SECTION D: SOME PERSPECTIVES IN MAMMAL ECOLOGY

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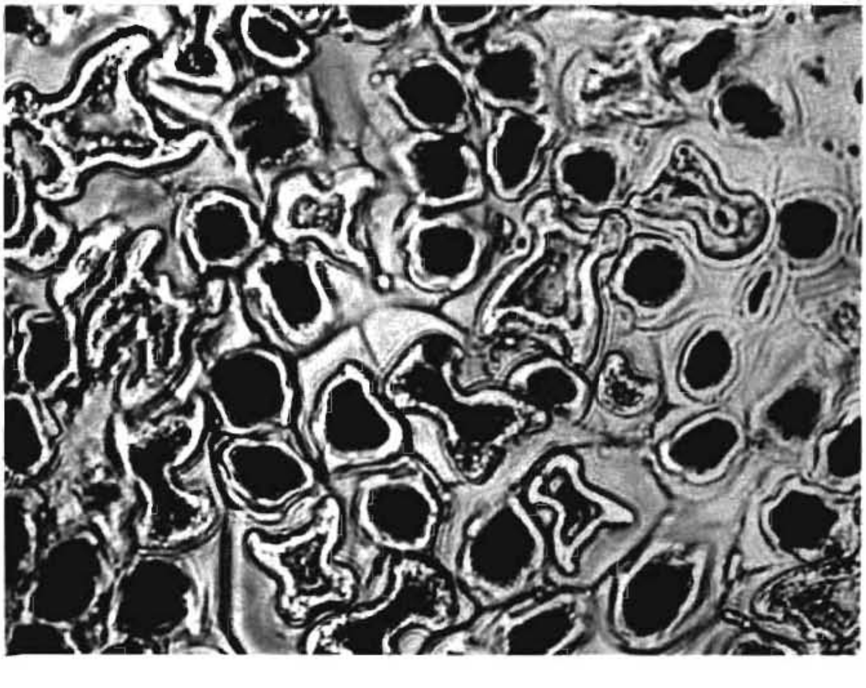
(Section Leader's Introductory Address)

When ecologists are talking together, the opinion is sometimes expressed that mammals are poor subjects for ecological work. The laws of ecology apply to them as to other animals, and it is possible to extract wide general principles from work done on mammals, as from work done on other animals. Nevertheless, there are certain undeniable difficulties in ecological research on mammals which render them relatively unpopular with students who wish merely to find the most convenient animal upon which to test a hypothesis. They are frequently shy and difficult to observe or capture; or they may be relatively scarce, so that it is not easy to accumulate a statistically significant series of observations; their physiological homeostatic mechanisms reduce to a low level their overt responses to many of the simpler, easy-to-measure physical factors of the environment. Worst of all, they are intelligent; even quite trivial interference with them may alter their behaviour enough to prejudice the validity of future observations to an indeterminate extent. In short, the fact must be faced that few groups of animals present so many barriers and difficulties to the ecologist as do mammals.

Yet the ecology of mammals must be studied, because for many reasons they are important animals. They may be important because of their individual size, because of the biomass which they represent, or because of an economic, medical or other direct relationship with man. Mammals are frequently a major factor, and sometimes a dominant factor, in the local ecosystem, and in no continent is this more clearly demonstrated than in Africa.

It is obvious, therefore, that the programme of sessions on population ecology in a Symposium on African Mammals ought to be varied in content and comprehensive in scope. I find it most encouraging that this description applies aptly to the papers to be presented—so much so that I needed to look no further than the Symposium programme when searching for inspiration for these introductory remarks. This programme demonstrates beyond doubt that important work on mammal ecology is being carried out in Africa today. It is only necessary for me to exhort others to explore more deeply, and cast the net more widely.

As a start I would like to commend the speakers who will give papers which are wholly or mainly concerned with techniques. It is very easy for practical details of methods to be lost because the only published record is so abbreviated as to be of very limited value; or to be difficult to find because the description is contained in the "Material and Methods" section of a paper, the title of which gives few clues to the presence of this vital information. The answer is, where a new technique has been developed, or major improvements made to an old one, to publish the method separately. Editors of journals are well aware of this problem, and many nowadays will look more kindly upon such papers than has sometimes been the case in the past.



