1 Introduction to the Study of Animal Populations

Information about animal populations is sought for a variety of purposes; but *the object* of a study will largely determine the methods used and thus this must be clearly defined at the outset. Very broadly, studies may be divided into *extensive* and *intensive* (Morris, 1960). Extensive studies are carried out over larger areas or longer time periods than intensive studies, and are frequently used to provide information on distribution and abundance for conservation or management programmes (e.g. monitoring the status of mammal populations; Macdonald *et al.*, 1998). Recent developments in remote sensing capability and geographical information system software have given great impetus to extensive studies in recent years (see Chapter 15). For pests or parasites they provide assessments of incidence or damage, and may also guide the application of control measures. Aphids, for example, are regularly monitored by the Rothamsted suction trap survey (http://www.rothamsted.ac.uk/insect-survey/STAphidBulletin.html; Harrington & Woiwod, 2007). In extensive surveys, an area will often be sampled once or at the most a few times per study period. The timing of sampling in relation to the life cycle of the animal is obviously of critical importance, and for many species, only limited stages in the life cycle can be sampled. Extensive studies produce information about the spatial pattern of populations, and it is often possible to relate the level of the population to edaphic, oceanographic or climatic factors. Recently, long-term data have proved invaluable to quantify the effects of climate change on distribution and phenology.

Intensive studies involve the *repeated* observation of the population of an animal. Usually, information is acquired on the sizes of the populations of successive developmental stages so that a life-table or budget may be constructed. Then, using this table an attempt is made at determining the factors that influence population size and those that govern or regulate it (Varley & Gradwell, 1963; Sibley & Smith, 1998). It is important to consider at the start the type of analysis (see Chapter 11) that will be applied and so ensure that the necessary data are collected in the best manner. Intensive studies may have even more limited objectives, such as the determination of the level of parasitism, the amount of dispersal, or the overall rate of population change.

The census of populations and the stages at which mortality factors operate are necessary first stages in the estimation of the productivity (see Chapter 14) of ecosystems.

In survey and conservation work, the species make-up of the community and changes in its diversity associated with human activities are most frequently the features it is desired to measure. The estimation of species richness invariably requires

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repeated sampling of the habitat, with special methods of analysis needed to estimate the total species number (see Chapter 13). The relative abundance of species is a key attribute which may give insight into the functioning and health of a community, though difficulties usually arise because of the impossibility of recording the abundance of all the species living within a habitat with equal efficiency.

1.1 Population estimates

Population estimates can be classified into a number of different types; the most convenient classification is that adopted by Morris (1955), although he used the terms somewhat differently in a later study (Morris, 1960).

1.1.1 Absolute and related estimates

For large animals that are easily observed and have small, countable, populations such as rhinos, elephants, tigers, whales or some birds, it may be possible to express the global or metapopulation size as a total number of individuals. However, for most animals, numbers will be expressed as a density per unit area or volume or per unit of the habitat. Such estimates are given by distance sampling and related techniques (Chapter 9), marking and recapture (Chapter 3), by sampling a known fraction of the habitat (Chapters 4–6) and by removal sampling and random walk techniques (Chapter 7).

1.1.1.1 Absolute population

This is defined as the number of animals per unit area. For planktonic animals, the number per unit volume can be more appropriate. It is almost impossible to construct a budget or to study mortality factors without the conversion of population estimates to absolute figures. This is because other measures of habitat are variable. For example, the amount of plant available to an insect is always changing; further, insects often move from the plant to the soil at different developmental stages. The importance of obtaining absolute estimates cannot be overemphasised.

1.1.1.2 Population intensity

This is the number of animals per unit of habitat, for example per leaf, per shoot, per plant, per host. Such a measure is often, from the nature of the sampling, the type first obtained (see also p. 146). When the level of the animal population is being related to habitat availability or plant or host damage, it is more meaningful than an estimate in absolute terms. It is also valuable when comparing the densities of natural enemies and their prey. However, the number of habitat units per area should be assessed, for differences in plant density can easily lead to the most intense population being the least dense in absolute terms (Pimentel, 1961). When dealing with different varieties of plants, differences in leaf area may account for apparently denser populations, in absolute terms, on certain varieties (Bradley, 1952). Thus, the choice of the leaf or of the

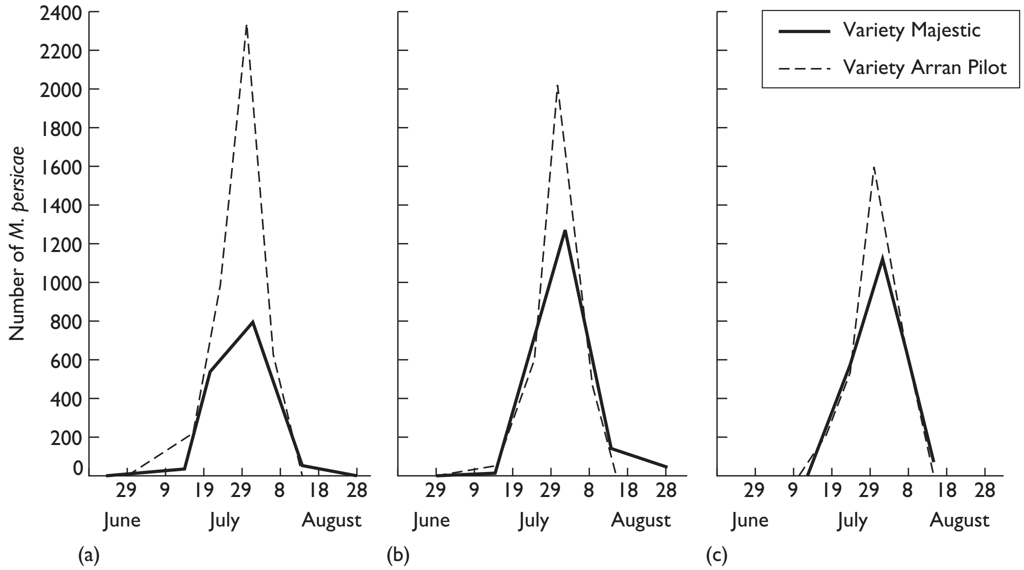

Figure 1.1 The influence of habitat unit on relative population levels when these are measured in terms of population intensity; the populations of *Myzus persicae* on different varieties of potato. (a) Per 100 leaves; (b) per plant; (c) per plant, corrected for proportions of upper, middle, and lower leaves. (Adapted from Broadbent, 1948.)

