A review of British mammals:

population estimates and conservation status of British mammals other than cetaceans

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Order: Rodentia

Red squirrel *Sciurus vulgaris*

Status: Native, but multiple introductions from continental Europe have produced a genetically mixed population. Red squirrels are vulnerable in England and Wales, and are already extinct in most parts of these two countries. They are locally common in Scotland.

Distribution: Isolated populations persist in southern England on three islands in Poole Harbour (Dorset), Cannock Chase (Staffordshire), the Isle of Wight and Thetford Forest (Norfolk). Introduced populations remain in north England, part of Wales and much of Scotland.

Population data: Red squirrels are found in small deciduous woods and copses, and also mature (older than 25 years) conifer forests, especially those larger than 100 ha. Densities over five years recorded in Scots pine *Pinus sylvestris* on Furzey Island (Dorset) ranged from 2·3 per ha pre-breeding to 7·5 per ha post-breeding (Kenward & Holm 1989); these densities are high, probably because the island provides a prime Scots pine habitat, with very large cone crops from mature, relatively uncrowded trees (R.E. Kenward pers. comm.). A mean density of 0·66 per ha recorded in January over two years in Cumbria (Tonkin 1983) probably reflects poor habitat quality (Kenward & Holm 1993). For coniferous woodlands, density estimates vary from 0·3-1·1 per ha (Shorten 1962; Tittensor 1977; Reynolds 1981; Moller 1986). Thus long term average densities of 0·5-1·5 per ha are normal for both coniferous and deciduous forest, but inter-annual fluctuations can be large and are affected by seed supplies and weather (Gurnell 1991a). Peak numbers occur in the autumn, with troughs in the spring before recruitment.

Red squirrel population size was estimated by J. Gurnell (pers. comm.) by taking the area of coniferous and broadleaved woodland in each of the three countries from a census in 1982, adjusting for the proportion of woodland greater than 15 years old, and calculating the proportion of woodland occupied by red squirrels. Assuming a minimum density of 0·1 per ha, a maximum density of 1·0 per ha and a median of 0·55 per ha, this gave median figures for England, Scotland and Wales of 30,000, 121,000 and 10,000 red squirrels respectively (with minimum and maximum figures of 6000 and 60,000 for England, 22,000 and 220,000 for Scotland, and 2000 and 20,000 for Wales).

Many of the English populations are fragmented, and most have very few red squirrels. Estimates of the size of the isolated populations in southern England were obtained as follows. In Poole Harbour there is a total pre-breeding population of 125 and 150-200 in the summer, as estimated by capture-mark-recapture studies (R.E. Kenward pers. comm.). In Cannock Chase and Thetford Forest the populations are too low to be estimated by conventional techniques, since red squirrels are seen only occasionally, but each population consists of fewer than 100 animals. On the Isle of Wight, the area of ancient woodland was 3695 ha (Spencer & Kirby 1992), and mean densities for the island were 0·3-1·6 per ha (Holm 1990), with a mean summer density for three sites over two years of 0·90 $\pm$ 0·17 per ha (Kenward & Holm 1993). Using the area of ancient woodland and the mean density figure gave a population for the Isle of Wight of 3330, but this does not include an estimate for the number of animals found in the coniferous plantations on the island. Densities on the island were dependent on the hazel nut crop, and numbers were lower when the hazel nut crop was poor (Holm 1990). For south Lancashire, between the Rivers Ribble and Mersey, red squirrels were present in 47 woods totalling 766 ha. The population estimate was based on an assumed density of 0·8 red squirrels per ha. This suggests a population of fewer than 600. However, this is probably an over-estimate since the habitats are mostly poor for red squirrels and because the 47 woods may include some transient sites

(P.W. Bright pers. comm.). The red squirrels at Formby were introduced from Europe about 60 years ago and now occupy 70 ha of mixed coastal forest, of which 40 ha are conifers (Gurnell & Pepper 1993). Due to supplementary feeding, densities are very high, up to ten times those found in natural habitats (Gurnell & Pepper 1993; Rice-Oxley 1993). Assuming a density of 10 red squirrels per ha of conifers gives a maximum population of 400 red squirrels at Formby. Thus the largest populations remaining in England are those in Cumbria, north Lancashire and Northumberland. These constitute about 85% of the red squirrel population in England.

Population estimates: A total pre-breeding population of about 161,000; 30,000 in England, 121,000 in Scotland and 10,000 in Wales. A more precise estimate needs up-to-date information on the current range of red squirrels, and more detailed studies of the densities of red squirrels in populations on the edge of their range. **Reliability of population estimate:** 3.

Historical changes: In Scotland, there appear to be no records to suggest that red squirrels are indigenous south of the Firths of Forth and Clyde (Harvie-Brown 1881a), but to the north of this area they were widespread and common. However, they became very rare due to widespread forest destruction during the 18th century, and persisted only in Rothiemurchus Forest in Inverness-shire. Populations were boosted by subsequent reintroductions from England (for details see Harvie-Brown 1881b), the increase in young woodlands, and possibly the control of predators (Millais 1904-1906). By the end of the 19th century, red squirrels were abundant in England and Scotland, and also in Wales according to Millais (1904-1906), although they were described as increasing in the newly wooded districts of Wales by Barrett-Hamilton & Hinton (1910-1921). However, there were further declines in the 1920s, with some, but not all, populations subsequently recovering. All these population changes occurred before grey squirrels were introduced to these areas.

Population trends: Following the spread of grey squirrels, the red squirrel has shown a steady decline in England and Wales in both range and numbers, although in Scotland red squirrels currently occupy more 10 x 10 km squares than they did 50 years ago due to increased afforestation (Gurnell & Pepper 1993). Using index numbers derived from the Forestry Commission's annual surveys over the period 1973-1988, Usher, Crawford & Banwell (1992) showed that there has been a dramatic decline in the distribution of the red squirrel in Wales, this being balanced by a modest expansion in Scotland. Compared to the 1988 situation, Usher, Crawford & Banwell (1992) predicted that the red squirrel would contract its range slightly, but none of the runs with their predictive model suggested that the red squirrel should become extinct in Britain or any of the three constituent countries.

However, when evaluating the status of individual populations, it is clear that the future of many is questionable. In England, the Isle of Wight population is probably secure, although it is possible that grey squirrels may become established on the island (Kenward & Holm 1989; Gurnell & Pepper 1993). Furthermore, the population is scattered and hence vulnerable. The populations in Poole Harbour are small and hence also vulnerable. The south Lancashire population is very vulnerable, especially since about half occurs in just one woodland complex, and the Welsh population is small, fragmented and vulnerable. Whether attempts to provide red squirrel sanctuaries in Cannock Chase and Thetford Forest will prove successful remains to be seen (Gurnell & Pepper 1993). Thus red squirrels appear vulnerable to extinction south of a line from Morecambe Bay to the Tees Estuary. Grey squirrels are already expanding into northern England, and the red squirrel populations there are threatened. A survey in 1991 showed that all but four reports of red squirrels in Wales were from state forests, and all but two 10 x 10 km squares with red squirrels also contained grey squirrels (Gurnell & Pepper 1993). The continued expansion of grey squirrels in eastern Scotland (Staines

1986) suggests that many Scottish populations are also threatened.

Population threats: The greatest single threat is competitive exclusion by grey squirrels (Kenward & Holm 1989) which, in deciduous woodland, live at higher densities. Modelling work has suggested that the rate of spread of grey squirrels was reduced due to competition with red squirrels (Okubo *et al.* 1989). Although the two species can co-exist for up to 20 years (Harris 1973/74; Reynolds 1985), red squirrels generally decline when grey squirrels colonise an area and are soon reduced to scattered 'island' populations that may persist for only a few years. In some parts of the Lothians red and grey squirrels appear to be currently co-existing (A.C. Kitchener pers. comm.); at what densities, and whether this is a stable situation, are unknown. Kenward & Holm (1993) showed that in oak-hazel woods, grey squirrel foraging, density and productivity were related to oak and acorn abundance, whereas red squirrels foraged where hazels were abundant, and their relatively low density and breeding success were related to the abundance of hazel nuts. In Scots pine, red squirrels can have densities and breeding success as high as grey squirrels in deciduous woodland.

Red squirrels cannot fully exploit acorn crops, and have a digestive efficiency for acorns of only 59%, apparently because they are much less able than greys to neutralise acorn polyphenols. Kenward & Holm (1993) developed a model to examine the competition for the autumn hazel crop, which was eaten by grey squirrels before the acorn crop, and showed that red squirrels are unlikely to persist with grey squirrels in woods with more than 14% oak canopy. They concluded that with oaks in most British deciduous woods giving grey squirrels a food refuge which red squirrels fail to exploit, replacement of red squirrels can be explained by feeding competition alone, exacerbated by the post-war decline in coppiced hazel. Furthermore, red squirrels increase their body weight in late autumn by about 10%, whereas grey squirrels increase their weight by about 20% (Kenward & Tonkin 1986). This makes red squirrels more vulnerable to food shortages during the winter period. This is most likely to occur where the two species coexist and are competing for food resources (Gurnell & Pepper 1993). Since maintenance of body weight is important for reproduction, reduced reproductive success rather than reduced survival may explain why red squirrels have declined in conifer forests that also contain grey squirrels. This may also explain why red squirrels have managed to coexist with grey squirrels in Thetford Forest but continued to decline (Gurnell & Pepper 1993).

Red squirrels feed mainly in the tree canopy and spend about 70% of their time off the ground (Kenward & Tonkin 1986); thus they need continuous tree canopy, and habitat fragmentation is likely to pose a significant problem. The impact of habitat fragmentation was demonstrated by Bright (1993), who found that, in south Lancashire, those woods more than 5 km from a major red squirrel nucleus were unlikely to have red squirrels. Also, small areas of woodland are unlikely to provide adequate food resources in years of seed shortage.

Overall, the threats to red squirrel populations suggest that it is unlikely that large numbers will survive except perhaps in a few areas of extensive conifer woodland in Scotland, and in smaller numbers on islands such as the Isle of Wight, so long as they remain free of grey squirrels. A management strategy for conserving red squirrels is described by Gurnell & Pepper (1993). A further problem to consider is the status of British red squirrels; originally a distinct sub-species, introductions of European stock during the 18th and 19th century may mean that the endemic red squirrel in Britain is no longer validly distinct (Lowe & Gardiner 1983).

Grey squirrel *Sciurus carolinensis*

Status: Introduced in the 19th and early 20th centuries; common and increasing.

Distribution: Generally distributed in most of England and Wales, and patchily distributed in the central belt of Scotland and the east coast north to Aberdeen.

Population data: Found in areas of mature broadleaved forest, mixed forest, and mature conifers; also in suburban and urban areas. There are occasional records of grey squirrels from virtually every other habitat, but these rarely represent resident populations. Densities averaged over several years are usually greater than 2·0 per ha and often much greater e.g. a mean of 7·4 per ha in oak woodland in southern England (Gurnell 1983), although annual densities ranged from 5·2-9·8 per ha (Gurnell 1989). Summer densities for all types of British woodland are likely to be 1·5-4·0 per ha, with spring densities even lower (R.E. Kenward pers. comm.). For three oak-hazel woods in England, the mean pre-breeding density was 2·3 per ha for 14 site years and the summer density was 2·7 per ha (Kenward & Holm 1993). For 34 mixed woodland sites, all with some plantation, pre-breeding density was 1·6 per ha and summer density 2·1 per ha (Kenward & Parish 1986). Densities in broadleaved and mixed conifer/broadleaved woodland range from 2 to 8 per ha (Gurnell 1987), although occasionally higher densities (up to 16 per ha) can occur (Shorten & Courtier 1955). Since grey squirrels show reduced trapability in the autumn and winter, these data refer to spring and summer populations.

Long-term densities in pure coniferous woodland are not known. In Wareham Forest, Dorset, densities of 2·0 and 3·6 per ha were recorded in good Scots pines *Pinus sylvestris*, and 1·1 per ha pre-breeding and 1·6 per ha for summer in mature Corsican pine *Pinus nigra* (R.E. Kenward & S.S. Walls pers. comm.). However, both these were good conifer habitats, and most plantations will have fewer grey squirrels. Thus a study in Thetford Forest, Norfolk, suggested that there were considerably fewer than 1 per ha. In eight upland conifer sites in the Upper Derwent valley in the Peak District, pre-breeding density was 0·5 per ha, and post-breeding density 0·7 per ha (R.E. Kenward & C.A. Walls pers. comm.).

There are a number of problems when trying to estimate the number of grey squirrels in Britain. Populations show annual cycles, with peaks in the autumn before dispersal and troughs in the spring before recruitment. In addition there are annual variations in numbers depending on food availability (Gurnell 1991b), and densities are dependent on the tree species present. The problem is confounded by the absence of data from low density habitats (Gurnell 1991b). Also, grey squirrel numbers are particularly difficult to estimate for suburban and urban areas. Bird table feeding, litter-bin scavenging and direct feeding in gardens and parks means that these habitats probably support higher numbers than the highest rural woodland populations, and one poison-baiting exercise on the outskirts of London suggested a kill approaching 14 grey squirrels per ha (H.W. Pepper pers. comm.).

In 1986 B. Mayle and J. Rowe (pers. comm.) calculated the minimum and maximum numbers of grey squirrels, taking the area of colonised woodland to be 431,826 ha in England, 28,280 ha in Scotland and 3790 ha in Wales, and minimum and maximum densities of 2 per ha and 12 per ha in England and Wales but with a maximum density of 6 per ha for Scotland. They concluded that there were 865,000-5,180,000 grey squirrels in England, 57,000-170,000 in Scotland, and 7600-45,000 in Wales, i.e. a total population between just under 1,000,000 and 5,400,000. However, the density estimates used for this calculation were considerably higher than the typical densities detailed above. Therefore, to calculate the pre-breeding population of grey squirrels, the area of suitable habitat in those counties currently colonised by grey squirrels and the following pre-breeding densities were used: 2·5 per ha in semi-natural broadleaved and mixed woodlands; 1·5 per ha in broadleaved and mixed plantations, parkland and tall scrub; 0·5 per ha in semi-natural coniferous woodlands and coniferous plantations; and a mean of 0·1 per ha for all built-up habitats.

Population estimates: A total pre-breeding population of about 2,520,000; 2,000,000 in England, 200,000 in Scotland and 320,000 in Wales. **Reliability of population estimate:** 3.

Historical changes: The first record in Britain was from Denbighshire in 1828, and a number of records exist for Montgomeryshire prior to 1830. The earliest documented introduction was to Macclesfield, Cheshire, in 1876. From then until 1929 there were a number of introductions around the country. It became illegal in 1938 to import grey squirrels or to keep them in captivity (Lever 1977). The subsequent spread of grey squirrels is described by Middleton (1931), Shorten (1954) and Lloyd (1983), amongst others. The period of greatest range increase in England and Wales was 1930-1945, when the species became entrenched in the midlands and most of the south of England apart from Cornwall. East Anglia remained largely free of grey squirrels but animals were found as far north as Cheshire and north Wales in the west and north Yorkshire in the east. Thereafter the spread has continued more slowly (Gurnell 1991b), but in the decade following World War Two they increased in abundance in the north, parts of East Anglia, and parts of Wales. A bounty system in the 1950s failed to reduce grey squirrel numbers or prevent their spread (Thompson & Peace 1962). In England, by the early 1960s only parts of Cumberland, East Anglia, north Lancashire and Westmorland remained largely uncolonised. Williamson & Brown (1986) described the pattern of spread as random dispersal with occasional major advances. Okubo *et al.* (1989), using Reynold's (1985) data from East Anglia for the period 1965-1981, estimated a mean rate of spread of 7·7 km per year.

Population trends: The spread of grey squirrels is continuing, but changes since 1973 have been relatively small. Using Forestry Commission survey results, and calculating index numbers, Usher, Crawford & Banwell (1992) showed that in England and Wales grey squirrel distribution is nearly stable, but in Scotland there has been a steady increase through the 1980s. However, grey squirrels continue to expand their range in north-west England; they are now more abundant than red squirrels in north Lancashire, and are well established in the Lake District as far north as Windermere and Ambleside (Lowe 1993). Predictive models suggest that the grey squirrel will continue to expand its range in Britain slightly, and should become more than twice as widespread as red squirrels (Usher, Crawford & Banwell 1992). Also, grey squirrels 'leap-frog' through unsuitable habitats (Reynolds 1985; Staines 1986), and in Scotland may spread (or possibly be spread) over hills to colonise river valleys (Staines 1986). Thus it is not clear what natural barriers will limit the spread of grey squirrels, nor what their final distribution or numbers will be. Their spread in Deeside has been slow; although they arrived in the early 1970s, they are still largely confined to estates or large gardens with mature deciduous trees and are very much restricted in range and density (B. Staines pers. comm.). However, a survey in 1991 found grey squirrels were present only 25 km south of Huntly in Aberdeenshire, and so the northern limit to their spread has not yet been established (Gurnell & Pepper 1993). The numbers killed nationally show no clear long-term trend, and overall have remained roughly constant from 1960-1990, although there are considerable annual variations, probably due to fluctuations in seed crops (Tapper 1992).

Population threats: None.

Bank vole *Clethrionomys glareolus*

Status: Native; very common.

Distribution: Found throughout mainland Britain and on Anglesey, Bute, Handa, the Isle of Wight, Mull, Raasay and Ramsey; the sub-species on the island of Skomer is dealt with separately below. Bank voles were found between 1966 and 1970 in the Brodick Castle area of the Isle of Arran, probably the result of an unrecorded recent introduction (Gibson 1973).

Population data: Bank voles prefer areas of mature mixed deciduous woodland with a thick shrub or field layer, but in Britain they are also found in grassland habitats, young deciduous plantations, conifer plantations and hedgerows (Alibhai & Gipps 1991). Populations in Britain are non-cyclic and do not attain very high densities. Numbers reach a peak in the autumn followed by a decline over winter and spring, and in some years numbers tend to increase from winter to summer after winter breeding. Numbers may fluctuate dramatically, and are significantly greater in the summer following a good seed crop than after a poor one (Mallorie & Flowerdew 1994). Thus densities can vary from 5 to (exceptionally) 130 per ha depending upon season and habitat. Good densities for bank voles in woodland would be 23 per ha in winter and 66 per ha in summer (H.C. Mallorie & J.R. Flowerdew pers. comm.). In linear features in arable areas, a density of 60 per km of hedgerow would be typical for hedgerows of reasonable quality; the actual density does not change significantly during the year, although during the summer bank voles will move from the hedgerows into the crops (Tew & Macdonald 1993; Tew 1994).

Samples from pellets (Table 5), bottles (Table 6) and traps (Table 7) all show that bank voles are rarer than wood mice, and overall the ratio of wood mice to bank voles is 1·7:1 (Table 8). This is in part due to the fact that wood mice colonise a greater range of habitats than bank voles, which are more dependent on cover. The following data were used to calculate pre-breeding population size: for linear features an average of 40 per km of all types of hedgerow in arable areas, 10 per km in pastoral areas and 5 per km in marginal upland areas; a mean of 10 per ha for semi-natural broadleaved woodlands; 5 per ha in semi-natural mixed woodlands and scrub, 2·5 per ha in broadleaved and mixed plantations and semi-natural coniferous woodlands, and 1 per ha in coniferous and mixed plantations and bracken.

Population estimates: A total pre-breeding population of about 23,000,000; 17,750,000 in England, 3,500,000 in Scotland and 1,750,000 in Wales. A high proportion of the population is in England because this is where the majority of the hedgerows in arable landscapes are found; hedgerows in arable landscapes in England alone contain over a third of the British pre-breeding bank vole population. This estimate for the total bank vole population also suggests a ratio of 1·7 wood mice per bank vole, which is the same ratio as in the samples summarised in Table 8.
Reliability of population estimate: 3.

Historical changes: Bank voles were not recognised until 1832, but were subsequently found to inhabit a wide area in Great Britain, although for many years bank voles were considered to be rather uncommon in places where they were found to be plentiful later that century (Harting 1887). It is unlikely that this observation reflects anything except a lack of recording (Millais 1904-1906), although at the turn of the century they were still thought to be scarce in northern Scotland.

Synchronous countrywide reductions in woodland rodent populations were indicated by Southern's (1970) analysis of tawny owl *Strix aluco* breeding success. In particular, bank vole (and wood mouse) numbers were low in the springs of 1955 and 1958, leading to low nesting activity and breeding success of the tawny owls in those two years. To look for evidence of, and reasons for, synchronous population fluctuations in woodland rodents, the Mammal Society initiated a long-term woodland rodent trapping survey, which involved trapping every May/June and November/December; the preliminary results for 17 sites for up to six years each during the mid-1980s are presented by Mallorie & Flowerdew (1994). This study confirmed the synchronous dynamics of bank vole populations over wide geographical areas, with tree seed crops having a strong influence on numbers the following summer and a weaker one on numbers in the winter following the seed crop. In addition there is evidence of density dependence in both summer-autumn and winter-spring periods, possibly regulated by the curtailment of the breeding season at high densities (Alibhai & Gipps 1985). Thus bank vole numbers were low in the summer of 1982, following the very cold winter of 1981-1982 and the failed seed crop the previous year (Tubbs 1986; J.R. Flowerdew pers. comm.).

Population trends: Unknown. In general, bank vole numbers are probably as great now as they have ever been. Future fluctuations in numbers will depend on the seed crop of woodland trees and to some extent the severity of winter weather (J.R. Flowerdew pers. comm.). Also, in view of the large proportion of the population found in arable landscapes, this species may benefit substantially from changes such as hedgerow planting, farm woodland schemes, and long-term set-aside. However, large-scale hedgerow losses (Barr *et al.* 1993) probably led to significant population declines.

Population threats: None known.

Skomer vole *Clethrionomys glareolus skomerensis*

Status: Native; locally common.

Distribution: Confined to the island of Skomer, south-west Wales.

Population data: They are closely associated with dense cover of bracken and bluebells, where peak densities can reach 475 per ha (T.D. Healing pers. comm.). Population estimates were made during surveys of small mammals on the island in 1960, 1981 and 1992 (Fullagar *et al.* 1963; Healing *et al.* 1983; T.D. Healing pers. comm.), combining live-trapping data from seven trap lines and two grids to produce a total population estimate. By this means, the population was estimated to be 21,536 in 1960 (Fullagar *et al.* 1963), 21,161 in 1981 (Healing *et al.* 1983) and 19,859 in 1992 (T.D. Healing pers. comm.). These were all late summer populations; assuming the winter population is roughly 35% that of the summer population suggests a pre-breeding population of 7000 voles.

Population estimates: A total pre-breeding population of about 7000 voles on an island of 290 ha, all in Wales. **Reliability of population estimate:** 1.

Historical changes: Unknown.

Population trends: The results of the surveys quoted above suggest that the population is stable, although interpreting data from such widely spaced surveys is difficult. About 70% of the voles on Skomer are found in dense bracken and bluebells. This habitat occupies about 15% of the surface area of the island, a proportion which has varied little in the last 30 years (Fullagar *et al.* 1963; Healing *et al.* 1983; T.D. Healing pers. comm.). Thus it is probable that the population of voles has also remained relatively stable. However, trapping on one grid in August from 1977 to 1981 inclusive revealed densities of 224, 145, 122, 218 and 318 voles per ha in each year; whether these fluctuations follow a regular cycle over the years is unknown (Healing *et al.* 1983).

Population threats: None known. The 1992 population survey found a significant increase in the number of wood mice on the island. Whether this will be detrimental to the vole population is unknown.

Field vole: *Microtus agrestis*

Status: Native; locally common.

Distribution: Widespread on the British mainland. Field voles occur on most of the Hebridean islands, but are absent from Barra, Lewis and some of the Inner Hebrides (Colonsay, Pabay, Raasay, Rum, Soay and South Rona). Field voles are also absent from the Isles of Scilly, Lundy, Orkney and Shetland.

Population data: Mainly found in rough, ungrazed grassland, including young forestry plantations with a lush growth of grass. Low population densities occur in marginal habitats such as woodlands, hedgerows, blanket bog, sand dunes, scree and open moorland; field voles have been recorded at over 1300 m in the Cairngorms (Gipps & Alibhai 1991).

There are both cyclic and annual changes in abundance. Richards (1985) reviewed the field vole studies carried out at the Wytham estate, Oxfordshire, from 1949 to 1978. He concluded that these populations showed annual, rather than cyclic, fluctuations, and he attributed this to the patchy nature of the habitat available to the field voles in Wytham. It seems likely that habitat type influences field vole population dynamics, and that vole cycles occur where there are extensive areas of habitat, such as upland forestry plantations, rather than in small patches of habitat. In Scotland and north England, there seems little doubt that field vole populations cycle (Snow 1968; Marchant *et al.* 1990). In southern England the situation is less clear; studies in Sussex farmland suggest cyclical fluctuations (Tapper 1979), whereas in Cambridgeshire and Leicestershire Village & Myhill (1990) found fluctuations in numbers that could be considered cyclic in arable land but not so much in mixed farmland. These cyclical changes make estimating population sizes difficult.

Estimating field vole numbers is also complicated by populations being very patchily distributed at the landscape level. This clumped distribution means that they are easily missed by trapping (D.J. Jefferies pers. comm.), and so density estimates for such a patchily-distributed species are largely meaningless. Although the species is both widespread and abundant, there are few estimates of population density, and most density estimates are from isolated fragments of suitable habitat, and so are probably atypical. Tapper (1979) calculated a density of 100 per ha for spring populations in suitable grasslands in southern England, with peak densities of 300 per ha. Ferns (1979) recorded 97 per ha in spring in a young larch plantation, reaching a peak of 128 per ha in early winter. Whilst field voles occur in the grassy banks of arable hedgerows, densities are low (Tew 1994). Densities vary from 1 to 15 per ha in mixed farmland in Morayshire (M.L. Gorman pers. comm.). There are no recent data on densities from upland areas, especially for Scotland and Wales, yet these habitats probably contain the great majority of the field vole population. The final problem when trying to estimate field vole numbers is calculating how much habitat is available to support such high densities.

Since there are few density estimates, and the availability of suitable habitats is unknown, the only basis on which to estimate the size of the field vole population is from their relative abundance in a wide range of samples (Table 8). This showed that, nationally, field voles were 1·9 times as common as wood mice and 1·8 times as common as common shrews. This suggests a pre-breeding population of 75,000,000 field voles. Estimating the distribution by country was more problematic, since there are relatively few samples from upland and other habitats from Scotland and Wales (see Tables 5-7). The figure for each country was obtained by deriving approximate ratios to common shrews and wood mice in arable, pastoral, marginal upland and upland habitats in Scotland and Wales, and using the availability of these habitat groupings and the estimated numbers of common shrews and wood mice in these habitat groups.

Population estimates: A total pre-breeding population of about 75,000,000; 17,500,000 in England, 41,000,000 in Scotland and 16,500,000 in Wales. The skewed distribution of field voles between the three countries (England: 56·6% of the land area and 23·3% of the field vole population; Scotland: 34·4% of the land area and 54·7% of the field vole population; and Wales: 9·0% of the land area and 22·0% of the field vole population) is because field voles now appear to be strongly biased in their distribution towards upland areas. In lowland areas this species is now very clumped in its distribution. It should be remembered that, in the absence of many density estimates, these figures are based on

relative abundance to other species of small mammal, and that for many habitats, e.g. upland areas of Scotland, there are very few samples on which to base this analysis.
Reliability of population estimate: 4.

Historical changes: At the turn of the century field voles were abundant throughout Great Britain wherever there was sufficient grassland (Thorburn 1920). Since then, field vole populations have almost certainly declined substantially due to the loss of rough grassland by both natural and anthropogenic changes, the removal of linear features and the general tidying-up of the rural landscape. This reduction in field vole numbers has led to a cessation of the vole plagues that were frequent until early this century (Ritchie 1920; Elton 1942). Whilst such vole plagues were comparatively rare in Britain, when they did occur, the numbers of voles were compared to swarms of locusts, devastating agricultural crops and barking young trees. In 1891-1893, for instance, there was a great increase in the vole numbers in the area of the Scottish border, and 370-470 km² were infested with voles, with parts of this area rendered useless (Millais 1904-1906).

The field vole is a major food item for a number of predators. Snow (1968) concluded that the number of fledgling kestrels *Falco tinnunculus* ringed showed a strong relationship with field vole numbers. Using ringing records for 1926-1966 from lowland Scotland, north England and north Wales, he concluded that peaks in vole numbers occurred in 1926, 1930, 1932/1933, 1937/1938, 1957, 1961 and 1964. The data in Marchant *et al.* (1990) suggest further peaks in 1968 and 1972/1973, and are then difficult to interpret until further peaks occurred in 1981 and 1984. A large-scale sampling programme in Cambridgeshire and Leicestershire (Village & Myhill 1990) also suggests that field vole numbers in arable farmland reached a peak in 1981 and 1984, and possibly in 1987. These peaks also coincided with the peaks in abundance of field voles in south-west Scotland (Taylor *et al.* 1988). Records from the early 1940s showed that in southern England cyclical fluctuations in kestrel numbers were barely detectable (Snow 1968; Marchant *et al.* 1990), possibly because of the lack of synchrony of local vole populations or a lack of cycles (J.R. Flowerdew pers. comm.).

