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Invasibility and Wildlife Conservation: Invasive Species on Nature Reserves [and Discussion]

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Invasibility and wildlife conservation: invasive species on nature reserves

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Nature reserves are often considered to be assemblages of species in natural or semi-natural communities. However, in many parts of the world they also contain exotic species that interact with the native flora and fauna. An International Working Group has been endeavouring to understand the management of invasive species in natural landscapes.

Data for four invasive species within the British Isles are analysed. The case studies investigated include Indian balsam (*Impatiens glandulifera*), rhododendron (*Rhododendron ponticum*), mink (*Mustela vison*) and coypu (*Myocastor coypus*). The rates of spread have been variable, usually increasing after an establishment phase.

The discussions concentrate on assessing the impact of invasive species, on deciding whether control measures are feasible and/or desirable, on deciding whether or not nature reserves are less prone to invasion than other habitats, and on assessing wildlife conservation values when invasive species are present.

Introduction

SCOPE's *International Working Group on the impact of invasions on nature reserves*

A small working group to investigate the impact of invasive species on nature reserves met in Paris in March 1985 under the chairmanship of Mr F. J. Kruger (South Africa). The other members of the group were Dr R. E. Brockie (New Zealand), Dr L. Loope (Hawaii, U.S.A.), Mr I. A. W. Macdonald (South Africa) and Dr M. B. Usher (U.K.). The specific objectives of the group were to seek generalities both about the nature of invasive species and about ecosystems prone to invasion, and to endeavour to understand the management of exotic plant and animal invaders of natural landscapes. The group felt that the best way to achieve these objectives was to collate a wide variety of case studies from which to search for general principles. It was felt that these case studies should primarily be drawn from tropical savannas, Mediterranean heaths (defined climatically, not geographically), arid lands, oceanic islands, and cold temperate Eurasia. These broadly defined habitats encompass several of the ecosystems known to have been invaded by alien species, as well as covering a wide climatic range. This paper adds to these studies, dealing primarily with the British Isles, but first it will consider briefly what is known of oceanic islands.

The oceanic islands can be used as an example of the case studies. Brockie (1985*a*) and Gressitt (1964) enumerated species on Campbell Island (52° S, 169° E), situated in a region of strong winds and low mean annual temperature. The island has 142 native species of flowering plants and ferns, none of which is endemic, and 77 introduced species, none of which seems particularly invasive. Three case studies are of tropical islands. The Haleakala National Park on Maui, in the Hawaiian archipelago, has about 660 species of native flowering plants and ferns, of which about 300 are island endemics. There are about 300 introduced species

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of which about 20 are invasive (Loope 1985). Similar data for the Galapagos Islands (Brockie 1985*b*; Porter 1983) indicate a native flora of 650 species with 239 endemic and 192 introduced species of which about 5 are invasive; and on the smaller Aldabra Island (Brockie 1985*c*; Wickens 1979) there are 178 species of vascular plants, 17 of which are endemic with a further 87 introduced species, only 4 of which are particularly invasive. Two general points are that endemism appears to be greater on larger than smaller islands, and that usually about one third of the flora is introduced (percentages are 23, 31, 33 and 35 for Galapagos, Maui, Aldabra and Campbell respectively). Similar data for birds, mammals, insects and so on are available in the reports cited.

The aim of this paper is to set data for the British Isles into this global context, remembering the needs of the SCOPE working party. Hence, concentration is focussed on nature reserves rather than enumerating the introduced and invasive species, which have been listed by Brown (1985).

Invasive species and wildlife conservation in the British Isles

In the British Isles there are probably no ecosystems that are unaffected by human activity, and hence in selecting nature reserves of national status (Ratcliffe 1977) the criterion of 'naturalness' was used. The more natural an ecosystem, the more it tends to be valued for wildlife conservation. Because there are no completely natural systems, examples cannot be used to resolve the question of whether or not completely natural ecosystems are resistant to invasion by alien species. However, it is possible to recognize degrees of naturalness and, possibly, to correlate these with the amount of invasion that has taken place.

The approach of the Working Group will be followed, first by considering case studies, and secondly by attempting to find some generalities. Two case studies are of alien species of flowering plant that have become widely distributed, and the other two case studies are of alien species of mammals, both of which have become established, although only one is widespread. Data on the distribution of these species were provided by the Biological Records Centre in the form of distributional maps, which record the presence of the species within 10 km squares of the national grid system. These data can only be used to give approximate rates of spread, because it is not known where in the 10 km square the sighting was made, and hence all calculations assume that the record is located at the centre of the square. Also these data have the disadvantage that they consist of only one kind of record: the sighting of a single specimen ranks equally with a documented breeding pair or with a known colony. The presence of a 'dot' on a map indicates that the species was present in that grid square: the absence of a 'dot' does not indicate the converse, only that the species was not recorded. Given these assumptions and weaknesses, distributional maps, which resulted from the observations of large numbers of people, can be used to gain an insight into the progress made by invasive species.

Invasive plants in the British Isles

General situation

Many species of plant have been introduced to the British Isles since neolithic times; some were intentionally introduced as crops, herbal medicines (see, for example, the discussion in Legg (1978) of the flora of Steep Holm) or ornamental species, and others were accidentally introduced, often by contamination of crop seeds. Webb (1985) discussed the criteria that can be used to decide whether or not a plant species is native, and Preston (1986) has extended these criteria. With doubt about the native or alien status of some plant species that may have been introduced at least a thousand years ago, it is difficult to estimate exactly what proportion of the British flora is introduced. Brown (1985) lists about 320 species; this result implies that about 20% of the flora is non-native. A summary of Brown's data is given by Williamson & Brown (this symposium). In relation to wildlife conservation, one example is rhododendron (*Rhododendron ponticum*), a woodland plant that is native from central and south Portugal to Lebanon and Asia Minor (Clapham *et al.* 1962). The other example is Indian balsam (*Impatiens glandulifera*), also known as the Himalayan balsam or policeman's helmet, which is a native of the Himalaya.

