Discussion

Prediction of regions that might now support pine marten populations must depend on extrapolation from both past and present marten distribution, habitat use and behaviour. In general, many carnivores show highly flexible behaviour allowing them to exploit a diverse array of habitat types. Such flexibility means simple models of habitat associations cannot readily be used to predict distribution. However, the available evidence suggests that pine martens show much less behavioural flexibility and consequently have more demanding habitat requirements, particularly for woodland. We argue that this permits clear predictions about habitat suitability to be made.

Model assumptions and attributes

The pine marten and American marten *Martes americana* are probably conspecific and their behaviour appears identical (Hagmeier, 1961; Anderson, 1970). Consequently we have used the behaviour of American martens on which more data exists, to draw inferences concerning pine martens.

Several measures of **woodland cover** were crucial attributes in our model of regional suitability for pine martens. The population density of both pine and American martens is related to landscape woodland cover, a reduction of which has been shown to result in a decrease in density (Grakov, 1972; Soutiere, 1979; Steventon & Major, 1982). Balharry (1993) found that the territories of breeding martens encompassed about 230ha of woodland, irrespective of whether landscape woodland cover was 3.5% or 27%; only non-breeding martens had territories largely outside woodland. A similar conclusion was reach by Allen (1984) for American martens, suggesting that there may be a minimum woodland area requirement.

Pine marten distribution appears to be strongly tied to areas of high woodland cover; for example a comparison of pine marten and woodland distribution maps for France (Labrid, 1986), shows approximately 80% of records are from 10-km squares with more than 20% woodland. By contrast, in the west of Ireland and Ross-shire marten populations occur in areas where woodland cover is less than five percent (O'Sullivan, 1983; Balharry, 1993). However, populations in such areas are known to occur at very low density ($0.2/km^2$; Balharry, 1993) and are probably at the edge of viability, surviving only because persecution, poisoning and road traffic accident rates are low. Rates of such violent mortality would be higher in most parts of England and Wales (see below) and at levels which a simulation model shows that low density marten populations would not withstand (Part 3).

Hence we can be confident that 10-km squares with a woodland block size of 2 or 3 which have mean woodland cover of 8.8% and 2.2% respectively (Table 1), would probably not support viable marten populations in most of England; they would certainly not be places where reintroductions or restockings should be conducted. Squares with a block size of three, however (>500ha of contiguous woodland) and a mean woodland cover of 19.8%, might well support viable marten populations, though, as discussed below, other factors will also be important.

Martens appear to prefer woodlands with sufficient canopy to provide them with cover, interspersed with patches of rough grassland rich in field voles which are their principal prey (Pulliainen, 1981; Balharry, 1993). Rough grassland within woods seems to be especially important, as it enables martens to forage under or close to cover (Balharry, 1993). Information on the distribution of such open woodland in Britain is not available, so we had to use **field size** as a surrogate attribute to describe potential habitat quality.

Field size is a measure of landscape enclosure (Rackham, 1986). More enclosed landscapes may generally support a greater diversity and biomass of the pine martens principal foods: there is a greater cover of unimproved grassland (c.f. Cresswell, Harris & Jefferies, 1990), the habitat of field voles (Corbet & Harris, 1991); there is a greater length of edge habitats supporting high densities of passerine birds and rabbits *Oryctolagus cunniculus* (Thompson & Worden, 1956), which may also be important prey (Balharry, 1993; and *pers. comm.*); and edge habitats further support berry-producing shrubs, such as *Rubus*, *Vaccinium* and *Sorbus*, which are major foods in season (Lockie, 1961; Balharry, 1993). Field size can thus be used to crudely partition areas in both lowland and upland Britain on the basis of their likely productivity of pine marten foods.

Total **length of roads** in each square was used as a measure of the likely rate of marten mortality due to road traffic accidents (RTAs). This was considered to be a more useful measure of the effects of roads than traffic density, as most mortalities of other mustelids occur on minor roads where traffic densities are low (SH & PWB, *pers. obs.*). RTAs are the most frequently recorded source of mortality of pine martens in England and Wales (D.J.Jefferies *pers. comm.*) and contribute 16% of known mortality in Scotland (Velander, 1983). Whether RTAs depress marten population size is not known. This happens with other mustelids, at least in lower quality habitats (badgers: Lankester *et al.*, 1991), though in high quality habitats populations may withstand high rates of RTAs (otters: Kruuk & Conroy, 1991). However, even a low rate of additional mortality is predicted to jeopardize the establishment of a new marten population following reintroduction (Part 3), and road density and traffic are much higher in many parts of England than in the marten's current Scottish range. Hence roads are likely be an important source of mortality affecting the viability of reintroduced marten populations.

