ONE

An Overview of the Study of the Population Dynamics of Large Mammals

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HISTORICAL BACKGROUND

Verhulst's interest in human populations and the publication of his application of the logistic equation in the 1830s may be viewed as some of the original work in the formal study of the dynamics of populations of large mammals (see also Chapter 14). Most of the progress in this field, however, has been realized within the last few years. Over time, the character of studies involving large mammal populations has changed as have studies on animal populations in general. Early investigations focused primarily on the capacity of populations to increase. The study of factors involved in preventing unlimited growth acquired more importance later. These same trends characterize the study of population dynamics at other taxonomic levels with an apparent tendency for studies of large mammal populations to lag behind studies of other groups. An excellent discussion of the general history of the study of populations can be found in Hutchinson (1978).

From a taxonomic perspective, the study of population dynamics has shown a tendency to focus on humans, microorganisms, insects, fish, birds, and, to some extent, on small mammals. Comparatively little of the effort expended in the field of population dynamics has involved large mammals other than humans. There are several factors that, in combination, have contributed to this discrepancy. Although often of importance to man, undomesticated large mammals in general are neither as influential as pests nor as important as food sources as are many smaller organisms. The study of the natural history and general biology of large mammals is easier than, and has often precluded or taken precedence over, the study of their population dynamics. The long-lived nature of large mammals (see Chapters 2, 22) prevents the rapid accumulation of data that is possible with populations of small organisms, especially those that can be reared in the laboratory. Obviously, there are fewer species of large mammals than of the smaller-bodied species. Together these factors seem to be the basic cause of a rather short and relatively unproductive history of the study of population dynamics of large mammals.

Most studies involving population dynamics within all taxonomic groups have involved either species of economic interest or man's own population. This has encouraged a narrow perspective oriented toward solving specific problems or achieving specific goals. By comparison, a philosophically more general or academic view of population dynamics has evolved through studies of birds, microorganisms reared in laboratories, and other groups of species that are relatively less important to man.

This trend is especially obvious among studies involving large mammals. As we will discuss them, most studies of the dynamics of large mammals involve three groups: (1) humans; (2) large terrestrial mammals (as predators, tourist attractions, or game animals); and (3) marine mammals (being larger and of economic value). In all cases, most studies involve species of direct importance to man. Few studies of the population dynamics of large mammals are conducted out of pure academic interest. Some of the studies on the George Reserve deer herd (McCullough, 1979), for example, provide a notable and very valuable exception.

The study of the dynamics of human populations has an interesting history. Having started with a conceptually holistic approach embodied in the logistic equation, the work on humans has become deeply engrossed in the effects of structure by age, sex, and reproductive potential, migration, socioeconomics, and other dimensions of importance to short-term projections. The concept of an upper limit to the population (or carrying capacity) has been of much less importance than would have been predicted on the basis of Verhulst's first consideration. Today the bulk of the theory involving dynamics in age-structured populations is to be found under the authorship of people who have worked with human populations.

Increasing impact, brought about by man's growing population and growing interest and concern by the public for the protection of certain species, has created new demands for a better understanding of the ways in which large mammal populations change over time. In terrestrial environments man has long had an interest in protecting, harvesting, or controlling the populations of specific species of large mammals. As in the case of studies involving humans, the study of these species has often progressed to a level of resolution that has, to a degree, prevented the development of holistic views. Studies in these situations have often emphasized minute details of the relationships between the animals and their environments, especially their resources. These studies have generally been less quantitatively oriented than have population studies of humans, insects, and fish. Most studies of terrestrial large mammals have thus resulted in a fairly detailed understanding of the natural history of the species involved. As a result we often know more about the husbandry of these species than we do about either how the populations are regulated or patterns in their dynamics. Specific needs for management and for short-term predictions have worked against the development of a holistic understanding of the population dynamics of large mammals.

Nonetheless, the general need for a holistic view of population regulation is growing in importance as increasing numbers of species of terrestrial large mammals are being managed within the context of their ecosystem. There is a growing need for a general perspective within which such management and future research may be conducted if management is to be realistically based on ecosystem principles.

The mathematical modeling of terrestrial populations of wild large mammals has been attempted only in recent years. Much of the delay in such activities has been a product of insufficient training (see Chapter 21). Most people who have worked with populations of large terrestrial mammals have not been given the mathematical background that is more characteristic of those studying fisheries, human populations, or marine mammals. Those who have attempted to undertake quantitative studies have tried to use life tables without realizing that such an approach is less of a dynamic model than a static description. This weakness is being avoided more in recent work as age-structured matrix models and other more elaborate but less analytically tractable models are being used with the help of computers. Many chapters in this volume exemplify the progress currently being made.