Rhododendron (*Rhododendron ponticum*)

Rhododendron is a common component of woods and copses throughout most of the British Isles (figure 1*a*). It was widely planted for decorative purposes in the Victorian era (Edlin 1956), but its naturalization tended to be documented neither with herbarium specimens nor

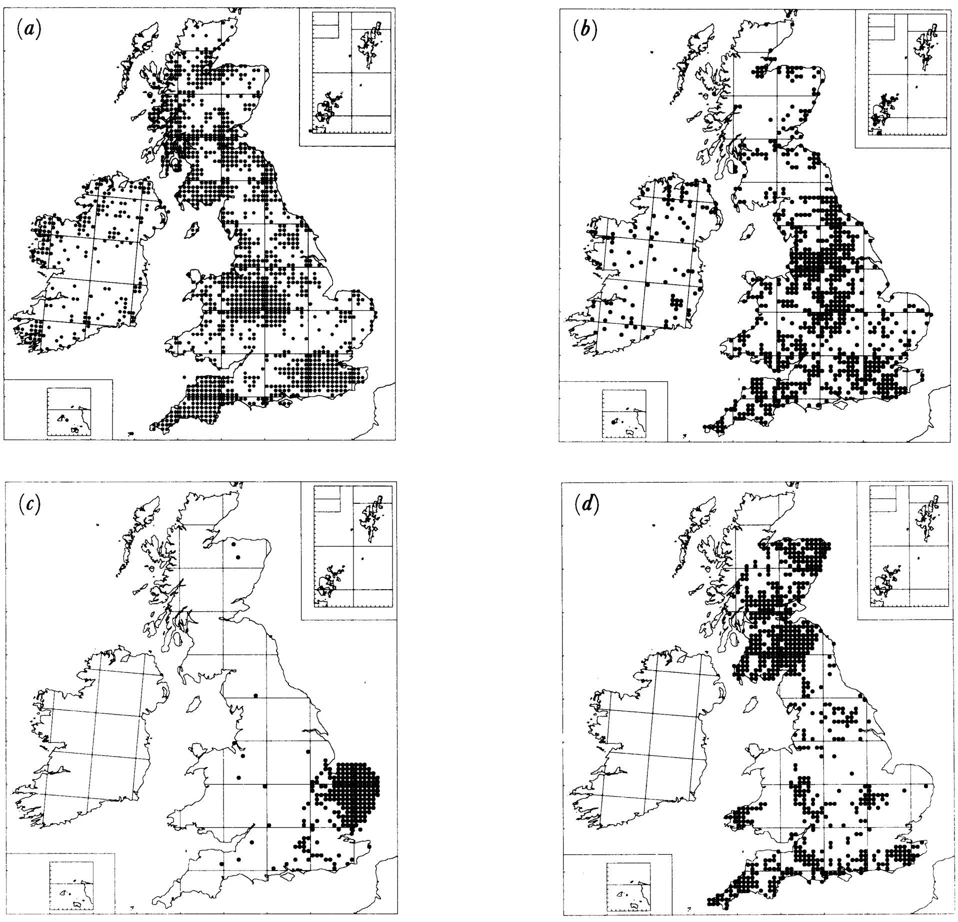

FIGURE 1. The current situation in the British Isles of the four invasive species discussed in the text. The maps are: (*a*), rhododendron (*Rhododendron ponticum*); (*b*), Indian balsam (*Impatiens glandulifera*); (*c*), coypu (*Myocastor coypus*); and (*d*), mink (*Mustela vison*). The vertical and horizontal lines represent the 100 km lines of the British and Irish national grids; presence of a species within a 10 km national grid square is indicated by an asterisk for *Rhododendron* and by a circle for the other species.

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with notes in natural history society journals (C. D. Preston, personal communication). Salisbury (1961) gave the date of introduction as 1763; the most recent account of its biology was given by Cross (1975). Owing to lack of recording and the length of time since introduction, it is not possible to give speeds of spread. However, the effects of rhododendron on communities that it has invaded can be described. In forestry, there are two main approaches to its control: mechanical and chemical. Whereas the former can do no more than contain the species, with the latter complete eradication can be attempted, although Robinson (1980) points out that these operations have serious implications for the profitability of a potential tree crop. The magnitude of the problem in a commercial forest is shown in table 1; nearly 70% of the area had been colonized.

Table 1. Rhododendron occurrence in Clogheen Forest, Killarney, Ireland

(Data derived for Robinson (1980); all figures, except the last column, are in hectares.)

Rhododendron cover	height of scrub: less than 1 m	1–2 m	more than 2 m	total area	percentage of total area
none	—	—	—	199.6	31
less than 5%	—	—	—	130.4	20
5–50%	53.8	58.5	16.0	128.3	20
51–80%	34.1	16.4	28.8	79.3	12
more than 80%	29.8	28.1	49.2	107.1	17

In the southwest of Ireland, invasion by rhododendron caused fears for the long-term conservation of the acidic Blechno–Quercetum (oakwood) community. The effects of invasion can be summarized under the following five headings (Cross 1980). First, it affects other plant formations, including dwarf shrubs, herbs, and, as stressed by Rose & Wallace (1974), bryophytes. The effect is probably due to light reduction, as Cross (1982) quoted 30, 9 and 2% daylight penetrations under oak, under mixed oak (*Quercus petraea*) and holly (*Ilex aquifolium*), and under woodland invaded by rhododendron, respectively. Second, rhododendron prevents regeneration of shrubs and trees, partly by the reduction in light and also by litter accumulation. These two effects are clearly seen in a reduction of plant-species diversity. Cross's (1982) data indicated that, in mixed oak and holly stands, there were seedlings of 4 tree species, 7 species of fern and herbaceous plant and 13 species of bryophyte, whereas in stands invaded by rhododendron these figures decreased to 0, 2 and 4 respectively, an overall reduction of 75% in species richness. The three other effects are less quantifiable, and may be of a longer term nature. One relates to the elimination of epiphytic bryophytes and lichens, largely due to shading and the gradual loss of a suitable habitat. The second relates to the reduction of fungal diversity, partly because fewer species are associated with rhododendron leaves and decomposition of rhododendron wood. The third relates to animal life, since rhododendron is unpalatable, or even toxic, to large herbivores and is associated with an impoverished arthropod fauna.

