A review of British mammals:
population estimates and conservation status of British mammals other than cetaceans

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Foreword

Historically, the health of the British fauna has been characterised by its distribution, with dots on maps denoting the presence of a particular species. In cases of drastic decline this sometimes proved an adequate tool - the disappearance of the otter from most of England, for example, was well illustrated by comparison of maps made at different times. For many widespread and common species, however, there can be serious declines in numbers that are not, until it is too late, mirrored in changes in distribution - a dot on a map can represent ten animals in a square where once there were a thousand.

Nature conservationists are increasingly asked to quantify their statements - *how many* otters, red squirrels or lesser horseshoe bats do we have and how many must we conserve? These simple questions identify the immediate problem: we often have little idea how many mammals there are, nor how their numbers change in annual (or longer) cycles.

For all but the rarest and most visible species, it is impossible to count the actual number of animals. Instead, one has to rely on extrapolation from empirical estimates of density for a particular habitat. Accuracy depends, therefore, on good field-derived estimates for that habitat and good estimates of the amount of the habitat. In some cases we have neither of these, and in many cases we have just one. In both these instances, we then turn to the opinions of experts.

For all the reasons outlined above, this report provides an estimate of population size, trends, threats and conservation status for every terrestrial mammal in Britain. Producing this report has been a considerable task - the authors have consulted widely and canvassed the opinions and data (both of which have been given voluntarily) of many mammal experts, all of whom deserve a great deal of thanks for their generous support.

Actually putting a figure on the number of some species that exist in Great Britain will inevitably be a controversial step - the exercise is certainly easier to criticise than it has been to do. We hope that this report will act as a focus for constructive debate on ways of improving the information for each species, and for initiating dedicated surveys of both species and habitats.

I am sure this report will be of great interest to all mammalogists; I hope it will further the conservation of British mammals by promoting discussion on the reliability of the figures, what they mean and how they can be improved.

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Vertebrate Ecology & Conservation Branch
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Executive summary

1. This review covers 64 species and one sub species of terrestrial mammal known, or believed, to breed in Britain. It includes those feral species that have persisted as breeding populations for at least fifteen years, but excludes the cetaceans.

2. For each species there is an assessment of the current status, historical and recent changes in numbers, population trends and population threats. For most species these assessments are based on subjective rather than objective criteria because there are few species for which there are long-term population data.

3. For each species except Nathusius' pipistrelle a pre-breeding population estimate was calculated to provide a base-line against which to measure future changes. Estimates are provided for Great Britain as a whole and separately for England, Scotland and Wales. The results are summarised in Table 14. The minimum aim was to achieve a population estimate with an accuracy to within an order of magnitude, but most are thought to be more accurate. A code is used to identify the level of confidence for each estimate. For nine species the estimate was graded 1 (most reliable), for 11 it was graded 2, for 20 it was graded 3, for 19 it was graded 4, and for five the estimate was graded 5.

4. Several problems were highlighted in the course of making these estimates. First, there are very few species for which an estimate of total population size was available; for most, population size was calculated either by estimating their abundance relative to other species and/or by multiplying the amount of suitable habitat by known population density estimates for those habitats. However, even this approach proved problematical for many species, either because density estimates were not available from Britain, or because these estimates were only available for a limited number of habitat types. Furthermore, most population sizes calculated in this way will tend to be over-estimates, because density estimates so derived are invariably based on a limited number of studies in some of the more suitable habitats for that particular species.

5. The review highlights the paucity of population data for many species of mammal, and density data are few or non-existent even for a number of common and/or widespread species such as the hedgehog, house mouse and common rat. Thus, further field studies are needed to improve our knowledge of the distribution and density of most species; only then will it be possible to refine many of the population estimates.

6. Absolute numbers of mammals are perhaps less important than trends in population size and degree of population fragmentation. The known or believed changes in British mammal populations over the last thirty years are summarised: two species have become extinct; eight are known, or believed, to have undergone substantial increases in range and/or numbers; nine have undergone some increase; for 23, population size was believed to have remained approximately stable; nine have undergone small declines in range and/or numbers; and for 14 there have been substantial declines. The species known, or believed, to be increasing in numbers include several already, or potentially, damaging to agriculture or silviculture, such as the rabbit, red deer, sika deer, roe deer and muntjac

and several species which are of conservation concern and which previously had been reduced to low levels, e.g. otter and polecat.

7. The population estimates for mammals are compared to those for other vertebrates. Few species of mammal are as rare as the species of bird listed on Schedule 1 of the Wildlife and Countryside Act 1981. However, mammals are less mobile, and minimum viable populations are likely to be larger. The commonest species of mammal have population sizes an order of magnitude larger than those of the commonest species of bird; the same relationship applies for the rarest species of mammals and birds.

8. There are a number of population threats faced by British mammals. Of the 65 mammals included in the review, seven are known, or believed, to be threatened by competitors, seven by climate change and/or adverse weather conditions, four by disease, seven by population fragmentation or isolation, 31 by habitat changes, five by inter-breeding, 18 by deliberate killing, 25 by pesticides, pollution or poisoning, four by predation and seven by road deaths.

9. The conservation status and legal protection afforded to all species of mammal in Britain are summarised. See Table 15.

10. The conservation status of each species is discussed from a European perspective. On this basis, most of the species of mammal that are rare in Britain have larger populations in Europe. The insectivores are generally about as common in Britain as in the rest of their European range; other than the Bechstein's and barbastelle bats, which are rare throughout Europe, the British populations of bats contribute only a small proportion of the European population; of the lagomorphs, the brown hare and rabbit populations are important in a European context; of the rodents, the grey squirrel and field vole populations constitute a significant proportion of the total European population; of the carnivores and pinnipeds, the otter, badger, common seal and grey seal populations are important in a European context; of the artiodactyls, the red, sika, fallow, muntjac and Chinese water deer populations constitute a major proportion of the European population, and the Soay sheep and wild goats that are of ancient origin are of particular interest because the populations in Britain are unique and constitute about half the ancient feral caprines in Europe.

11. The monitoring of endangered wild mammal populations is now a statutory responsibility under European Union legislation. This review identifies those species of particular conservation concern from both a British and a European perspective and provides a basis on which to develop a comprehensive monitoring scheme for British mammals.

Contents

Introduction

There are few data on population sizes and/or population trends for most British mammals, although the National Game Bag Census data provide an indication of population trends for some species (Tapper 1992). For many others, however, even such basic data as population densities are absent for more than a few habitats (see review in Corbet & Harris 1991). Detailed surveys have been undertaken for a few species, e.g. badger *Meles meles* (Cresswell, Harris & Jefferies 1990) and wildcat *Felis silvestris* (Easterbee, Hepburn & Jefferies 1991), and for others there are periodic monitoring exercises, e.g. otter *Lutra lutra* (Andrews & Crawford 1986; Green & Green 1987; Strachan *et al*. 1990), or annual counts over much of their range, e.g. red deer *Cervus elaphus*; see Clutton-Brock & Albon (1989) for an analysis of the data collected for red deer. Overall, however, unlike the regular monitoring of bird populations (e.g. Stroud & Glue 1991), there is no comprehensive monitoring scheme for British mammals. Neither has there been any attempt to estimate the population size for most species of British mammal, unlike the British avifauna (Morris 1993a), although the status of some of the rarer species has now been reviewed (Morris 1993b). Thus for many species of mammal substantial population changes could go unrecorded, as has occurred for the water vole *Arvicola terrestris* (Strachan & Jefferies 1993) and may have occurred for the hedgehog *Erinaceus europaeus* (P.A. Morris unpubl.). Whilst there are data on the number of hedgehogs killed by gamekeepers, these are not suitable for monitoring changes in hedgehog populations (Tapper 1992). This comparative lack of information on British mammal populations is largely due to the difficulties of counting mammals. For birds, counts are often based on habitat type (e.g. gardens), and hence include large numbers of species, whereas for mammals, survey or census techniques need to be tailored to suit the ecology of individual species or, more rarely, groups of species.

Despite the hitherto rather fragmented approach, there is now an increasing amount of information available on the status of many British mammals and, for a small number, good population estimates are available. This review attempts to assess the abundance of all British mammals, to show where deficiencies in knowledge exist, to highlight their status and population trends, and to comment on any potential population threats or other factors that may affect future population size. Finally, the importance of the British mammal fauna is assessed in a European context.

Methods

Basis of the calculations: This review covers all 63 species of native and introduced mammal that are known to have bred in Great Britain in the last thirty years and one species that may have bred in Britain; it also includes one sub species for which there are data on population size, but excludes the cetaceans. The review covers an area of 230,367 km^2, and includes off-shore islands but not the Channel Islands and Isle of Man (Table 1). Records for vagrant or migratory species, and those not known, or not believed, to have bred in Britain, are also summarised. However, introduced species that have not persisted as breeding populations for at least 15 years, such as Mongolian gerbil *Meriones unguiculatus*, golden hamster *Mesocricetus auratus*, raccoon *Procyon lotor* and Himalayan porcupine *Hystrix brachyura* (Smallshire & Davey 1989; Baker 1990), have been excluded. The selection of species included in the review was largely based on the third edition of *The handbook of British mammals* (Corbet & Harris 1991). Where historical records are quoted, the county name used is that given in the original report, and these have not been adjusted to take account of any changes in county names.

Data have been collated from published sources or from specialists for each species, with the minimum goal of producing an 'order of magnitude' population estimate. For many species, there are significant inter-seasonal or inter-annual changes in population size and so, for comparisons between species, we have estimated the size of the overwintering or pre-breeding population. For some species, where accurate population estimates were already available, minimum/maximum figures are given or, where appropriate, estimates with 95% confidence limits. Where no published data on population size were available, for some species these have been provided by key workers. For species where no other population estimates were available, population densities and/or home range sizes for different habitat types were extracted from the literature or supplied by workers on that species, and were used to estimate the total population size, based on the distribution of the species and the area of suitable habitats available. As a general rule, only data from mainland Britain were used for these calculations, since information from the rest of Europe, where there are likely to be differences in both habitat and faunal composition, are unlikely to be representative of Britain.

To estimate habitat availability, data on 42 main habitat types in each of the 32 land classes devised by the Institute of Terrestrial Ecology (Bunce, Barr & Whittaker 1981a, 1981b) were used. The distribution of land classes within England, Scotland and Wales is shown in Table 2. When calculating population size of some species, four land class groups, rather than individual land classes, were used. Thus land classes 2, 3, 4, 9, 11, 12,14, 25 and 26 formed the arable land class group, land classes 1, 5, 6, 7, 8, 10, 13, 15, 16 and 27 formed the pastoral land class group, land classes 17, 18, 19, 20, 28 and 31 formed the marginal upland land class group and land classes 21, 22, 23, 24, 29, 30 and 32 formed the upland land class group (Barr *et al.* 1993). The habitat data were collected by surveying 2455 1 x 1 km squares during the period November 1985 to February 1988 as part of a national badger survey; full details of the habitat data recorded are given in Cresswell, Harris & Jefferies (1990). In addition, a further 165 1 x 1 km squares from land classes on the Scottish islands, not included in the original badger survey, were subsequently surveyed for habitat data only, to ensure that the habitat data were not biased due to the exclusion of islands uninhabited by badgers. For the habitat data, all areas over 0·5 ha or linear features over 50 m long were included. For each land class, mean areas of each habitat type were calculated, excluding areas of sea. Details of the area of the main habitat types in the area covered by this review are given in Table 3. For aquatic species such as water voles, mink *Mustela vison* and otters, data on abundance were available for water authority regions, and so figures for the lengths of riparian habitats in each authority region are given in Table 4. Data on the rates of habitat change in Britain are given by Barr *et al*. (1993).

When the calculations included in this review were undertaken, there were no habitat data available for Britain as a whole, although there were some data on the land-use changes in England (Sinclair 1992). Subsequent to the calculations being completed, a report was published on the pattern of land use in Britain in 1990 (Barr *et al*. 1993). This presented land cover data from two different sources: satellite imagery and a very detailed survey of 508 1 x 1 km squares, stratified by land class, with a greater number of squares surveyed within larger land classes. Habitat classifications for these two surveys differed slightly from those used here, and so direct comparisons are difficult. However, the broad results are very similar. For example, in this survey it was estimated that there were 528,000 km of hedgerow, compared to 549,000 km estimated by Barr *et al*. (1993). Thus the habitat data used here provide a reliable basis for estimating the size of the mammal populations in Britain.

Problems with producing the population estimates: There are very few, if any, species for which the population estimates presented here could not be improved. Counting mammals is notoriously difficult, and even for well-monitored species there are uncertainties inherent in the estimates. For example, for the seals, there will be uncertainties about what proportion of the population is hauled-out when the counts are undertaken. Some of the weakest population estimates are those based on population density figures and the area of suitable habitat available. The problem with such an approach is that inevitably there are few density estimates, and those are for a limited range of habitat types, even for the commonest species. Since most workers base their study of a particular species in an area where that species is common and hence easiest to catch, it is difficult to know how typical such density estimates are for the rest of that species' range. For this reason, population estimates using this approach were generally based on density estimates slightly below those reported in autecological studies.

Of particular difficulty in this respect are all the small mammals, the bats and the deer. Hence for the small mammals and the bats, the relative proportions of the different species in a variety of samples were used as a cross-check to determine if at least the relative size of the population estimates were correct, and that the rank order of abundance for the species was appropriate. Thus for small mammals, data were collated from a variety of pellet analyses (Table 5), bottle studies (Table 6) and trapping studies (Table 7); the relative proportions from these studies are summarised in Table 8. These tables are not comprehensive in that they deliberately do not include all the data that were available, since these were strongly biased to southern England, and there were few samples from Scotland or Wales. Thus the samples included in these tables were designed to provide as wide a coverage as was possible, both geographically and by habitat, without excessively biasing the data to a few habitats in southern England. For species such as the water shrew *Neomys fodiens*, for which few, if any, density estimates were available, population size could only be calculated by comparing abundance relative to a common species in a variety of samples from different habitats; in the case of the water shrew, abundance relative to common shrew *Sorex araneus* and pygmy shrew *Sorex minutus* was used. For the bats, few density estimates were available. For greater horseshoe bat *Rhinolophus ferrumequinum* and lesser horseshoe bat *Rhinolophus hipposideros*, total population size was reasonably well known, but for most others there were few data on which to base a population estimate. Thus relative abundance was the only approach available for calculating population size for most bats, and the estimates had to be based on the subjective assessment of relative abundance by experienced bat workers.

For the deer, with the exception of red and to some extent sika *Cervus nippon*, there were few density estimates because counting deer, even in a small area, is notoriously difficult. Most deer census figures tend to be an under-estimate (Springthorpe & Myhill 1985), and using these to calculate total population size is therefore inherently unreliable. The problem is compounded for those species where the latest distribution maps (Arnold 1993) were used to provide an estimate of the occupied range, since these maps provided at best only the minimum distribution for a species. For instance, a survey into the distribution of muntjac *Muntiacus reevesi* increased the number of 10 x 10 km square records from 417 (Arnold 1993) to 745 (Chapman, Harris & Stanford 1994), an increase of 79%. Whilst muntjac may be an extreme example, in that they were still expanding their range, even species with established ranges were likely to have been under-recorded, and probably by a significant amount.

For each species, a separate population estimate was also calculated for each of England, Scotland and Wales. Where there were regional counts, e.g. for the seals and some of the deer, the three estimates were based on these counts. Where the estimate was based on the area of suitable habitat and known population densities, the figures were based on the availability of suitable habitats in each country. For total population estimates based on abundance relative to other species, e.g. many of the bats, the estimates for each country were based on the proportion of the 10 x 10 km square records in each of the three countries (Arnold 1993), excluding the Channel Islands and the Isle of Man. There are problems with each approach. For instance, the quality of counts from different regions often varied. When using density estimates, it had to be assumed that the same population density occurred in similar habitats throughout the range. Using the proportion of 10 x 10 km square records in different parts of a species' range of necessity placed equal weight on squares with one record and those with many. Thus these regional figures are intended only to give an indication of the relative status of a species in different regions of the British Isles.

