

3 Population Biology and Life-History Variation of Gamebirds

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3.1 Introduction

This chapter considers further aspects of the population biology of gamebirds and discusses how some of the patterns observed might have evolved through the process of natural selection. Ecologists usually consider such studies under the general heading of 'life-history strategies'. Essentially, the studies aim to ascertain how different species maximise their lifetime reproductive success, defined as the total number of offspring produced within its lifetime, that survive to the age of first reproduction. As this is determined by a variety of different facets of the species' ecology, many life-history studies are concerned with whether there are consistent trends in the way that survival and fecundity rates vary between and within species.

The study of how natural selection has tuned the survival and fecundity of different species is particularly important in the case of managed populations. Many aspects of management aim to increase or decrease certain population parameters in relation to those that have evolved for the species in the unmanaged state. For example, hen pheasants are caught and placed in laying pens where they produce large numbers of eggs which are then incubated artificially (35 eggs per female is not uncommon). Such a level of egg production is much greater than the average clutch size recorded for 'wild' pheasants. Management of wild populations also tends to increase population densities to levels far greater than in the unmanaged habitat. On some estates red grouse have been recorded at densities of 115 pairs km⁻², while in the natural state density is probably closer to 3 pairs km⁻² (Hudson and Watson, 1985). In biological terms management may be thought of as a subtle form of experimental manipulation that reveals more about the population biology of the species. For example, populations which are harvested at different intensities may be used to determine whether increased mortality leads to increases in fecundity or changes in the rates of dispersal.

3.1.2 *Single population studies versus comparative studies*

Two complementary approaches may be made when studying life-history variations. One approach is to obtain data from a long-term study of a single species where information is gathered throughout the life of as many individuals as possible. Studies of this type tend to emphasise differences between individuals in their net lifetime reproductive success: a classic study of the sparrowhawk in the south of Scotland showed that a high proportion of the population's recruitment is undertaken by only a few individuals (Fig. 3.1).

Although long-term studies of gamebirds have been conducted (Jenkins *et al.*, 1963; Potts, 1980, 1986; Watson *et al.*, 1984; Hudson, 1986a), none has collected data on lifetime reproductive success. Detailed observations of individual gamebirds over a long period of time would be invaluable in providing this data.

When limited amounts of long-term data are available for a population, specific aspects of life-history theory can be tested by undertaking carefully designed experiments. Such experiments have been particularly important in examining the factors determining clutch size in birds. However, to truly monitor evolutionary changes in bird populations fairly unique circumstances are usually required; for example, the small gene pools of Darwin's finches in the Galapagos Islands have enabled Grant (1986) to undertake some of the classic studies of micro-evolution in bird populations. Nonetheless, even these studies required relatively long periods of time, of the order of five to ten generations for the species studied.

In the absence of a detailed long-term study or manipulative experiments, a comparison of the available life-history data for a range of species is often useful. Such an approach enables us to correlate interspecific variations in survival and fecundity with other aspects of species' ecology, such as variations in the types of habitats used or the mating and feeding strategies of different species. Provided a series of sensible but rigorous statistical procedures is followed when undertaking these multi-species comparisons (see Clutton-Brock and Harvey, 1984), the life-history strategies of different species may be compared. This occasionally permits more quantitative speculation on how natural selection may have operated in tuning the observed life-history parameters in a single species or population.

In this chapter we shall adopt both strategies. Initially we shall consider the key life-history variables in turn and give examples from detailed studies of single species. We shall then make some larger inter-specific comparisons using a set of data for European ducks and gamebirds.

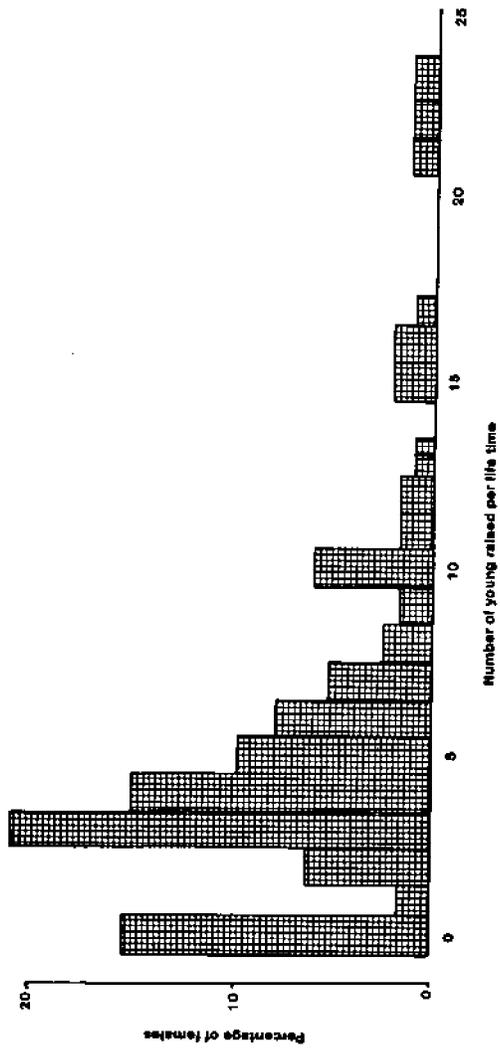


Fig. 3.1 Lifetime reproductive success in a population of sparrowhawks (after Newton, 1986). The histogram shows the percentage of females which produce different numbers of offspring; about 50% of the offspring are produced by 15% of the population.

3.2 Clutch size

Ornithologists have investigated the adaptive significance of clutch size for many years. Lack (1948) proposed that the number of chicks the pair could feed determined the number of eggs a female laid. He suggested that the survival of individual chicks declined with clutch size so that larger clutches do not always lead to larger numbers of chicks fledging. However, observational studies into clutch size of birds have found that the average clutch size is often lower than that which produces the most fledglings: for example, most red grouse lay a smaller clutch than the level which produces the maximum number of chicks (Fig. 3.2). Cody (1966) pointed out that increases in predation on larger clutches may be a factor which tends to reduce clutch size. Later, Charnov and Krebs (1974), in a paper that builds on the work of Williams (1966), suggested that as increased production of offspring may lead to increased mortality in the mother so the 'optimal' clutch size may be less than that suggested by Lack. Where some cost to the parent accrues with increased reproductive effort, selection will favour the clutch size that maximises lifetime productivity of the parent. This is not necessarily the one that maximises the number fledged within one season and in general will tend to be less than this value (Fig. 3.3).