The invasion of the Irish oakwoods led Tansley (1939) to state '...if this displacement of *Ilex* by *Rhododendron* in really progressive it is an interesting example of an apparently rare phenomenon, the successful invasion of an undisturbed community by an exotic species'. Cross (1981) investigated the factors leading to disturbance of the Killarney woodlands and subsequently to the germination of rhododendron seedlings. Much of the disturbance is due to overgrazing by the introduced sika deer (*Cervus nippon*), and holly, a native species, is in fact able to compete with rhododendron in the absence of such grazing. Since rhododendron is ungrazed, whereas native species such as holly and birch (*Betula pubescens*) are extensively grazed, the large population density of deer favours the spread of rhododendron. The paradox is that removal of rhododendron, which also disturbs the environment, also favours the germination of its extremely small, and widely distributed, seeds.

In Great Britain, rhododendron also causes considerable problems for nature reserve management. The Nature Conservancy Council's (NCC's) Event Records Scheme contains data on the control of rhododendron on 19 National Nature Reserves (NNRS). Many techniques have been used, including cutting, spraying and hand-pulling of regrowth, but the virtual yearly repetition of the operations in the same compartment of the same reserve indicates that Robinson (1980) was correct in saying that mechanical control could only contain the problem. In nature reserves, containment, rather than eradication, is probably going to be the aim of management. In the survey of the prime wildlife conservation sites in Great Britain (Ratcliffe 1977), rhododendron was referred to a number of times, generally with comments that its spread was largely under control. In Ireland, controlling the spread will be a more difficult process (Foras Forbartha 1981). Rhododendron seems to be having its greatest effect in the more oceanic climate of Ireland, where it is a long-term threat to the existence of the native acidic oakwood formation and a shorter-term threat to a number of species of understorey plant, especially the Atlantic bryophytes (Ratcliffe 1968).

Indian balsam (*Impatiens glandulifera*)

This balsam is established and widespread in the wild (Brown 1985). Salisbury (1961) indicated that is was introduced in 1839, but the data in the Biological Records Centre contain only one 10 km grid square record by 1880, and only eight records by 1900. These seven additional records were all south of the first record, and have a mean distance of 246 km (standard error 17.5 km) from it. There is no indication that this was a natural range extension, and is probably a result of repeated introductions and escapes. By 1920 there is evidence that balsam was spreading from sites where it had previously been recorded (see figure 2).

During the 20 years from 1900, the mean minimum distance of new records was 109 km (standard error 18.1 km). Between 1920 and 1940 (figure 2) there was considerable spread; the number of recorded grid squares increased from 29 to 75. A mean rate of range expansion during this period was 1.9 km a^{-1}. Considerable expansion of distribution took place between 1940 and 1960 (see figure 2), when there were 614 recorded grid squares in England, Scotland and Wales, and the first records from Ireland (90 grid squares). Although it is impossible to estimate rates of spread when there are so many foci, nevertheless a rate of 1.9 km a^{-1} would have been insufficient for the 1940 distribution to expand to the 1960 distribution. A study of some isolated range expansions, such as the Moray Firth, Scottish Borders and North Yorkshire, indicates that range expansion between 1940 and 1960 was of the order of 3–5 km a^{-1}. This may be partly due to increased survey work, because the Botanical Society of the British Isles started their mapping scheme during this period. Thus during the first 80 years after escape there was virtually no range expansion, and this has been followed by expansion rates of approximately 2 km a^{-1} and at least 4 km a^{-1} during each of the subsequent two 20 year periods.

