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NEW FACTORS CONTROLLING POPULATIONS OF LAND VERTEBRATES IN GREAT BRITAIN

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ABSTRACT: The vertebrate fauna of Britain is impoverished by nature. Further, virtually the whole land surface has been altered radically by Man, and all vertebrate species have been profoundly affected both unconsciously and consciously by Man. The rate of change during the last quarter of a century has been far greater than at any other time; new deleterious factors - increased habitat destruction, increased human pressure and motor traffic, myxomatosis and a vast increase in pesticide use have coincided in this period. The public's attitude to several common species (e.g., rabbit, woodpigeon, fox and birds of prey) has been equivocal and has altered in time. In Britain the cost of effective population control of most vertebrate pest species would be far greater than the value of the damage done by them; but local control operations are often necessary. Pest control and conservation are seen as different sides of the same coin; in thickly populated industrial countries with rapidly changing environments such as Britain, the emphasis is likely to shift from pest control to conservation in the future.

INTRODUCTION

Great Britain is extensively industrialised and thickly populated; in 1969 there were 594 persons per square mile, in other words, the population density is more than ten times that of the United States. Also, British agriculture has been mechanised to an extent which is greater than in any other country. Therefore, the ecological situation in Britain today is unusual, but it represents one which is likely to be more frequent in other countries in the future. In this review an attempt has been made to identify the principal factors which have controlled population size of vertebrate species in Great Britain. Its theme is that Man has been one of the principal factors for centuries, and that control and conservation should be considered as different aspects of one type of activity.

THE BRITISH LAND VERTEBRATE FAUNA AND ITS HISTORY

The flora and fauna of the British Isles are impoverished. There are two main causes. First, Britain was separated from the continent of Europe about 6,000 years ago under climatic conditions which differ from those of today, and hence many species adapted to present climatic conditions were unable to colonise the islands. Secondly, from Neolithic times (3,400 - 1,700 B.C.) onwards Man has had profound effects both on animal species and on their habitat. Originally, most of the country was covered by broad-leaved forest (Godwin 1956) but today only 9 per cent of the land contains any form of woodland. The species which were almost certainly exterminated directly by over exploitation or indirectly by destruction of the habitat, or by both activities in historical times are given in Table 1. On the other hand, other species have been introduced intentionally or unintentionally and have become members of the wild fauna. These are shown in Table 2. In addition, the capercaillie (*Tetrao urogaillus*) became extinct in the 18th Century but was reintroduced successfully in 1837. At least six avian species which had become extinct in the 19th century have recolonised the country during the present century, largely thanks to effective conservation measures. About fifteen avian species have colonised Britain for the first time since 1800 (Parslow 1968). To conclude, fifteen out of fifty-eight (26 per cent) of the British mammalian fauna owe their extinction (five species) or introduction (ten species) to Man, and seven species out of one hundred and ninety (4 per cent) of the breeding avian fauna owe their extinction (four species) or introduction (three species) to Man.

Most of Britain consists of agricultural land. Owing to the decline of British agriculture from 1875 to 1939 the agricultural landscape changed remarkably little from the time of the enclosures (mainly 16th and 18th and early 19th century), but the second World War and developments resulting from it completely altered the situation in subsequent years. A large proportion of the remaining woodlands were felled, much waste land reclaimed and numerous hedges were removed in order to make fields a more convenient size for the operation of combine harvesters and in order to reduce maintenance costs. These developments were particularly manifest in the southeastern half of England. For example, the area of lowland heath in Dorset was reduced by 30,000 acres in the 123 year period 1811-1934, and by 35,000 acres in the 26 year period 1934-1960 (Moore 1962). Hedge mileages in three parishes in Huntingdonshire were reduced by five miles from 1850 to 1946 and by fifty-one miles from 1946 to 1965 (Moore et al 1967).