plant as the unit for expressing population intensity can affect the relative population estimate obtained (Broadbent, 1948) (Fig. 1.1). Similarly, with litter fauna – owing to the effects of seasonal leaf fall – the intensity measure (on animals/weight of litter) will give a different seasonal picture from an absolute estimate per square metre (Gabbutt, 1958). These examples also underline the importance of absolute estimates when interest lies primarily in the animal population.

1.1.1.3 Basic population

In some habitats, especially forests and orchards, it is often convenient to have an intermediate unit between that used for measuring intensity and absolute measures of ground area, for example 1 m^2 of branch surface (Morris, 1955) or branches of apple trees (Lord, 1968).

1.1.2 Relative estimates

These estimates, in which the number caught cannot be expressed as a density or intensity per area or habitat unit, allow only comparisons in space or time. They are especially useful in extensive work on species distributions, monitoring changes in species richness, environmental assessments, recording patterns of animal activity, and investigating the constitution of a polymorphic population. The methods employed are either the catch per unit effort type or various forms of trapping, in which the number of individuals caught depends on a number of factors besides population density (Chapter 7). There is no hard and fast line between relative and absolute methods, for absolute methods of sampling are seldom 100% efficient and relative methods can sometimes be corrected in various ways to give density estimates.

Relative methods are important in applied areas such as fisheries or game management, where most of the information available may be derived from fishing or hunting returns. In fisheries research, catch per unit effort is often difficult to calculate from landing statistics because of changes in catch efficiency as fishing technology and the economy changes. The behaviour of fishermen frequently changes with the abundance of the target species.

1.1.3 Population indices

These are generated when the animals themselves are not counted, but their products (e.g. frass, webs, exuviae, tubes, nests) or effects (especially plant damage) are recorded.

Both, population indices and relative estimates of population can sometimes be related to absolute population (if this is measured at the same time) by regression analysis. If such a study has been based on sufficient data, subsequent estimates from relative methods or indices can be converted to absolute terms using various correction factors; such an approach is common in fisheries research (e.g. Beverton and Holt, 1957).

1.2 Errors and confidence

The statistical errors of various estimates can usually be calculated and the upper and lower boundaries of an estimate are referred to as the fiducial limits (the estimate (x) being expressed as $x \pm y$ where y = fiducial limits). These are sometimes incorrectly referred to as 'confidence' limits, but the distinction between the two terms is in practice unimportant. The fiducial limits are calculated for a given probability level, normally 0.05, which means that there are only five chances in 100 that the range given by the fiducial limits does not include the true value (hence the expressions 5% probability level and 95% fiducial limits). If more samples are taken the limits will be narrower, but the estimate may not move closer to the actual value. Biologists are often worried that assumptions about sampling efficiency (e.g. does the 'knockdown' method really collect all the weevils on a tree?) may be incorrect. Intuitively, most believe – quite correctly – that this estimate should be compared with another method that has *different* assumptions. If the estimates are of the same order of magnitude, then the investigator can have much greater confidence that the result of the study is not misleading. It is therefore sound practice for the ecologist to *contemporaneously estimate the population or other variables by more than one method.*

When two estimates have been obtained from different sampling procedures, and provided they are internally consistent (e.g. a t-test shows that the means are not significantly different), they may be combined to give a weighted mean, weighting each estimate inversely as its variance (Cochran, 1954). Under some circumstances Bayes' theorem could be used (see p. 88, equation 3.29) to give the combined estimate. Laughlin (1976) has suggested that the ecologist may be satisfied with a higher probability level (say 0.2) and thus narrower fiducial limits for estimates based on more than one method, because such estimates have a qualitative, biological assurance, additional to that from the consistency of the data, that the true mean lies close to the estimate.

Most population studies are based on sampling, and the values obtained are considered to have a generality that scales with the area from which the samples were drawn. All estimates have fiducial limits and the level of accuracy that should be aimed at is difficult to determine. Morris (1960) has aptly said that '…we are not likely to learn what precision is required by pessimistic contemplation of individual fiducial limits'. Excessive concerns about accuracy can always be used by those who favour the warmth of the hearth to being in the field. As the amount of time and labour that can be put into a problem is limited, it should always be borne in mind that the law of diminishing returns applies to the reduction of the statistical errors of sampling. In the long run, more knowledge of the ecology of the animal may be gained by studying other areas, by making other estimates, or by taking further samples than by straining for a very high level of accuracy in each operation. Against this must be set the fact that when animals are being extracted from samples, the errors all lie below the true value as animals will occasionally be missed. A number of very carefully conducted control samples may allow a correction factor to be applied, but the percentage of animals missed may vary with density; sometimes, more are overlooked at the lowest densities (Morris, 1955).

An alternative to sampling is the continuous, or regularly repeated, study of a restricted cohort, such as the population of an aphid on a particular leaf or leaf-miners on a bough. These studies have a very high level of accuracy but they sacrifice generality. A combination of some cohort studies with larger-scale sampling often provides valuable insights.

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