.

The initial differences of point of view are not the only difficulty. In the following section an analysis of a rather formal kind of one of the concepts frequently used in animal ecology, namely that of the *niche*, is attempted. This analysis will appear to some as compounded of equal parts of the obvious and the obscure. Some people however may find when they have worked through it, provided that it is correct, that some removal of irrelevant difficulties has been achieved. It is not necessary in any empirical science to keep an elaborate logicomathematical system always apparent, any more than it is necessary to keep a vacuum cleaner conspicuously in the middle of a room at all times. When a lot of irrelevant litter has accumulated the machine must be brought out, used, and then put away. It might be useful for those who argue that the word environment should refer to the environment of a population, and those who consider it should be the environment of an organism, to use the word both ways for a couple of months, writing "environment" when a single individual is involved, "Environment" when reference is to a population. In what follows the term will as far as possible not be used, except in the non-committal adjectival form environmental, meaning any property outside the organisms under consideration.

2. The Formalization of the Niche and the Volterra–Gause Principle

2.1. Niche space and biotop space. Consider two independent environmental variables x_1 and x_2 which can be measured along ordinary rectangular coordinates. Let the limiting values permitting a species S_1 to survive and reproduce be respectively x_1', x_1'' for x_1 and x_2', x_2'' for x_2. An area is thus defined, each point of which corresponds to a possible environmental state permitting the species to exist indefinitely. If the variables are independent in their action on the species we may regard this area as the rectangle ($x_1 = x_1'$, $x_1 = x_1''$, $x_2 = x_2'$, $x_2 = x_2''$), but failing such independence the area will exist whatever the shape of its sides.

We may now introduce another variable x_3 and obtain a volume, and then further variables $x_4, \ldots, x_n$ until all of the ecological factors relative to S_1 have been considered. In this way an n-dimensional hypervolume is defined, every point in which corresponds to a state of the environment which would permit the species S_1 to exist indefinitely. For any species S_1, this hypervolume $\mathbf{N}_1$ will be called the *fundamental niche** of S_1. Similarly for a second species S_2 the fundamental niche will be a similarly defined hypervolume $\mathbf{N}_2$.

It will be apparent that if this procedure could be carried out, all X_n variables,

* This term is due to MacArthur (1957). The general concept here developed was first put forward very briefly in a footnote (Hutchinson, 1944).

both physical and biological, being considered, the fundamental niche of any species will completely define its ecological properties. The fundamental niche defined in this way is merely an abstract formalization of what is usually meant by an ecological niche.

As so defined the fundamental niche may be regarded as a set of points in an abstract n-dimensional **N** space. If the ordinary physical space **B** of a given biotop be considered, it will be apparent that any point $p(\mathbf{N})$ in **N** can correspond to a number of points $p_i(\mathbf{B})$ in **B**, at each one of which the conditions specified by $p(\mathbf{N})$ are realized in **B**. Since the values of the environmental variables $x_1\ x_2, \ldots, x_n$ are likely to vary continuously, any subset of points in a small elementary volume $\Delta\mathbf{N}$ is likely to correspond to a number of small elementary volumes scattered about in **B**. Any volume $\mathbf{B}'$ of the order of the dimensions of the mean free paths of any animals under consideration is likely to contain points corresponding to points in various fundamental niches in **N**.

Since **B** is a limited volume of physical space comprising the biotope of a definite collection of species $S_1, S_2, \ldots, S_n$, there is no reason why a given point in **N** should correspond to any points in **B**. If, for any species S_1, there are no points in **B** corresponding to any of the points in $\mathbf{N}_1$, then **B** will be said to be *incomplete* relative to S_1. If some of the points in $\mathbf{N}_1$ are represented in **B** then the latter is *partially incomplete* relative to S_1, if all the points in $\mathbf{N}_1$ are represented in **B** the latter is *complete* relative to S_1.

2.2. Limitations of the set-theoretic mode of expression. The following restrictions are imposed by this mode of description of the niche.

(1) It is supposed that all points in each fundamental niche imply equal probability of persistance of the species, all points outside each niche, zero probability of survival of the relevant species. Ordinarily there will however be a optimal part of the niche with markedly suboptimal conditions near the boundaries.

(2) It is assumed that all environmental variables can be linearly ordered. In the present state of knowledge this is obviously not possible. The difficulty presented by linear ordering is analogous to the difficulty presented by the ordering of degrees of belief in non-frequency theories of probability.

(3) The model refers to a single instant of time. A nocturnal and a diurnal species will appear in quite separate niches, even if they feed on the same food, have the same temperature ranges, etc. Similarly, motile species moving from one part of the biotop to another in performance of different functions may appear to compete, for example, for food, while their overall fundamental niches are separated by strikingly different reproductive requirements. In such cases the niche of a species may perhaps consist of two or more discrete

hypervolumes in N. MacArthur (1957) proposed to consider a more restricted niche describing only variables in relation to which competition actually occurs. This however does not abolish the difficulty. A formal method of avoiding the difficulty might be derived, involving projection onto a hyperspace of less than n-dimensions. For the purposes for which the model is devised, namely a clarification of niche specificity, this objection is less serious than might at first be supposed.

(4) Only a few species are to be considered at once, so that abstraction of these makes little difference to the whole community. Interaction of any of the considered species is regarded as competitive in sense 2 of Birch (1957), negative competition being permissible, though not considered here. All species other than those under consideration are regarded as part of the coordinate system.