After myxomatosis, vole populations benefited from the increased grass growth, and their habitats expanded greatly (Sumption & Flowerdew 1985). This is corroborated by studies of the numbers of weasels taken by gamekeepers; after myxomatosis the numbers of weasels killed increased markedly until the early 1970s in both Suffolk and Sussex (Tapper 1982; King 1989), suggesting higher levels of prey availability, at least until the early 1970s. In addition, peaks in the number of weasels killed and vole peaks are probably correlated (with a slight delay); thus in Suffolk the number of weasels killed peaked in 1953, 1956, 1960, 1964, 1967, 1970 and 1973, probably as a direct result of field vole peaks (Tapper 1979), but thereafter the recovery of rabbits and stoats confuses the picture. Some at least of these peaks in vole numbers appear to be widespread. There was a vole plague in the Carron Valley, Stirlingshire, in 1953/1954 (Lockie 1956), and in 1956/1957 vole numbers throughout Wales reached plague levels, and this was more widespread than any previous vole plague in living memory. During this plague, damage to forestry was extensive (Cadman 1957), as used to occur earlier this century (Elton 1942). Thus it seems likely that there was a general increase in field vole numbers, and in distribution on a local scale, in the mid-1950s to early 1970s, which subsequently fell from the mid-1970s as rabbit numbers increased and suitable habitats consequently declined.

Population trends: Numbers have been declining since the mid-1970s, when habitats were lost due to an increase in grazing pressure following the increase in rabbit numbers and intensive agriculture, especially in the south. Field voles also like 'marginal land', exactly the sort of habitat that has positively attracted development in the south-east, so that much suitable habitat has been lost to roads, houses and out-of-town industrial and trading estates. There has also been a significant loss of habitat because grassland is a transitional type of vegetation, and it is lost by scrub encroachment if not managed. Managing grassland in a way that maintains its suitability for field voles is not cost-effective in the lowlands. This reduction in field vole numbers, and perhaps also a reduction in their accessibility to aerial predators, seems to have contributed to the decline in the numbers of barn owls *Tyto alba* (Shawyer 1987). An increase in permanent (but not rotational) set-aside (Brockless & Tapper 1993), woodland planting schemes and other landscape management practices that increase the area of rough grassland should increase the amount of available habitat, and hence field vole numbers. However, the increase in rabbit numbers will further increase grazing pressure and thereby help limit field vole numbers, and so if there is any overall population increase due to changes in agricultural policy, it is unlikely to be as large as that which occurred in the mid-1950s.

Population threats: Continuing loss of habitat may lead to a further decline in numbers, especially in the south, and this problem is likely to be exacerbated by the increasing number of rabbits, although this may be partially off-set by the increase in long-term set-aside.

Orkney vole *Microtus arvalis orcadensis*

Status: Introduced to Orkney, probably by Neolithic settlers before 3500 BC. The skull characteristics of Orkney voles suggest that their affinities are more with populations in south Europe than elsewhere, and that they probably came with early settlers from the eastern Mediterranean (Berry & Rose 1975). It is common where it occurs.

Distribution: Confined to six of the Orkney islands: Mainland, Rousay, Sanday, South Ronaldsay, Stronsay and Westray. There is a pellet record from Eday in 1965, and two recorded introductions to the same island involving a few voles in 1987 and 1988 (Arnold 1993).

Population data: Within the intensively managed agricultural landscapes that now dominate Orkney, the voles are largely confined to linear features which maintain very high population densities and also serve to connect otherwise fragmented pieces of natural habitat (Gorman & Reynolds 1993). Voles used to be present in agricultural habitats in Orkney e.g. in rich grass and clover fields (Millais 1904b) and in both pasture and arable fields in the 1940s (Hewson 1951). The current marked absence of voles from agricultural areas in Orkney, may be due to the particularly intensive nature of current land management on the islands, especially the high stocking rates and the extensive areas devoted to silage (Gorman & Reynolds 1993).

To calculate total population size, density estimates were made for a variety of habitat types on Mainland in July-August by snap trapping and Longworth trapping over a three-year period and averages calculated. These gave densities of: damp heath 273 per ha, heather moorland 102 per ha, marsh 57 per ha, coniferous plantation with grass understorey 129 per ha and pasture 0 per ha (Gorman 1991). Land cover estimates for those Orkney islands which have voles were based on the Macaulay Land Use Research Institute's land classification system. Combining these figures produced an estimated annual low in April of 1,000,000 voles, and an annual high in September of 4,000,000 voles (M.L. Gorman pers. comm.).

Population estimates: A total pre-breeding population of about 1,000,000, all in Scotland.
Reliability of population estimate: 1.

Historical changes: Only recognised as a member of the British fauna at the turn of the century (Millais 1904b); at that time it was widespread (but probably locally distributed) in Orkney in both natural and man-made habitats. However, Orkney voles have disappeared from agricultural areas in the last fifty years, and it is likely, therefore, that there has been a very substantial decrease in vole populations since the Second World War (Gorman & Reynolds 1993).

Population trends: Numbers have been declining, probably substantially, through agricultural pressures, especially the loss of heath and moorland. On Orkney Mainland alone it is likely that habitat that could support over 100,000 voles has been lost from what was once moorland (Gorman & Reynolds 1993). However, this decline may have halted, since the rate of loss of habitat to agriculture has decreased (M.L. Gorman pers. comm.).

Population threats: Since 1936 the area of Orkney used for agriculture has increased from 37% to 81% at the expense of natural habitats. This has led to a very substantial reduction in vole populations, and population fragmentation and isolation has increased (Gorman & Reynolds 1993).

Water vole *Arvicola terrestris*

Status: Native, and probably still moderately common, although declining.

Distribution: Found throughout mainland Britain but mainly confined to lowland areas near water. Water voles are very locally distributed in north and north-west Scotland and absent from most islands, but present on Anglesey, Bute, the Isle of Wight, and a few small islands. In Scotland they are found in headstreams up to 660 m altitude, but most populations occur at altitudes of less than 50 m (D.J. Jefferies pers. comm.). They are more numerous in upland and peatland habitats than formerly thought (Green & Green 1993).

Population data: Estimating population size is difficult because, on some river systems at least, water voles are patchily distributed around 'core sites', and their distribution is discontinuous because some sites are unsuitable or are too remote from existing populations (Lawton & Woodroffe 1991). Of 2970 sites surveyed in Britain in 1989-1990, 47·7% were positive for water voles (Strachan & Jefferies 1993). For each water authority region in England, the percentage of sites positive for water voles and the number of water voles per km of bank (in brackets) were: Anglian 63·2% (42·5); North West 34·5% (29·3); Northumbria 52·6% (32·7); Severn Trent 34·9% (32·7); South West 8·1% (17·2); Southern 68·5% (42·6); Thames 70·8% (41·5); Wessex 34·5% (28·6); Yorkshire 35·7% (29·6); and in mainland Scotland 26·5% (32·1) and Wales 15·0% (28·0) (Strachan & Jefferies 1993). The actual number of animals per km was calculated from the number of latrines found, using the formula described by Woodroffe, Lawton & Davidson (1990a). Based on the lengths of aquatic habitats given in Table 4, this gave a total population size of 3,895,000 water voles, with 2,506,000 in England (Anglian region 768,000, North West region 137,000, Northumbria region 221,000, Severn Trent region 315,000, South West region 20,000, Southern region 380,000, Thames region 379,000, Wessex region 103,000 and Yorkshire region 183,000), 1,254,000 water voles in mainland Scotland and 135,000 water voles in Wales. For this calculation it was assumed that for rivers and canals both banks are used by the same water voles. For wider waterways this will not be true, and for these the length of bank should theoretically be doubled, thus increasing the population estimate slightly. Also, these figures are for the summer, and the winter population is likely to be only 30% of this (Woodroffe 1988) i.e. 1,168,500.

Population estimates: A total pre-breeding population of about 1,169,000; in England 752,000, in Scotland 376,000 and in Wales 41,000. **Reliability of population estimate:** 3.

Historical changes: At the turn of the century water voles were abundant in all suitable localities in England, were found in all low-lying districts of Scotland except Argyll, and were common in the streams of Anglesey and North Wales, but were comparatively scarce in south Wales (Millais 1904-1906). Subsequently there has been a long-term decline (Jefferies, Morris & Mulleneux 1989; Strachan & Jefferies 1993). Jefferies, Morris & Mulleneux (1989) showed a statistically significant decline in the use of words such as 'common' to describe water voles in local mammal reports, although such information could not be used to quantify the magnitude of the decline. A recent field survey (Strachan & Jefferies 1993) showed that there has been a steady long-term decline this century, with two periods of accelerated site loss, the first in the 1940s/1950s, and the second within the last two decades. The first decline was most marked in northern and western Britain and may correlate with increased afforestation and subsequent acidification of waterways (Harriman & Morrison 1982; Nature Conservancy Council 1986). The second period of loss, most marked in the 1980s, is correlated with the spread of mink (Strachan & Jefferies 1993). Prior to, and in addition to, the escape of mink from farms, habitat destruction by riparian engineering works causing fragmentation and isolation of colonies, coupled with water pollution, acted as cumulative factors which also contributed to this decline. Since 1900, 68% of occupied water vole sites have been lost, and this could be as high as 77% (Strachan & Jefferies 1993). Also, the number of voles at each site is believed to decline with the percentage of occupied sites, and so the reduction in water vole numbers has been even greater (D.J. Jefferies pers. comm.).

Population trends: Continuing to decline. Calculating the rate of decline this century, Strachan & Jefferies (1993) estimate that by the end of this century 94% of formerly occupied sites may be lost, with an even greater reduction in water vole numbers, making this the most dramatic population decline of any British mammal this century .

Population threats: There is no conclusive evidence as to what has led to the decline; predation by mink *Mustela vison*, habitat destruction, human disturbance, pollution (especially by organochlorine insecticides in the 1950s and 1960s), increasing numbers of cattle grazing river banks and thereby reducing the available cover, and climatic changes have all been mooted as causal factors. Nationally, the relative contribution of any or all of these is at present unknown (Jefferies, Morris & Mulleneux 1989). A study in the North Yorkshire Moors National Park showed that gaps occur in the distribution of water voles because some habitats are unsuitable (approximately 45% of sites examined), and of sites with suitable habitat, about 30% lack water voles because they are too isolated, thereby reducing colonisation rates, and/or suffer very high levels of mink predation (Lawton & Woodroffe 1991). Other studies have shown that mink predation can have a significant impact, at least locally (Woodroffe, Lawton & Davidson 1990b), and a survey in 1989-1990 showed that water voles had declined in numbers, particularly where mink were present (Strachan & Jefferies 1993). The questionnaire survey by Jefferies, Morris & Mulleneux (1989) also identified the presence of mink as being an important factor leading to the decline of water voles. However, there is good evidence that the population decline had begun well before mink became widespread, probably due to pollution and habitat degradation, and so a number of, probably inter-acting, factors have played a role in the decline of water voles.

It appears that the effects of predation are exacerbated by the water vole's specialised habitat requirements, and the loss of populations in marginal habitats due to predation can lead to increasing fragmentation of populations in prime habitats, thereby increasing the potential for population losses due to chance events. The interactions of predation, isolation, fragmentation and habitat quality are presently unknown (Lawton & Woodroffe 1991). However, Howes (1979) presented some interesting data from Yorkshire comparing fox and barn owl predation on water voles in adjacent areas where the vegetation had or had not been removed. Water voles occurred in 24·5% and 8·1% of fox scats and represented 13·2% and 1·6% of barn owl prey items respectively from sites without and with bankside vegetation. Clearly, vegetation loss renders water voles susceptible to a wide variety of predators and not just mink. The relative impact of different types of predators on water vole populations has yet to be determined. The results from a questionnaire survey suggest that disturbance, particularly dredging operations, also have a significant impact on water vole populations (Jefferies, Morris & Mulleneux 1989).

Wood mouse ***Apodemus sylvaticus***

Status: Native; widespread and very common.

Distribution: Found throughout mainland Britain, although absent from many small islands, e.g. the Isle of May, Lundy, North Rona and from the Isles of Scilly other than Tresco and St Mary's (Flowerdew 1991). Many island populations are the result of accidental introductions (Berry 1969).

Population data: Wood mice are highly adaptable and inhabit most habitats if they are not too wet, including woodland, arable land, ungrazed grassland, heather, blanket bog, sand dunes, rocky mountain summits and vegetated parts of urban areas (Flowerdew 1991). Densities vary seasonally, with autumn/early winter peaks and spring/summer troughs; densities of 1-40 per ha are usual in mixed deciduous woodland, but after a good seed crop densities of 130-200 per ha have been recorded, although such high densities are very rare. Montgomery (1989) suggested that the average April-June density for wood mice in mixed deciduous woodland is about 7 per ha. This would also be the typical spring density for coniferous woodland, although densities vary a little depending on the age of the trees and extent of ground cover (W.I. Montgomery pers. comm.). In arable and pastoral landscapes, the length and nature of the field boundary per unit area may be more important than land use in determining absolute density (W.I. Montgomery pers. comm.). In arable areas of Britain, seasonal variation in density is from 0·5 per ha in the summer to 17·5 per ha in winter, with winter peaks as low as 8·4 per ha (Green 1979; Wolton 1985; Attuquayefio, Gorman & Wolton 1986; Wilson, Montgomery & Elwood 1993; Tew & Macdonald 1993; Tew 1994). In mixed farmland on the Moray coast, Grampian, wood mouse numbers varied from 2 to 30 per ha (M.L. Gorman pers. comm.). These low spring densities in arable fields may simply reflect the large size of fields.

There are no data on wood mouse populations in pastoral areas of northern and western England, Scotland or Wales. A study in Northern Ireland in a very similar habitat, where there were 1·9 farms and 9·2 km of field boundaries per km^2, found a density of 3·0 per ha in summer and 2·5 per ha in winter, with 99% of these in field boundaries and only 1% in buildings (Montgomery & Dowie 1993). A study on sand dunes in Scotland suggested that densities range from less than 0·5 per ha in spring to around 12 per ha in the autumn (Gorman & Zubaid 1993). In urban areas, densities can be very high in isolated habitat patches due to restricted dispersal (Dickman & Doncaster 1987), although suitable habitat patches are scattered and overall densities in urban areas are much lower. Marginal habitats for wood mice, such as moorland, grasslands and sand dunes, do not show as marked a seasonal cycle as woodland populations.

Median figures for spring populations were used to calculate the population size. These were: 7 per ha in all types of woodland and scrub; 2·5 per ha in bracken, unimproved grassland and marshy areas; 1 per ha in arable land; and 0·5 per ha in sand dunes, moorlands, improved and semi-improved grasslands, urban areas and other marginal habitats. To calculate the autumn population size, spring densities were multiplied by three (W.I. Montgomery pers. comm.).

Population estimates: A total pre-breeding population of about 38,000,000; 19,500,000 in England, 15,000,000 in Scotland and 3,500,000 in Wales. The autumn population would be about 114,000,000. **Reliability of population estimate:** 3.

Historical changes: As for bank voles, synchronous countrywide reductions in woodland rodent populations were indicated by Southern's (1970) analysis of tawny owl breeding success. In particular, the numbers of both species were low in the springs of 1955 and 1958. The preliminary results for 17 sites monitored for up to six years during the mid-1980s as part of the Mammal Society's survey (Mallorie & Flowerdew 1994) confirmed the synchrony between the dynamics of wood mouse populations over wide geographical areas. During this period, wood mouse numbers were lowest in the summer of 1982, following a poor seed crop the previous autumn and the very cold winter of 1981/1982. The survey showed that wood mouse densities were significantly greater in the winter and the summer following a good seed crop, and that population highs and lows tended to coincide at different sites. This is due to widespread heavy tree seed crops, although at each site different species of tree may be involved. Mallorie & Flowerdew (1994) suggested that weather synchronised the seed crop between species: frosts in spring will destroy newly fertilised tree seeds and fruits, flowers and early seed may be lost during high winds and heavy rain or hail in May/June, and cool wet weather in summer may prevent ripening.

Population trends: Assumed to be stable.

Population threats: There are a number of threats to populations on arable land. Laboratory and field studies have shown that wood mice are susceptible to poisoning by insecticidal seed treatments, herbicidal sprays and methiocarb molluscicide pellets (Tarrant & Westlake 1988; Tarrant *et al.* 1990). They are particularly susceptible to seed treatments because of the attractiveness of seeds as food. Johnson, Flowerdew & Hare (1991) showed that the surface application of molluscicide pellets drastically reduced field populations of wood mice, although applications over several years on the study site failed to produce any long-term depression of wood mouse numbers. This was possibly due to the small size of the study fields, and the presence of hedgerows and nearby woods which supported reservoir populations. The problem would possibly be more significant on larger fields with fewer hedgerows and few nearby wood mouse populations to recolonise the treated fields. Johnson, Flowerdew & Hare (1991) also showed that drilling molluscicide pellets substantially reduced wood mouse mortality.

In addition, harvest has a dramatic affect on recruitment and population density in arable areas. Whilst harvesting itself leads to little mortality, 60% of the wood mice in one study disappeared within ten days of the harvest, and increased predation risks were a major factor (Tew 1992). Further mortality occurred due to stubble burning, although sufficient wood mice survived to overwinter and sustain the following year's population (Tew & Macdonald 1993). A reduction in the use of herbicides, e.g. to produce 'conservation headlands' around the edges of arable fields, leads to an increase in the abundance of both floral and invertebrate food supplies and hence to increased populations of wood mice (Tew, Macdonald & Rands 1992).

Yellow-necked mouse *Apodemus flavicollis*

Status: Native; locally common.

Distribution: Mainly eastern and south-eastern England, the English/Welsh border and southern Wales. There are occasional records outside this range in south-west England and further north to Northumberland.

Population data: This species is largely confined to mature deciduous woodland, and there is some evidence of an association between the distribution of yellow-necked mice and areas of ancient woodland (Montgomery 1978). Marginal habitats include hedges, rural gardens and buildings (Montgomery 1991), and yellow-necked mice enter houses more frequently than wood mice, generally in the autumn (Arnold 1993). An association between the distribution of yellow-necked mice and arable fields has been reported in Essex (Corke 1977), but there is no evidence for this being more widespread (Montgomery 1978).

Yellow-necked mouse numbers reach a peak in late autumn/early winter, and decrease throughout winter and spring. Although a long-term study in Gloucestershire found a marked seasonal cycle (Montgomery 1985), it is likely that this was more extreme than that seen in many populations, and overall autumn populations are around three times higher than spring ones (W.I. Montgomery pers. comm.). There are also variations in peak abundance between years which are positively correlated with mast production. Patterns of woodland management, in particular increasing amounts of conifer planting and the concomitant loss of seed-producing trees, reduce yellow-necked mouse numbers (Yalden & Shore 1991).

Whilst densities can reach 50 per ha in good habitats in the late autumn, long term trapping in an area of ancient woodland in Gloucestershire suggested that good sites would have 10 per ha in the spring and average sites 2 per ha (Montgomery 1980; D.W. Yalden unpubl.). Studies in Kent suggested similar figures, i.e. 3-12 per ha (D. Roberts pers. comm.). Population size was therefore estimated as follows. Based on the figures in Spencer & Kirby (1992), there are approximately 230,000 ha of ancient woodland within the main yellow-necked mouse range (Avon, Berkshire, Dorset, Essex, Gloucestershire, Gwent, Hampshire, Herefordshire, Hertfordshire, Kent, Shropshire, Surrey, Sussex, Wiltshire and Worcestershire). It was assumed that yellow-necked mice are found in all the ancient woodland in these counties, since the documented distribution almost certainly represents under-recording. This is primarily because it is not easy to differentiate the skulls of wood mice and yellow-necked mice (Fielding 1966), and so there are very few records from bottles (Morris 1970) or owl-pellets (Glue 1974). Thus the spring population, at an average density of 2 per ha of ancient woodland, would be around 450,000. This calculation takes no account of yellow-necked mouse populations in habitats other than ancient woodland, and there are also a number of isolated populations outside the contiguous range (Arnold 1993). However, in many areas of apparently suitable habitat the species is transient (J. Gurnell pers. comm.), and coppicing (M. Hicks pers. comm.) and other woodland management practices (Yalden & Shore 1991) adversely affect yellow-necked mouse numbers. Thus, even allowing for these other populations, the total population is unlikely to exceed 750,000. The separate numbers for England and Wales were calculated from the areas of ancient woodland (Spencer & Kirby 1992) and the relative distribution of records (Arnold 1993).

Population estimates: A total pre-breeding population of about 750,000; 662,500 in England, none in Scotland and 87,500 in Wales. **Reliability of population estimate:** 4.

Historical changes: Records from Neolithic and Roman sites indicate that the range was formerly more extensive (Yalden 1984b), and the current distribution suggests that this is a relict of a formerly widespread woodland species (Montgomery 1978; Yalden 1992). It was only recognised as a separate species in 1894 when de Winton (1894) described it as very local, and even at the turn of the century yellow-necked mice were thought to be sporadic in their distribution (Barrett-Hamilton & Hinton 1910-1921).

Population trends: In recent years yellow-necked mice are believed to have been declining, probably both in range and abundance, although the rate and magnitude of any population change is unknown.

Population threats: Being a species that is probably closely associated with ancient woodland, it is very vulnerable to the effects of habitat loss and fragmentation (Harris & Woollard 1990). In addition, a long term study at one site in Gloucestershire has shown that relatively small changes in habitat management can have a significant impact on yellow-necked mouse numbers (Yalden & Shore 1991). In this site, the replacement of deciduous woodland with conifers, and the loss of elms (*Ulmus* spp.) and some yew trees (*Taxus baccata*), caused a significant decline in yellow-necked mouse numbers (Montgomery 1985), probably because they depend on seeds more than other rodents (Hansson 1985). As this one example shows, the combined effects of exacting habitat requirements and habitat fragmentation can have a significant effect on yellow-necked mouse numbers.

Harvest mouse *Micromys minutus*

Status: Probably a post-glacial introduction (Sutcliffe & Kowalski 1976); limited in distribution but locally can occur in large numbers.

Distribution: England south and east of central Yorkshire, plus parts of the coastal belt of Wales; scattered colonies outside this area probably represent long-standing introductions, possibly from last century (Harris 1979a). In particular, most, if not all, the Scottish records represent isolated colonies established as the result of accidental introductions. The only recent record from Scotland was of a colony to the south of Edinburgh that was first reported in the nineteenth century (Harris 1979a). This site has now been destroyed by a housing estate (S. Pritchard pers. comm.). However, searches of suitable habitat in the south and east of Scotland may reveal other colonies.

Population data: Harvest mice are found in areas of dense monocotyledonous vegetation. Most records collected during a survey in the 1970s (Harris 1979a) were from linear features such as hedgerows, ditches, field edges and roadside verges; nowadays they are rarely found in cereal fields. Harvest mice are often the most abundant small mammal in wetlands (M.R. Perrow & A. Jowitt pers. comm.). There are few density estimates because there are particular difficulties in calculating densities for this species. Harvest mice may be patchily distributed, both spatially and temporally. Accurate population estimates in tall vegetation require above-ground sampling, and although the proportion of catches on the ground increases in winter, it is still often less than 10% of the total catch (M.R. Perrow & A. Jowitt pers. comm.). Occasionally, densities can be very high (>200 per ha), but such high numbers are very localised, and peak densities are often followed by several years of low numbers (Trout 1978; Harris & Trout 1991). Mean density estimates between July and October for the following habitats were supplied by M.R. Perrow & A. Jowitt (pers. comm.): 0·05 per ha in barley; 0·4 per ha in wheat; 2·5-5·0 per ha in rough and damp meadows; 20 per ha in reedbeds, although numbers in reedbeds built up to a peak later in the year. Also, the over-winter mortality of harvest mice (from a peak in November) can be greater than 95%, and this is matched by an equally rapid population increase in late summer/early autumn.

In view of the paucity of density data, especially pre-breeding densities, the fragmented nature of the habitats used by over-wintering populations of harvest mice, and the very clumped, and often ephemeral, nature of harvest mouse populations (Harris 1979a), it was impossible to calculate population size from the available density data. Instead the ratio of harvest mice to wood mice in a variety of samples was used. This suggested that there were 26·6 wood mice per harvest mouse (Table 8) i.e. a pre-breeding population of 1,425,000 harvest mice. The distribution of harvest mice in Wales is very patchy, and they seem to be most frequently recorded in *Molinia* grassland on bogs. However, there are no data on which to accurately estimate population size, and so the population in Wales was estimated as follows: pre-breeding density was assumed to be 0·1 per ha of blanket bogs and marginal inundations, and 2 per km of hedgerow in arable areas.

Population estimates: A total pre-breeding population of about 1,425,000; 1,415,000 in England, no colonies currently known in Scotland and about 10,000 in Wales. We need to know a great deal more about population ecology of this species before this estimate can be improved. **Reliability of population estimate:** 5.

Historical changes: Harvest mice are believed to have been accidentally introduced in Neolithic times (Sutcliffe & Kowalski 1976; Harris 1979a; Yalden 1992), and their spread was largely dependent on the clearance of woodlands. How much of this spread was due to natural colonisation as opposed to further accidental translocations is unknown. Many of the isolated populations on the edge of the range are almost certainly due to accidental transport in hay and cereals (Harris 1979a). The species is predominantly eastern in its distribution, and whilst it spread naturally into eastern Europe in post-glacial times, it only became common in Poland in Neolithic times (Nadachowski 1989). It would appear that their subsequent spread into western Europe generally is probably due to accidental Neolithic translocations, and that the current abundance of harvest mice in much of Europe is therefore a comparatively recent event.

This species is easily overlooked (Harris 1979a) and even Thorburn, a competent naturalist living in the centre of its range, recorded that 'I have never succeeded in finding the nest' (Thorburn 1920). Millais (1904-1906) described it as a scarce and local resident in all the counties in which it was found. Thus the paucity of harvest mouse records, other than when specific surveys have been undertaken, means that there are no data on which to assess any long term population changes. A survey in the 1970s recorded harvest mice in 23 Watsonian vice-counties for which there had been no previous records (Harris 1979a), and there is no evidence that there has been a decline in range this century, although some isolated populations that were the result of introductions are known or believed to have disappeared. However, widespread changes in agricultural practice during the course of this century have removed large areas of suitable habitat in which harvest mice appeared to be abundant (Harris 1979b), and numbers must have declined substantially. Even at the turn of the century writers were reporting that harvest mice were much less common than in the middle of the 19th century (Barrett-Hamilton & Hinton 1910-1921), and this decline was attributed to the advent of close-cutting reaping machines. Hardy (1933) even called for the reintroduction of the harvest mouse, arguing that the species was in imminent danger of extinction in Britain. Yet as late as the 1950s, large numbers of harvest mice were still being recorded in cereal ricks, e.g. Rowe & Taylor (1964). However, this habitat disappeared soon afterwards. There are other changes in agriculture which have probably caused declines in harvest mouse numbers since the 1950s. The sowing of winter cereals promotes earlier harvests, before the peak of the harvest mouse breeding season (Harris 1979c), and the shorter-stemmed cereals now grown are less suitable for nest building (Harris 1979a).

Population trends: Since a substantial proportion of the population may now be living in linear features in agricultural landscapes, further agricultural improvements leading to the loss of linear features are likely to lead to further population declines. However, set-aside will rapidly supply additional habitat adjacent to existing populations, and so should benefit this species.

Population threats: As a species living in marginal habitats and wetland areas, populations are vulnerable to habitat changes. A survey in the mid-1970s found that each year 12% of known sites were destroyed (Harris 1979a). In addition, mean litter sizes have declined from 6·75 $\pm$ 0·40 pre-1917 to 5·40 $\pm$ 0·16 in the 1970s; why this decline occurred is unknown (Harris 1979c). Harvest mice seem to favour dry continental climates, and it has been suggested that their distribution in Britain is limited by summer rainfall (Adams 1913). Heavy rain can lead to high juvenile mortality (S. Harris unpubl.), and cold and wet are important climatic factors that terminate the breeding season (Harris 1979c). Thus climate changes could have a significant impact on numbers. Although there are no quantitative data on the diet of harvest mice in Britain, they are known to have a mixed insectivorous and granivorous diet, and so the increasing use of insecticides (O'Connor & Shrubb 1986) could also have contributed to a decline in numbers.

House mouse *Mus domesticus*

Status: Introduced; present in Britain from at least the Iron Age. Locally abundant.

Distribution: Widespread but very patchily distributed throughout mainland Britain and most inhabited off-shore islands. The St Kilda race became extinct following the evacuation of the human population in 1930, apparently due to an inability to compete successfully with wood mice (Berry & Tricker 1969).

Population data: It is particularly difficult to provide a total population estimate, since the reproductive behaviour of house mice is 'boom and bust': very large populations may build up quickly in favourable, often temporary, habitats, and then disappear even more quickly (R.J. Berry pers. comm.). The classic example of this is in the cereal, particularly wheat, ricks that used to be built in the early autumn and then broken down for threshing the following spring. Southern & Laurie (1946) found that almost all ricks were infested with house mice, with some populations exceeding 2000 in a single rick, and with a population doubling time of around two months. However, at threshing these rick populations underwent a very high mortality, even if the statutory barriers around the rick were not used (R.J. Berry pers. comm.). Thus, whilst the national rick population of house mice could be extremely large, it was temporary, but did serve to maintain a constantly-replenished field population. However, threshing is now confined to a few farms (mainly in Somerset and Devon) where long-stalk wheat is grown for thatching, and some of the Scottish islands (R.J. Berry pers. comm.). The main concentrations of house mice in Britain today are probably in hen houses (R.J. Berry pers. comm.).