Unfortunately few data unequivocally support the survival-fecundity interaction which is required for the Charnov/Krebs model of clutch size determination. Although the most common brood size in many species is less than the brood size that produces the maximum number of young per season, this only provides circumstantial evidence that such an effect may be operating. In altricial species (those with young born naked, blind and dependent on parents for food), the increased cost of large broods to the parents is apparent: more young mean, quite simply, more mouths that must be fed and more work for the parents. Although this factor is certainly an integral part in determining the 'optimal' brood size, the long-term effects of repeated seasonal stress from relatively larger broods is difficult to assess. While such observational studies provide interesting data, only experimental manipulations of clutch size can be used to rigorously compare the different hypotheses. Unfortunately, studies that have artificially increased clutch sizes in passerine species have given equivocal results about compensatory reductions in survival (DeSteven, 1980; Nur, 1984). However, an elegant study by Bryant (1979) clearly shows that double-brooded female house martins (*Delichon urbica*) have lower survival than single-brooded females. This suggests that the time the birds devote to breeding may be an important component of the effort

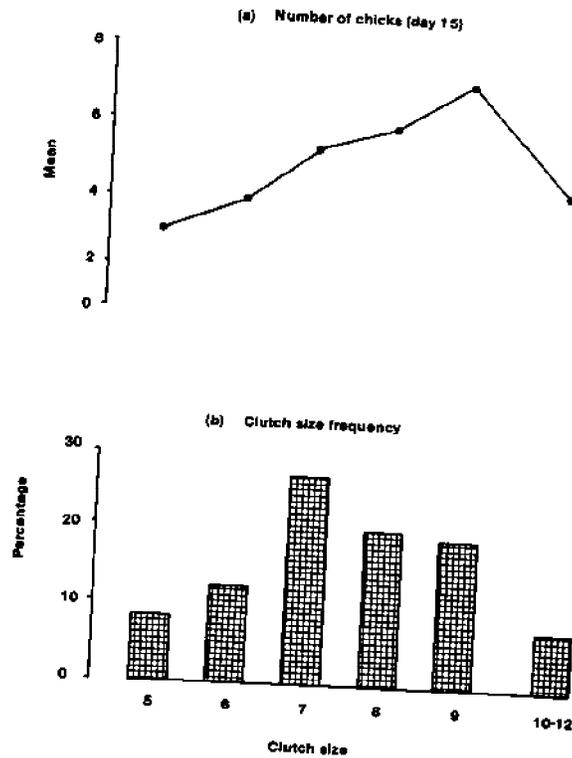


Fig. 3.2 Frequency distributions of clutch size and brood size for red grouse. The lower graph is the percentage of clutches of different sizes observed in the population while the upper graph shows the mean brood size produced relative to clutch size; the most productive clutches were of 9 eggs. (After Moss *et al.*, 1981.)

they put into rearing any individual clutch (see Section 3.6).

If determining the ultimate consequences of increased parental effort is complicated in altricial birds, it is even more so in birds such as gamebirds with nidifugous young (those that leave the nest soon after hatching; see Winkler and Walters, 1983). Since the parents do not feed their young, the increased energetic costs to the parent are either relatively low or must come from some other aspect of brooding which may be still more difficult to assess. For example, there may be costs to the parents in protecting the chicks from predators (Safriel, 1975), the physiological demands of producing more eggs (Inglis, 1977; Ankney and MacInnes, 1978) and, of course, having to incubate them. In a study on Canada geese, Lessells (1986) manipulated the numbers

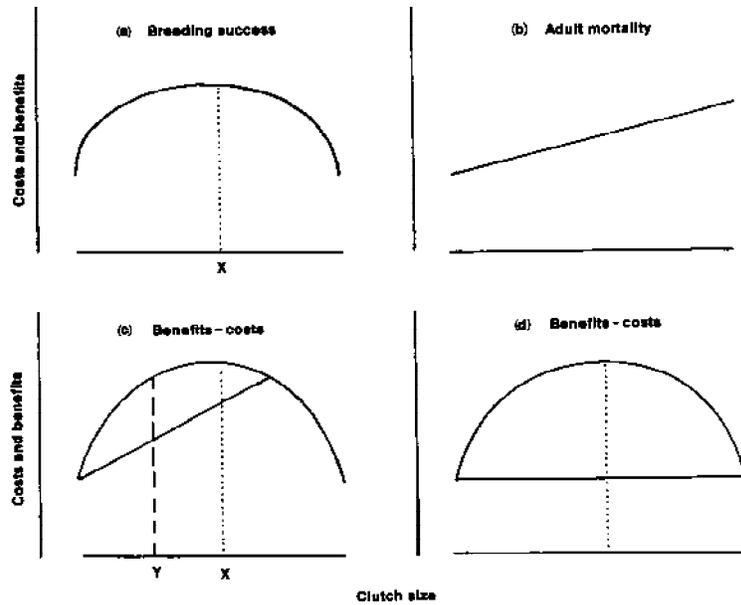


Fig. 3.3 Trade-off between clutch size and adult survival.
 (a) Relationship between breeding success (benefit) and clutch size; Lack's hypothesis predicts that the commonest clutch size (X) is also the most productive.
 (b) The costs of breeding increase with clutch size.
 (c) Combining the benefit curve and the cost function, the greatest net benefit occurs at Y, a clutch size less than X.
 (d) If the costs of breeding are independent of clutch size, X and Y coincide. (*Modified from Charnov and Krebs, 1974, and Perrins and Birkhead, 1984.*)

of goslings in broods to study the effects of brood size on both the goslings and the adults. Her study found no detrimental effects on the offspring (measured by gosling growth, survival and age at first breeding) or on adult over-wintering survival. However, the females with larger broods moulted later, weighed less, and bred later the following season, although this did not affect their clutch size in the second year. Lessells concluded that the number of eggs laid was determined by some factor other than the fitness consequences of brood size, such as the female's reserves before laying. In addition, as Lessells acknowledges, the study was done on a population of sedentary geese. Most populations in North America migrate, and the consequences of lighter weight and delayed moulting may be more significant for migrant populations (Barry, 1962).

