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The feasibility of reintroducing Wild Boar (*Sus scrofa*) to Scotland

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Abstract

The feasibility of reintroducing Wild Boar *Sus scrofa* to Scotland was investigated using the predictions of a Geographical information System (GIS) and a Population Viability Analysis (PVA). In the first stage of this study we summarized information from published literature on the biology, habitat requirements, home range use and population densities of Wild Boar, and using a GIS we identified four suitable sites of significant size, all located in Highlands. In the second stage we used a Population Viability Analysis (RAMAS/age), parameterized with published information on survival and fecundity of European Wild Boar populations, to calculate the number of animals required in a 'release population' if it were to survive on average 50 years. At the two largest sites that we considered, a release population of 50 animals would be likely to produce a viable population. The study concluded that biologically, the reintroduction of the Wild Boar is possible. However, a complementary study examining both the environmental and the potential wider ecological and socio-economic impacts of Wild Boar will be required before reintroduction is seriously considered.

Keywords: GIS, reintroduction, Scotland, *Sus scrofa*

INTRODUCTION

Species reintroduction is increasingly seen as a valuable tool for conservation: to save species from extinction, to reinstate species that have become locally extinct, and to encompass modern ideas of conservation that give consideration to the wider social, cultural and economic environment. Scientifically, politically and legally, reintroductions are being promoted as part of a commitment to what has become termed 'creative conservation' (Yalden, 1986; Olney, Mace & Feistner, 1994). To date in the UK, the most comprehensive study of a possible reintroduction of a mammal has dealt with the Beaver (*Castor fiber*) (Macdonald *et al*., 1995), and Scottish Natural Heritage (SNH) currently undertaking a three year feasibility study on its reintroduction. This study examines the case for the reintroduction to Scotland of Wild Boar (*Sus scrofa*).

After several decades of constant increase in range and numbers (Sáez-Royuela & Tellería, 1986) the Wild Boar is now found throughout most of Europe. The Wild Boar is extinct in the UK, but remains of Wild Boar are common from Mesolithic sites (Clutton-Brock, 1991), although they are difficult to distinguish from domestic swine (Aybes & Yalden, 1995; A. Kitchener, pers. comm.). There is good documentary evidence for the survival of Wild Boar in England through to the 14th century (Rackman, 1986), when it became extinct due to direct persecution and habitat loss. However, populations may have been maintained for a long while after then by introductions of new stock from the Continent and by interbreeding with domestic and feral

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pigs (Yalden, 1986, 1999).

The UK Biodiversity Action Plan (HMSO, 1994) aims to conserve and enhance biological diversity in the UK, and where practicable it also aims to enhance populations and the natural ranges of native species (Macdonald *et al.*, 1995). Article 22 of the Habitats and Species Directive (EC 92/43) states that member states of the European Union should investigate the possibility of reintroducing species in Annex IV, that are native to their territory, where this might contribute to their conservation (EEC, 1992). Furthermore, under article 11 (2) of the Convention of European Wildlife and Natural Habitats, the UK government should encourage the reintroduction of native species.

In Scotland the responsibility for implementing wildlife legislation falls to SNH. Wild Boar are not listed under Annex IV of the Species and Habitats Directive, due to the expansion of European populations (Sáez-Royuela & Tellería, 1986). Furthermore SNH have no current plans to consider Wild Boar for reintroduction (M. Cooper, pers. comm.). However, as a species whose extinction in historical times was mainly due to human activities, we assert that Wild Boar should be included on any list of species to be considered for reintroduction to the UK.

The IUCN (1987) advise that the first phase of any reintroduction programme should be a feasibility study. A recent paper (Howells & Edward-Jones, 1997) investigated the feasibility of reintroduction of Wild Boar in Scotland by analysing the availability of suitable woodland habitat that could support a minimum viable population. The authors concluded that the goal of establishing a self-sustaining population of Wild Boar in Scotland was unrealistic. The aim of the present study is to re-assess the feasibility of reintroduction of Wild Boar in Scotland through a more integrated approach, in which the area of woodland available is only one of the many factors involved.

The specific objectives of the study were:

1 To establish Wild Boar habitat requirements and life history characteristics by summarizing relevant information on its biology from the available literature.

2 To use a Geographical Information System (GIS) to assess the availability of suitable release sites for Wild Boar in Scotland.

3 To use predictive population modelling (RAMAS/age) to suggest how many animals would be required in an initial ‘release population’.

1 A REVIEW OF THE BIOLOGY AND HABITAT REQUIREMENTS OF WILD BOAR

The Wild Boar is the most widely distributed species of the Old World Suidae. Its range extends from Western Europe and the Mediterranean basin to the Russian Taiga, through India and south-east Asia to the islands of Sri Lanka and Japan. In Northern Europe, the species has recently recolonized Sweden, Finland, Estonia and Soviet Karelia, its presence being recorded up to 65°N (Erkinaro *et al.*, 1982). European Wild Boar have been introduced to North America (Barrett, 1978) and feral pigs, belonging to the same species, exist in Australia and New Zealand, and many Pacific islands (Tisdell, 1982; Caley, 1993). In Europe, increases in Wild Boar in the last few decades have been attributed to several factors including socio-economic changes (de-population of rural areas) which improve environmental conditions for the species, variations in the type of dominant crops, reintroductions, lack of predators, limited hunting, additional food and climatic changes (Genov, 1981b; Erkinaro *et al.*, 1982; Sáez-Royuela & Tellería, 1986).

In Europe the body size of adult Wild Boar varies from 35 to 230 kg along a NE-SW cline, the smallest individuals being found in Mediterranean countries (Sjarmidi & Gerard, 1988). Males are generally bigger than females (Nowak & Paradiso, 1991).

Diet

The Wild Boar is omnivorous, although predominately a herbivore with plant material forming between 80 and 90% of the diet (e.g. Briedermann, 1976; Genov, 1981a; Massei, Genov & Staines, 1996). In north-eastern and western Poland, where Wild Boar inhabit deciduous forests and field margins, Genov (1981a) found that 131 plant species were consumed over the course of the year; cultivated species made up 71% of stomach contents (by mass), woodland and meadow species 21%, and animal matter 9%. A conspicuous part of the diet of the Wild Boar is formed by underground food items such as roots, bulbs and soil invertebrates (Genov, 1981a).

Animal food plays only a minor role in the diet of the Wild Boar, with estimates of 2–9% (e.g. Genov, 1981a; Sjarmidi, Spitz & Valet, 1992; Groot Bruinderink, Hazebroek & Van der Voet, 1994). Agricultural crops are heavily used, and in Europe Wild Boar consume mainly potatoes, grapes and cereals (Lescourret & Genard, 1985; Dardallion, 1987; Gerard & Campan, 1988).

The Wild Boar is monogastric and thus less capable than ruminant ungulates of extracting carbohydrates from cellulose. When crops and supplementary food are not available, energy-rich food such as acorns and beech mast are the preferred natural diet of the Wild Boar (Barrett, 1978; Groot Bruinderink *et al*., 1994; Jedrzejewska *et al*., 1994; Massei *et al*., 1996). Wild boar also live in areas dominated by coniferous forests, alder marshes and reeds and then the diet is based on a mixture of underground food, the bark of trees, invertebrates and carrion (Erkinaro *et al*., 1982; Kristiansson, 1985; Welander, 1995).