2.3. Terminology of subsets. If $\mathbf{N}_1$ and $\mathbf{N}_2$ are two fundamental niches they may either have no points in common in which case they are said to be *separate*, or they have points in common and are said to *intersect*.

In the latter case:

$(\mathbf{N}_1 - \mathbf{N}_2)$ is the subset of $\mathbf{N}_1$ of points not in $\mathbf{N}_2$
$(\mathbf{N}_2 - \mathbf{N}_1)$ is the subset of $\mathbf{N}_2$ of points not in $\mathbf{N}_1$

$\mathbf{N}_1 \cdot \mathbf{N}_2$ is the subset of points common to $\mathbf{N}_1$ and $\mathbf{N}_2$, and is also referred to as the *intersection subset*.

2.4. Definition of niche specificity. Volterra (1926, see also Lotka, 1932) demonstrated by elementary analytic methods that under constant conditions two species utilizing, and limited by, a common resource cannot coexist in a limited system.* Winsor (1934) by a simple but elegant formulation showed that such a conclusion is independent of any kind of finite variations in the limiting resource. Gause (1934; 1935) confirmed this general conclusion experimentally in the sense that if the two species are forced to compete in an undiversified environment one inevitably becomes extinct. If there is a diversification in the system so that some parts favor one species, other parts the other, the two species can coexist. These findings have been extended and generalized to the conclusion that two species, when they co-occur, must in some sense be occupying different niches. The present writer believes that properly stated as an empirical generalization, which is true except in cases where there are good reasons not to expect it to be true,† the principle is of

* I regret that I am unable to appreciate Brian's contention (1956) that the Volterra model refers only to interference, and the Winsor model to exploitation.

† Cf. Schrödinger's famous restatement of Newton's First Law of Motion, that a body perseveres at rest or in uniform motion in a right line, except when it does not.

fundamental importance and may be properly called the Volterra–Gause principle. Some of the confusion surrounding the principle has arisen from the concept of two species not being able to co-occur when they occupy identical niches. According to the formulation given above, identity of fundamental niche would imply $\mathbf{N}_1 = \mathbf{N}_2$, that is, every point of $\mathbf{N}_1$ is a member of $\mathbf{N}_2$ and every point of $\mathbf{N}_2$ a member of $\mathbf{N}_1$. If the two species S_1 and S_2 are indeed valid species distinguishable by a systematist and not freely interbreeding, this is so unlikely that the case is of no empirical interest. In terms of the set-theoretic presentation, what the Volterra–Gause principle meaningfully states is that for any small element of the intersection subset $\mathbf{N}_1 \cdot \mathbf{N}_2$, there do not exist in $\mathbf{B}$ corresponding small parts, some inhabited by S_1, others by S_2.

Omitting the quasi-tautological case of $\mathbf{N}_1 = \mathbf{N}_2$, the following cases can be distinguished:

(1) $\mathbf{N}_2$ is a proper subset of $\mathbf{N}_1$ ($\mathbf{N}_2$ is "inside" $\mathbf{N}_1$): (a) competition proceeds in favor of S_1 in all the elements of $\mathbf{B}$ corresponding to $\mathbf{N}_1 \cdot \mathbf{N}_2$, given adequate time only S_1 survives; (b) competition proceeds in favor of S_2 in all elements of $\mathbf{B}$ corresponding to some part of the intersection subset and both species survive.

(2) $\mathbf{N}_1 \cdot \mathbf{N}_2$ is a proper subset of both $\mathbf{N}_1$ and $\mathbf{N}_2$; S_1 survives in the parts of $\mathbf{B}$ space corresponding to $(\mathbf{N}_1 = \mathbf{N}_2)$, S_2 in the parts corresponding to $(\mathbf{N}_2 = \mathbf{N}_1)$, the events in $\mathbf{N}_1 = \mathbf{N}_2$ being as under 1, with the proviso that no point in $\mathbf{N}_1 \cdot \mathbf{N}_2$ can correspond to the survival of both species.

In this case the two difference subsets $(\mathbf{N}_1 - \mathbf{N}_2)$ and $(\mathbf{N}_2 - \mathbf{N}_1)$ are, in Gause's terminology, refuges for S_1 and S_2, respectively.

If we define the realized niche $\mathbf{N}'_1$ of S_1 in the presence of S_2 as $(\mathbf{N}_1 - \mathbf{N}_2)$, if it exists, plus that part of $\mathbf{N}_1 \cdot \mathbf{N}_2$ as implies survival of S_1, and similarly the realized niche $\mathbf{N}'_2$ of S_2 as $(\mathbf{N}_2 - \mathbf{N}_1)$, if it exists, plus that part of $\mathbf{N}_1 \cdot \mathbf{N}_2$ corresponding to survival of S_2, then the Volterra–Gause principle is a statement of an empirical generalization, which may be verified or falsified, that realized niches do not intersect. If the generalization proved to be universally false, the falsification would presumbly imply that in nature resources are never limiting.

2.5. Validity of the Gause–Volterra principle. The set-theoretic approach outlined above permits certain refinements which, however obvious they may seem, apparently require to be stated formally in an unambiguous way to prevent further confusion. This approach however tells us nothing about the validity of the principle, but merely where we should look for its verification or falsification.