In addition to the energetic demands on the parents that may limit clutch size, there are also physiological constraints on the number of eggs a female can lay. Prior to breeding, females have a given store of reserves which they can invest in egg production, either a few large eggs or many small ones. Many studies of gamebirds have stressed the importance of chick survival in the first two weeks of life, and it seems reasonable to suppose that chicks which hatch at an advanced stage with good yolk reserves are going to survive relatively well (Ankney, 1980). Therefore, the clutch size laid will also be a result of a trade-off between the amount of food reserves available to the hen and the size of egg which produces a chick with good survival chances. In this respect, we may expect to see large variation in clutch size and/or egg size in relation to female condition and the available reserves (Ankney and Bisset, 1976; Ankney and MacInnes, 1978). Variation in egg size within a species tends to be small and in some gamebirds, like the red grouse (Moss *et al.*, 1981) and the willow ptarmigan (Erikstad *et al.*, 1985), the size of the eggs does not vary with clutch size. One interpretation of this finding is that birds will lay the size of egg that provides the optimal chances for the chick's survival (Smith and Fretwell, 1974). Eggs tend to be larger in second than in first clutches (Parker, 1981; Erikstad *et al.*, 1985), possibly because the chicks will be hatching after the optimal time and additional yolk reserves may help the chick to survive through the first few days of life.

Predation may also have a role in influencing the clutch size of birds with nidifugous young (Perrins, 1977). Clutch sizes may be lower in birds suffering high predation during laying and incubation simply because females take longer to lay larger clutches and the longer the eggs are in the nest, the more vulnerable they are to predators. Robertson and Hill (1987) used data from two nest record schemes and found that 10% of pheasant nests were lost per day during laying and 2.8% per day during incubation.

In many gamebird species, clutch size is also dependent upon the age of the parent, with birds breeding for the first time having lower clutch sizes than older or more experienced birds (Fig. 3.4). As hatching and fledging success may also be a function of parental experience, analyses of factors affecting clutch size should take care to allow for these variables. This may be particularly important in populations where survival and recruitment vary erratically due to environmental or meteorological conditions, as these lead to variations in the proportion of birds of different ages in the population.

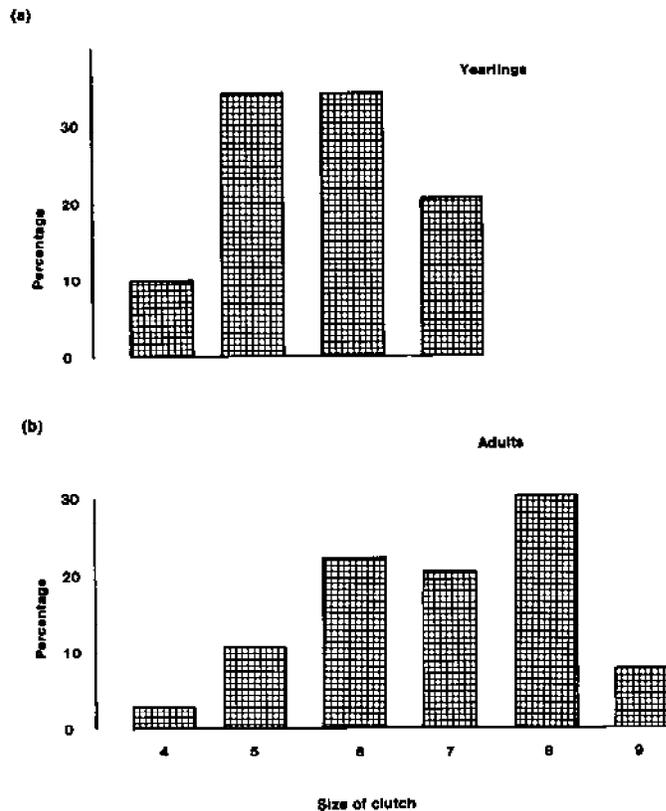


Fig. 3.4 Effect of age on clutch size in blue grouse: (a) the percentage of clutches of different sizes laid by yearling birds; (b) the clutch sizes of adults. (From Zwickel, 1975.)

3.3 Survival

Survival is much harder to measure than fecundity in wild populations of most bird species. Although excellent textbooks exist which describe methods for estimating the values of these life-history traits (Southwood, 1978; Caughley, 1977; Brownie *et al.*, 1978), the data are often fraught with statistical biases, and few field experiments ever produce data of sufficient quality or quantity to satisfy the statistical assumptions of these techniques. Nevertheless, it is important in any study of population dynamics to obtain some indication of the survival rates of birds of different ages (Fig. 3.5). Although we occasionally obtain estimates of the mean or maximum life expectancy of a game species, we rarely obtain any information about how different hunting

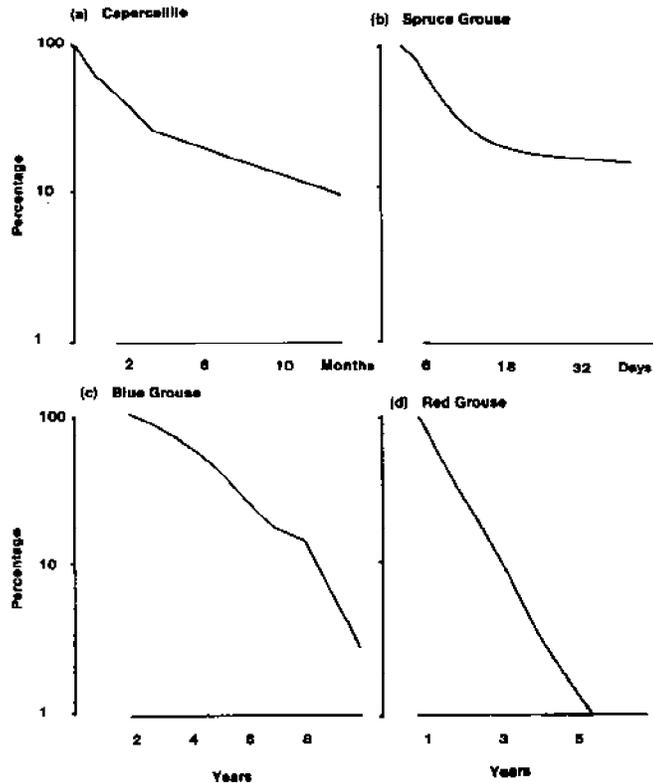


Fig. 3.5 Survival curves of four species of game birds. The upper two graphs show survival over the early months of life. The data for the capercaillie are from Linden (1981), those for the spruce grouse are from Smyth and Boag (1984). Note that in both cases 80 to 90% of birds born die within the first year of life. The lower two graphs show survival curves for birds that have survived to start reproducing. The data for blue grouse are from Lewis and Zwickel (1982), those for red grouse are from Jenkins *et al.*, (1963).