Wild Boar respond to temporal and spatial variation in food availability and abundance by feeding opportunistically, often through the exploitation of cultivated crops, or by migrating over long distances. (Jezierski & Myrcha, 1975; Andrzejewski & Jezierski, 1978; Genov, 1981a; Singer *et al*., 1981; Meriggi & Sacchi, 1992). The extent of habitat fragmentation is also a significant factor in resource exploitation; where the boundary line between field and woodland is extensive, Wild Boar make greater use of cultivated fields (Genov, 1981b).

Social organization and population dynamics

The sex ratio of Wild Boar, determined by trapping or shooting is, on average, 1 : 1 (Gerard & Campan, 1988; Ahmad *et al*., 1995; Boitani *et al*., 1995).

The basic social group is organized around a nucleus of closely related females and their most recent litters (Dardallion, 1988), with the adult males being solitary. The dynamics of the basic group include the isolation of the preparturient female in spring, her re-entry to the group with her new born, the entry of nulliparous females and in the autumn, the arrival of adult males during the rutting season with simultaneous departure of subadult males (Spitz, 1986; Gerard & Campan, 1988). Males fight for access to females and, having achieved matings, they move to another group. The age of puberty ranges from 8 to 24 months of age and females do not usually breed until the second year of life. Synchronized farrowing is generally observed within a group of females (Mauget *et al*., 1984). The reproductive activity of the Wild Boar is seasonal, with rutting in autumn-winter and breeding in spring (Mauget *et al*., 1984). Compared with other ungulates, that show a well-defined rutting period, the timing of reproduction in Wild Boar is strongly related to autumn–winter food availability (Mauget *et al*., 1984; Pepin *et al*., 1987). Abundance of energy-rich foods such as acorns influences both the proportion of females that breed and the litter size (e.g. Aumaitre *et al*., 1984; Groot Bruinderink, 1994; Massei *et al*., 1996). The proportion of breeding females in each year varies between 11 and 90% and mean litter size varies between 1.5 and 4.5 (Boitani *et al*., 1994; Groot Bruinderink *et al*., 1994; Massei *et al*., 1996). Fecundity is also related positively to the age and body mass of females (Sáez-Royuela & Tellería, 1987; Briedermann, 1990; Groot Bruinderink *et al*., 1994).

Wild Boar in a natural habitat can live for up to 11 years (Massei *et al*., 1997a). However, they generally have a lower life expectancy than this due to hunting. In a study of a hunted population in Poland, Jezierski (1977) found that Wild Boar lived for 4 years. In the same population, mortality was greatest in the first and second year of life, when 48% and 36% of a cohort died, respectively. Mortality is highest in the first few years of life, but it decreases significantly in later life (Jezierski, 1977). In particular, high piglet mortality may be related to late winter frosts since piglets do not have a fully developed capacity for thermoregulation. Mortality may also be related to the acorn crop of the previous year in that an abundant acorn crop may lead to a sudden increase in numbers which then crash the following year (Okarma *et al*., 1995; Massei *et al*., 1997b).

Habitat use and home range

Habitat use by Wild Boar is determined by food availability, shelter and weather conditions (e.g. Kurz & Marchinton, 1972; Meriggi & Sacchi, 1992; Boitani *et al*., 1994; Massei & Genov, 1995). They select habitats that offer high-energy food, cover from predators (hunters included), and they avoid those areas where weather conditions may be extreme, for example, where snow cover hampers movement (Singer *et al*., 1981). In hot summers, Wild Boar prefer shady areas because, lacking sweat glands, they need to thermoregulate by wallowing and resting in cool places (Saunders & Kay, 1991). Water is essential to Wild Boar survival. Resting places are often located in areas with dense vegetation cover where Wild Boar lie in a ground depression sometimes lined with nesting material (Spitz, 1986).

Meriggi & Sacchi (1992) showed that the most preferred habitat types in Northern Italy were those that could assure food and shelter, e.g. old coppiced trees. In the Camargue, southern France, and in the Great Smoky Mountains National Park (USA) the use of habitat appeared to be affected by the availability of energy-rich food such as acorn and beechmast, as well as by crops (Singer *et al*., 1981; Dardallion, 1987). Spatial segregation of the sexes in different habitats has been suggested by Singer *et al*. (1981) and by Boitani *et al*. (1994). Spitz & Janeau (1995) showed that subadult males selected habitats primarily for their food potential and females with dependent piglets selected for a combination of food-rich and secure habitats.

Wild Boar are primarily nocturnal (Singer *et al*., 1981; Russo, Massei & Genov, 1997). The size of their home range varies considerably in relation to several factors such as abundance and dispersion of food resources, age, sex and physiological status of the animal, habitat quality and population density, and human disturbance (Gerard & Campan, 1988). Home range size is usually larger in males than in females and increases during the hunting season, probably due to human interference (Maillard & Fournier, 1995). Estimates of annual home range size vary from 4.0 to 21.8 km^2 (Saunders & Kay, 1991), between 4.6 and 16.4 km^2 (Massei *et al*., 1997a) or average 26 km^2 (Jullien *et al*., 1990). When hunting occurs, the annual home range increases: for instance Boitani *et al*. (1994) found that annual home range increased from 3.1 to 12.3 km^2 and Janeau & Spitz (1984) reported 50–150 km^2, Spitz & Janeau (1990) looked at a variety of European studies and suggested that mean home ranges were small, around 4 km^2. In particular, sows reduce their movements and tend to centre their activities around nests before farrowing (Janeau & Spitz, 1984; Gerard & Campan, 1988).

Home range size can increase when food availability decreases (Belden & Pelton, 1975; Singer *et al*., 1981). In the Great Smoky Mountains National Park (USA), Wild Boar seasonal home ranges were smaller when mast was abundant (Singer *et al*., 1981). Factors such as population density and physiological stress might also influence the size of the home range. In contrast Massei *et al*. (1997a) found that in a mast rich year the annual home range averaged 14 km^2 and decreased to about 6 km^2 the following year, which was characterized by low mast, high population density and high mortality of Wild Boar. Boar responded to high population densities and shortage of food by *decreasing* home range size and *increasing foraging* activity. Andrzejewski & Jezierski (1978) have also shown that individual Wild Boar spend more time foraging when the population density increases.

Annual ranges of different individuals overlap extensively (Singer *et al.*, 1981; Jullien *et al.*, 1990) although Boitani *et al.* (1994) found that males ($n = 3$) maintained exclusive home ranges during the rutting season, which suggested territoriality.

Radio-tracking studies have revealed that over a single night, boars can travel between 2 and 15 km, although the direct distance between resting places varies between 0 and 7 km (Spitz, 1986). During seasonal migrations between high-(above 1000 m) and low-elevation ranges (below 1000 m), Wild Boar can move over longer distances, from 12 km to 250 km (Andrzejewski & Jezierski, 1978; Singer *et al.*, 1981). A French study showed that 25% of 262 Wild Boar had moved more than 10 km from the initial trapping site (Cargnelutti, Spitz & Valet, 1992).