For example, in a recently completed study of the food and feeding of the stoat *Mustela erminea* and the weasel *M. nivalis* which was carried out at Exeter (Day 1963), it was found necessary to examine large numbers of guts and scats of the predators to determine the species of prey animals. Since these small mustelids reject large bones, and break up very finely such bones and other hard parts as they swallow, such valuable aids to prey identification as teeth and large bone fragments are virtually absent from their gut. Prey identification must therefore depend on the only parts which are swallowed intact and not destroyed by digestion—hair and feathers. Identification of hairs is not, of course, a new technique—forensic scientists, for example, have used it for many years. Dr Day's contribution lies in some refinements of techniques, and in constructing a key which makes possible the identification from their hairs, at least to genus in most cases, of such mammals as are likely to become the prey of small mustelids in Britain (Plate 1). A similar key makes possible the identification from their covert feathers, at least as far as order in most cases, of such birds as are similarly likely to be eaten by stoats and weasels in Britain (Pl. 2).

It would be inconvenient and cumbersome in a general account of the results of Dr Day's investigation, to publish a description of his technique in detail, or to include his keys in their entirety. It is proposed, therefore, to publish a separate paper devoted to the methods of hair and feather identification with the keys and a full bibliography, so making these available to any worker who wishes to use the technique as it stands, or who wishes to adapt and improve it still further. Similarly, I hope that speakers on matters of technique at this symposium will feel able to express their ideas and experience in print.

Turning from this general point to matters more specifically ecological; it might be argued that one of the greatest steps in the emergency of ecology as a science was the quantification of observations. The relative simplicity by which this may be achieved is demonstrated by a paper which we are to hear based on counts of game animals drinking at water holes during dry weather. Large numbers of tourists in many parts of Africa have derived great pleasure from watching aggregations of game at water holes. Yet when trouble is taken to count the animals, and analyse the results, how much more exciting and significant the phenomenon becomes.

The way in which important conclusions may be drawn from relatively simple, quantitative observations is well exemplified by the work of Boyd (1959) on St. Kilda. Only one small mammal is to be found on this island, the common wood mouse of Britain, *Apodemus sylvaticus.* Boyd trapped these wood mice, using groups of 10 traps set in a standard manner, at 30 places at altitudes from 25 feet to 1,250 feet above sea level (the highest point on the island