rates or variations in meteorological conditions affect survival.

3.3.1 Adult survival

In most bird species, adult survival is usually assumed to be fairly constant. Although there are several flaws in this assumption, particularly for long-lived birds, it is extremely difficult to detect senescence in studies of gamebirds, as few individuals survive to old

age. However, the greatest changes in mortality rate occur over the first year of life, initially starting fairly high and then declining to some lower level (Fig. 3.5). The quantity of data available to estimate the mortality rate at any age similarly declines exponentially, and estimates of mortality for immature birds are often heavily biased due to differences in recovery rates of birds in the different months of their first year of life. Although maximum life expectancy is sometimes used as an index of longevity in studies of gamebirds, it is important to realise that estimates of this parameter increase systematically with the quantity of data used to estimate it; this can create a large systematic bias and make common species appear longer-lived than rare species. Conversely, although larger quantities of data may be available to estimate mortality from managed populations, the increased mortality due to hunting may produce a steeper mortality curve. (Compare Fig. 3.5c and d, for lightly exploited blue grouse and heavily exploited red grouse.)

3.3.2 Additive and compensatory mortality

The effects that hunting has on a population are not well understood. Perhaps the most fundamental question that still remains is whether hunting mortalities act in an additive or a compensatory manner. That is to say, does hunting kill birds in addition to the number that normally die over the winter, or does the hunting simply kill off the excess that would have died during the winter and thus lower or compensate for winter mortalities?

Many studies suggest that hunting acts in a compensatory manner, but such results can be misleading. Since management practices strive to maintain populations at maximum densities, much of the over-winter mortalities are due to starvation or dispersal off the range. In such cases, hunting may tend to act in a compensatory manner by alleviating the mortalities from overpopulation. However, hunting kills may appear to be compensatory in what would otherwise be an increasing population: the hunting may not lower the spring breeding density from the previous year, but the population will certainly not grow as a protected population would.

In general the level of compensation is likely to be variable, with low levels of hunting mortality usually compensated for and higher levels of mortality only occasionally so. A more quantitative answer requires a more detailed knowledge of how population density affects rates of



Plate 3.1 The first 20 days of life for gamebird chicks are critical. They must (a) grow rapidly and (b) avoid predation. Chick mortality through starvation and predation can reach 90% and is therefore a major determinant of lifetime reproductive success.

recruitment and adult survival. This is discussed in the next section.

3.3.3 Chick survival

In a number of gamebirds, mortality over the first year of life can be in the region of 80 to 90% (Fig. 3.5). The critical stage for most species is within the first 20 days of life, a time when growth rate is greatest and when the chicks must develop thermogenesis (Pedersen and Steen, 1979) and become capable of avoiding predators (often by flight). Studies on various gamebirds indicate that two factors are believed to play a significant role in influencing chick survival: first, the influence of maternal nutrition on the quality of the egg and second, the role of insects in the diet of chicks. Poor female condition can be influenced by poor nutritional state or heavy parasite burdens. It has been suggested that maternal condition influences the quality of eggs laid, which in turn causes annual changes in chick survival (Siivonen, 1957). In a study of red grouse, Jenkins *et al.* (1965) collected clutches of grouse eggs from the wild and reared them under bantams. The proportion of chicks reared in captivity was correlated with the ratio of young to old birds reared in the wild, suggesting that egg quality was an important factor influencing chick survival. However, Hanssen *et al.* (1982) believed this method inadequate for testing egg and chick quality in the willow ptarmigan and so looked at annual variations in the chemical composition of eggs. They found that chick survival was not related to any discernible measure of egg quality but to June temperatures and the level of predation, influenced in turn by the abundance of lemmings (Hanssen and Utne, 1985). In an analysis of chick survival in clutches from captive and wild red grouse, Moss *et al.* (1981) came to the conclusion that over 50% of the observed variation in chick survival was related to intrinsic differences amongst hens; however, it is still not clear whether this is due to genetic or environmental effects on the mother.

Although intrinsic factors may play a role in influencing chick survival, it is clear that extrinsic factors, and in particular food quality, are important to survival as well. In a wide range of studies, workers have found associations between the abundance of insects in the chicks' diet and survival (Cross, 1966; Potts, 1970, 1973, 1980, 1986; Green, 1984; Hill, 1985; Rands, 1985, 1986a; Hudson, 1986a). The importance of the insects on the chicks' diet has been demonstrated experimentally in grey partridges (Cross, 1966; Potts, 1980, 1986) and red grouse (Hudson, 1986a). Workers were unable to rear chicks