Environmental effects of Wild Boar

Wild Boar often cause substantial damage to agricultural crops, particularly when other energy-rich food is scarce (Mackin, 1970; Andrzejewski & Jezierski, 1978; Meriggi & Sacchi, 1992) and are therefore considered as a pest in many areas. The results of many studies on the effects of Wild Boar on the environment however, are controversial. Rooting by Wild Boar is thought to accelerate decomposition of organic matter by incorporating forest litter into the soil (Jezierski & Myrcha, 1975). In Germany the introduction of Wild Boar to young conifer plantations resulted in the removal of competitive vegetation (weeds), which enhanced the regeneration and growth of Norway Spruce (*Picea abies*) (Kepka, 1989 cf. Brownlow, 1994). In Austria Wild Boar living in stands of Norway Spruce caused an additional 35.2% mortality in the population of the sawfly (*Cephalcia abietis*) (Führer & Fischer, 1991, cf. Brownlow, 1994). In Sweden, the rooting activity of the Wild Boar was found to increase plant species richness (Welander, 1995) in reed beds, alder marshes and pine forests. Conversely, a study by Bratton (1975a,b) in the Great Smoky Mountains National Park (USA), showed that there was a significant decrease in number of plant species. In a study of the Veluwe region in the Netherlands by Groot Bruinderink & Hazebroek (1996), regeneration of Oak (*Quercus rober*, *Q. petraea*), Red Oak (*Quercus rubra*) and Beech (*Fagus sylvatica*) was negatively correlated with rooting activity. Howe, Singer & Ackermann (1981) also found that Wild Boar rooting significantly reduced herbaceous forage and caused a decrease of 82% in soil macroinvertebrate populations in hardwood forest stands. In the same area, Singer & Ackermann (1981) and Singer, Swank & Clebsh (1984) showed that two vertebrates living in the leaf litter, the Red-Backed Vole (*Clethrionomys gapperi*) and the Short-Tailed Shrew (*Blarina brevicauda*) were nearly eliminated from intensively rooted areas. Wild boar were found to predate eggs of ground nesting birds such as the Red Legged Partridge (*Alectoris rufa*) in Spain (Calderon, 1977), and it was suggested that they could predate nests of Pheasants (*Phasianus colchicus*) in Northern Italy (Marsan, Schenone & Spano, 1990).

Criteria for release sites

In the first stage of this study we have reviewed Wild Boar life history characteristics and habitat requirements. Here we summarize this information as a set of 'criteria', i.e. habitat type, habitat size and management, which can be used to judge the quality of potential release sites. Release sites should be carefully chosen to maximize the chances of establishment and breeding, to minimize mortality and conflict with humans (Macdonald *et al.*, 1995), and to fulfil the species requirements through all stages of its life cycle.

Habitat type

Deciduous woodlands provide optimal habitat for Wild Boar and oak and/or beech woodlands will be most suitable given that the preferred natural foods of the Wild Boar are acorns and beechnuts. We suggest that 'mature' woodlands are best since oak only starts to yield seed at about 40 years of age and beech slightly later at 50 years (Worrel & Nixon, 1991); both species produce the heaviest crops between 80 and 120 years (Newbold & Goldsmith, 1981; Evans, 1988). Mature deciduous woodlands would also be most appropriate because of their high structural and species diversity. Although Wild Boar prefer mast, they exploit a wide variety of plant species found in the shrub and ground layers of woodlands (Genov, 1981a). In addition dense vegetation provides Wild Boar the ideal shelter for resting and bedding.

Wild Boar can also utilize other woodland habitats, including pinewoods and mixed woodlands. However, in Scotland, many Scots pinewoods (*Pinus sylvestris*) are of limited suitability, due to the extent of overgrazing by Red Deer (*Cervus elaphus*). We suggest that pinewoods with mixed stands of birch and/or oak would be preferable, but should be regarded as suboptimal compared to deciduous woodland.

Wild Boar will also use open habitats such as heathland and grassland. Although these offer little shelter, they do provide alternative food resources when mast is scarce. Oak and beech produce seed crops which vary greatly from year to year (Newbold & Goldsmith, 1981; Worrel & Nixon, 1991), the frequency of seeding decreasing with increasing latitude, elevation and oceanity, and therefore fluctuations in mast availability can be complex (Jones, 1959; Matthews, 1963). Generally good years for oak occur every two to four years and for beech once every five to 10 years (Newbold & Goldsmith, 1981). Between good mast years there are partial mast years and years of general or local scarcity. Hence Wild Boar will search for alternative food resources. They will consume plant species associated with grassy heathland habitats, for example, the leaves of broad-leaved grasses such as *Molinia*, *Poa*, *Holcus*, and *Agrostis* spp., the leaves of *Trifolium repens*, and the roots of *Vaccinium* spp. *and Pteridium aquilinum* (Groot Bruinderink *et al*. 1994). Hence these habitats may also be important to Wild Boar although again they should be regarded as suboptimal. Water is essential to Wild Boar survival, therefore any habitats must contain water bodies. The availability of water is unlikely be a limiting factor in Scotland.

Habitat patch size

The size of a habitat patch required to maintain a viable population of boar is of great importance and in part will depend on the 'carrying capacity' of the environment. Jezierski & Myrcha (1975) estimated a stocking density of 2 individuals km^{-2} in their study in Poland and Spitz (1986) has suggested that populations living at densities of 5 individuals km^{-2} may occupy an area of 500–700 km^2. The density of Wild Boar, can however, vary dramatically. For example, Andrzejewski & Jezierski (1978) reported that in the Kampinos National Park, Poland, population density peaked at 10 individuals km^{-2} as the artificially increased food resource triggered exponential growth in the population. However, densities declined to 1.2–1.6 individuals km^{-2} when factors such as increased juvenile mortality, decreased reproductive capacity and increased emigration began to take effect. The quality of the habitat occupied by Wild Boar also affects densities. For example, Jedrzejewska *et al*. (1994) reported that in the Bialowieza National Park, Poland, Wild Boar densities were highest in 'pristine' as opposed to 'exploited' forest environments, where silvicultural treatments and supplementary feeding had not reduced the carrying capacity of sites. In the pristine forest dominated by mature Oak (*Quercus* spp.), Hornbeam (*Carpinus betulus*), Lime (*Tilia cordata*) and Field Maple (*Acer campestre*), Wild Boar densities were 2–5 times higher than in the exploited forest, dominated by Spruce

(*Picea* spp.) and Pine (*Pinus* spp.). Winter populations reached 23.8 individuals km^{-2} following a good acorn crop, and averaged 5.9 individuals km^{-2} in the long term, whereas in the exploited forest densities averaged 3.5 individuals km^{-2}. The authors concluded that this difference was attributable to differences in food availability, with oak trees covering 20% of the pristine forest area yielding on average 16.4 tonnes of acorns km^{-2} but coniferous species covering 54% of the exploited forest yielding no edible seeds. Given the densities of boar observed in these European studies we suggest that it will be reasonable to expect maximum Wild Boar densities in Scotland of 3–5 individuals km^{-2}.

Management

The spatial distribution of Wild Boar must also be considered, given the potential conflict they may have with human land use. Wild Boar will move from the core area of their home range to surrounding areas such as meadows, grasslands or agricultural land, especially when energy-rich food is scarce (Mackin, 1970; Andrzejewski & Jezierski, 1978; Meriggi & Sacchi, 1992) and will use crops heavily when available, hence it would be undesirable to introduce them close to agricultural areas. Proximity to urban areas will also be undesirable given the high possibility of road accidents.