Vulnerability to persecution

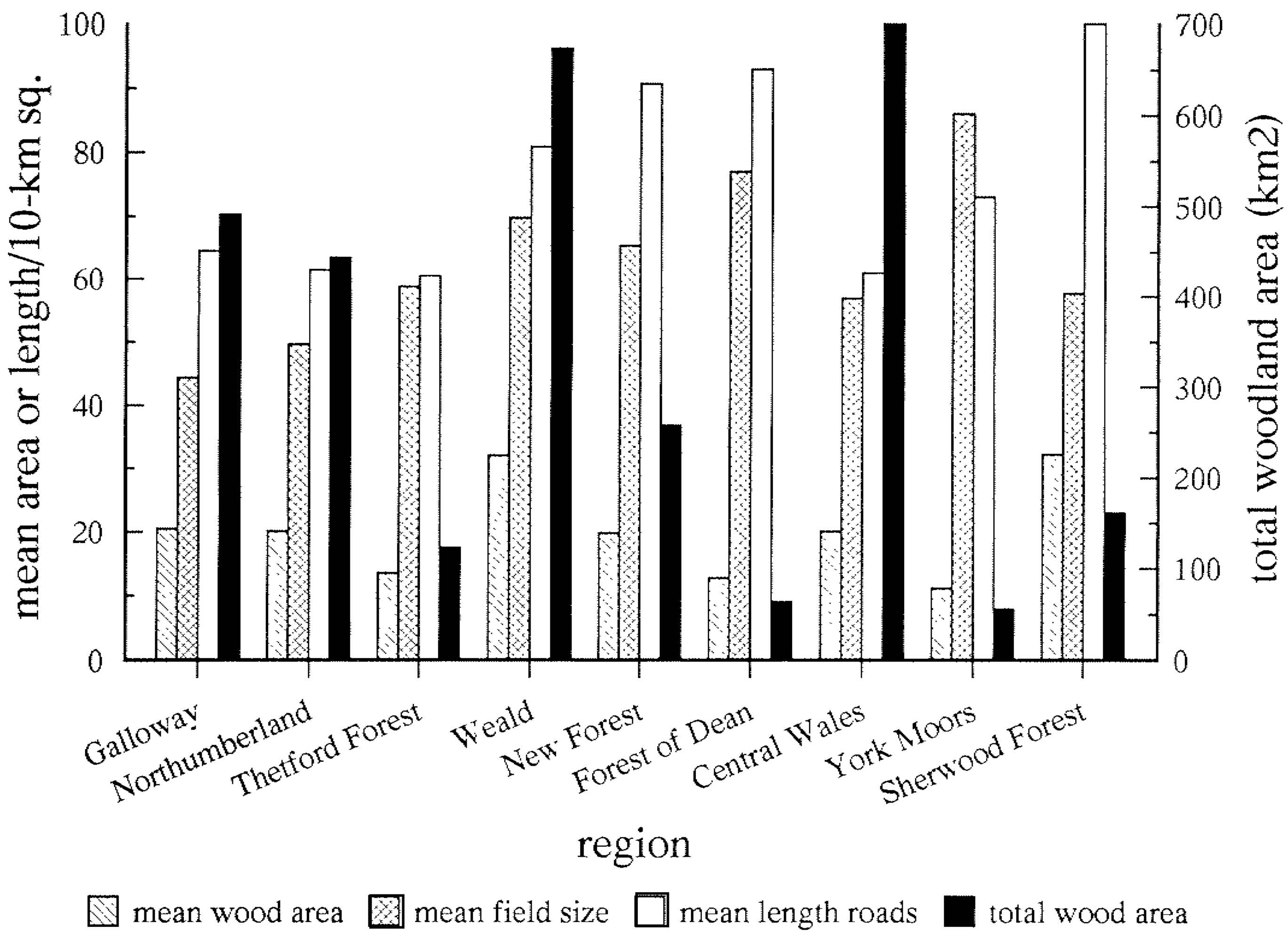
Inflexible territorial behaviour seems to enhance the vulnerability of marten populations to persecution (Balharry, 1993), which was the direct cause of past extinctions (Langley & Yalden, 1977). Martens are easily trapped or snared and would be caught in Fenn traps that are widely set in England but not in Scotland. Mortality due to inadvertent persecution would be likely to cause high mortality in England, but its potential prevalence was very difficult to measure. The best available information came from the Game Conservancy's surveys, which may not record the distribution of people who undertake more limited part-time gamekeeping (Tapper, 1993), which could nevertheless have important impacts on marten populations. Detailed field surveys of gamekeeping activity would be required before translocations could go ahead (Part 5).