Many large mammals in marine environments are of economic value. The history of the harvest of these species is long and, in some cases, relatively well documented. Technological advances in harvesting techniques have resulted in the extinction, or near extinction, of a number of species. Compared with our view of the population dynamics of terrestrial species, we have a more holistic view of the dynamics of marine mammal populations. This situation has been forced on us by the nature of their environment; detailed examinations of the relationships between marine animals and their environment is prohibitively difficult. Most of the information useful for studying the population dynamics of marine mammals has come from harvest records. As in the case of fish, these data are collected in terms of numbers, ages, pregnancy rates, and weights. The dynamics of each of these attributes of harvested populations has been scrutinized in relationship to the other attributes without the benefit of a detailed understanding of their behavior, physiology, and interaction with other species.

It was not until the 1960s that quantitative syntheses of the data for marine mammals began to take the shape of population models (e.g., Chapman, et al., 1964). The studies that were of greatest importance involved the effects of harvest on exploited populations. Unfortunately, many of these studies were based on previous studies of fish and, to some extent, insect populations. The study of fish was also characterized by data involving numbers, weight, and age, as indicated by the catch. This similarity in data led to a natural tendency to borrow models from older work on fisheries to be applied to marine mammals. As is the case for terrestrial populations, much of the current work on marine mammals is beginning to take on its own identity, overcoming the sometimes inappropriate approaches inherited from early studies in the field of fisheries.

GENERAL APPROACH

Most approaches taken in the study of populations take one of three basic forms. The first is the approach taken by natural historians. This is least formal and is basically descriptive. Little if any attention is paid to the utility of any paradigm developed. The intuitively appealing, intriguing, and visually apparent aspects of a given species' population biology are emphasized. The second approach involves conceptual models formalized in written narrative. This makes a conscious recognition of the existence of the animals in the context of a population. The third approach uses formal mathematical models to describe these populations. Although parts of a continuous and complementary spectrum, these overlapping categories of approaches are useful for discussing the field of population dynamics. It is the more formal approach that we attempt to emphasize through the chapters that make up this volume. Our bias is toward this type of study and, when overwise left unspecified, we will be referring to this approach with the term "population dynamics."

Studies of terrestrial large mammals have often been primarily a process of developing a description of their natural history. Partly because of the length of time required for sufficient data to accumulate, only recently have more holistic, formal treatments of the population dynamics of terrestrial large mammals been developed. An examination of the chapters in this volume, the literature cited herein, and a bibliography of population dynamics in large mammals (Fowler et al., 1980a) illustrates that relatively few organized or specialized efforts have been made along such formal avenues. In many cases, however, there exist relatively unutilized data sufficient for studies involving the production of a formal synthesis. Many populations in Europe, Asia, and North America have been monitored for years. An important need is to identify such sets of data and to utilize this information in formal syntheses to improve our understanding of the dynamics of terrestrial large mammal populations.

Compared with that of terrestrial large mammals, our knowledge of the natural history of marine mammals is limited. Basic biological data often have come solely from animals captured in the harvest, rather than from observations of animals in their natural environment. Motivated by international as well as national concerns, various studies focusing primarily on the dynamics of marine mammal populations were first seriously approached during the 1960s when several formal mathematical models were first applied. The pioneering work of D. G. Chapman on the northern fur seal (Chapman, 1961, 1964, 1973) and with others on the great whales (Chapman et al., 1964; and subsequent volumes of the Reports of the International Whaling Commission) was important in this regard. As mentioned earlier, these studies drew heavily on techniques and concepts developed in earlier studies of fish populations. As will be amplified later, the governments sponsoring such research needed relatively precise evaluations of the size and rate of production of the populations in question in order to provide specific advice for management.

For both terrestrial and marine large mammals, there is a growing need to refine the underlying conceptual models. In most instances, this means that the basic biology or natural history of the species involved should be better utilized in the construction of these models. For terrestrial species this involves using the existing information to extract general principles, while for marine populations this involves the need for more such information. By virtue of this contrast we encounter one of the basic differences in studies of large mammals in these two environments—the difference in resolution—an attribute discussed in the next section.