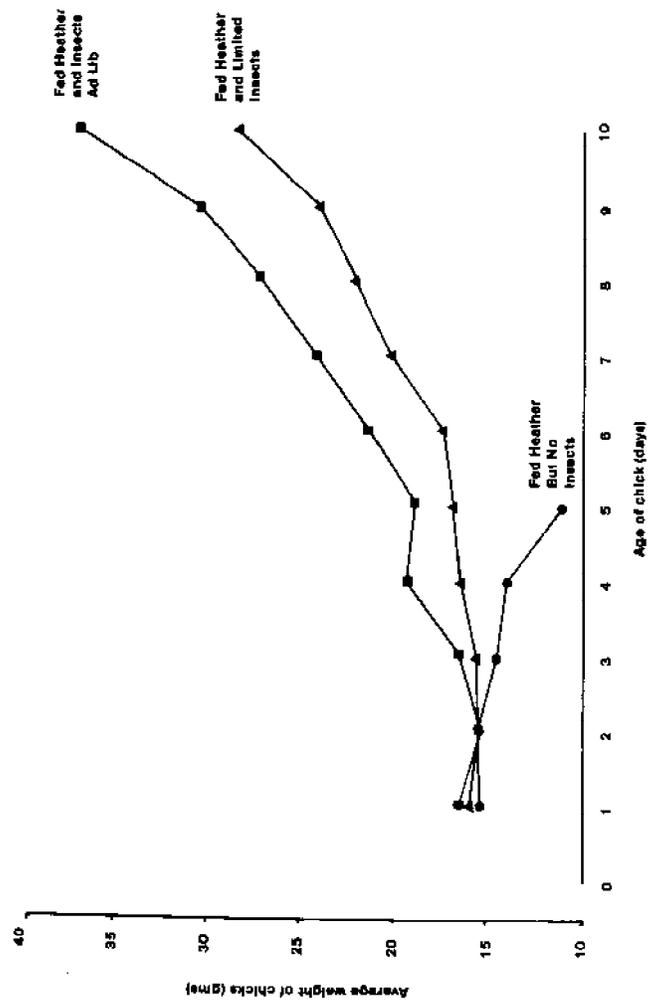


Fig. 3.6 The growth of captive red grouse chicks fed differing quantities of insects. Chicks provided with heather alone did not gain weight and died within 6 days, while chicks provided with insects grew well and survived. (After Hudson, 1986a.)

successfully on the adults' diet, and chick growth and survival were improved when insects or some other nutrient-rich supplement was provided (Fig. 3.6). By extrapolating from research on poultry, Wise (1982, 1985; see also Moss, 1985; Potts, 1986) demonstrated that the sulphur-based amino acids, cystine and methionine, were likely to be the limiting nutrients in chick growth. As these are in relatively low concentrations in the adults' diet, the chicks would be required to eat incredible quantities of the adults' food in order to survive and grow. Insects carry relatively high levels of methionine and cystine (four times that of wheat and more than 15 times that of heather), and it seems reasonable to suppose that eating insects will benefit chick growth and survival. Thus, although many intrinsic and extrinsic factors play some role in determining chick survival, a gamekeeper can at least partially reduce chick mortality by providing an abundance of preferred insects.

3.4. Density-dependence and recruitment

Studies of the factors determining clutch size, fledging success and survival of individuals within a population have found that many of these parameters are dependent upon the density of the population in different years. In most species where data on clutch size and fledging success have been collected over a range of population densities, we tend to see a negative relationship between population density and per-capita recruitment (Fig. 3.7).

The survival of immature birds through their first winter is also likely to be dependent upon the density of adult birds in the population. These relationships can be important in regulating the size of the population from year to year. Where relationships between simple measures of recruitment and population density appear equivocal, it is important to appreciate that more subtle mechanisms may be determining how density affects rates of recruitment to the population. For example, as density rises, the prime habitats may be used first, forcing additional birds into marginal habitats which are less productive. This will tend to decrease the average per-capita rate of recruitment and may be a very powerful density-dependent mechanism in populations that live in heterogeneous habitats. In a study of partridge, Rands (1987b) found the relationship between recruitment rate and density varied from one farm to the next due to variation in available nesting habitat. As the goal of habitat management on many game estates is to maximise the areas of suitable

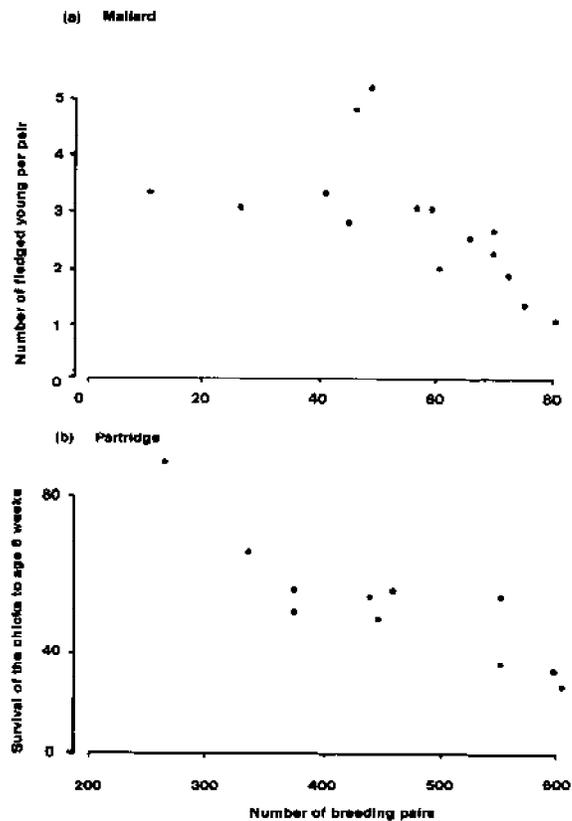


Fig. 3.7 Effect of density on different parameters of fecundity or recruitment in mallards and grey partridge: (a) shows the decline in the number of young fledged per pair as the number of breeding pairs increases (after Hill, 1984a); (b) shows the change in survival of chicks to age six weeks in a population of grey partridge. (After Blank *et al.*, 1967).

breeding habitat for different species, it is important to bear in mind that altering the mosaic of habitats will also tend to alter the shape of the recruitment function.

3.4.1 Mechanisms of population change

In ecology, the debate about the relative importance of the mechanisms that regulate population size has tended to centre on relatively few species; the grouse and ptarmigan have been one such group. Some

of the mechanisms, such as the role of predation and parasitism, are discussed in their respective chapters (see also the review by Angelstam, 1987). These explanations can account for cycles observed, often operating through the effects of breeding production (Bergerud *et al.*, 1985). However, as Watson and Moss (1987, and references therein) point out, a fall in a population can occur after breeding success is high. A number of theories have arisen to explain this observation.