Table 1. Species extinct in historical time in Great Britain

| Class | Species | Date of Extinction |
|---------|---|--------------------|
| Mammals | Beaver (<u>Castor fiber</u>) | 12th Century AD |
| | Wolf (<u>Canis lupus</u>) | 18th Century AD |
| | Brown Bear (<u>Ursus arctos</u>) | ? 10th Century AD |
| | Wild Boar (<u>Sus scrofa</u>) | 17th Century AD |
| | Reindeer (<u>Rangifer tarandus</u>) | 12th Century AD |
| Birds | Great Auk (<u>Alea impennis</u>) White tailed | 1812 |
| | Eagle (<u>Haliaeetus albidilla</u>) | 1916 |
| | Kentish Plover (<u>Charadrius alexandrinus</u>) | 1956 |
| | Great Bustard (<u>Otis tarda</u>) | 1832 |

Table 2. Species introduced into Great Britain

| Class | Species | Date of Introduction |
|---------|--|----------------------|
| Mammals | Rabbit (<u>Oryctolagus cuniculus</u>) | c 1100 |
| | American Grey Squirrel (<u>Sciurus carolinensis</u>) | 1876 |
| | Black Rat (<u>Rattus rattus</u>) | Middle Ages |
| | Brown Rat (<u>Rattus norvegicus</u>) | c 1700 |
| | Edible Dormouse (<u>Glis glis</u>) | 1902 |
| | Coypu (<u>Myocastor coypus</u>) | c 1930 |
| | American Mink (<u>Mustela vison</u>) | 1929 |
| | Indian Muntjac (<u>Muntiacus muntjak</u>) | 1890 |
| | Chinese Muntjac (<u>Muntiacus reevesi</u>) | 1900 |
| | Sika Deer (<u>Cervus nippon</u>) | Mid 19th Century |
| | Chinese Water Deer (<u>Hydropotes inermis</u>) | c 1900 |
| Birds | Little Owl (<u>Athene noctua</u>) | 19th Century |
| | Red legged Partridge (<u>Alectoris rufa</u>) | 1770 |
| | Canada Goose (<u>Branta canadensis</u>) | 17th Century |

At the same time as the drastic reduction of habitat other deleterious factors have increased, notably the greatly increased use of pesticides from the late 1940's onwards, and a great increase in motor traffic and hence an increase in new roads and of wildlife casualties during the same period. The relative importance of all these new factors cannot be quantified in most cases, but it is significant that they have coincided in time. Thus, wild land vertebrates of Britain have experienced unprecedented pressures during the last quarter of a century. Control measures, where they are designed to cause population declines as in some pest control measures, or population increases as in some conservation measures, have to be considered against this background.

In Britain very few vertebrate species cause sufficiently serious losses to justify official spending on total population control measures. Most of the pest species are introduced ones, notably the rabbit (*Oryctolagus cuniculus*), brown rat (*Rattus norvegicus*), coypu (*Myocastor coypus*), grey squirrel (*Sciurus carolinensis*) and American mink (*Mustela vison*). Some native species are also serious pests; notably the house mouse (*Mus musculus*), wood-pigeon (*Columba palumbus*) and house sparrow (*Passer domesticus*). The declared or implied aim for each of these species is to reduce their numbers in those districts where they are known to be, or are thought to be pests, to levels which will not cause serious economic damage; in some cases, e.g., coypu and mink, extermination would be preferred if it were possible. A few other species also do damage at times, but since they are valued for sport, higher population densities are acceptable than would be the case if they were not hunted or shot; the fox (*Vulpes vulpes*) and the red deer (*Cervus elephas*) are in this category. Birds of prey are frequently killed because they are believed to affect game bird populations. All other species are tolerated or are encouraged by official and voluntary conservation bodies. The greatest expenditure on the conservation of a single species is on game birds, especially the pheasant (*Phasianus colchicus*), partridge (*Perdix perdix*), red-legged partridge (*Alectoris rufa*), red grouse (*Lagopus scoticus*) and on the mallard (*Anas platyrhynchos*); it is mostly non-official.

When any one species in Britain is studied it becomes apparent that conscious or unconscious human activity largely determines its numbers, and that there is considerable feedback in the system. This is illustrated in the examples given below.