The study of the dynamics of human populations has developed very differently from the study of the population dynamics of marine and terrestrial large mammals. Studies of human populations involve very formal mathematical models, the third approach discussed above. These models are firmly grounded with precise and detailed descriptions of vital rates, almost always on an age-specific basis. But the underlying conceptual models do not appear to be self-contained. For example, the fact that vital rates (birth, mortality, and so forth) do change is accounted for, but as external input rather than as changes that can be accounted for within the models. (See Chapters 15 and 19 for work of this type on animals other than humans.)

A great deal of attention in the models used in the study of human populations is given to structure, distribution, and details of importance in short-term predictions. Precision over short time spans is more important than are long-term changes, trends or patterns. Very little emphasis is placed on factors of ultimate importance in establishing an upper limit to the human population. Feedback by way of density dependence is rarely if ever included. In comparison to the classic models of marine mammal populations, the models of human populations are quite resolute. In contrast to most models of terrestrial large mammals, and many for marine mammals, models of human populations involve a great deal of internal dynamics relating to age and sex structure.

Because of technological support behind the growth of human populations, relatively little evidence has been found for the existence of density dependence (see Fowler, 1981, Chapter 23). This has led to the abandonment of the logistic that was one of the earliest models to be applied to populations of large mammals (Pollard, 1973). By contrast, considerable evidence for density dependence in large mammals (Fowler et al., 1980b, Chapter 23) exists. Most of the formal models of large mammal population dynamics for nonhuman species involve density dependence as seen in many of the chapters in this book.

As a result of research involving human populations and the supporting theory, we have a very detailed understanding of the process of population growth as it relates to such factors as age structure, reproductive schedules (reproductive value by age), age at first birth, and life span. This is an example of study that has taken a very resolute formal quantitative approach to specific aspects of population dynamics. It is to be contrasted to attempts to incorporate a great deal of resolution into our representations of the interactions between populations and their environments, a matter of scope as discussed in the next section. Such approaches include a larger system, but often with less detail or resolution involving the population itself.

SCOPE AND RESOLUTION

Among the most important aspects of the design of studies of large mammal populations are those of scope and resolution. The breadth of a study and the degree of detail involved are determined by the questions to be addressed. Several dimensions of scope and resolution as involved in studies of large mammal populations are addressed here.

It is important to point out that separate studies of the same population, with different scope and resolution, can be mutually complementary to our understanding of the dynamics of that population. Studies of marine mammals, of terrestrial mammals, and of humans, however, have each tended historically to retain separate sets of goals that are different among, and consistent within, groups. Too frequently this has led to marine mammals being studied nearly consistently at one level of resolution, and humans, for example, at an entirely different level. In view of the fact that studies at different levels of scope and resolution are complementary, it would seem useful to design two studies of an elephant population, for example—one to answer questions generally asked about whales, and a second to answer questions generally asked about humans. Such complementary studies, applied on a large scale, would enhance our overall understanding of the dynamics of large mammal populations.

In all cases the design of studies of populations of large mammals must deal with the overriding problem of resolution, or the degree to which detail is involved. The proper resolution of any particular study is determined by the questions being addressed. The realizable resolution is determined by the existing data, logistical constraints, time, and money. Practical considerations or management-oriented questions often demand precision and predictability at the expense of generality. General principles that often emerge from questions that are more academic in nature, and that demand more generality in approach, are often sacrificed.

Of similar importance is the scope of factors thought to be influential in determining the nature of the dynamics of populations. Can a population be represented adequately by a model involving only the population's numbers and its essential internal characteristics alone? Or do we need to include other elements, such as those of the ecosystem, to capture the essential features of the dynamics of interest. As with the resolution of a model, the scope of a model must be determined largely by the questions being addressed. However, a growing body of theoretical and empirical background would indicate that the proper scope of such studies depends in part on the species involved. Small-bodied "r-selected" species seem to be more at the mercy of their environment than are large "K-selected" species, and hence may require more scope in the models developed to represent them.

Even so, greater scope may be required in meeting the objective of much of the current work on large mammals. In managing the harvest of the great whales and the Alaska fur seals, for example, it has become increasingly clear that the degree of interspecific interactions, both among harvested species and between the harvested populations and their food sources, is considerable (see Chapters 2, 14, 17). It has been estimated that southern hemisphere sei whales may have increased by more than 60% in population size owing to changes in their reproductive rates prior to their being exploited (Smith, 1977; but see also Mizroch, 1980). Similarly, a major area of research is the possible effect of changes in fish populations in the Bering Sea, due to increased fishing effort, on fur seal population size. In both cases the traditional models of limited scope, in providing advice for management, cannot be realistic in accounting for these interactions; but these models can and do provide advice that is precise (discussed below).