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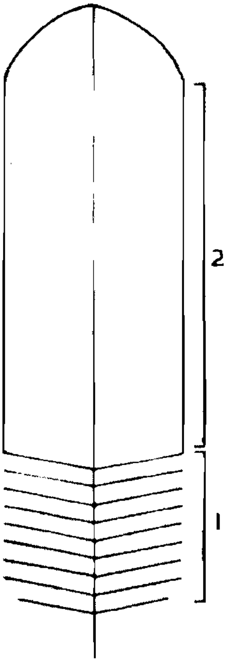
PLATE 1. Three criteria are used in the identification of mammal genera from hairs, viz. the appearance of the surface scale pattern as seen in an impression made on a thin film of gelatine; the appearance of the medullary "cells" of the hair and the profile view of the scales seen in a whole mount of a hair; and the outline and medullary "cells" seen in cross sections of hairs. A. Gelatine cast of the base of a guard hair of a vole, showing an irregular scale pattern. B. Whole mount of the base of a guard hair of a shrew—note single row of medullary "cells" and row of scales protruding on one side only. C. Cross section of the hairs of a shrew. The large outlines are guard hairs—note the single compartment in the medulla, and the bizarre H-shaped outline (From Day 1963).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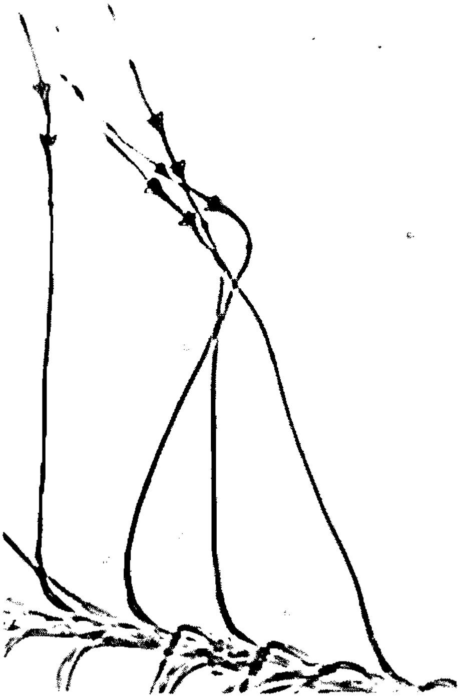
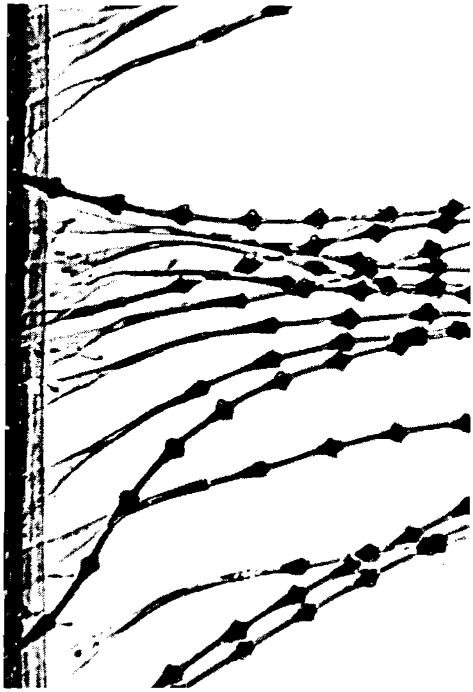




has an altitude of 1,396·8 ft.). Pointing out that exposure (which he defined as "a complex of climatic and topographic variables") was a direct function of altitude, Boyd was able to demonstrate a highly significant inverse correlation between heights above sea level of the trapping stations, and weights of total catch at each station. Weights of catch were used because the maximum possible catch size of 10 individuals left too little scope for variation. I carried out similar observations several years after Boyd, using groups of 50 traps instead of 10. Since the sample sizes were larger, it was possible to correlate numbers of mice caught with altitude. The results confirmed Boyd's finding of a simple general relationship between the frequency of occurrence of a mammal and height above sea level on this isolated wind-swept island.

Returning to the previously mentioned paper on the occurrence of game animals at water holes, we find that a further point of the greatest significance is demonstrated: proper interpretation of observations is dependent upon a thorough understanding of behavioural relationships, both interspecific and intraspecific, between the animals using the water holes. Clearly a mammal ecologist cannot consider himself fully equipped without a general knowledge of theories of behaviour, and a specific knowledge of the behavioural characteristics of the species with which he is working.

In a recent study with the primary object of elucidating the nature of the relationship between an animal (the short-tailed vole *Microtus agrestis*) and the traps used to catch it (E. E. Shillito 1960) it was found necessary to pay careful attention to the whole problem of the relation of the vole to its environment, and in particular the vexed question of exploratory behaviour (E. E. Shillito 1963). The work of Dr. Elizabeth Shillito and others reveals very clearly that the home range of many mammals, large and small, is an area by no means of equal value throughout to the animal. Within the range are areas used intensively, and areas which are seldom if ever visited; there are in many cases well-defined pathways which the animal habitually uses when moving from one part of its home range to another. Of course, there may well be times when an animal moves more or less at random; during feeding, perhaps, or when reconnoitring a previously unknown area. But many movements of mammals are specifically orientated towards definite areas, objects or situations, the orientation being determined by the drive which initiates the movement. Even in the case of large mammals, where it may be quite easy to identify the different uses to which different parts of the home range are put, the extent of the animal's dependence on its knowledge of its home range, and the restrictions which knowledge and lack of knowledge impose on movements, are not always fully realised.