Since there are limitations in the data used to produce any of the estimates in this review, they must be viewed as the first stage in a process of estimating the population size for British mammals, and in monitoring population changes and trends. With better data on the distribution and ecology of each species, the estimates for most, if not all, species will be improved.

Reliability of the population estimates: Since there were limitations in the data used to produce the population estimates, a reliability score is provided to give some indication of the level of accuracy that is thought to have been achieved. The scores are as follows:-

1. A widely distributed species for which there had been a recent census or for which there were regular counts that were believed to have a high degree of accuracy, or a rare species for which most of the populations were thought to be known and regularly monitored. For these species it was believed that any improvements in census techniques were unlikely to alter the population estimate by more than 10% either way.
2. A widely distributed species for which the population estimate was based on good data on population densities in different habitat types, or a rare or local species for which the estimate was based on a good understanding of the factors that were limiting its distribution or numbers, and good information on population densities in a reasonable range of habitat types. For these species, there was scope for improving the population estimate, but any improvements were unlikely to be substantial, and any resulting change in the population estimate would probably be less than 25%.
3. A widely distributed species for which the population estimate was based on a

limited amount of data on population densities in different habitat types, or for which the population estimate was obtained by scaling abundance relative to a species for which there was a reasonable population estimate. For rare species, the estimate was based on only a limited knowledge of the factors limiting its distribution or numbers, or on only a few density estimates from a limited range of habitats. Any improvement in the population estimate could result in a change of up to 50%, but on current knowledge it was considered unlikely that the estimate would be wrong by a greater margin.

4. An estimate based on a very limited amount of information on the species, for which there was a need for much more information on either its distribution in Britain, or population densities in a variety of habitat types, or relative abundance. Any improvement in knowledge would greatly improve the basis on which the estimate was achieved, but may not necessarily have made a substantial difference to the estimate presented here, since all species have been ranked in order of relative abundance and its position in the rankings was thought to be correct.
5. A species for which there was so little information on its distribution and/or abundance in different habitat types, and for which the data were so inadequate or biased, that it was not possible to scale its abundance relative to other species reliably. For these species the estimate was believed on subjective criteria to be within the right order of magnitude, but no greater degree of accuracy was thought to have been achieved.

Of the 65 species and sub species covered in the review, for one there was no population estimate, for nine the estimate was graded 1, for 11 it was graded 2, for 20 it was graded 3, for 19 it was graded 4, and for five it was graded 5.

Population trends and factors likely to affect population size: Population size *per se* is not the only, nor necessarily the major, factor to consider when assessing the status of British mammals, and population trends and factors likely to affect future population size are at least as important. Thus absolute numbers are often considered to be less important than the degree of habitat, and hence population, fragmentation (see review by Bright 1993). So for each species the available information on population trends, and significant factors that might affect future population size either locally or nationally, are reviewed. For the latter, only factors likely to have an impact on population size, rather than normal mortality factors, were considered. Since there are so few data on population size or trends for many species, any assessment of the factors likely to have an impact on population size are, of necessity, based on subjective, rather than objective, criteria. Hence the sections on population threats for each species must be viewed as a preliminary assessment of perceived, rather than known, risk. Methods of assessing change in population size, and the value of conservation measures to improve the status of threatened species of mammal, are discussed by Jefferies & Mitchell-Jones (1993).

Species accounts

Order: Marsupialia

Red-necked wallaby *Macropus rufogriseus*

Status: Introduced; two recent populations in England were founded in 1940 and a third in about 1985, and one in Scotland in 1975.

Distribution: Colonies are still present in the Peak District and on the island of Inchconachan, Loch Lomond, Scotland; the colony in Ashdown Forest, Sussex, and that near Teignmouth, Devon, are now extinct. In addition there are occasional escapes from wildlife collections.

Population data: The last record from the Sussex colony was in 1972 and this population is assumed to be extinct. The Teignmouth population originated from an unknown number of animals that escaped, probably early in 1985; an animal killed on the road in 1994 was believed to be the last survivor (C.J. Wilson pers. comm.). Survey techniques for the Peak District population are detailed in Yalden (1988). The population was divided into two, and each sub-population counted on a separate day. The total population size is based on 'best counts'. Intensive field work in 1978 showed that, with enough visits, 'best counts' seemed to provide a total population estimate, and no other individuals were known to occur away from the two sub-populations. In January 1993 the Peak District colony stood at only three animals (D.W. Yalden unpubl.). The size of the Loch Lomond population in 1992 was 26 (Weir, McLeod & Adams 1995).

Population estimates: The total free-living population of wallabies in 1993 was 29 individuals: 3 in England, 28 in Scotland and none in Wales. In addition, there is a free-ranging colony of 400-600 animals at Whipsnade Park, Bedfordshire. **Reliability of population estimate:** 1.

Historical changes: A number of other populations have existed in the past. In the 1850s several escaped into woods near Cromer, Norfolk; there were rumours of feral wallabies in the Pennines early this century; and several were released near Rothesay on the Isle of Bute about 1912, one of which was self-supporting for about three years. In the 1920s a number were released on Lundy; they were later accidentally drowned (Lever 1977). The present colony in the Peak District originated from five animals that were released from a collection at Leek, Staffordshire in 1939 or 1940; the early history of this population is described by Lever (1977). The Sussex colony originated from a captive colony at Lower Beeding, near Horsham, and by 1940 there was a small but apparently fully naturalized and breeding colony in the Ashdown Forest and St Leonard's Forest district (Lever 1977). The population at Loch Lomond started with two pairs from Whipsnade that were introduced in 1975 (Weir, McLeod & Adams 1995).

Population trends: Although four free-living populations have become established in recent times, one is certainly extinct, one is probably extinct, one no longer appears viable, and there is no evidence that the Scottish population is spreading. Overall, the number of feral wallabies in Britain appears to be declining. Most data on population trends are for the Peak District population, which increased from five in 1940 to around 50 in 1962. Thereafter numbers declined, ranging between 10 and 20 during 1970-1985, followed by a further recent decline (Yalden 1988).

Population threats: Harsh winters reduce numbers and they suffer heavy mortality in severe snow falls. Traffic and other accidents are also a significant cause of death in the Peak District, and many of these may result from animals fleeing following disturbance by dogs or people (Yalden 1991). In the Peak District, disturbance appeared to be a significant factor limiting their distribution (Yalden 1990).

Order: Insectivora

Hedgehog *Erinaceus europaeus*

Status: Native; locally common.

Distribution: Found throughout mainland Britain up to the treeline, but scarce or absent from very wet habitats, areas of large arable fields and conifer plantations. Although there are occasional records of animals foraging at higher altitudes (Arnold 1993), they are probably absent from many upland areas, especially in Scotland. They are also found on many islands, often as a result of introductions; for details see Morris (1991). Recent (1970s and 1980s) introductions include North Ronaldsay (Orkney) and St Mary's (Isles of Scilly).

Population data: Hedgehogs are most abundant where there is close proximity of grassland to woodland, scrub or hedgerow, and they are present in virtually all lowland habitats where there is sufficient cover for nesting. They are common in suburban areas, but generally scarce in coniferous woods and marshy and moorland areas (Morris 1991). Hedgehogs appear to be patchily distributed, and the National Game Bag Census suggests that hedgehogs are more regionally aggregated than species such as the stoat *Mustela erminea* and the weasel *Mustela nivalis* (Tapper 1992), a finding also supported by the distribution of road-deaths (P.A. Morris unpubl.). Road-kill data collected during July-September for 1989-1992 inclusive showed large regional differences, with a rank order of decreasing abundance of: north-east England, north-west England, East Anglia, Wales, east midlands, south England, Scotland, south-west England, west midlands and south-east England. There was a four-fold difference in the number of dead hedgehogs recorded per 100 km of road between north-east and south-east England (P.A. Morris unpubl.). Doncaster (1992) suggested that predation by badgers may account for this patchy distribution; he showed that high densities of badgers in one area in Oxfordshire appeared to enhance dispersal and mortality of introduced hedgehogs. The regional differences in hedgehog numbers indicated by the road-kill survey seem to support the suggestion that hedgehogs are most common where badgers are rarer (cf. Cresswell *et al.* 1989).

Approximately 1 per ha were recorded on a golf course with a particularly high density of hedgehogs (Reeve 1982). In north-east London a minimum density for the urban area, based on public sightings and road mortality figures, was 0·0735 per ha (Plant 1979). In a woodland in the Yorkshire Dales, Morris, Munn & Craig-Wood (1993) recorded 1 per 1·5 ha. In an ancient field system with a mosaic of hedgerows, small copses and unimproved grassland, the density was 1 per 4·5 ha (Morris 1988). Studies elsewhere have suggested that this density is probably typical for mixed farmland in southern England (P.A. Morris unpubl.), although numbers are likely to be lower in areas with large fields, where there may be a shortage of nesting sites (Reeve 1994).

The few data on hedgehog population densities were collected during the summer, and so are greater than would be expected for the pre-breeding population at the end of hibernation. Thus the following densities were used to estimate population size: 1 per 2·5 ha for semi-natural broadleaved, mixed and recently felled woodlands, parkland, scrub, lowland unimproved grasslands and amenity grasslands; 1 per 10 ha for built-up areas; and 1 per 20 ha for broadleaved, coniferous and mixed plantations, semi-natural mixed woodlands, bracken, semi-improved and improved grasslands and arable areas.

Population estimates: A total pre-breeding population of about 1,555,000; 1,100,000 in England, 310,000 in Scotland and 145,000 in Wales. This clearly is an approximate figure, because there were few data available on hedgehog densities in different habitat types. **Reliability of population estimate:** 4.

Historical changes: At the turn of the century hedgehogs were described as plentiful throughout the greater part of Great Britain, in spite of constant persecution by farmers and gamekeepers, though scarce in the northern highlands of Scotland (Millais 1904-1906; Thorburn 1920). They were said to have been introduced to western Ross-shire in 1890 in baled hay and were also introduced to the eastern parts of Sutherland and Caithness (Millais 1904-1906). Hence it would appear that hedgehogs were extending their range in Scotland in the second half of the 19th century (Millais 1904-1906).

Burton (1969) suggested an average density in the early 1950s of 1 per acre, i.e. 1 per 0·405 ha, throughout the country, although he admitted this was derived largely from guess work. Excluding the marginal upland and upland land classes, this would still give a population of around 36,500,000 hedgehogs for the arable and pastoral land classes, or more than twenty times the present population estimate. Based on his subjective impressions of hedgehog numbers in a rural area of Surrey, Burton (1969) suggested that 1947 was a year of particular abundance, and that hedgehog numbers had fallen in the 1960s when compared with the 1950s. However, he also suggested that there had been little change in the numbers living in the vicinity of small towns and in the suburbs of larger towns.

Population trends: The National Game Bag Census data suggest a steady reduction in the numbers killed, possibly dating from before the 1960s. Whether this denotes a population decline due to an increasing loss of suitable habitats, or a change in gamekeeping practice, is unclear (Tapper 1992). In an attempt to get a subjective assessment of whether hedgehog numbers were changing, P.A. Morris & S. Wroot (unpubl.) sent a questionnaire survey to the National Federation of Women's Institutes in 1990; over 1200 members participated. Of these, 36% thought that hedgehog road kills were less common than 10 years previously, compared with 25% who thought they were more common; the rest either did not know or thought they were about the same. However, in the south-west, significantly more people thought that hedgehogs had become less common, and in the south-east more respondents thought there were fewer hedgehogs in 1989 than in previous years. The south-west and south-east were two of the areas the road-kill survey (see above) identified as currently having the lowest hedgehog densities. Whilst it is difficult to draw firm conclusions from opinion surveys, it is clear that only a minority of people felt that hedgehogs were becoming more numerous, and it is probable that in the 1980s the hedgehog population was either static or declining.

Estimating population trends is further complicated because in some years hedgehogs may be particularly abundant. It has been suggested that this may occur when conditions are suitable for a significant proportion of the population to rear second litters successfully (Jefferies & Pendlebury 1968). However, this is unlikely to be the case because few second litters attain sufficient body weight to survive the winter (Morris 1984). A study in southern Sweden showed that annual mortality varied greatly between seasons, and that population size was influenced predominantly by environmental factors such as food availability, the availability of suitable winter nest sites and winter climate (Kristiansson 1990); thus adult population size in an area of 50 ha varied by a factor of 2·7.

The rate of growth for island populations is largely unknown. Two hedgehogs were introduced to North Ronaldsay in 1972; the population is now thought to be about 500, but may be as low as 100 (H. Warwick pers. comm.). An unknown number of hedgehogs was introduced to the Isles of Scilly before the mid-1980s; the current population size is also unknown.

Population threats: These have been discussed in general terms by Burton (1969). The effects of predation by badgers (see above) are unclear, but if this does lead to population declines, then any increase in badger numbers is likely to have an impact on hedgehog populations. Mortality on roads may also be a significant population threat. A survey during July-September suggested an average count of 2·26 killed per 100 km of roads in 1990, 1·88 per 100 km in 1991 and 2·14 per 100 km in 1992 (P.A. Morris unpubl.). It is not clear how these figures should be used to estimate the total killed on the whole road network. The 1990 survey suggested at least 20,000 hedgehogs are killed annually, but figures up to 100,000 have been quoted (Stocker 1987). A similar figure (102,400) is obtained by extrapolating the results of a five-year survey in Surrey (R. Ramage pers. comm.), where 49 km of road were travelled daily and all road kills recorded. The survey included a wide variety of habitats, but was confined to major roads. The figure of around 100,000 is obtained by extrapolating the data to all principal, trunk, motorway, minor and unclassified roads in Britain. Whilst this ignores lower hedgehog densities in parts of Britain, this is offset by the fact that the Surrey results were very much minimum figures. Only animals seen whilst driving were recorded, and so some casualties would have been missed, as would all animals that had managed to crawl off the carriageway. Also, the survey in Surrey was undertaken in a part of Britain having the lowest recorded density of hedgehog road deaths (see above). Whether losses on the roads constitute a significant threat to long-term survival is unclear; Reichholf (1983) has suggested that in Germany road mortality can lead to the extinction of isolated populations. In Sweden, however, Kristiansson (1990) found that while sub-adult and adult hedgehog mortality averaged 47% per annum over seven years, the majority (average 33%) was winter mortality; winter temperatures much lower than normal were associated with higher mortality. In contrast, road deaths were less important.

Rural habitat changes probably constitute a more significant threat to hedgehog populations, particularly the change from permanent grassland and rough grazing to arable land, which is less suitable for hedgehogs because of its lower earthworm population. In addition, the removal of hedgerows and concomitant increase in field sizes limits the availability of nesting sites, further reducing the suitability of arable land for hedgehogs; a shortage of suitable nesting sites generally may be a factor limiting hedgehog numbers. Such landscape changes may account for the decline in hedgehog numbers in the returns for the National Game Bag Census (Tapper 1992). Pesticide residues from agrichemicals and garden pesticides, especially molluscicides, potentially have an impact through the food chain, but no data are currently available on the pesticide levels present in hedgehogs, with still less available on their effects on the hedgehog population overall.

Finally, climatic changes could have a significant impact on hedgehog numbers. Hedgehogs have to reach a minimum weight of 450 g in order to survive a normal period of hibernation (Morris 1984). Hot dry summers reduce the availability of earthworms and other invertebrates, and this may have a significant impact on hedgehog numbers and/or the survival of young.

Mole *Talpa europaea*

Status: Native; common.