Two major ways of approaching the problem have been used, one experimental, the other observational. In the experimental approach, the

method (e.g. Gause, 1934; 1935; Crombie, 1945–1947) has been essentially to use animal populations as elements in analog computers to solve competition equations. As analog computers, competing populations leave much to be desired when compared with the more conventional electronic machines used for instance by Wangersky and Cunningham. At best the results of laboratory population experiments are qualitatively in line with theory when all the environmental variables are well controlled. In general such experiments indicate that where animals are forced by the partial incompleteness of the **B** space to live in competition under conditions corresponding to a small part of the intersection subset, only one species survives. They also demonstrate that the identity of the survivor is dependent on the environmental conditions, or in other words on which part of the intersection subset is considered, and that when deliberate niche diversification is brought about so that at least one non-intersection subset is represented in **B**, two species may co-occur indefinitely. It would of course be most disturbing if confirmatory models could not be made from actual populations when considerable trouble is taken to conform to the postulates of the deductive theory.

The second way in which confirmation has been sought, namely by field studies of communities consisting of a number of allied species also lead to a confirmation of the theory, but one which may need some degree of qualification. Most work has dealt with pairs of species, but the detailed studies of *Drosophila* of Cooper and Dobzhansky (1956) and of Da Cunha *et al.* (1957), to name only two groups of investigators, the investigation of about 18 species of *Conus* on Hawaiian reef and littoral benches (Kohn, in press) and the detailed studies of the food of six co-occurring species of *Parus* (Betts, 1955) indicate remarkable cases among many co-occurring species of insects, molluscs and birds, respectively. However much data is accumulated there will almost always be unresolved questions relating to particular species, though the presumption from this sort of work is that, in any large group of sympatric species belonging to a single genus or subfamily, careful work will always reveal ecological differences. The sceptic may reply in two ways, firstly pointing out that the quasi-tautological case of $\mathbf{N}_1 = \mathbf{N}_2$ has already been dismissed as too improbable to be of interest, and that when a great deal of work has to be done to establish the difference, we are getting as near to niche identity as is likely in a probabilistic world. Occasionally it may be possible to use indirect arguments to show that the differences are at least evolutionarily significant. Lack (1947b) for instance points out that in the Galapagos Islands, among the heavy billed species of *Geospiza*, where both *G. fortis* Gould, and *G. fuliginosa* Gould co-occur on an island, there is a significant separation in bill size, but where either species exists alone, as on Crossman Island and Daphne Island the bills are intermediate and presumably adapted to eating modal sized food. This is hard to explain unless the small average difference in food size believed to exist

between sympatric *G. fortis* and *G. fuliginosa* is actually of profound ecological significance. The case is particularly interesting as most earlier authors have dismissed the significance of the small alleged differences in the size of food taken by the species. Few cases of specific ecological difference encountered outside *Geospiza* would appear at first sight so tenuous as this.

A more important objection to the Volterra–Gause principle may be derived from the extreme difficulty of identifying competition as a process actually occurring in nature. Large numbers of cases can of course be given in which there is very strong indirect evidence of competitive relationships between species actually determining their distribution. A few examples may be mentioned. In the British Isles (Hynes, 1954; 1955) the two most widespread species of *Gammarus* in freshwater are *Gammarus deubeni* Lillj: and *G. pulex* (L.). The latter is the common species in England and most of the mainland of Scotland, the former is found exclusively in Ireland, the Shetlands, Orkneys and most of the other Scottish islands and in Cornwall. On northern mainland Scotland only *G. lacustris* Sars is found. Both *deubeni* and *pulex* occur on the Isle of Man and in western Cornwall. Only in the Isle of Man have the two species been taken together. It is extremely probable that *pulex* is a recent introduction to that island. *G. deubeni* is well known in brackish water around the whole of northern Europe. It is reasonable to suppose that the fundamental niches of the two species overlap, but that within the overlap *pulex* is successful, while *deubeni* with a greater tolerance of salinity has a refuge in brackish water. Hynes moreover shows that *G. pulex* has a biotic (reproductive) potential two or three times that of *deubeni* so that in a limited system inhabitable by both species, under constant conditions *deubeni* is bound to be replaced by *pulex*. This case is as clear as one could want except that Hynes is unable to explain the absence of *G. deubeni* from various uninhabited favorable localities in the Isle of Man and elsewhere. Hynes also notes that Steusloff (1943) had similar experiences with the absence of *Gammarus pulex* in various apparently favorable German localities. Ueno (1934) moreover pointed out that *Gammarus pulex* (*sens. lat.*) occurs abundantly in Kashmir up to 1 600 m, and is an important element in the aquatic fauna of the Tibetan highlands to the east above 3 800 miles, but is quite absent in the most favorable localities at intermediate altitudes. These disconcerting empty spaces in the distribution of *Gammarus* may raise doubts as to the completeness of the picture presented in Hynes' excellent investigations.

Another very well analyzed case (Dumas, 1956) has been recently given for two sympatric species of *Plethodon*, *P. dunni* Bishop, and *P. vehiculum* (Cooper), in the Coastal Ranges of Oregon. Here experiments and field observations both indicate that *P. dunni* is slightly less tolerant of low humidity and high temperature than is *P. vehiculum*, but when both co-occur *dunni* can exclude *vehiculum* from the best sites. However under ordinary conditions in

nature the number of unoccupied sites which appear entirely suitable is considerable, so that competition cannot be limiting except in abnormally dry years.