Such considerations do not negate, however, the utility of single species models for many purposes. A production model (such as the generalized production model discussed in Chapman, 1960; Richards, 1959; Pella and Tomlinson, 1969) with stochastic properties may capture the essential elements of the dynamics of a broad spectrum of species. Greater degrees of stochasticity (more variance) may be needed for those species that are more subject to their physical and biological environment. The interaction of the species with its biological environment (the ecosystem aspect) may, in large part, be captured by the parameters of such models (e.g., see Fowler, 1980a, 1981).

Obviously, permanent or unusual changes in the ecosystem are not going to be reflected in simple models (see Chapter 17). In addition, it may facilitate our understanding of the ways in which simple models should be parameterized to conduct studies in which a greater scope is included. Thus the more complex ecosystem models are of obvious value, and work along these lines should be encouraged. Progress along these lines will, by necessity, be slow, however, because the quantity of information required often proves prohibitive. (See Fowler et al., 1980b; Chapter 14.)

PRECISION, REALITY, AND GENERALITY

Levins (1966) identified three features of models constructed to represent natural systems. These were generality, precision, and realism. He points out the difficulty (if not impossibility) of obtaining strength in all three of these attributes in one model. One or more must be sacrificed to obtain a strong representation of the others. Different tradeoffs have strength and utility in particular applications. In the study of population dynamics, these principles can be used in evaluating and comparing the various approaches being taken.

Some of the chapters in this book argue that more reality should be included in models of the population dynamics of large mammals, through an increase in scope, especially in terms of the interaction of populations with their environment (Chapters 2, 15-19, 23). It is argued that simple models, such as the logistic, although they implicitly reflect interactions with environments, are often not sufficiently realistic. Some generality and realism are sacrified despite the fact that such models capture several basic concepts of importance. Botkin et al. (Chapter 19) present examples of how specific types of information concerning factors external to populations can potentially affect our views of the ways they behave. Both Caughley (Chapter 18) and Fowler (Chapter 23) argue that interactions between trophic levels may produce overriding effects on the types of dynamics to be expected. These latter arguments attempt to achieve some degree of generality and realism by sacrificing precision. Horwood's chapter (Chapter 17) deals with other interactions between species, sacrificing precision and some generality in an attempt to be realistic. Generality is of less importance than either precision or reality in McCullough's work on grizzly bears (Chapter 9). Somewhat of a balance seems to have been struck by the model behind the chapter by Pojar (Chapter 12), in which only a limited proportion of all three features is achieved.

As argued earlier, one way of dealing with the impossibility of producing a complete representation of reality in one model is to produce several models of the same system. As Walters et al. (Chapter 16) have described, several models of different levels of resolution (and hence precision, reality, or generality) may be produced for examining questions from different points of view. Frequently not well recognized is the possibility of constructing several different models of the same system, instead of developing one in great detail. Although difficult to implement, such an approach emphasizes the problems created by the fact that no model is perfect. Relying on one imperfect model regardless of its resolution can create serious problems.

An interesting example of the balance among realism, precision, and generality appears in the population studies developed to provide advice for the management of several groups of marine mammals. The constraint of providing specific defensible advice to regulatory bodies such as the International Whaling Commission, the United States National Marine Fisheries Service, and the North Pacific Fur Seal Commission has prompted models that emphasize realism and precision—especially the latter—at the expense of generality.

Studies by Chapman and others referenced above for the International Whaling Commission were designed to provide advice to the political decision-making body. The results of these studies had increasing impact on the actual decisions about quota levels that were made through the 1960s and into the 1970s. For different points of view on this, see McHugh (1974), McVay (1974), and Smith (1976). In order to be useful in a sometimes adversarial context, it was necessary that the advice given be quite specific, requiring very high precision in the models being used. It was generally more important that estimates of the effect of various harvest levels be precise than that they be obtained using realistic models. Certainly both of these aspects far outweigh the need for generality in this context.

Very likely, in the interest of providing advice in a usable fashion, the precision of the results of studies on the population dynamics of the great whales has, from time to time, been oversold (Smith, 1976). Certainly decisions have been made primarily on the basis of point estimates, rather than on statistically more meaningful interval estimates. Indeed, in some instances simple sensitivity analyses of the models being used have only recently been undertaken.