In the case of the small mammals, it is possible to find many instances where movements of animals are assumed to be random, particularly for the purpose of making population esti-

PLATE 2. In identifying orders of birds the coverts (body feathers) are most useful, since the diagnostic features of the downy barbules of these feathers stand up well to the rigours of ingestion and digestion. A. Diagram of covert showing downy (1) and non-downy (2) regions. B. Downy barbules of a member of the Passeriformes, showing villi on the bases. C. Portion of downy barbule of a member of the Galliformes, showing how in some regions the nodes loosen and slip together into groups of two (as here) or more. D. Downy barbules of anseriform bird, showing how the nodes are confined to the tip (From Day 1963).

mates (Southern and Linn 1964). Yet this may be very far from the truth. In the course of some work currently in progress at the University of Michigan, H. W. Ambrose III and W. J. Graham (pers. comm.) have been following the movements of individual voles *Microtus pennsylvanicus pennsylvanicus*, tagged with radioactive isotopes, using a scintillation counter. In the case of one particular female, it became clear after her movements had been followed for some days that she habitually spent her nights in a very restricted area, and her days in a larger area some yards away, moving between the two morning and evening, habitually using a curved path. Inasmuch as the area in which this female had established her home range was apparently homogeneous, it was difficult to see why it took this particular form. It is not to be assumed that all individuals of *M. p. pennsylvanicus* would establish such eccentric home ranges, and the situation described may be extreme and atypical. Be that as it may, it would be interesting to know why this situation occurred; and extrapolating from this it would be most valuable if enough information were available from a wide range of mammals to enable the ecologist to interpret readily both normal and unusual behaviour patterns so that he might be able to judge their ecological significance. There is a clear need for greater understanding of the behaviour of wild mammals, and greater appreciation of the profound influence of behaviour patterns upon ecology.

Although in mammals there is greater flexibility in behaviour patterns, and thus greater scope for variability according to the particular experience of each individual, and although mammals show to a much less extent than, say, birds, the typical stereotyped innate response to environmental situations, the inherited aspects of behaviour patterns common to all individuals of a species may frequently be recognised. Since these patterns to a large extent set the rules by which an animal lives, a knowledge of their nature, of the extent to which they are innate and therefore largely standard and common to all individuals of the species, or are learned and therefore more or less variable in the light of individual experience, is a most valuable asset to a mammal ecologist. Correct interpretation of data may depend on an understanding of the reasons for particular kinds of behaviour.

The concept of behaviour may, of course, be extended from the individual to the population, or even to the community. Such an extension is valuable, since it conveys something of the sense of dynamics which is essential to good ecological thinking. Descriptions of static ecological situations are of course not without value. Indeed, they may be all that can be managed with available time and resources. Yet so often much of their interest lies in speculation about the factors which led to them, and about their future development. Wherever possible, the ecologist should contemplate a process, not an entity, although this is not always easy.

Later in this programme we shall hear a paper which promises to be most interesting, in which advantage was taken of an unusual opportunity to determine the age structure of a population of black rhinoceros. The modern ecologist is now quite familiar with the concept of the age structure of a population. Moreover, he understands in a general way the significance of different kinds of age structure (Fig. 1) and he is familiar with diagrams demonstrating changes of age structure with time (Fig. 2). It is abundantly clear that in any attempt to define the interrelationships between population and habitat, or to predict the pattern which this