Although a highly successful commensal species, house mice can live completely independently of man provided that potential competitors are absent (Berry, Cuthbert & Peters 1982). Thus house mice have successfully colonized many islands, where high populations may be attained e.g. up to 500 on the 250 ha island of Faray, Orkney (Berry *et al.* 1992), 450-3250 on the 57 ha Isle of May (Triggs 1991) and 150-5000 on the 100 ha island of Skokholm, with densities of 60 per ha recorded in rock outcrops and grassland (Berry & Jakobson 1975). However, their distribution on the mainland is limited by competition with other small mammals, particularly wood mice (Berry 1991). Hence house mice are rare in British woodlands, and avoid open fields with little cover, although in the late 1950s they were as common as wood mice in agricultural habitats in north-west Scotland and the Hebrides (Delany 1961).

Infestations in farm buildings range from 7 to 362 (mean 70, n = 44), based on trap-outs, with mean population size being lowest in ancillary stores (22) and highest in dairy units (109), with granaries (80) and mixed-food stores (87) being intermediate (Rowe, Swinney & Quy 1983). A survey of 14 different types of agricultural premises in 1974 showed that, in decreasing order of priority, pigs and poultry holdings, general crop holdings, cereal holdings, dairy holdings, mixed holdings, specialist dairy holdings and mainly poultry holdings were most likely to be infested with house mice, all with over 60% levels of infestation. The least likely to be infested were mainly vegetable and mainly fruit holdings, both with less than 25% levels of infestation (Ministry of Agriculture, Fisheries and Food unpubl.). Highest densities have been recorded in buildings with an abundance of food and an absence of common rats (*Rattus norvegicus*): house mouse numbers in buildings seem to be severely restricted by the presence of rats (R.J. Quy pers. comm.). Thus the highest numbers occur in isolated buildings that are rat proof. In Britain 130-300 per ha have been recorded in piggeries (Tattersall 1992), 70,000 per ha in a

Texas hen house (Berry 1991) and even higher densities in commensal situations elsewhere. However, unlike some other parts of their range, British house mouse populations do not exhibit population explosions leading to mouse plagues.

Whilst there is little information on house mouse populations in arable landscapes, there is even less information on house mouse populations in pastoral landscapes. In Northern Ireland, Montgomery & Dowie (1993), in an area with 1·9 farms and 9·2 km of field boundary per km², found a mean density of 6·7 and 35·9 per km² in winter and summer respectively. In winter they were all confined to buildings, but in summer 89% were in field boundaries. However, the numbers indoors in winter varied five-fold between years, from 4 to 20 per km².

In urban areas, house mice are probably more numerous than common rats, and are generally rare away from buildings (Yalden 1980). Thus in London it was estimated that in 1972 9% of buildings were infested with house mice (Rennison & Shenker 1976), although locally higher levels of infestation can occur e.g. nearly 50% in an area of central London (Meyer & Drummond 1980). Anecdotal evidence suggests that urban infestations average 4-5 house mice (R.J. Quy pers. comm.). A survey of house mouse (and common rat) infestations in non-agricultural premises in England and Wales from 1976 to 1979 inclusive showed that house mice were significantly less prevalent in either large towns, i.e. more than 20,000 inhabitants (3·8%), or small towns, i.e. 3000-20,000 inhabitants (3·8%), than they were in rural areas, i.e. those including a village or town up to 3000 inhabitants (5·6%). Infestations showed a regular seasonal pattern, with winter peaks and summer troughs. Also, over the four years of the survey, in all areas the level of prevalence was declining (Rennison & Drummond 1984). In Britain, non-commensal populations increase approximately eight-fold during the breeding season (Berry 1968), but in farm buildings and other situations breeding occurs throughout the year when there is a year-round food supply (Rowe, Swinney & Quy 1983).

Estimating population size is very difficult, because local infestations are erratic in occurrence but may attain many hundreds in number. However, to provide a guide-line on population size, for arable landscapes a pre-breeding density of 20 per km², and for pastoral landscapes a density of 10 per km², were assumed, based on the data from Montgomery & Dowie (1993) and the fact that infestations in farm buildings in Britain (Rowe, Swinney & Quy 1983) generally seemed higher than those recorded in Ireland. This gave a population of 1,540,000 in rural areas in England, 335,000 in Scotland and 23,000 in Wales. To estimate the number of house mice in domestic premises, details of the number of urban and rural households recorded in the 1981 census were obtained from Office of Population Censuses and Surveys (1984). Based on the survey of Rennison & Drummond (1984), it was assumed that 3·8% of urban and 5·6% of rural premises were infested, with a mean of 4·5 house mice per infestation. This gave a total of 2,600,000 house mice in urban, and 395,000 in rural, domestic premises in England; 275,000 in urban, and 47,000 in rural, domestic premises in Scotland; and 140,000 in urban, and 43,000 in rural, domestic premises in Wales.

Population estimates: A total pre-breeding population of about 5,192,000; 4,535,000 in England, 657,000 in Scotland and 206,000 in Wales. These estimates must be considered as minimum figures, since there are no data on the frequency of high-density populations in farms and other premises, and no information on the numbers of house mice in buildings other than domestic premises. **Reliability of population estimate:** 5.

Historical changes: House mice used to be the third most common small mammal (after wood mice and bank voles) in arable land in southern England, forming about a fifth of the small mammals trapped on farmland in the Oxford area (Southern & Laurie 1946).

However, with the advent of combine harvesters and the decline of cereal ricks, house mouse numbers in agricultural land have declined (Southern & Laurie 1946; Davis 1955), probably considerably (R.J. Berry pers. comm.). More recently, Rowe, Taylor & Chudley (1959) only caught house mice on arable land in the late summer/early winter, and several studies in hedgerows on cereal land in East Anglia caught few or no house mice (Pollard & Relton 1970; Eldridge 1971; Jefferies, Stainsby & French 1973). The paucity of house mice in owl-pellets (Table 5), bottles (Table 6) and traps (Table 7) also suggests that house mice are now rare in agricultural landscapes. The presence of common rats around farm buildings seems to reduce the number of house mice (R.J. Quy pers. comm.).

Population trends: It would appear that there has been a dramatic decline in house mouse numbers during this century (see above), although numbers may now be stable, at least in non-rural habitats. During 1993 the Ministry of Agriculture, Fisheries and Food organised a new national rodent survey. The preliminary results show that since the late 1970s there has been no significant change in the overall levels of infestation in non-agricultural premises. Within this broad trend, there has been a significant reduction in the levels of infestation of properties used for business purposes, but there has been a significant rise (from 3·7% to 5·9%) in infestation levels in domestic premises in rural areas. There has been no significant change in infestation levels in domestic properties in urban areas (A. Mayer & A. Shankster pers. comm.)

Population threats: Competition limits the numbers of house mice in non-commensal situations (Tattersall 1992). In commensal situations, pest control measures have substantially reduced house mouse numbers over the last fifty years. However, field and laboratory trials have shown that the toxic effects of agrichemicals such as paraquat and carbofuran on population size and structure may be ameliorated through behavioural mechanisms such as feed aversion and toxicant avoidance (Linder & Richmond 1990). Richards (1989) suggested that a decline in urban infestations in the late 1970s may have been due to the introduction of more effective mouse toxicants.

Common rat *Rattus norvegicus*

Status: Introduced in the first half of the 18th century; common.

Distribution: Found throughout Great Britain except in the most exposed mountain regions and on some of the small off-shore islands (Taylor, Fenn & Macdonald 1991). There are few records from the Outer Hebrides and Shetland (Arnold 1993), but whether this reflects the true status of the common rat there is unclear.

Population data: Common rats are generally limited to habitats where competing species are few or absent or where food supplies are augmented by humans. Very dense populations can occur in favourable habitats. Typically they are associated with farms, refuse tips, sewers, urban waterways and warehouses, and the number of common rats in and around farm buildings increases in October and November as rats move in from the surrounding area (Clark & Summers 1980), although the presence of resident common rat populations may prevent field populations becoming established in farm buildings in the autumn (Taylor 1978). They occur in hedgerows around cereal crops, principally in summer and autumn; in winter around cover crops such as maize and kale planted for game birds; and in root crops, particularly sugar beet, all year round. Certain features nearly always guarantee the presence of common rats away from farm buildings. They are hedgerows, copses and ditches bordering fields of wheat, oats, barley, maize, kale, stubble, turnips and sugar beet, but not oil-seed rape and linseed. Rat numbers are further boosted by game-rearing practices, since wide hedgerows, shelter belts and supplementary feeding of birds provide all that rats need (R.J. Quy pers. comm.). Common rats also occur in areas with dense ground cover close to water, occupying grassland as well as all types of coastline (Taylor, Fenn & Macdonald 1991). Populations independent of man occur in many coastal habitats, and on many islands (e.g. Lundy and Rum).

Populations tend to be high in the autumn and early winter and low in the spring. However, estimating population density is particularly difficult for this species, and a study on three rural rubbish tips showed that estimates based on capture-mark-recapture data and on the rate of bait uptake under-estimated population size by factors ranging from 1·3-7·0 (Taylor, Quy & Gurnell 1981). In 1987, 53% of farm grain stores were infested with rats, and, based on trap-outs, the mean size of infestations on farms on the English/Welsh border ($n = 50$) was 52; in Hampshire ($n = 16$) 155; and in Surrey/Sussex ($n = 24$) 89. Since it is likely that those caught formed about 90% of the rat populations (Quy, Cowan & Swinney 1993), the mean population sizes were 58, 172 and 99 respectively. These variations reflect differences in the area covered by farm buildings, the dominant agricultural activity of the area (the border farms are mainly livestock, the Hampshire farms mainly cereals, and the Surrey/Sussex farms mixed arable crops with livestock rearing) and the ability to control rats (rats on arable farms are more difficult to control than on livestock farms, and Hampshire contains rats that are resistant to many poisons, whilst most rats in Surrey/Sussex are susceptible) (R.J. Quy pers. comm.). This pattern of common rat distribution on farms is also reflected in the pattern of rodenticide usage. A survey in 1990 of 706 farms growing arable crops showed that 54% by weight of all the rodenticide used was in the eastern region, 20% in the northern region and 11% in the south-western region (Olney & Garthwaite 1990).

In the absence of more detailed data on the size of rural rat populations, it was assumed that the pre-breeding population was associated with farm buildings and that there were none in field situations. Data from a survey in 1970 detailed below (Ministry of Agriculture, Fisheries and Food unpubl.) were used to estimate that a mean of 45% of all agricultural premises over 2 ha in England and 34% in Wales were infested with common rats. There were no data for Scotland, but a figure of 40% was selected, which was slightly lower than that for agricultural holdings in the north of England. Data on the number of holdings in 1986 in each of the three countries was obtained from the Government Statistical Service (1988). It was assumed that an average pre-breeding infestation was 60 common rats. Using these figures suggested a rural common rat population of 3,860,000 in England, 870,000 in Scotland and 680,000 in Wales. These must be minimum figures, since there are no data on pre-breeding rat populations in canal banks and other non-agricultural rural habitats.

In urban areas rat populations are smaller, but small and distinct colonies on the surface may be linked to a large population in the sewers. During the 1960s and 1970s, Drummond, Taylor & Bond (1977) trapped out surface infestations in Folkestone, Kent. None were found in open areas such as rough ground, parks or allotments, and at any one time only 0·16% of Folkestone's rateable properties were infested, with an average of 2·2 common rats each. A more extensive survey in England and Wales found that the average level of infestation in rural areas was 7·8% of premises and in urban areas 3·8% of premises in towns of less than 20,000 inhabitants and 2·7% in larger towns (Rennison & Drummond 1984).

To estimate the size of the common rat populations in domestic premises, data for the number of households in rural and urban areas in each country were obtained from the 1981 census (Office of Population Censuses and Surveys 1984). It was then assumed that there was a mean of 7·8% of rural, and 3·25% of urban, domestic premises infested with common rats, with a mean of 2·2 rats per infestation. This gave a common rat population of 270,000 in rural, and 1,110,000 in urban, domestic premises in England, 30,000 and 120,000 respectively in Scotland and 30,000 and 60,000 respectively in Wales. These must also be minimum estimates, since there are no data on which to calculate the size of urban rat populations in buildings other than domestic premises, or in sewers and rubbish tips.

Population estimates: A minimum pre-breeding population of about 6,790,000; 5,240,000 in England, 870,000 in Scotland and 680,000 in Wales. These are minimum estimates because there are no data from a number of habitats permanently occupied by common rats. **Reliability of population estimate:** 4.

Historical changes: The common rat reached England around 1728 and its subsequent spread was rapid. It first appeared in Scotland between 1764 and 1774, but its spread appears to have been slower, and in some remote areas was described as 'recently introduced' as late as 1855 (Matheson 1962). Whilst there was no reliable estimate of the size of the common rat population at the start of the century, it was clearly considered to be a major economic pest, and there were a number of publications on how to exterminate rats, e.g. Ministry of Agriculture and Fisheries (1932). A widely quoted figure for the number of common rats was that of Boelter (1909) who, after a long series of enquiries, assumed that there was not less than one rat to each cultivated acre, or alternatively one rat per human; this gave a minimum population of 40,000,000 common rats. The figure of one common rat per person in Britain is still widely quoted today. However, Hinton (1920) reported that, even when this estimate was produced, it was generally viewed as a significant under-estimate.

In view of the current estimated population size, there must have been a dramatic decline in common rat numbers since the early part of this century. However, there are no accurate data on recent changes in the size of the common rat population in Britain. A survey in 1970 of the distribution and percentage of farms infested with rats in England and Wales found that 20·6% of agricultural holdings over 2·025 ha (5 acres) in size in south-east England had field infestations, whereas 38·3% had infestations in farm buildings. Comparable figures for south-west England were 11·8% and 47·8%, for the east midlands 30·2% and 56·0%, for the west midlands 13·4% and 37·9%, for east England 64·1% and 55·7%, for north England 9·9% and 43·5%, and Wales 7·7% and 34·1%. Rat infestations were more numerous on farmland in east and south-east England and the east midlands than in the remaining four regions, and were most numerous in east England. Infestations in farm buildings were most numerous in east England and the east midlands. The highest infestation rates occurred in the regions with the most arable land, and there was a significant relationship between the incidence of farmland infestations and the percentage of agricultural land under cereals and under root, fodder and vegetable crops and also between the incidence of farm building infestations and the percentage of land under cereals. A survey of 14 different types of agricultural premises in 1974 showed that, in decreasing order of priority, pigs and poultry holdings, cereal holdings and mixed holdings were the most likely to be infested with rats, all with over 60% levels of infestation. The least likely to be infested, in decreasing order, were sheep rearing, mainly vegetable and mainly fruit holdings, all with less than 35% levels of infestation. This second survey also suggested that since the 1970 survey there had been an increase in the number of premises infested (Ministry of Agriculture, Fisheries and Food unpubl.).

A survey of common rat (and house mouse) infestations in non-agricultural premises in England and Wales from 1976-1979 inclusive showed that common rats were associated with 3·6% of the 62,055 premises inspected. Of these, 73·8% were confined to the gardens or other outdoor areas, and only 10·1% were wholly within buildings; of the remaining 16·1%, rats were present both indoors and outside. The situation in towns was significantly different to that in rural areas. In towns, 77·3% of the infestations were wholly external, 12·6% wholly internal and 10·0% mixed. In rural areas the figures were 70·6%, 7·9% and 21·5% respectively. The situation in domestic premises was also significantly different from non-domestic premises. In the former, 84·6% of infestations were wholly external, 7·2% wholly internal, and 8·2% mixed. For non-domestic premises, the figures were 59·0%, 12·8% and 28·2% respectively. Rat-infested premises were most prevalent in rural areas (7·8%), and also significantly more prevalent in small towns, i.e. less than 20,000 inhabitants (3·8%), than in larger towns (2·7%). The percentage of rat-infested premises fell each spring to a low summer value, and then rose each autumn to a winter peak (Rennison & Drummond 1984).

Population trends: The National Game Bag Census data show that the number of common rats killed by gamekeepers has decreased; since this has been coupled with an improvement in control techniques, it is probable that this reflects a real decline in rural rat populations (Tapper 1992). Other factors, such as the loss of habitat, will also have contributed to this decline. These changes include the removal of hedgerows, ditches, etc. to make larger fields and the loss of cereal ricks where, in inter-war years, populations would build up during the winter to reach very high numbers (Venables & Leslie 1942; Matheson 1962). Thus since 1945 the numbers killed in rural areas have been only a small proportion of those recorded earlier (Tapper 1992).

Whilst there has been a dramatic decline in numbers over the last fifty to a hundred years due to the control of rick and urban populations, and the loss of farmland populations, this trend may now have been reversed. During 1993 the Ministry of Agriculture, Fisheries and Food organised a new national rodent survey (for house mice and common rats) in both urban and rural areas. The preliminary results show a significant rise in common rat infestation levels of non-agricultural premises from 4·4% to 4·8%. This rise was most marked in domestic premises in both urban and rural areas, where the rise was from 3·3% to 4·6% (A. Meyer & A. Shankster pers. comm.). One possible factor contributing to this increase is higher crop yields over at least the last 20 years. As a result, there is more food available, and improvements in storage facilities have not kept pace with the increased production, so that more food is stored where it is accessible to rats (R.J. Quy pers. comm.).

Population threats: Populations are locally controlled where numbers become noticeable. However, the spread of resistance to currently available rodenticides is likely to hinder attempts at population control, especially in southern England (R.J. Quy pers. comm.). The general improvements in urban hygiene may have led to population declines in urban areas. In the countryside, however, there has been no such general improvement, and old farm buildings, untidy yards, agricultural dumps, 'fly-tipping' and landfill rubbish tips all contribute to a greater availability of habitats suitable for rats. This will have been offset by the loss of hedgerows and ditches to make larger fields; such changes will have led to population declines (R.J. Quy pers. comm.). Populations used to be extensive in drift mines (Twigg 1961), and the size of the infestation increased with the size of the installation. Furthermore, urban mines had more rats than rural mines, and those in farmland more than those in moorland areas; this agreed well with the distribution of common rats generally (Twigg 1975). However, common rat infestations of drift mines were particularly high around stables, but now that pit ponies are no longer used, these populations of rats have also declined (Twigg 1975). Common rats have never been a problem in shaft mines.

Unlike urban house mouse populations, it is possible to largely eliminate common rats from urban areas, and the concept of 'rat-free towns' has been popular in Europe for some years (Drummond 1985). This involves an active campaign to eliminate existing populations, followed by a substantial improvement in environmental hygiene (Richards 1989). At present only the control of rat populations in sewers is routine in British urban areas.

Ship rat *Rattus rattus*

Status: Introduced at least as early as the 3rd century, with further introductions from ships, which continue to the present day. Since the 1950s, there has been a continued contraction in distribution and most mainland populations appear transient (Twigg 1992).

Distribution: Except for populations on Lundy, Devon, and Carnach Mhor on Garbh Eilean, the main island of the Shiants, Inner Hebrides, records are largely (but not exclusively) confined to port areas. In the period 1985-1989, a questionnaire survey showed that there was an increase in the number of mainland localities (Twigg 1992).

Population data: The following estimates by G.I. Twigg (pers. comm.) were based on the 1989 distribution and how many ship rats were likely to be present at a mainland site, based on a subjective estimate of abundance. At four localities, where control of black rats was needed or was being carried out, it was estimated that an average of 50 rats were present. At those sites where rats were seen occasionally, a mean of 15 rats was assumed. The presence of up to five rats was assumed for temporary occurrences, e.g. the loading bays of multistores and other rapidly changing and unpredictable environments where numbers cannot build up. There were also seven occurrences of isolated animals, in which no more were seen once one animal had been killed, for example at food importers. These estimates suggest 200-300 ship rats were to be found in Britain in 1989 excluding the populations on Lundy and Garbh Eilean (G.I. Twigg pers. comm.).

For Lundy, it is not possible to estimate the total population size. Ship rats persist despite a poisoning campaign in the early 1990s against rats in general, but only four were caught during a survey in 1991 (Smith *et al.* 1993). Whilst a survey in 1992 suggested that the population was very high and occurred all over the island (P. Smith pers. comm.), the pre-breeding population is unlikely to exceed 500 animals, and is likely to be substantially fewer. On Garbh Eilean, there is similarly no estimate of the total number present, but it is believed to be in the low hundreds (D. Bullock pers. comm.), and so we have assumed that this population also numbers no more than 500.

Population estimates: A total pre-breeding population of at most 1300 animals; fewer than 750 in England, about 550 in Scotland and none currently known to occur in Wales. Since there are no data on which to estimate the size of the two major populations, it is impossible to be more precise. For this estimate, we have assumed that each numbers no more than a few hundred animals, and there may well be fewer on each island.
Reliability of population estimate: 2.

Historical changes: From Roman times, the ship rat was widespread and common, but following the introduction of common rats in the early 18th century, its numbers rapidly declined. However, in 1780 it was still the prevailing species in London, although it had been replaced by common rats in many of the shires (Batten, n.d.). Ship rats were still common in parts of Scotland well into the 19th century. They still infested Benbecula in the Outer Hebrides until the 1880s and Shetland as late as 1904 (Millais 1904-1906; Lever 1977). In Orkney, they declined during the 18th century, but persisted until the 1930s in South Ronaldsay and possibly the 1940s in Kirkwall (Booth & Booth 1994). However, in 1939 a German grain ship went aground on Westray, Orkney, and ship rats became established on the island, where they were locally a pest; the last definite record was in 1968, and they are now presumed extinct (Booth & Booth 1994).

In mainland Britain, ship rats were more or less extinct by 1890, although they were still fairly common in parts of Cheshire and north Wales. However, Millais (1904-1906) reported that in 1905 ship rats were very numerous in Yarmouth. During the Second World War in those ports where ship rats abounded, they were more abundant than common rats, and in London there were roughly four ship rats to every common rat in the port (Twigg 1975). By 1956 ship rats were restricted to a few sea ports and major cities, and some small islands (Bentley 1959). A survey in the 1960s showed a further loss of ground due to improved methods of rodent control, better buildings, disinfection of ships, etc., and extinction seemed likely (Bentley 1964). However, populations persist, although most are impermanent, and ship rats were reported from only 23 mainland sites between 1981 and 1989 (Twigg 1992).

Although there are no quantitative data on the size of the ship rat population on Lundy, it seems to have undergone substantial changes in size in recent years. The population probably arose from survivors of ship wrecks several hundred years ago (Smith *et al*. 1993). A survey in 1962 showed that ship rats were more widely distributed on the island and in greater numbers than common rats (Anon. 1963), a situation that was reversed by 1983 (Smith 1985). In the second half of the 1980s, there was a significant decline in common rat numbers following a poisoning campaign, and in 1991 ship rats were probably restricted to the south-east part of the island (Smith *et al.* 1993). It was concluded that their future looked bleak. Yet a survey in 1992 showed that ship rats were widespread throughout the island, and greatly outnumbered common rats (P.A. Smith pers. comm.). Whether this increase was due to a reduction in competition with common rats is at present unclear (P.A. Smith pers. comm.). Nothing is known about the history of the ship rat population on Garbh Eilean, but it is believed to be long established (D. Bullock pers. comm.).

Population trends: Current trends are unclear. Future ship-borne entry of large numbers seems unlikely because of effective inspection systems, but lorry-borne entry does occur and is more difficult to prevent, and increased vehicular traffic through the Channel Tunnel may increase the number of ship rats entering the country. The potential effects of climate change are also unknown (Twigg 1992).

Population threats: Ship rats are generally controlled whenever populations or individuals are located. The populations on Lundy and Garbh Eilean are of particular interest. Whilst there is much speculation as to their possible impacts on the sea bird colonies on these two islands, based on experiences elsewhere, proof of any impact in Britain is currently lacking.

Common dormouse *Muscardinus avellanarius*

Status: Native; localised and declining.

Distribution: Widespread but patchily distributed. Dormice are most common in England in Avon, Buckinghamshire, Devon, Dorset, Gloucestershire, Hampshire (including the Isle of Wight), Kent, Somerset, Surrey and Sussex, and in Wales in Gwent (P.W. Bright pers. comm.). Elsewhere in England this species is sparsely distributed, although isolated populations occur as far north as Cumbria and Northumberland. Dormice are probably under-recorded in east Wales along the English border and also in south Wales (P.W. Bright pers. comm.). A recent survey in south-east Dyfed produced 27 records, and the species is believed to be widespread, if sparsely distributed, in the area (A. Lucas pers. comm.).

Population data: The principal habitat for dormice is ancient woodland (Bright, Mitchell & Morris 1994), although they may be absent from isolated fragments due to chance events or historical patterns of management (Bright & Morris 1990, 1992). In addition, an unknown proportion of the population lives in secondary woodland, and in hedgerows, perhaps particularly in south Wales. Therefore, to calculate the population size, the total area of semi-natural ancient woodland in the eleven counties in which dormice are most common (approximately 168,000 ha) was obtained from Spencer & Kirby (1992). Dormice live at very low densities, only attaining 8-10 per ha even in prime habitat (Bright & Morris 1992), and a typical density would be nearer 5 per ha (P.W. Bright pers. comm.). At such a density, the total population of dormice would be 840,000. Allowing for scattered populations in other counties would suggest a total population figure of around 1,000,000. However, dormice are unlikely to persist in woods with an area of less than 20 ha, or isolated by more than 1 km (Bright, Mitchell & Morris 1994). Moreover, they are often absent from areas of ancient woodland altogether, perhaps as a consequence of past management. Thus the total could be substantially lower due to populations being lost as a consequence of long periods of isolation from larger populations (Bright, Mitchell & Morris 1994). Whilst the extent of these past losses is unknown, we have assumed that dormice are absent from about half of the available suitable habitat.

Population estimates: A total pre-breeding population of about 500,000; 465,000 in England, none in Scotland and 35,000 in Wales. More information on the local distribution of, and the effects of past patterns of woodland management on the survival of, common dormouse populations is needed in order to improve this estimate. **Reliability of population estimate:** 3.

Historical changes: Dormice occurred much more widely last century, although even where they were common they were still patchily distributed (Thorburn 1920). Their distribution and status at the end of last century was summarised by Rope (1885). In England they were more widely distributed in the north than now, although they were rare in the midlands and absent from some eastern areas. In Wales dormice were found in all counties, including Anglesey, and were more frequent in the north and west of Wales (Barrett-Hamilton & Hinton 1910-1921). A recent survey in Dyfed revealed that dormice were still widespread in the area, and it is possible that this species has still to be 'rediscovered' in many other parts of Wales. However, in the absence of records, dormice are generally perceived to have declined in both range and abundance during this century, although there are no data on the rate or pattern of decline. A survey from 1975 to 1979 (Hurrell & McIntosh 1984) provided widespread evidence of a decline, including no recent records from seven counties where dormice had been reported a century earlier by Rope (1885). The frequency of common dormouse records in local mammal reports declined by approximately 50% from the 1930s to the 1970s (Morris 1993b).

Population trends: Being on the edge of its range, the distribution of common dormice in Britain has always been very patchy. Thus whilst an absence of records does not prove that the species is absent (the recent confirmation of sites in Cumbria and Northumberland shows how easy it is to miss fringe populations), it is likely that local extinctions have already occurred and continue to occur in many areas of England. The common dormouse population that is likely to be viable in the long term can be estimated by excluding those areas of semi-natural ancient woodland below 20 ha in size. These comprised 83% of the woods, using the size class distribution given by Spencer & Kirby (1992). This would suggest a viable population of only 150,000. However, in Dyfed common dormice were frequently recorded in woodlands of less than 20 ha, occupying small pieces of ancient woodland, hazel-rich hedgerows, and the scrub at the edges of conifer plantations. Thus in some areas fragmented habitats can still sustain dormice.

Population threats: Dormice are threatened by absolute loss of habitat, especially the removal of ancient woodland or its substitution by plantations (especially softwoods), and the incidence of dormice is higher in ancient semi-natural woodland than in ancient replanted woodland (Bright, Mitchell & Morris 1994). Dormice are also threatened by the management of woodland in ways that are inappropriate to their requirements, including clear-felling, short coppice rotations or neglect (Bright & Morris 1989). The problems are exacerbated by the fact that the dormouse raises few young per year, but compensates by breeding for more than one year. It is thus a relative *k*-strategist (compared to the wood mouse or bank vole, which are more prolific breeders). This strategy is poorly suited to an animal on the fringe of its distributional range, where climatic uncertainties may reduce successful breeding for several years in succession. Dormice are specialist feeders that require a succession of fruiting trees and shrubs to maintain a regular food supply; thus they are confined to woodland with a high diversity of tree types, and those with a species-rich understorey that is not heavily shaded by taller trees (Bright & Morris 1990, 1993). Poor woodland management that leads to heavy shading and loss of the shrub layer leads to extinction even if the woodland itself persists. Their reluctance to cross open areas at ground level also means that they require aerial pathways to interconnect feeding sites and so proper habitat management is crucial for their survival (Bright & Morris 1989).