Another result of this emphasis on precision is that the scope of the models developed within the context of management has remained quite narrow. They are almost always single-species descriptions, and are heavily dependent on the concepts of density dependence, carrying capacity, and maximum sustainable yield. In fact, the emphasis on precision has, at times, resulted in these concepts being built into the legal framework (national and international) that provides the context in which management decisions are made. Thus the stated management objective for the northern fur seal is maximum sustainable yield. Similarly, the much more general concept of optimum sustainable population level (OSPL), as used in the U.S. Marine Mammal Protection Act (MMPA, Public Law 92-522, 1972), has been interpreted for purposes of managing the incidental kill of porpoises by tuna fishermen as a population size between the level giving maximum sustained yield and the carrying capacity (Smith, 1979).

The problems of management in the context of not being able to provide relatively precise advice are very great. When it becomes apparent or likely that the models being used are rather more precise than they are realistic, or accurate, what is to be done? In the case of the great whales the information available is insufficient to allow creation of new models of greater realism without greatly sacrificing precision. Yet without the level of precision that management decisions have come to depend on, these decisions are more likely to be based on political and economic pressures, too often to the detriment of the long-term productivity and viability of the populations.

Studies of the populations of porpoise in the eastern tropical Pacific illustrate this point in directly acknowledging the problems of realism. Animals of these populations are known to associate closely with schools of yellowfin tuna. Fishermen using purse seines utilize the surface-swimming porpoise as indicators of the presence of tuna, resulting in the incidental killing of some porpoise. Management decisions about allowable incidental kill levels are based, in part, on fairly precise, but rather simple, population models (Smith, 1979; Smith and Polalcheck, 1978). Because of the apparent symbiotic relationship between the tuna and some populations of porpoise, the co-occurrence of several species of porpoise and of tuna, and the reduction in abundance of both the porpoise and the tuna populations, it is reasonable to expect some interspecific relationships to be important. Current management actions are based on a model that is precise, but more general than realistic.

This single-species model was selected as the best for generating management advice when it was realized how difficult it would be to deal with the interspecific interactions. It was *not* decided that a less precise but more realistic multispecies or ecosystem model would be appropriate for management advice. The loss in precision to gain this realism would have been so great as to preclude any utility of the management advice that would be produced. Interestingly, in court challenges to the management decisions that have been made on this advice, the adequacy of the scientific advice is being attacked not in terms of the realism of the models, but rather in terms of the precision of specific parameter estimates used. Thus the decision that precision could not be sacrificed to gain realism is probably reasonable from the perspective of management. Frequently this emphasis on precision over realism has been shown to be a necessity if rational management decisions in adversarial context are to prevail. Indeed, without reliance on such concepts as carrying capacity and maximum sustained yield, the management of marine mammal populations would be governed far more by short-term economic interest than by interests concerning long-term renewability.

COMPARATIVE APPROACHES

Another way of gaining insights into the nature of any specific population and its dynamics is to view it as an example of particular types of populations, and on the basis of the properties of each of the larger groups to deduce the properties of the particular case. This approach presupposes that groupings of populations can be described on the basis of samples of populations drawn from that group. Comparison of the dynamics of populations of various categories should lead, in theory, to general principles of use in deducing properties of specific populations.

It is the apparent lack of attempts to make comparisons and to formulate generalizations concerning the nature of the population dynamics of large mammals that provided the general stimulus for convening the conference at which the contributions to this volume were originally presented. In this volume the chapters by Bunnell and Tait (Chapter 4), Chapman (Chapter 14), Goodman (Chapter 22), and Fowler (Chapter 23) (as well as the unpublished papers by Holt and Beddington presented at the conference) deal with this issue directly. Others treat the issue less directly. As more papers of similar nature are produced, the potential for such approaches will become more apparent. The work of Harestad and Bunnell (1979) and Smith (1974) falls into this category along with work recently completed by Fowler (1980a, 1981). The principles having their origin in such studies can help provide a perspective within which each special case may be considered. Such studies must rely, however, on a general background of information contained in papers similar to those in this volume and in the general literature. It is hoped that this book will be of help in stimulating further work along such lines.

