When intra-specific competition for food does occur, the amount of food produced at the next lower trophic level imposes an overall limit on the yield obtainable from a fishery, although the yield must inevitably be much less than the amount of food available from the lower level. Two factors contribute to the difference: the efficiency of conversion of food into the bodies of the fish; and the efficiency of cropping of the fish population by the fishery. Efficiency of conversion increases with the rate at which the fish are growing and therefore generally tends to diminish as the fish become older; it rarely exceeds 20%. Efficiency of cropping is reduced both by the loss of fish which die from natural causes before reaching the age at which they begin to be caught, and by natural mortality after this age. In the presence of competition, therefore, both efficiency of conversion and efficiency of cropping are increased by reducing the age at which fishing is started and both therefore tend to cause the optimum size limit to be less in the presence than it is in the absence of competition.

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THE EXPLOITATION OF BIRDS

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In comparison with fish or mammals, birds offer little scope for large-scale exploitation. Although for centuries they have provided food, feathers, oil, nitrogen-rich guano and sport for man's use and enjoyment, the volume of products obtainable by periodic harvesting from even large populations of birds has seldom attracted more than local interest. Attempts to satisfy wider markets, e.g., to provide plumage for millinery, have invariably led to disaster; primitive and civilised man alike have frequently been misled by the apparent abundance and stability of breeding colonies and migrating flocks. Even when the need for conservation has been fully recognised, the temptation to over-exploit has seldom been resisted, and the history of man's exploitation of birds is a sorry and almost consistent record of devastation.

Populations cropped closely for food but otherwise protected by resident humans have generally fared better than those open

to predation by nomads. A few primitive communities have for centuries exploited neighbouring colonies, taking a heavy but sustained annual yield. Up to the year of evacuation (1930), the inhabitants of St. Kilda took annually for food between 4000 and 12,000 fulmar petrels (*Fulmarus glacialis*) or approximately 115 birds a year per inhabitant (Fisher & Lockley 1954:93); in addition large numbers of puffins (*Fratercula arctica*) were taken for food and feathers, and Manx shearwaters (*Puffinus puffinus*) were hunted as a subsidiary source of food. Although the St. Kildans are estimated to have consumed half the annual production of some of their bird colonies, the number of breeding birds was not appreciably reduced during a century of recorded predation. This is one of very few instances in which birds are known to have formed the staple food of a community throughout the year.

Similarly gannets (*Sula bassana*) were for many years cropped successfully from breeding colonies in Scotland, Orkney, the Faeroes, and islands off Iceland during the 19th century, by small communities which intentionally or otherwise devised successful conservation methods (Fisher & Lockley 1954:82). The species as a whole decreased steadily in numbers, however, between 1834 and 1894, due largely to the devastation of a vast population on Bird Rocks in the Gulf of St. Lawrence, visited regularly by itinerant fishermen as a source of food and bait. There is evidence that garefowl or great auks (*Alca impennis*), once plentiful at a number of breeding stations in the North Atlantic, were successfully exploited in passage off the Mediterranean coast some 20,000 years ago (Fisher & Lockley 1954:65). The species later suffered heavy predation from fishermen at the main breeding grounds off Newfoundland and the last known specimens were killed in 1844.

Bent (1921) has described the destruction of gull and tern colonies along the eastern coast of North America during the late 19th and early 20th centuries, when both plumes and eggs were in demand. Greenway (1958) has shown clearly the effects of advancing European civilisation on the birds, particularly the highly adapted endemic species (p. 36), of the North American continent. Extinction of the passenger pigeon (*Ectopistes migratorius*), the heath hen (*Tympanuchus cupido cupido*), the wild turkey (*Meleagris gallopavo sylvestris*), and the Carolina parakeet (*Conuropsis carolinensis carolinensis* and *C. c. ludovicianus*), is " . . . so closely related in time to the penetration of the continent by Europeans and their civilisation that it is impossible not to believe that the one is the result of the other. Destruction of habitat, loss of food supply, and finally persecution by men are undoubtedly the causes, and this last is the most important" (p. 39). Thus passenger pigeons, nesting colonially in huge, wandering flocks, were taken in hundreds of thousands at a time when their mortality was in any case likely to be high due to the destruction of their feeding grounds by timber-felling. Extinction of moas in New Zealand may similarly have been due to man's predation following climatic changes and alteration of habitat which reduced the stock (Archey 1941:99, Oliver 1949:194–5). On the Mascarene Islands pigs, rats and monkeys introduced during the 16th and 17th centuries began the destruction of some 24 species of birds, including the dodos and solitaires, but commercial hunting in the 18th century completed their extirpation (Greenway 1958:105). As Hachisuka (1955: 65 & 91) has pointed out, the common dodo of Mauritius (*Raphus cucullatus*) was almost certainly exterminated between 1681 and 1695, while the white dodo (*Victoriornis imperialis* or *Raphus solitarius*) survived at least until 1735 on the more sparsely populated island of Reunion.