In both these cases, which are two of the best analyzed in the literature, the extreme proponent of the Volterra–Gause principle could argue that if the investigator was equipped with the sensory apparatus of *Gammarus* or *Plethodon* he would know that the supposedly suitable unoccupied sites were really quite unsuitable for any self respecting member of the genus in question. This however is pure supposition.

Even in the rather conspicuous case of the introduction of *Sciurus caroliniensis* Gmelin and its spread in Britain, the popular view that the bad bold invader has displaced the charming native *S. vulgaris leucourus* Kerr, is apparently mythological. Both species are persecuted by man; *S. caroliniensis* seems to stand this persecution better than does the native red squirrel and therefore tends to spread into unoccupied area from which *S. vulgaris leucourus* has earlier retreated (Shorten, 1953; 1954).

Andrewartha (see also Andrewartha and Birch, 1954) has stressed the apparent fact that while most proponents of the competitive organization of communities have emphasized competition for food, there is in fact normally more than enough food present. This appears, incidentally, most strikingly in some of Kohn's unpublished data on the genus *Conus*.

The only conclusion that one can draw at present from the observations is that although animal communities appear qualitatively to be constructed as if competition were regulating their structure, even in the best studied cases there are nearly always difficulties and unexplored possibilities. These difficulties suggest that if competition is determinative it either acts intermittently, as in abnormally dry seasons for *Plethodon*, or it is a more subtle process than has been supposed. Thus Lincoln Brower (in press) investigating a group of species of North American *Papilio* in which one eastern polyphagous species is replaced by three western oligophagous species, has been impressed by the lack of field evidence for any inadequacy in food resources. He points out however, that specific separation of food might lower the probability of local high density on a given plant, and so the risk of predation by a bird that only stopped to feed when food was abundant (cf. de Ruiter, 1952).

Unfortunately, there is no end to the possible erection of hypothesis fitted to particular cases that will bring them within the rubric of increasingly subtle forms of competition. Some other method of investigation would clearly be desirable. Before drawing attention to one such possible method, the expected limitations of the Volterra–Gause principle must be examined.

2.6. Cases where the Volterra–Gause principle is unlikely to apply. Skellam (1951; see also Brian, 1956b) has considered a model in which two species occur

one (S_1) of much lower reproductive potential than the other (S_2). It is assumed that if S_1 and S_2 both arrive in an element of the biotops S_1 always displaces S_2, but that excess elements are always available at the time of breeding and dispersal so that some are never occupied S_1. In view of the higher reproductive potential, S_2 will reach some of these and survive. The model is primarily applicable to annual plants with a definite breeding season, random dispersal of seeds and complete seasonal mortality so all sites are cleared before the new generation starts growing, S_2 is in fact a limiting case of what Hutchinson (1951; 1953) called a fugitive species which could only be established in randomly vacated elements of a biotop. Skellam's model requires clearing of sites by high death rate, Hutchinson's qualitative statement a formation of transient sites by random small catastrophes in the biotop. Otherwise the two concepts developed independently are identical.

When competition for resources becomes a contest rather than a scramble in Nicholson's admirable terminology, there is a theoretical possibility that the principle might not apply, If the breeding population be limited by the number of territories that can be set up in an area, and if a number of unmated individuals without breeding territory are present, food being in excess of the overall requirements, it is possible that territories could be set up by any species entirely independent of the other species, the territorial contests being completely intraspecific. Here a resource, namely area, is limiting but since it does not matter to one species if another is using the area, no interspecific competition need result. No case appears yet to be known, though less extreme modifications of the idea just put forward have apparently been held by several naturalists. Dr Robert MacArthur has been studying a number of sympatric species of American warblers of the genus *Dendroica* which might be expected to be as likely as any organism to show the phenomenon. He finds however very striking niche specificity among species inhabiting the same trees.

The various cases where circumstances change in the biotop reversing the direction of competition before the latter has run its course. Ideally we may consider two extreme cases with regard to the effect of changing weather and season on competition. In natural populations living for a time under conditions simulating those obtained in laboratory cultures in a thermostat, if the competition time, that is, the time needed to permit replacement of one species by another, is very short compared with the periods of the significant environmental variables, then complete replacement will occur. This can only happen in very rapidly breeding organisms. Proctor (1957) has found that various green algae always replace *Haematococcus* in small bodies of water which never dry up, though if desiccation and refilling occur frequently enough the *Haematococcus* which is more drought resistant than its competitors will persist indefinitely. If on the contrary the competition time is long compared with the environmental periods, then the relevant environmental determinants

of competition will tend to be mean climatic parameters, showing but secular trends in most cases, and competition will inevitably proceed to its end unless some quite exceptional event intervenes.*

Between the two extreme cases it is reasonable to suppose that there will exist numerous cases in which the direction of competition is never constant enough to allow elimination of one competitor. This seems likely to be the case in the autotrophic plankton of lakes, which inhabits a region in which the supply of nutrients is almost always markedly suboptimal, is subject to continual small changes in temperature and light intensity and in which a large number of species may (Hutchinson, 1941; 1944) coexist.