In attempting to generate comparisons, schemes must be formulated that result in classifications across which comparisons can be made. Examples can be produced on the basis of the chapters in this book. One of our first objectives was to provide a sampling of marine and terrestrial work that could be used for initial contrasts and comparison in the format of the conference and this book. It was hoped that consideration of what is known in terrestrial settings could be of material help in gaining a better understanding of the dynamics of the marine species, and vice versa. As noted earlier, one difference seen in comparing these two groups of papers is that the terrestrial species are represented by studies with greater resolution than are the marine species. A further difference to be kept in mind is that the major problem facing many species of marine mammals is the danger of their being overharvested. They are less likely to be subject to habitat destruction, a problem common to many terrestrial species.

It is difficult to determine which comparisons will result in the greatest progress in our understanding. There are, however, a number of dimensions across which theoretical and empirical comparisons could be made to help develop our view of the population dynamics of large mammals in particular and of animals in general. In addition to longevity, initial survival, age at first reproduction, birth, and mortality, as discussed by Fowler in Chapter 23, there are such factors as social organization, territoriality, and taxonomic categories. The 12 characteristics mentioned by Eberhardt and Siniff (1977) as potentially useful for evaluating a population may serve as bases for comparison as well. Some of the attributes mentioned above are part of the "life-history strategy" that must serve as a basis for comparison as discussed by Goodman (Chapter 21) and Fowler (1981). Various categories of specialization and behavioral types may serve as fruitful categories for comparison. Growth rates and specific productivity are further dimensions for potential comparisons.

There are numerous studies on species of terrestrial herbivores (such as the ungulates in general). There is relatively less work that deals with terrestrial carnivores, but progress is being made (see, e.g., Chapters 6 and 16). As emphasized in the chapters by Fowler (Chapter 23) and Caughley (Chapter 18), the dimension of trophic level may be an important dimension across which to make comparisons. Specific arguments for expecting differences between trophic levels were developed by May (1973), Fowler (1980a, 1980b), and May et al. (1979).

Numerous types of comparisons can be made across the dimensions identified above. As discussed in Fowler (1980a; Chapter 23), the shape of productivity curves can be compared. These are of special interest in management and from the point of view of the roles played by the populations in their respective ecosystems. Comparison may be made between such attributes, since they may be correlated. There may be a tendency for populations of large-bodied species to exhibit regulation through change in birthrate, as opposed to change in juvenile survival, which may be of more importance in the regulation of smaller-bodied species. Such correlations, if they exist, can only be recognized through comparison. As shown by Harestad and Bunnell (1979), there are relationships between the size of territories (range) and body size, trophic status, and resource productivity.

There are a number of specific questions and hypotheses that need to be addressed as they relate to matters of practical importance. In particular, the scientific committee of the International Whaling Commission is in desperate need of insights useful in developing more realistic approaches to setting quotas or deciding which stocks should receive protection. As carnivorous large-bodied and socially organized large mammals, do cetaceans exhibit dynamics that can be described on the basis of what we know about large-bodied species combined with what we know about the socially organized species and carnivores in general? Do social groups of cetaceans exhibit territoriality in ways in which our growing knowledge of the effects of territoriality in terrestrial systems may be applied? Are there genetically determined differences between the various taxa, or are population dynamics more a product of the nature of a species as independent of its taxonomic relationship to other groups?

Before leaving the topic of comparative population dynamics, it should be noted that we do not wish to underemphasize the need to make comparisons across a much wider spectrum of species types than is encompassed by large mammals alone. The study of large mammals in particular and animals (and possibly plants) in general should profit from broad comparisons. As pointed out by Fowler (1980a, 1981), patterns concerning population dynamics seem to be emerging as a result of comparisons made across the spectrum of body size, *r-K* strategies, longevity, and productivity. These comparisons need both theoretical and empirical underpinnings to provide the progress we need toward a better understanding of the population we wish to manage. Through such studies we may better appreciate the errors made in adapting models developed in the study of fish and insects to the study of large mammals.

THE SCOPE OF THIS BOOK

The chapters included in this book are examples of studies of large mammals that provide a basis for comparisons of two types. First, each chapter contains information concerning individual species such that species may be compared as outlined in the previous section and as discussed in Chapter 23. Second, the studies themselves can also be compared, as outlined in earlier sections. Such comparisons are a necessary part of coming to grips with a truly comparative study of population dynamics. The basis for comparisons in each case is not always well defined; indeed, it is the principal problem of comparative science to explore the possible bases, searching for those from which new insights can be obtained.