THE RABBIT (*Oryctolagus cuniculus*)

The rabbit owes both its increase and its decline to Man. It was introduced by the Normans, and originally was confined to carefully preserved warrens. It probably became widely distributed in England by the 16th century, but many parts of Wales and Scotland were not colonised until the 19th century. With the passing of the Ground Game Act in 1880, rabbits became an important article of food, particularly among rural populations in periods of agricultural depression; and extensive industries based on this species both for food and clothing were built up and maintained until 1953; it is estimated that from 160 to 100 million rabbits were cropped each year. Until the Second World War the rabbit was thought of as a species which should be tolerated, but during the War and the immediate post-war period its role as a pest became more generally recognised - it was estimated that it caused 40-50 million pounds sterling worth of damage each year. Then the public's attitude to the species became equivocal and local control was sponsored officially. The apparently accidental introduction of myxomatosis in 1953 at once reduced its numbers substantially and at the same time virtually destroyed the wild rabbit industry and the esteem in which the species was held. Despite the reduction of direct human predation, the rabbit has never returned to its pre-myxomatosis numbers in Great Britain. It is kept down legally by ferretting, trapping and shooting, and illegally by the spread of myxomatosis, which also occurs naturally. The extent to which rabbit populations are affected by vertebrate predators (principally the stoat (*Mustela erminea*), the fox and the buzzard (*Buteo buteo*)) is not known. Originally the rabbit was too numerous for it to be controlled by these predators, but it is conceivable that in some areas its numbers are now low enough for it to be controlled by the action of the whole "predator force" in some districts at certain times. For a short time in 1954 it seemed possible that the rabbit could be exterminated by myxomatosis, but public opinion prevented the legal, and hence controlled use of this highly specific method of biological control, and the opportunity passed. Since then the virus has become attenuated in some districts. It is conceivable that it will eventually cease to control the species; then the memory of diseased rabbits may grow dim and the species may again become a desirable prey for the shooter; but so long as prosperous agriculture is maintained in Britain, the rabbit is unlikely to be tolerated at the population levels which existed between the wars, and so population control might be attempted in the future.

The history of the rabbit in Britain is closely linked with human attitudes towards it. So abundant was this species that its rapid decline in the mid 1950's had extensive repercussions on the flora and fauna of the country. (Anon 1956, Thompson & Worden 1956).

The fox is a native species occurring throughout the country except for most of the outlying islands, (Southern 1964). It is found in all habitats including towns. The public's attitude towards it has been equivocal - the fox frequently takes poultry, game birds and sometimes lambs, but it has long been valued as a quarry for the huntsman. At least 50,000 foxes are killed each year by hunting and shooting, but this has no overall effect on the population. Myxomatosis greatly reduced one of its main prey species, but the fox turned to alternative prey and no decline of its population was recorded. From 1959 to 1960, 1,300 foxes were reported as having died in eastern England; the fox population was severely depleted in some districts. Field and laboratory studies showed that the deaths were mainly due to foxes eating pigeons which had acquired a lethal or near lethal dose of aldrin or dieldrin as a result of feeding on wheat seed dressed with these substances; the fox is unusually sensitive to them. Badgers (*Meles meles*) and birds of prey (see below) also died from the same cause. In 1962 the use of aldrin, dieldrin and heptachlor as cereal seed dressings for use in spring was withdrawn by voluntary agreement between Government and Industry, and casualties to foxes and other predators were greatly reduced as a result. (Blackmore 1963, Southern 1964).

In some districts at least, the fox is preserved in order to be hunted. However, there is increasing public pressure to ban those field sports in which mammals are hunted with hounds. If hunting were to be banned, it is probable that the fox would lose its present protection and so might decline in areas where the shooting of game birds remains an important activity. On the other hand, if some new factor arose which was seriously detrimental to the fox, there is no doubt that conservation interests would take measures to ensure the survival of the species, as is already done with other rarer British carnivora (*Martes martes* *polecat* (*Mustela putorius*) and wild cat (*Felix silvestris*)).