There is interesting evidence derived from the important work of Brian (1956a) on ants that the completion of competitive exclusion is less likely to occur in seral than in climax stages, which may provide comparable evidence of the effect of environmental changes in competition. Moreover whenever we find the type of situation described so persuasively by Andrewartha and Birch (1954) in which the major limitation on numbers is the length of time that meteorological and other conditions are operating favorably on a species, it is reasonable to suppose that interspecific competition is no more important than intraspecific competition. Much of the apparent extreme difference between the outlook of, for instance, these investigators, or for that matter Milne on the one hand, and a writer such as Lack (1954) on the other, is clearly due to the relationship of generation time to seasonal cycle which differs in the insects and in the birds. The future of animal ecology rests in a realization not only that different animals have different autecologies, but also that different major groups tend to have fundamental similarities and differences particularly in their broad temporal relationships. The existence of the resemblances moreover may be quite unsuspected and must be determined empirically. In another place (Hutchinson, 1951) I have assembled such evidence as exists on the freshwater copepoda, which seem to be reminiscent of birds rather than of phytoplankton or of terrestrial insects in their competitive relationships.

It is important to realize, as Cole has indicated in the introductory contribution to this Symposium, that the mere fact that the same species are usually common or rare over long periods of time and that where changes have been observed in well studied faunas such as the British birds or butterflies they can usually be attributed to definite environmental causes in itself indicates that the random action of weather on generation is almost never the whole story. Skellam's demonstration that such action must lead to final extinction

* If there were really three species of giant tortoise (Rothschild, 1915) on Rodriguez, and even more on Mauritius, and if these were sympatric and due to multiple invasion (unlike the races on Albemarle in the Galapagos Islands) it is just conceivable that the population growth was so slow that mixed populations persisted for centuries and that the completion of competition had not occurred before man exterminated all the species involved.

must be born in mind. It is quite possible that the change in the phytoplankton of some of the least culturally influenced of the English lakes, such as the disappearance of *Rhizosolenia* from Wastwater (Pearsall, 1932), may provide a case of random extinction under continually reversing competition. The general evidence of considerable stability under most conditions would suggest that competitive action of some sort is nearly always of significance.

2.7. Rarity and commonness of species and the non-intersection of realized niches. Several ways of approaching the problem of the rarity and commonness of species have been suggested (Fisher *et al.*, 1943; Preston, 1948; Brian, 1953; Shinozaki and Urata, 1953). In all these approaches relatively simple statistical distributions have been fitted to the data, without any attempt being made to elucidate the biological meaning of such distribution. Recently however MacArthur (1957) has advanced the subject by deducing the consequences of certain alternative hypotheses which can be developed in terms of a formal theory of niches.

It has been pointed out in a previous paragraph that the Volterra–Gause principle is equivalent to a statement that the realized niches of co-occurring species are non-interesting. Consider a **B** space containing an equilibrium community of n species $S_1 S_2 \ldots S_n$, represented by numbers of individuals $N_1\ N_2 \ldots N_2$. For any species S_K it will be possible to identify in **B** a number of elements, each of which corresponds to a whole or part of $\mathbf{N}'_K$ and to no other part of **N**. Suppose that at any given moment each of these elements is occupied by a single individual of S_K, the total volume of **B** which may be regarded as the specific biotop of S_K will be $N_K \Delta\mathbf{B}\ (S_K)$, $\Delta\mathbf{B}(S_K)$ being the mean volume of **B** occupied by one individual of S_K. Since the biotop is in equilibrium with respect to the n species present, all possible spaces will be filled so that:

$$\mathbf{B} = \sum_{K=1}^{n} N_K \Delta\mathbf{B}(S_K).$$

We do not know anything *a priori* about the distribution of $N_1\Delta\mathbf{B}(S_1)$, $N_2\Delta\mathbf{B}(S_2), \ldots, N_n\Delta\mathbf{B}(S_n)$, except that these different specific biotops are taken as volumes proportional to $N_1 N_2 \ldots N_n$, which is a justifiable first approximation if the species are of comparable size and physiology. In general some of the species will be rare and some common. The simplest hypothesis consistent with this, is that a random division of **B** between the species has taken place.

Consider a line of finite length. This may be broken at random into n parts by throwing $(n-1)$ random points upon it. It would also be possible to divide the line successively by throwing n random pairs of points upon it. In the first case the division is into non-overlapping sections, in the second the sections overlap. MacArthur, whose paper may be consulted for references to the

mathematical procedures involved, has given the expected distributions for the division of a line by these alternative methods (Fig. 1). He has moreover shown that with certain restrictions the distribution (I) which corresponds to non-intersecting specific biotops and so to non-intersecting realized niches, fits certain multispecific biological associations extremely well. The form of this distribution is independent of the number of dimensions in **B**. The alternative distribution with overlapping specific biotops predicts fewer species of intermediate rarity and more of great rarity than is actually found; proceeding from the linear case (II), to division of an area or a volume, accentuates this discrepancy. Two very striking cases in which distribution I fits biological multispecific populations are given in Figs 2 and 3 from MacArthur and in Fig. 4 from the recent studies of Kohn (in press).