Home range estimates of Wild Boar vary widely, although the actual size and configuration of a range will be influenced by many factors. For example, ranges can increase when populations are hunted (Boitani *et al*., 1994; Maillard & Fournier, 1995). However, a number of European studies have shown that mean home ranges are generally small, and of the order of 4 km^2 (Spitz & Janeau, 1990). Daily and seasonal travelling distances also vary widely, but again the majority of European studies report small distances, up to 15 km (Spitz, 1986; Cargnelutti *et al*., 1991). Given the variability of Wild Boar movement it is difficult to define an optimum distance of potential release sites from intensive agriculture or urban areas. Ideally release sites should be as far as possible from human land use and in this study we suggest that release sites should, *at the very least* be 5 km or more from areas of intensive agriculture and urban land use. Finally existing conservation designations should also be considered, as these may influence the management of a newly reintroduced population.

2 IDENTIFYING SUITABLE RELEASE SITES USING A GEOGRAPHICAL INFORMATION SYSTEM (GIS)

Introduction

Having identified the criteria which can be used to judge the quality of release sites, the second stage of our study examines the availability of potential release sites in Scotland using a Geographical Information System (GIS). GIS has become a useful tool for site assessment in feasibility studies and is currently being employed by SNH in a feasibility study concerning the Beaver (M. Cooper, pers. comm.).

Increasingly, GIS methodologies are employed by ecologists to predict the likely distribution of an animal species from an assessment of spatial data describing environmental or other features where the species is known to occur. This has involved the application of criteria ('rules') through GIS overlay facilities to identify the co-occurence of the specified conditions. These rules are usually derived from known general relationships and the resulting model is generally descriptive (Aspinall, 1992).

Our aim was to use a GIS to identify habitat patches in Scotland that would be suitable as release sites for Wild Boar. Given this information we could then specify the expected carrying capacity of these sites, based on our expectation that maximum Wild Boar densities in Scotland could reach 3–5 individuals km^{-2}.

Table 1 Criteria used in the GIS identification of suitable release sites for Wild Boar

Criteria		Value
1	Fundamental habitat requirement:	a. 10 km^2
2	Deciduous, seminatural and mixed woodland, including a 1-km buffer of heathland, grassland or seminatural pine	b. 20 km^2
		c. 50 km^2
		d. 100 km^2
		e. 200 km^2
		f. 500 km^2
3	Distance of habitat patches to urban settlements	≥5 km
4	Distance of habitat patches to agricultural land	≥5 km
5	Distance of habitat patches to major roads (motorways, A and B roads)	≥1 km

Methods

We used published data on the biology and habitat requirements of Wild Boar, in order to devise a set of simple criteria that, firstly, defined habitat patches that would fulfil the species' requirements, and, secondly, would minimize mortality and conflict with humans. These rules are summarized in Table 1.

We defined the fundamental habitat requirement for Wild Boar as deciduous, seminatural and mixed woodland. Since Wild Boar can move from woodland to open areas, we also included a 1-km buffer around patches of suitable woodland. The buffer contained any heathland, grassland and seminatural pine, since Wild Boar often utilize such habitats for food and shelter. The fundamental habitat patch was then further categorized as a 'patch size' (shown in Table 1), of which there were six 'values' or areas (chosen arbitrarily). Hence in the GIS analysis we would be able to identify the number of patches of the six different size classes we had chosen. To minimize mortality and conflict with humans, we specified that habitat patches should be located *at least* 5 km or more (an arbitrary distance) from urban and agricultural areas (arable) and at least 1 km or more from major roads (A class, B class and motorways). Sites with conservation designations were also included in the GIS.

These criteria were then associated, through GIS overlay routines, with information on the digitized land cover of Scotland LCS 1988 (MLURI, 1988), the location of roads (A class, B class and motorways) and conservation designations (in the form of vector datasets or *cover types*), to identify the co-occurence of the specified conditions. This employed ARC/INFO® 7.0.1. software. We used 9 of the 24 single cover types available in the LCS 1988, and 6 of the nationally significant mosaics (see Appendix 1), which included woodland, heathland and grassland habitats, and arable and urban land use.

Results

Table 2 shows the number of different sized suitable habitat patches that were identified by the GIS, and Fig. 1 shows the locations of those areas that are deemed suitable release sites for Wild Boar as defined by the quality criteria used in this study. The sites in Fig. 1 have been classified by 'expected maximum carrying capacity' according to the expected maximum density of 3–5 individuals/km^2 in Scotland.

Figure 1 and Table 2 show that there are only 2 patches large enough to support 600–1000 Wild Boar. These are found in the Highlands; in Ardgour between Loch Eil and Loch Linnhe and Moidart, west of Loch Shiel. There are also 2 patches large enough to support 300–500 Wild Boar, one bordering Loch Ness, and one north of Loch Hourn in the Highlands.

The GIS also identified 30 patches large enough to support 150–250 Wild Boar, 20 of these are found in the Highlands, two notable sites are found bordering Loch Ness, and in Speyside. In addition others are found at Deeside in Grampian, at Glen Esk in Tayside and at Lammermuir

Table 2 Number of different sized habitat patches available in Scotland

Size of patch (km^2)	Expected maximum carrying capacity of animals at each site	Number of patches identified
≤10	30–50	> 200
≤20	60–100	75
≤50	150–250	30
≤100	300–500	2
≤200	600–1000	2
≤500	1500–2500	0

Information taken from ARC/INFO® database. Range calculated using the expected density of 3–5 individuals km^{-2}

in the Borders. Seventy-five patches large enough to support 50–100 Wild Boar were identified, and many more smaller patches, supporting a maximum of 50 Wild Boar, are scattered all over Scotland. Figure 1 also shows that a significant number of smaller patches are within close proximity of each other. The close proximity of the smaller patches, for example, those found close to Loch Ness and in Deeside and Glen Esk suggest that were these areas to be considered together, they would also be suitable sites for reintroduction.

One possible constraint to all the sites identified is the proximity of major roads, for example, nearly all of the largest sites are bounded by major roads. Finally, it must be noted that few of the suitable sites identified are found to be currently covered by conservation designations.