The species has become increasingly common along riverbanks and in wet wasteland

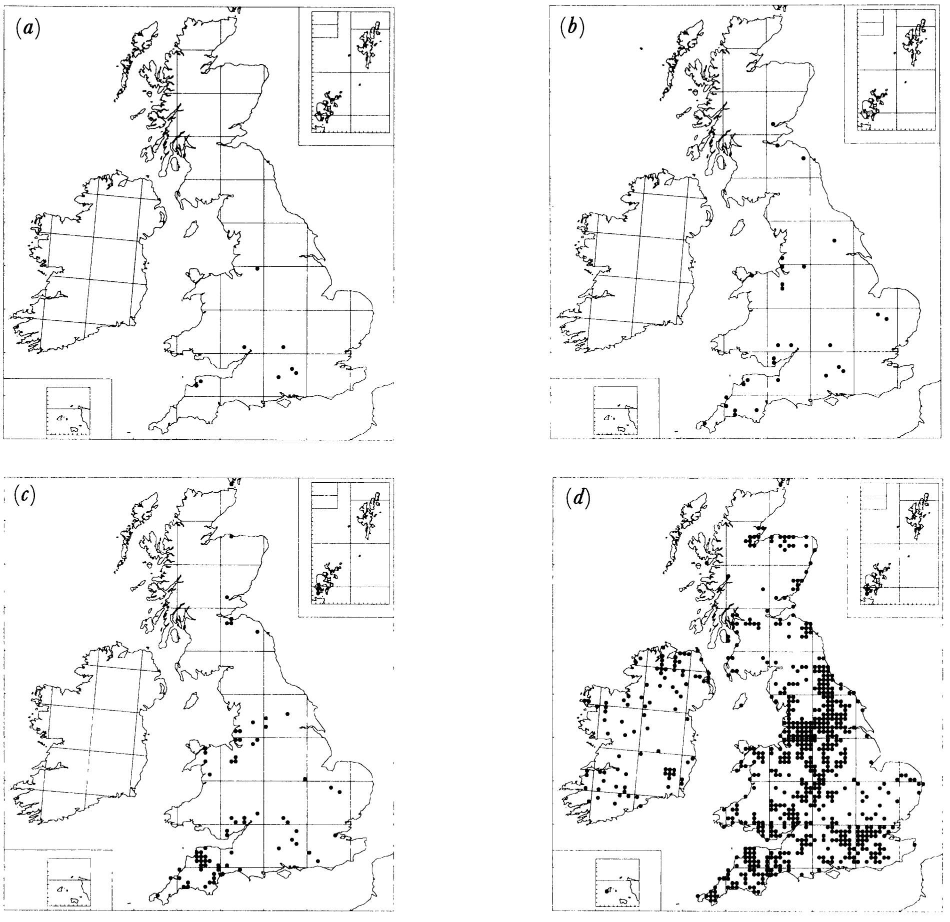

FIGURE 2. The spread of the Indian balsam (*Impatiens glandulifera*) in the British Isles. The illustrations show all records up to 1900 (*a*), 1920 (*b*), 1940 (*c*) and 1960 (*d*). The vertical and horizontal lines represent the 100 km lines of the British and Irish national grids.

habitats. It is an annual herb that grows to a height of 1–2 m (Clapham *et al.* 1962). The fruit opens explosively, each fruit releasing 10–20 seeds. A single plant may have over 100 fruits, though in Yorkshire many fruits do not ripen because of the onset of autumnal frosts. At the present time this species appears to be neutral for conservation management. It was not referred to in Ratcliffe's (1977) review, nor is there any mention to if in the NCC's Event Records Scheme. Why has the balsam not yet featured as an unwanted alien despite its wide distribution (figure 1*b*)? Gilmour & Walters (1954) recognized that the species flourished in garden soils, but that it was mostly invasive on river banks, especially those of heavily polluted rivers in the north of England. It would appear, therefore, that this species may be unable to invade undisturbed environments, but can be highly invasive where the native species have been killed or reduced in numbers by pollution.

Conclusions

It is not possible to survey the impacts of all introduced plants on the nature reserves of this country. Brown (1985) indicated that about 320 species have become established, and that about 150 species that were introduced have failed to become established. Tansley (1939), quoted above, argued that it was rare to find an undisturbed community being invaded by a plant, and this argument tends to be supported both by the examples quoted above and by observations of other pest species (Brown 1985). Disturbance of communities can result from many factors. The Indian balsam has been able to form its largest populations on the banks of polluted rivers. Such habitats will have a reduced diversity from their pre-pollution state, but the arrival of the balsam will have reduced the diversity even further, as few other plants survive under a dense balsam stand. The disturbance to the oakwoods invaded by rhododendron was by another introduced species, the sika deer. By selectively grazing the native flora, by not grazing rhododendron seedlings, and by keeping the moss depth to less than 1 cm (which makes an ideal seed bed for germination of rhododendron seeds), the sika deer has disturbed the oakwood sufficiently to make it prone to invasion. Probably the only other invasive plant species in the NCC's Event Records Scheme is the pirri-pirri-bur (*Acaena anserinifolia*), from Australia and New Zealand, which has formed an extensive population on the Lindisfarne NNR. This is a sand-dune system that is naturally disturbed by wind and sea, as well as being subjected to some recreational pressure. With invasive plants in the British Isles, there does seem to be a correlation between the degree of disturbance of a nature reserve and the ability of potentially invasive species to establish large populations.

Invasive mammals in the British Isles

General situation

Twenty-three species of mammal, listed by Brown (1985), have been introduced to the British Isles either intentionally or unintentionally. Six of these are currently recognized as having widespread pest status. These include the house mouse (*Mus musculus*) and rabbit (*Oryctolagus cuniculus*), which were introduced many centuries ago, the brown rat (*Rattus norvegicus*), introduced accidentally about three centuries ago, and the grey squirrel (*Sciurus carolinensis*), coypu (*Myocastor coypus*) and mink (*Mustela vison*), all introduced within the last century or so. The first three of these species were already widely spread within the British Isles before distributional recording began, and hence it is not possible to assess the speeds of spread or the effects of their invasion on the ecosystems being invaded. Squirrels are well documented in the conversation literature (see, for example, Usher (1973), Williamson & Brown (this symposium)), and hence the review below concentrates on the coypu and mink, the two species that have been most recently introduced. Historical accounts of the introduction of many of these species, together with the musk rat (*Ondatra zibethicus*), are given by Matthews (1952), and more recent biological accounts are given by Corbet & Southern (1977).

Coypu (*Myocastor coypus*)

The present status of the coypu (figure 1*c*) shows that the majority of the records are from East Anglia and surrounding counties, with only sporadic records (mostly pre-1944) elsewhere. Detailed recording has been carried out in East Anglia, where the changes in the species distribution can be assessed from the data held by the Biological Records Centre (figure 3).

The coypu was introduced in 1929 for fur farming, and animals soon escaped from captivity (Warwick 1935). Feral populations were established in reed-beds, river banks and marshes and along the feeder streams to such areas (Southern 1964). The animals feed predominantly on