The limitation which is imposed by the theory is that in all large subdivisions of **B** the ratio of total number of individuals ($m = \sum_{i=1}^{n} N_i$) to total number of species (n) must remain constant. This is likely to be the case in any biotop which is what may be termed *homogeneously diverse*, that is, in which the elements of the environmental mosaic (trees, stones, bushes, dead logs, etc.) are small compared with the mean free paths of the organisms under consideration. When a heterogeneously diverse area, comprising for instance stands of woodland separated by areas of pasture, is considered it is very unlikely that the ratio of total numbers of individuals to number of species will be identical in both woodland and pasture (if it occasionally were, the fact that both censuses could be added would not be of any biological interest). MacArthur finds that at least some bodies of published data which do not fit distribution I as a whole, can be broken down according to the type of environment into subcensuses which do fit the distribution. Data from moth traps and from populations of diatoms on slides submerged in rivers would not be expected to fit the distribution and in fact do not do so.* Such collection methods certainly sample very heterogeneously diverse areas.

The great merit of MacArthur's study is that it attempts to deduce operationally distinct differences between the results of two rival hypotheses, one of which corresponds essentially to the extreme density dependent view of interspecific interaction, the other to the opposite view. Although certain simplifying assumptions must be made in the theoretical treatment, the initial results suggest that in stable homogeneously diverse biotops the abundances of different species are arranged as if the realized niches were non-overlapping; this does not mean that populations may not exist under other conditions which would depart very widely from MacArthur's findings.

2.8. The problem of the saturation of the biotop. An important but quite inadequately studied aspect of niche specificity is that of the number of species

* I am indebted to Dr Ruth Patrick for the opportunity to test some of her diatometer censuses.

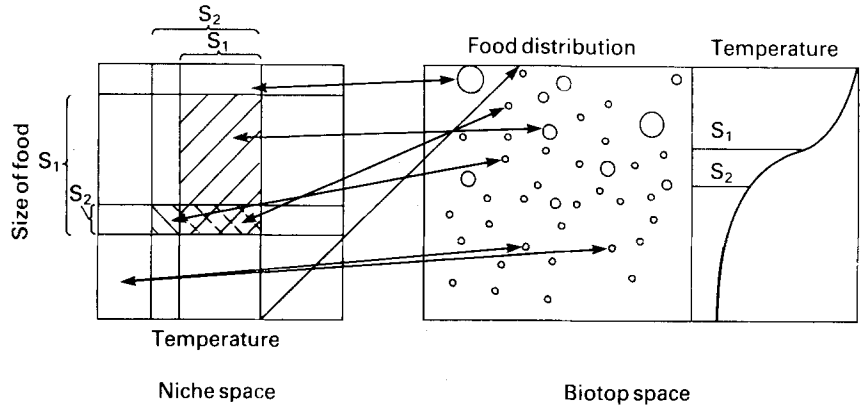

Figure 1. Two fundamental niches defined by a pair of variables in a two-dimensional niche space. Only one species is supposed to be able to persist in the intersection subset region. The lines joining equivalent points in the niche space and biotop space indicate the relationship of the two spaces. The distribution of the two species involved is shown on the right-hand panel with a temperature depth curve of the kind usual in a lake in summer.

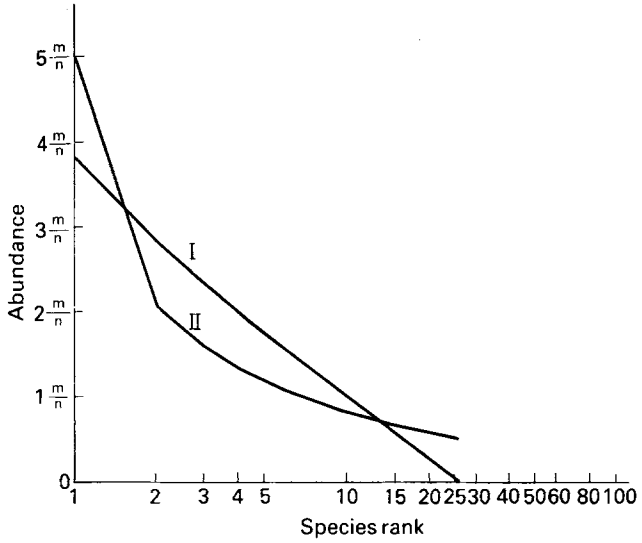

Figure 2. Rank order of species arranged per number of individuals according to the distributions I and II considered by MacArthur.

that a given biotop can support. The nature of this problem can be best made clear by means of an example.

The aquatic bugs of the family *Corixidae* are of practically world wide distribution. Omitting a purely Australasian subfamily, they may be divided

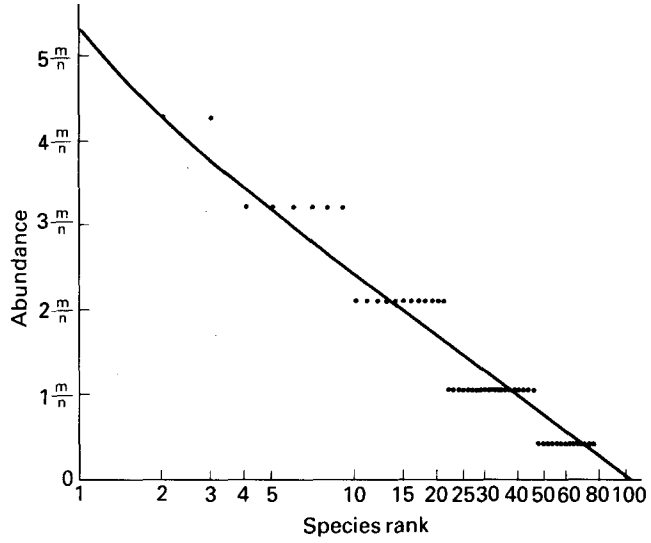

Figure 3. Rank order of species of birds in a tropical forest, closely following MacArthur's distribution I.