Poor summers, leading to a late start to the breeding season, may reduce survival of offspring, particularly if they do not reach a minimum weight of 15 g before the onset of winter (P.W. Bright & P.A. Morris unpubl.). A succession of poor summers could therefore lead to local extinctions. The problems that dormice face are exacerbated by low breeding rates and low population densities. In Dyfed, the main threat to populations is open-cast mining, which destroys and fragments the woodlands in which the dormice are found (A. Lucas pers. comm.).

Fat dormouse *Glis glis*

Status: Introduced to Tring Park, Hertfordshire, in 1902. Locally common, but fat dormice have spread slowly from their point of release. Both numbers and range are still increasing.

Distribution: Found in conifer plantations, mixed and deciduous woodland, orchards, gardens and houses in Buckinghamshire and Hertfordshire. A survey in 1980-1988 showed that fat dormice were present in 70 1 x 1 km squares, with records as far west as the Bledlow Ridge, east at least to Potters Bar and south to High Wycombe (L.M. Jones-Walters unpubl.). There is an outlying record from Sandy, Bedfordshire, in 1974, and earlier records from Shropshire, Warwickshire, Wiltshire and Worcestershire, with unconfirmed records in Berkshire, Gloucestershire, Hampshire, Northamptonshire, Oxfordshire and Surrey. These scattered records suggest that there were other introductions that did not persist (Lever 1977; Arnold 1993).

Population data: In Europe densities fluctuate from 1-30 per ha, and 1-5 per ha is normal (Storch 1978). Whether such high densities are achieved in Britain is unknown, but a small pilot study in the Chilterns recorded densities of 1 per ha in suitable woodland (Hoodless & Morris 1993). No other British data are available, although very high numbers have been recorded inside single houses (P.A. Morris unpubl.). Assuming that half of the 70 1 x 1 km squares constitute suitable habitat for fat dormice, at densities of 1 per ha the total population size would be 3500 animals, and at densities of 5 per ha the population would be 17,500. The actual population probably lies around the mid-point i.e. approximately 10,000 animals. Since there are about 15,000 ha of woodland in the Chilterns as a whole, not all of which is suitable for fat dormice, this suggests that the estimate of 10,000 is reasonable.

Population estimates: A total pre-breeding population of about 10,000, all in England.
Reliability of population estimate: 3.

Historical changes: Following their introduction to Tring Park in 1902, fat dormice multiplied very quickly and caused considerable damage to thatch and to corn and other crops. As a result a campaign was conducted which was thought to have exterminated them. However, between 1925 and 1927 a number were seen in Tring Park and in the surrounding countryside. Subsequent early records are detailed by Lever (1977). The spread has been slow, and in the first 85 years the average rate of spread from Tring Park was about 380 m per year (Jones-Walters & Corbet 1991), with most records still within 25 km of the release site.

Population trends: It is increasing both in range and numbers, albeit slowly. Most spread has been to the south and east, and this is assumed to be due to an absence of suitable habitat to the north and west. However, translocations are known to have occurred, with at least one of them leap-frogging a major barrier to natural dispersal. This was of a fat dormouse caught in Wytham Wood, Oxfordshire, on the other side of the treeless Vale of Aylesbury. Should fat dormice become established in areas beyond the natural barriers that have so far limited their spread, there is every reason to expect that they will become far more widely distributed. This seems almost inevitable, since people who trap fat dormice in their house are often reluctant to kill them, and so release them in a piece of woodland, sometimes some distance away.

Population threats: None known, but control measures in houses may have some effect on local populations.

Coypu *Myocastor coypus*

Status: Introduced. There have been no sightings since December 1989, when one was trapped in the Fens, Cambridgeshire, and this species is now believed to be extinct in Britain.

Distribution: Coypu were first brought to Great Britain for their fur in 1929, with most of the early farms in Hampshire, Surrey and Sussex. Most escapes occurred between 1932 and 1939, mainly in these three counties but with some in East Anglia, Scotland and Wales. However, from about 1940 feral coypu colonies from the south largely disappeared (Lever 1977), with only those in East Anglia persisting. All the fur farms had closed down by 1945 (Gosling & Baker 1991). Feral populations only became established near Slough, Berkshire, and in the valley of the River Yare in Norfolk, whence they spread throughout much of East Anglia. By 1965 they extended north to Lincolnshire, west to Huntingdon and Peterborough, and south to Essex and Hertfordshire (Gosling & Baker 1991).

Coypu were very destructive to crops. They also damaged natural aquatic macrophyte communities of conservation importance and which were vital to the stability of river banks in the face of wash from passing boats. Also, their large burrows were a threat to the integrity of the flood defences in a part of England where much valuable farmland and property lies below river level. In view of these threats a major trapping campaign was instigated, and this led to the eradication of the species (Norris 1967).

Population data: During the eradication campaign, population size was estimated using a retrospective census technique based on trapping results (Gosling, Watt & Baker 1981). This was possible because most adult animals were eventually killed by trapping (Gosling & Baker 1989).

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

Historical changes: The size of the Slough population is unknown, although it was believed to be small, and disappeared about 1954 (Norris 1967). The Norfolk population had spread throughout much of East Anglia by the late 1950s, when the population, based on capture returns, was believed to number about 200,000 (Norris 1967), although this figure may have been an over-estimate (Gosling & Baker 1989). Thereafter numbers declined, but increased from 2000 in mid-1970 to nearly 19,000 in late 1975 because of mild winters and low trapping intensity (Gosling, Watt & Baker 1981). However, in the late 1970s more trapping and colder winters kept the population below 14,000 and the population declined to fewer than 6000 following the cold winter of 1978/1979. From 1981, a coypu eradication policy was introduced, with the aim of exterminating coypu within ten years. The population declined from around 6,000 adults in 1981 to 15 in 1987, 3 in 1988 and 1 in 1989; the success of the trapping campaign was enhanced by an above-average number of cold winters (Gosling & Baker 1989). No coypu have been recorded since 1989, and this species is now extinct in Britain.

Population trends: The Coypu (Prohibition of Keeping) Order 1987 prohibits the keeping of coypu in Britain and so this species should not become established again, since only small numbers are now kept in secure conditions in a number of zoos.

Order: Carnivora

Red fox *Vulpes vulpes*

Status: Native. Animals were introduced from Europe last century to reinforce populations for hunting (Vesey-Fitzgerald 1965). Increasing in range and probably in numbers.

Distribution: Foxes are found throughout mainland Britain. They are present on the Isle of Wight. They were absent from Anglesey until 1962 when they were introduced, and until recently they were absent from all the Scottish islands except Skye (Harris & Lloyd 1991). However, foxes appear to have been recently introduced to Harris in the Outer Hebrides (A.C. Kitchener pers. comm.).

Population data: A population estimate was produced by Macdonald, Bunce & Bacon (1981) by selecting 256 1 x 1 km squares, eight from each of the 32 land classes, and subjectively estimating fox densities for each square. By this means they estimated a spring population of approximately 252,000 resident adult foxes, noting that these figures could double by late summer by the inclusion of juveniles and itinerant adults. What proportion of this increase would be due to itinerant adults is unclear, but presumably they would also have to be added to the spring estimate of adult population size.

When Macdonald, Bunce & Bacon (1981) produced their population estimate, only a small proportion of the 1 x 1 km squares in Britain had been assigned to a land class, and the subjective estimates of fox density were interpolated for unclassified regions by averaging values of the surrounding classified squares. This estimate took no account of a number of variables such as non-resident adult foxes and regional variations in fox social group size. For many areas of Scotland, this approach seemed to over-estimate fox densities significantly (Hewson 1986). Also it ignored fox densities in urban areas.

In view of these problems, density estimates for rural areas were obtained for a number of habitats in England (Insley 1977; J.C. Reynolds pers. comm.), Scotland (Hewson 1986, 1990b) and Wales (Lloyd 1980). These were assigned to land classes, and mean densities were estimated as the number of social groups per km². Those land classes for which there were no density estimates were graded on a sliding scale based on subjective estimates of habitat suitability and ranked between land classes for which there were density estimates. Thus densities of one fox social group per km² were used for land classes 1, 2, 5, 6 and 7; one per 2·5 km² for land classes 3, 4, 8, 9, 10, 11, 12, 13, 14, 15 and 16; one per 5·0 km² for land classes 19, 20, 26 and 27; one per 7·5 km² for land classes 17, 18, 25 and 28; one per 10 km² for land classes 21, 22, 29 and 31; and one per 25 km² for land classes 23, 24, 30 and 32. This gave a total British fox population of around 75,500 social groups: 60,000 in England, 7500 in Scotland and 8000 in Wales. However, it should be remembered that for many land classes there were no density estimates at all, and virtually none with more than one estimate.

There are few data on the demography of rural fox populations. To estimate how many foxes there are per social group, data from Kolb & Hewson (1980) and Lloyd (1980) were used. Thus it was assumed that each rural fox family group had an adult male and a breeding female. In addition the data from Lloyd (1980) suggested that in Britain on average about 25% of vixens are barren. Thus, in addition to the 75,500 breeding vixens, there would be a further 19,000 barren vixens. There are no data on the ratio of itinerant:resident foxes, and so it was assumed that there were a further 0·5 itinerants per family group. This gives a mean social group size significantly below that recorded in urban areas, and reflects the higher levels of persecution of rural fox populations.

For urban areas, much more precise data are available, and population size was estimated as follows. Detailed population surveys were undertaken in nine English towns (Harris 1981; Harris & Rayner 1986a), and the results of these surveys were used to develop a predictive model to estimate fox numbers in other urban areas (Harris & Rayner 1986b). The distribution of foxes in urban areas of Britain is given by Harris & Rayner (1986c). Mean population estimates for all these urban areas were obtained by Harris & Smith (1987a) using a simplified version of the predictive model of Harris & Rayner (1986b), and total fox population sizes were estimated for every urban area with a population of more than 50,000 people in 1951. These density estimates were calculated as social groups per km^2, and these were converted to actual fox numbers using the demography data for Bristol (Harris & Smith 1987b). The demography data for Bristol were applied to all urban areas, since few urban fox populations are now controlled. This also applied to London, where fox control was much less than when the data for London given by Harris & Smith (1987b) were collected. The Bristol data showed that at the start of the breeding season an average urban fox family group consisted of 3·4 adults; thus to obtain the adult urban fox population, the estimated number of family groups was multiplied by 3·4.

This technique provided a detailed estimate of the number of foxes in all the major urban areas in Britain. It did not include small towns and villages, since many of these have only low numbers of resident foxes, and a high proportion of those seen in settlements at night are likely to be foraging animals that are normally resident in the surrounding rural area (Harris & Smith 1987a).

Population estimates: A total pre-breeding population of about 240,000; 195,000 in England, 23,000 in Scotland and 22,000 in Wales. Of these, the urban fox population was as follows: total 33,000, England 30,000, Scotland 2,900 and Wales 100. In addition, assuming a mean litter size of five, around 425,000 cubs are born each spring. The paucity of population data for this species in rural habitats meant that it was particularly difficult to produce a population estimate.
Reliability of population estimate: 4.

Historical changes: At the turn of the century, the fox was common in many parts of Britain, and this was attributed to its status as a beast of the chase; otherwise, foxes would have disappeared from many areas as a result of the activities of gamekeepers (Millais 1904-1906). Although then perceived to be common, foxes have increased their range in Britain this century, particularly in parts of Norfolk and coastal areas in eastern Scotland, where until recently they were absent or uncommon (Harris & Lloyd 1991). In Scotland, changes in fox numbers and distribution have been described by Hewson & Kolb (1973), Kolb & Hewson (1980) and Hewson (1984b). They showed that there were large changes in demography and the number of foxes killed in relation to food abundance. With the onset of myxomatosis, the abundance of diseased rabbits led to an increase in the number of foxes killed. Later poor reproductive success and cub survival coincided with the period of reduced rabbit numbers. However, the massive reduction in the numbers of rabbits led to an increase in vegetation cover, which in turn promoted an increase in the numbers of field voles and an improved food supply for the foxes. With an increase in the number of adult foxes killed, there was a decrease in the cub:adult ratio, probably due to a decrease in the proportion of breeding vixens as population density rose. Changes in over-winter mortality, which were associated with food supply, appeared to be the main cause of the fluctuation of numbers.

Records of the numbers killed by gamekeepers show a steady increase in the mean number of foxes killed per km² since 1960 for all regions of mainland Britain (Tapper 1992), with four times as many killed per km² in 1990 as in 1960. The increase has been greatest in south-east England (seven fold) and East Anglia, and lowest in Scotland (two fold). Although these data suggest an increasing fox population, it is impossible to quantify the scale of any increase from such data. In East Anglia and the east midlands, the fox population in 1960 was probably very low, since foxes are very sensitive to dieldrin poisoning, and large numbers were found dead after having consumed poisoned wood pigeons *Columba palumbus* (Taylor & Blackmore 1961). Lloyd (1980) reported 1,300 dead foxes being found by huntsmen, and there was evidence of a substantial reduction in fox numbers (Rothschild 1963; Lloyd 1980). Also, a gamekeeper will kill not only resident territorial foxes but also itinerants immigrating from other areas, so that the number killed locally can sometimes far exceed the pre- or post-breeding density. Thus the trend towards larger numbers killed may result from increasing productivity, increasing breeding density, less effective control by man, or most likely a combination of all these factors. The increasing number killed per unit area certainly reflects a real increase in population density in East Anglia and coastal areas of eastern Scotland, where foxes were absent or rare prior to 1960 (Harris & Lloyd 1991; Tapper 1992). Whether it reflects a real increase in other parts of the country is unclear.

Control by man may have become less effective for two reasons. First, the number of gamekeepers roughly halved during the 30 years after 1960 (Tapper 1992), so that each shooting estate was more likely to be adjoined by unkeepered land, leading to increased immigration. Secondly, there has been a shift from spring and summer control using snares, cyanide gas and (formerly) gin-traps, to night shooting using a rifle and spotlight, a method which is easiest in late autumn, winter and early spring when cover is short and visibility therefore good. Since this is the main dispersal period (Trewhella & Harris 1988), shot foxes are likely to be quickly replaced, thereby allowing large numbers to be shot per unit area and thus giving the impression of an actual population increase.

Changes in food resources must also have influenced fox breeding density and/or productivity. Whilst a four-fold increase in productivity of a fox population is theoretically possible in response to changes in food availability (see review by Lloyd 1980), this would be extreme, and it seems unlikely that increased productivity and/or increased cub survival alone have contributed to the increase in the number killed by gamekeepers. Thus it seems likely that there has also been an increase in fox breeding density. Evidence from at least some estates and from other studies (Hewson & Kolb 1973; Lloyd 1980) suggests that fox numbers were very low in 1960, perhaps as a result of myxomatosis in rabbits. However, myxomatosis was introduced in 1953, and the number of foxes killed per km² in 1990 was four times the number killed pre-myxomatosis in 1946 on the same estates (Tapper 1992). Thus the increase in fox numbers cannot be explained solely by increasing rabbit numbers. The presence of large numbers of foxes in urban areas in southern England is unlikely to be responsible for the increase in the number of rural foxes killed since a study in Bristol showed that the urban fox population was self-regulating, with little net emigration (Harris & Smith 1987b).

Population trends: It appears that fox numbers may be increasing, although this assessment is based on the numbers killed by gamekeepers rather than any measure of changes in actual population densities. Thus the magnitude of any change is unclear. The reasons for any population increase are unknown, but an increased rabbit population and other food supplies, such as the very large increase in the number of reared pheasants (Reynolds & Tapper 1994), the presence of sheep carrion in upland areas, the exploitation of urban food resources, and the relaxation of control by man, are all likely to be contributory factors.

Population threats: Very high mortality rates, e.g. up to 100,000 per year killed in the late 1970s for their skins (Harris & Lloyd 1991), had no discernible effect on overall fox numbers in Britain, although a decline was reported in Ireland due to the numbers killed for the skin trade (Wilson 1982). At present the very low price for wild British fox skins means that this trade is negligible. Foxes are extensively culled by gamekeepers, and this can locally reduce numbers. Foxes are also the most common wild mammalian victims of deliberate poisoning incidents in England and Wales but these are unlikely to pose a significant population threat except locally. The most frequent reasons for such abuse of pesticides were game and sheep/lamb protection (Greig-Smith 1988).

Pine marten *Martes martes*

Status: Native. Locally common in parts of Scotland, very rare in England and Wales.

Distribution: In England found in Cumbria, Durham, Northumberland and North and West Yorkshire; in Wales found in Clwyd, Dyfed, Gwynedd and Powys, with a 1994 sighting on Anglesey (D.J. Jefferies pers. comm.); and in Scotland found in Dumfries & Galloway, Grampian, Highland, Strathclyde and Tayside. In 1980-1981 12 animals were released in Dumfries by the Forestry Commission (Shaw & Livingstone 1992). Some survived and are now breeding (Velander 1991; G. Shaw pers. comm.).

Population data: Field surveys in England and Wales were undertaken in 1987-1988 by surveying transects 2 km long in suitable habitats. Even where martens were present, evidence was sparse, rarely exceeding ten droppings per 2 km compared to up to 30 scats for similar tracks 2 km long in Scotland. This suggests that pine martens in England and Wales survive only at a low density. Most signs were found in coniferous plantations or at sites adjacent to crag outcrops or scree slopes (R. Strachan pers. comm.). Population sizes in England and Wales were estimated subjectively from these field signs. This approach suggested that in the late 1980s in England there were fewer than 100 individuals: fewer than 50 in the Kielder Forest region, Northumberland, fewer than 30 in the Lake District, and fewer than 20 in North Yorkshire. Records in the area between North Yorkshire and the Kielder Forest populations may only represent wanderers. In north Wales it was estimated that there were fewer than 50 pine martens.

An analysis of the records from the 1987-1988 survey and historical data showed that only the Northumberland/Durham population was possibly spreading. The populations in Cumbria, North Yorkshire and West Yorkshire appeared to be contracting, and that in Wales was static (D.J. Jefferies pers. comm.). Surveys in the Lake District in 1993 and north Wales in 1994 suggested that there had been further significant declines in numbers (P.W. Bright, S. Harris & R. McDonald unpubl.), and that these populations were probably no longer viable. In the absence of a corpse or reliable sighting, despite appeals for records, D. Brown and S. Parr (pers. comms) were pessimistic about the status of the pine marten in north Wales. Morgan (1992/93) has summarised the information on the distribution and status of the pine marten in mid and south Wales. Based on the frequency of records, his survey suggested that pine martens could be established, albeit in very small numbers, in the upland areas of mid and south-west Wales. At this stage it is impossible to estimate the number of animals involved, but they are unlikely to push the total population for England and Wales above the maximum estimate of 150 individuals calculated by R. Strachan (pers. comm.), who believes that the total number is probably much smaller, with a minimum number of around 40.

In Scotland, Balharry (1993) estimated densities of 1 per 4 km^2 to 1 per 10 km^2 depending on the area of woodland within the territory. Woodland habitats were found to be selected in preference to open vegetation types, and regardless of territory size, there were no significant differences in the area of woodland (126 ha per individual) contained within marten territories. Also, territorial structure was intrasexual. Thus population size was estimated by Balharry (1993) as follows. The average area of woodland in each pine marten territory 126 ± 40 ha (s.d.) and there is 273,240 ha of woodland in the Highland region, all of which was assumed to be spatially orientated such that it was available to pine martens. This suggested a total population of around 2200 (range 1650-3150) individuals in the Highlands. For the other regions of Scotland (Dumfries & Galloway, Grampian, Strathclyde and Tayside), it was assumed that there was a 50% occupancy of woodland, thus giving a total maximum population of 3500-6800. D. Balharry (pers. comm.) suggested that the population lies at the lower end of this range.

Population estimates: A total pre-breeding population of about 3650; <100 in England, about 3500 in Scotland and <50 in Wales.
Reliability of population estimate: 2.

Historical changes: Until the 19th century, pine martens were widespread throughout mainland Britain, the Isle of Wight, Jura and Lewis. In the middle of the 19th century a rapid decline of the pine marten took place. Millais (1904-1906) documented the last records for each English county, and its decline in the latter part of that century has been described by Langley & Yalden (1977). Persecution by gamekeepers had led to its extinction in some English counties by 1800, and it was rare in many others. During the 19th century most of the remaining English populations became extinct, as did many in Scotland and Wales. In the late 1930s pine martens remained only as a relict population in north-west Scotland, but by the 1940s there were a few signs of recovery. By 1959, the main population was still north and west of Loch Ness but with animals reported in the Grampian region (Lockie 1964). By 1982 the range extended further south and east, although there was little evidence of animals in the far north (Velander 1983). By 1987, pine martens were again being seen in the northern areas as far east as Bettyhill, Highland (Velander 1991), and in the mid-1980s they were more widespread in the southern Highlands than reported by Velander (1991). In 1985 they colonised the area south-west of Loch Tay, Tayside, and have subsequently moved south into Strathyre and Loch Lomond-side, Strathclyde. Also in 1985 a pine marten was killed on the road near Dunfermline, Fife, well beyond the established range (J. & R. Green pers. comm.). Of the two release sites chosen in the Galloway Forest Park, Dumfriesshire, only one led to the establishment of a breeding population, and this population seems to be consolidating in a radius of 12 km south and west of Glen Trool (Shaw & Livingstone 1992).

Population trends: Their spread southwards from the Highlands and in south-west Scotland seems to be continuing, although whether they would have recolonised the south-west without the help of an introduction in the 1980s is unclear. However, in the 1960s, an animal was killed on an estate in south-west Scotland (J. & R. Green pers. comm.). This may have been a vagrant, suggesting perhaps that natural colonisation would have occurred with time. Alternatively, this animal may have resulted from an undocumented translocation. There continued to be records from the area in the 1970s (Shaw & Livingstone 1992). Total colonisation of north-east and south-east Scotland may be prevented by factors such as natural barriers, interspecific competition and conflict with man (Balharry 1993). Based on the total area of woodland in Scotland, the maximum potential population could be 6800-13,100 individuals, i.e. double the present population (Balharry 1993).

Population threats: Pine martens breed relatively slowly (1-5 young per year when over three years old), and live at very low densities. Isolated populations are therefore likely to be susceptible to population perturbations, local persecution or high levels of, for example, road mortality, and the death of relatively few pine martens may result in the removal of the breeding population from a wide area (Balharry 1993). Thus their continued persistence at such low population levels is probably unlikely. In Scotland unselective methods of predator control are still widespread, and this is probably limiting further spread (D. Balharry pers. comm.). It is not known whether pine martens will spread naturally through large areas of unsuitable habitat to colonise new areas. Also, it is possible that the presence of wildcats or feral cats may limit the distribution and density of pine martens or *vice versa*. Slight differences in food supply or habitat may allow one to gain the competitive edge and exclude the other, or both could co-exist at sub-optimal densities (Balharry 1993).

Stoat *Mustela erminea*

Status: Native. Common and possibly declining.

Distribution: Found throughout mainland Britain at all altitudes, and on many islands, including Anglesey, Islay, Jura, Mull, Skye and the Isle of Wight. Introduced to both Orkney and Shetland, stoats became extinct in Orkney but persist on Mainland Shetland.

Population data: Stoats are found in a wide variety of habitats, including any type of woodland cover, farmland, moors, marshes and in linear features in open areas. The National Game Bag Census data show that there is no large variation in the regional distribution of stoats killed per unit area by gamekeepers, although slightly more are killed in East Anglia and some southern counties than in counties with large areas of upland grouse moor (Tapper 1992). Density and distribution are more closely related to prey availability than to habitat *per se*, and there are marked variations in density both within seasons and between years - stoat numbers may follow cycles in prey abundance. There are no density estimates for Britain, although autumn densities in Europe and Canada probably average 3-10 stoats per km^2 (King 1991a). However, mean body size in those populations is much smaller (King 1989), and so extrapolation of those densities to Britain is questionable (C.M. King pers. comm.). Much higher densities were recorded in some areas before myxomatosis (Jefferies & Pendlebury 1968), but these were based on the numbers killed by gamekeepers in a comparatively small area, and this is not a reliable basis for estimating population density. To obtain a population estimate for Britain, we assumed a density of 6 per km^2 for all types of woodland, parkland, scrub, bracken and coastal sloping cliffs; 2 per km^2 for coastal sand dunes, lowland heaths, heather moorlands, bogs, upland and lowland unimproved grassland and arable land; and 1 per km^2 for semi-improved and improved grasslands.

Population estimates: A total pre-breeding population of about 462,000; 245,000 in England, 180,000 in Scotland and 37,000 in Wales. Obviously this is only an approximate estimate, since there are no density estimates for British habitats, and there is little information on variations in density both between years and between habitats. However, Tapper's (1992) figure for the number of stoats killed by gamekeepers each year (average of about 1·5 per km^2) suggests that this estimate for the pre-breeding population (approximately 2·0 per km^2 for Britain as a whole) is reasonable. **Reliability of population estimate:** 4.

Historical changes: At the turn of the century stoats were still abundant despite relentless persecution (Millais 1904-1906). However, populations were severely reduced for 15 to 20 years following the outbreak of myxomatosis. On one Suffolk estate, there was a ten-fold reduction in the number of stoats killed in 1960 compared to 1950. From 1960 to 1976 the number of stoats killed, as recorded in the National Game Bag Census, doubled, but the number killed in northern areas declined again after 1965. This was probably because the increase in rabbits had been less in northern areas (Trout, Tapper & Harradine 1986). However, since the mid 1970s, the number of stoats killed by gamekeepers throughout Britain has declined again. Reasons for this decline are unclear; since the number of rabbits killed nationally has continued to increase (Tapper 1992), a further rise in the stoat population might be anticipated. However, any rise in fox numbers may be a contributory factor to the failure of the stoat population to increase in response to rising rabbit numbers, since increasing fox numbers can lead to a decline, or even local extinction, of stoat populations (Mulder 1990). The impact of fox predation on stoat numbers may be further enhanced by habitat simplification, particularly the loss of linear features in the countryside (Harris & Saunders 1993).

Population trends: Continuing to decline.

Population threats: Unknown. The reasons for the apparent recent decline are not clear, but it may at least in part be due to reductions in the numbers of farmland birds and larger mammalian prey such as common rats, which are important prey items in areas where rabbits are not readily available, and possibly to increased competition with foxes. Also, stoats may be at risk from secondary poisoning in arable areas by consuming rodents contaminated with insecticides and/or molluscicides.

Weasel *Mustela nivalis*

Status: Native, common.

Distribution: Found throughout mainland Britain and on some islands, including Anglesey, Sheppey (Kent), Skye and the Isle of Wight, but not found on smaller islands or those without native stoat populations.

Population data: Weasels are found in a wide range of habitats, although most are killed in arable farming counties (Tapper 1992). The correlation between the local density and distribution of weasels and small rodents is well-established (King 1991b). Being closely related to fluctuations in rodent numbers means that weasel populations are very unstable, varying over a wider range of densities than do stoats. For instance, in Wytham Woods, Oxfordshire, weasel densities in different years varied from 4·5 per ha to less than 1 per ha, depending on small mammal abundance (King 1989). Moors (1974) recorded an average density of one weasel per 7·7 ha on farmland in north-east Scotland. Lockie (1966) recorded peak densities of 10 males and 3 females on 32 ha in the Carron Valley, Stirlingshire, but this was when field vole numbers were high, and the weasels resident with stable territories; after the first year the system broke down, and weasel numbers were much lower. Also, weasels show cyclic fluctuations in numbers with a 3-4 year quasi-cycle that correlates with cycles in field vole numbers. However, not all weasel populations are cyclic, and this may be because in woodland habitats they feed on other rodents such as bank voles, which are less cyclic than field voles (Tapper 1992), and because field voles are only cyclic in certain habitats (see field vole account).

Estimating a typical density of weasels for particular habitat types is very difficult, and there are few density estimates for British habitats. Whilst home range sizes suggest that weasels could attain densities of 30 per km^2, i.e. three times the density of stoats (see figures in King 1991b), this density figure is unrealistic since home ranges are invariably measured in favourable patches of habitat much less than 100 ha in size, and extrapolation to larger areas is invalid (C.M. King pers. comm.). Thus densities cannot be calculated from home range estimates. In the absence of data from a range of habitat types, weasel numbers were calculated based on their abundance relative to the number of stoats. The ratio of stoats to weasels probably depends on the proportion of prey of different sizes; where small rodents are common, weasels outnumber stoats, and *vice versa* where small rodents are less common. Whilst weasel densities probably vary more on a regional basis than stoat densities (Tapper 1992), kills by gamekeepers suggest that, overall weasels probably equal stoats in abundance (C.M. King pers. comm.). The relative abundance of weasels in each of the three countries was determined from the distribution of records in Arnold (1993) and the relative numbers killed per km² recorded by Tapper (1992).

Population estimates: A total pre-breeding population of about 450,000; 308,000 in England, 106,000 in Scotland and 36,000 in Wales. **Reliability of population estimate:** 4.