Some sample bases for comparison of both types are shown in Table 1. In this table the columns are grouped into six categories. The first two categories represent material for comparisons over the characteristics of the species involved. The remainder represent comparisons that may be drawn between and among the studies themselves. In all cases Table 1 contains an indication of how each chapter has been categorized, to show the scope included in this book. In addition to the bases for comparison outlined above we have indicated the continent of origin of the senior author of each chapter.

The absence of chapters dealing with studies of human populations (see columns labeled *Group of Mammals*, Table 1) is regrettable. Although two contributions were planned, conflicts in schedules resulted in cancelations. This lack is unfortunate, as much of the theory of population growth has been developed within the context of research involving humans (see, e.g., Pollard, 1973; Keyfitz, 1968). The work on humans, however, has taken on a very different character from studies of other large mammals as discussed above. Inter-

Table 1 Classification of Chapters in This Volume Across Several Dimensions

First Author	Chapter	Group of Mammals: Terrestrial	Marine	Human	Trophic Level: Herbivores	Carnivores	Omnivores	Approach: Descriptive	Conceptual	Formal	Scope: Single Species	Multispecies	Ecosystem	Levins's Categories: Realism	Precision	Generality	Continent: Africa	Europe	Australia	N. America	S. America	Asia
Allen	13		x			x			x	x	x				x	x			x			
Botkin	19	x			x				x	x			x	x		x				x		
Bunnell	4	x				x	x	x	x			x		x		x				x		
Burgoyne	21	x			x				x	x	x			x		x				x		
Caughley	18	x			x			x	x			x		x		x			x			
Chapman	14		x			x			x	x	x				x	x				x		
Croze	15	x			x				x	x		x		x		x	x					
DeMaster	20		x			x			x	x	x			x		x				x		
Eberhardt	10		x			x			x	x	x			x	x					x		
Fowler	23	x	x		x	x	x		x	x	x	x		x		x				x		
Goodman	22	x	x		x	x	x		x	x	x			x		x				x		
Hanks	3	x			x			x	x			x					x					
Harris	11	x			x				x			x		x		x				x		
Harwood	8		x			x			x	x	x			x	x			x				
Horwood	17		x			x			x	x			x	x		x		x				
Laws	2	x	x		x	x		x	x			x						x				
Lett	7		x			x			x	x	x				x	x				x		
McCullough	9	x				x	x	x	x	x	x			x	x					x		
Pojar	12	x			x				x			x		x		x				x		
Smith	5		x			x			x	x	x			x	x					x		
Starfield	6	x				x			x	x	x			x	x		x					
Walters	16	x			x	x			x	x		x		x		x				x		

action between students of human populations and students of other large mammal populations is needed, as humans are large mammals.

The collection of chapters in this book may be distributed along a spectrum ranging from single species to ecosystems. As mentioned earlier, the single-species approach makes the assumption that the essential dynamics of a population can be characterized as abstracted from its environment. The ecosystem approach carries the philosophy that the ecosystem may provide the overriding driving forces that determine the dynamics of any particular species. As shown in the columns labeled *Scope* in Table 1, there is preponderance of chapters that take the single-species approach. This partly expresses our bias toward working along these lines as well as the fact that most work is being conducted at this level. The latter should be viewed as a gap in the approaches being taken, and the recommendations being given by Botkin et al. (Chapter 19), Croze et al. (Chapter 15), Caughley (Chapter 18), and others in this volume should be taken seriously. Ecosystem models and results of research conducted at this level should be examined for a better understanding of the cause-and-effect relationships contributing to particular types of dynamics. Simple, general, single-species models should be examined for the differences and similarities that exist between various groups or types of populations as categorized on the basis of their interactions with their ecosystems.

There is a relatively large number of species of terrestrial herbivores in comparison to carnivores. In spite of this differential, this book contains a number of chapters that deal with carnivores (see columns labeled *Tropic Level*, Table 1). McCullough's chapter on bears (potentially classified as omnivores, Chapter 9), the chapter by Starfield et al. on lions (Chapter 6), and the treatment by Walters et al. on wolves (Chapter 16) exemplify advances being made in our understanding of the population dynamics of these higher trophic levels. It is apparent that interactions *within* the populations of such species is of great importance. It is important to know to what degree these interactions override those with other elements of their ecosystem.

Three levels of approaches to the study of populations were identified above: descriptive, conceptual, and formal. The chapters in this book are categorized in these terms in Table 1 under the column labeled *Approach*. Most include aspects in two of these three categories, and all include some level of conceptual modeling. All the chapters, of course, rely on descriptive studies at some point, even if this is not specifically discussed.