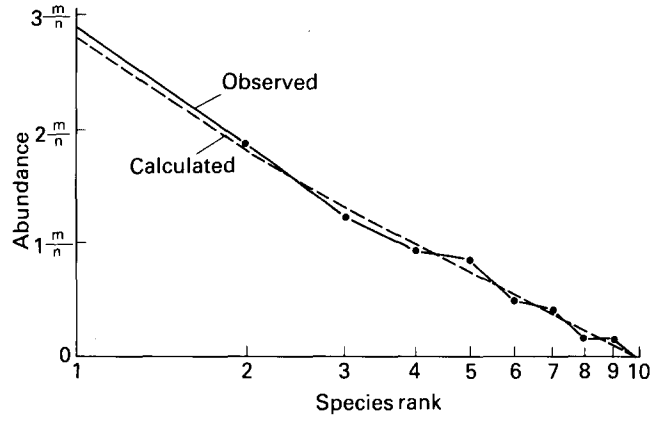

Figure 4. Rank order of species of *Conus* on a littoral bench in Hawaii (Kohn).

into the *Micronectinae* which are nearly always small, under 5 mm long and the *Corixinae* of which the great majority of species are over 5 mm long. Both subfamilies probably feed largely on organic detritus, though a few of the more primitive members of the *Corixinae* are definite predators. Some at least suck out the contents of algal cells, but unlike the other Heteroptera they can take particulate matter of some size unto their alimentary tracts. There is abundant evidence that the organic content of the bottom deposits of the shallow water in which these insects live is a major ecological factor regulating their occurrence.

No *Micronectinae* occur in temperate North America and in the Old World this subfamily is far more abundant in the tropics while the *Corixinae* are far more abundant in the temperate regions (Lundblad, 1934; Jaczewski, 1937). Thus in Britain there are 30 species of *Corixinae* and three of *Micronectinae* (Macan, 1956), in peninsular Italy 20 or 21 species of *Corixinae* and five of *Micronectinae* (Stickel, 1955), in non-Palaeartic India about a dozen species of *Corixinae* and at least ten species of *Micronectinae* (Hutchinson, 1940) and in Indonesia (Lundblad, 1934) only three *Corixinae* and 14 *Micronectinae*. A reasonable explanation of this variation in the relative proportions of the two subfamilies is suggested by the findings of Macan (1938) and the more casual observations of other investigators that *Micronecta* prefers a low organic subtratum; in tropical localities the high rate of decomposition would reduce the organic content.

In certain isolated tropical areas at high altitudes, notably Ethiopia and the Nilghiri Hills of southern India the decline in the numbers of *Micronectinae* with increasing altitudes, and so lower average water temperatures, is most noticeable, but there is no increase in the number of *Corixinae*, presumably because the surrounding fauna is not rich enough to have permitted frequent invasion and speciation. Thus in the Nilghiri Hills between 2 100 and 2 300 m, intense collecting yielded three *Corixinae* of which two appear to be endemic, and one non-endemic species of *Micronecta*. Very casual collecting below 1 000 m in south India has produced two species of *Corixinae* and five species of *Micronectinae*. The question raised by cases like this is whether the three Nilghiri *Corixinae* fill all the available niches which in Europe might support perhaps 15 or 20 species, or whether there are really empty niches. Intuitively one would suppose both alternatives might be partly true, but there is no information on which to form a real judgement. The rapid spread of introduced species often gives evidence of empty niches, but such rapid spread in many instances has taken place in disturbed areas. The problem clearly needs far more systematic study than it has been given. The addition and the replacement of species of fishes proceeding down a river, and the competitive situations involved, may provide some of the best material for this sort of study, but though much data exists, few attempts at systematic comparative interpretation have been made (cf. Hutchinson, 1939).

3. The Future of Comparative Demographic Studies. Perhaps the most interesting general aspect of the present Symposium is the strong emphasis placed on the changing nature of the populations with which almost all investigators deal. In certain cases, notably in the parthenogenetic crustacean *Daphina* (Slobodkin, 1954), it is possible to work with clones that must be almost uniform genetically, but all the work on bisexual organisms is done under conditions in which evolution may take place. The emergence in

Nicholson's experiments of strains of *Lucilia* in which adult females no longer need a protein meal before egg laying provides a dramatic example of evolution in the laboratory; the work reported by Dobzhansky, by Lewontin, and by Wallace, in discussion, shows how experimental evolution, for which subject the Carnegie Laboratory at Cold Spring Harbor was founded, has at last come into its own.

So far little attention has been paid to the problem of changes in the properties of populations of the greatest demographic interest in such experiments. A more systematic study of evolutionary change in fecundity, mean life span, age and duration of reproductive activity and length of post reproductive life is clearly needed. The most interesting models that might be devised would be those in which selection operated in favor of low fecundity, long pre-reproductive life and on any aspect of post-reproductive life.