Historical changes: At the turn of the century weasels were exceedingly common in England, Scotland and Wales (Millais 1904-1906). The outbreak of myxomatosis in the early 1950s led to a flush of vegetation and a great abundance of small rodents in 1957-1958; this led to a record catch of weasels on game estates (Sumption & Flowerdew 1985). The National Game Bag Census shows that there has been a progressive decline in the number of weasels killed since 1961; this is most marked in East Anglia and the east midlands but barely apparent in the south-west and Scotland (Tapper 1992). The gradual recovery of the stoat from the early 1960s to the mid-1970s was accompanied by a substantial decline in the number of weasels, perhaps due to interference competition. However, since the mid-1970s the number of stoats killed by gamekeepers has declined again, but there has been no apparent increase in the number of weasels killed.

Population trends: Continuing to decline, although weasels have not yet declined to the pre-myxomatosis ratio of 2-3 stoats per weasel (King 1991b).

Population threats: Unknown. As for stoats, recent declines may, at least in part, be due to scarcity of prey or to secondary poisoning but it is doubtful whether these provide a full explanation. Nor is it clear why weasel numbers have not responded to declining stoat populations. If stoat numbers are being reduced by increased levels of fox predation, this would also act to reduce weasel numbers (King 1989), although for both stoats and weasels, population density is more likely to be controlled by productivity rather than mortality (C.M. King pers. comm.).

Polecat *Mustela putorius*

Status: Native. Locally common and increasing.

Distribution: Found throughout Wales except Anglesey, and in England in 12 to 15 counties from Cheshire south to Avon and apparently as far east as Leicestershire and Northamptonshire (J.D.S. Birks pers. comm.). There have been introductions into Cumbria (two), in the Oban area of Argyll (two) and on Speyside in the 1970s and 1980s, but both the purity of the stock used for the releases and their subsequent fate are currently unknown (A.C. Kitchener pers. comm.).

Population data: Densities apparently are not great, and studies in mid-Wales found a mean territory size of 101 ha, with territories clumped for no obvious reason (Blandford 1987; Blandford & Walton 1991). However, polecats are generally regarded as a lowland species, so Blandford's data from hill areas of mid-Wales may not be typical. Also, cull data in Tapper (1992) suggest that population densities in the English midlands are currently lower than in parts of Wales closer to the historical stronghold of the species. Whether this is part of the recolonisation process or a function of habitat quality is currently unknown (J.D.S. Birks pers. comm.).

Weber (1987) estimated polecat population density in Switzerland to be 0·1 per km² in the areas with fewest polecats and 0·5-1·0 per km² in areas with the highest polecat densities. K.C. Walton (pers. comm.) calculated British polecat population estimates by applying these Swiss density figures to the area of each county colonised by polecats (including upland areas, but making allowance for areas populated by humans). Thus, if the British range supported polecats at the lowest Swiss density, 0·1 per km², the British population would be 2143; and at the highest Swiss density, 1·0 per km², the British population would be 21,429 polecats. A second estimate was provided by N. Teall (pers. comm.), using figures from Tapper (1992) of <0·015 to >1·5 polecats killed per km². The current distribution is approximately 235 10 x 10 km squares (Arnold 1993), of which half were thought to have a density of 1·5 polecats per km² and half no more than 0·15 polecats per km². By this means N. Teall (pers. comm.) estimated around 19,000 polecats. Recently, preliminary results of live-trapping in Herefordshire farmland by J.D.S. Birks (pers. comm.) has suggested a density of 0.5-1.0 animals per km², so the population estimates used by Teall for his calculations are likely to be minimum figures. Also, the distribution of records from estates in Wales is biased, and there appear to be no records from the former counties of Merionethshire and Caernarvonshire, nor from the large estates in central east Wales, all areas with high densities of polecats (K.C. Walton pers. comm.). How this bias in returns from the National Game Bag Census data will affect the population estimate is unclear.

Two other estimates were obtained, the first by using the home range sizes presented in Blandford (1987) and the distribution given in Arnold (1984); this suggested a population of 19,200 polecats. The second assumed that polecats in Wales were more or less confined to rivers, and at densities of 1 per km of river. This calculation suggested a total population of around 12,000. How realistic it is to assume that polecats are confined to river valleys is unclear; K.C. Walton (pers. comm.) questions the validity of assuming linear territories, and there are few data to support such an assumption. Whilst most road deaths in Wales are from river valleys, this may simply be because in Wales roads tend to follow valleys, although it may reflect prey distribution (Blandford & Walton 1991).

Whilst a variety of approaches were used to calculate population size, they all produce broadly similar estimates, and thus a minimum population estimate of 15,000 seems reasonable.

Population estimates: A total pre-breeding population of about 15,000; 2500 in England, it is not known whether the introductions to Scotland survived, and 12,500 in Wales.
Reliability of population estimate: 3.

Historical changes: The decline and subsequent spread of polecats early this century has been documented by Langley & Yalden (1977). In the 19th century polecats were still common over most of Britain, although they were already scarce in the south-east. However, by the end of that century there had been a marked decline, with the situation being reviewed in detail by Millais (1904-1906). Their decline in Scotland was hastened by the high value of their pelts (Ritchie 1920), and it was this rather than just their impact on gamekeeping interests that led to their extirpation (A.C. Kitchener pers. comm.).

It is frequently stated that at their minimum, at the onset of the First World War, polecats were probably only common within an area of approximately 70 km radius around Aberystwyth, Dyfed. However, this area excludes the north of Caernarvonshire and Denbighshire, always polecat strongholds, and includes large areas of Dyfed that did not have polecats until the 1960s. Thus an area of approximately 70 km radius around Aberdovey would be a more realistic description of the minimum range (K.C. Walton pers. comm.). At this time polecats were either extinct or virtually so over most of England and Scotland. However, polecats never became extinct in Herefordshire and Shropshire (Langley & Yalden 1977), a view supported by gamekeepers in these counties (J.D.S. Birks pers. comm.).

Since the 1920s, however, polecats have been expanding their range and numbers. The main increase occurred in the 1950s, possibly aided by the cessation of gin-trapping for rabbits. This period of rapid increase also coincided with the rapid decline in otter numbers, so polecats may have benefited from the decline of a potential competitor. Whilst otters were suffering from the effects of organochlorine insecticides, polecats, having a predominantly mammalian diet, only accumulated very low levels of organochlorine pesticides, and so were able to rapidly increase in numbers during this critical period (Jefferies 1992). Thus, by the 1960s polecats had recolonised virtually all of Wales (Walton 1964, 1968), and in subsequent decades spread into many of the English border counties.

Population trends: The spread into England seems to be continuing (J.D.S. Birks pers. comm.), and it is assumed that this spread is associated with a continuing population increase. The situation is currently very dynamic, and there have been reports of animals as far east as Leicestershire and Northamptonshire which, in appearance, appear to be typical polecats (J.D.S. Birks pers. comm.). It has been suggested that this spread of the polecat has probably been aided by the increase in young forestry plantations (Blandford 1987) and the rise in rabbit numbers (Tapper 1992). However, K.C. Walton (pers. comm.) believes that rabbit numbers *per se* were not the major contributory factor. In the 1940s 3,000,000 rabbits per annum were sent from Cardiganshire, Carmarthenshire and Pembrokeshire to London (Thompson & Worden 1956), yet polecats were virtually unknown over much of the area. Gin-trapping rabbits was prohibited after 1958, and it was the cessation of commercial rabbit trapping rather than the increase in rabbit numbers that led to the increase in polecat numbers and distribution. However, after increasing steadily since the 1960s, the National Game Bag Census data show that the numbers of polecats (and mink) killed each year per km^2 have levelled out or decreased since 1983 (Tapper 1992). The rapid increase in polecat (and mink) numbers following the decline in otter numbers, and a subsequent reversal of this trend as otter numbers built up in Wales and the English border counties, suggest that there may be a negative interaction here, and that if the increase in otter numbers continues, polecat numbers may expand much more slowly (Jefferies 1992).

Population threats: The future of polecats in Britain seems to be assured, and the current distribution in Britain is half as large again as 20 years ago, but it would be unrealistic to expect a full recovery (unaided) to its former range (Blandford & Walton 1991). The high incidence of road casualties is surprising, considering the relatively low density of traffic in Wales during the autumn, the main period of mortality, and the lack of foraging activity near roads (Blandford 1987). Why polecats are susceptible to road deaths is unclear; it may be because roads provide a reliable source of carcasses to scavenge (K.C. Walton pers. comm.). This susceptibility to road mortality may reduce the rate of spread into areas of England, where road traffic is heavier. However, polecats have colonised the outer suburbs of one large urban area (Llanelli) despite some road casualties (K.C. Walton pers. comm.). Extensive drainage and agricultural improvements may pose a threat in some areas (Blandford & Walton 1991). Polecats have also been reported as victims of secondary poisoning in areas where anticoagulant rodenticides were in use (Walton 1970), and in England, where polecats hunt rodents around farm buildings, some animals have accumulated high levels of second generation rodenticides (J.D.S. Birks pers. comm.). What effect this may have on numbers or the rate of spread in England is currently unclear. Finally, as the range of the polecat expands, the risk of hybridisation with feral ferrets increases; how much of a risk this will be is unknown.

Feral ferret *Mustela furo*

Status: Introduced. Established on a few islands and some mainland areas, occasionally with records elsewhere.

Distribution: Established on Harris, Islay, Mull, Shetland and the Uists. Ferrets appear to survive best on off-shore islands with lots of rabbits and few other carnivores (J.D.S. Birks pers. comm.). Whilst records of individual animals also exist for many counties in England, Scotland and Wales, these probably represent relatively recent escapes. Colonies have been reported in several places on the mainland, but their size and persistence is currently unclear. For instance, from at least 1977 to 1987 feral ferrets were present throughout Strathearn, Tayside, and it was not unusual to see more than ten on a gamekeeper's gibbet (J. & R. Green pers. comm.). On Mull, they have been present since at least the late 1920s (Pocock 1932).

Population data: None available. There is no known preferred habitat type for feral ferrets, nor has there been any attempt to estimate population density. It is also unclear whether records on the mainland represent free-living populations or a 'standing crop' of escapees.

Population estimates: The total pre-breeding population is unlikely to exceed 2500, but it is impossible to be more precise; in England 200, in Scotland 2250 and in Wales 50. **Reliability of population estimate:** 5.

Historical changes: Unknown.

Population trends: Unknown. An eradication campaign was attempted on Islay in the late 1980s. This lasted two years and had temporary success, but feral ferrets are now common again (J. & R. Green pers. comm.). There have also been attempts to reduce the numbers on Shetland, but their success, if any, is unknown.

Population threats: None known.

American mink *Mustela vison*

Status: Introduced. Although escapes from fur farms occurred from 1929, the number of animals was low in these early years and they did not establish free-living populations. The first records of wild-bred young were from Devon in 1956 (Thompson 1964). Now common and widespread.

Distribution: Widespread, with records from most areas except north-west Scotland and north-west Wales (Arnold 1993). Numbers appear to be low in East Anglia and east Yorkshire (Tapper 1992). The greatest density of records is from south-west England, Sussex, the English/Scottish border counties, and south and east Scotland (Arnold 1993). The low productivity of upland rivers may limit their spread in the Highlands (Chanin 1981). In the Outer Hebrides mink have colonised all of Lewis and Harris following their escape from fur farms in the 1960s, but have yet to extend significantly further southwards. In the Inner Hebrides they have been recorded on Mull since 1990 (Green & Green 1993). They are now also on Islay (A.C. Kitchener pers. comm.), and there are unconfirmed reports from Jura. They have been present on the Isle of Arran since their escape from fur farms in the 1960s.

Population data: Mink are found in a wide range of aquatic habitats, particularly favouring eutrophic streams, rivers and lakes with abundant waterside vegetation; they are less abundant on oligotrophic waters or where waterside cover is sparse or absent (Dunstone 1993). Relatively dense populations may also occur in undisturbed rocky coastal habitats with a broad littoral zone (Birks & Dunstone 1991). On mainland Britain, mink occupy coastal habitats around Slapton in south Devon, north-east England, the whole of the Solway Firth and the west coast of Scotland, but coastal mink are probably not as widespread as coastal otters because of their need for a wider range of prey items (mammals and birds) and their requirement for a suitable foraging habitat, i.e. relatively shallow, sloping, boulder strewn, beaches or abundant rock pools (Dunstone & Birks 1983; N. Dunstone pers. comm.).

On mainland Britain, density varies with habitat. On the River Teign, an oligotrophic river in Devon, densities were 0·46 mink per km of river when rabbits were common, but only 0·23 mink per km of river when rabbits were scarce (Birks 1989). Seasonal variations in density are influenced by vacation of territories by rutting males in the spring and re-settlement after the mating season, and by the settlement of the juveniles following dispersal in August. From studies of mink inhabiting rivers and lakes in Devon (Chanin 1976; Birks & Linn 1982), it was calculated that the mean territory length for the two sexes was 2·28 per km, i.e. 0·44 mink per km of riparian habitat. Assuming a complete overlap of the territories of the two sexes, since Birks & Dunstone (1991) say that there is 'much overlap', this gives a density of 0·88 mink per km of river/lake shore. Obviously, assuming total overlap of territories between the sexes is likely to inflate the population estimates a little, but this is probably not by a substantial amount. In each water authority region in England the percentage of sites found to be occupied by mink during the national water vole survey were: Anglian - 20·5%; North West - 39·7%; Northumbria - 55·5%; Severn Trent - 33·6% South West - 66·0%; Southern - 33·0%; Thames - 25·0%; Wessex - 52·7%; Yorkshire - 48·0%; and 27·3% in Scotland and 39·3% in Wales (Strachan & Jefferies 1993). Using these figures for percent occupation, the lengths of riparian habitats in Table 4, and a density of 0·88 mink per km, D.J. Jefferies (pers. comm.) calculated that there are 4500 mink in the Anglian area, 4500 in the North West, 5750 in the Northumbrian, 7500 in the Severn Trent, 7000 in the South West, 3500 in the Southern, 2750 in the Thames, 4250 in Wessex and 6750 in Yorkshire, a total of 46,500 in England; plus 31,250 in mainland Scotland and 9750 in Wales. These estimates exclude coastal habitats.

The number of coastal mink was calculated as follows. The main known populations in England were in Slapton, Devon, the north-east coast of England, and the south coast of Solway, occupying lengths of coastline of approximately 10, 100 and 60 km respectively (N. Dunstone pers. comm.). A study on the Solway coast found a mean territory length of 1·30 km, or 0·77 mink per km (Dunstone & Birks 1985). Again, assuming a complete overlap of the territories of males and females gives a density of 1·54 mink per km of coast i.e. about 250 coastal mink in England. On the west coast of Scotland, coastal mink are only found north to about Skye i.e. approximately 4000 km of coast (N. Dunstone pers. comm.). Assuming the same density as in Solway would give a population of about 6000 coastal mink in Scotland. Off the west coast of Scotland, the only islands with mink are the Isle of Arran and Harris and Lewis (Birks & Dunstone 1991). Nothing is known about the numbers on the Isle of Arran. For Harris and Lewis, the densities (adult females per km) were higher in coastal habitats (0·85) than rivers (0·75) or lochans (0·63); productivity was also higher in the coastal habitats (Hudson & Cox 1989). Using these figures, Hudson & Cox (1989) estimated there were about 7500 breeding female mink on Harris and Lewis. Assuming an equal number of males and non-breeding females gives a total population of about 15,000 mink.

The otter survey in England in the early 1990s suggested that coastal-living mink are much more common than the figures used in this calculation, and of 204 coastal sites examined, 63·2% had mink (R. Strachan pers. comm.). This survey also suggested that the rocky coasts and estuaries of south-west England may provide mink with better foraging and denning opportunities compared with the flatter saltmarsh and reedbed-dominated estuaries of the east coast. Thus it seems probable that relatively high densities of coastal-living mink occur in south-west England and west Wales (R. Strachan pers. comm.), and more data on these will increase the population estimate presented here.

Population estimates: A total pre-breeding population of at least 110,000; 46,750 in England, 52,250 in Scotland (plus an unknown number on the Isle of Arran) and 9750 in Wales. More data on coastal and island populations of mink are needed to enable this estimate to be improved. In addition, in 1994 there were 15 mink farms in the UK; the number of mink being kept on mink farms in the UK was 100,000 in 1987 and 47,000 in 1992 (Ministry of Agriculture, Fisheries and Food pers. comm.). **Reliability of population estimate:** 3.

Historical changes: Mink were first imported into Britain in the late 1920s, and from then until 1945 the industry was small. The business then expanded and by 1962 the number of mink keepers had risen to a peak of around 700. With the introduction of the Mink (Keeping) Regulations, 1962, the number of farms dwindled to about 240 in 1971, but annual pelt production rose steadily from 6000 in 1953 to 160,000 in 1962 and 300,000 in 1971 (Johnston 1974).

Breeding mink were discovered in Devon in the mid-1950s. Their range and numbers increased considerably in the late 1950s and early 1960s, and within three years had expanded from a few kilometres of the River Teign to an area of 2600 km² (Linn & Stevenson 1980). A similar pattern was probably occurring elsewhere, as evidenced by the number of animals being killed. Thus by 1960 wild mink had been caught in five counties in England and Wales and two in Scotland. With the introduction of the Mink (Keeping) Regulations, 1962, the efforts to control feral mink were stepped up. In 1963 wild mink had been caught in 31 counties in Britain, and by 1967 this had risen to 63 (Thompson 1968). The number of wild mink caught each year rose throughout the 1960s, and by mid-1970 4875 mink had been caught in England and Wales, mostly in Devon (1317), Lancashire (594), Sussex (411) and Wiltshire (403). In Scotland the total caught was 1946, with most from Aberdeenshire and Kirkcudbrightshire. By 1971, mink had been caught in 41 counties in England and Wales, and 29 counties in Scotland (Johnston 1974). Much of this apparently rapid spread was the result of small scale escapes in which the mink were subsequently recaught, but elsewhere new feral populations were established and counties colonised from neighbouring areas (Chanin 1981). In Scotland, the early history of mink has been reviewed by Cuthbert (1973). By the end of the 1970s, mink were widely distributed throughout mainland Scotland south of the Great Glen. Since then expansion appears to have slowed, but mink are gradually extending northwards up the east and west coasts (Green & Green 1993). Recently there has been a clear increase in the number killed in eastern England (Tapper 1992), suggesting that numbers are also now building up in this area.

Evidence of the rate of increase in recent years comes from the otter surveys of England. In 1977-1979, mink were recorded in 196 (15·1%) of the 1300 10 x 10 km squares surveyed (Lenton, Chanin & Jefferies 1980), compared with 334 (22·3%) of the 1500 10 x 10 km squares surveyed in 1984-1986, an increase of roughly 50% in seven years. The water vole survey in 1989-1990, though stratified differently and hence not directly comparable with the otter surveys, found mink in 543 (62·8%) of 864 10 x 10 km squares surveyed in mainland Britain, and 34·4% of all 600 m stretches of waterway searched showed signs of mink (Strachan & Jefferies 1993).

Population trends: Mink are continuing to increase both in range and numbers, but probably at a reduced rate. The possibility that low otter numbers helped the spread of mink has been mooted several times, e.g. Chanin & Jefferies (1978), and there is some recent evidence to support this assertion. Firstly, in three separate areas of Britain where otters have made a significant recovery in the last ten years, the mink population has independently been described as being lower than in earlier years (Birks 1990). Also, the National Game Bag Census data show that the numbers of mink (and polecats) killed each year per km² increased steadily in several years from the 1960s, but has levelled out or decreased since 1983 in Wales and the English border (Tapper 1992). These trends coincide with the decline and subsequent increase of otters in the same area, suggesting some form of negative interaction (Jefferies 1992).

Population threats: Following the 1988 epizootic in common seals, phocine distemper virus caused distemper outbreaks in Danish mink farms in 1989 (Heide-Jørgensen *et al.* 1992). Whether the virus transferred to free-living mink in Britain is unknown, but with coastal populations of mink the risk of transmission was probably high.

Badger *Meles meles*

Status: Native and generally common, particularly in southern England (Cresswell *et al. 1*989).

Distribution: Found throughout mainland Britain, plus Anglesey, the Isle of Arran, Canvey Island, Isle of Grain, Isle of Sheppey (Kent) and Isle of Wight. Badgers are most common in areas below 100 m, and are rare in upland areas.

Population data: Early attempts to estimate population size were based on the results of the Mammal Society's sett survey. Hardy (1975) suggested that there were about 35,000 badgers in Britain, and Clements, Neal & Yalden (1988) estimated a population of 36,000 social groups or about 216,000 adult badgers. These estimates were hampered by the lack of data from many areas, and by a failure to differentiate between different types of sett. Based on a stratified survey of 2455 1 x 1 km squares from November 1985 to February 1988, in which setts were classified into one of four types, the number of social groups was estimated to be 41,894 $\pm$ 4404 (95% confidence limits) (Reason, Harris & Cresswell 1993). Mean densities for different land classes range from 0 to 0·646 $\pm$ 0·135 (s.e.) social groups per km^2 of land. Locally, densities may reach six social groups per km^2 (Kruuk 1978). Mean group size from a number of studies averaged six adults (Cresswell, Harris & Jefferies 1990), although individual group sizes of as few as two in Speyside (Kruuk & Parish 1987) and more than 20 adults in Gloucestershire have been recorded (C.L. Cheeseman pers. comm.). In areas of low population density mean group size may be smaller (Skinner, Skinner & Harris 1991). Assuming a mean group size of six adults, the total British badger population is approximately 250,000 adult badgers, and 172,000 cubs are born each spring (Harris *et al.* 1992). Of the total British badger population, 24·9% is in south-west England and 21·9% in south-east England, with overall 76.1% in England, 9.9% in Scotland and 14.0% in Wales (Cresswell *et al.* 1989).

Population estimates: A total pre-breeding population of about 250,000; 190,000 in England, 25,000 in Scotland and 35,000 in Wales. In addition there are about 172,000 cubs born each year. **Reliability of population estimate:** 2.

Historical changes: The distribution and numbers of badgers in Britain are clearly dependent on the pattern of agriculture (Reason, Harris & Cresswell 1993). The effects of changing patterns of agriculture on badger numbers since the Domesday Book of 1086 have been discussed by Cresswell *et al.* (1989). Even in the last 150 years, badgers have undergone major changes in status and possibly also distribution; these changes are summarised by Cresswell, Harris & Jefferies (1990). At the turn of the century, badgers were probably rarer than they had been 100 years earlier or would be half a century later, almost certainly the result of persecution by gamekeepers. Millais (1904-1906) described them as 'somewhat scarce'. During this century badger numbers have increased overall, although in East Anglia in the early 1960s badger deaths were recorded as a result of dieldrin poisoning (Cramp, Conder & Ash 1962; Jefferies 1969), and whilst the full effects of these insecticides on the badger population in East Anglia are unknown, a number of well-known setts became inactive for extended periods, and some still remain so (Cresswell, Harris & Jefferies 1990).

Population trends: At present these are unclear. Griffiths & Thomas (1993) have suggested that the British badger population may be stable, although a definitive estimate of population changes will not be available until the national badger survey is repeated. However, in some areas the rates of sett loss are substantial, and in the absence of a comparable rate of establishment of new setts, the badger population is likely to be declining, at least locally. In Essex, for instance, in the 20 year period up to the mid-1980s, 36% of known setts disappeared, and of those remaining, the number occupied by badgers fell to 14%. Also, the modal sett size declined from six holes to three. In south and west Yorkshire, 81% of 278 setts were occupied in the mid-1970s, but only 38% in 1978 (Paget & Patchett 1978). Conversely, in parts of the south-west anecdotal reports suggest that the badger population may be expanding, at least locally, in some areas.

Population threats: Annual adult mortality is believed to total approximately 61,000 animals, while annual cub mortality is 64,500 pre-emergence and 41,500 post-emergence (Harris *et al.* 1992). The pre-emergence cub mortality is thought to be largely due to infanticide (Cresswell *et al.* 1992). Road deaths are probably the next major cause of death, with approximately 50,000 badgers killed per annum. Whilst this figure may seem high, a comparable figure (60,000) is obtained by extrapolating the results of the Surrey road deaths survey (R. Ramage pers. comm.); see the hedgehog account for details of the survey. In addition, an estimated 10,000 badgers are killed illegally by diggers and a further 1000 killed each year in an attempt to control bovine tuberculosis in cattle in the south-west (Harris *et al.* 1992). Despite these various mortality factors, cub survival to the end of the first year approximately equals adult mortality, and so mortality at the individual level (i.e. ignoring sett losses and their associated mortality - see below) is probably not affecting population size (Harris *et al.* 1992). Persecution by badger diggers and other forms of illegal killing probably have had only a minor impact on population size in recent years, although there was a more substantial impact earlier this century (Cresswell, Harris & Jefferies 1990). In the absence of past persecution, it has been estimated that there could be 43,437 ± 4731 badger social groups in Britain, an increase of 3·7% on the present population. Most of this loss occurred in Norfolk and Suffolk as a consequence of persecution by gamekeepers last century (Harris 1993; Reason, Harris & Cresswell 1993).

However, sett losses, rather than mortality of individual badgers, probably pose the most significant population threat. Sett destruction often involves the death of the resident badgers, and where this is the main sett, can lead to the loss of an entire social group. Landscape changes, particularly those associated with agricultural activities, were the major cause of sett losses in Essex in the 20 years up to the mid-1980s (Skinner, Skinner & Harris 1991), and Reason, Harris & Cresswell (1993) estimated that small increases in landscape diversity (in the absence of past persecution) could produce an increase in the badger population to 58,284 ± 5640 social groups, an increase of 40%. Obviously, this is a theoretical calculation. It assumes that any population increase will occur in a linear fashion in response to increasing habitat availability, an assumption that may not hold true. However, it does serve to show that with small habitat improvements, there could be substantial increases in badger populations. Fragmentation of populations by loss of setts or new road schemes, particularly in low density areas, may pose a substantial threat (Skinner, Skinner & Harris 1991).

Otter *Lutra lutra*

Status: Native. Localised, but generally increasing.

Distribution: In England otters are absent from the central area, rare in the east, north-west and south, but reasonably common in the south-west, north-east and the English counties bordering central Wales. They are found throughout most of Scotland, but with reduced numbers in areas of intensive agriculture and the industrial central lowland belt. In Wales, they are absent from parts of the south and Anglesey.

Population data: These were calculated for England, Scotland and Wales from the length of river in each water authority region and the percent of occupation of sites in the latest published otter surveys, using 1984-1986 data for England (Strachan *et al.* 1990), 1984-1985 data for Scotland (Green & Green 1987) and 1984-1985 data for Wales (Andrews & Crawford 1986). From these surveys, the site occupation rate for each water authority region was as follows: Anglian - 1·1%; North West - 9·3%; Northumbria - 9·8%; Severn Trent - 3·6%; South West - 43·8%; Southern - 3·0%; Thames - 0%; Wessex - 0·6%; Yorkshire - 2·2%; and 65·0% in mainland Scotland and 38·0% in Wales. The density of otters in different habitat types is unclear. D.J. Jefferies (pers. comm.) used the following data to calculate the otter population size. A study of rehabilitated otters in East Anglia found that three adults (one male, two females) occupied a minimum polygon range of 74·7 km² (Jefferies *et al.* 1986), and in Perthshire four adult otters (one male, three breeding females, plus some juveniles) occupied a minimum convex polygon range of 57·4 km² (Green, Green & Jefferies 1984). This gave an estimated 24·9 km² per adult otter in low density areas such as England and Wales, and 14·4 km² per adult otter in high density areas such as Scotland. From the figures for the length of all waterways in Table 4, and the area covered by each water authority, there were 1·10 km of waterway per km² in England and Wales, and 1·66 km of waterway per km² in Scotland, i.e. 27·32 km of waterway per adult otter in England and Wales (minimum convex polygon range multiplied by the length of waterways per km²) and 23·77 km of waterway per adult otter in Scotland. Using these figures, the lengths of all waterway (Table 4) and the percentage occupation to give the occupied length of waterway in each region, produced an estimated total adult otter population of about 350 in England (Anglian - 10, North West - 42, Northumbria - 43, Severn Trent - 34, South West - 196, Southern - 13, Thames - 0, Wessex - 2 and Yorkshire - 13), 3567 in mainland Scotland and 391 in Wales. These figures do not include of the number of immature animals living on their natal range.

To estimate the otter population in Shetland, Kruuk *et al.* (1989) conducted a stratified survey of holts, covering 35% of the coast. In smaller, intensively-studied areas, they found there were 0·331 resident female otters per holt, and that resident females comprised 54·5% of the otter population. Allowing for sampling errors and statistical errors, they concluded that there were 700-900 adult otters in Shetland in 1988. There are no reliable data on which to calculate the number of adult otters in other coastal regions of Scotland, but D.J. Jefferies (pers. comm.) has provisionally estimated these as 1000 on the west coast of Scotland from the Mull of Kintyre north to Cape Wrath and 1200 on Orkney and the Western Isles by assuming densities comparable to those found in Shetland.