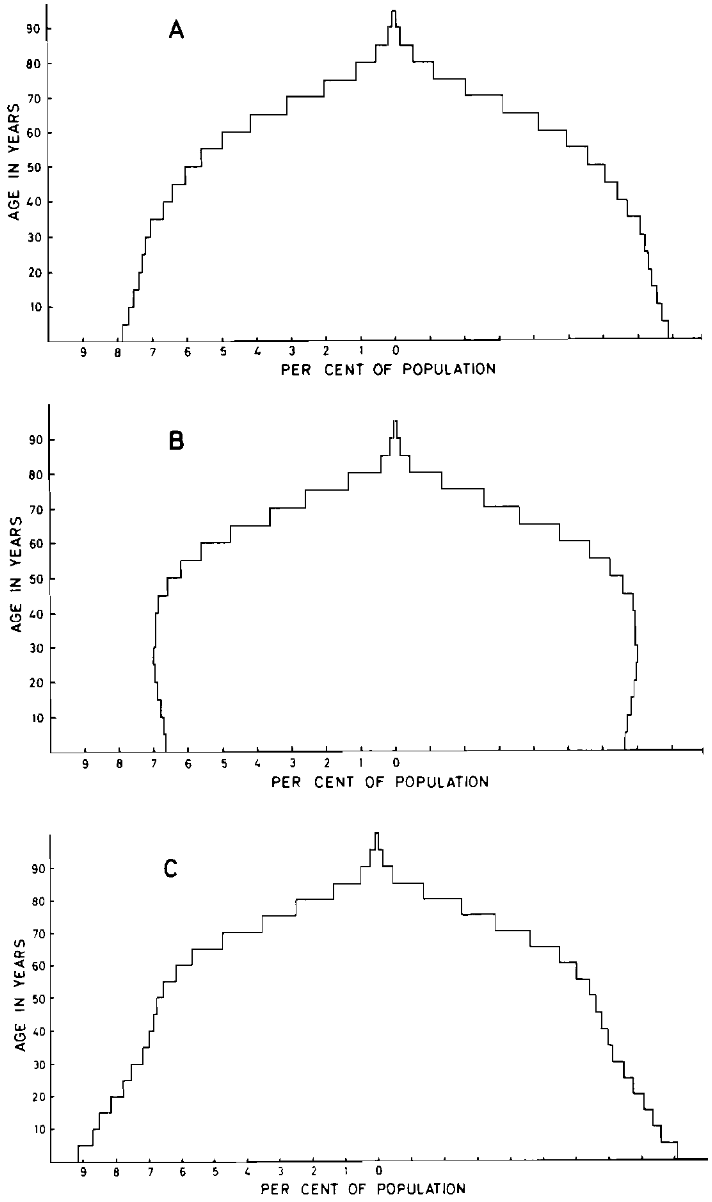


FIGURE 1. Age distribution of white males *Homo sapiens* in U.S.A. in 1930. A. Stationery population. B. With rate of *decrease* of 0·005 per head per year. C. With rate of *increase* of 0·005 per head per year. (From Southern and Linn 1964, after Dublin and Lotka 1936). Lotka (1925) has shown that populations tend to stabilize towards the type of distribution shown in A above. (Figure reproduced by kind permission of authors and publisher).

relationship is likely to follow in any given situation, an understanding of the part played by age structure in determining the course of events is of prime importance. Unfortunately, in spite of the time which has elapsed since the attention of biologists was drawn to these demographic matters (Lotka 1925, Bodenheimer 1938), we are very far from understanding this important factor beyond the simplest approximations. This is at least in part due to the very great technical difficulties of obtaining the necessary information in the field, but problems of analysis and interpretation are also important. It may well be that the first break-through will come from work on laboratory populations of some conveniently short-lived species of animal. Yet the field data must eventually be collected, and the operation of this factor in natural situations will, we hope, be understood. We must eventually be able to recognise the patterns which are formed as age structure changes with time, as this will give valuable information about the nature of the population and the type of ecological process in which it is involved. It would also, since no population exists in isolation, open a useful window on many aspects of the functioning of the local ecosystem. The theoretical groundwork has yet to be laid for this kind of exploration, and the practical difficulties are daunting, and this is all the greater reason why a start should be made now, so that the ultimate aim may be reached the sooner.