Distribution: Moles are found throughout mainland Britain wherever the soil is sufficiently deep for them to burrow. There are occasional records as high as 930 m in Scotland (Arnold 1993) and 1000 m in Wales (Milner & Ball 1970). Moles are absent from most islands except Anglesey, the Isle of Wight and a few of the Inner Hebrides.

Population data: Moles are present in most habitats. Originally they were inhabitants of deciduous woodland, but they have spread into agricultural habitats and thrive in pastures. In arable land colonisation from field boundaries occurs after ploughing. They are uncommon in coniferous forests, on moorland and in sand dune systems (Stone & Gorman 1991). There are very few density estimates available. In English pastures 8-16 per ha have been recorded in the summer (Larkin 1948), but in north-east Scotland densities in woodland and pasture remained similar throughout the year at 4-5 per ha (Stone 1986). Typical pre-breeding densities would be 1·3 per ha in poor habitats and 4·0 per ha in good habitats (M.L. Gorman pers. comm.). Thus population size was estimated by assuming a density of 1·3 per ha in coniferous plantations and woodlands, lowland heaths, arable habitats and lowland improved grasslands, and 4·0 per ha in all types of woodlands except coniferous plantations, parkland, scrub, bracken and lowland unimproved and semi-improved grasslands. Moles were assumed to be absent from all the other types of habitats, although they will occur in low densities in some of these, e.g. gardens on the edge of built-up areas.

Population estimates: A total pre-breeding population of about 31,000,000; 19,750,000 in England, 8,000,000 in Scotland and 3,250,000 in Wales. These are approximate figures, since there are very few density estimates for Britain, and these are limited to a small range of habitats. **Reliability of population estimate:** 3.

Historical changes: In eastern and northern Scotland the mole was common in the late 1800s, whereas it had been rare previous to 1860 (Millais 1904-1906). There are no other data on historical population changes.

Population trends: Unknown; the reduction in persecution may have led to an increase in numbers, whereas agricultural changes and high-intensity arable land-use may have led to population decreases. Deep ploughing is likely to be especially detrimental to mole populations.

Population threats: The current level of persecution by man is much less than in the past, and there are no known population threats. Agricultural operations such as ploughing and re-seeding significantly reduce earthworm populations (Edwards & Lofty 1972), and the removal of hedgerows and areas of rough land eliminates the sanctuary areas from which moles could recolonise an area following cultivation. The impact of agricultural chemicals, particularly insecticides, on mole numbers is unknown.

Common shrew *Sorex araneus*

Status: Native; common.

Distribution: Found throughout mainland Britain at all altitudes, and on many islands except the Isles of Scilly, Orkney, Outer Hebrides, Shetland and some of the Inner Hebrides.

Population data: Common shrews are found almost everywhere where there is some low vegetation cover. They are most abundant in thick grass, bushy scrub, hedgerows and deciduous woodland. Occasionally they are found amongst heather and stable scree (Churchfield 1991a). Densities are very variable, but reach a summer peak of 42-69 per ha in deciduous woodland and grassland, and 7-21 per ha in dune scrub and scrub-grassland. In winter, densities in deciduous woodland and grassland are much lower (5-27 per ha) (Churchfield 1991a). Typical densities would be 6 per ha for grassland at Wytham, Oxfordshire (Pernetta 1977), 1·7-6·9 per ha (April and November) in Wytham Woods, Oxfordshire (Buckner 1969), 26 per ha in woodland near Exeter, Devon (Shillito 1960, 1963a), 4·9-13·5 per ha (July and November) in a larch plantation in south Wales (B.A.C. Don unpubl.), a mean density of 60 per ha over 16 months in grassland in Berkshire (Churchfield & Brown 1987) and 42 per ha in coarse herbage at Woodchester, Gloucestershire in July (Yalden 1974). Densities in arable areas are generally low, and in such habitats common shrews are largely confined to hedgerows (Tew 1994).

Since there are only a few density estimates for pre-breeding population densities, the population size was calculated using the following figures: a density of 10 per ha in low scrub, bracken, lowland unimproved grassland and sloping cliffs, 2·5 per ha in semi-natural broadleaved and semi-natural mixed woodlands, broadleaved and young plantations, parkland, tall scrub, lowland heaths, semi-improved and improved grasslands and arable land, 1 per ha in semi-natural coniferous woodlands, coniferous and mixed plantations, sand dunes, heather moorlands and upland unimproved grasslands, and 0·5 per ha for blanket and raised bogs, and in built-up areas.

Population estimates: A total pre-breeding population of about 41,700,000; 26,000,000 in England, 11,500,000 in Scotland and 4,200,000 in Wales. Comparing this with the estimated population size for the wood mouse *Apodemus sylvaticus* gives a ratio of 1·1 common shrews per wood mouse, which is in complete concordance with the overall ratio of common shrews to wood mice from a large variety of samples - see Tables 5-7, and the summary in Table 8. **Reliability of population estimate:** 3.

Historical changes: Unknown.

Population trends: Unknown; the loss of ancient grassland and meadows, plus the continuing widespread use of insecticides (MacGillivray 1994), have probably led to a population decrease, but numbers may have been locally increased by long-term set-aside (Brockless & Tapper 1993).

Population threats: The continued loss of prime habitats (see above) and use of agricultural insecticides may cause continued declines. Also, one study found that liming upland catchment areas to improve water quality reduced surface activity by common shrews for two to three months but, in contrast to pygmy shrews *Sorex minutus*, had no effect on common shrew numbers (Shore & Mackenzie 1993).

Pygmy shrew *Sorex minutus*

Status: Native; common.

Distribution: Found throughout mainland Britain at all altitudes. Pygmy shrews are absent from the Isles of Scilly and Shetland, but otherwise are widespread on small and large islands (Churchfield 1991b). Their presence on remoter islands (e.g. Barra, Lewis and Orkney) is almost certainly due to introductions. This is the only shrew present on Orkney and the Outer Hebrides.

Population data: Pygmy shrews are found in all types of terrestrial habitat, especially where there is plenty of ground cover; they show a preference for grassland over woodland. A maximum density of 12 per ha in summer but 5 per ha in winter was recorded in grassland in southern England (Pernetta 1977), and a mean density of 14 per ha over 16 months in grassland in Berkshire (Churchfield & Brown 1987). In lowland habitats they are generally less abundant than common shrews (Churchfield 1991b), e.g. one pygmy shrew per 4·3 common shrews in grassland in Berkshire (Churchfield & Brown 1987), but in moorland areas pygmy shrews outnumber common shrews, e.g. near Glossop, Derbyshire a ratio of 8·7 pygmy shrews per common shrew was found in pitfall traps (Yalden 1981). In the Peak District, pygmy shrews outnumbered common shrews by 2:1 on blanket bog, and were more numerous than common shrews above around 450 m (Yalden 1993). Based on 42 sites sampled over two years, the ratio of pygmy to common shrews in different moorland habitats were as follows: *Calluna* 8·2:1, *Calluna/Eriophorum* 7·1:1, *Eriophorum vaginatum* 19·0:1, *Juncus squarrosus* 6·7:1 and grasses 1·3:1 (Butterfield, Coulson & Wanless 1981).

Since there are so few data on densities but a lot more information is available on relative abundance, population size was estimated using the relative abundance of common:pygmy shrews in samples from a wide variety of sources and habitat types (Tables 5-8). From these a mean ratio was obtained of 5·4 common shrews per pygmy shrew in England, 5·0:1 for Scotland, and 2·8:1 for Wales. These data suggest that pygmy shrews are more common in Wales, yet in upland areas of Scotland pygmy shrews do not appear to be as common, relative to common shrews, as they are in upland areas of England. These ratios were used to calculate the size of the pygmy shrew population in each of the three countries.

Population estimates: A total pre-breeding population of about 8,600,000; 4,800,000 in England, 2,300,000 in Scotland and 1,500,000 in Wales. To improve this estimate, more information is needed on the population densities of pygmy shrews in a range of habitats. **Reliability of population estimate:** 4.

Historical changes: Unknown. At the turn of the century, pygmy shrews were thought to be generally, but sparsely, distributed (Millais 1904-1906). At that time, the distribution of pygmy shrews in Scotland was unclear, and there are no quantified data on which to assess any population changes.

Population trends: Unknown. The increasing use of insecticides and the loss of habitat have probably led to a population decrease, but numbers may have been increased locally by long-term set-aside (Brockless & Tapper 1993).

Population threats: Liming of watersheds is used to mitigate the effects of acidification on water quality, but one study found that this practice reduced the surface activity of pygmy shrews for up to 18 months, and this was associated with reduced food availability (Shore & Mackenzie 1993). Furthermore, liming also reduced the populations of pygmy shrews by 30-55%. This effect lasted from five months to over three years at different sites. Hence liming of upland catchment areas can have detrimental effects on pygmy shrew populations. Heavy grazing of moorlands by increased upland sheep and deer populations potentially also have removed much of the thick vegetation which pygmy shrews require. Conversely, Environmentally Sensitive Area schemes and better grouse moor management should favour this species.

Water shrew *Neomys fodiens*

Status: Native; locally common.

Distribution: Widespread in mainland Britain but thought to be locally distributed in parts of northern Scotland. Present on Anglesey, the Isle of Arran, Bute, the Garvellachs, Islay, the Isle of Wight, Kerrera, Mull, Pabay (Skye), Raasay, Skye, South Shuna and possibly other islands (Churchfield 1991c). There are three records from Hoy (Orkney) from 1847-1964, but whether there are still water shrews on the island is unknown (Green & Green 1993).

Population data: Few water shrew density estimates are available. Peak numbers occur in the summer, and a maximum of 3·2 per ha was recorded in water-cress beds in southern England (Churchfield 1984). Whilst this may have been an under-estimate, water shrews were present at lower densities than common shrews even in this apparently optimal habitat. Other than this figure, there are no density estimates, and calculating numbers based on habitat availability is fraught with difficulties because there are no data on habitat preferences of water shrews. Whilst they are often associated with clear, fast-flowing, unpolluted rivers and streams, they are also found by ponds and drainage ditches, in north-west Scotland they occur amongst boulders on rocky beaches, and they are often found considerable distances from water in deciduous woodland (Shillito 1963b; Churchfield 1991c). However, Shillito (1963b) suggested that populations in woodland are transient and only present in the summer when there is an adequate food supply. Similarly, Tew (1994) recorded water shrews in hedgerows in arable areas, but noted that they were only transient, and suggested that linear features in farmland were important corridors for movement between preferred habitats. Even in apparently suitable habitats such as water-cress beds, Churchfield (1984) found that water shrews were intermittently nomadic, with frequent shifts of home range.

Since there is so little information on the population ecology of water shrews, population size was estimated using the relative abundance of common:water shrews in samples from a wide variety of sources and habitat types (Tables 5-8). From these a mean ratio was obtained of 22·1:1 for England, 31·7:1 for Scotland and 15·3:1 for Wales. These data suggest that water shrews are relatively more abundant in Wales, and relatively less common in Scotland.

Population estimates: A total pre-breeding population of about 1,900,000; 1,200,000 in England, 400,000 in Scotland and 300,000 in Wales. This estimate tends to agree with the relative paucity of records despite its very wide distribution - only 1228 records from 654 10 x 10 km squares (Arnold 1993). Information on water shrew population densities and behaviour in different habitat types is needed, both to improve this estimate and to understand how the species maintains such a wide distribution with a low population size. Even in an apparently favourable habitat, water shrews appear to be unable to compete with common shrews, and this may explain why populations seem to be more mobile than those of common shrews (Churchfield 1984). It may also explain why the species exists at low population densities. **Reliability of population estimate:** 4.

Historical changes: Unknown. At the turn of the century it was described as 'not by any means a rare animal, but would appear to be of local distribution' (Barrett-Hamilton & Hinton 1910-1921), and 'fairly common in England and Wales, as well as in Scotland' (Millais 1904-1906). Whether the current paucity of records indicates a population change is unknown.

Population trends: Unknown; there are no data on which to assess population changes. Water shrews may be declining, but since they are patchily distributed and populations are sometimes ephemeral, the problems of monitoring population changes are considerable.

Population threats: Although there is no firm evidence, it has been suggested that water shrews may be threatened in Britain by habitat destruction, particularly in southern England, and by disturbance and modification of waterside banks and vegetation (Churchfield 1991c). Water quality may also be a significant factor affecting water shrew populations, although the precise effect of water quality on water shrew populations is unknown (Churchfield 1991c). A survey of the quality of rivers, canals and estuaries in England and Wales in 1990 found that 89% of rivers, 90% of canals and 90% of estuaries were of either 'good' or 'fair' quality, as defined by the National Water Council, and 2%, 1% and 3% respectively were of 'bad' quality. These figures suggest that overall water quality in Britain is declining. Compared to a similar survey in 1985, about 15% of the total river length was downgraded, about 11% upgraded. Comparable changes for canals were 15% and 7%, and for estuaries 3% and 1% (National Rivers Authority 1991).

Lesser white-toothed shrew *Crocidura suaveolens*

Status: Introduced to the Isles of Scilly, probably in the Iron Age or earlier.

Distribution: Found on all but some of the smaller of the Isles of Scilly, with records from Bryher, Gugh, St. Agnes, St. Mary's, St. Martin's, Samson, Tean and Tresco. Lesser white-toothed shrews are also thought to occur on Annet (Spencer-Booth 1956).

Population data: They are commonly found in tall vegetation such as bracken, hedgebanks and woodlands, but are also found amongst boulders and vegetation on the shores. The peak density recorded is 1 per 30 m^2 (Pernetta 1973), but a more realistic average density is likely to be around 1 per 100 m^2. Spencer-Booth (1956, 1963) suggested that densities are higher at the top of the beaches than inland.

To estimate population size, a map of scale 1:10,560 was used to calculate the areas of suitable habitat on the main islands colonised by lesser white-toothed shrews. There were approximately 70 km of shoreline, 100 km of hedgerows and 500 ha of natural heathland-type vegetation. Densities of 1 per 10 m of shoreline, 1 per 50 m of hedgerow and 10 per ha of natural vegetation were used to estimate population size.

Population estimates: A total pre-breeding population of about 14,000, all in England. A great deal more information is needed on the habitat selection and population density of this species in different habitats to improve the population estimate. **Reliability of population estimate:** 4.

Historical changes: Unknown.

Population trends: Unknown.

Population threats: The species appears to be well-established, and there are no known population threats.

Order: Chiroptera

Because the population threats, population trends and methods of estimating population size were similar for many of the species of bat, a general section is included, and specific comments only made as they apply to individual species. In particular, producing population estimates for bats was especially difficult since there were few density estimates and little quantified data on bat numbers in relation to habitat associations and patterns of land use. Thus many of the population estimates were based on subjective estimates of relative abundance. Whilst such estimates may not be supported by quantitative data, those included here were based on the considerable amounts of field experience of the workers consulted, and since these workers were in general agreement as to the size of the estimate, the figures are the best available. However, there is clearly scope to improve the quality of the data available on bat population sizes and population trends in Britain.

Population data: For greater and lesser horseshoe bats, population sizes are reasonably well documented from regular roost and/or hibernacula counts, but for most species of bat there are few data on population sizes. Therefore the population of pipistrelles *Pipistrellus pipistrellus* was estimated by Speakman (1991) by multiplying independent estimates of population densities of these bats in three areas (two in Scotland, one in Yorkshire) by their known current range. For those species for which there were no direct density or population estimates, Speakman (1991) calculated population sizes from the frequency of reports of roosts of those species relative to those for pipistrelles, using returns made to the Nature Conservancy Council. Details of the roost records he used are given in Mitchell-Jones *et al.* (1986). The figures were adjusted to take into account mean roost size relative to that for pipistrelles. Since most of the roost records he used refer to nursery roosts in houses, the same technique could not be used for Daubenton's bat *Myotis daubentonii* and the noctule *Nyctalus noctula*, which rarely use houses for their nursery roosts. Their populations were estimated from general reports of abundance relative to other species in surveys undertaken by local bat groups, and so their population estimates were likely to be the least accurate (Speakman 1991).