Suitability of the nine regions

A new marten population could withstand only a low rate of violent mortality due to RTAs or inadvertent trapping, to which it would remain vulnerable (Part 3). Translocations should thus only be attempted to regions likely to support high marten densities and where violent mortality would be low.

In the following discussion it is important to appreciate that the area names used refer to *regions* that are sometimes more extensive than the name implies. For example the Weald region includes parts of the South Downs and the New Forest region encompasses tracts of Hampshire and Dorset outside the New Forest *per se*.

Fig. 4. Attributes of nine regions defined using TWINSPAN and contiguous 10-km squares. Attributes used in the TWINSPAN are shown (mean woodland area, mean field size, mean road length) per 10-km square, together with the total woodland area for the region.



The **Galloway** and perhaps **Northumberland** regions provide an example of habitats known to be suitable for martens against which to assess regions further south. They both have large areas of contiguous woodland and, assuming that each breeding marten territory requires 230ha of woodland (see above), might each sustain breeding populations of about 200 individuals (Table 3). Both regions probably support high biomass of potential marten foods (c.f. small field size) and low rates of mortality from RTAs and persecution are probable. If martens cannot survive in these places it is unlikely they would do so further south, unless their population productivity was higher. This emphasises the need to determine whether martens have existed in Northumberland in the recent past and now declined (Part 1). Understanding the reasons for any such decline would be a vital prerequisite for translocations elsewhere (Part 5).

Unsurprisingly the TWINSPAN classification showed that parts of **central Wales** have similar attributes to Galloway and Northumberland. A very large expanse of contiguous woodland is centred on the Cambrian Mountains, which might support about 350 pine martens. By analogy with Galloway, martens should thrive in this area and indeed may still be present. The Countryside Council for Wales will commission a survey of martens in 1994 and conservation measures must await the results of this work. Nevertheless, it is clear that the area of woodland and low potential rates of mortality from gamekeeping and roads (gamekeeper density $0.1/km^2$, mean road density, 40km/10-km square) make central Wales an ideal region to pursue the reintroduction or restocking of pine martens.

Thetford Forest, suggested by Yalden (1986) as a potential area for reintroductions, has very similar attributes to the two northern sites, but covers a small area and is mostly in Norfolk, where there is a high density of gamekeepers (Table 3). Release sites away from persecution pressure might be found, for example on the Ministry of Defence Stanford Battle Area, but a marten population in the region would have little future. We suspect a reintroduced population would not reach viable size before both the area of suitable habitat and anthropogenic sources of mortality limited its growth. Furthermore English Nature and the Forestry Commission are currently mounting a conservation programme for red squirrels *Sciurus vulgaris* in Thetford Forest. Pine martens are widely believed to prey on red squirrels, but in fact there is scant evidence to support this idea (Pulliainen, 1981). Nevertheless, they might not be welcome in Thetford while the squirrel population there remains in jeopardy. The Institute of Terrestrial Ecology at Banchory are currently studying the influence of martens on red squirrel populations. We suspect that squirrel populations at very low density might be depressed by marten predation, as those of capercaille may be reduced by fox predation (M. Gorman, *pers. comm.*), but other limiting factors are likely to be more important. Several factors thus at present militate against Thetford Forest as a potential region for reintroductions.

In the south of England, the **Weald** region is unique in terms of its high woodland cover and very extensive area of contiguous woodland, being second only in size to that of central Wales (Table 3; Fig. 4). There is enough woodland cover for a potential breeding population of nearly 300 pine martens, but a full understanding of prey availability and potential rates of violent mortality in the region is needed. Field sizes in the region are moderately small, implying heterogeneous habitats and perhaps abundant prey for martens. However deciduous Wealden woodlands may lack areas of rough grassland, that are a common feature of thickets of regenerating conifers in Galloway and Northumberland. This probably means that field vole densities within woods on the Weald are lower. Harris *et al.* (1994) estimated that 55% of the field vole population of Britain is in Scotland, 22% in Wales and only 23% in England. Since England has the largest land area, field voles must be more sparsely distributed there.