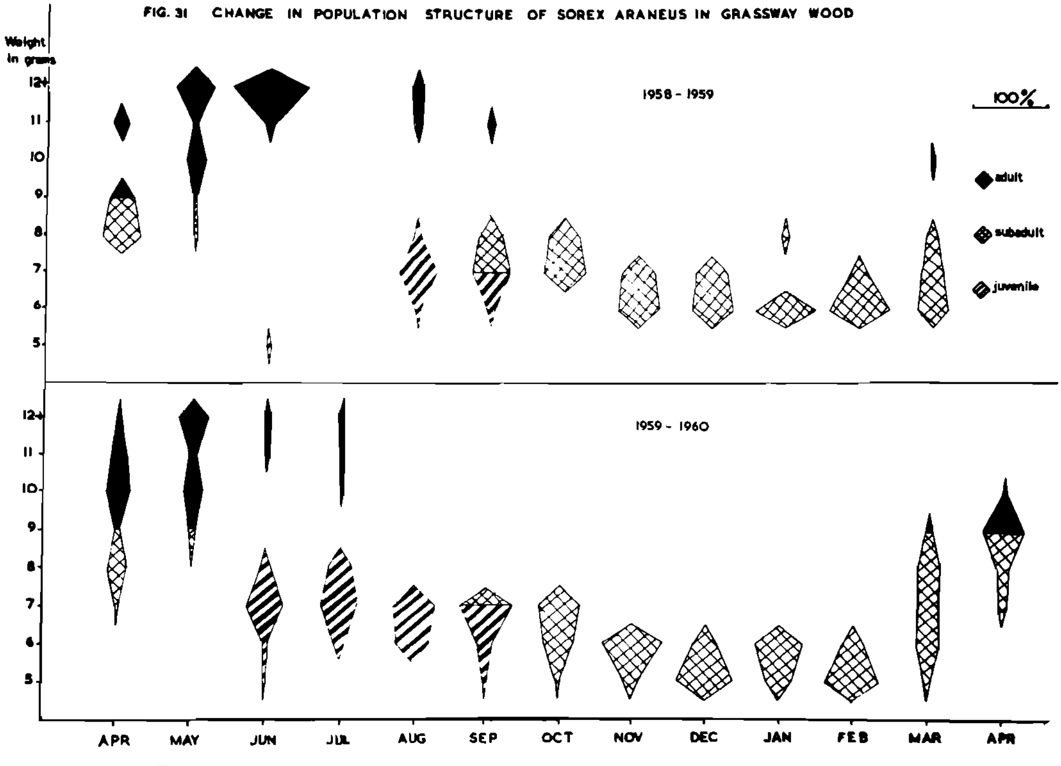


FIGURE 2. Diagram to show the change in population structure of a woodland population of *Sorex araneus* over two complete years. (From J. F. Shillito 1963a). Note the rapid extinction of adults after breeding. Age was determined by pelage condition and weight; winter weight loss accounts for the downward distortion of the age trend in subadults. (Reproduced by kind permission of the author and of the Zoological Society of London).

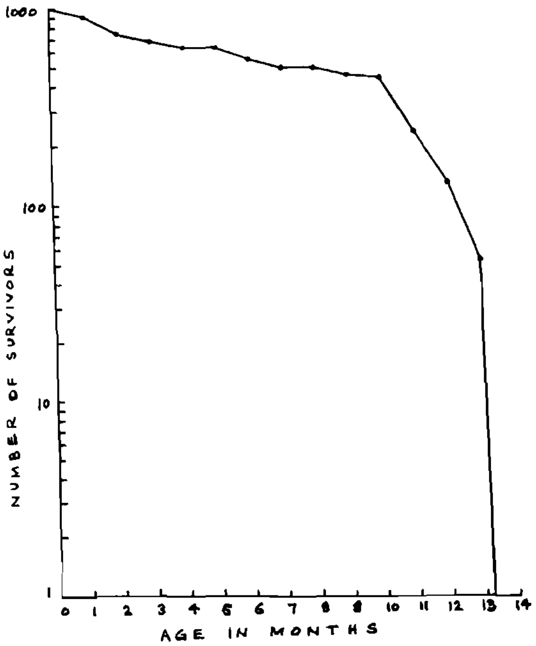
Another set of parameters which crops up with increasing regularity is the life table, and what is perhaps its most significant immediate derivative, the survivorship curve. A few years ago I was involved in an investigation of the ecology of the common shrew of Britain, *Sorex araneus* (J. F. Shillito 1960, 1963a, 1963b, 1964). From the data collected, an attempt was made to construct a life table for this species, and a survivorship curve was drawn (Fig. 3). While in itself interesting, this work led me to consider some of the important aspects of the interpretation of demographic data of this kind. The survivorship curve for *Sorex araneus* is I believe quite a good one. It is possible to see that there is, over most of the period of survival of the group, a steady improvement in the mortality rate, until the sudden terminal onset of mortality which extinguishes the group quite quickly. This is a good example of the rectangular type of survivorship curve, but it must be remembered that this particular curve is drawn from data obtained only from animals entering the active population. No data are available on mortality among nestlings, so that the curve is to this extent incomplete. Such incomplete curves are often of considerable value in analyses of the survival patterns of species which have very high early mortality, so high as to obscure the pattern of the rest of the life span. In mammals, with their well-developed parental care, such a problem would be most unlikely to arise. The point of origin of the life table should therefore be as early in the animal's life as possible, to assess the importance of infant mortality.