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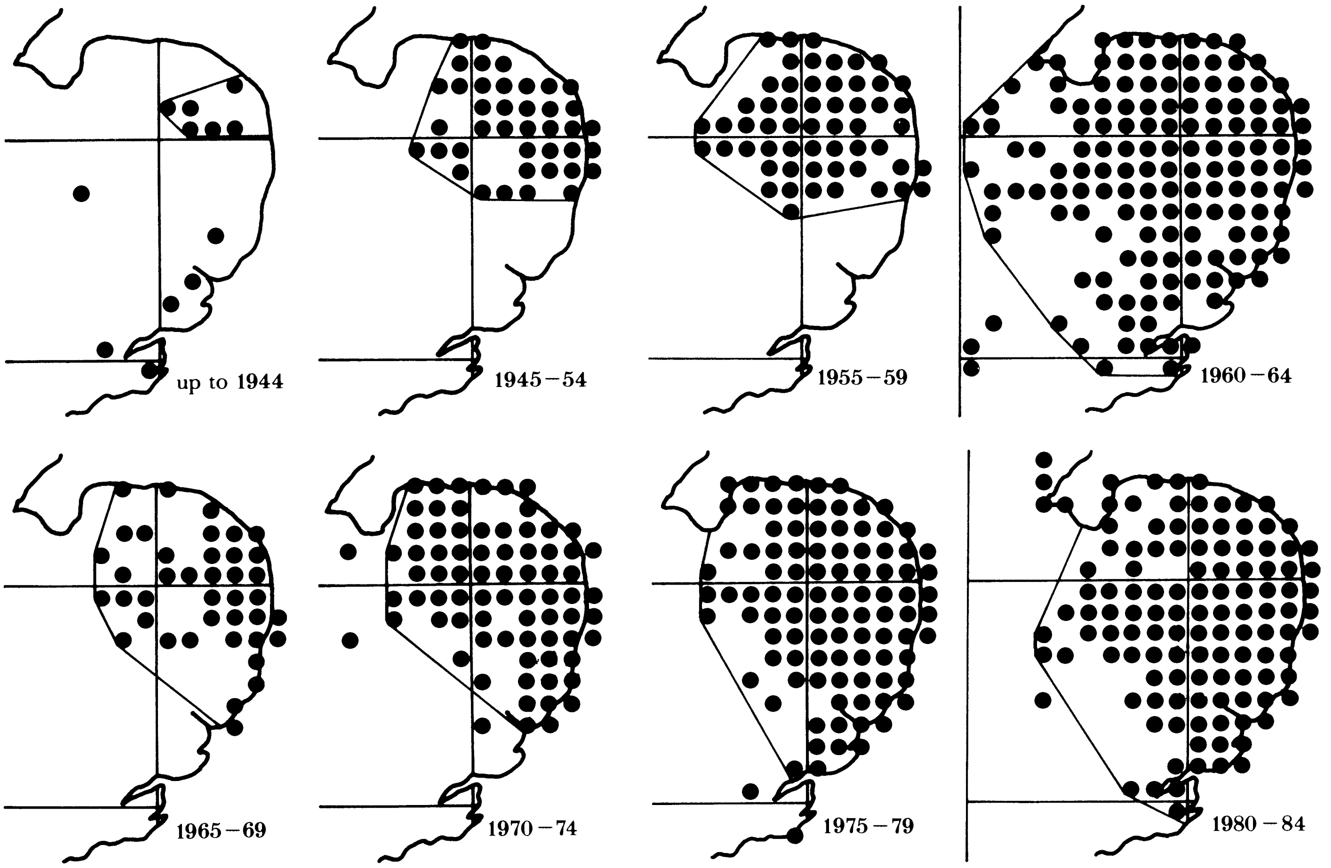

FIGURE 3. The range expansion of the coypu (*Myocastor coypus*) in and near East Anglia (from the Wash to the Thames). Records were collected between the dates indicated. The upper series shows the range, before the 1962–3 winter, when there was virtually no control. The lower series shows the expansion in range during the period of active coypu control. Except for the first of each series of maps, a convex line has been drawn from coast to coast so as to enclose all contiguous 10 km grid square records.

water and marsh plants, although, particularly in winter, they will feed up to 1.5 km from wetlands on agricultural crops, especially sugar beet (a list is given by Morton *et al.* (1978)).

Control measures started in 1960, and an intensive M.A.F.F. campaign began in 1962 (Morton *et al.* 1978). This campaign coincided with the exceptionally cold winter in 1962–63, when it was estimated that between 80 and 90 % of the coypu population died of hypothermia, starvation or disease. The data in figure 3 can therefore be viewed as two series. The first four diagrams indicate the range extension when there was no control. The second four diagrams indicate the extension, after the cold winter, in the face of control by trapping and shooting. Estimates from these maps indicate that the front of the area occupied by coypus advanced by approximately 3 km a^{-1} from 1944 to 1959, and then increased to approximately 20 km a^{-1} from 1959 to 1962 (the majority of records on the 1960–64 map in figure 3 were made before the 1962–63 winter). There seems to be no known reason for this relatively sudden increase in the speed of range expansion. In the decade following the cold winter the range expansion over the same region as previously was about 2 km a^{-1}, but from 1974 to 1984 this increased to a mean of about 3 km (2 km a^{-1} in a westerly direction and 4 km a^{-1} in southerly and south-westerly directions).

The conservation importance of the coypu can be assessed by its impact on the nature reserves of East Anglia. The NCC's Event Records Scheme indicates that trapping and/or shooting has occurred more or less annually on the Bure Marshes NNR since 1970 and on the Walberswick NNR since 1973. Intermittent control has been carried out on the Holkham, Calthorpe Broad and Hickling Broad reserves. Grazing impacts have been large on certain favoured food species, such as frogbit (*Hydrocharis morsus-ranae*) and water soldier (*Stratiotes aloides*), the latter having become so rare in Great Britain by the early 1970s that it was considered for inclusion in the *Red Data Book* (Perring & Farrell 1977). Ellis (1965) reports that such locally common species as cowbane (*Cicuta virosa*) and great water dock (*Rumex hydrolapathum*) have been virtually eliminated from Broads in which they were frequent before invasion by coypu. Perhaps more importantly, coypu grazing has caused a considerable modification in wetland communities, as detailed in Appendix VII of Morton *et al.* (1978).

Although the original control programme aimed at extermination of the species, doubt has been cast on the possibility of achieving such an aim. This is due to the coypu's fecudity (two litters per year, average litter size 5, sexual maturity at 3.5 to 5.5 months, longevity probably in excess of 5 years) and to the inaccessibility of the habitat of the feral populations. While the impetus for control came from the agricultural interests, the conservation interests were faced with a dilemma. Coypus undeniably affect the structure and composition of many plant communities, but the disturbance caused by active and intensive control could adversely affect birds, such as the marsh harrier (*Circus aeruginosus*) and bittern (*Botaurus stellaris*), and mammals, especially the otter (*Lutra lutra*). Reserves have not shown themselves resilient to invasion by coypus; indeed, the reserves of the Norfolk Broads substantially provided the areas referred to as 'the inner redoubts' by Morton *et al.* (1978) and were the foci for the second range expansion following the 1962–63 winter. The speed of advance of the coypu (approximately 3 km a^{-1} initially and subsequently increasing, though slower in the face of the post-1962 control programme) and the coypu's ability to invade any wetland habitat, whether recently disturbed or a wildlife reserve, both have relevance for conservation management.