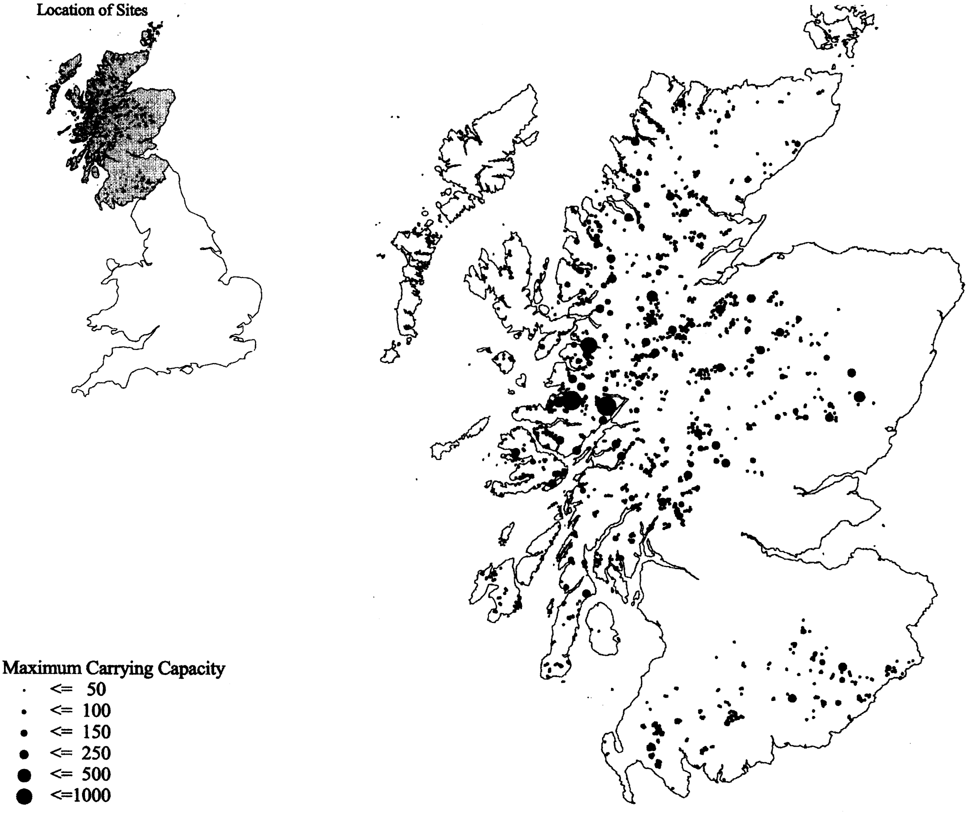

Fig. 1 The land cover of suitable sites for Wild Boar in Scotland, classified by their expected maximum carrying capacity (animals per site).

3 A POPULATION VIABILITY ANALYSIS USING RAMAS/AGE

Introduction

Having established that there are large sites in Scotland that meet our quality criteria, the final stage of our feasibility study considered the question, 'what is the smallest size that a Wild Boar population can be to retain a reasonable chance of surviving for some time in the future?' Assessing the likelihood that a population will persist for some arbitrary chosen time into the future is known as 'population viability analysis' (PVA). Generally PVA is any systematic attempt to understand the processes that make a population vulnerable to extinction (Primack, 1993), but in practice the term really refers to the use of computer models to simulate the likely fate of a population and to estimate minimum viable populations (MVPs).

PVA is a particularly useful approach in assessing the feasibility of a reintroduced population. Small populations, such as those of newly reintroduced animals, are inherently more at risk from demographic and environmental stochasticity than are larger populations (Caughley, 1994). PVA can therefore be used to test the viability of various population sizes for given environmental conditions.

Computer simulations have been a popular choice for conducting PVAs and several models are available. One such model is RAMAS/age (Ferson & Akçakaya, 1991), and it has been used to model many populations including the Red-Cockaded Woodpecker (*Picoides borealis*) (Maguire, Wilhere & Dong, 1995), the Grizzly Bear (*Ursus arctos horribilis*) (Mills *et al*., 1995) and the Brook Trout (*Salvelinus fontinalis*) (Power & Power, 1995).

RAMAS/age is a modelling technique for the development and analysis of single species population models. It allows the computation of the dynamics of a model population using a modified Leslie matrix approach so that time proceeds in fixed unit steps (Ferson & Akçakaya, 1991). A RAMAS/age model may include age structure, density dependence, and demographic and environmental stochasticity. Specifically, it incorporates nonlinearity in density dependence, and emulates demographic and environmental stochasticity using observed means and variances of biological parameters such as survival and fecundity (Ferson & Akçakaya, 1991). RAMAS/age simulates the population over a set period of time, estimates how many individuals there will be in the population or in any age class in the future and computes the probability that the population will exceed or fall below some threshold size.

Our aim therefore was to assess how many animals would be required in an initial 'release population' under a chosen acceptable level of risk of loss of the population. There is no definitive level, but a ≤ 5% risk of extinction over a 50-year period was chosen, 50 years being deemed an appropriate timescale for a management programme.

Methods

Using the published data on the biology and habitat requirements of Wild Boar, and the size of suitable release sites available, we used RAMAS/age to assess the percentage probability of extinction for different populations with particular characteristics.

The GIS used in this study revealed that in Scotland there are two sites that we would expect to support 300–500 animals at capacity and two sites that we would expect to support 600–1000 animals. Therefore, for modelling purposes we defined two 'carrying capacities' based on the mid point of these ranges, i.e. 400 and 800 animals.

In the first stage in the modelling we developed two 'basic' deterministic models, based on suitable release sites that we would expect to support a maximum carrying capacity of 400 animals (**Model A)** and 800 animals (**Model B)**. Vital rates, in this case age-specific fecundity and survival, maximum age (7 years), and sex ratio (1 : 1), were determined using data from a Czechoslovakian population (Kratochvíl, Kux & Pikula, 1986), shown in Appendix 2. We assumed that release populations would consist of Wild Boar in their third year of life, as individuals of this age have high survival probabilities. Each model also included density-dependence, using the logistic function, given by the equation:

$$Z = E\,[1 + r\,(K - E/K)] \quad (1)$$

where Z represents recruits to the population, E represents individuals before they enter the zeroth age class, r determines the strength of the nonlinearity in the logistic function, and K determines the greatest recruitment possible

In the second stage in the modelling we extended the two basic models to incorporate two different levels of demographic and environmental stochasticity. The first, **Scenario 1**, included only demographic stochasticity, and the second, **Scenario 2**, included both demographic and environmental stochasticity. Environmental stochasticity was determined using coefficients of variation (CVs), and these were specified for zero age class (that is Wild Boar in their first year of life) and adult survival, and fecundity, from the vital rates defined in the basic model. Each model was simulated 100 times. The values used for the parameters of the logistic function and the CVs specified in all the models are summarized in Appendix 3.

In summary, four sets of models were simulated to determine the size of the 'release population' required at the suitable sites identified by the GIS: model **A** (scenario **1** and **2**), and model **B** (scenario **1** and **2**). Each model was run with six different initial population sizes namely 5, 10, 25, 50, 75 and 100 animals, in their third year of life, and a 1 : 1 sex ratio.

Results

The population growth of the two deterministic model populations, A and B, together with a population growing without density dependence are shown in Fig. 2. Figure 3(a) and (b), show the percentage extinction probabilities under the four sets of models used in this study. Model A, Scenario 1, assumes a release area with an expected maximum carrying capacity of 400 animals, populations subject to natural demographic stochasticity, and 5, 10, 25, 50, 75 and 100 animals released. Releases involving 10 or more animals suggest a less than 5% risk of extinction over 50 years. In Model A, Scenario 2 (where both demographic and environmental stochasticity is included) the release of 50 or more animals would suffer the same extinction risk. Hence under Scenario 1, release populations of less than 10 animals have extinction probabilities that exceed the defined 'acceptable risk'. Under Scenario 2, release populations of less than 50 animals have extinction probabilities that exceed the defined 'acceptable risk'.