There is in many groups, notably *Daphnia*, dependence of natality on food supply (Slobodkin, 1954) though the adjustment can never be instantaneous and so can lead to oscillations. In the case of birds the work of the Oxford school (Moreau, 1944; Lack, 1947a, 1954 and many papers quoted in the last named) indicates that in many birds natality is regulated by natural selection to correspond to the maximum number of young that can be reared in a clutch. In some circumstances the absolute survival of young is greater when the fecundity is low than when it is high. The peculiar nature of the subpopulations formed by groups of nestlings in nests makes this reasonable. Slobodkin (1953) has pointed out that in certain cases in which migration into numerous limited areas is possible, a high reproductive rate might have a lower selective advantage than a low rate. Actually in a very broad sense the bird's nest is a device to formalize the numerous limited areas, the existence of which permits such a type of selection. It should be possible with some insects to set up population cages in which access to a large number of very small amounts of larval food is fairly difficult for a fertile female. If the individual masses of larval food were such that there was an appreciable chance that many larvae on a single mass would die of starvation while a few larvae would survive, it is possible that selection for low fecundity might occur. This experiment would certainly imitate many situations in nature.

The evolutionary aspects of the problem raised by those cases where there is a delay of reproductive activity after adult morphology has been achieved is much harder to understand. Some birds though they attain full body size within a year (or in the case of most passerines in the nest) are apparently not able to breed until their third or later year. It is difficult to see why this should be so. In any given species there may be good endocrinological reasons for the delay, but they can hardly be evolutionarily inevitable. The situation has an abvious *prima facie* disadvantage, since most birds have a strikingly diagonal survivorship curve after the first year of life and this in itself indicates little

capacity for learning to live. One would have supposed that in the birds, mainly but not exclusively large sea birds, which show the delay, any genetic change favoring early reproduction would have a great selective advantage. Any experimental model imitating this situation would be of great interest.

The problem of possible social effects of long post-reproductive life, which can hardly be subject to direct selection, provides another case in which any hints from changes in demographic parameters in experiments would be most helpful. The experimental study of the evolutionary aspects of demography is certain to yield surprises. While we have Nicholson's work, in which the amplitude of the oscillation in *Lucilia* populations appear to be increased or at least not decreased as a result of the evolution he has observed, though the minima are less low and the variation less regular, we do not know if this sort of effect is likely to be general. Utida's elegant work on bean weevils appears to be consistent with some evolutionary damping of oscillations which would be theoretically a likely result.

The most curious case of a genetic change playing a regular part in a demographic process is certainly that in rodents described by Chitty. In view of the large number of simple ways which are now available to explain regular oscillations in a population, it is extremely important to heed Chitty's warning that the obvious explanation is not necessarily the true one. To the writer, this seems to be a particular danger in human demography, though the mysteries of variation of the human sex ratio, so clearly expounded by Colombo, should be a warning against over-simple hypotheses, for here no reasonable hypotheses have been suggested. Human demography relies too much on what psychologists call intervening variable theory. The reproducing organisms are taken for granted; when their properties change, either as the result of evolution or of changes in learned behavior, the results are apt to be upsetting. The present "baby boom" is such an upset, and here a tendency to over-simplified thinking is also apparent. If, as appears clear at least for parts of North America, the present birth rate is positively correlated with economic position, it is easy to suppose that couples now have as many children as they can afford, just as most small birds appear to do. There is, however, a difference. If at any economic level a four child family was desired, but occasionally owing to the imperfections of birth control a five child family was actually achieved, we should not expect the fifth child to have a negligible expectation of life at birth, so that the total contribution to the population per family would be the same from a four and five child family. Yet this is exactly what Lack and Arn (1947) found for the broods of the Alpine swift *Apus melba*. In man the criterion is never purely economic; it is not how large a brood can be reared, but how large a brood the parents think they can rear without undue economic sacrifice. Such a method of setting limits to natality is obviously extremely complicated. It involves an equilbrium between a series of desires,

partly conscious, partly unconscious, and a series of estimates of present and future resources. There is absolutely no reason to suppose that the mean desired family size determined in such a way is a simple function of economics, uninfluenced by a vast number of other cultural factors. The assumption that a large family is *per se* a good thing is obviously involved; this may be accepted individually by most parents even though it is at present a very dubious assumption on general grounds of social well being. Part of the acceptance of such an assumption is certain to be due to unconscious factors. Susannah Coolidge in a remarkable, as yet unpublished, essay,* "Population *versus* People", suggests that for many women a new pregnancy is an occasion for a temporary shifting of some of the responsibility for the older children away from the mother, and so is welcomed. She also suspects that it may be an unconscious expression of disappointment over, or repudiation of, the older children and so be essentially a repeated neurotic symptom. Moreover, the present highly conspicuous fashion for maternity, certainly a healthy reaction from the seclusion of upper-class pregnant women a couple of generations ago, is also quite likely fostered by those business interests which seem to believe that an indefinitely expanding economy is possible on a non-expanding planet.

An adequate science of human demography must take into account mechanism of these kinds, just as animal demography has taken into account all the available information on the physiological ecology and behaviour of blow flies, *Daphnia* and bean weevils. Unhappily, human beings are far harder to investigate than are these admirable laboratory animals; unhappily also, the need becomes more urgent daily.

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* I am greatly indebted to the author of this work for permission to refer to some of her conclusions.

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