There are several problems with this approach. In particular, densities calculated for north-east Scotland by Speakman *et al.* (1991a) were minimum estimates, and the number of new bat roosts being found on their study area showed no signs of reaching an asymptote. What proportion of roosts had been found is unknown, and so how much influence this had on Speakman's (1991) estimate for the size of the pipistrelle population, and hence every species of bat scaled in abundance relative to pipistrelles, is unknown. Also, Speakman (1991) based his calculations on the mean size of pipistrelle roosts in north-east Scotland in the early summer, i.e. 117 (Speakman *et al.* 1991a), yet in recent years Scottish roosts have tended to be larger than those in England, and mean roost size for Britain as a whole, excluding records of only one or two bats, is $75{\cdot}00 \pm 1{\cdot}82$ (s.e.) (n = 2679) (A.J. Mitchell-Jones pers. comm.). This will have biased those of Speakman's (1991) estimates which included a measure of roost size relative to pipistrelles. There are other confounding effects, since colonies for some species (e.g. pipistrelle) are relatively mobile, whereas those for others, e.g. serotine *Eptesicus serotinus* are not, and for species such as the pipistrelle a number of roost reports may refer to one colony. Finally, Speakman's calculations were based on the area of the British Isles (308,700 km^2, i.e. including all of Ireland), whereas this review only covers Great Britain excluding the Channel Islands and the Isle of Man, a land area of 230,367 km^2; thus for this review his figures have been adjusted accordingly for species that occur in Ireland. The population estimates obtained were for adult bats only at the start of the breeding season.

Independent estimates were also provided by A.M. Hutson, A.J. Mitchell-Jones and R.E. Stebbings, who all based their estimates on the calculations made by Speakman (1991) and the known distribution and relative abundance of each species of bat. Whilst this is a subjective approach, population size for some species (e.g. greater and lesser horseshoe bats) is reasonably well documented, and so there is a known basis from which to calculate relative population sizes. Thus, to determine whether the estimates for each species of bat were accurate at least to the right order of abundance, the relative proportions of each species in a variety of samples were compared (Table 9). Obviously each sample is biased. Those species that habitually roost in houses (Table 10) predominated in the enquiries made to the Nature Conservancy Council (and subsequently the country agencies). Yet even within house-roosting species there are biases. For example, inspections of lofts revealed a higher proportion of brown long-eared bats *Plecotus auritus* relative to pipistrelles than did records of bats seen emerging from lofts. This is because pipistrelles leave their roost earlier than long-eared bats, and tend to occur in larger colonies (A.J. Mitchell-Jones pers. comm.). In contrast, Daubenton's bat was over-represented in records submitted to the Biological Records Centre because it is frequently recorded whilst seen hunting over water and at hibernation sites. Whilst the pipistrelle is the commonest bat, it was the species most likely to be under-reported to the Biological Records Centre, since recorders are more prone to report rare species or unusual records.

The least biased sample is probably the carcasses submitted for rabies examination, and when the relative proportion of each species in this sample is compared with the estimates of population size (Table 11), there is a good overall level of concordance. The exceptions to this are Daubenton's bat, whose riparian life style suggests that corpses are likely to be under-represented in the sample; brown long-eared bat, a species likely to be over-represented because it is prone to injury, such as by cats (A.M. Hutson pers. comm.); and the serotine, whose comparative over-representation may have been due to its large size and/or dependence on houses and as a result of the current research interest in this species (J.R. Speakman pers. comm.), so that carcasses were particularly likely to be submitted for examination. However, overall the agreement between the relative proportions in the sample submitted for rabies examination and the population sizes estimated here is remarkably close, and where the figures differ there are explanations to account for the disparity. Since the relative proportions for the two horseshoe bats, whose actual population sizes are reasonably well known, agree well, it suggests that the estimates for other species are also likely to be correct, at least to the right order of magnitude.

Population trends: These are particularly difficult to evaluate, since there is a paucity of historical data on bat population sizes, and so the following assessments are tentative. For the 14 species known to be breeding in Britain, only one (the lesser horseshoe) is considered to be increasing in some areas. The populations of two species (Natterer's bat *Myotis nattereri* and barbastelle *Barbastella barbastellus*) may be stable. Three species (greater horseshoe, noctule and brown long-eared) are believed to have declined this century or currently are believed to be declining, and for the rest current population trends are even less clear.

Counting bats emerging from roosts during the summer has been used to monitor population trends (R.E. Stebbings pers. comm.). These roosts are predominantly, but not exclusively, pipistrelle nursery roosts, and these counts provide a valuable long-term data set on population trends for the commonest species of bat (Table 12). However, care must be taken when interpreting these data. People tend to count large colonies as they are more obvious and impressive, and any such bias is most likely to exert an influence in the early days of the survey, when the number of roosts surveyed was small. With time, some roosts are abandoned, whereas others are either located for the first time or are genuinely new roosts. Whether the loss of a roost indicates a decline in bat numbers or a decline in the suitability of that particular roost site is usually unknown, as is whether new roosts indicate a change in location or an increase in bat numbers. Also, a mean decline in colony size could represent more small colonies rather than an actual decline in bat numbers, or else be due to a combination of the two factors. Finally, although a large number of roosts were involved in estimating the change from 1991 to 1992 (387), the number of colonies in 1979 was much lower, and for each of north England, Scotland and Wales was five or fewer. Thus changes are calculated against a very small baseline, and for Wales, mean colony size was particularly large, whereas for Scotland it was below average. Not surprisingly, against this baseline Wales has subsequently shown the greatest decline and Scotland the greatest increase. If 1980 is taken as the baseline, when the total number of roosts counted exceeded 200, a similar but generally less extreme pattern is seen (Table 13). Using the current estimate of 2,000,000 pipistrelles, these figures on roost declines suggest that in 1980 the population was 3,500,000. If 1978 is used as the baseline, it suggests that there were then 7,500,000 pipistrelles. This figure does seem very high, and it is also difficult to see why 4,000,000 pipistrelles died in the two years 1978-1980. In the absence of any evidence to explain this dramatic change over two years, it seems more likely that the small samples in 1978 produced a skewed baseline figure.

Whilst it is not possible to use colony counts to produce an exact measure of bat population changes, especially since many of the yearly differences shown in Tables 12 and 13 were not statistically different, they do provide data on relative and regional trends. Thus the most significant changes occurred prior to the mid-1980s, and thereafter bat population changes have been much smaller. Also, the declines appear to have been greatest in south-east England, the midlands and Wales, whereas in Scotland mean roost size has increased (R.E. Stebbings & H.R. Arnold pers. comm.). In Scotland, pipistrelles appear to be found in fewer, larger roosts, and so roost size itself is not a measure of population density. However, whilst the declines have been greater in Wales, because mean colony size was originally largest in Wales (Table 12), mean colony size in 1992 (91, n = 32) was still larger than that for England (64, n = 324). In 1992 Scotland had a mean colony count of 279 (n = 31), and in fact although only 8% of the counts were from Scotland, over half the colonies that had in excess of 500 bats were recorded there (R.E. Stebbings & H.R. Arnold pers. comm.).

Population threats: These are numerous and have been discussed by Stebbings (1988). They generally fall into three main categories. Firstly, landscape changes can cause a significant reduction in foraging area due to loss of old pasture, deciduous woodland and the improvement and clearance of water courses. Woodland can be improved as a foraging habitat for bats by increasing the number of tree species and structural diversity (Mayle 1990). The removal of hedgerows and other linear features may lead to habitat fragmentation and the loss of foraging areas for the smaller species of bat, which are reluctant to cross open areas (Limpens *et al.* 1989). Furthermore, the removal of hollow trees, especially in hedgerows, is likely to have a serious impact on tree-roosting species, due to the loss of roost sites. A recent analysis indicated that in some landscapes in Britain there is a shortage of suitable foraging habitats, and this may be limiting bat numbers in these areas (Walsh, Harris & Hutson 1995). Secondly, the use of harmful pesticides, the insulation of cavity walls, the repointing of walls and the reroofing and the renovation of bridges and old buildings may be killing and/or excluding many species of bat that roost in buildings. In particular, the use of persistent insecticides such as lindane to protect timber in buildings from insects has been a serious threat (Mitchell-Jones *et al.* 1989). In the 1970s it was estimated that in Britain over 100,000 buildings underwent remedial timber treatment for wood-boring insects each year, and this posed a significant conservation problem for bats. However, following the discovery that timbers treated with lindane are potentially lethal for long periods (Racey & Swift 1986; Boyd, Myhill & Mitchell-Jones 1988), the number of timber-treatment products containing lindane or pentachlorophenol has declined from 72% to 10% from 1988 to 1992, and the lindane-based products should soon disappear from use (Mitchell-Jones, Hutson & Racey 1993). Bat population declines due to organochlorine insecticide poisoning may have been occurring for the last thirty years. Jefferies (1972) reported high levels of dieldrin and DDT in bats from the east midlands in the 1960s; it was thought that these pollutants were acquired from their insect prey. Laboratory tests showed that pipistrelles were particularly sensitive to DDT. Jefferies (1972) found that during 1968/1969, bats sampled from the east midlands were carrying one third of the lethal level of organochlorine insecticides as 'background' residues, this rising to just under the lethal level after hibernation. D.J. Jefferies (pers. comm.) suggested that organochlorine insecticides were causing declines in bat populations from the late 1950s until at least 1975. The third main threat is disturbance; this is a particular threat for species that roost and/or hibernate underground. Disturbance of hibernating bats causes a significant decline in a bat's potential duration of hibernation due to a reduction in the fat stores associated with metabolic activity (Speakman, Webb & Racey 1991). Also, the large numbers of mines that have been solidly capped are lost both as hibernacula and as nursery sites for cave-dwelling species. Thus to help maintain bat populations, it is probable that roost sites, hibernation sites, foraging areas and corridors for movement must all be maintained. A conservation strategy that does not consider all these aspects is unlikely to be successful.

One other problem is that British bats are generally *K*-strategists (Gaisler 1989). They produce only one young annually, rarely twins, but compensate by living far longer than other small mammals, sometimes over 20 years. Features of their reproductive strategy such as low fecundity, delayed reproduction and a low intrinsic rate of population growth all mean that bats are slow to increase their population size following a decline, and so are vulnerable to further perturbations. Thus small population sizes are likely to put bats at greater risk than other groups of British mammals.

Greater horseshoe bat *Rhinolophus ferrumequinum*

Status: Native; very rare and endangered.

Distribution: Confined to south-west England and south Wales, south of the line Cardigan-Cheltenham-Southampton, including the Isle of Wight; vagrants are occasionally recorded elsewhere. Last century greater horseshoe bats were found in and around

London, including Hampstead Heath and Regents Park (Mickleburgh 1988; Stebbings 1989a).

Population data: There are a number of recent population estimates, and these are based on counts of summer roosts and hibernacula; there are now 35 known breeding and all-year roosts, and 369 hibernation sites (A.J. Mitchell-Jones pers. comm.). Recent increases in the number of known roosts has resulted in increased estimates of population size but these do not represent an actual population increase. Thus there were believed to be about 2200 greater horseshoe bats in 1983 (Stebbings & Griffith 1986), and 3500-3800 in the late 1980s (R.E. Stebbings pers. comm.). The minimum population size in 1992 was estimated by R.D. Ransome (pers. comm.) to be 2500, but that did not include counts from a new site discovered in Cornwall. Recently, R.E. Stebbings (pers. comm.) suggested the figure for the current population should be 4000, since two more traditional nurseries had been found since his last estimate. Hutson (1993) also estimated the population to number 4000. R.E. Stebbings (pers. comm.) estimated population size from the number of young born in all the nurseries and relating those figures to an average proportion of the number of adult bats in the nursery cluster compared with estimates of total population sizes for three colonies as determined by detailed capture-mark-recapture studies. This gave a total population estimate that was three to four times the size of the nurseries. A.J. Mitchell-Jones (pers. comm.) also suggested that, in the absence of better information, the total population was three times the number seen emerging from summer nursery roosts. Based on this technique, he estimated the maximum population size to be 6600. P. Chapman (pers. comm.) also suggested that 4000 is probably too low, and that 6600 is a more reasonable figure.

Population estimates: A total pre-breeding population of at least 4000, and possibly nearer 6600; in England 3650, in Scotland 0 and in Wales 350. Intensive searches for this species suggest that very few new colonies will be found, although a better understanding of the percentage of the population recorded at nursery roosts is likely to refine the estimate for total population size. **Reliability of population estimate:** 2.

Historical changes: Yalden (1992) argued that this large and characteristic inhabitant of caves ought to be prominent in sub-fossil and fossil cave faunas, and that its relative scarcity suggests that it was neither more widely distributed nor, perhaps, more abundant in former times. In more recent times, it was present in Kent until *circa* 1900 and at the turn of the century was considered to be fairly numerous on the Isle of Wight (Millais 1904-1906). It was also abundant in some parts of the south-west (Barrett-Hamilton & Hinton 1910-1921). This century there was a significant population decline and a loss of over half of its previous range (Stebbings 1988). It has been suggested that the population earlier this century may have numbered around 300,000 (Stebbings & Arnold 1989); this estimate was based on an estimated earlier distribution of about 6,000,000 ha and a known bat density for one particular colony of 0·05 per ha. Recently R.E. Stebbings (pers. comm.) has revised his estimate to about 330,000. Obviously, this estimate is based on a number of assumptions, many of which cannot be tested. In particular, the density at one colony may not be typical for the whole range. In optimum habitat the population density may have been considerably higher but there would also have been areas that were sparsely occupied (R.E. Stebbings pers. comm.).

Stebbings (1988) suggested that this decline in numbers occurred mostly during 1950-1980; of at least 58 nursery colonies that were known then, only 12 now produce more than five young per year. However, Ransome (1989) argued that the long-term studies in Devon from 1948 (Hooper & Hooper 1956; Hooper 1983) showed that this population did not number many thousands in the early 1950s, a view supported by J.H.D. Hooper (pers. comm.), because there is a shortage of suitable hibernacula over large areas of the range estimated by Stebbings (1988). J.H.D. Hooper (pers. comm.) suggested that, in the 1950s, up to 600 was a reasonable estimate for the population in south Devon, a long way short of the many thousands suggested by R.E. Stebbings (pers. comm.). Similarly, Ransome (1989) questioned the estimate of Stebbings & Arnold (1987) that the population in Dorset alone declined from 15,000 before 1953 to 90 in 1986; Ransome (1989) also argued that the British population before 1950 was probably considerably lower than 300,000. Ransome (1989), monitoring greater horseshoe bats around Bristol, found a significant decline from the winter of 1962/1963 until 1966/1967, followed by a temporary recovery and fall again between 1967/1968 and 1971/1972. This was followed by a slow recovery up to 1978/79, and relative stability until 1985/1986, with a further major reduction in 1986. The minimum number of bats alive in 1987/1988 was only 42% of the number alive in 1968/1969. J.H.D. Hooper (pers. comm.) estimated that the greater horseshoe bats in the Buckfastleigh/Chudleigh area in 1993 had increased to around 680, a very similar figure to when he started work in the late 1940s.

Population trends: Following a decline through the 1970s and 1980s, the population in Dorset is increasing following protection (R.E. Stebbings pers. comm.). The same applies in south Devon, where summer and winter surveys indicate that numbers have more than doubled in the last 20 years, although it is possible that this does not reflect a genuine increase but is due to immigration or to the adoption of improved monitoring techniques (P. Chapman pers. comm.). The south Wales population is believed to be stable or undergoing a small decline. The population in the Cotswold area is continuing to decline. Ransome (1989) has shown that population growth is limited by summer weather: poor summers lead to late births and, when followed by unfavourable weather and poor food supplies in late August and early September, lead to slow growth of juveniles, thereby reducing their chances of over-winter survival. Thus, at small population sizes, greater horseshoe bats seem to be particularly vulnerable to population declines as a result of a series of cold and wet summers.