Exploitation of the eggs of wild birds has been investigated in some detail by Cott (1953, 1954), who considers the sooty tern (*Sterna fuscata*) to be "perhaps the world's most important wild egg producer" (1954: 129). On the Seychelle Islands this species, together with other colonial sea-birds, has been exploited systematically for many years (Vesey-Fitzgerald 1941, Ridley & Percy 1958). During the 19th century eggs were taken annually for food from the vast breeding colonies, providing a valuable source of protein for the human population. The establishment of an export market for yolk led to increased exploitation, in which little control was exercised until yield (shown principally by customs receipts) was considerably reduced. At the end of the century

some seven million eggs were collected annually; by the middle of the present century less than 140,000 eggs were available in a season. Thus a plentiful supply of inexpensive food was virtually destroyed by uncontrolled or ill-managed exploitation.

The heavy exploitation of song-birds in England during the 19th century was described by Mayhew in his account of the London poor, originally published in 1851. Mayhew estimated that some 70,000 goldfinches (*Carduelis carduelis*), 70,000 linnets (*C. cannabina*), 60,000 larks (*Alauda* spp.) and 35,000 song-thrushes (*Turdus ericetorum*), together with other species in similar numbers, were taken annually for the London market (Quennell 1951:240 *et seq.*). Large numbers of nests and eggs were also taken, mostly from the home counties. The trade seems to have had little lasting effect on the numbers of song-birds, possibly because many were taken as juveniles between May and August and would in any case have been subject to heavy mortality from other causes during their first year; the numbers taken would also have been small compared with untouched populations outside the zone of heaviest predation.

Similar factors may be responsible for the apparent continuing success of New Zealand mutton birds (*Puffinus griseus*), of which some 250,000 unfledged juveniles are taken annually for local consumption and export (Richdale 1944:93). Only a small proportion of the total population is at present subject to human exploitation, and only juveniles (many of which, if comparisons may be drawn with other species, would probably die during their first migration) are removed from the breeding grounds. Very little is known of the population ecology of this important species and no accurate tally of the annual yield is kept. While it is possible that the population may be considerably under-exploited and that the industry it supports could be expanded without damaging stocks, in our present state of biological ignorance the necessity for retaining controls and restrictions can not be over emphasised.

Protection of birds is now recognised as a duty by civilised communities and the introduction of game laws and other conservation measures, particularly during the last half century, has done much to save remaining stocks of wild birds throughout the world. Interest in birds as animals has also spread, particularly in Europe and North America, so that public opinion is marshalled on the side of the conservationist and protector. However, many species of birds, particularly game birds, wild-fowl and those with large, palatable eggs, are still regarded as exploitable and continue to provide a wide range of human communities with food and sport. Over-exploitation in the past may be blamed on ignorance, lack of interest in animals, and absence of protective legislation; today it is inexcusable. Biologists, publicists and legislators are available in abundance to ensure that exploitation, where considered necessary, shall be conducted on sensible, economic lines. The first need is always for an adequate ecological survey of the species, for authorities administering game laws and protection must know the strong and weak points of their animals' ecology if they are to make full and intelligent use of their powers.

Natural populations large and stable enough to be exploited are already subject to natural exploitation by predators and parasites, and regularly suffer losses due to climate, seasonal food restriction, inexperience and other natural causes. Thus normal populations usually have a high mortality of eggs, nestlings and juveniles; only 8-18% of eggs laid giving rise to adult birds (Lack 1954:87). With no knowledge of the species which he is attempting to exploit, man merely superimposes his own pattern of predation on a delicately balanced system and may add to the difficulties of an already overburdened stock. Knowing the ecology of the species, he may selectively replace other forms of predation, anticipate other forms of loss, and perhaps increase the rate of exploitation which the population can support. The organised shooting of game birds and wild-fowl is a form of exploitation popular in many civilised countries, and one to which the principles of ecological research can well be applied. Surprisingly few populations exploited in this way have been studied in detail to discover the highest economic level of exploitation. The exploitation of birds, as of any other natural resource, should be both efficient and economical if it is deemed necessary at all, and

efficient exploitation demands a steady yield at the highest level which the population can provide. This level can be reached only when the population dynamics of the stock are known, and when every practical form of stock improvement has been applied.