One theory is that variations in summer productivity (influenced by extrinsic factors such as resource abundance and meteorological conditions) lead to changes in the yearling to adult ratio in the following spring (Smyth and Boag, 1984). As density is increasing, many young are recruited to the population; and since yearlings often have smaller clutches than adults (Zwikel, 1975; Smyth and Boag, 1984; Fig. 3.4), the recruitment rate drops, and population density falls. However, in Zwikel's study, although the difference in productivity between yearlings and adults was significant, the proportion of young in the population corresponded neither to the average clutch size produced nor to the average number of chicks per female.

Moss and Watson (1985), on the other hand, attribute the regular changes in red grouse densities to intrinsic cycles in the levels of aggression which limit territory size and hence the breeding densities of this species. Aggressive behaviour, they argue, is selected against as density decreases; presuming that neighbours are most likely to be kin, giving them room to breed increases the individual's inclusive fitness. However, at greater densities, when pre-territorial summer emigration is high, the likelihood of neighbours being kin is much less (Green, 1983), and aggression is selected for. Some support for this theory has been provided by removal experiments (Krebs, 1971; Watson and Jenkins, 1968). When territorial individuals are removed, they are often replaced by others who subsequently breed. This suggests that there are birds both available and capable of breeding, an important prediction of the spacing behaviour theory. Even so, it is necessary to know more about the degree of relatedness between individuals in the population and whether the replacement birds would have bred or not, had the removal experiment not been conducted.

The major difficulty with the spacing behaviour theory is distinguishing cause and effect: any factor that is operating to increase the population density is likely to bring a corresponding increase in visible displays of aggression; thus, the levels of aggression could be a response to, not responsible for, the fluctuating densities.

The controversy between intrinsic and extrinsic factors has tended to obscure the fact that the two hypotheses are by no means mutually exclusive. Chick production, adult mortality (in most studies, a measure of dispersal and deaths in the study area), territory establishment and weather all influence spring densities. The problem of determining which mechanisms are important to population regulation may best be examined by considering a simple, general model of a bird population.

3.4.2 *A life-history model for gamebirds*

A suitable model for the dynamics of a hypothetical bird population is illustrated in Fig. 3.8. Essentially, the model assumes that the numbers of birds in year $t+1$, will equal the number of adult birds that survive from year t , plus the numbers of birds that are born in year t that survive to age one. The functions $f_1(N_t)$ and $f_2(N_t)$ represent the possible effects of population density on survival and recruitment. Note that it is quite possible for either of these functions to equal unity at all population sizes if density has no effect on either survival or fecundity. However, that both of these functions will equal unity is unlikely, as this would imply a totally unregulated population. Similarly, it is important to realise that when $f_1(N_t)$ equals unity, there can be no compensatory mortality from hunting. The degree of compensatory mortality depends entirely on the shape of this function; if it has a strong negative slope then compensation is likely, if it has only a weak negative slope then compensation is only going to be minor. The other diagrams in this figure illustrate how different shaped density-dependent functions may be produced by different biological mechanisms such as limitations of food supply or finite numbers of breeding territories. The figures illustrate idealised hypothetical cases; in reality the shape of these functions will be moulded by a mixture of these different functions. Notice that in general management always tends to reduce the slope of these density-dependent relationships (e.g. by increasing the amount of food available or by increasing the numbers and quality of breeding territories).

It is also important to realise that there may be some interaction between fecundity and survival in individual birds (as is discussed in the section on clutch size above). This would require the inclusion of a third function $f_3(E_t)$ which modifies adult survival as fecundity changes (Fig. 3.9). If this effect is significant, we may see an apparent positive interaction between adult survival and density in a system

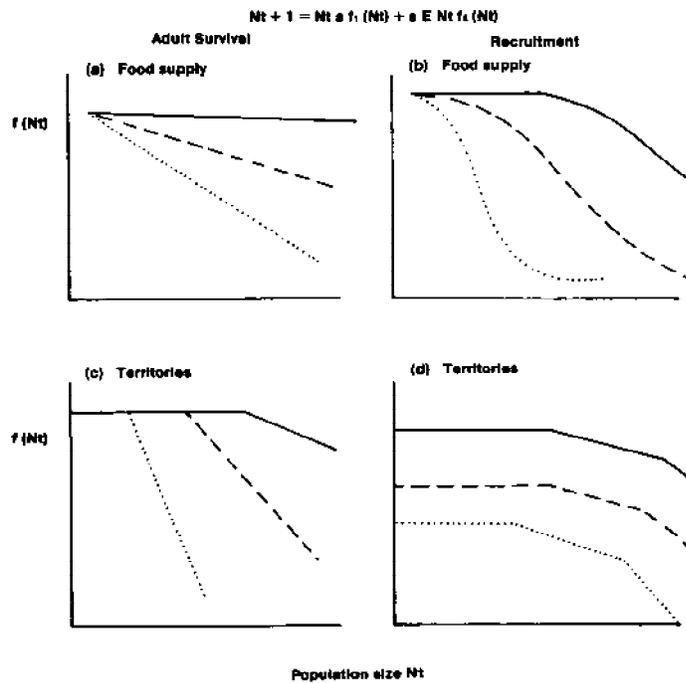


Fig. 3.8 Simple model of population dynamics of a game bird species and the factors that determine the shape of potential density-dependent factors. Two functions are assumed to be potentially operating: $f_1(N_t)$ determines the influence of population size, N_t , on adult survival; $f_2(N_t)$ determines the influence of population size on production and survival of young birds. The graphs sketch out how various biological and management options affect the shape of these functions. The graphs on the left depict how (a) food supply and (c) number of available breeding territories affect survival. In (a) decreasing supplies of food are indicated by increasingly broken lines, whereas in (c) the number of available territories decreases as the lines become more fragmented. Note that in (a) increases in population density give a steady decrease in survival, essentially because there is less food per bird. In (c) survival is assumed constant until all the available territories are full after which it declines so that sN_t always equals the number of territories.

The graphs for the number of young birds produced in any year again depict idealised cases for the effects of (b) available food and (d) numbers of territories. The conventions of increasing fragmentation of the line with diminishing resources follows that of (a) and (c). In (b) increasing population density leads to steady decline in recruitment, while in (d) recruitment remains constant until all territories are taken, when recruitment declines. The lines of different slope depict the possible case of more marginal habitats being used for nesting once the best quality areas are full.

where only the fecundity term was strongly linked to density. In a system where population density affects both survival and fecundity, increased costs of reproduction associated with increased fecundity may countermand the benefits of increased survival at low population density. Unravelling the relative strengths of these different interactions requires a lot of data from experiments conducted at a range of population densities.