Model B, Scenario 1 assumes an area with an expected maximum carrying capacity of 800

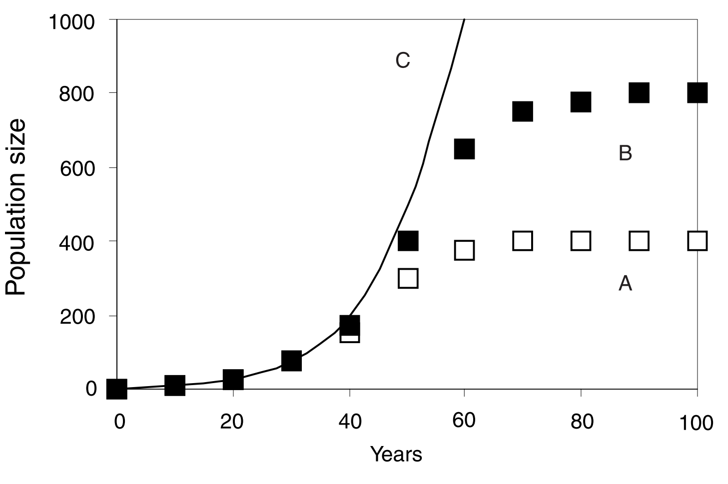

Fig. 2 Growth trajectories of deterministic models A (expected maximum carrying capacity of 400 animals) and B (expected maximum carrying capacity of 800) with density dependence, and C without density dependence.

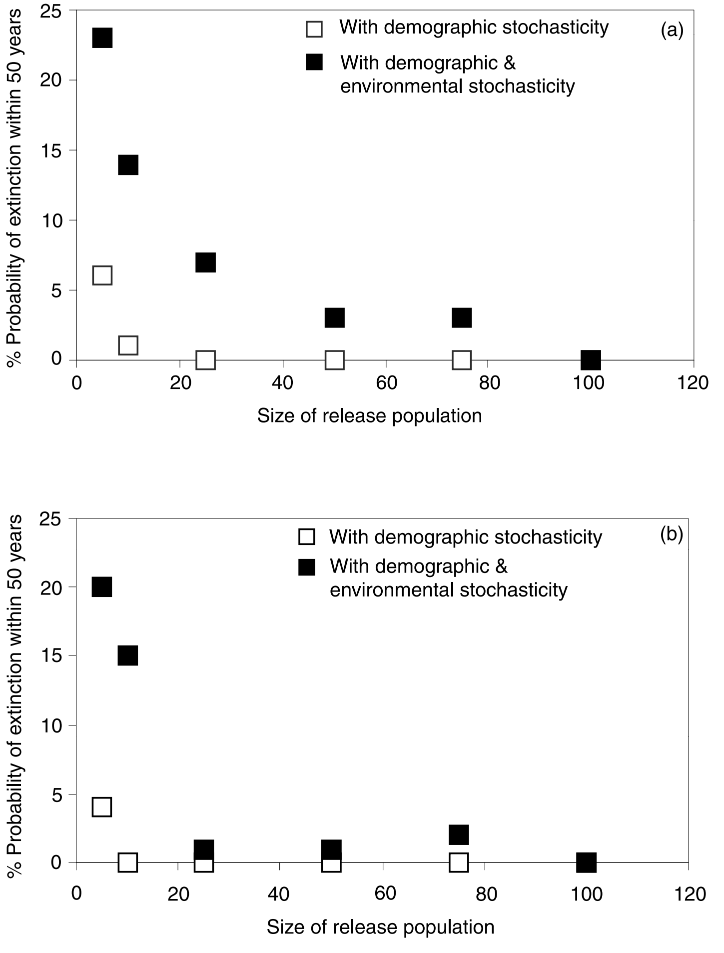

Fig. 3 The percentage probability of extinction of different 'release populations' under Scenario 1, a population modelled with demographic stochasticity, and Scenario 2, a population modelled with both demographic and environmental stochasticity. (See Appendix 3 for the logistic function and CV values). (a) At a site with an expected maximum carrying capacity of 400 animals (b) At a site with an expected maximum carrying capacity of 800 animals

animals, populations subject to natural demographic stochasticity, and 5, 10, 25, 50, 75 and 100 animals released. In this case releases involving 5 or more animals are shown to have a less than 5% risk of extinction over 50 years. However, in Model B, Scenario 2 (where both demographic and environmental stochasticity are included), the same risk would require ≥25 to be released.

DISCUSSION

The GIS shows that, in total, there are 1309 suitable habitat patches for Wild Boar available in Scotland. Only four sites are of significant size, i.e. two sites capable of supporting 300–500 animals and two sites supporting 600–1000 animals were identified, each in the Highlands. We suggest that these are the most suitable sites for a reintroduced population due to the large number of animals they can potentially support.

We chose to model populations at two patch sizes, i.e. 400 animals and 800 animals to approximate the largest sites that had been identified by the GIS, described above. Different sized release populations were modelled under demographic stochasticity only and under both demographic and environmental stochasticity. Demographic stochasticity, that is variation in vital rates at the level of the individual, can cause populations to fluctuate in size (Gilpin & Soulé, 1986; Menges, 1992). Demographic stochasticity arises from the fact that individuals exist as discrete entities and, for instance, can have one or two offspring but not 1.5. It is usually negligible in large populations but is especially pronounced in small populations and K-selected species. Environmental stochasticity, that is random variation in biological communities and the natural environment, can also cause fluctuations in the population size of a species. As environmental conditions change over time, a population's vital rates will change too since they are partially a reflection of the suitability of the environment for growth. Hence in contrast to demographic stochasticity, environmental stochasticity affects all individuals in the population.

The results of the PVA showed that including environmental stochasticity into the models, predictably, resulted in greater extinction probabilities for a given release population. More specifically, with the inclusion of environmental stochasticity to a model including demographic stochasticity, larger release populations were necessary; 50 rather than 10 animals at a patch with a carrying capacity of 400 animals, and 25 rather than 5 animals at a patch with a carrying capacity of 800 animals. Our results support the modelling efforts of Menges (1992), who showed that environmental stochasticity is generally more important than demographic stochasticity in increasing the probability of extinction for a given release population. We suggest that the models that also include environmental stochasticity are the more realistic. This is due to the fact that a reintroduced Wild Boar population, as well as being subject to demographic stochasticity, will certainly be subject to the effects of random variation in the natural environment, for example changes in resources, climatic conditions or even infrequent catastrophic events, such as the outbreak of disease.

It must be emphasized that these results *do not* provide a prediction of the *precise* number of animals required in a release population. Rather, the results should be taken as providing an estimate of the number of animals that will be required to ensure a reasonable chance of success in a reintroduction programme. When relating the predictions of the GIS to those of the PVA, if populations are to be viable over a 50-year period, we conclude that one should consider releasing approximately 50 animals with a 1 : 1 sex ratio in the suitable sites identified.