Population threats: Populations benefited from mines for limestone, ochre and metal extraction falling into disuse early this century. More recently, many closures for safety reasons are thought to have seriously depressed numbers in Dorset and, to a lesser extent, in Avon, Gloucestershire, Somerset and Wiltshire (Ransome 1991a). Of 426 known hibernacula, 97 (23%) are SSSIs or proposed SSSIs, and these cover 72% of the known hibernating population of greater horseshoe bats (Mitchell-Jones, Hutson & Racey 1993). Although formerly roosting in caves in both summer and winter, this species now depends on buildings during the summer, since few cave sites provide sufficiently high temperatures for successful breeding (Arnold 1993). Large colonies are also known to have died following the use of pesticides (Stebbings 1988). The decline in numbers of large beetles (a major food source) following habitat changes, especially the loss of old pasture, potentially poses a major threat to the survival of greater horseshoe bats in many areas (Stebbings 1988).

Lesser horseshoe bat *Rhinolophus hipposideros*

Status: Native; rare and endangered.

Distribution: Widely distributed in south-west England and Wales, south and west of a line from Chester to Southampton. At the turn of the century lesser horseshoe bats were also found in Durham, the Peak District, North Yorkshire and Northumberland (Millais 1904-1906) and were still present in Surrey and Kent in the 1950s. Hibernating records from Yorkshire in the early 1980s have yet to be confirmed. Records elsewhere are of vagrants.

Population data: These were based on counts of known colonies. Heaver (1987) estimated a total population in 1985 of 4800

(1300 in south-west England, 1000 in the English border counties and 2500 in Wales), based on details of 261 hibernacula and 151 summer roosts known to have been in use since 1980. Stebbings (1988) suggested that the adult population was probably nearer 8000. More recently, as a result of intensive roost surveys, there are now 227 known breeding and all-year roosts, and 605 hibernation sites. Thus Hutson (1993), using estimates of known summer colonies plus estimates for colonies in areas where only hibernating populations were known, estimated that there were 7000 lesser horseshoe bats in Wales alone, with a comparable number in England, giving a total population of 14,000 (Hutson 1993). A.J. Mitchell-Jones (pers. comm.) provided a second estimate based on the maximum number of bats counted at each site since 1981 for 381 sites in England and 273 in Wales. The results were very similar to Hutson's (1993) estimate, i.e. 6947 in England and 6747 in Wales.

Population estimates: A total pre-breeding population of about 14,000; 7000 in England, none in Scotland and 7000 in Wales. Recent intensive searches for this species have improved the data on which the population estimate is based, and it is unlikely that further work will substantially increase this population estimate. **Reliability of population estimate:** 2.

Historical changes: Since this species seems to feed more in scrubby deciduous woodland and less over grassland than does the greater horseshoe bat, it may have been more abundant and/or widespread when woodland was more abundant (Yalden 1992). In the early 1900s, the lesser horseshoe bat was, as today, more widely distributed than the greater horseshoe bat (Kelsall 1887; Millais 1904-1906), and was found locally in some numbers, but was not common (Thorburn 1920). Since 1950 the lesser horseshoe bat has disappeared from much of the north of its European range, and colonies appear to be declining (often by up to 90%) over its European range (Stebbings 1988).

Population trends: Current population trends are less clear, since populations are highly localised and variable in size. The loss of abandoned mine sites probably depressed numbers and/or led to a range reduction, whereas densities in forested areas have increased recently (Ransome 1991b). Consequently this species has probably benefited from increased afforestation. The survey by Heaver (1987) suggested that there had been a range reduction, but with increased densities within the range. Based on roost counts, R.E. Stebbings (pers. comm.) estimated that, in the seven years up to 1992, there had been an overall size reduction of 12% in 36 roosts in England and Wales, but for the 24 roosts in Wales this reduction was 22%, although it is unlikely that this represented a real population decline. Certainly, there appears to have been a recent slight increase in range, with bats occurring further east in Dorset, although this may be due to increased recorder effort, and there has been an increase in population size in south Wiltshire (R.E Stebbings pers. comm.). Data from hibernacula in south-west England suggest that there has also been a population increase in this area (G. Jones pers. comm.). Overall, in the absence of hard winters for a number of years (see below), it seems that lesser horseshoe bats have been maintaining population levels and increasing in some areas (R.E. Stebbings pers. comm.).

Population threats: Reasons for the dramatic range reduction in much of northern Europe are unclear; in Britain the loss of mine sites has probably led to a range reduction. The loss of roosts is a continuing problem, and the lesser horseshoe bat is thought to be very vulnerable to severe winters since many colonies appear to lack suitable hibernacula to protect them from low temperatures (R.E. Stebbings pers. comm.). Of 909 known hibernacula, 161 (18%) are SSSIs or proposed SSSIs, including 53% of the known hibernating population of lesser horseshoe bats (Mitchell-Jones, Hutson & Racey 1993).

Whiskered bat *Myotis mystacinus*

Status: Native; locally distributed.

Distribution: Probably found throughout England and Wales. There are a few records from southern Scotland as far north as the Firth of Forth (Ayrshire, Borders, Dumfriesshire and Midlothian); it is probably absent from the highlands. Its status in Scotland is uncertain, although it is probably rare (Haddow, Herman & Hewitt 1989; J. Herman pers. comm.).

Population data: Speakman (1991) based his estimate on the ratio of the number of recorded whiskered/Brandt's roosts relative to pipistrelles, with the assumptions that whiskered bat roosts were on average the same size as pipistrelle roosts, that both species have an equal propensity to roost in buildings and that the roosts are equally mobile. Until 1970 whiskered and Brandt's bats were regarded as one species. They are difficult to tell apart, and most recent records still do not differentiate the two species. Speakman's (1991) estimate (adjusted for the area covered in this review) for the two species combined was 131,600. Of those records that do differentiate (n = 155), 69·4% were for whiskered bats (Arnold 1993). Assuming that this represents the true ratio of occurrence of the two species, the number of whiskered bats would be 90,000, based on Speakman's (1991) calculations. However, whiskered bat roosts are, on average, probably much smaller than the 117 (the mean for pipistrelle roosts) used by Speakman (1991) (A.M. Hutson pers. comm.). R.E. Stebbings (pers. comm.) suggested that whiskered bat colonies are approximately one third the size of pipistrelle colonies, and so estimated a population size of 30,000 to 40,000. A.J. Mitchell-Jones (pers. comm.) also estimated a population size of around 40,000, using the same arguments as R.E. Stebbings.

Population estimates: A total pre-breeding population of about 40,000; in England 30,500, in Scotland 1500 and in Wales 8000. At present there is only a limited amount of information on this species, in particular on its abundance in different parts of Britain and its abundance relative to Brandt's bat. **Reliability of population estimate:** 4.

Historical changes: At the end of last century Harting (1888) suggested that whiskered/Brandt's bats were either overlooked or mistaken for pipistrelles. Thus the early status of this bat in Britain is unclear, partly because of confusion between whiskered/Brandt's bats and pipistrelles and partly because, until 1970, Brandt's bat was not recognised as a separate species in this country. However, in the late 1800s whiskered/Brandt's bats were considered to be generally distributed, and abundant in some counties such as Yorkshire, where they equalled brown long-eared bats and pipistrelles in abundance (Millais 1904-1906; Barrett-Hamilton & Hinton 1910-1921). Thorburn (1920) described them as numerous in various parts of the southern, western and midland counties, and not uncommon in Wales. In Scotland there were no confirmed records prior to 1987 (Haddow, Herman & Hewitt 1989).

Population trends: If this assessment of their relative abundance last century was correct, it would suggest there has been a significant decline in their relative abundance compared to pipistrelles, and hence a disproportionately large decline in the number of whiskered/Brandt's bats, although their range appears to be much as it was a century ago.

Brandt's bat *Myotis brandtii*

Status: Native; common in west and north England, rare or absent elsewhere.

Distribution: This is unclear because of confusion with whiskered bats, but Brandt's bats are believed to be widespread in England and Wales. The status of this species in Scotland is less clear. There is one record for 1874 from Rannoch, Perthshire (Haddow, Herman & Hewitt 1989), one recent record from England close to the Scottish border

(Arnold 1993), and several recent records in southern Scotland, particularly Dumfriesshire (R.E. Stebbings pers. comm.).

Population data: Speakman (1991) based his estimate on the ratio of the number of whiskered/Brandt's roosts relative to pipistrelles, and the assumption that the roosts of Brandt's bat were, on average, the same size as pipistrelle roosts. This assumption on roost size was unrealistic (see whiskered bat). This approach also assumed that both species have an equal propensity to roost in buildings and that the roosts are equally mobile. An estimate for the number of Brandt's bats was calculated from Speakman's (1991) adjusted estimate for whiskered/Brandt's bat, as described for whiskered bat; this suggested a population size of 40,000. However, Brandt's bat roosts probably contain, on average, far fewer bats than the 117 used by Speakman (1991) as the average size of pipistrelle roosts (A.M. Hutson pers. comm.). R.E. Stebbings (pers. comm.) suggested that Brandt's bat is only slightly rarer than whiskered bat, and so estimated that there are 30,000 Brandt's bats, based on his calculation of the number of whiskered bats. However, from hibernacula in Kent and Sussex, A.M. Hutson (pers. comm.) found that Brandt's outnumbered whiskered bats by about 1·5:1, and S. Bradley (pers. comm.) also thought that Brandt's predominated over whiskered bats in hibernacula in northern England. Clearly further work is needed to determine the relative abundance of Brandt's and whiskered bats.

Population estimates: A total pre-breeding population of about 30,000; 22,500 in England, 500 in Scotland and 7000 in Wales. Very little is known about this species in Britain, and it is not even clear whether Brandt's bat is more or less common than the whiskered bat. **Reliability of population estimate:** 5.

Historical changes: These are unknown due to early confusion with whiskered bats; see above for an account of whiskered/Brandt's bats.

Population trends: Unknown due to early confusion with whiskered bats; see above for an account of whiskered/Brandt's bats.

Natterer's bat *Myotis nattereri*

Status: Native; fairly common throughout much of Britain.

Distribution: Found throughout England and Wales; recent records have extended the known range of Natterer's bats in Scotland to all areas except the extreme north-west (Haddow 1992).

Population data: Speakman (1991) based his estimate on the ratio of the number of known Natterer's bat roosts relative to pipistrelle, and the assumptions that Natterer's bat roosts were, on average, the same size as pipistrelle roosts, that Natterer's bats have an equal propensity to roost in houses, and that the roosts are equally mobile. Correcting Speakman's (1991) estimate for the area covered by this review produced a population estimate of about 60,000. However, Natterer's bat maternity roosts are usually smaller than those for pipistrelles (A.M. Hutson pers. comm.), although Natterer's bat is a very widespread species, and R.E. Stebbings (pers. comm.) suggested that the population size is larger than that estimated by Speakman (1991). A.M. Hutson (pers. comm.) agreed, and he estimated 100,000 Natterer's bats, based on the belief that they are more common than whiskered and Brandt's bats combined.

Population estimates: A total pre-breeding population of about 100,000; 70,000 in England, 17,500 in Scotland and 12,500 in Wales. Since there is little information on this species, further data on its abundance relative to other species are needed in order to refine the population estimate. **Reliability of population estimate:** 4.

Historical changes: At the turn of the century, Natterer's bats were thought to be generally distributed but somewhat local

(Millais 1904-1906), and the known distribution (Harting 1889a; Millais 1904-1906) was very similar to that today, suggesting that there has been no significant change in distribution. Whether there has been any significant change in status is unknown.

Population trends: Currently unknown.

Bechstein's bat *Myotis bechsteinii*

Status: Native; very rare in central southern England.

Distribution: Most records are from south-west England and the Isle of Wight; there are some recent records from the south-west midlands (R.E. Stebbings pers. comm.), and one was found in Brecon in Wales in 1993 (J. Messenger pers. comm.).

Population data: All the records in Britain up to 1989 are detailed by Stebbings (1989b). There are no recent records of breeding colonies in Britain, the only accepted record of a nursery cluster being from Hampshire in 1886, and all the summer records are of single individuals. Since 1960, Bechstein's bat has only been recorded from 19 10 x 10 km squares (Arnold 1993). This is a truly woodland species which lives almost exclusively in hollow trees, and hence is difficult to find. In the absence of any firm information on this species, it is difficult to calculate the actual population size except on subjective criteria.

Speakman (1991) estimated the population to be *circa* 100 individuals, but assuming that this is a resident species that breeds in Britain, this is almost certainly far too low an estimate for a breeding population found over a relatively large area. A.M. Hutson and A.J. Mitchell-Jones (pers. comms) suggest that a population of at least 1000 would be needed to maintain a viable population over such a large area, and R.E. Stebbings (pers. comm.) suggests 1500-2000, although he argued that even this may be too low an estimate. This population estimate is based on the assumption that the species is resident and breeding. However, in the absence of known breeding colonies, and in view of the paucity of records, it could equally be argued that the species is only a vagrant in Britain (J.R. Speakman pers. comm.).

Population estimates: A total pre-breeding population of about 1500, all in England; whether there is an established population in Wales is currently unknown. **Reliability of population estimate:** 4.

Historical changes: There is some archaeological evidence that Bechstein's bat was much more abundant over 2000 years ago both in Britain and Poland, and being a 'foliage-gleaner', it appears to have been a major casualty of the post-Neolithic clearance of deciduous woodland (Yalden 1992). At the turn of the century records were few, and even then it was considered to be the rarest British bat (Barrett-Hamilton & Hinton 1910-1921); Millais (1904-1906) listed three known records, and fifteen years later this had only increased to six (Thorburn 1920).

Population trends: It may be that the species is, and in recent times always has been, rare throughout its range, and that populations are stable at low levels. If so, the current low numbers do not represent a recent decline. However, fragmentation of woodlands (see below) may have led to a population decline (R.E. Stebbings pers. comm.).

Population threats: If the population is as low as is currently believed, this species is one of Britain's rarest resident mammals and, in view of the low numbers, it must be very vulnerable to further population declines due to chance events. Also, it is thought to be characteristic of ancient deciduous woodland (Yalden 1992), and because it does not like flying in open areas, fragmentation of woodland is likely to pose a significant threat which may have led to population declines.

Greater mouse-eared bat *Myotis myotis*

Status: Records last century from southern England were discounted, but it is possible that this species occurred as an occasional vagrant, although there is no evidence that it was resident in Britain before the 1940s (Stebbings 1992). Colonies reported this century were probably never well established and are now extinct.

Distribution: All recent records are confined to south coast counties of England.

Population data: A small hibernating population was discovered in Dorset in 1956 and numbered at least 12 in December 1960. However, one of the nursery sites, discovered after the colony had effectively died out, suggested that the population was larger in the 1950s (Stebbings 1992). This colony was extinct by 1980. A stray migrant was recorded in Kent in the winter of 1985. The last known hibernating population was in Sussex; discovered in 1969 (Phillips & Blackmore 1970). The sex ratio of bats marked, and ringing returns, suggest that the colony probably numbered around 50 individuals (Stebbings 1992). However, it appears that the nursery colony was destroyed in 1974 (its whereabouts was unknown) (Stebbings & Griffith 1986), and only one male remained from 1985 to 1990. There have been no more recent records of this species (Stebbings & Hutson 1991).

Population estimates: Extinct. **Reliability of population estimate:** 1.

Historical changes: This species has probably never been other than an occasional resident in Britain, and at the turn of the century there were only a few occasional confirmed occurrences, although records were more widely distributed (Barrett-Hamilton & Hinton 1910-1921).