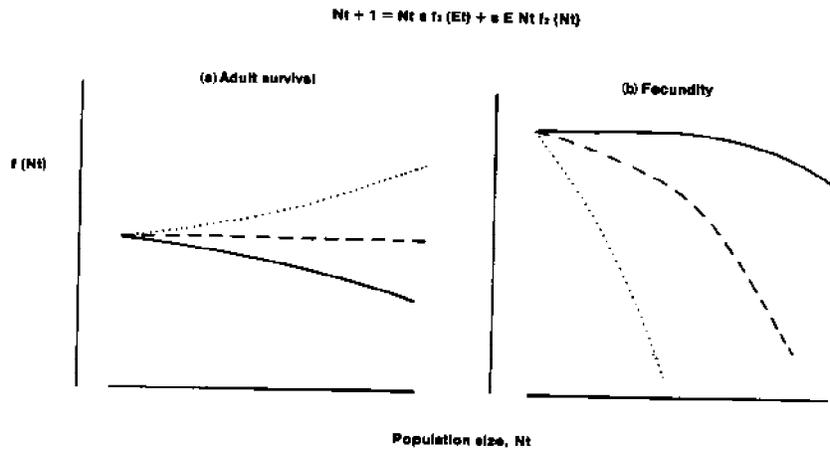


Fig. 3.9 The effects of including in costs to increased reproduction on the model of game bird population dynamics. The function $f_2(N_t)$ is the same as in Fig. 3.8. An additional function, $f_3(E_t)$, assumes that increased levels of fecundity lead to reductions in survival. The curves again illustrate different intensities of density-dependent relationship and the curves in (a) correspond to those in (b). Thus when recruitment is only weakly linked to density (solid line), reductions in fecundity at high population density hardly affect survival. In contrast when fecundity is tightly linked to population density (dotted line), the large reductions in fecundity as population density rises lead to increases in survival.

3.4.3 Problems with determining the shape of recruitment curves

Determining how clutch size and fledging success vary with population density is probably the most important task if a population is to be managed efficiently. However, the data necessary to ascertain the shape of this curve need to be collected over a wide range of population densities. As the most efficient type of management will tend to maintain the population at some constant density, these data are often hard to obtain. Populations that are recovering from severe environmental perturbations, such as a bad winter, or those that

fluctuate over a wide range of abundances, such as many grouse species, are likely to give more useful information about the shape of these functions than populations which remain relatively constant. Thus, until these data are collected and more is known about the relative intensity with which density-dependent effects operate on survival and fecundity in populations of gamebirds, we will be unable to make anything other than speculative guesses about whether hunting operates additively or compensatorily to other sources of mortality. As changes in management will alter the shape of these functions, populations should be monitored especially accurately at times when management practices change; it is then that much useful information may be gained about the relative strength of the wide variety of different mechanisms that may contribute to population regulation.

3.5 Dispersal

Statistical and logistic problems plague attempts to estimate dispersal rates in wild animal populations. Here we have problems not only in determining the shape of the frequency distribution of dispersal distances for a species but also in estimating the extent of dispersal and differentiating between animals which have dispersed out of the study site and those that have died and decomposed or have been eaten. Although studies involving radio-telemetry may help to reduce some of the problems in this area, obtaining large sample sizes or assessing just how much the telemetry techniques bias the estimates will still be hard.

3.5.1 *Natal and breeding dispersal*

Two types of dispersal are usually recognised: natal dispersal – the distance between where an animal is born and where it breeds – and breeding dispersal – the distance between where an adult breeds in successive breeding seasons (Greenwood, 1980). In general, females tend to disperse further than males (Fig. 3.10; Greenwood, 1980), and natal dispersal distances are greater than those between breeding seasons.

Breeding dispersal may be affected by either reproductive success in the previous breeding season or population density. In the former case, unsuccessful breeders tend to disperse further than successful breeders, which tend to reneest at a site where they have previously been

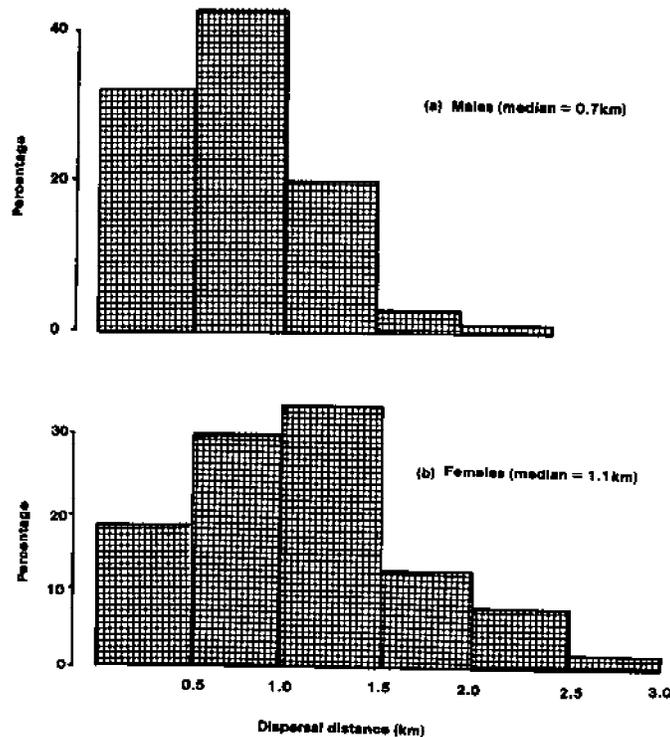


Fig. 3.10 Dispersal data for male and female blue grouse; (a) data for males, (b) data for females. In both cases frequency distributions are illustrated for the distance moved by birds from where they were radio-tagged as juveniles to where they were found breeding in the next breeding season. (After Hines, 1986.)

successful. Dispersal may also be higher when population density is higher, but note that this may also be because breeding success is lower and because birds have to move further to locate an available territory. The evidence to support this is somewhat varied. Hines (1986) found dispersal was not density-dependent in blue grouse and, in a re-analysis of the data presented by Jenkins *et al.*, (1963), found that dispersal in red grouse, too, was not related to density. However, more recent studies by Watson *et al.*, (1984) have suggested that dispersal in red grouse may indeed have a density-dependent component.