In a recent study in north-east Scotland, Kruuk *et al.* (1993) argued that area of waterway, rather than length of waterway, should be used when calculating the amount of waterway per otter, since there was an exponential decline in otter utilisation with mean stream width. This finding is very similar to a possible relationship they noted between fish biomass and river width (smaller streams showed much larger fish productivity). Thus, if it was possible to calculate the area of waterways, it should produce a more accurate otter population estimate. In an area where otters were common Kruuk *et al.* (1993) calculated a median value of one otter per 15·1 km of stream. If this figure is used, it suggests a population of 5600 otters in mainland Scotland. However, since their data are based on the proportion of spraints deposited by otters marked with radionuclides, their estimate is likely to include spraints from unmarked otters of a variety of ages, not just adults, as was used in the calculation above. Furthermore, the calculation presented here is based on occupancy levels in the mid-1980s, since when the population has increased (see below). Thus the results from the study in north-east

Scotland suggest that the estimate presented here for the adult population is probably reasonably accurate.

Population estimates: A total pre-breeding population in the mid-1980s of about 7350; 350 in England, 6600 in Scotland (3600 on the mainland and 3000 on the islands) and 400 in Wales. When the results of the current otter resurveys are all available, they will produce significantly higher population estimates, since there has been an increase in the levels of occupancy since the mid-1980s, e.g. Northumbria 9·8% to 25·8%, Thames 0% to 2·2%, Wessex 0·6% to 12·3% and Yorkshire 2·2% to 9·3% (J. & R. Green pers. comm.).
Reliability of population estimate: 3.

Historical changes: These are described by Chanin & Jefferies (1978) and Jefferies (1989). Otter populations were relatively high until at least the mid-18th century. Otter hunting with hounds had started by 1796 (Bell 1874), and in the 18th and 19th centuries otters were increasingly persecuted for fishery protection and sport. Local declines in otter populations in the 18th century accelerated, and by the end of the 19th century these had become so severe that in some areas there was a shortage of otters to hunt (Jefferies 1989). There are few data on the effects of persecution on otter populations, but severe local effects did occur. For example, between March 1831 and March 1834 the Duchess of Sutherland's estate paid five shillings each for 263 otters (Ritchie 1920), and otters were entirely exterminated from the Inner Hebridean islands of Colonsay and Oronsay by keepers; otters did not return to these islands until the 1950s (J. & R. Green pers. comm.). In fact, persecution for pelts was widespread and led, for instance, to the development of 'otter-houses' on Shetland in which the animals were periodically trapped.

However, during the First World War the cessation of hunting and reduced pressure from gamekeepers led to a small population increase. Intensive hunting with packs of hounds during the 1920s and 1930s altered the age structure of the population, and probably had a significant population impact; in the 1930s the annual kill was around 400 animals. This declined to an annual mean of 199 in the 1950s (Chanin 1991). A catastrophic decline occurred simultaneously over England, southern Scotland and Wales, but most severely in the south-east, starting in 1957-1958. This was due to a combination of hunting pressure and the pollution of rivers by organochlorine insecticides. The trough in this decline seems to have occurred around 1977-1979. In the mid-1970s the population in Norfolk was down to 17 pairs (Macdonald & Mason 1976), and on the Somerset Levels in 1983/84 there were only about 12 otters (Scott 1985). There was markedly less decline in Scotland. Green & Green (1980) showed that in 1979 the otter population in southern Scotland was fragmented, but that the Northern and Western Isles, the Inner Hebrides, the west coast and south-west Scotland supported good otter populations.

Population trends: A recovery seems to have commenced in the early 1980s, although the population in East Anglia continued to decline (Chanin 1992). This general increase seems to be continuing, and a survey of England in progress in 1993 reported many new areas with signs of otters (R. Strachan pers. comm.). In Scotland a survey underway in 1994 showed substantial increases in distribution, particularly in the central and eastern lowlands, and that there is now a significant urban otter population, most markedly within Greater Glasgow (J. & R. Green pers. comm.). Improvements in water quality and good baseline populations seem to be major factors leading to this rapid recolonisation of Scotland. However, whilst otters seem to have a good future in those areas with established populations, current pollutant levels in lowland areas of England may prevent consolidated range expansion (Mason & Macdonald 1992). A study in Wales and the west midlands suggested that the colonisation of lowland areas of England is inhibited by the organochlorine pesticide residues in the otter's food chain, but that if contamination levels can be reduced, otters will spread rapidly (Mason & Macdonald

1993a). Furthermore, levels of PCBs in some lowland areas may be sufficiently high to adversely affect the reproduction or physiological competence of otters so that such populations may not be self-sustaining (Mason & Macdonald 1993b).

Because the otter population in East Anglia did not follow the general pattern of increase, a restocking programme commenced in 1983 (Jefferies *et al.* 1986), and up to the end of 1989 18 animals had been released at six localities in East Anglia (Wayre 1989). By that time it was considered that suitable habitat for any further releases was limited (Anon. 1989), and the current East Anglian otter population is derived largely, if not entirely, from these releases (Mason & Macdonald 1993c). Subsequently, a further six animals were released at two sites in the Lee catchment north of London (Mason 1992). In addition a few otters have been released in south-west England not far from the zone of expansion of the wild population. In East Anglia it has been claimed that there have been 21 litters, 19 from released animals and two from second generation females (Wayre 1989). However, the value of these releases and the reported successes have been seriously questioned by Mason (1992).

Population threats: Otters are relatively short-lived animals with, on average, a short breeding life-span in which to produce sufficient cubs to sustain the population. Hence any factor which reduces either otter survival or breeding success, even by only a small amount, could be detrimental to the survival of otter populations (Conroy 1992). Thus road mortalities may be important to isolated relict populations. Natural, as opposed to violent, mortality appears to be highest during times of food shortage. This applies to both Shetland (Kruuk & Conroy 1991) and north-east Scotland (Kruuk *et al.* 1993), and it is at these times that most alternative prey items (mammals and birds) occur in spraints (Kruuk *et al.* 1993). However, samples from a range of habitats do not reflect this seasonal pattern of violent mortality (Mason & Madsen 1990).

One study in riparian habitats in Scotland showed that food is limited (Kruuk *et al.* 1993), with the otters taking 60-118% of the mean standing crop or 53-67% of the annual production of salmonids. This finding has important implications for the conservation of otters, since if otters are food limited, improving otter habitats (e.g. by providing bankside vegetation, reducing human disturbance, etc.) may not be of value unless fish biomass is also raised (Kruuk *et al.* 1993). Similarly, events that lower fish stocks, such as short-term pollution or commercial fishing, are more likely to affect otter populations if they happen at those times of the year when the food supply is critical.

Pollution of rivers and seas may still be a significant threat to otters, particularly in lowland areas. Mason (1989) has reviewed all the various pollution threats to British (and other) otters. Mason & Macdonald (1992) argue that in many lowland areas both rivers and fish are still too contaminated to support otters, and PCB levels alone appear sufficient to cause reproductive problems. In mink, reproductive failure occurs when PCB concentrations exceed 50 mg per kg fat (Jensen *et al.* 1977), and such concentrations have been exceeded in otters from eastern England and elsewhere in Europe where numbers have declined sharply. In contrast, thriving otter populations, such as that in northern Scotland, have generally contained low levels of PCBs (Foster-Turley, Macdonald & Mason 1990). Some high PCB levels have been recorded in very young animals. For instance, a cub born in eastern England to a mother released as part of a restocking programme was killed by a car when only 11 weeks old and not yet weaned. It had already accumulated 62 mg of PCBs per kg fat in its liver (Jefferies & Hanson 1987). Two animals from eastern England, containing high concentrations of PCBs, exhibited pathological symptoms such as ulcers and skin abnormalities (Keymer *et al.* 1988). These symptoms were similar to those recorded in Baltic seals where PCB-induced adrenocortical hyperplasia is thought to have resulted in a failure of the immune system

(Bergman & Olsson 1986). Mason & Macdonald (1993c) concluded that contamination, particularly by PCBs, may mean that the otter populations in East Anglia may not be viable without repeated releases of captive-bred animals.

In south-west Scotland and northern England, there was an increase in dieldrin, DDE and PCBs in otter scats from west to east, suggesting that organochlorines may still be having an impact on otters (Mason 1993). A similar negative correlation between mean PCB concentrations and otter population performance was found in Wales and the adjacent English counties (Mason & Macdonald 1993d). However, interpreting the significance of PCB residues is not easy, and residues in otters from East Anglia are as high as those from parts of Wales, where otter numbers are increasing (D.J. Jefferies pers. comm.). Whether the absence of otters in much of lowland England is due to an absence of otters to colonise the area, a lack of suitable habitat or a high level of pollutants is as yet unclear.

In both Scotland and Wales, acidification of upland rivers reduces invertebrate populations, and hence reduces the fish population on which the otters feed, possibly leading to local population declines (Mason & Macdonald 1989; Green & Green 1993) rather than a contraction in distribution (Mason 1991). It has been suggested that in lowland areas, increased public pressure on waterside amenities means that disturbance and destruction of bankside vegetation renders many areas unsuitable for otters. However, Jefferies (1987) showed that the effects of disturbance may be overrated. He found that the behaviour of males was little affected, but females were more affected, using more underground holts than hovers, and that the effects of disturbance were most pronounced on females with cubs. The loss of wet woodlands, carrs and riverside trees, habitats favoured as resting sites by otters, may be particularly significant (Macdonald & Mason 1983; Jefferies *et al.* 1986).

With current legal protection and with improvements in water quality, population increases should continue, although the changes in waterside habitats probably mean that otters will never regain their former numbers. Where numbers have reached very low levels, restocking may aid population growth (Jefferies *et al.* 1986; Jessop 1992). For those areas where numbers are low, heavy losses in commercial fish and crustacean traps (Jefferies, Green & Green 1984) may be significant, although, generally, violent deaths have not posed a serious threat to otter populations. The potential impact of oil spills, such as the *Esso Bernicia* spill in Sullom Voe in 1978 and the *Braer* incident in Shetland in 1993, could be considerable on coastal otter populations. One major incident in this area could destroy a significant proportion of the British otter population.

Wildcat *Felis silvestris*

Status: Native. Uncommon but wildcats increased in numbers and range throughout much of this century following a reduction in persecution (Langley & Yalden 1977).

Distribution: Wildcats are only found in Scotland north of a line between Edinburgh and Glasgow (Easterbee, Hepburn & Jefferies 1991), and are normally confined to low altitudes. Since 1987 there have been a number of reports from Galloway; whether these represent true wildcats, and if so whether a natural colonisation or an undocumented release, remain to be determined (J. & R. Green pers. comm.).

Population data: Only two density estimates are available. In east Scotland, Corbett (1979) estimated a density of 30·3 wildcats per 100 km² in Glen Tanar, Deeside. In west Scotland, R. Scott (pers. comm.) estimated about 8·0 per 100 km² in Ardnamurchan. These two estimates were obtained about 15 years apart. Whether wildcats are still present in Deeside at the densities prevalent when Corbett was working there is unclear, and it is possible that there has been an overall decline in density to the approximate levels currently seen in Ardnamurchan (R. Scott pers. comm.). Analysing the data collected by N. Easterbee during 1983-1987, D.J. Jefferies (pers. comm.) found that wildcats were rare or absent in the central area, with density increases to the north, south, east and west. The density in the east (based on the number of sightings per five year period) was still higher than in Ardnamurchan. Thus within their current range, density appears to decline from east to west and possibly from south to north (R. Scott pers. comm.). If wildcats occur throughout their current range at the lower density (8·0 per 100 km²), the total population would be 2800, and if at the higher density (30·3 per 100 km²), the total population would be 10,700.

An independent estimate was supplied by D.J. Jefferies (pers. comm.), who used the distribution of wildcats on a 10 x 10 km square basis as shown in Easterbee, Hepburn & Jefferies (1991). Each occupied 10 x 10 km square was allocated to one of four status categories based on the frequency of sightings (which was known for 82% of the occupied squares), and the status in particular squares was related to the known density in the two field study sites described above. This produced an estimated population of about 3500 wildcats. This estimate was of animals of independent-age (over five months old) and of wildcat appearance, although it undoubtedly included some hybrids (D.J. Jefferies pers. comm.).

Population estimates: A total pre-breeding population of about 3500, all in Scotland. **Reliability of population estimate:** 3.

Historical changes: Wildcats were once widespread, but persecution and loss of habitat led to a population decline (Langley & Yalden 1977). In 1800 wildcats were still widespread in Scotland and Wales, and they were present in at least six, and possibly eight, English counties. By the mid-1800s, they were extinct or virtually so in England, although there is one apparently reliable record from Hutton Roof, Cumbria, in 1922; two wildcats were seen, and one was shot and preserved (Arnold 1993). The last reliable record from Wales was probably in 1862. The wildcat's decline in Scotland continued into the early 20th century. It reached its nadir around the First World War, when wildcats were confined to a small area of north-west Scotland. Ritchie (1920) supposed that it still survived in Argyll, Inverness-shire, Sutherland and Wester Ross, but was not optimistic about its future.

The range expansion earlier this century was undoubtedly associated with an increase in numbers. After the First World War, wildcats expanded their range, and by the end of the Second World War occupied much of their current range (Taylor 1946). A questionnaire survey in the early 1960s showed that wildcats were increasing in abundance (Jenkins 1962), but since the 1960s there has been little range expansion.

Population trends: These are unclear. The recent survey by Easterbee, Hepburn & Jefferies (1991) found that wildcats were reported to have declined in 34% of the occupied 10 x 10 km squares in the years before the survey, whereas they had increased in only 8%. Interpreting subjective data is difficult, but Easterbee, Hepburn & Jefferies (1991) concluded that most populations of wildcats in Scotland were showing little change. Relatively few population increases were recorded and these were mostly in the areas where wildcats were classified as established, whereas the areas where wildcats were occasional and rare showed few increases, but frequently showed a decrease, of 32% and 44% respectively.

It appears that most of the suitable habitat in Scotland north of the central industrial belt has now been recolonized by wildcats, and that further opportunities for spread or population expansion are limited. It seems unlikely that wildcats will cross the central industrial belt naturally, although there is a substantial area of suitable habitat which could support wildcats in south Scotland (Easterbee, Hepburn & Jefferies 1991).

Population threats: During the 1983-1987 survey, persecution was found to be widespread, and 19% of reported cases affected established populations, whereas 81% affected lower density populations. The Game Conservancy's National Game Bag Census return for 1984/85 recorded the killing of 274 wildcats on 40 shooting estates in central, eastern and north-eastern Scotland. This figure, which excludes many estates and persecution from other sources, still amounts to an annual mortality of nearly 10% of the population estimated by D.J. Jefferies (see above). This level of persecution was recorded prior to wildcats receiving legal protection in 1988. Current levels of persecution are unquantified but are still thought to be high in some areas (McOrist & Kitchener 1994). The continued persecution of low density populations could lead to localised population declines and even extinctions, since many of the populations are small and isolated (Easterbee, Hepburn & Jefferies 1991). Furthermore, some of these decreases have been in the relict population in the north-west highlands, which was thought to have least hybridisation with domestic cats.

Overall, hybridisation with domestic cats is believed to pose the major conservation problem, and is probably a continuing event which commenced several centuries ago (French, Corbett & Easterbee 1988). Recent genetic studies (Hubbard *et al.* 1992) have suggested that much interbreeding is occurring with consequent DNA hybridisation; of 42 putative wildcats from remote areas of northern and western Scotland, only eight showed clear genetic differences from domestic cats. However, discriminant analysis of skull measurements of Scottish wildcats suggests that in the last 30 years there has been a reduction in hybridisation with natural selection for the original wildcat skull morphology (French, Corbett & Easterbee 1988; Kitchener 1992). Hybridisation was most frequent from 1940-1965, when wildcats were rapidly expanding their range but numbers were low and hence there was a shortage of potential mates. Since 1965 the skulls of wildcats have partially reverted in size and shape to those of wildcats collected before 1940 (French, Corbett & Easterbee 1988). It is unknown whether wildcats will fully revert to their original wild-type morphology, or whether they have evolved a new skull morphology after a period of hybridisation with domestic cats.

Other threats include accidental killing by dogs, snares, poison baits set for other species, and road traffic accidents. Corbett (1979) found that on the Glen Tanar estate 58% of wildcat deaths were due to snaring, 8% were shot, 8% were killed by cars, 8% trapped, and only 17% were due to natural causes. Most viral diseases in domestic cats seem to readily infect wildcats. Active feline leukaemia virus infections have been found in several wildcats from Scotland (McOrist *et al.* 1991).

Since wildcats are mostly found in the less developed and more remote areas, development programmes and road building to boost local economies could be detrimental to wildcat populations (McOrist & Kitchener 1994). Although increasing afforestation helped the spread of wildcats, as forest plantations mature they become less suitable for the small mammals on which wildcats prey (Easterbee, Hepburn & Jefferies 1991). Forestry management should therefore aim to diversify the age of plantations. Finally, two wildcats collected in Aberdeenshire had significant levels of dieldrin in their livers, and one other contained traces of DDE (McOrist & Kitchener 1994). If dieldrin is still present in the food chain of wildcats, it may constitute an additional threat to populations already under pressure.

Feral cat *Felis catus*

Status: Introduced. The term 'feral cat' is widely applied, and difficult to define precisely. Cats living independently of humans vary from totally free-living populations on islands, through urban colonies that are at least in part provisioned, to straying individuals in urban areas and cats loosely associated with farms.

Distribution: Feral cat colonies are most common in six areas of Britain. These are Cleveland, Durham, Northumberland and Tyne and Wear; Greater London and south-east England; Greater Manchester, Humberside, Lancashire, Merseyside and Yorkshire; the midlands; the central lowlands of Scotland; and South Wales (Rees 1981). The majority of colonies (69%) were found on hospital, industrial and private residential sites (Rees 1981). They are found on most (if not all) inhabited islands, including those such as Lundy with very small human populations (Rees 1981). They have been deliberately introduced to many islands, e.g. Holm of Melly, Noss and South Havra in the Shetlands in the 1890s to control rats, and St Kilda in 1930, although they are now extinct on St Kilda. There are truly feral populations on some uninhabited islands, e.g. the Monach Isles, Outer Hebrides, where they were introduced to control rabbits (Corbett 1979; Macdonald 1991).

Population data: Of 287 colonies, nearly 50% consisted of ten or fewer cats, and only 7% consisted of more than 50 cats (Rees 1981). Occasionally very large colonies occur. In Portsmouth dockyard, colony size varied from 252-351 over three years, and adult population size from 164-203, an average density of over 2 per ha (Dards 1981). Rural densities are much lower. On Devon farmland and the Monach Isles densities of 6 per km² were recorded (Macdonald & Apps 1978; L.K. Corbett unpubl.). A survey found that about two-thirds of English farms had cats that were, to varying extents, independent or semi-feral, and that the mean colony size was four (Macdonald *et al.* 1987).

In the 1980s it was estimated that there were over 6,000,000 cats in Britain, and a widely quoted figure was that about 20% of these, i.e. 1,200,000, were feral (e.g. Tabor 1981). However, this figure was derived from a questionnaire survey that located 704 colonies, and it was suggested that the total number of animals thought to occur in these colonies (12,302) represented 1% of the total feral cat population, which might therefore number 1,200,000 (Rees 1981). There was no quantitative evidence for this assessment. Therefore, to calculate the size of the feral cat population in Britain, it was assumed that their density was 6 per km² in rural habitats in the arable and pastoral land class groups but that feral cats were absent from marginal upland and upland land class groups. This gave a rural population of 600,000 feral cats in England, 125,000 in Scotland and 55,000 in Wales. To calculate the size of the urban feral cat population, four detailed surveys in Bristol, Oldham, Swindon and the Wirral and Ellesmere Port were used. In these surveys, feral cat colonies were located and the number of cats present in each was estimated, suggesting a mean density of around 1·4 feral cats per km² (R.J.C. Page pers. comm.). This density was applied to all the built up areas in England, Scotland and Wales.

Population estimates: A total pre-breeding population of about 813,000; 625,000 in England (600,000 in rural areas, 25,000 in urban areas), 130,000 in Scotland (125,000 in rural areas, 5,000 in urban areas) and 58,000 in Wales (55,000 in rural areas, 3,000 in urban areas). These must be minimum figures, since there are no data on the numbers of free-living cats in urban areas that are loosely or temporarily associated with households, and which do not live in colonies. **Reliability of population estimate:** 4.

Historical changes: Feral cats have probably been present in Britain in considerable numbers for a long time, having possibly arrived in Britain with the Normans in the 11th century (Zeuner 1963). Hudson (1898) estimated that there were at least 500,000 cats in London, of which 80,000-100,000 were feral, and Matheson (1944) estimated that there were 30,000 cats in Cardiff, of which 6,600 were feral. Both these estimates suggest that in the period up to the Second World War about 20% of the total urban cat population was feral. Current estimates suggest that this proportion has declined dramatically, and with improved welfare, particularly the neutering of entire colonies (Neville 1989), this proportion should decline further.

Population trends: Possibly declining in urban areas due to neutering of animals in colonies. However, recently the Cats Protection League (1993) estimated that 25% of United Kingdom families (i.e. 5,400,000 households) owned at least one domestic cat, and that the total domestic cat population was approximately 7,600,000 animals. It was estimated that this will approach 8,000,000 by the year 2000. Whether this will also lead to a growth in the feral cat population, particularly in the number of free-living urban cats that do not live in colonies but are loosely associated with particular households, is unknown. There is no evidence to indicate any change in the size of the rural population of feral cats.

Population threats: None known. Neutering of colonies (Neville 1989) will locally reduce problems and limit the growth of individual colonies, but is unlikely to have a significant impact on the total number of feral cats in Britain, especially since the technique is usually applied to urban colonies, and most feral cats are found in rural habitats.

Order: Pinnipedia

Common seal *Phoca vitulina*

Status: Native; locally common.

Distribution: The coasts of east England, east Scotland, north and west Scotland, the Hebrides, Orkney and Shetland. There are very few records from Wales (Arnold 1993), and breeding colonies are only found in England and Scotland.

Population data: Until 1984 population estimates were based on haul-out counts made from boats at the end of the pupping season. However, common seal pups are capable of swimming within hours of birth, so at any one time a proportion of pups will not be observed (Reinjders & Lankester 1990). Also, the pupping season is lengthy, so early born pups will disperse before late ones are born. Therefore, common seals are now counted between late July and mid-August during the annual moult (Thompson *et al*. 1989), when the largest number of seals are usually recorded. An aerial survey in Orkney in 1985 during the moult produced a mean population estimate approximately three times that obtained in previous surveys; much of this increase was due to the change of survey period rather than any change in common seal numbers (Thompson & Harwood 1990). The relationship between the number of seals counted and total population size has yet to be established owing to the uncertainty over the proportion that is at sea at any given time, although this is only a small proportion of the total population (Thompson 1989; Thompson & Harwood 1990). However, so long as standardised survey techniques are used for different areas, improved methods can be used to re-evaluate old survey data (Thompson & Harwood 1990).

Because the breeding grounds and moulting sites of common seals are more dispersed than those of grey seals, common seal surveys are made less frequently and several areas have yet to be covered using the more effective moult surveys (Thompson 1992). In July/August 1991 an aerial survey was carried out in Shetland, the north coast of Scotland and reference locations on the west coast of Scotland using a helicopter and a thermal imager. A thermal imager was used because it is difficult to discriminate seals on rocky shores. Separate counts are needed to estimate pup production, and thermal imaging is also used here, since it helps differentiate between dead and live pups; failure to recognise dead pups can lead to over-estimates of pup production (Thompson & Harwood 1990). Sites where common seals haul-out on to sandbanks, such as the Wash, Firth of Tay and Moray Firth, are surveyed using a fixed-wing aircraft (Hiby, Duck & Thompson 1993).

By these means, the minimum number counted was 24,640. Studies of common seals in Orkney fitted with radio-transmitters have shown that almost all males and 42-75% of females are likely to be counted in aerial surveys in August. If the behaviour elsewhere in Britain is the same as that observed in Orkney, total population sizes could be 23-59% higher than these values (Sea Mammal Research Unit unpubl.). Thus the population could be between 30,310 and 39,180. Individual counts were: 1551 in the Wash in 1991; 1663 on the east coast of Scotland in 1991; 8205 on the north and west coast of Scotland and Inner Hebrides in 1988-1991; 1300 in the Outer Hebrides in 1974; 7137 in Orkney in 1989; 4784 in Shetland in 1991 (Hiby, Duck & Thompson 1993).

Population estimates: A total pre-breeding population of about 35,000; 2200 in England, 32,800 in Scotland and none in Wales (based on colony counts, although there are occasional sightings of animals off the Welsh coast). **Reliability of population estimate:** 2.

Historical changes: Common seals were once more widely distributed around the coasts of Britain, with colonies on the Isle of Wight in the 19th century and in the Bristol Channel until quite recently (Bonner 1972; Bonner & Thompson 1991). Their disappearance from these two areas is probably due to increased human pressure (Anderson 1990). Similarly in the early years of the 19th century, common seals bred in great numbers in the mouth of the River Tees, and from around 1820 or 1830 about 1000 frequented the mouth of the Tees, but by 1862 the number had been reduced to three (Millais 1904-1906). Thorburn (1920) described common seals as constantly persecuted, and only abundant in the Hebrides, Orkney and Shetland. They were thought to be thinly distributed on the western coasts of England, and on the east coast there were some on the Farne Islands, Northumberland but they were rare south of the Wash.

Lockley (1966) suggested a minimum population of common seals in Britain of 8000, excluding pups. This rose to 11,000-12,000 by the early 1970s (Bonner 1972). However, following the introduction of grey seal hunting in the 1960s, hunting was soon extended to common seals on the west coast of Scotland and in the Wash, and the long-established hunt in the Shetlands intensified, since common seal pups produced a much more valuable pelt (Bonner 1989a). In the Wash, the annual kill of pups averaged 607 from 1962 to 1970, and never rose above 870 (Vaughan 1978). This represented only 38% of the calculated production (Bonner 1976), and was not thought to seriously endanger common seals in the Wash (Bonner 1989a). The same applied to kills of 400-600 in the west of Scotland. However, in Shetland before 1960 the cull probably accounted for about 300-400 pups, but after 1962 the number killed increased substantially until, in 1968, about 900 young seals were taken, a very high proportion of the annual production of pups (Bonner, Vaughan & Johnston 1973). A survey of Shetland in 1971 (Bonner, Vaughan & Johnston 1973) found that the common seal population had declined, possibly at a rate of around 7·5% per annum over the previous 15 years. Public antipathy to these hunts led to the introduction of the Conservation of Seals Act 1970, which for the first time provided a close season for common seals. Comparisons of surveys conducted in Shetland in 1971 and 1984 showed that the population still had not fully recovered from the effects of hunting by the mid 1980s.

Population trends: These are unclear. Counts made on the Wash between late July and early August showed an average increase of 3·5% per annum between 1969 and 1988 (Hiby, Duck & Thompson 1993). Conversely, in Shetland a helicopter count in 1991 showed almost exactly the same population size as estimated in 1984 from boats (4784 compared to 4700 in 1984), yet helicopter surveys generally have yielded substantially higher counts than those obtained from boats. Thus the 1991 result may suggest that common seals in Shetland have declined since 1984 (C. Duck pers. comm.).

In 1988, the phocine distemper epizootic killed more than 18,000 common seals in the North Sea, the Kattegat-Skagerrak and the southern Baltic (Heide-Jørgensen *et al*. 1992). Populations in Denmark and Sweden were reduced by up to 60% in 1988, but are expected to reach pre-epizootic levels by 1995 (Heide-Jørgensen *et al*. 1992). In the Wash the common seal population was reduced by about 50% following the epidemic, and counts since that time have not shown any recovery in numbers. Populations on the east coast of Scotland were thought to have experienced 10-20% mortality. Common seals in Orkney, Shetland and the west coast of Scotland, however, were not significantly affected by the epizootic (Harwood *et al*. 1991; Thompson & Miller 1992; Hiby, Duck & Thompson 1993). Prior to the phocine distemper virus outbreak, the British common seal population may have been 46,000-47,000 (P.M. Thompson pers. comm.). Overall, however, the effect of the epizootic on the total British population was much less than elsewhere in Europe (Sea Mammal Research Unit unpubl.).

Population threats: The effects of the observed levels of organochlorine contamination are not fully understood (Thompson 1992). Reijnders (1986) demonstrated reproductive suppression in common seals from the Netherlands as a result of PCB contamination, but these pollutant levels were some 200 times (PCBs) and four times (total DDTs) greater than those found in British seals. However, during illness or starvation, the mobilisation of fat reserves and the consequent increase in circulating PCBs may be sufficient to compromise an animal's physiology (Law, Allchin & Harwood 1989). Evidence to support this assumption was provided by Hall *et al*. (1992), who found significantly greater concentrations of organochlorines in the blubber of common seals which died as a result of contracting phocine distemper virus, than in live seals which had been exposed to the virus. However, it is possible that the dead animals were already ill and mobilising their fat reserves at the time they contracted the virus, and so the higher concentrations of organochlorines could have been the consequence of fat metabolism entirely unrelated to the events that caused their deaths. The high mortality rates seen during the phocine distemper virus epizootic were probably the consequence of introducing a highly pathogenic virus into a naive population with no specific immunity to the infectious agent. Thus no contributory external factors are necessary to explain the severity of the outbreak, but synergistic effects due to organochlorine pollution or crowding of seals at haul-out sites may have exacerbated the impact of the disease in some areas (Heide-Jørgensen *et al*. 1992). Whilst the epizootic led to a marked reduction in common seal populations in several parts of the North Sea, they appear to have recovered remarkably well (Thompson & Hall 1993).