Other important aspects of survival which were brought home to me during the work on the common shrew were the obvious enough facts that survivorship changes with time, and is different in different sections of the same population at the same time. The first point is well enough exemplified by comparing the survivorship curve of the female inhabitants of Massachusetts in 1890 with that of their counterparts in 1910 (Fig. 4). The change in the infant mortality alone is startling. In this case the probable major causes of the change are clear enough—advances in hygiene an easy first, with better nutrition and advances in medicine also of some importance. In wild populations it might be more difficult to assess the causation of changes.

On the second point, it is well understood that different sections of human populations have different specific mortalities. Insurance companies issuing motor car policies may quote very different premium rates for undergraduates and clergymen! On a wider scale the survival curves for India, Italy and Australia show the very distinct influence that local conditions have on human life (Fig. 5). Similar differences undoubtedly exist in wild mammal populations—in temperate countries, for example, it seems possible that small rodents born early in the breeding season have a different survival pattern from those born later on. It would be interesting to compare the survivorship curves of these different groups of animals.

Throughout this discussion of demography I find once again that I am emphasising the study of the pattern of process. It is again clear that the most exciting progress is to be made by viewing the ecological situation as dynamic—continually developing and changing. If we can understand the nature of these changes, we may one day have a firmer basis for assessment of causation.

One of the most vexed questions in ecology today concerns the part played by food supplies in population regulation. Views tend to be extreme—food is represented sometimes as the



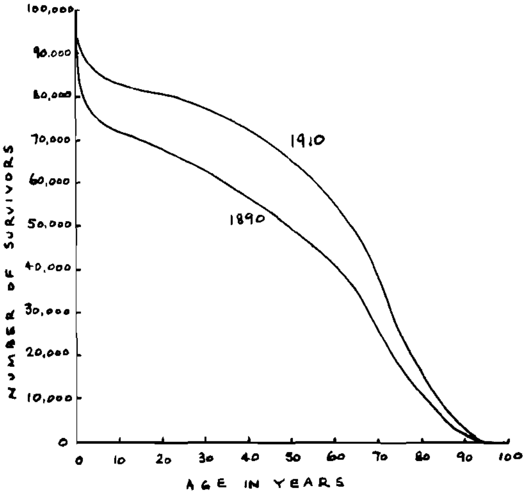
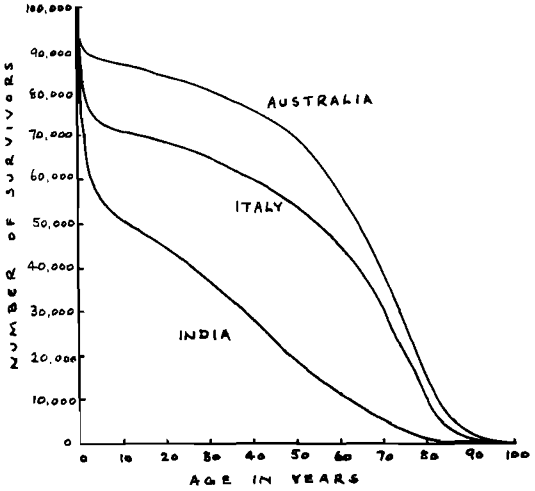


FIGURE 3. Survivorship curve for a woodland population of *Sorex araneus* (From J. F. Shillito 1960).