The fox is an example of an active species which can be a pest, whose sporting value may disappear but whose conservation value would become apparent if its population declined severely. Owing to its habits and wide distribution, acceptable measures taken to control its population would cost far more than the cost of the damage it causes, and so it is most unlikely to be the subject of organised control.

RAPTORIAL BIRDS OF PREY

The rabbit and the fox are both species which have been able to adapt to the severe environmental pressures to which they have been subjected in recent years. The raptorial birds of prey, despite catholicity in breeding sites and food, have been less successful. In Britain, at the beginning of the 19th century, thirteen species were abundant to moderately common and two were local. Since then, one has become extinct, eight now only exist in very small numbers and only three are moderately common.

From the earliest times birds of prey have been persecuted because most of them take, or are believed to take, poultry and game birds. Originally only the peregrine (*Falco peregrinus*) and the merlin (*Falco columbarius*) were protected since they provided the most valued hawks for falconry. The rapid decline of the birds of prey began to occur in the mid 19th century at the time of the invention of the breach loader and of widespread preservation of game birds. The result was that species like the common buzzard, which formerly occurred throughout the country in all types of habitat, became extinct or much less common in the agricultural areas in the east where pheasants and partridges were preserved, and survived only in the western mountains and moorlands. Recoveries of bird of prey populations in both World Wars strongly suggests that game preservation had been the main factor controlling birds of prey during the last hundred years. Until 1953, the rabbit was the main food of the buzzard in most of Britain. Its sudden disappearance caused a decline in reproductive activity, but the buzzard, like the fox, was able to turn to other prey and it has not suffered any marked decline. (Moore 1957 and unpublished). On the other hand, pesticides have had very marked effects on raptors which feed on other birds. The whole story is complex and not completely understood; briefly it is as follows: -

Severe population declines of the peregrine, kestrel (*Falco tinnunculus*) and the sparrow hawk (*Accipiter nisus*) occurred in the late 1950's and early 1960's as a result of acute poisoning due to feeding on prey which had eaten wheat seed dressed with aldrin, dieldrin

and heptachlor (Jefferies & Prestt 1966). Decline in reproductive success occurred in these species and in the golden eagle (*Aquila chrysaetos*) concurrently. Associated with the declines were increased egg breakage and a decline in eggshell weight (Ratcliffe 1967); in the peregrine and sparrow hawk these began at the time that DDT was introduced. Field studies (Hickey and Anderson 1968, Ratcliffe 1970) showed a close correlation of organochlorine insecticides content and eggshell thinness both among different species and within one species. Laboratory studies (e.g., Porter and Wiemeyer 1969) showed that DDT and dieldrin are among those substances which can cause changes in eggshell thickness. Restrictions on seed dressings containing aldrin, dieldrin and heptachlor came into force in 1962, numerous other restrictions on aldrin, dieldrin in 1965 and on dieldrin sheep dip in 1966. Since the time of the restrictions there have been marked recoveries in populations and breeding success of all the affected species, although the populations of the peregrine and sparrow hawk are still much reduced. (Ratcliffe and Prestt unpublished).

Thus the bird of prey populations have largely been controlled by intentional predation by Man in the interests of game preservation, and unintentionally by lethal and sublethal side effects of pesticides. Acts of Parliament aimed at reducing predation by Man have been flouted widely, and probably have had little effect in protecting birds of prey. On the other hand, restrictions on insecticides proposed by conservation biologists and implemented by Government with the agreement of Industry, have been effective in reversing the trend towards the extinction of British raptors. Birds of prey are so rare that their effects on most game birds - which normally form only a small percentage of their prey - must be very slight. When this comes to be more fully realised they may cease to be considered as outlaws to be destroyed at all costs, and with the help of conservation measures may be expected to recover their original status to some extent.