Although we did not model populations in the PVA for those sites with an expected maximum carrying capacity lower than 300 animals, many of the suitable smaller sites are found to be in close proximity to each other. Wild Boar is a wide ranging species having good dispersal abilities. Where small patches are close to each other, and when considered together, i.e. the effective carrying capacity of the site is greater than 300 animals, then we suggest that such areas could also be considered as suitable release sites, as reintroduced populations will be viable over 50 years. However, it is important to consider whether it is actually *possible* for Wild Boar to move between sites. With respect to the smaller sites identified, the results of the GIS suggest that in some cases the presence of roads may inhibit movement between sites, if they are bordered by high physical barriers for example. At Loch Ness the A82 may prevent movement between the suitable sites bordering the Loch. Similarly, at Speyside the A95 and A9 may prevent movement between suitable sites. At Deeside, the A93 runs straight through the suitable sites identified, furthermore towns are nearby. Similarly other 'barriers' such a walls or fences may inhibit movement between sites, although Wild Boar are large animals and able to demolish most fencing. A GIS cover of water bodies, such as streams, rivers and Lochs was not used in this study and therefore the spatial distribution of these is not known. However, Wild Boar can swim very well, are thus well able to cross rivers and lakes. This study reveals therefore that whilst potential suitable sites can be identified on a large scale, a feasibility study must examine the sites and their surrounding region at a finer spatial scale. It is certainly possible to investigate areas of interest more closely using a GIS, and therefore this study recommends that more detailed investigations are carried out. Specific land-use characteristics, that may facilitate or constrain movement, may then be considered more closely. For example, the travelling routes of Wild Boar are generally sheltered by tree lines and wood perimeters (Genov, 1981b), and the presence of such habitat features will presumably encourage movement between sites in certain cases. Therefore, identification of such features either using a GIS or Ordnance Survey (OS) maps may also be important. Hence, we may further conclude that some of the smaller patches may also be considered as suitable release sites, as long as Wild Boar have the potential to move freely between them, and do not come into conflict with human land use.

In this study we have used biological information predominately from published information on European Wild Boar populations, assuming that environmental conditions on the Continent will best resemble those found in Scotland. However, it is important to note that the environmental conditions found on the continent are not totally representative of the conditions found in Scotland. Several factors may be important. For example, in many cases the diet of Wild Boar is influenced by human activities such as agriculture and supplementary feeding; crops may account for a great proportion of the diet of Wild Boar (Genov, 1981a,b). Similarly supplementary feeding is commonly used to improve the condition of Wild Boar in areas where they are regarded as game (Groot Bruinderink *et al.*, 1994). Hunting has a great influence on the behaviour of Wild Boar, altering habitat use, activity patterns and home range size, at least periodically (Singer *et al.*, 1981; Massei, 1995). Furthermore, climatic conditions in continental Europe, especially winter weather conditions, may be more extreme than those in Scotland. For example, in the Balowieza National Park, Poland, mean January temperatures can range from – 13.4–1.3 °C (Jedrzejewska *et al.*, 1994), compared to 0–6 °C (Met. Office., 1997) on the West Coast in Scotland where the potential suitable sites are located. In the Kampinos National Park, Poland, snow cover ranges from 66 to 103 days (Jezierski & Myrcha, 1975) compared to 3.6 in Scotland (Met. Office 1997). Presumably a newly reintroduced population will be not be hunted in the short term, or be given supplementary feed, in the long term. In the initial stages of a reintroduction programme, additional factors such as stress caused to animals during transportation and disruption to the social organization and behaviour of animals removed from the wild may also be of importance. The behaviour of the animals may be affected due to the disruption of their social organization. Therefore, the factors described above may all have implications for the results that have been presented in this study. A reintroduced population could actually have higher extinction probabilities than those predicted by the PVA in this study. However, populations will remain viable in the long term (as the PVA demonstrated) due to several aspects of the ecology of Wild Boar which will account for this uncertainty. For example, the diverse diet and good dispersal abilities of the species means that they adapt efficiently to sudden and unpredictable resources, by searching for alternative food resources. Secondly, although piglet survival is low, animals that do survive to adulthood have high survival probabilities and when combined with high fecundity, the intrinsic rate of growth in Wild Boar populations is high.

In this study we have implied that the suitable release sites identified by the GIS have a ‘carrying capacity’. This notion is misleading and implies that a reintroduced population, once established, will reach and remain at some kind of equilibrium size, which in reality may not the case. If population densities reach the expected maximum number of animals, in response to the decrease in available food resources and space, not only may mortality increase, but some animals may also disperse from these sites to new areas (Belden & Pelton, 1975; Singer *et al.*, 1981). Dispersal to new areas is usually led by subadult males (Cargnelutti *et al.*, 1992). The incentive to disperse from these sites may be even more significant if Wild Boar find cultivated crops within their home range. Therefore, although the two largest sites can support a significant number of animals, ultimately a proportion of animals may not be contained within these sites alone *if* the capacity is reached. Given this, one could argue that the 5 km buffer defined in this study was rather small, given the dispersal ability of Wild Boar. However, 5 km was chosen as a *minimum* distance, and therefore it does not mean that the potential suitable sites were actually this close to human land use. In fact on closer inspection of the site locations on an OS map, neither of the two sites that we considered as potential suitable release sites were less than 10 km from human land use. In addition, there is little intensive agriculture on the West Coast of Scotland and it is sparsely populated, therefore for these two sites at least, conflict with human land use would be minimal. Subsequently we conclude that the choice of a 5-km buffer was reasonable.

The results of the present study contrast to those of a study by Howells & Edward-Jones (1997), who concluded that the goal of establishing a self-sustaining population of Wild Boar in Scotland was unrealistic in the short term. More specifically they identified a founding minimum viable population (MVP) of 300 animals, an estimate far higher than the predicted 25–50 animals of this study, and suggested that no woodland in Scotland was large enough to support this MVP alone. The only suitable habitat they considered was woodlands containing seminatural stands. In addition, the study modelled populations with genetic stochasticity using the package VORTEX (Lacy, 1993), as well as demographic and environmental stochasticity.

Several reasons account for the different conclusions reached in these two studies. (i) As shown by previous studies, Wild Boar use a number of habitats, other than woodland. When taking more habitat types into account, the sites available for reintroducing Wild Boar increase considerably in number and area. (ii) Although small populations may be theoretically subject to rapid extinction due to the loss of genetic variability, the key question is whether genetic variability (especially inbreeding depression) will be important in Wild Boar. To our knowledge there is presently no published evidence for inbreeding depression in Wild Boar populations. Demographic and environmental stochasticity should therefore be far more important than genetic stochasticity for a newly reintroduced population of Wild Boar. When Howells & Edward-Jones (1997) model without inbreeding depression, the estimate of 75 animals as a founding population is much closer to our prediction. (iii) Some of the values used by Howells & Edward-Jones (1997) in their model, such as mortality rate and litter size, were based on a small number of studies and differ from ours: for example, a mean litter size of 9 piglets used in their Vortex model is inappropriate, as it is almost double the average litter size of Wild Boar.