Levins's (1966) three attributes of realism, precision, and generality discussed above provide another basis for comparison of the chapters in this volume. Our categorization of the studies presented in this volume as they achieved a balance among these aspects are indicated in Table 1 in the column labeled *Levins's Categories*. Although classifying chapters into these categories is a matter of judgment, it appears that most of the contributions favor realism and generality at the expense of precision. Somewhat fewer favor realism and precision, while fewest favor precision and generality. These relationships are different for studies on terrestrial and marine mammals.

In trying to obtain a diverse sampling of workers and populations we attempted to attract to the conference a number of individuals from countries other than the United States. As shown in the columns labeled *Continent* in Table 1, we succeeded in obtaining three contributions from Africa, two from Australia, and three from Europe (plus two not published). Financial constraints and a large population of workers in the United States resulted in an imbalance, wherein almost one-half the participants represent North America.

It should be noted that a great deal of work has been conducted by the Japanese. In particular, there has been a considerable effort spent in dealing with marine mammals, especially fur seals as well as both large and small cetaceans. The Soviets have conducted some work along these lines, and considerable data exist among the western Asian and European countries concerning several terrestrial species. There seems to be an opportunity for progress in these areas.

DIRECTIONS FOR THE FUTURE

We have tried to present a general description of our view of the history and perspective of studies involving the population dynamics of large mammals and to place this book within that perspective. In presenting the history we have tried to point out the important differences between approaches taken by various disciplines within the general field. The strengths of each approach may be used to aid progress in the others. We have provided a general perspective with the view that each type of model has its own merits. Specific questions require specific avenues of research. We have discussed general comparisons and emphasized this aspect of the study of the population dynamics of large mammals because, in the past, little attention has been paid to academic issues, general principles, and overall perspective.

To promote the progress that seems possible, several things are required. The first is a need to standardize the definitions and concepts behind terms being used within the field of population dynamics, especially as they are used by biologists studying large mammals. The term "carrying capacity" is a good example. Most theoretical population biologists and population dynamicists working in the fields of fisheries and entomology use the term to refer to that mean population level that would be observed under conditions unaltered by man. It is often referred to as the constant K in the deterministic logistic equation. Range specialists, however, as investigators who deal with many species of terrestrial ungulates, define carrying capacity in terms of the conditions of the forage. Such differences must be resolved before any meaningful communication between disciplines can take place.

Second, the specialists working in the field of population dynamics of large mammals need to recognize the existence of other work both within their specific field as well as in the general field of population dynamics. As mentioned earlier, there is a need to identify existing sets of historical data and to subject them to formal analysis to help overcome the problems created by the long-lived nature of large mammals. A specialized course in this field at several major universities would prove fruitful and could draw on the resources now available in the published literature. Symposia and conferences such as that which resulted in this book are to be encouraged. One or two specialized centers for research in this field would help provide coherency. The publication of a journal specializing in the population dynamics of large mammals would be of considerable help. The field has an identity and integrity of its own, and recognition of the existence of the collections of published papers, data, and workers doing this type of work will help promote the progress needed.

Hand in hand with recognizing and being familiar with the breadth of work in other aspects of the field of population dynamics in its application to large mammals is the need to undertake complementary studies, as mentioned earlier. Work on any single population or species can be made much more productive by taking separate approaches with different scope, resolution, levels of formalism, realism, precision, and generality. Since most of these attributes are determined by practical considerations, there is a need to emphasize academic studies—studies presenting more general and less restricted questions and hypotheses. Broader interest in conducting such studies should be encouraged.

There is clearly a great need for catalyzing and supporting further work on the population dynamics of large mammals. As man's population continues to rise, we encounter increasing numbers of problems that involve the populations of other large mammals. Many species such as the elephant and bison are restricted to ranges much smaller than previously occupied. In many cases these ranges continue to decrease because of habitat destruction. Other populations are either depleted or are overharvested. There are conflicts involving other resources, such as exemplified in the cases of tuna, porpoise, and gray seals (see Chapters 8 and 17). Predator control and its direct and indirect effects continues to be of concern. Growing public concern over sound management or complete protection places us in a particularly good position for requiring more understanding of the effects of various alternatives. More thought is needed regarding future options in place of current demand. One of the purposes of this chapter and of the book as a whole is to provide new insights of value in making this progress, to underline the need for continued effort, and to help provide some alternatives for fruitful study.

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