Population trends: Its largely south coast distribution in Britain suggests that colonies are periodically established, and it is possible that colonies will become established again. However, at present, populations of greater mouse-eared bats are much reduced in the whole of north-west Europe, and the chances of recolonisation would appear to be remote until such time as populations generally have built up again (Stebbings 1992; Hutson 1993).

Population threats: It is probable that the Dorset colony was destroyed by excessive disturbance and popular interest. In addition it has been suggested that some were lost due to timber treatment of a roost, and that the nursery roost of the Sussex colony was destroyed by an unrecorded event (Stebbings 1992; R.E. Stebbings pers. comm.).

Daubenton's bat *Myotis daubentonii*

Status: Native; common throughout much of Britain.

Distribution: Widespread north at least to Inverness, and probably occurs throughout all of mainland Scotland, but only one roost is currently known north of the Great Glen (J.R. Speakman pers. comm.). The known distribution in Scotland is documented by Haddow (1992). A survey around Sheffield, South Yorkshire showed that Daubenton's bats are absent or rarely seen at altitudes greater than 200 m or in urban and industrial areas (Clarkson & Whiteley 1985).

Population data: Although a widespread species, it is to a large extent associated with riparian habitats and colony size tends to be small, i.e. 5-25 bats (R.E. Stebbings pers. comm.). Speakman (1991) based his adjusted estimate of 160,000 on the ratio of Daubenton's bats to other species in surveys organised by local Bat Groups. In Great Britain as a whole R.E. Stebbings (pers. comm.) estimated that Daubenton's bat is probably of similar abundance to Natterer's bat. Thus he suggested a population of 90,000-100,000. A.M. Hutson (pers. comm.) also argued that the very few known summer roosts, and the paucity of winter records from underground sites, gives a false impression of rarity. The species is widespread, associated with any area of open water, and he suggested that overall it is one and a half times as common as Natterer's bat. Thus he estimated a population size of 150,000. However, it is equally true that the concentration of this species around open water could give a false impression of its relative abundance, and so this could lead to an over-estimate of population size (A.M. Hutson pers. comm.).

Population estimates: A total pre-breeding population of about 150,000; 95,000 in England, 40,000 in Scotland and 15,000 in Wales. These estimates are based on its abundance relative to other species and the belief that the paucity of roost records gives a false impression of rarity. **Reliability of population estimate:** 4.

Historical changes: For a long time this was considered to be one of the rarer British bats, although even last century Harting (1889b) suggested that it had been overlooked or mistaken for other species. At the turn of the century Daubenton's bat was considered to be abundant in every part of England and Wales that afforded suitable combinations of water and woods (Barrett-Hamilton & Hinton 1910-1921), and in Scotland it was widespread but local with records as far north as Banffshire. However, this species is subsequently thought to have declined in the north. A survey in north-east Scotland suggested that at the start of the century Daubenton's bat may have been the commonest bat in the area but it is currently the rarest (Speakman *et al.* 1991b). Reasons for this perceived change are unknown, although different sampling methods may be partly responsible.

Population trends: There is no specific information on current population trends in Britain, but in Europe there have been significant increases in the numbers of Daubenton's bat (e.g. Daan 1980; Gaisler, Hanák & Horácek 1981). These increases may be because aquatic insects, which form the major source of food, have not declined in the same way that terrestrial insects have as a result of the use of insecticides (Daan 1980). In particular, eutrophication of fresh waters may even have increased food availability for Daubenton's bats (Daan 1980). Changes in water quality in Britain (National Rivers Authority 1991) may lead to changes in the availability of suitable insect prey, and potentially affect the number of Daubenton's bats in the long term.

Serotine *Eptesicus serotinus*

Status: Native; widespread in southern Britain.

Distribution: Well established south-east of a line from Bristol to Great Yarmouth (including the Isle of Wight), with a few records from south-west England, central and south Wales, and one each from Nottinghamshire and Yorkshire (Arnold 1993). These latter records may be vagrants or evidence of a recent range extension.

Population data: Based on the ratio of the number of serotine roosts relative to pipistrelles, and a mean roost size for serotines of, on average, one tenth the size of pipistrelle roosts (C.M.C. Catto unpubl.), Speakman (1991) estimated the population size to be 15,000. R.E. Stebbings (pers. comm.) calculated the population size to be 10,000-12,000 by separating nursery from other roosts, and from the fact that serotine roosts are one quarter the size of pipistrelle roosts and not one tenth (mean $21{\cdot}4 \pm 1{\cdot}7$, $n = 94$; Stebbings & Robinson 1991). A.J. Mitchell-Jones (pers. comm.) agreed with this larger estimate of mean serotine roost size; his figure was $18{\cdot}4 \pm 2{\cdot}0$ ($n = 66$). He found that the number of nurseries was rather less than predicted from the number of casual records. A.M. Hutson (pers. comm.) suggested that whilst the species is not common, these figures could be a substantial under-estimate because there is no asymptote in the number of new roosts being found.

Population estimates: A total pre-breeding population of about 15,000; 14,750 in England, none in Scotland and 250 in Wales. However, this may be a significant under-estimate. J. Messenger (pers. comm.) believes that the species is under-recorded in Wales, and that the estimate for Wales in particular is too low. **Reliability of population estimate:** 4.

Historical changes: The known distribution and probable status at the turn of the century were much as today. Millais (1904-1906) described it as decidedly rare and local. There were only a few records from south-west England, and the serotine was regarded as rare north of the Thames (Barrett-Hamilton & Hinton 1910-1921) and rare except in a few districts in the south and south-east of England (Thorburn 1920). Thus it has always had a restricted range in Britain, but was considered to be numerous in some localities in the south-east in the mid-1800s.

Population trends: Some nursery colonies are known to have declined substantially since 1960 (Stebbings & Griffith 1986). R.E. Stebbings (pers. comm.) reported that a detailed study in East Anglia showed that the serotine population had declined by about 90% in ten years, with some colonies disappearing completely. Recent records from Nottinghamshire, Yorkshire and Wales may be indicative of a range expansion but are more likely to reflect the greater number of people recording bats; although a large bat, the serotine's crevice-dwelling habits and small colony size render it inconspicuous (Stebbings & Robinson 1991). Thus there is an absence of hard data on which to assess current population trends.

Noctule *Nyctalus noctula*

Status: Native; generally uncommon, but more numerous in well-wooded areas.

Distribution: Widespread over most of England and Wales. Vagrants were recorded in Orkney in 1976, 1978 and 1988 (Arnold 1993); there were records last century for Scotland (e.g. Millais 1904a) and there are some recent records from south-west Scotland, including a large colony near Newton Stewart (Haddow 1992). This is one of the few species of bat seen feeding over open moorland (Whiteley 1985). There have also been some recent records from North Sea oil rigs (J.R. Speakman pers. comm.).

Population data: Speakman (1991), basing his estimate on the ratio of the abundance of noctules relative to other species in surveys organised by local Bat Groups, suggested a population of about 40,000. R.E. Stebbings (pers. comm.) suggested a figure of 30,000-50,000, but had no firm data on which to base this estimate. A.M. Hutson (pers. comm.) produced an estimate of 50,000 based on their abundance relative to serotines.

Population estimates: A total pre-breeding population of about 50,000; 45,000 in England, 250 in Scotland and 4750 in Wales. The upper end of the suggested range seems a reasonable estimate, based on the relative abundance of noctules to other species of bat in the samples submitted for rabies testing. **Reliability of population estimate:** 3.

Historical changes: At the turn of the century the noctule was considered to be a common species, being described as plentiful in suitable localities in southern, eastern and midland counties, common throughout Yorkshire, abundant in Cheshire, and more or less plentiful in Lancashire (Millais 1904-1906). Further north it was rare, but there were a few records from as far north as Elgin in Scotland (Barrett-Hamilton & Hinton 1910-1921). Observations suggest a substantial and rapid decline both in range and numbers during this century, particularly after the 1940s, but there are no data with which to quantify this change (Stebbings & Griffith 1986).

Population trends: No quantitative information is available on current population trends. Although widespread, there are not many roosts in buildings and so there are few data on which to base an estimate of population trends. The loss of ancient woodlands and old hedgerows may have removed both foraging habitats and roost sites.

Leisler's bat *Nyctalus leisleri*

Status: Native; widespread but scarce in Britain.

Distribution: There are few records from Britain, and these are mostly from eastern and central England and the Welsh borders. The record from Holyhead, Gwynedd, in 1992 was probably of a vagrant (J. Messenger pers. comm.). R.E. Stebbings (pers. comm.) suggests that further work may show that the distribution covers the whole of Wales. There are two recent records from south-west Scotland (Haddow 1992), and one vagrant recorded from Shetland in 1968.

Population data: Colonies of up to 200 individuals have been recorded in a few buildings, but it is essentially a woodland species and is sometimes recorded from bat boxes in conifer plantations (Stebbings & Griffith 1986). Records from the area around Sheffield, South Yorkshire (19 in 1985) suggest that it is moderately widespread (Whiteley & Clarkson 1985). Speakman (1991) based his population estimate on the ratio of the number of Leisler's roosts relative to pipistrelle roosts, and the assumption that Leisler's roosts were on average half the size of pipistrelle roosts. This suggests that the population numbers about 4,000. However, R.E. Stebbings (pers. comm.) reported that whilst colony size can be up to 200 bats, the average is probably only a quarter that of pipistrelle roosts. Based on the distribution of the species and the number of records, R.E. Stebbings (pers. comm.) argued that Speakman's (1991) figure is far too low, and suggested that the population is around 15,000. A.M. Hutson & A.J. Mitchell-Jones (pers. comm.) based their estimate on the abundance and distribution of Leisler's bats relative to serotines. They suggested that the population is somewhere between 5000 and 15,000.

Population estimates: A total pre-breeding population of about 10,000; 9750 in England, 250 in Scotland and none currently known to occur in Wales. More information is needed to refine this estimate. **Reliability of population estimate:** 4.

Historical changes: At the turn of the century Leisler's bats appeared to be very local and were thought to be nowhere common (Millais 1904-1906), only being known from three districts viz. the Avon valley in Gloucestershire, Warwickshire and Worcestershire; Cheshire; and the West Riding of Yorkshire (Barrett-Hamilton & Hinton 1910-1921), and there is no evidence of a significant change in abundance in the last hundred years.

Population trends: Unknown, but it seems probable that this species has always had a restricted range and occurred at relatively low population levels in Britain. There has been a proportional increase in the number of recent Leisler's records, and the species may be increasing slightly (R.E. Stebbings pers. comm.).

Pipistrelle *Pipistrellus pipistrellus*

Status: Native; common in most areas. At present it is unclear whether this is a single species. Jones & van Parijs (1993) showed that the echo-location calls of pipistrelle bats fall into two distinct frequency bands, with frequencies containing most energy averaging 46 kHz and 55 kHz. The two phonic types also showed small differences in average morphometrics. Although both phonic types are found throughout Britain, they are reproductively isolated with separate maternity colonies. Thus *Pipistrellus pipistrellus* may actually consist of two cryptic sibling species, and further genetic work seems to support this view (G. Jones pers. comm.). Although the data are preliminary, there is some evidence that the low frequency type predominates on the south coast, whilst the high frequency type predominates in Scotland (G. Jones pers. comm.).

Distribution: Found throughout the British Isles and on many islands but probably not now resident in Orkney or Shetland, although pipistrelles were resident in Orkney in the 1970s (P.A. Racey pers. comm.). There were records from earlier this century from the Outer Hebrides (Millais 1904-1906; Barrett-Hamilton & Hinton 1910-1921; Thorburn 1920), and there is one recent Hebridean record, from Stornoway (R.E. Stebbings pers. comm.).

Population data: Speakman (1991) based his estimate of pipistrelle numbers on three early summer surveys of nursery roosts; these consist almost entirely of females. The estimated densities from the three studies were all similar. Walsh, Stebbings & Thompson (1987) found 0·05 females per ha in 500 km² around York, whilst J.S. Pritchard & F.M. Murphy (unpubl.) found 0·2 bats per ha in two glens in the centre of Scotland, which gave an overall estimated density of about 0·05 females per ha when the adjacent unsuitable moorland was included. Similarly, in an area of 3200 km² in north-east Scotland, Speakman *et al.* (1991a) found 0·18 bats per ha, which again was equivalent to about 0·05 bats per ha when surrounding areas of unsuitable habitat were included in the estimate. However, the number of new roosts found by Speakman *et al.* (1991a) never reached an asymptote, and so the density estimates (and hence total population figures) represent minimum numbers; what proportion of the total number of roosts was found is unknown. Thus these three independent estimates suggest a minimum of 0·05 breeding female pipistrelles per ha, at least in northern Britain.

To calculate population size, Speakman (1991) assumed that there are equal numbers of males and females in pipistrelle populations. However, the validity of this assumption is in doubt, since mist-netting samples caught at foraging sites contained fewer males than females (Speakman *et al.* 1991a), and a lower population of males might be anticipated from their lower survival rates (Lundberg 1989). Thus, using Speakman's (1991) adjusted figures, there would be 2,400,000 pipistrelles if the sex ratio is 1:1, but only 1,800,000 if the sex ratio is two females per male, as was found for a small sample of free-flying bats caught at a feeding site in Scotland (Speakman *et al.* 1991a). R.E. Stebbings (pers. comm.) calculated the population size from an estimated density of pipistrelle colonies in England. He extrapolated this density to comparable areas in Scotland and Wales, and used an average nursery cluster of 80 bats with a 40:60 sex ratio (because of higher male mortality). By this means he estimated 1,300,000-1,600,000 pipistrelles in Britain.

Population estimates: A total pre-breeding population of about 2,000,000; 1,250,000 in England, 550,000 in Scotland and 200,000 in Wales. To improve this estimate, more information is needed on the population structure of pipistrelles, and density estimates from areas in southern Britain. Also, since the density estimates used by Speakman (1991) in his calculations may have been some way below the actual density, this figure is likely to be an under- rather than over-estimate.
Reliability of population estimate: 3.

Historical changes: At the turn of the century pipistrelles were probably numerous in every locality where bats could exist (Barrett-Hamilton & Hinton 1910-1921), and generally were the commonest species (e.g. Lilford 1887), although outnumbered by Daubenton's and long-eared bats in some parts of England and Scotland (Millais 1904-1906), or by whiskered, brown long-eared and noctule bats in parts of England (Barrett-Hamilton & Hinton 1910-1921). In Scotland pipistrelles were found in most if not all counties, but were less numerous in Sutherland and rare in Caithness. During the course of this century, the relative abundance of pipistrelles and other species of bats in north-east Scotland appears to have changed, and pipistrelles are now much more abundant than indicated in 19th century records (Speakman *et al.* 1991a). Why the population has increased in this part of Scotland is unclear, but the adaptability of pipistrelles and their ability to use modern buildings as nursery sites may be important factors.

Population trends: Overall, pipistrelles are thought to have undergone a substantial population decline since 1960; annual surveys of colonies in houses from 1978-1983 suggested declines of 55%, and average colony size fell from 119 to 53 (Stebbings & Griffith 1986). By 1987 population levels were only 38% of those in 1978 (Stebbings 1988), and there were few known colonies of more than 1000 individuals, although such large colonies were not unusual before 1960. Also, whilst there are regional differences in mean pipistrelle colony size (south-west England 56, mean of 44 colonies per year counted 1986-1992; south-east England 64, mean of 173 colonies per year counted 1986-1992; midlands 70, mean of 78 colonies per year counted 1986-1992; north England 85, mean of 122 colonies per year counted 1986-1992; Scotland 262, mean of 41 colonies per year counted 1989-1992; Wales 99, mean of 56 colonies per year counted 1986-1992) (R.E. Stebbings pers comm.), it is unclear whether these mean colony sizes represent different population densities. Although two studies in Scotland and one in Yorkshire found very similar population densities (Speakman 1991), mean colony size in Scotland was three times that in north England. Hence differences in mean colony size may not represent different population densities, and interpreting data on roost sizes is difficult. Thus, whilst it is likely that there have been declines in pipistrelle numbers, the magnitude of any decline is unclear.