FIGURE 4. Survival curves for female *Homo sapiens* in the State of Massachusetts, 1890 and 1910 (From Lotka 1925, after Glover).

FIGURE 5. Survival curves for *Homo sapiens* in India, Italy and Australia (From Lotka 1925, after Glover).



vital controlling factor for all populations, or at other times as a factor of no great importance. The truth, of course, lies somewhere in between. Many populations stabilise at a level well within the limitations of their food supply, as a result of the operation of mechanisms in which food supply has no part. Wynne-Edwards (1962) has recently speculated at length upon this subject. At other times and places, food limitations impose rigorous sanctions on the increase in size of a population (Dare 1961). Between these extreme situations are all manner of intermediate possibilities, in which food plays a greater or lesser rôle in the regulation of the numbers of an animal. What is quite certain is that the relationship between an animal and its food supply is of the greatest importance, since food is an essential requisite for survival. It is therefore encouraging to see that two of the papers we are to hear are concerned with the food of mammals.

In any study of the food relationships of animals it is important to recognise the reciprocity of the relationship. A topic which is commonly discussed is the extent to which predation may or may not control prey populations. Here again is a subject over which passions become inflamed—often to no good purpose. What is much more rarely discussed is the no less real and important question of the extent to which prey populations control the numbers of their predators.

A few years ago I was involved in an investigation which brought this last point home to me very firmly. Work was in progress on the ecology of the common buzzard *Buteo buteo* on Dartmoor in England (Dare 1961), and an important part of this work was a quantitative study of the food of this predator. As the results came in it became clear that the breeding success of the buzzard was closely linked with supplies of rabbits *Oryctolagus cuniculus*. The rabbit had recently been decimated by myxomatosis, so that some buzzard breeding territories had very few rabbits, while on others they were much more plentiful. Pairs of buzzards holding rabbit-rich territories were usually able to breed successfully, but on rabbit-poor territories, although the adults were able to find enough alternative prey animals (particularly the short-tailed vole *Microtus agrestis*) for their own maintenance, breeding failure was the rule. Some pairs of buzzards attempted to breed, others did not make the effort. Where nestlings were hatched not all died directly of starvation. Some were killed by stronger nest mates, others were killed by crows during their parents' prolonged absences in the vain search for food; but increases in these other causes of mortality were directly linked with food shortage. There could be no mistaking the fact that here, in this particular place, over the short period of a few years that the investigation covered, prey shortage was having a marked depressing effect on the buzzard population. Though this effect may only have been transient, it was real enough, and a clear-cut example not only of the reduction of a predator population by scarcity of a prey species, but also of much of the mechanism by which this reduction came about. Another interesting aspect of this work is the dependence of the buzzard for breeding on a single prey species, the rabbit, although many others were taken—at least one of them, the short-tailed vole, in considerable numbers.

In conclusion, it remains only to welcome in the programme the appearance of papers on production ecology. It seems clear that a study of the flow of energy and materials through the ecosystem is one of the fundamentals of modern ecology. Interest in this aspect of ecology has increased enormously in recent years, and will undoubtedly continue to do so. Anyone not entirely familiar with the subject will find that its essentials are lucidly explained by Odum (1959). It seems likely that the dynamics of ecosystemic working will come to be regarded as the unifying principle in ecology, in much the same way that organic evolution is regarded as the unifying principle of biology. As such, work on production ecology is bound to be of great and continuing importance, and I earnestly commend to this conference the view that the part played by mammals in the great ecosystemic engine of Africa deserves close and immediate attention.

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