Mink (*Mustela vison*)

Mink, like coypu, were introduced to the British Isles in 1929. Although individuals soon escaped, Southern (1964) stated that it was not known to have bred in the wild until 1956. The data for the mink are difficult to interpret because there were about 700 fur farms by 1962 (Swan 1981), and releases occurred in many areas. The current position is that the mink occurs widely throughout the British Isles (figure 1*d*). A control programme started in 1962, but this did not prevent the mink extending its range rapidly (see figure 4). Estimates of the speed of spread can be obtained for some areas. In 1960 there was only one recorded grid square in Scotland, in Aberdeenshire. By 1963 there were ten grid squares in this area (figure 4*a*), up to 60 km distant in a westerly direction and 40 km in an easterly direction where the North Sea prevented further spread. The number of recorded grid squares by 1966 had increased to 42 (figure 4*b*). Spread northwards and eastwards was prevented by the coast, but westwards and southwards the new records were up to about 60 km distant from the 1963 records. Range expansion in the Grampian region effectively stopped until the mid-1970s, after which it seemed to expand towards the west and south-west (figure 1*d*).

The first mink were recorded in the Firth of Forth area between 1960 and 1963 (figure 4*a*), and by 1966 there were 56 records in this area. Range expansion was not uniform; there had

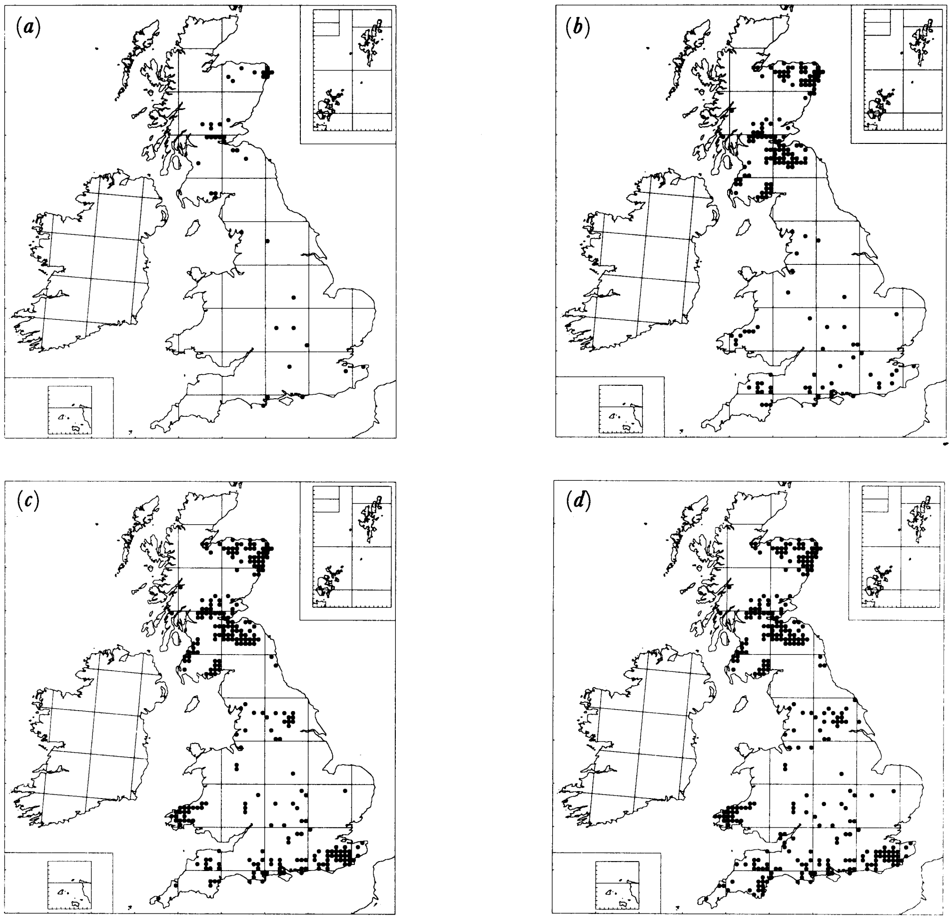

FIGURE 4. The spread of the mink (*Mustela vison*) in the British Isles. The illustrations show all records up to 1963 (*a*), 1966 (*b*), 1969 (*c*) and 1974 (*d*). The vertical and horizontal lines represent the 100 km lines of the British and Irish national grids.

been virtually no expansion northwards, some expansion, up to 20 km, to the east and west, but expansion of about 50 km to the south (figure 4*b*). Mink in the Firth of Clyde and Galloway expanded its range by between 50 and 60 km between 1963 and 1966. Again there was relatively little change in the range of these lowland Scottish infestations from 1966 until the mid-1970s (figure 4*c*, *d*), after which range expansion began again. An analysis of Scottish trapping records is given by Cuthbert (1973).

Although releases also occurred in England and Wales, there is relatively little evidence of the spread from release points when the 1960, 1963 and 1966 maps are compared. However, range expansions can be seen by comparing the 1966, 1969 and 1974 maps (figures 4*b*, *c*, *d*). The speed of range increase is similar to that observed in Scotland, with rates up to 20 km a^{-1}.

The maps showing coypu range expansion indicate records for most 10 km grid squares within the zone of expansion (figure 3), except at the periphery. The mink contrasts with this; there are many 10 km grid squares, within the zone, without records. Swan (1981) states that male mink, which were radio tracked, ranged up to 11 km in 14 days in Scandinavia, and that one mink in Scotland is known to have moved 20 km in 6 days. Females are, however, more sedentary than males. Fecundity is not great; females come into breeding conditions only once per year, and they produce litters of three or four (Swan 1981) or five or six (Southern 1964) kits, which are weaned at eight weeks but remain with their mother until late summer. There seems to be no information about the longevity of feral mink.