In this study, we have shown the value of a GIS as a tool for assessing the availability of suitable release sites for Wild Boar. First, GIS allows investigation of a large area, in this case the whole of Scotland. Secondly, the output of the GIS offers a simple and speedy visualization of those areas that may be suitable. Thirdly, because GIS can simultaneously consider a multitude of factors that determine the suitability of a site, it can be a far superior way of investigating an area to traditional map-based surveys; these often require a considerable amount of time and effort. Hence, a GIS has many advantages, but there are some important limitations to consider. The rules used to identify the co-occurence of the specified conditions will ultimately determine the quality of the resulting output of the GIS. Therefore, one must be sure that these criteria best define the habitat requirements of Wild Boar. The criteria must be valid and the results obtained must seem reasonable. We believe that the rules used in this study do best define the habitat requirements of Wild Boar, given the available biological information. As just one example, by including a buffer around woodland patches we have taken into consideration the fact that Wild Boar, when mast is scarce, will move from such patches to alternative habitats in search of alternative food resources. Furthermore, the GIS used in this study is restricted by the number of ‘cover types’ that are available for spatial analysis. For example, the structural and species diversity of a woodland is an important consideration when assessing the suitability of habitats for a Wild Boar population. Structurally diverse woodlands offer great sheltering potential, a vital habitat requirement of Wild Boar. Because neither the structure of woodlands or the species diversity of woodlands are represented in the form of a GIS cover type, important aspects of the available habitats in Scotland are lacking in the final output. Hence, including other criteria in the GIS analysis, such as the structural diversity of woodlands, may have led to a different conclusion. Finally, it is important to stress that whatever the quality of the GIS output, those sites identified as suitable must always be investigated by further field surveys, so that particular features of the site can be identified and evaluated. Perhaps the value of GIS is that it leads the investigator quickly and easily to a stage where field studies can be considered.

The PVA, using RAMAS/age also proved to be a useful tool for assessing the number of animals required in a release population. RAMAS/age can simulate biologically realistic populations by allowing the investigation of complex population models, which incorporate the action of density dependence and the effects of demographic and environmental stochasticity. Traditionally PVA has approached the problem of persistence by considering simple birth and death models (Soulé, 1987). As RAMAS/age computes the probability of extinction for different sized populations, it suggests the minimum number of Wild Boar required in a release population. Although there are many advantages to RAMAS/age a number of important limitations also need to be considered. The data required to parameterize the models in RAMAS/age can be obtained from life history data, but in the case of Wild Boar (as with many other species), limited data are actually available. This is not surprising given the time and cost involved in gathering life history data for one species. As this study demonstrates, one is limited to using data from just one study. This may make it difficult to define accurately the parameters required by RAMAS/age. For example, a considerable amount of data is needed to specify the coefficients of variation used to represent environmental stochasticity. In addition, data may be incomplete. We were able to find only one study that gave data for all the vital rates required by RAMAS/age. Furthermore RAMAS/age models only density-dependence of reproductive success. In a real population, density-dependence may operate on adult survival, migration or sex ratio, but these are not explored in RAMAS/age. Although we cannot be certain that the predictions of the PVA exactly mirror the future of a reintroduced Wild Boar population, and despite the limitations of the PVA used in this study, we are confident that the biological information used to define the parameters of the models in RAMAS/age is accurate enough to provide reasonable estimates of the size of release populations required for a reintroduction programme.

The predictions of the GIS and PVA have shown that biologically, the reintroduction of Wild Boar is feasible. However, we must also finally consider the advantages and disadvantages of reintroducing Wild Boar to Scotland with respect to the biology of Wild Boar. Wild Boar will without doubt have an effect on the Scottish environment. It has been shown that in Europe, Wild Boar have considerable potential to alter the ecological character of their environment. Firstly, there is evidence to suggest that the impact of Wild Boar on ecosystems can be critical in situations involving either competition with sensitive or endangered species or damage to forest resources through rooting activities. Boitani *et al*. (1994) argue that, although this may be true in areas where Wild Boar occur as non-native populations, as illustrated in the Great Smoky Mountains National Park (Howe *et al*., 1981; Singer *et al*., 1984), it would also apply to native ecosystems. Rooting can have a strong impact on the structure and nutrient status of the soil, with consequences for tree growth (Brownlow, 1994). Predation and rooting-induced changes can lead to a decline or character change in soil animal populations. Rooting is also reported to cause erosion and accelerated leaching of calcium, phosphorus, zinc, copper, and magnesium from leaf litter and soil. In areas of rooting nitrate concentrations may increase in soil, soil water and stream water, suggesting alterations in nitrogen transformation processes (Singer *et al*., 1984). Reduction in ground layer vegetative cover in woodlands has also been reported and can be associated with a loss of diversity and changes in the relative population sizes of different plant species (Howe *et al.*, 1981). With regard to other fauna, there is evidence to suggest that Wild Boar may disturb ground-nesting birds. In Scotland, this imperils populations of Capercaillie (*Tetrao urogallus*) and Black Grouse (*Lyrurus tetrix*), listed as birds of high conservation concern (RSPB, 1996). Certainly all the impacts described above may occur with a reintroduced population, especially when we take into account the fact that Wild Boar have been absent from Scotland for many years. Hence, it may be unwise to reintroduce Wild Boar to the release sites suggested in this study if they contain rare or sensitive species. However, the fact that the sites identified in this study were not currently covered by conservation designations suggests that competition with sensitive or endangered species may actually be limited. The impacts of Wild Boar may also be beneficial. For example, Peterken (1996) has explained that although rooting by Wild Boar is conspicuously patchy, and the patches themselves are aggregated into clusters, the cumulative effect of Wild Boar may be significant but not substantial. Singer *et al.* (1984) reported that accelerated decomposition of organic matter might occur, which may increase nutrient availability and hence benefit tree growth.

The main advantage of reintroducing Wild Boar to Scotland would be to replace a species that until recently was part of the native fauna of Britain and should still be so.

This study has considered only the biological feasibility of reintroducing Wild Boar to Scotland, and concludes that it would be feasible. However, a feasibility study must also consider the desirability of reintroduction of a species within the wider, ecological and socio-economic, aspects of ecosystem protection and restoration. Hence, the 'environmental impact' of reintroduced Wild Boar must be considered; specifically whether the Wild Boar have an impact (positive or negative) on human activity such as agriculture, forestry and conservation; whether Wild Boar can be easily controlled; and the potential risk of Wild Boar introducing diseases that can affect other species. Such issues require a separate but complimentary investigation to this study.

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Appendix 1 The cover types taken from the LCS 1988 (MLURI, 1988) used in the GIS.

Single cover types	Nationally significant mosaics
Arable	Heather moorland, peatland
Improved grassland	Poor rough grassland, heather moorland
Good rough grassland	Good rough grassland, heather moorland
Heather moorland	Good rough grassland, poor rough grassland
Semi-natural coniferous	Improved grassland, good rough grassland
Mixed woodland	Good rough grassland, bracken
Broad-leaved	
Scrub	
Urban	

Appendix 2 Life history parameters used in the RAMAS/age models

Age class	Fecundity	Survival
0–1	0.0	0.580
1–2	2.5	0.219
2–3	3.0	0.586
3–4	6.0	0.626
4–5	7.0	0.367
5–6	7.0	0.273
6–7	5.0	0.334
7–8	4.0	0.001
8–9		

Data taken from Kratochvíl *et al.* (1986)

Appendix 3 Values used for the logistic function and coefficients of variation in the RAMAS/age models.

	Model A		Model B	
	Scenario 1	Scenario 2	Scenario 1	Scenario 2
Logistic function				
r	0.065	0.065	0.00325	0.00325
k	0.7	0.7	0.7	0.7
Coefficients of variation				
zero age-class survival	0.0	0.13	0.0	0.13
adult survival	0.0	0.596	0.0	0.596
fecundity	0.0	0.37	0.0	0.37