Harwood & Hall (1990) have discussed the rôle of periodic mass mortalities in managing marine mammal populations. They argued that these events are the most important factor determining the long-term average population size in the absence of human exploitation. Density-dependent mechanisms such as small changes in infant survival or in the fecundity of the youngest age classes will serve to set an upper limit on population size, but the pattern of phocid social behaviour, such as periodic aggregations to breed or feed, exacerbates the risk of disease spread irrespective of total population density. However, long-term fidelity to particular breeding sites limits the exchange of individuals between neighbouring breeding groups, and hence limits the spread of disease.

The Scottish populations are susceptible to oil spills. Whilst seals have short hair which may become coated in oil, they do not preen and ingest that oil (Thompson 1992). However, should these animals be in the vicinity of a recent spill, the inhalation of toxic fumes could result in neural damage (Geraci 1990). Also, domestic sewage may contain toxic chemicals as well as human pathogens which may survive in sea-water and are known to cause infections in captive seals (Thompson 1992).

Common seals are particularly susceptible to disturbance at breeding sites, since mothers and pups can become separated, and the time available to nurse pups, already limited by their preference for inter-tidal haul-out sites, may be reduced (Thompson 1992). This may account for their disappearance from the Isle of Wight and Bristol Channel. Plans to reclaim areas of the Wash pose a threat to one population, both due to the loss of inter-tidal haul-out sites and increased levels of disturbance; this occurred in the Tees estuary during the 1960s (Thompson 1992). It is possible that the poor rate of increase in the number of common seals in Shetland over the past 20 years is in part due to the intensive fishing activities, particularly industrial fisheries, in the area (F.G.L. Hartley pers. comm.).

The seal epizootic in 1988 was not a new phenomenon to British common seals; similar events were recorded in Orkney in 1813, 1836 and 1869/70, and Shetland in the 1930s (Harwood & Hall 1990). The British common seal population is still under threat from a recurrence of the phocine distemper epizootic, since a large proportion of the population has not come into contact with the infection and has yet to develop an immune response (Harwood *et al.* 1989; Harwood & Grenfell 1990; Carter *et al.* 1992). However, whilst common seal mortality from the phocine distemper virus was only 10-20% in the Moray Firth, the high prevalence of antibodies in the survivors suggests that the low mortality in this area was not due to the seals lacking contact with the virus. It is possible that the seals in that area are either more resistant to the phocine distemper virus, or else the virus had mutated to a less virulent form (Thompson & Miller 1992; Thompson *et al.* 1992).

Grey seal *Halichoerus grypus*

Status: Native; locally common.

Distribution: There are important colonies in the Farne Islands, Northumberland, south-west Wales, Firth of Forth, Hebrides, Orkney and Shetland, with smaller populations in south-west England, Donna Nook/the Wash and the Humber Estuary.

Population data: The main grey seal breeding colonies on the Isle of May in the Firth of Forth, the Hebrides and Orkney are surveyed annually during the breeding season using conventional aerial photography. Each colony is covered three to five times during the pupping season, with pups counted from the photographs. In addition, the colony on the Farne Islands, Northumberland is counted from the ground. Since the breeding season exceeds the period that any one pup remains ashore, the counts only provide figures for the maximum number of pups at the site at any one time, and mathematical models incorporating life history parameters have been applied to the data since 1988 (Harwood *et al.* 1991). A maximum likelihood model is used to derive pup production figures from these counts (Ward, Thompson & Hiby 1987). Total pup production from these main colonies accounts for some 85% of all pups born in Britain each year. The total female population and total production figures are derived from models based on the overall pup production in each breeding area (Sea Mammal Research Unit unpubl.). It is believed that the 95% confidence intervals for the pup production estimates are within 10% of the point estimate. Those for the estimate of the number of adult females are within 35% below and 73% above the point estimates. It is not possible to give 95% confidence limits for the number of males, but these are almost certainly at least as large as for the female part of the population (Sea Mammal Research Unit unpubl.). In addition, less frequent counts are carried out of the numbers of pups born in the Humber Estuary, south-west Britain, mainland Scotland and Shetland but confidence limits cannot be provided for these population estimates (Hiby, Duck & Thompson 1993).

Overall, these counts suggest a total population of 93,500 grey seals at the start of the 1991 pupping season, when approximately 27,000 pups were born. Of the total population, 7100 were around England and Wales (Farne Islands, Northumberland - 3200; Humber Estuary - 800; south-west Britain - 3100) and 86,400 around Scotland (mainland Scotland - 3500; Inner Hebrides - 8700; Outer Hebrides - 37,500; Isle of May - 4200; Orkney - 29,000; Shetland - 3500) (Hiby, Duck & Thompson 1993).

Population estimates: A total pre-breeding population of about 93,500; 5500 in England, 86,400 in Scotland and 1600 in Wales.
Reliability of population estimate: 1.

Historical changes: In the early part of this century, grey seals were rather rare in England and Wales. A fair-sized colony inhabited the Isles of Scilly, a few still persisted on the Farne Islands, Northumberland and some were found on the Pembrokeshire coast. In Scotland they were much more plentiful, especially on the north-western coasts and the Hebrides, Orkney and Shetland (Thorburn 1920). However, at the time of the enactment of the Grey Seal Protection Act 1914, the British grey seal population was put at only 500 animals, although this was undoubtedly a significant under-estimate. In 1928 the population was estimated to have reached 4000-5000 (Rae 1960), and by 1932, when a new Act extended the close season for grey seals, the population was put at 8,000, again with no information as to how this estimate was derived (Bonner 1982).

In the 50 years up to 1980, several populations of grey seals showed dramatic increases (Bonner 1981). It is unclear to what extent this increase in grey seal numbers was due to a reduction in hunting pressures, the change in economic circumstances which reduced the human population in the areas frequented by the seals (the abandonment of islands such as the Monachs in the Outer Hebrides and Holm of Faray in Orkney provided new secure breeding places for the seals), or the almost total disappearance of the crofter-fisher lifestyle which regarded seals as a valuable asset, thereby allowing the seals to exploit their new breeding places in comparative safety (Bonner 1982). Whatever the relative importance of the various factors, grey seal populations improved. For example, pup production on the Farne Islands, Northumberland increased from less than 100 in the early 1930s to 751 in 1956 and 2010 in 1971 (Coulson & Hickling 1964; Bonner 1975) and on the Monach Isles from about 50 in 1961 to 1400 in 1974 (Bonner 1976). Overall, the British grey seal population doubled from 34,200 in the mid-1960s (Smith 1966) to 69,000 in the mid-1970s (Summers 1978).

The growth in seal numbers led to concern over their impact on fish stocks. The grey seal and fisheries controversy has been described in detail by Bonner (1982; 1989b). In 1959 the Nature Conservancy set up a Consultative Committee on Grey Seals and Fisheries, which in 1963 recommended (Nature Conservancy 1963) that grey seal numbers should be reduced by 25% in the Orkneys and the Farne Islands to preserve fish stocks. At that time, the population of grey seals in Scotland was estimated to be 29,500. The Farne Island population was culled from 1963 to 1965 under the auspices of the Ministry of Agriculture, Fisheries and Food, but thereafter the cull was halted because the National Trust argued that the fisheries case, as it related to the Farne Islands, Northumberland, was insufficiently proven. The cull in Orkney continued, whilst that on the Farne Islands was reintroduced in 1972 because increasing seal numbers were damaging the fragile environment and leading to increased pup mortality. The benefits and failures of these control programmes are discussed by Bonner (1982). Reviewing the pattern of population growth, Harwood & Greenwood (1985) concluded that in the years up to the early 1980s, some undisturbed grey seal populations had grown at rates of 6-7% per annum, whereas others had not. Thus for the Inner Hebrides, from 1976-1981, the increase was 7% per annum (Natural Environment Research Council 1982), for the Outer Hebrides 6·5% per annum from 1969-1975 (Summers 1978), and for Orkney until 1969 6% per annum, when the effects of pup culling became apparent, and thereafter 3% per annum (Summers 1978). For the Farne Islands, the growth rate was 8% per annum from the 1930s until 1951 (Coulson 1981), and then 7% per annum from 1951 to 1971, with a decline thereafter as a result of control measures.

Renewed controversy over the impact of seals on fisheries led, in 1977, to an annual culling programme being introduced in Orkney and the Outer Hebrides, with the aim of reducing grey seal numbers in these populations from 50,000 to 35,000 by 1982. Originally planned as an annual cull of 4000 moulted pups and 900 breeding cows and other pups (Summers 1979; Bonner 1982), it was revised after the first year to a pup-only hunt because of widespread public concern. Also, the effects of culling adults at breeding colonies was not as predicted; around 15% of cows were deterred from coming ashore, and of those that did come back, some deserted their pups if the colony was disturbed again and some of the cows failed to return to breed in subsequent years. At the colonies where cows were culled in 1977, pup production in 1978 was up to 40% lower than in 1971 (Harwood & Greenwood 1985).

Population trends: The grey seal population is continuing to increase and the 1991 count was 9·9% higher than equivalent figures for 1990 (Hiby, Duck & Thompson 1993). The number of pups born each year in Orkney has increased more than 60% since 1984, although not all the Orkney colonies have increased at the same rate. Whilst some have shown a steady increase, others have declined and some have shown little change; reasons for this disparity are unknown (Sea Mammal Research Unit unpubl.). The 1988 phocine distemper virus had less impact on grey than common seals. Although only a few grey seal carcasses were found, it was estimated that there was a substantial but undetected mortality of 12%. This led to pup production in 1988 being 24%, 20% and 13% lower than expected for Orkney, the Isle of May and the Farne Islands respectively (Harwood *et al.* 1991; Hall, Pomeroy & Harwood 1992; Hiby, Duck & Thompson 1993). Since 1989, pup production has risen steadily at all sites except the Farne Islands, although it is still lower than expected. The reasons for the continued reduction in pup production at the Farne Islands are unknown.

Harwood & Prime (1978) showed that both juvenile and adult survival are probably affected by the density of animals within a breeding assembly, and thus as long as suitable breeding sites are available, there is a mechanism to ensure that the density at any one site does not rise to a level which would significantly affect the rate of increase of the population. However, since many potential grey seal breeding sites have yet to be occupied, it is likely that the British grey seal population will continue to increase.

Population threats: Bonner (1981) reviewed the literature on pollutant levels in grey seals, and concluded that generally they have not suffered any toxic effects from the levels of pollutants found, even though levels in blubber can be quite high (Blomkvist *et al.* 1992). However, recent studies of seals in the Baltic suggest that very high pollutant burdens may cause pathological changes which could ultimately affect reproductive performance (Olsson, Karlson & Ahnland 1992). Other work has shown that trace metal and organochlorine levels in grey seals on the eastern coast of Britain were considerably lower than those from grey seals that had suffered reproductive disorders elsewhere in the North Sea (Reijnders 1986; Law, Allchin & Harwood 1989; Law *et al.* 1991). Also organochlorine contaminants in grey seals from the Farne Islands in 1988 were lower than in 1972, suggesting a gradual decline with time (Law, Allchin & Harwood 1989). As for common seals, the risks posed by the discharge of untreated sewage are unknown (Thompson 1992).

Grey seals are potentially at risk from oil spills. Although in general seals seem able to avoid oil patches at sea, they often become stained by crawling over oil-covered rocks (Bonner 1972). Thus when the *Torrey Canyon* discharged 119,000 tonnes of crude oil off south-west England in 1967, there were an estimated 200-250 grey seals in the area affected by the spillage, but few seal deaths were reported (Bonner 1972). Whilst the *Exxon Valdez* incident in North America demonstrated that substantial seal mortality can be caused by massive releases of crude oil in enclosed waters, this type of pollution is unlikely to affect British seals, as shown by the *Braer* incident in Shetland (W.N. Bonner pers. comm.).

Grey seals are very sensitive to disturbance of their breeding sites; hence the dramatic increase in use of islands off north-west Scotland following depopulation of the area (Summers & Harwood 1979). Unlike common seals, nearly all grey seals now show immunity to the phocine distemper virus (Carter *et al.* 1992; Hiby, Duck & Thompson 1993), and so it would appear unlikely that a recurrence of this disease will have a significant impact on grey seals in the near future.

Order: Artiodactyla

Red deer *Cervus elaphus*

Status: Native, with a number of feral populations in England and Scotland. Deer from native stocks are only confirmed in parts of Scotland and north-west England (Lowe & Gardiner 1974); all other populations are introduced. Common and increasing.

Distribution: Cumbria, East Anglia, Hampshire, south-west England, south-west Scotland, Scotland north of the central industrial belt, and with scattered records from elsewhere in England and Wales. Red deer are also found on numerous Scottish islands (Staines 1991).

Population data: They are found on open moorland, and in coniferous and deciduous forest. Densities vary with the quality and structure of the habitat. Densities of 5-40 (exceptionally) per km² occur in forestry plantations, and 12-15 per km² are typical for hill land, although densities from less than 10 to over 30 per km² occur (Ratcliffe 1984; Stewart 1985; A.J. de Nahlik pers. comm., B. Staines pers. comm.). In Hampshire, the size of the herd in the New Forest and Avon Valley was estimated from counts to be around 300, with two-thirds of these in the New Forest area (M. Clarke and R.J. Putman pers. comms). In north-west Essex the population was estimated subjectively by N.G. Chapman (pers. comm.) to be around 50. In Breckland in 1992, 100 were counted on Forestry Commission land and surrounding estates within an 8 km radius (R. Whitta pers. comm.), and in the Dunwich area of Suffolk there were 200 in 1994 (E. Calcott pers. comm.). In northern England, the population in Cumbria numbered about 1000 (J. Cubby and V.P.W. Lowe pers. comms), with the 600 in the southern part of the Lake District so extensively hybridised with sika deer *Cervus nippon* that it was unlikely that any pure red deer remained in the area (Lowe & Gardiner 1975). The Peak District population was estimated subjectively and by sign (rutting-stand) surveys to be around 200 (D.W. Yalden unpubl.). In addition, there are scattered records and small populations in England from north Staffordshire northwards, but these populations are generally small, and the total number is probably less than 300. In south-west England the population size on Exmoor was estimated in 1991/92 by a combination of faecal counts, vantage point counts and a simultaneous vantage point count over the whole area (Langbein & Putman 1992) and on the Quantocks in 1989/90 by assessing faecal density (F. Winder & P.R.F. Chanin unpubl.). These gave a spring population of 4750 in the Exmoor National Park, a further 1000 within 10 km of the park boundary, 800-900 on the Quantocks (Langbein & Putman 1992), plus an unknown number elsewhere from mid-Devon to Cornwall, suggesting a population in south-west England of at least 10,000 (R.J. Putman pers. comm.). In addition, red deer roam large distances from these main centres of distribution, and records are widely scattered (Arnold 1993). Thus, allowing for some animals away from the main areas, the total

English population lies at around 12,500. Red deer have also been recorded occasionally in Wales (Arnold 1993).

In Scotland, the population size in the Highlands was estimated for 1986 by Clutton-Brock & Albon (1989) using the Red Deer Commission's census figures and standardised counts of different blocks within a common time frame, using a multiple regression model that included both year and block identity as independent variables. This approach suggested an early spring population of 297,000 ± 40,000, compared with the Red Deer Commission's estimate of 265,000 for the highlands. Of these, 30% were in three contiguous areas in the eastern and central Highlands. Populations in Scottish woodlands were estimated by Staines & Ratcliffe (1987) to be 27,000-50,000, using vantage point counts and indices of faecal abundance. Since deer are notoriously difficult to count in woodlands, it is likely that the population lies at the upper end of this range.

Hingston (1988) estimated that there were approximately 5000-6000 red deer in parks, whilst J. Langbein (pers. comm.) put this figure at 7500. In addition there were 18,500 red deer on farms in Scotland in 1989 (Callander & MacKenzie 1991) and 33,625 farmed red deer in England and Wales in 1993 (Ministry of Agriculture, Fisheries and Food pers. comm.).

Population estimates: A total pre-breeding population of about 360,000; 12,500 in England, 347,000 in Scotland and fewer than 50 in Wales. In addition, there are a further 7500 in parks and 52,125 on farms.

Reliability of population estimate: 2.

Historical changes: The red deer herd in north Devon and west Somerset was estimated to number 250 in 1871, and over 500 in the early 1900s. In Cumbria it was thought that there were about 300 at the turn of the century, although they had been much rarer fifteen years earlier (Millais 1904-1906). The number of red deer in English parks at the turn of the century was around 6000 (Whitaker 1892). In Scotland, deforestation of native woodlands and persecution led to the probable extinction of all native stocks in the lowlands by the 17th century (Ritchie 1920). Red deer only survived on remote hill lands of the Scottish Highlands and islands. Red deer numbers were probably lowest at the end of the 18th century, but increased in the 19th century with a rising interest in deer stalking (Staines & Ratcliffe 1987) and introductions. From a peak around 1914, numbers are thought to have declined during the First World War. The situation in the 1920s and 1930s is unclear, but the population may still have been 200,000 at the start of the Second World War, following which the population declined by up to 50% to approximately 100,000 by 1950 (Callander & MacKenzie 1991). Red Deer Commission census figures for Scotland since 1960 have shown a steady increase in numbers, suggesting that the population has doubled in the last 30 years, with a possible temporary reduction in the late 1970s due to increased natural mortality during two severe winters (Callander & MacKenzie 1991). In 1975, Gibbs *et al.* (1975) estimated the total red deer population in Britain to be 190,000, but gave no details as to how this estimate was obtained.

Population trends: Until recently, the red deer population in Scotland was continuing to increase due to a number of factors. These included lower than average levels of natural mortality, reduced competition with hill sheep and the underculling of hinds (Clutton-Brock & Albon 1989; Callander & MacKenzie 1991). However, with an annual cull now in excess of 50,000 and perhaps the effects of winter weather, the red deer population in Scotland may now be relatively stable (C.B. Shedden pers. comm.). Red deer are also increasing in both range and numbers in south-west England. Lloyd (1975) estimated that there were 500-800 red deer in the Exmoor National Park during the 1970s, and Allen (1990) estimated 1500 during the 1980s. Using faecal pellet counts over limited areas and extrapolating these to the rest of the Park, Malcolm *et al.* (1984) suggested a figure of around 1900 red deer in the early 1980s. All these figures were undoubtedly gross under-estimates. Based on a retrospective analysis of current rates of population growth, Langbein & Putman (1992) suggest that the population was around 1400 in 1975, rising to just under 3000 by 1985, with a further 50% increase over the last seven years. Continued growth at the same rate would produce a population in excess of 9000 in the Exmoor National Park by the turn of the century. Elsewhere, numbers are low, and populations seem to be stable or declining slightly. Reasons for this remain unclear, but poaching is thought to maintain the Peak District population at around 200 (D.W. Yalden unpubl.).

Population threats: In some areas there is hybridisation with the increasing populations of sika deer (see below). However, red deer populations in Galloway, south-west Scotland and most English populations (except Cumbria) are non-native. Almost all of the English populations are of park origin, and most of the park herds were of continental rather than Scottish origin. In addition, many were probably red deer-wapiti crosses (R.J. Putman pers. comm.). Since these populations are not pure native stock, further hybridisation in these areas may not be a major conservation issue. More recent information suggests that hybridisation is occurring between native red and sika deer, and introgression of genes from sika to red deer seems likely to increase. Also, sika-like hybrids seem to be better competitors in dense woodland, and so it is possible that sika-like deer may completely replace red deer in such habitats (Balharry *et al*. 1994).

Sika deer *Cervus nippon*

Status: Introduced; locally common.

Distribution: Large populations occur in Argyll, Inverness-shire, Peeblesshire, Ross and Cromarty and Sutherland. Small populations occur in Cumbria, Dorset (including Brownsea Island in Poole Harbour), Hampshire, Lancashire and Northamptonshire, with a few deer in Bedfordshire. The Dorset population now extends into east Devon, particularly around Axminster (J. Langbein pers. comm.). A small population is maintained on the island of Lundy.

Population data: Sika deer are found in dense woodland and scrub, and the thicket stages of coniferous forests. In England, populations are still small enough to be estimated by counts. Transect counts, adjusted for areas of different habitats, and population reconstruction from cull data, suggested there were about 200 in the New Forest in the 1980s (Mann 1983; Putman 1986), although this population has recently been subjected to a heavy cull and may now only number about 100 (R.J. Putman pers. comm.). The Dorset population is expanding into parts of Devon; based on counts of the main sub-populations, the total number, including those on Brownsea Island, was less than 2000 (R.J. Putman pers. comm.) in the early 1990s. There were a further 200 in the Forest of Bowland in Lancashire (J. Cubby pers. comm.) and around 40 on Lundy. Thus the total population of sika deer in England is under 2500.

In Scotland approximately 140,000 ha are colonised by sika (P.R. Ratcliffe pers. comm.). Assuming that at any one time *circa* 25% of this area is suitable for sika deer, this gives 35,000 ha of suitable habitat with densities of 20-25 deer per km² (A. Chadwick pers. comm.). This suggests 7000-8750 sika occur in Scotland. The Red Deer Commission put the number of sika in Scotland at 10,000 (Scottish Development Department 1990), although there are no details as to how this figure was calculated.

In addition, Hingston (1988) suggested there were about 500 Japanese sika in parks, plus approximately another 400 of the Formosan and Manchurian subspecies. J. Langbein (pers. comm.) estimates a total of 1500 for all subspecies since Hingston (1988) did not include all the parks with sika deer.

Population estimates: A total pre-breeding population of about 11,500; fewer than 2500 in England, 9000 in Scotland and none in

Wales. In addition, there are a further 1500 in deer parks. **Reliability of population estimate:** 2.

Historical changes: The first Japanese sika to reach Great Britain were a pair presented to the Zoological Society of London in 1860. In the same year, a stag and three hinds were imported to Enniskerry, Co. Wicklow, and they formed the source for a number of parks in England and Scotland (Lever 1977). However, at the turn of the century they were still held in fewer than ten English (and some Scottish) deer parks, and numbered only a few hundred (Whitaker 1892). Details of the early introductions to deer parks in Britain are given in Whitehead (1964), who also documented the early range extensions. In the mid-1970s, Gibbs *et al.* (1975) estimated a total population in Britain of 1000, but no details are given as to how this estimate was obtained. Data on their range expansion has been updated by Ratcliffe (1987). The origins and genetic identity of the sika deer in Britain are discussed by Ratcliffe (1987), Ratcliffe *et al.* (1991) and Putman & Hunt (1993).

Population trends: The increases in some populations but not others reflect the availability of suitable habitat (young coniferous plantations) for colonisation. Whilst the populations in the New Forest, Ross and Cromarty and Argyll are spreading only slowly, most populations in northern Scotland are expanding their range rapidly in areas where there is suitable habitat. Juvenile males will apparently travel long distances, and colonisation by stags can precede the appearance of hinds by up to 10 years. The rate of range expansion in Argyll was 3-5 km per year (Ratcliffe 1987).

Population threats: It would appear that where substantial populations of both red and sika deer occur, hybridisation is rare (Harrington 1982). However, once a first cross has been established, further introgression is rapid, and other than F1 hybrids, it is very difficult to distinguish hybrid stock from pure red or pure sika deer (Putman & Hunt 1993). Thus selective culling of apparent hybrids is not an effective management practice. Multivariate analysis of skull measurements shows that the only population that can be considered to be pure is that in Peeblesshire, because the original introductions (to Dawyck in 1908) came directly from Japan and native red deer do not occur in the area. Similarly, the sika deer in the New Forest appear to have retained their identity, perhaps also reflecting an introduction of purer stock and their relative isolation from the red deer in the area (Putman & Hunt 1993). The high degree of variability in the Lake District population reflects the high numbers of hybrid deer observed there during the last 10-20 years, and the population in the Lake District may now be comprised entirely of hybrids between sika and red deer. It seems that the remaining sika deer populations were derived from mainland Asiatic deer which had previously hybridised with red deer (*Cervus elaphus xanthopygus*), and all the Scottish populations other than that in Peeblesshire have been exposed to some hybridisation with red deer since their introduction (Ratcliffe 1987; Ratcliffe *et al.* 1991; Putman & Hunt 1993).

Since only the populations in the New Forest and Peeblesshire appear to be relatively pure bred, there could be a case for managing these to ensure their continuing genetic integrity.

Fallow deer *Dama dama*

Status: Introduced; widespread and locally common.

Distribution: Found throughout much of England and in parts of Wales. Local in Scotland, where its distribution includes three west coast islands. Fallow deer prefer deciduous/mixed mature woodland and conifer plantations with open areas.

Population data: There are very few reliable population estimates from any habitats, except Forestry Commission counts from large areas of continuous woodland. Densities normally range from 18-43 fallow deer per km² (N.G.

Chapman pers. comm.). However, these populations are often heavily managed, and so the density is maintained at a particular level that is not related to the carrying capacity of that habitat type but often at a level that is subjectively believed to limit their grazing impact (R.J. Putman pers. comm.). Since these populations are maintained at an arbitrary level (e.g. 2400 in the New Forest), any density estimates or extrapolations based on these counts are largely meaningless. Even where accurate counts are available, it is rarely possible to relate these counts to the areas covered by the deer. In agricultural landscapes, densities are particularly hard to estimate, since they can vary tremendously with no apparent environmental cause, although levels of human disturbance and intensity of culling may be more important here than environmental quality *per se* (R.J. Putman pers. comm.). Thus in one agricultural area in Lincolnshire there was a minimum of 40 per km², based on minimum counts (R.J. Putman pers. comm.). However, more typical densities for agricultural land in Hampshire, based on transect counts adjusted for the area of each habitat sampled, were 8·0 per km² in an arable landscape with small fields and scattered small copses, 6·8 per km² on rolling downs with scattered coverts and copses and 4·6 per km² in an area of mixed arable and pasture with more extensive woodlands (Thirgood 1990). Pellet counts in a mixed agricultural woodland and moorland area of Devon suggested *circa* 17·5 fallow deer per km² (J. Langbein pers. comm.).

It is difficult to relate fallow deer numbers to land classes, or to particular habitat types, although density does change with habitat (Putman 1986; Chapman & Putman 1991). Many populations are still centred on ancient deer forests, or around the parks from which they originally escaped (J. Langbein & R.J. Putman pers. comm.); see, for example, Chapman (1977) for a description of the situation in Essex. Thus, despite being a long-standing introduction, their distribution is patchy and their numbers and distribution are dominated by human influence, and so it was not possible to use habitat characteristics to estimate population size. Therefore the recorded distribution and estimated density were used to calculate population size. B. Mayle (pers. comm.) calculated a population size of 32,400 in 1986, based on the distribution given by Arnold (1984) and the results of the Forestry Commission's survey of its own woodlands. She based her calculation on a figure of 50 deer in each of the 648 10 x 10 km squares believed to contain fallow deer. This figure is a minimum estimate, since the current distribution map almost certainly under-estimates the number of 10 x 10 km squares containing fallow deer, and because fallow deer populations also are very clumped and locally can reach very high densities. For most of the recorded range, densities will be much higher than 0·5 per km². Gibbs *et al.* (1975) estimated that the total fallow deer population in Britain was 50,000, although they gave no details as to how this figure was obtained. A third figure was produced by Gliksten (1993), who estimated 60,000-70,000 fallow deer, based on a subjective estimate of density and the known distribution. The Red Deer Commission put the number of fallow deer in Scotland at 1000-2000 (Scottish Development Department 1990), although there is no information as to how this figure was calculated.

Whilst this approach was subjective, it is hard to be more precise. R.J. Putman (pers. comm.) tried to produce a quantitative estimate based on the areas of known distribution, the areas of suitable habitat, and densities estimated in a variety of habitats. However, the estimate produced by this means was unrealistically high because the available data on densities are heavily biased due to the clumped distribution of the species. In view of all the problems in trying to calculate a population size, and since most attempts to count fallow deer numbers under-estimate them, it is probable that the total population is about 100,000, but it is impossible to be more precise.

In addition, Hingston (1988) estimated that there were 11,580 fallow deer in 81 parks, but some parks were not included at the request of the owners. J. Langbein (pers. comm.) estimates that there are 17,000 in parks. In 1993 there were 6,710 farmed fallow deer in England and Wales (Ministry of Agriculture, Fisheries and Food pers. comm.). Gliksten (1993) estimated that 15% of all farmed deer are fallow. Based on the number of farmed red deer in Scotland in 1989 (Callander & MacKenzie 1991), this would suggest about 3250 farmed fallow deer in Scotland.

Population estimates: The best estimate possible is that the total pre-breeding population is about 100,000; in England 95,000, in Scotland fewer than 4000 and in Wales fewer than 1000. In addition, there are a further 17,000 in parks and about 10,000 on farms. **Reliability of population estimate:** 4.