3.6. Interspecific comparisons

To examine variations in survival and fecundity at higher taxonomic

Table 3.1 Nested analysis of variation in selected life-history variables at different taxonomic levels in European ducks and gamebirds. The figures given are the percentage of variation in the data at each taxonomic level.

<i>Variable</i>	<i>Species</i>	<i>Genus</i>	<i>Family</i>	<i>Order</i>
Female body weight	11.89	62.18	0.00	25.93
Adult mortality	6.88	45.67	0.00	47.45
Clutch size	13.87	57.28	28.84	0.00
Egg weight	6.16	37.35	0.00	56.48
Incubation time	21.82	45.14	0.00	33.04

levels, we collated data on these variables for the European gamebirds from Cramp and Simmons, 1977, 1980. Analyses performed at both the species and generic levels, as nested analysis of variance, suggested that this was where the majority of variation in the data lay (see Table 3.1). The main results, presented in Table 3.2, tend to confirm those of

Table 3.2 Relations between different life-history variables for European gamebirds and ducks. Parallel regressions were fitted to the data for each group, but no significant difference was detected between the slopes. Figures given in each case are the correlation coefficient, *r*, the slope of the major axis regression, *b*, and in parentheses, the sample size. Statistical significance is indicated as follows: *** = $p < 0.10$, ** = $p < 0.05$, * = $p < 0.01$, n.s. = no significant correlation, F.wght = female weight.

<i>Variables</i>	<i>Genus</i>	<i>Species</i>
Clutch size × log F.wght.	$r = -0.568$ ** $b = -11.6$ (18)	-0.590 *** -10.5 (30)
Adult survival × log F.wght.	$r = -0.499$ * $b = -66.2$ (14)	-0.669 *** -47.5 (24)
Clutch weight × log F.wght.	$r = 0.89$ *** $b = 0.15$ (18)	0.91 *** 0.14 (30)
Log clutch weight × log F.wght.	$r = 0.86$ *** $b = 1.01$ (18)	0.87 *** 0.98 (30)
Log egg weight × log F.wght.	$r = 0.97$ *** $b = 1.81$ (20)	0.97 *** 1.87 (48)
Log incubation time × log F.wght.	$r = 0.70$ *** $b = 0.26$ (19)	0.72 *** 0.26 (47)
Log incubation time × log Egg wght.	$r = 0.63$ *** $b = 0.12$ (19)	0.69 *** 0.13 (47)

a similar analysis of North American gamebirds (Zammuto, 1987). Both mean clutch size and annual survival decline with increases in body size, suggesting that larger birds not only are longer lived but also tend to lay fewer eggs per season. No interactions are apparent between clutch size and mortality once the effects of body size are removed (Table 3.3). An interesting interaction appears to emerge between reproductive effort and body size. In general all the species tend to lay total clutches whose weight is approximately equal to 35% of their total body weight. However, larger species tend to lay smaller numbers of eggs and so lay disproportionately larger eggs. As the slope between incubation time and female body size has a slope less than that of the relation between incubation time and egg size, and both have slopes less than unity, this suggests that larger species may be reducing incubation time *relative to their body size*, by laying fewer, larger eggs. This may mean that time is as important a constraint on fecundity/survival interactions as energy. Larger birds may therefore lay fewer but larger eggs in order to speed development and reduce the length of time for which the parents must care for the eggs.

Although part of this analysis contrasts with that of Zammuto (1987) in finding no pay-offs between survival and fecundity, the data are of a very heterogeneous quality and much better estimates of survival and juvenile mortality would be required before the analysis could be said to give other than speculative results. In addition, it is important to bear in mind that the patterns we see at the interspecific level are not necessarily representative of those at the intraspecific. Where detailed studies have been done on individual populations, for example the sparrowhawks studied by Ian Newton (1986, Fig. 3.1), those individuals with the highest annual fecundity and lifetime reproductive success were those that lived the longest. Analysis of these data gives a positive relationship between survival and fecundity.

Table 3.3 Partial correlations between mortality, M , clutch size, CS , and female body weight, $F.wght$. In each the correlation between two variables with the effects of the third removed are given at the species and generic level. Levels of significance indicated as in Table 3.2.

<i>Variables</i>	<i>Genus</i>	<i>Species</i>
$\text{Log}(F.wght) \times M - CS$	-0.372 n.s.	-0.370 n.s.
$\text{Log}(F.wght) \times CS - M$	-0.506 *	-0.475 **
$CS \times M - \text{Log}(F.wght)$	0.311 n.s.	0.375 n.s.
Sample size	14	19

3.7. Conclusion

Both ecologists and the managers of game estates are concerned with determining the factors which maximise the lifetime reproductive success of gamebirds. The analysis of how life-history parameters such as clutch size and survival are tuned in gamebirds will obviously benefit from more studies where management is used, or considered, as a controlled experiment. The two models outlined in Figs. 3.8 and 3.9 suggest that really quite complex and carefully designed experiments have to be undertaken if we are to understand how fecundity and survival interact with each other in any particular habitat to produce the observed variations in life-history variables. Carrying out these experiments not only aids estate managers who are concerned with producing a constant yield of birds for sportsmen to hunt, but also allows biologists to answer questions about the evolution of life-history strategies in birds.

Although the interspecific comparisons of life-history data raised some interesting points, a further analysis would benefit from additional information. Here, as with the single species studies, it would be interesting to know if the costs of reproduction, required by the Charnov and Krebs (1974) model of clutch size, are paid in energetic units or in time units. Essentially we need to know whether the constraints on the numbers or size of eggs laid are due to energy lost for survival or whether the length of the breeding season restricts breeding effort in any individual season. It seems likely that the answer to this question will best be determined by manipulative field experiments. Joint interactions between game managers and ecologists may be most useful in addressing this problem.