Control is largely by trapping: Corbet & Southern (1977) record that about 1000 mink are killed per year. There are very few records of mink control in the NCC's Event Records Scheme. In the East and West Midlands there have been isolated trapping activities in Wicken Fen and Rostherne Mere NNRS, and in Scotland periodic control at the Loch Leven and Whitlaw Mosses NNRS. The initial fear of conservationists was that mink, being carnivorous and associated with water bodies, would compete with the otter (*Lutra lutra*) and would affect colonies of ground-nesting birds, especially on offshore islands. Whereas the latter is probably a real fear, studies of the food of the mink and otter (Chanin & Linn 1980; Chanin 1981; Wise *et al.* 1981) indicate that there is not a large (about one third) overlap in the diets of the two species, this overlap being the fish component of the diet. D. J. Jefferies (personal communication) has pointed out that it is unlikely that mink were a factor in the decline of the otter in England, and that the areas in England currently with the most otters often also have the largest mink populations.

This example raises a few general points. The speed of range expansion has been variable. Because individual mink can migrate for long distances, the mean range expansion can be 20 km a^{-1}, but, unlike the coypu, the species does not 'fill in' all suitable habitats behind this front. For some periods the front appears static, but the factors that influence the stationarity or advance of the front are unknown. Conservationists had a perception of this predator being able to exterminate many native species. Despite the wide range of food taken by the mink (Jenkins & Harper 1980; Wise *et al.* 1981), the most apparently vulnerable species, the otter, appears not to have been adversely affected, nor have other native fish, bird or mammal populations (Chanin & Linn 1980). Also, nature reserves seem to have had no greater resistance to colonization than other suitable wetland habitats.

Conclusions

Both coypu and mink were introduced to the British Isles for fur farming, and subsequently escaped. Their consideration would not be complete without mention of the musk rat (*Ondatra zibethicus*), which was also introduced in 1929 and had established feral populations by 1930. Extensive infestations occurred in central Scotland and Shropshire, with other smaller infestations (Corbet & Southern 1977). The potential damage to the natural environment was tremendous, due to animals eating aquatic vegetation and burrowing into stream banks. Matthews (1952) records the problem in Continental Europe where riverside pastures were transformed into marshes by burrowing. Control measures in Britain were speedy: keeping musk rats was prohibited, and an intensive trapping programme led to the extinction of the species in the British Isles by 1937.

Campaigns against mink have, in general, not been very successful, but the continuing campaign against coypu seems to be succeeding. The campaign against musk rats was extremely successful, and the reasons for this should be examined. The fecundity of the musk rat is large; females can produce 6 or 7 litters, each of about 8 young, in the breeding season. Of the three species of fur farm mammals that established feral populations in the British Isles, the musk rat has the greatest fecundity and the mink the lowest fecundity. Since the success of control campaigns has been inversely proportional to the species' fecundity, it appears that the ability to control an invasive mammal is related more to the species' dispersal than to its fecundity. Morton *et al.* (1978) pointed out that the pattern of migration of coypu at very low population densities was unknown, and they perceived that control could only be effective if migration did not increase as population size decreased.

For wildlife conservation, there must always be a balance between the disadvantages of having an invasive species and the disadvantages of killing or disturbing wanted species during the control campaign. Matthews (1952) documents a musk rat campaign in Scotland during which 945 musk rats were killed, but there were also unintentional deaths of 2305 water voles, 2178 moorhens, 1745 brown rats, 101 ducks, 57 weasels, 36 stoats, 18 herons, and small numbers of many other species. The prevention of disturbance of breeding bittern and marsh harriers has been an important feature of coypu control. Although an invasive species can harm the nature resource of the country, care should be taken not to cause even more harm to that nature resource as a result of measures to control the invasive species.

Discussion

What makes a species become invasive? Brown (1985) did not use a category of 'invasive', but he used categories of 'introduced and widely distributed' and of 'pest' species. Terminology for various categories of introduced species is difficult, but some recommendations are given by Shafland & Lewis (1984). In relation to nature reserves it seems useful in the continuum of species categories to use the term 'invasive' for those introduced species that require management operations either to control their population size or to control their continued spread. Invasive species are thus introduced species that have become pests. In the case studies three of the four species are thus invasive on nature reserves as control operations have been carried out; Indian balsam would not qualify as an invasive species, although its abundance in some areas may mean that it could enter this category on some wetland or riparian reserves in the future. However, none of the examples shows the spectacular rates of spread that have been observed in other parts of the world. For example, Baumgartner & Greenberg (1984) document rates of spread up to 3.2 km d^{-1} of *Chrysomya* flies in South America.

Tansley's (1939) contention concerning the rarity of invasions of exotic plant species into undisturbed communities seems largely to have been supported by the case studies quoted here. It seems unlikely that any of the plant pest species listed by Brown (1985) would be invasive in nature reserves that are undisturbed, since most in his list were weeds of arable land. Although the contention seems to be well-founded for plant communities in the British Isles, studies of native vegetation in other parts of the world have shown undisturbed communities to be vulnerable to invasive species. The studies of Ogle (1987) and Timmins & Williams (1987) on the invasive species of natural vegetation in New Zealand indicate that the most invasive species are the most vagile. The seeds tend either to be wind-dispersed or to be succulent and bird-dispersed, and the species tend to be short trees that have rapid growth and are short-lived (less than 80 years). The exceptions to these general rules, such as old man's beard (*Clematis vitalba*), are frequently invasive only in forest remnants or along the margins of larger areas. Such habitats are clearly suffering from a climatic disturbance following removal of adjacent areas of native vegetation. Physiological adaptation may also be an important aspect of the ability of a plant species to colonize otherwise undisturbed communities. The work of Pammenter *et al.* (1986) on *Agrostis stolonifera* invading natural communities on Marion Island

(46° 54′ S, 37° 45′ E) showed that its competitive ability was due to its response to low photon flux densities and to its carbon allocation patterns.