Historical changes: Their early history in Britain is described by Whitehead (1964). By the middle of the 17th century, there were over 700 parks in England that held fallow deer. During the Civil War, many were broken up and the deer escaped and, although the majority were killed, a few survived in the more inaccessible areas to establish feral populations. In the 18th century there was renewed interest in establishing deer parks, and by the end of last century there were about 390 parks in England with 71,000 fallow deer (Whitaker 1892). The number of parks with fallow deer subsequently declined, and in 1988 only about 120 remained (J. Langbein pers. comm.).

At the turn of the century the number of feral fallow deer herds was small Millais (1904-1906) described a number of herds, and although his list is not exhaustive, it does suggest that feral fallow deer were comparatively few. In Essex, for instance, Laver (1898) only refers to the herd in Epping Forest, yet eighty years later Chapman (1977) showed that there were many feral herds, all centred around deer parks. It is probable that fallow deer numbers throughout Britain have increased this century as a result of repeated escapes from parks.

Population trends: Numbers are possibly slowly increasing, but the magnitude of the increase is unknown and is believed to vary between different areas. Gill (1992) considered that fallow deer were possibly the only species of deer in Britain not increasing either in range or numbers.

Population threats: Fallow deer have been established for around nine centuries, possibly from a relatively small founder stock. Certainly, electrophoretic studies of blood proteins have so far failed to reveal any evidence of genetic polymorphism in British fallow deer (Pemberton & Smith 1985). A second sub-species of fallow deer (*Dama dama mesopotamica*) is larger and has a different antler morphology, and has been hybridised with *Dama dama dama* on deer farms in New Zealand, the United States of America and elsewhere, either by natural or artificial methods. A cross-bred herd exists in Kent, and stock has been advertised for sale in Britain. Free-ranging fallow deer populations are often in close proximity to deer parks and farms, and escapes do occur. Thus there is a potential risk of hybrid or pure Persian fallow deer cross-breeding with the long-established stock, and at present there are no measures to reduce this risk (N.G. Chapman pers. comm.).

In some areas, such as Cannock Chase in Staffordshire (P. James pers. comm.) and Epping Forest, Essex (Chapman & Chapman 1969), road mortalities can be high, and these may lead to local population reductions.

Roe deer *Capreolus capreolus*

Status: Native in Scotland. Roe deer became extinct in England during the 18th century, and populations in south, east and north-west England were re-established by reintroductions in the 19th century.

Distribution: Roe are the most widely distributed species of deer in Britain. They are found throughout Scotland and northern England, southern England and parts of East Anglia, with scattered records from Wales and the English counties along the Welsh border. They occur on a few of the larger islands in the Inner Hebrides and the Clyde Islands (Arnold 1993).

Population data: Roe deer are found in open mixed coniferous and purely deciduous woodland, in agricultural landscapes, and, in some parts of Scotland, on moorland without access to cover. Woodland density estimates vary from 0·5±0·5 (95% confidence interval) to 24·8±0·5 per km², based on pellet counts at 20 sites in Scotland (J. Latham pers. comm.). Densities in sitka spruce forests in the Scottish borders and the pine forests of East Anglia range from 8-25 deer per km², with densities being greatest (25 per km²) in stands 5-15 years old, declining to 8 deer per km² prior to the first thinning, and subsequently rising to 15 per km² as the forest is further thinned (Loudon 1982; Staines & Ratcliffe 1991). Locally, densities of 75 deer per km² have been recorded in isolated woods in southern England (Loudon 1982), but such estimates probably only include part of the animals' ranges (A.L. Johnson pers. comm.). At Porton Down, Wiltshire, in an area of open downland, there were 6·9 per km², as determined by helicopter and ground-based counts (Johnson 1984). At Alice Holt, Hampshire, an area of mixed broadleaved and coniferous forest, there were 12·8 deer per km² as estimated by pellet counts (K. Otim unpubl.). Other than these, there are few density estimates on which to base a population estimate.

B. Mayle (pers. comm.) estimated the number of roe deer in Britain to be 62,950 by assuming a density of 50 animals for each of the 1259 10 x 10 km squares thought to contain roe deer, as indicated by Arnold (1984) and from the Forestry Commission's own surveys. However, this is almost certainly a very substantial under-estimate, since it assumes a mean density of only 0·5 deer per km². If it is assumed that for the 1237 10 x 10 km squares in which roe deer are currently recorded (Arnold 1993), 5-10% of the habitat was suitable for roe deer at a mean density of 15 per km², the population would number 93,000-186,000. However, even 186,000 is likely to be a significant under-estimate. The Red Deer Commission for Scotland obtained an estimate for the Scottish population in 1980 of 125,000-175,000, and in 1990 the figure was put at 200,000 (Scottish Development Department 1990), although there is no information as to how this figure was calculated. Shedden (1993) believed this figure to be a substantial under-estimate for the following reasons. Scottish roe deer populations have relatively low levels of recruitment, and so a 15% cull should prevent population growth. Since the roe deer population in Scotland was expanding, the cull must have been under 15%. Shedden (1993) therefore calculated a roe deer population in Scotland of 305,000-400,000 based on the number of stalkers, the estimated cull size, and the assumption that this represented 10% of the total roe deer population in Scotland. Despite the number of assumptions, this probably provides the most realistic population estimation for Scotland. Assuming that the true population in Scotland is around 350,000, based on the distribution of roe deer in Britain as a whole, it is probable that the total population in Britain is around 500,000.

Population estimates: A total pre-breeding population of about 500,000; 150,000 in England, 350,000 in Scotland and around 50 in Wales. **Reliability of population estimate:** 3.

Historical changes: Once widespread, in historical times roe deer became extinct throughout much of Great Britain, and by the beginning of the 18th century were thought to survive only in remnant woodlands in parts of the central and north-west Highlands of Scotland (Ritchie 1920). The reasons for this decline are unclear; several explanations have been put forward, but none are convincing. An increase in woodlands during the 18th century led to a range expansion in Scotland, with roe deer reaching the Scottish border by 1840. Roe deer of unknown origin were re-introduced to Milton Abbas, Dorset, in 1800, and Millais (1904-1906) estimated that at the start of the century there were 300-400 in

Dorset, and that they were still spreading. At that time there were also populations in the New Forest, Surrey and Sussex, and they were re-introduced to Epping Forest, Essex, although these did not persist. The population in East Anglia originated from an introduction of German deer to the area between Brandon and Thetford in 1884 (Chapman *et al.* 1985), and the roe deer in the Lake District are thought to be of Austrian origin (Staines & Ratcliffe 1991). From these centres, roe deer have spread throughout much of eastern, northern and southern England during the course of this century. Full details of these changes are given by Whitehead (1964). By the mid-1970s, Gibbs *et al.* (1975) estimated the total roe deer population in Britain to be 200,000, although no details are given as to how this figure was obtained.

Population trends: Still increasing in range in England, and this range increase is almost certainly associated with an increase in numbers, although the rate of increase is unknown.

Population threats: None known.

Chinese muntjac ***Muntiacus reevesi***

Status: Introduced. Locally common and rapidly increasing in numbers.

Distribution: Following the original introduction to Woburn Park, Bedfordshire in 1894, Chinese muntjac are now established in most of southern England as far north as Derbyshire, Lincolnshire and Nottinghamshire, including some urban areas. In addition, there are scattered records outside this range, including Cheshire, Cumbria, Northumberland, South Yorkshire and in Scotland, although a number of the Scottish records have yet to be confirmed (Chapman, Harris & Stanford 1994), and parts of north Wales and most of the counties along the south Wales coast. They have also been introduced to Steep Holm, in the Bristol Channel.

Population data: Muntjac seek areas of cover (Chapman *et al.* 1985) and are most common in deciduous woodland, mixed/coniferous woodland and areas of scrub. However, despite their wide distribution (which includes virtually every English county plus several in Wales and possibly in Scotland), their distribution is very clumped. A recent survey, in which large numbers of records were collected from members of the public, found that 50% of the reports came from just five counties - Berkshire, Buckinghamshire, Hertfordshire, Oxfordshire and Warwickshire. Elsewhere numbers were low and/or populations were scattered, either due to recent colonisation, or deliberate or accidental releases outside the main area of distribution (Chapman, Harris & Stanford 1994). This patchy distribution makes estimating population size particularly difficult. In addition, there are few detailed density estimates, but in one area of coniferous woodland in East Anglia, densities of up to 30 animals per km^2 were recorded (K. & M. Claydon pers. comm.). This high density occurred in the absence of culling. A similar high density was recorded in a small (43·5 ha) deciduous wood in Oxfordshire (Harding 1986). However, where populations are heavily managed, densities are likely to be lower.

Population size was estimated as follows. For the counties of Berkshire, Buckinghamshire, Hertfordshire, Oxfordshire and Warwickshire, adult densities were assumed to be 30 per km^2 in prime habitats (semi-natural broadleaved and mixed woodlands, young plantations and scrub) and 15 per km^2 in broadleaved, coniferous and mixed plantations. For this calculation, adults were taken to be animals that had reached adult size, i.e. they were at least seven months of age. Based on the distribution of records, the estimated number of muntjac in these five counties was taken to represent 50% of the total population in Britain.

Population estimates: A total pre-breeding population of about 40,000; in England around 40,000, in Scotland fewer than 50 and in Wales fewer than 250. Whilst muntjac are widely recorded in Wales, most of these records are of scattered individuals, and the population is unlikely to exceed 250 adult animals. It must also be remembered that muntjac breed throughout the year, with no evidence of seasonal trends in productivity or survival (Chapman, Chapman & Dansie 1984). Thus at any time of the year there will also be a number of fawns and immature animals in the population, and one study (Claydon, Claydon & Harris 1986) suggested that these would add about 30% to the total population, i.e. around 12,000 animals that have not reached adult size. **Reliability of population estimate:** 3.

Historical changes: Their spread is documented in detail by Lever (1977), Anderson & Cham (1987) and Chapman, Harris & Stanford (1994). The first feral muntjac was observed at Wrest Park, 11 km east of Woburn, Bedfordshire in 1922, and another a few years later at Ashridge Park, Hertfordshire, 19 km south of Woburn (Lever 1977). In the first 60 years the spread was relatively slow, extending to a radius of 72 km from Woburn (Whitehead 1964). By the early 1990s this had extended to 300 km to the south-west, 200 km to the north and north east, and 120 km to the south-east (Chapman 1991). However, natural spread only seems to occur at a rate of about 1 km per year, and the wide distribution is in large part due to many deliberate and accidental releases (Chapman, Harris & Stanford 1994). In the mid-1970s, Gibbs *et al.* (1975) estimated that the total population in Britain was 5000, although no details are given as to how this figure was obtained.

Population trends: Numbers are increasing rapidly, and in many parts of the current range numbers are still well below carrying capacity. The population model detailed below gives an intrinsic rate of population growth of almost 10% per year; thus at current rates the population will double in less than 8 years. However, modelling work has suggested that the potential for further natural range expansion is more limited than generally perceived, and most spread is likely to be in Kent and Sussex, and to a lesser extent north in Lincolnshire, Nottinghamshire and South Yorkshire, and west into Cheshire and Shropshire (Chapman, Harris & Stanford 1994).

Whilst the estimate presented here may seem large considering the small size of the founder population (Chapman, Harris & Stanford 1994), and the slow early spread, a population of 40,000 is entirely feasible. A simple population growth model based on certain assumptions (that the founder population was introduced at the turn of the century; there were 24 animals with equal numbers of bucks and does; that all does bred; that culling was not introduced until 1925 and that until then all animals died at eight years of age) and demography data supplied by N.G. Chapman from several sites in southern England (sex ratio of the population is equal; 47% of fawns die before two months of age; mortality by 1 year is 56%, by 2 years 69%, by 3 years 75%, by 4 years 81%, by 5 years 88%, by 6 years 94%, by 7 years 95% and by 15 years 100%; an interbirth interval of 8 months; no does are pregnant before 6 months of age, 60% are pregnant at 10 months, 80% at 12 months, 100% at 15 months) showed that the muntjac population in 1993 could have reached 292,000 animals (S. Wray pers. comm.). Obviously not all of the assumptions in the model would have been met. For example, not all the does in the founder population would have bred, not all would have lived to 8 years, etc., but the model does serve to show the potential rapid rate of growth, and also that the estimate of 40,000 is a long way below the maximum number that could have been achieved in a hundred years.

There are several reasons why the population is well below the theoretical maximum that could have been achieved. In particular, the population growth model made no allowance for the effects of the severe winters of 1939/1940, 1946/1947 and 1962/1963 on the muntjac population, although there was a very significant level of mortality (Pickvance & Chard 1960; Chapman, Harris & Stanford

1994). Three large die-offs in a quarter of a century must have had a significant impact on the rate of population growth and hence rate of spread, especially since muntjac had not long been established outside Woburn Park (Chapman, Harris & Stanford 1994). The rapid spread since 1963 is probably in part due to the long period without winters severe enough to induce high levels of mortality. The other significant factor in limiting the rate of spread is the high level of culling that often occurs when muntjac are first colonising an area, which is often undertaken in an attempt to prevent the species becoming established.

Population threats: A field study in East Anglia estimated that 47% of fawns die before the age of two months, probably largely due to predation (K. & M. Claydon pers. comm.). For older animals, culling and road traffic accidents are probably the main causes of mortality, and heavy culling can severely limit the rate of spread into some areas. Although extreme winter conditions, and in particular long periods of snow cover such as in 1962/1963, may cause heavy mortality, there is no evidence of increased fawn mortality in most winters, and it is unlikely that adverse weather conditions will limit population growth other than temporarily.

Chinese water deer *Hydropotes inermis*

Status: Introduced; uncommon and local.

Distribution: Free-living populations occur in Bedfordshire/Hertfordshire, Berkshire, Cambridgeshire, Norfolk and Suffolk. Records elsewhere (Arnold 1993) relate to individual animals rather than established populations.

Population data: There are few density estimates. At Whipsnade Park, Bedfordshire, densities of 2 per ha have been recorded, and at Woodwalton Fen, Cambridgeshire 0·3 per ha (Farrell & Cooke 1991). The population in Bedfordshire/Hertfordshire was estimated to be 40-100 by field censuses (Nau 1992); the population at Shinfield, Berkshire, was estimated by sightings to be about 20 (S. Wray pers. comm.); that in Cambridgeshire in the area around Woodwalton Fen, Holme Fen and Monks Wood was estimated to be 100-200 by A.S. Cooke & L. Farrell (pers. comm.) based on personal observations; the population near Newmarket, Suffolk, was estimated to be about 20 based on sightings (N.G. Chapman pers. comm.); that at Minsmere, Suffolk, was estimated by counts to be three (L. Farrell pers. comm.); and that on the Norfolk Broads was estimated at about 300 based on sightings, although this may be an under-estimate (R. Engeldow pers. comm.). Thus the free-living population is approximately 480-650. However, in addition there are a number of itinerant animals not included in these figures. Since there are reports well away from the main centres of distribution, and other small populations have arisen from escapes from collections, the true figure probably lies at the upper end of this range.

There are also 400-600 free-roaming in Whipsnade Park on the Bedfordshire Downs and 200-300 at Woburn Park.

Population estimates: The total pre-breeding population probably lies around 650, all in England. **Reliability of population estimate:** 2.

Historical changes: Chinese water deer were introduced to Woburn Park around the turn of the century, and from 1929 to 1931 a total of 32 were transferred to Whipsnade Park. From these populations animals were sent to a number of parks around England, including two in Hampshire, one in Montgomeryshire, one in Norfolk, two in Shropshire and one in Yorkshire, amongst others (Lever 1977). Some of these led to free-living populations, not all of which persisted, and the early history of these is summarised by Whitehead (1964) and Lever (1977). The populations in Hampshire had died out by 1963, and those in Northamptonshire and Shropshire also appear to have died out. The populations in Berkshire and Suffolk originated in the 1980s.

Population trends: The low numbers (especially when compared with muntjac, which were introduced at around the same time), widely scattered records of vagrant/itinerant animals, and impermanence of many feral populations, suggest that conditions are not ideal for the establishment of this species, and that numbers are likely to remain low.

Population threats: Harsh winters can cause heavy mortality, and fox predation may be a significant cause of mortality of young animals. Road casualties are probably also significant. Whether any of these mortality factors pose a threat to population survival is unknown.

Reindeer *Rangifer tarandus*

Status: The native population became extinct approximately 9500 years ago. Swedish stock was re-introduced to the Cairngorms in 1952, when there were 15 animals (4 bulls, 9 cows, 2 calves). Subsequently there have been additional introductions of Norwegian and Russian reindeer.

Distribution: Until May 1991 the whole herd was kept in the Cairngorms, where The Reindeer Company leases approximately 2400 ha. However, since May 1991 the herd has been split into two approximately equal sized groups, the second being on a 200 ha hill farm on the Glenlivet Estate near Tomintoul, Grampian.

Population data: Herd numbers are taken from actual counts and recorded in annual herd lists (E. Smith pers. comm.). Thus in February 1993 there were 77 animals in total, with an expected calving in May of about 30 animals.

Population estimates: A pre-breeding population of up to 80 animals, all in Scotland. **Reliability of population estimate:** 1.

Historical changes: The early history of the herd is summarised by Whitehead (1964). From 1952 to 1960, the herd remained below 25 animals. There was a period of slow increase in the 1960s, and since 1970 the herd has been maintained at approximately constant size (E. Smith pers. comm.).

Population trends: A constant herd size is maintained, with a maximum number in June just after calving of around 100 animals.

Population threats: None.

Park cattle *Bos taurus*

Status: A number of herds of park cattle survived to the beginning of this century, but their origins are unknown. Their status at the turn of the century was summarised by Anon. (1887). The principal strains which survive today are Cadzow, Chartley, Chillingham, Dynevor and Vaynol. All are horned cattle. Only the Chillingham herd has been kept pure; they are remarkably homozygous and show no affinity with any other breed (Hall & Hall 1988). All the other strains have been, or are being, crossed with other breeds, including longhorn and highland cattle, to produce the white park breed, which must be distinguished from the Chillingham cattle (Hall 1991). Whilst the Vaynol cattle were at one time considered to be part of the white park breed, they are now considered to be separate (Anon. 1993). The conformation of the white park is that of a typical early 20th century British beef breed, but skeletally the Chillingham cattle resemble mediaeval British cattle. Whilst Chillingham and white park cattle are horned, British white cattle are genetically hornless and arose from another park herd. In addition, since 1978 a herd of Aberdeen Angus cross shorthorn cattle has been allowed to run feral on the island of Swona (Orkney). The Chillingham cattle and the Swona herd are among the very few cattle in the world that are completely feral, i.e. with a natural sex ratio and age distribution (Hall & Moore 1986).

Distribution: Chillingham cattle were found only in Chillingham Park, Northumberland, until a reserve herd was established in Morayshire in 1972. White park cattle are mostly found in farm parks, whereas the British white is becoming a commercial proposition (Hall 1991). The Swona herd is confined to Swona, Orkney.

Population data: Data are available from herd counts. In addition, the white park, Vaynol and British white cattle are fully pedigreed (S.J.G. Hall pers. comm.). Thus in March 1993 the Chillingham Park herd of Chillingham cattle consisted of 19 males and 26 females, and the reserve herd in Morayshire contained four males and six females. In February 1993 there were six male and 17 female cattle of the Vaynol strain. In January 1993 there were 24 male and 250 female white park cattle, and in September 1992 there were 83 male and 730 female British white cattle. Precise numbers of the Swona herd are unknown, but there are 20 at most (S.J.G. Hall pers. comm.).

Population estimates: In March 1993 the number of Chillingham cattle was 55: 45 in England, 10 in Scotland and none in Wales. **Reliability of population estimate:** 1.

Historical changes: Chillingham cattle declined to only 13 animals in 1947. The number then increased steadily to about 40 around 1970, since when numbers have fluctuated between 40 and 65. The sex ratio is biased because of better survival of adult females (Hall 1991).

Population trends: The numbers of white park cattle are increasing, but only slowly. British white cattle are increasing more rapidly. The size of the Swona herd fluctuates and numbers have reached the low 30s in the past (Hall & Moore 1986).

Population threats: None known. The reserve herd of Chillingham cattle is self-sustaining, and no animals are moved from this herd to Chillingham or anywhere else, although occasionally calves are sent from Chillingham to join the herd. The reserve herd is maintained as a nucleus to repopulate Chillingham Park in the event of the latter herd being wiped out by disease. In March 1993 semen was being stored from three Vaynol cattle and six white park cattle.

Feral goat *Capra hircus*

Status: Introduced; well established.

Distribution: Generally hilly and mountainous areas of England, Scotland and Wales plus a number of islands (Bute, Cara, Colonsay, Holy Island (Isle of Arran), Islay, Jura, Lundy, Mull, Rathlin and Rum (Bullock 1991).

Population data: Populations are generally small and discrete. Unless otherwise stated, population estimates were based on visual counts that include kids of the year. In southern England there are the following populations: Brean Down, Somerset - maintained at 15-20 animals by culling (M. Oates pers. comm.); Lundy, Devon - in 1991 the population of six was augmented by the introduction of six from the Valley of the Rocks to give a total of 12; Valley of the Rocks, Devon - since 1988 the maximum number of goats has never risen above 40, and in 1991 six were removed to Lundy and in 1992 nine were removed to the Isle of Wight; Ventnor, Isle of Wight - in 1992 nine goats were introduced to Bonchurch Down for scrub control. In northern England/southern Scotland feral goats occur at: College Valley, Northumberland - 34; Nether Hindhope, Roxburgh - 43; Kielderhead Moors, Borders Region and Northumberland - in 1992 about 100 but a cull was planned to reduce the population to about 75; Langholm-Newcastleton Hills, Dumfries & Galloway and Borders - estimated 130, with a maximum of 145; Moffat Hills, Dumfries & Galloway - 184. Feral goats are found in south-west Scotland as follows: Cairnsmore of Fleet, Dumfries & Galloway - on the whole massif, *circa* 400; 'Wild Goat Park', Dumfries & Galloway - an enclosure established by the

Forestry Commission with 35 goats in 1992 and the number maintained at between 30 and 50 (J. Livingstone pers. comm.); Glentrool, Central Galloway - 200; Corserine and the Rhinns of the Kells, Central Galloway - 150; Loch Dee and Loch Doon, Central Galloway - 150-200 (all J. Livingstone pers. comm.). Western Scotland supports several populations. In the Clyde area there were estimated to be 355 in the mid-1980s, and subsequent counts of parts of the area suggested there had been little change or a small increase. For the period 1960-1978 the population on Rum showed six-yearly cycles, with population estimates ranging from 98-185 (Boyd 1981). In 1981 the population was estimated to be 200 (R.I.M. Dunbar pers. comm.), and although there are no recent data, the population on Rum is unlikely to have decreased and may be as high as 300. From Islay, Jura, Mull and the west coast of mainland Scotland there is an estimate of over 400 in the mid-1980s. In the central and north Scottish Highlands, information from the 1980s suggests a population of over 300. Since 1980 several new populations of feral goats have been established in Scotland in the interests of trophy hunting and/or the cashmere industry but no data are available on these herds (D.J. Bullock pers. comm.). In Wales a survey in Snowdonia in 1991 estimated 282 goats, and there is thought to be a similar number in the Rhinogau/Maentwrog area (Hellawell 1992).

Population estimates: A total pre-breeding population of over 3565. About 315 in England, over 2650 in Scotland and 600 in Wales. **Reliability of population estimate:** 2.

Historical changes: Goats were probably one of the earliest domesticated animals to be introduced to Britain. The early history and distribution of feral goats in Britain is documented by Whitehead (1972).

Population trends: Probably there is little overall change. No populations have declined since 1980 (D.J. Bullock pers. comm.) and the Scottish population has remained constant since the late 1960s (Greig 1969). The severe winter of 1978/1979 caused significant losses, but a series of milder winters up to 1992/1993 has led to an increase in many populations that are not controlled by culling. Between 1980 and 1990 a number of populations were culled in the interests of afforestation, and these culls were augmented by large scale removals (more than 20 goats at a time) for the cashmere industry, although demand for the latter declined after 1990 (D.J. Bullock pers. comm.).

Population threats: None known.

Feral sheep *Ovis aries*

Status: Introduced; long-standing feral populations.

Distribution: Soay sheep are found on Soay and Hirta, St Kilda, and there have been introductions to Ailsa Craig (Strathclyde), Cardigan Island (Dyfed) and a number of other Welsh Islands, Holy Island (Isle of Arran), Lundy (Devon) and Sanda Island (Strathclyde). Boreray blackface sheep are confined to Boreray, St Kilda.

Population data: Soay sheep numbers are based on population counts in May/June and include the surviving lambs of the year. The population of Soay sheep on Hirta fluctuates in a cyclical manner between about 600 and nearly 1600 (Clutton-Brock *et al.* 1991). The population on the neighbouring island of Soay may cycle in synchrony with the one on Hirta. In 1966 the minimum size of the population on the island of Soay was 115, and 140-160 in 1967 (Jewell, Milner & Boyd 1974). Recent counts have been made from the neighbouring island of Hirta, from which most of the grazings can be seen. In summer 1991 the count was 250-300, in August 1992 it was 110-120 (A. MacColl & I. Stevenson pers. comm.); the true numbers would be no more than 30 more. The population on Cardigan Island was reduced to about half in October 1990 and now numbers less than 100. There are no recent counts for the population on Holy Island, and the Lundy population is managed at around 150 by annual culls. There are three or four on Sanda Island (B. Zonfrillo pers. comm.). The size of the sheep population on the island of Boreray was estimated by land- and sea-based counts in 1992 to be 302 (A. MacColl & I.R. Stevenson pers. comm.).

Population estimates: The average size of the pre-breeding Soay sheep population is around 1800; 150 in England, 1550 in Scotland and 100 in Wales. The total pre-breeding feral population probably never exceeds 2500 animals. There are also many in parks, in farm parks, and on some farms. The pre-breeding population of Boreray sheep is around 300, all in Scotland. **Reliability of population estimate:** 1.

Historical changes: The Soay sheep resemble the original wild species and the domesticated Neolithic sheep brought to Britain about 5000 BC. Those on Soay may be the direct descendants of these sheep, although there is a faint possibility that they were originally introduced by the Vikings in the 9th and 10th centuries AD (Campbell 1974). When St Kilda was evacuated in 1930, the Soay sheep were left on the island of Soay, as were the flock of primitive blackface sheep on Boreray. In 1932, 107 Soay sheep were transferred from Soay to the larger island of Hirta by the St Kildans, who returned annually to tend the sheep on Boreray and Hirta until the outbreak of the Second World War, when the Soay sheep on Hirta were said to number about 500. In 1947 the flock was said to number 400-450 and in 1948 650-700 (Lever 1977). Annual counts from 1955 to 1973 showed that the Soay population on Hirta fluctuated between 610 and 1783 (Boyd 1974). Nine counts of the Boreray blackface sheep between 1951 and 1971 showed that the minimum flock size varied between 330 and 466 (Lever 1977). In 1934 six Soay sheep were introduced to Skokholm, in 1944 eight were introduced to Cardigan Island, two to Middleholm Island in 1945, four to St Margaret's Island near Tenby in 1952, and in 1958 a few were introduced to Skomer. In 1975 the only Welsh island still to have Soays was Cardigan, where there were 80. Soay sheep were introduced to Lundy around 1927, and by 1959 numbered over 80. The Soays on Ailsa Craig were introduced direct from St Kilda in the 1930s; in 1956 they numbered 14 (Lever 1977), but do not persist today.

Population trends: The Soay sheep on Hirta, and possibly those on Soay, show cyclical changes in numbers and these are probably density-dependent. Thus on Hirta, high winter mortality occurs every three to four years following summers when population density exceeds 2·2 sheep per ha. During these die-offs, more than 50% of adults, 70% of yearlings and 90% of lambs die and population density falls by around 65% (Clutton-Brock *et al.* 1992). Despite these perturbations, there are no long-term population changes. On Hirta, changes in population size occur as a result of high over-winter mortality from starvation and this is particularly pronounced among lambs and rams (Clutton-Brock *et al.* 1991), thereby giving an adult population with a varying bias towards females. Recent calculations, taking into account this unusual demography, suggest that the effective population size of the Hirta Soay sheep is in the range 200-250 (D.R. Bancroft pers. comm.).

Population threats: None known. Despite their isolation and population dynamics, the Soay sheep on Hirta have substantial genetic variation at the phenotypic and molecular level (Jewell, Milner & Boyd 1974; J.M. Pemberton & D.R. Bancroft pers. comm.), a conundrum that is the subject of current research. There is the potential threat from diseases or parasites introduced from the mainland. An example is the presence of the nematode *Nematodirus battus* on the island. It was first identified in England in 1951, and it is unclear whether the parasite was a recent introduction or had previously been over-looked. Yet this parasitic worm was found in most of the 120 Soay sheep carcasses examined on Hirta in 1989/1990, despite these sheep being separated from mainland stocks since the 1930s (Gulland 1991; I.R. Stevenson pers. comm.). Also, Gulland (1991) reported that

50% of the Soay sheep examined had cysts of the tapeworm *Taenia hydatigena*, yet there are no carnivores on the island and the last resident dog left with the islanders in the 1930s.