Nathusius' pipistrelle *Pipistrellus nathusii*

Status: Currently thought to be a migrant winter visitor (Speakman *et al.* 1991b), although two young animals with barely fused epiphyses were caught outside a church near Peterborough, Cambridgeshire in 1992. Thus further surveys may show that this species is breeding in Britain (R.E. Stebbings pers. comm.), although at present there are no British records during the breeding period. Rare.

Distribution: There are occasional records throughout Britain from Shetland to the south coast and the Channel Islands.

Population data: Most records are of single bats, except a possible occurrence of three together in Cornwall (Speakman *et al.* 1991b), and the two young animals from Peterborough. Up to the end of 1989, there had been 13 confirmed records from the area covered by this review (one in each of Cornwall, Dorset, Essex, Hertfordshire, London and Shetland, two from north-east Scotland and five from the North Sea). In addition, a 1940 record from Whalsey, Shetland, has now been documented (Herman 1992). By 1994 the total number of records, including the Channel Islands and North Sea, was well over 30 (J.R. Speakman pers. comm.).

Population estimates: Unknown; there are very few records, most of which are from May or September. This temporal distribution does not coincide with winds of a particular direction, and hence suggests that some bats migrate across the North Sea and English Channel to hibernate in Britain, returning to mainland Europe the following spring (Speakman *et al.* 1991b). However, R.E. Stebbings (pers. comm.) has suggested that the species may be breeding in Britain (see above), and their regular occurrence amongst the bats submitted for rabies testing (around 1% of bats submitted - Table 9) suggests that the species may be under-recorded (A.M. Hutson pers. comm.). However, this sample is biased by the inclusion of bats from North Sea oil rigs that are automatically sent for rabies testing (J.R. Speakman pers. comm.).

Historical changes: Unknown, since the species was first identified in Britain in 1969.

Population trends: Unknown. The recent spate of records may be due to a change of status and the species expanding westwards

(Stebbings 1988), but more critical recording by volunteer Bat Groups is likely to have been a significant factor contributing to the increased number of records (Speakman *et al.* 1991b).

Barbastelle *Barbastella barbastellus*

Status: Native; widespread but rare.

Distribution: Widely distributed throughout England and Wales, south of a line from the Mersey to the Tees (Arnold 1993), with early records as far north as Cumbria (Millais 1904-1906).

Population data: Since there are only 10-15 records each year (R.E. Stebbings pers. comm.), very little is known about this species and there are no known breeding colonies. Whilst the records are all of single animals, the number of records is increasing. In the absence of objective criteria on which to base a population estimate, Speakman (1991) suggested there are around 100 individuals. However, for such a widely distributed resident species, it is hard to believe that the population could be so low. A.M. Hutson and A.J. Mitchell-Jones (pers. comm.) suggested a population size of around 5000 would be needed to maintain the population over such a wide area, and R.E. Stebbings (pers. comm.) argued that it would need to be even higher, around 5000-10,000.

Population estimates: A total pre-breeding population of about 5000; 4500 in England, none in Scotland and 500 in Wales. Until we know more about the biology of this species, it is impossible to estimate population size more precisely. **Reliability of population estimate:** 5.

Historical changes: At the turn of the century the barbastelle was described as 'well-known, although not abundant' in Essex, Norfolk and Warwickshire, with definite colonies in Somerset, Worcestershire and Wales, and there were records from every county south of the Wash and east of the Dee (Barrett-Hamilton & Hinton 1910-1921). These authors concluded that it was widely distributed but in small numbers, a situation that is probably comparable to the current situation.

Population trends: Currently unknown. Arnold (1993) reported that despite the increase in records for most species of bat due to the recent increase in bat recording, the number of barbastelle records has declined after a peak in the 1950s and 1960s. He suggested that this might represent a population decline. An alternative explanation for the decline in the number of records is that barbastelles are known to respond to severe weather by entering caves, where they are more likely to be detected. Thus severe winters may have produced peaks of records that do not imply a subsequent real decrease. R.E. Stebbings (pers. comm.) questioned the reported decline in the number of records, and suggested that there has been an increase in records in the last decade in line with the increased activity of Bat Groups.

Brown long-eared bat *Plecotus auritus*

Status: Native; common.

Distribution: Occurs everywhere except in open uplands and perhaps in exposed regions of north-west Scotland and off-shore islands; there is one record of a specimen from North Uist, Outer Hebrides (Thorburn 1920).

Population data: Speakman (1991) calculated the population size using two estimates of brown long-eared bat population density from coniferous woodland in Norfolk (Boyd & Stebbings 1989) and from north-east Scotland (Speakman *et al.* 1991a). He suggested that brown long-eared bats occur at a density of about one tenth that of pipistrelles, i.e. 0·005 bats per ha. Since brown long-eared bats occupy about 80% of the range of pipistrelles, Speakman (1991) assumed that the population of brown long-eared bats is 8% that of pipistrelles. Since his figure for pipistrelles was 2,400,000 for

Britain, this produced an estimate of about 190,000 brown long-eared bats. He further suggested that an independent confirmation of this estimate comes from roost reports: 30·4% are for long-eared bats compared with 58·5% for pipistrelles (Mitchell-Jones *et al.* 1986), although A.J. Mitchell-Jones (pers. comm.) argued that the proportion of pipistrelle roosts is under-estimated because the majority of unidentified roosts were probably pipistrelles. Since brown long-eared bat roosts are about 14% as large as those of pipistrelle roosts, this also suggests that the population of brown long-eared bats is about 8% that of pipistrelles. R.E. Stebbings (pers. comm.) disagreed with the assumption that brown long-eared bats occupy about 80% of the range of pipistrelles because, whilst they are found throughout England, Scotland and Wales, they are restricted to woodland habitats. A direct comparison with pipistrelles is difficult, so he based his estimate on the relative abundance of the two species, and suggested a population size of the order of 150,000-200,000. A.M. Hutson (pers. comm.) also based his estimate on their abundance relative to pipistrelles. He suggested that the brown long-eared bat population was 10% that of pipistrelles, i.e. about 200,000.

Population estimates: A total pre-breeding population of about 200,000; 155,000 in England, 27,500 in Scotland and 17,500 in Wales. For the second most common bat in Britain, there is a surprising lack of information on which to base a more precise population estimate. **Reliability of population estimate:** 4.

Historical changes: At the turn of the century this was the most widely distributed bat and was also considered to be one of the most common, if not the commonest, species (Millais 1904-1906). Lilford (1887) recorded that it was 'exceedingly common' in most parts of England, although he also suggested that the pipistrelle was 'the' common bat in Britain. Brown long-eared bats were not known from Orkney and Shetland (Millais 1904-1906), but were recorded from the north of mainland Scotland, where they outnumbered all other species, and were recorded from the Isle of Arran, Islay, Mull and North Uist (Barrett-Hamilton & Hinton 1910-1921). During this century brown long-eared bats have undergone a long-term decline in relative abundance, and also probably in their distribution. The reasons for this decline are unknown.

Population trends: These are currently unclear. Brown long-eared bats are very dependent on roof spaces and so, during the last 30 years, they have been at risk from timber treatment in buildings using organochlorine pesticides. Since this was coupled with the loss of deciduous woodland, a habitat of great importance to brown long-eared bats, R.E. Stebbings (pers. comm.) argues that the species has declined in recent decades and that this decline may have been substantial.

Grey long-eared bat *Plecotus austriacus*

Status: Native; very rare, and only a few small colonies are known.

Distribution: Found only in Devon, Dorset, Hampshire (including the Isle of Wight) and Somerset.

Population data: These are all subjective, based on the limited distribution and paucity of records. Speakman (1991), A.M. Hutson (pers. comm.) and A.J. Mitchell-Jones (pers. comm.) all suggested that the population is around 1000 individuals, and R.E. Stebbings (pers. comm.) suggested that the figure was in the range 500-1500.

Population estimates: A total pre-breeding population of about 1000, all in England. In view of the limited range and information on the species, this is the best available estimate. **Reliability of population estimate:** 3.

Historical changes: Unknown, but in view of its largely Mediterranean distribution, it has probably always been rare in Britain.

Population trends: Any long-term population trend is unknown. Grey long-eared bats are generally rare in north-west Europe, but common in southern areas, particularly around the Mediterranean. Thus they are vulnerable to harsh winters, and in the cold winter of 1962/1963 one colony in Dorset declined from 22 to 4 individuals (Stebbings & Griffith 1986). Three colonies in Dorset and one in north-west Devon have all declined to extinction in the last 20-30 years (R.E. Stebbings pers. comm.).

Order: Lagomorpha

Rabbit *Oryctolagus cuniculus*

Status: Introduced; in most areas numbers are expanding again following a dramatic decline after the introduction of myxomatosis.

Distribution: Rabbits are widespread throughout mainland Britain up to the treeline and on most small islands but absent from Rum and Tiree. Their distribution on islands is documented by Flux & Fullagar (1992).

Population data: The most suitable habitats are areas of short grasses, whether these are natural or agricultural. However, they are found in a wide variety of habitat types. Densities vary seasonally, with numbers relatively stable over winter (<1 to 15 per ha) followed by highly variable summer peaks (<1 to 40 per ha) (Tittensor 1981). Summer peaks are higher on sandy soils, and over-winter numbers are higher on sand and chalk than on clay soils (Cowan 1991). The following density estimates were available for over-wintering rabbit populations in specific habitat types: 8·4 per ha on chalk grassland, Oxfordshire, based on a capture/mark/recapture study averaged over six winters (Cowan 1984); 14-22 per ha on sand dunes, Holy Island, Northumberland, based on marking and population counts (MacDonald 1989); 2·1 per ha on sand dunes, East Lothian, using Leslie's trap out method (Kolb 1991a); 1·7 per ha on forestry/hill grazing, Borders, using marking and Leslie's trap out method (Kolb 1991b); hill farm/open grazing, Borders, using Leslie's trap out method - (H.H. Kolb pers. comm.); 12·6 per ha on grassland/broom, Strathmore, Tayside, using Petersen/Bailey capture/mark/recapture calculations (H.H. Kolb pers. comm.).

These figures are for densities that are locally quite high, and if they were typical for all the areas of comparable habitat, they would suggest an over-winter rabbit population approaching 100,000,000. This would be comparable to the estimates of the rabbit population before the introduction of myxomatosis. Whilst the rabbit population is rapidly recovering, it has not reached pre-myxomatosis levels (see below). Thus, for the population estimate, the following density figures were used: 5 per ha for scrub, bracken, sand dunes and sloping coastal cliffs; 2·5 per ha for parkland, lowland heaths, lowland grasslands and arable land; 2 per ha in semi-natural broadleaved, semi-natural coniferous, semi-natural mixed and recently felled woodlands, and broadleaved, coniferous, mixed and young plantations; 0·5 per ha in upland unimproved grassland; and 0·1 per ha in heather moorlands.

Population estimates: A total pre-breeding population of about 37,500,000; 24,500,000 in England, 9,500,000 in Scotland and 3,500,000 in Wales. Compared to pre-myxomatosis days, there has been a very significant change in the relative abundance of rabbits in each of the three countries, with the change being most dramatic in Wales (see below). **Reliability of population estimate:** 3.

Historical changes: Rabbits were originally held in warrens, and there were only substantial increases in wild populations from the mid-18th century onwards, when changes in agricultural practice created favourable habitats and an increased interest in game led to intensive predator control (Thompson & Worden 1956). In Scotland, rabbits were for a long time mainly confined to a few islands and to coastal sand dunes. Early in the 19th century rabbits were rare north of the Tay and Clyde, and their range extension throughout Scotland was gradual (Millais 1904-1906). The natural spread of rabbit populations can be quite slow (Kolb 1994), and their spread in Scotland was largely due to 18th and 19th century introductions throughout the highlands and the north-west (Lever 1977). A similar pattern of events occurred in Wales. Until the early 19th century rabbits were mostly confined to large warrens on islands, but introductions to the mainland, coupled with agricultural changes and large-scale predator control, led to rapid increases in numbers (Lever 1977). At the turn of the century rabbit numbers were high, and average bag returns remained high until the onset of myxomatosis in 1953 (Tapper 1992). At that time the British rabbit population was estimated to be 60,000,000-100,000,000, with about 40,000,000 being culled each year for the meat and fur trade (Thompson & Worden 1956). Thompson & Worden (1956) believed that the upper limit was a conservative estimate, and that the spring and summer population was in excess of 100,000,000 rabbits. Myxomatosis destroyed over 99% of the British rabbit population (Thompson 1956). Assuming that the original estimate was reasonably accurate, this implies that fewer than 1,000,000 rabbits were left in Britain following the introduction of myxomatosis.

Population trends: For an *r*-selected species such as the rabbit, it is difficult to be precise about trends, because even several years of decline can be recouped remarkably quickly. However, its powers of recruitment are not as high as sometimes suggested by calculations based on counts of corpora lutea or of late term foetuses, since these ignore the rate of nestling mortality, which can be considerable (Bell & Webb 1991).

Since the advent of myxomatosis, bag records suggest that nationally the rabbit population has steadily recovered (Tapper 1992), although locally this may not be the case. On Forvie sand dunes, Grampian, rabbit numbers have declined from a peak in 1976, with considerable and possibly regular fluctuations in abundance (I.J. Patterson pers. comm.). Long-term data from agricultural areas show that in 1953, before the onset of myxomatosis, 94% of farm holdings in England and Wales had rabbits on cultivable land. By 1970 this figure had only recovered to 59% (Lloyd 1970), and by 1986 rabbit numbers were still only around 20% of pre-myxomatosis levels (Cowan 1991). Assuming that the estimate of up to 100,000,000 rabbits pre-myxomatosis was correct, Cowan's (1991) estimate suggests that the rabbit population in the mid-1980s was around 20,000,000.

It is also clear that the rabbit population is still well below that recorded before myxomatosis. The National Game Bag Census data (Tapper 1992) suggest that rabbit numbers are currently between a third and a half of the pre-myxomatosis numbers, which is supported by the estimate presented here. In Scotland, 92·9% of farms had rabbits pre-1954. The corresponding figure was only 60·7% in 1970 and 80·7% in 1991. The number of farms with serious infestations fell from 54·9% pre-1954 to 0·4% in 1970, and recovered to 16·6% in 1991 (Kolb 1994). In addition to dramatic changes in rabbit numbers, there has also been a significant change in the distribution of rabbits. During the 1970s eastern and south-eastern regions consistently showed the highest rises in rabbit numbers, the south-west intermediate, and Wales and the north relatively low increases (Trout, Tapper & Harradine 1986; Kolb 1994). Pre-myxomatosis populations were high in the south-west and in Wales (Thompson & Worden 1956), whereas Wales now has one of the lowest rabbit populations. In Scotland, there have consistently been more farms with rabbit infestations in the east, Highlands and north-east. These areas also had more farms with serious infestations when compared with the rest of the country, both before and after myxomatosis (Kolb 1994). Trout *et al.* (1986) concluded that in many areas the carrying capacity for rabbits had still to be reached, and so further population increases are to be expected. All these observations agree well with the estimates for the size and distribution of the rabbit population presented here.

Population threats: Fresh outbreaks of myxomatosis cause local depletions, and rabbit control measures can suppress populations locally. Whilst myxomatosis is still prevalent in many areas, mortality during such out-breaks has fallen to 40-60% (compared with over 99% at the start of the epidemic) as a result of increasing levels of genetic resistance (Ross 1982; Ross & Sanders 1984). Also, from 1992 there have been reports of viral haemorrhagic disease in wild rabbits in Britain (Duff *et al.* 1994); whether this calicivirus will have a significant impact on British rabbit populations remains to be seen.