Why are there apparently no invasive plant species of undisturbed vegetation in the British Isles when these are examples of invasive species of undisturbed natural vegetation in other parts of the world? The answer may possibly be historical, as species have been introduced to the British Isles since the neolithic culture arrived, and what is observed now shows the fragmentation of the original vegetation, virtually all of which is disturbed, with invasive species of a thousand or more years ago appearing as native members of the community. The introduction of plant species to New Zealand, and especially to Marion Island, is historically more recent, and hence the effects of invasion are currently being observed. The historical factor can be used to pose an unanswerable question: will New Zealand communities be less prone to invasion by plant species in a thousand years' time?

The case studies of the mammals may support the historical interpretation. A few mammal species were introduced to the British Isles a thousand years ago; the rabbit and house mouse are examples. Many species have been introduced within the last 100 years, and at least four of these are invasive in nature reserves in the British Isles. The case of tropical island reserves (Brockie 1985*a*, *b*, *c*; Loope 1985) indicate that the majority of introduced mammals have become invasive. Natural island communities in most parts of the world do not appear to have any resistance to invasion by mammals, especially the brown rat or feral populations of domestic mammals such as cats, dogs, goats and pigs. The Irish oakwoods were invaded by sika deer, the earliest introduction being the Japanese subspecies. This is an interesting example of an apparently undisturbed community being invaded by a mammal, which then disturbed the community sufficiently to facilitate invasion by an introduced plant.

With an 'invasive' species' defined as above, control measures will already have been started. These follow similar patterns of mechanical culling (trapping or shooting animals, cutting and uprooting plants) or poisoning (herbicide sprays). Control measures in the British Isles have rarely been successful, although the musk rat control is an exception to this rule. The case studies of both plants and animals indicate that fecundity may not be the primary factor affecting the success of a control programme; the ability of a species to disperse is perhaps the most important factor. Species with low dispersal abilities can be contained readily and eradication can be achieved by intensive culling. Species with high dispersal ability will continue to re-establish populations, and eradication seems not to be a management option. However, in any eradication or containment programme, the disturbance caused to a nature reserve can have adverse side effects, either by the death or disturbance of wanted species or by the disturbance making the reserve more prone to invasion by other species. There needs to be a balance between the disadvantages of the presence of the invasive species and the disadvantages of the disturbance caused by its elimination or containment.

Having rather implied that introduced species, especially strongly invasive ones, reduce the value of semi-natural areas as nature reserves, it should be remembered that some introduced species can increase values. Margules & Usher (1981) reviewed criteria that were used in assessing wildlife conservation values, and they pointed out that the list of rare plant species in the British Isles, contained in the *Red Data Book* (Perring & Farrell 1977), included several species that were known to be introduced, such as *Iris versicolor*, as well as many species that were possibly introduced, such as *Iris spuria*. The value of an area for wildlife conservation purposes depends upon the integration of many values of single attributes of that area. Invasive species tend to make the area less natural, to reduce the diversity of other species, and, with control programmes, to make the area more disturbed. All of these attributes are perceived as reducing the value of the area for wildlife conservation purposes. It is only the uncommon and long-established alien, such as the *Iris* species above, valued for its rarity, that could increase the conservation value of an area. Thus, invasive species invariably lead to a reduction of the value of an area in wildlife conservation assessments, whereas non-invasive introduced species may either increase or decrease that value.

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Discussion

Sir Hans Kornberg, F.R.S. (*Department of Biochemistry, University of Cambridge, U.K.*). Dr Usher demonstrated that coypu breed more rapidly than mink, yet it has remained restricted to East Anglia whereas mink have spread widely. Why does he think this is?

M. B. Usher. Coypu only travel short distances. Mink have a much larger home range and much greater dispersion capability.

J. W. Horwood (*Ministry of Agriculture, Fisheries and Food, Fisheries Laboratory, Lowestoft, Suffolk, U.K.*). The role of fecundity was stressed in discussing birds, and Dr Usher has now referred to its importance in mammals. It is easier to demonstrate than mortality as a key factor, but is it possible that invasive species also have a lower death rate? Is it possible that invading plants are similarly less affected by herbivores?

M. B. Usher. There are no data on the death rates in these feral mammals. I did give some longevity for coypu, but could not find it for feral mink. There is no evidence that any large herbivores crop *Rhododendron*, but it has a small associated insect fauna.

Sir Richard Southwood, F.R.S. (*Department of Zoology, South Parks Road, Oxford, U.K.*). There are only a few insects on *Rhododendron* in Britain and those are mostly introduced: a lace bug, a hopper, one or two other types, and one native hemipteran that seems to have transferred from birch. Do we know anything of the diversity of *R. ponticum* woods in southeast Europe, where it occurs naturally?

P. D. MOORE (*Department of Biology, King's College, 68 Half Moon Lane, London, U.K.*). As Dr Usher pointed out, Tansley was wrong in his assertion that *Rhododendron ponticum*, in displacing *Ilex aquifolium*, was invading a stable habitat. *Ilex* is favoured by woodland disturbance, as demonstrated by pollen analytical studies and population studies such as those of Peterken & Tubbs. In Germany, Richard Pott has shown that grazed coppice woodland (Hudewald) is particularly favoured by *Ilex*. So replacement of *Ilex* by *Rhododendron* is a case of one grazing resistant weed being replaced by another.

M. B. USHER. I should like to thank Dr Moore for his comments about *Ilex aquifolium*. How much is known about the ecology of *Ilex* in the Atlantic (maritime) environment of Western Ireland as opposed to the more continental environment of Germany? On the sea cliffs of the Island of Rhum NNR, Inner Hebrides, especially above the path from Kinloch to Papadil, *Ilex* occurs as scattered shrubs, many of which appear to be extremely old. Could it be possible that *Ilex* is more frequent, and hence less dependent upon disturbance, in woodlands along the Atlantic coasts of northwest Europe?

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