

CHAPTER 10

A REVIEW OF DENSITY DEPENDENCE IN POPULATIONS OF LARGE MAMMALS

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1. INTRODUCTION

The study of population regulation has been central to much of the work on the population biology of both animals and plants, as seen in much of the literature (for example, Lack, 1954; Slobodkin, 1961; MacArthur and Connell, 1967; McLaren, 1971; Ricklefs, 1973; Emmel, 1976; Tamarin, 1978). Recent developments in the theoretical aspects of population dynamics have led to a growing union of the concepts of life history analysis with those of population regulation, both in an evolutionary context (for example, Boyce, 1984). Much of the literature dealing with population regulation covers research on fishes and insects, with some work devoted to the study of birds (Nikolskii, 1969; Lack, 1966; Clark et al., 1967; Weatherly, 1972; Varley et al., 1973; Hassel, 1975; Gulland, 1977). Wynne-Edwards (1962) presents information on density dependence for a number of taxonomic categories. Reviews of the literature dealing with density dependence exist for fish (McFadden, 1977) and small mammals (Christian, 1963; Krebs and Myers,

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1974). A preliminary review for large mammals was produced by Fowler et al. (1980).

This paper is a review of the broad concept of density dependence as applied to large-mammal populations. It is an expansion of the material dealing with population regulation presented in Fowler et al. (1980) to include other density-dependent aspects of large-mammal populations. It also includes material published in the last 10 years, primarily as found in the English language. This paper has the objectives of (1) providing a list of literature dealing with density dependence in large mammals; (2) helping to bring to the attention of biologists dealing with individual species the results of research dealing with other taxonomic groups, other habitats, and trophic levels, thereby promoting interchange of information among researchers in this field; and (3) promoting comparisons both within the category of large mammals (for example, marine versus terrestrial), and between large mammals and other major categories of animals as a basis for finding important patterns in population dynamics such as those described by Fowler (1981). The utility of density-dependent information will be discussed along with brief considerations of the ways in which much of the information on large mammals relates to some of the questions that seem to be at the forefront of evolutionary population dynamics today.

The term "large mammals" is not clearly defined. The bimodality in the size distribution of mammals pointed out by Bourliere (1975) is helpful in this regard. Mammals weighing between a few kilograms and tens of kilograms occur less frequently than those above and below this range. Most large terrestrial animals are either herbivores (such as the ungulates included in this review) or carnivores (such as many of the bears, canids, and felids). All marine mammals, including sea otters, are relatively large. Based on these observations, the sizes of animals included in this review are roughly comparable to those observed in the marine environment, with the exception of a few smaller species, such as coyotes (*Canis latrans*) and monkeys (*Macaca*).

Material in this review involves both direct and indirect forms of density dependence and both internal and external mechanisms of expression (terms defined in Fowler et al., 1980, and Fowler, 1984). Thus, any change in a large-mammal population that correlates with change (or difference) in population size or density reflects density dependence as defined for this review. The main focus of this paper will be the population level parameters of mortality and reproduction along with growth. Additional material will be reviewed as it relates to the comparison of behavior, diseases, parameter variability, physiology, and population structure at varying population levels. Such com-