Ecological research takes time and may prove expensive; when conservation is the aim, the expense is unlikely to be balanced by income derived directly from the conserved stock. Exploitation, on the other hand, should prove profitable and capable of supporting the research on which it is based. The differences between conservation and exploitation, and the different methods required to achieve one or the other, are not always appreciated by landowners and licensing authorities responsible for maintaining stocks and providing sport. The practice of basing a permitted annual bag on game bags of previous years is, for instance, a conservation measure widely used in exploitation. Records of game bags are an interesting population index and may, in certain species, show the level of yield at which conservation is assured. They do not provide information on which the efficiency of exploitation may be increased, and may hide important trends in the population which would be exposed by more efficient ecological studies.

The point is illustrated by recent studies of red grouse (*Lagopus scoticus*) undertaken for the Scottish Landowners' Federation by a team of ecologists under the direction of Dr. David Jenkins. Although the problems studied by the team are peculiar to grouse moors and to British methods of exploitation and maintenance, the findings of the enquiry and the underlying ecological principles are important wherever avian populations are exploited. For many years large areas of moorland have been maintained throughout Scotland as grouse reserves; shooting is normally restricted to four months following 12 August each year, and considerable expense is involved in maintaining stocks, gamekeeping and the provision of amenities for shooting. In the last two to three decades a steady decline in game bags has been reported, and in 1956 a three-year investigation into the causes of the decline was begun. Local landowners and keepers had suggested variously that sheep tick, disease, bad weather during nesting, predominance of old birds producing small broods, predation and overshooting contributed to the decline. The results of the survey (extended after its original term and now continuing under the auspices of the Nature Conservancy and the University of Aberdeen) have shown that more basic causes are responsible, and that expensive remedial measures, including re-stocking, vermin destruction, and even the setting of lower bag limits, are unlikely to halt the decline.

Studies began with population counts, marking, and the collection of basic data on clutch size, sex ratio, etc. The importance of food supply as a factor limiting population size soon became apparent. Food of red grouse consists mainly of the shoots of young heather, and a supply of shoots is ensured under management by selective burning. Behaviour studies indicated that the birds keep feeding territories, the size of which varies with the food available, so that over a given area the size of breeding population depends mainly on the efficiency of the management in maintaining food supplies. The policy of burning is hallowed by long usage, but also received additional support from the findings of the Committee of Enquiry on Grouse Disease (Lovat *et al.* 1911) as a prophylaxis against parasites. It now seems probable that burning, particularly the widespread burning of large areas practised in recent years, has led to heavy losses of minerals from the surface soil and consequent impoverishment both of the heather and of the grouse which depend on it. Jenkins regards the mineral losses as the most important single factor contributing to the decline in grouse numbers. In his view attempts to increase stocks artificially by hand rearing and introduction from other areas, and intensive drives against predators, are probably wasted effort (Elliott in Jenkins 1959:22) as the birds colonise the moor as intensively as its resources permit. Introduced birds, in common with the annual surplus produced each breeding season, die because they are unable to find feeding territories among the established population. It follows that, despite the long-term decline in numbers, the annual bag at present taken in autumn (a conservative figure based on the assumption that breeding density in spring depends on the number

of birds left after autumn shooting) could be increased without over-exploiting the stock and without accelerating the decline, which is due to other causes (Jenkins *et al.* 1961:4). Research is gradually extending to cover soil sampling, botany, detailed behaviour studies and large-scale experimental alteration of population balance. Results at present indicate the need for resting and replenishing the land, possibly by allowing it to revert to scrub or woodland and introducing alternative game animals to maintain productivity. Thus the ecological research, although expensive and time consuming, has already helped to reduce expenditure on useless remedies, has shown the need for new methods of exploitation consistent with good farming, and has provided instruction on an economically important but neglected form of land management.

Similar research is required, and should be demanded, in every case where exploitation of birds is permitted under legislation or control. Only through such studies are we likely to gain the knowledge required to safeguard stocks, and at the same time allow a fair and efficient form of management in which interests both of licence holders and of protecting authorities are safeguarded.

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UTILISATION OF MARINE INVERTEBRATES

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The utilisation of marine invertebrates extends from prehistoric nomad times through all levels of communal development to our present civilisation. The invertebrates have provided hard parts such as shells for tools, ornaments, symbols, a source of lime, jewellery, dress, weapons, fibres for cloth, dyes, and soft-parts for food. We retain today more of these usages than we have abandoned, and in some cases increased our utilisation in proportions greater than the increase in population. The requirement for commercial sponge has not extended and only a few hundred tons are now landed each year but the demand for ornamental corals is in the order of 4,000,000 pounds and more each year, while the demand for pearls is unsatisfied even with the tremendous production from Japan's pearl culture development.