Annual changes in reproductive success, and particularly the onset of the breeding season, are affected by climatic factors, especially higher minimum ground temperatures and hours of daily sunshine in winter. Following mild winters, the first young of the year appear above ground about two months earlier (in February rather than April), and one study found that, over four years, annual average reproductive success per adult female ranged from 6·1 to 10·1 (Bell & Webb 1991). These data demonstrate the possible effects of predicted global warming on the productivity of rabbits, and hence the potential for an increase in rabbit numbers.

Brown hare *Lepus europaeus*

Status: Probably introduced to Britain by the Romans. There have been many subsequent introductions to islands. Common but has undergone a substantial decline this century.

Distribution: Widespread, and most common in agricultural areas. In Scotland brown hares are absent from the north-west and western Highlands, where they are replaced by mountain hares on heather moorland. Present on Anglesey and the Isle of Wight; they have been widely introduced to Scottish islands (Millais 1904-1906; Barrett-Hamilton & Hinton 1910-1921).

Population data: Three population estimates are available. The first was obtained by Tapper & Stoate (1992). Hares were counted on 12 areas between January and March 1988 and 1989, using spotlight counts as described by Barnes & Tapper (1985). These gave an absolute estimate of brown hare density within a given area; for each area the cropping pattern and presence or absence of a gamekeeper were recorded. From these an index of field size and habitat diversity was calculated. Habitat data from the Institute of Terrestrial Ecology's land classes were then used to calculate a relationship between an index of crop diversity and brown hare numbers, which in turn was used to estimate the number of brown hares that would be present both with and without the presence of gamekeepers to control the numbers of predators. By this means, Tapper & Stoate (1992) estimated that the number of brown hares in Britain in late winter lay between 1,250,000 and 1,911,000, the figures being, respectively, in the absence or presence of predator control. Whilst this approach gave a reasonable estimate of total population size using the data then available, it had its limitations. First, only a minority of land classes were surveyed for brown hares, and the results from 12 sample sites predominantly in southern and eastern England were extrapolated to produce a national estimate of hare numbers. Also, the 12 survey sites chosen were areas with known hare populations, and generally areas with reasonable population densities; no areas with few or no hares were included in their calculation of the relationship between hare numbers and habitat features. This is likely to produce an over-estimate. A second estimate was derived by the Game Conservancy from the National Game Bag Census, extrapolated to the whole country, based on the assumption that about 40% of hares are shot during winter hare shoots (Tapper & Stoate 1992). This suggested a population of about 1,000,000 hares before the main culling season.

A third estimate was produced by M. Hutchings & S. Harris (unpubl.), who organised a stratified national survey in which

734 randomly selected 1 x 1 km squares were surveyed for hares. This survey was undertaken in the winters of 1991/1992 and 1992/1993. A transect in each square (mean length 2950 m) was walked three times between mid-October and mid-January, and the position of each hare seen was recorded in relation to the transect line. The data were analysed using the program DISTANCE, an updated version of Burnham, Anderson & Laake's (1980) program TRANSECT. This program was used to calculate population densities in each of the four land class groups, based on a detection function. By this means, a mid-winter brown hare population of 817,500 $\pm$ 137,250 (95% confidence limits) was obtained. This figure is lower than the other two because a much wider range of habitats were sampled, including many 1 x 1 km squares with few or no hares. The relatively large 95% confidence limits are due to the very clumped distribution of the hare population, so that comparable habitats can have widely different hare numbers. This clumping is due to various anthropogenic factors, most notably the willingness of the land owner to tolerate the presence of hares. In many areas hare numbers are drastically reduced so that poachers are not attracted onto the land (M. Hutchings & S. Harris unpubl.).

Population estimates: A mid-winter population, at the start of the breeding season but before the onset of the main hare-culling season, of about 817,500; 572,250 in England, 187,250 in Scotland and 58,000 in Wales. Organised shoots at the end of the winter may lead to a 40% decline (Tapper & Stoate 1992). **Reliability of population estimate:** 2.

Historical changes: At the turn of the century brown hares were considered to be abundant throughout England, Scotland and Wales except on the higher parts of mountains, and in the 19th century were even found on open areas in London (Barrett-Hamilton & Hinton 1910-1921). Reports in the *Victoria Histories of the Counties of England* show that they were certainly much more abundant in the western parts of England than at present, but at the start of this century declines were already beginning in the south-west (M. Hutchings & S. Harris unpubl.). Prior to the Ground Game Act of 1880, the abundance of hares in some districts was described as 'quite extraordinary', but the Ground Game Act removed the protection that was enjoyed by brown hares and is thought to have led to a dramatic decline in numbers, followed perhaps by an increase around the turn of the century. Thorburn (1920) described brown hares as plentiful in cultivated areas, especially grasslands, when not driven away by persecution.

More recently, National Game Bag Census data (Tapper 1992) have shown that hare bags were highest in the early part of the century, and that after the late 1920s they declined until the latter half of the Second World War. Thereafter numbers increased until 1960 (but not to pre-1920 levels). This increase in the later half of the 1950s may have been aided by the decline in rabbit numbers, providing a niche into which the hares expanded (Rothschild 1963). This was followed by a further decline in hare numbers during the 1970s and 1980s. This decline occurred in virtually all regions (Tapper 1992). Tapper & Parsons (1984) concluded that it represented a real decrease in abundance, and that the hare bag was declining at a more or less steady rate when considered nationally. However, autumn counts from 1976-1992 in the Dane Valley, Cheshire, showed no evidence of any overall population change, although there were marked inter-annual variations (D.W. Yalden unpubl.).

Population trends: Many estates no longer hold as many large hare shoots as previously, which complicates the interpretation of the National Game Bag Census data. However, the available information suggests that overall hare numbers have remained constant for the last ten years (mean 2·80 shot per km^2 for the years 1983-1987, mean 2·95 per km^2 for the years 1988-1992), although there will be significant annual and seasonal fluctuations due to the effects of summer weather conditions on breeding success. Hunting records also suggest that, nationally, hare numbers have remained constant over the last few years (Stoate 1993). This index is based on the number of hares seen whilst out hunting with packs of beagles and is the average of all hunting trips for the entire season, and then averaged between packs. Thus the index is based on many data which are independent of the game returns. Neither source of data shows any change in hare numbers over the last ten years. This general pattern of population change over the last thirty years has occurred throughout much of Europe, and generally hare numbers appear to have stabilised at a relatively low level (S.C. Tapper pers. comm.). However, a recent national survey suggested that population declines may be continuing since hares are heavily culled in many areas in eastern England because they attract poachers. These declines would not be detected by the National Game Bag Census and hunting data, which are biased towards large keepered estates and hunting areas where hare populations receive a degree of protection. Also, it appears that hares may be continuing to decline in low density areas in the west, and again the National Game Bag Census and hunting data are not suitable for monitoring changes in such low density hare populations (M. Hutchings & S. Harris unpubl.).

Population threats: Numerous explanations have been advanced for the decline in brown hare numbers, but none is in itself totally satisfactory. Barnes & Tapper (1986) concluded that there was a boom in hare numbers in the late 1950s and early 1960s as a consequence of the myxomatosis epizootic in rabbits, which removed a potential competitor. However, the subsequent decline in hares could not be explained adequately either by the increase in rabbits or a series of poor breeding seasons for the hares. High hare numbers in bag returns are associated with mild springs (Barnes & Tapper 1986), and mild autumns appear to lengthen the breeding season, sometimes significantly (Hewson & Taylor 1975). Thus weather can have a dramatic impact on hare breeding success.

The most generally accepted cause of the decline of the brown hare is change in the agricultural ecosystem (Tapper & Barnes 1986; Tapper & Stoate 1994). This in itself does not explain the actual cause of the decline. We do not know the relative importance of habitat simplification, use of agrichemicals, changes in farming practice such as cutting silage instead of hay, increasing use of complex machinery, etc. All these factors are likely to have played a role in the decline of hares, and their relative impact will vary in different regions of the country. In addition, hare numbers have increased where fox *Vulpes vulpes* numbers have been reduced experimentally (Tapper, Potts & Brockless 1991), but whether predation has played a role in their general decline is currently unclear, as is whether hares are now more vulnerable to predation as a consequence of habitat simplification (Harris & Saunders 1993). Whilst the reasons for the decline in brown hare numbers are probably complex, and at present are poorly understood, it is clear that many factors are involved. Anecdotal observations suggest that the five-year set-aside scheme led to an increase in brown hare numbers in some areas.

Mass mortalities of brown hares are sometimes reported from parts of East Anglia, most often in the summer. A number of factors may be responsible: food shortage due to agricultural changes, such as the change from growing spring to winter cereals (G. McLaren & S Harris unpubl.), grass sickness (Whitwell 1991; Griffiths & Whitwell 1993), or European brown hare syndrome (Duff *et al.* 1994), although this disease is most prevalent in the autumn (Gavier-Widén & Mörner 1991), whereas the mass mortalities occur earlier in the year. Their impact on brown hare populations is at present unknown.

In the Royal Museum of Scotland, Edinburgh, there are about 20 skins and skulls of specimens that appear to be brown hare/mountain hare hybrids, although whether they actually are hybrids has yet to be determined (Balharry *et al.* 1994). These came from Argyll, Ayrshire, Dumfriesshire and

Peeblesshire, i.e. those parts of Scotland where mountain hares were introduced in the middle of last century. Whether hybridisation is frequent in these areas needs to be determined (A.C. Kitchener pers. comm.). However, the current evidence suggests that wild hybrids occur only rarely, and so do not represent any real threat to the population (Balharry *et al*. 1994).

Mountain hare *Lepus timidus*

Status: Native but widely introduced outside its natural range; locally common in some upland areas.

Distribution: In the British Isles, mountain hares are indigenous only in the Highlands of Scotland; all the populations south of the Clyde and Forth are the result of introductions. Mountain hares are most numerous on grouse moors in north-east Scotland, and uncommon in west Scotland. They were present on Orkney in mediaeval times and died out; the modern population is the result of a recent introduction. Other introductions, mostly during the 19th century, were to Eigg (now extinct), Hoy, Islay (now extinct), Jura, Mull, Outer Hebrides, Raasay, Scalpay, Shetland and Skye. They were introduced into Ayrshire, Lanarkshire and Peeblesshire in the 1830s and 1840s, from where they dispersed widely (Barrett-Hamilton & Hinton 1910-1921), and to the Pennine area of South Yorkshire and Derbyshire about 1880. Introductions to the Cheviots and Lake District have not persisted. The population in North Wales, originating from introductions to the Vaynol estate near Bangor about 1885, is now extinct (Hewson 1991). No mountain hares have been reported in Wales for at least 15 years (R. Lovegrove pers. comm.).

Population data: Mountain hare populations are very localised; they reach the highest densities in north-east Scotland, and are particularly scarce in north and west Scotland (Watson & Hewson 1963). Population densities range from 3 to 46 per km^2, depending upon habitat type. The highest densities occur on heather moors overlying base-rich rocks, with the lowest densities where there are acidic rocks; locally densities may reach 300 per km^2 (Hewson 1991). In Scotland there are approximately 12,000 km^2 of heather moorland. Using a simple population estimate based on this area of heather moorland, and a mean density of 30 hares per km^2, the population in Scotland would be about 300,000. An alternative estimate was based on the following assumptions. Arnold (1993) recorded mountain hares in 363 10 x 10 km squares, including the Scottish islands and the Pennines. It was assumed that they were found in these squares but nowhere else, that they occurred at an average density of 2 per km^2 on the Scottish islands and north-west of the Great Glen (an area of about 5500 km^2). Over the rest of Scotland a density of 20 per km^2 was assumed where they are present (an area of about 35,200 km^2). However, hares are likely to be absent from large areas of this range which do not consist of heather moorland. Based on these two mean densities, and assuming that only half the range was suitable for hares, the population in Scotland would be about 360,000. In the Peak District, extensive surveys showed that the annual late winter density varied between 1·4 and 3·3 per km^2 (average 2·1 per km^2) (Yalden 1984a). Since they occupy an area of 246 km^2, the late winter population for the Pennines is about 500 animals.

Population estimates: A total pre-breeding population of about 350,000 animals, split into several sub-populations; 500 in England, 350,000 in Scotland and none in Wales.
Reliability of population estimate: 3.

Historical changes: Millais (1904-1906) described the distribution of mountain hares at the turn of the century. The National Game Bag Census records (Tapper 1992) show that high numbers were shot around the turn of the century, and even more after the First World War. They reached a peak around the early 1930s. Low numbers during the Second World War were followed by a recovery by

1950 to some 50% of those in the 1930s. There was then a decline which lasted from the mid-1970s to the early 1980s, since when the numbers shot have increased to equal the bag levels of the 1950s. At present the reasons for these population changes are unknown.

Population trends: Tapper (1987) showed that, whilst just over half of the populations he examined show irregular fluctuations in numbers, the rest showed a weak tendency towards regular population cycles with a periodicity of about 9·5 years. With species such as the mountain hare that fluctuate widely in number, it is difficult to detect long-term population changes.

Population threats: The main threat is probably population fragmentation. Populations in the Pennines, Mull, Orkney and Shetland are all relatively small and isolated. Furthermore, most recoveries of marked mountain hares are close to the point of capture; the maximum recovery distance in one study was 12 km (Hewson 1990a). Assuming that mountain hares will rarely cross more than 20 km of unsuitable habitat, the Scottish population is effectively fragmented into a number of sub-populations, particularly in the north and west (see map in Arnold 1993), and some of these could be quite small. The number of introduced populations that have died out shows the vulnerability of small mountain hare populations - see Millais (1904-1906). The Pennine population is also potentially vulnerable because of its small size, wide distribution, and the pressures placed upon it by high visitor use of the area.

It is possible that mountain hares are susceptible to climatic instability, and that adverse weather conditions affect juvenile mortality. Thus there is considerable variation in recruitment rate from place to place and possibly also from year to year (Flux 1970). Such chance events will enhance the vulnerability of small populations. Also, reduced management of heather moorland, and substantial reductions in the area of heather resulting from increased sheep-grazing, pose a threat to mountain hares (Anderson & Yalden 1981; Hewson 1984a). However, current Common Agricultural Policy reforms may reduce grazing pressure in the uplands, as may some of the new Environmentally Sensitive Areas. The new Southern Uplands Environmentally Sensitive Area is specifically targeted at increasing the regeneration of heather moorland, and may thus benefit mountain hares (J. & R. Green pers. comm.).

In the Royal Museum of Scotland, Edinburgh, there are about 20 skins and skulls of specimens that appear to be brown hare/mountain hare hybrids. These come from Argyll, Ayrshire, Dumfriesshire and Peeblesshire, in those areas where the mountain hare population was established following introductions to Ayrshire in the middle of the last century (Hewson 1991). Whether hybridisation is frequent in these areas needs to be determined (A.C. Kitchener pers. comm.). However, the current evidence suggests that wild hybrids occur only rarely, and so they do not represent any real threat to the population (Balharry *et al.* 1994). Moreover, Irish hares were introduced to south-west Scotland in about 1923 (Hewson 1991), and J. & R. Green (pers. comm.) have suggested that the colour varieties seen in the hares in that part of Ayrshire may be the descendants of that introduction. Certainly, Irish hares have been introduced to a number of areas where mountain hares were present, e.g. Mull and Vaynol Park, and the two races remained distinct. The colony on Mull, for instance, was introduced around 1860, and the descendants were still identifiable fifty years later (Barrett-Hamilton & Hinton 1910-1921). Thus it is possible that Irish hares are still recognisable in Ayrshire 70 years after their introduction. These observations suggest that the two races may be reproductively isolated (Balharry *et al.* 1994).