THE WOODPIGEON (*Columba palumbus*)

The woodpigeon is a woodland species which has become well adapted to living in agricultural land. In Britain it greatly increased as a result of certain changes in agriculture in the 19th and 20th centuries, notably the introduction of turnips and clover, both of which provide food at a critical time in the winter. The species has also benefited considerably from the numerous conifer plantations by the Forestry Commission from the 1920's onwards. The population of woodpigeons in Britain today probably lies between five to ten million. They do damage to crops to the extent of 1 - 2 million pounds sterling per year. They are much shot and eaten, but in Britain, unlike in many European countries, the pigeon is not classed as a game species. In 1954 a scheme was introduced by the Ministry of Agriculture to control woodpigeons by means of providing cheap cartridges for recognised pigeon shooters. The scheme failed completely to control the woodpigeon population. Dr. R. K. Murton shows why this was in his outstanding monograph on the species. (Murton 1965). Government support for cheap cartridges was withdrawn in 1965. It is quite clear that the cost of controlling the woodpigeon in Britain would be far greater than the cost of the damage done. However, local control by various means will continue to be worth while to individual farmers. Similarly, the populations of the house sparrow and grey squirrel are uncontrollable from the practical point of view.

COYPU (*Myocastor coypus*)

The South American coypu can only just survive the British climate; its numbers are greatly reduced by abnormally cold winters such as that of 1962/3. A combination of this form of natural control and control measures by the Ministry of Agriculture have prevented the spread of this species and have prevented it becoming a serious pest in the areas where it does occur.

RATS AND HOUSE MOUSE

These species provide the most serious vertebrate pest problems in Britain. They have certainly been aggravated by urbanisation and possibly by the destruction of predators by the preservers of game and by organochlorine insecticides. Despite great efforts by national and local authorities and by individuals, rats and mice continue to be a health hazard and to destroy large quantities of food. Relatively few effective and practical rodenticides are available, and some local populations are already resistant to warfarin.

OTHER SPECIES

A wide range of non-pest species e.g., all birds except sixteen species in England and nineteen in Scotland receive legal protection. Considerable efforts to protect rare verte-

brates are made by Government and voluntary conservation bodies. This is done principally by two methods. First the Nature Conservancy, a Government body, has set up national nature reserves representing all the main habitat types found in the country. Secondly, the Nature Conservancy and voluntary bodies such as the National Trust, the Royal Society for the Protection of Birds and County Naturalists' Trusts set up nature reserves to protect populations of rare or threatened species. Birds, mammals and reptiles are all protected in these two ways. Conservation by law has had little apparent effect, but conservation by protection of habitat has been relatively successful.

CONCLUSIONS

Man has affected the populations of all British vertebrates both directly and indirectly, unconsciously and consciously; and the man-made factors have interacted in a complex way. Except in the case of birds of prey which have relatively small populations, his conscious efforts at control have usually had far less effect than his other activities. From the earliest time Man has protected some species and waged war on others, but his attitude to some important species has been equivocal and has changed in time. For example, the rabbit and woodpigeon were at one time valued, but under changed conditions have come to be regarded principally as pests. On the other hand, the status of birds of prey, is changing from that of pest to that of protected species. Some species, notably the fox, rabbit and birds of prey, have been persecuted and conserved at the same time. In the past, conscious human action reflected different opinions of different vested interests, and rarely resulted from an overall critical assessment of the value of the species concerned or of the damage done by it. In recent years much more has become known about many of the pest species and it is becoming possible to cost both their depredations and the amount of money required to effect population control.

The general conclusions can be drawn from a study of human effects on vertebrates in Britain. First, a distinction has to be made on the one hand between local control, in which a farmer protects a given crop, game or poultry from the depredations of animals and, on the other, with population control. It is apparent that the expense of controlling populations of most abundant pests in Britain would be far greater than the damage done. The important exceptions are the human commensals, the rats and mice, over which medical considerations arise.

Secondly conservation and pest control are, and always have been, different sides of the same coin; in both the aim is to manage populations of wild animals to human advantage. All the indications in over-crowded, industrialised Britain are that applied biologists in the future will become less concerned with vertebrate pest control and more concerned with vertebrate conservation. However, fundamental knowledge of the biology of the species concerned remains the essential requirement for both activities.

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