However, the Weald probably supports a high biomass of alternative prey such as rabbits and passerine birds, which the pine marten may readily take (c.f. Pulliainen, 1981; Balharry, 1993). Field surveys of the prey base are clearly needed (Part 5). If the prey base is large, a reintroduced marten population might withstand the high levels of violent mortality (due to a moderate to high density of gamekeepering and roads) that seem likely in the Weald region. In this respect the abundance of rabbits on the edges of the South Downs might be crucial. Comparative surveys of gamekeeping activity in the Weald and its influence on martens in those areas of Scotland which they are currently recolonising are essential (Part 5).

In summary, we believe that the Weald has great potential as a region to reintroduce pine martens as was suggested by Yalden (1986), but further research is essential to determine whether it really is suitable; this should include trial translocations elsewhere (Part 5).

The **New Forest** region is the only other area in England that might be suitable for a reintroduction, having broadly similar attributes to the Weald. However, it has significantly lower woodland cover and just over one-third of the total contiguous woodland present in the Weald. It also has the third highest density of roads of any region examined, a high density of gamekeepers ($0.6/km^2$) and may also have a rather low density of field voles due to heavy grazing pressure (Putman, 1986); though in places fenced exclosures around conifer plantations might provide vole-rich patches. Intensive use for outdoor recreation might also make the New Forest unsuitable for martens, if as has been suggested, they cannot tolerate high levels of disturbance as has been suggested (Velander, 1983). The suitability of the New Forest region could be investigated further if a reintroduction to the Weald went ahead and was successful.

All other regions of contiguous woodland resolved by our analysis are too small to be considered as suitable for pine martens at present. This includes the **North York Moors** where the 1987-1988 survey reported pine martens present, but where reliable local mammalogists have no evidence of martens. Our results suggest that this region would support only about 25 breeding martens, even if they occurred at high population density ($0.5/km^2$). The probability that such a small population would persist cannot be high. Similarly it is noteworthy that the Lake District has only four 10-km squares which encompass large areas of contiguous woodland (Fig. 3). Such a low density of woodland, fragmented by high ground, would seem unlikely to have been the refuge for a relict marten population that was apparently present until recently (D.J. Jefferies, *pers. comm.*). However, it is known that martens were present in the Lake District, at least in the last century (Millais, 1905). Perhaps the loss of ancient woodland (Spencer & Kirby, 1992), the huge increase in road traffic and in outdoor recreation since then may have promoted the extinction of a population that was probably already at low density due to lack of woodland.

Yalden (1986) suggested that the Weald, Thetford Forest and the Quantocks might be suitable areas for pine marten reintroductions. D.J.Jefferies (*pers. comm.*) has further suggested that parts of Devon or the Wyre Forest (near Kidderminster) might be suitable. Our results show that the Quantocks, Devon and the Wyre Forest have only small areas of contiguous woodland and would thus probably not support viable marten populations. On this basis alone they would not be suitable for first attempts at marten reintroductions.

PART 3: FACTORS AFFECTING THE SUCCESS OF A REINTRODUCTION OR RESTOCKING PROGRAMME

The sections on public attitudes were compiled with help from John A. Burton

Introduction

Despite the large number of translocations of scarce species that have been conducted, there is little specific information from which to predict whether a proposed translocation programme would succeed (Griffith *et al.*, 1989). However, successful translocations seem often to result from release methods tailored to the behaviour of particular species (Part 4; Bright & Morris, 1994) and from the rapid growth of founder populations (Stanley Price, 1989). In general, two types of factors will affect the success of translocations: ecological ones, which will be mostly unmodifiable, and anthropogenic factors, many of which might be modified. Kellert (1985) suggested that anthropogenic influences have received insufficient attention from those involved in translocations and that such considerations would be especially important for translocations of taxa, particularly carnivores, that are perceived to impact on human activities.

There is more published information on the translocation of American martens that for most other species that have been translocated. They are one of only three species on which controlled tests of translocation techniques have been conduced (Davis, 1978; the others being swift fox *Vulpes velox* [Carbyn, Armbruster & Mamo, 1993] and dormouse *Muscardinus avellanarius* [Bright & Morris, 1994]). Since American martens and pine martens are probably conspecific (Hagmeier, 1961; Anderson, 1970), this information should be directly relevant to pine marten translocations.

In Part 2 we suggested that some regions in England are potentially suitable for pine marten reintroductions or restockings, but that success might critically depend on habitat quality and persecution pressure. There are no directly relevant field data on these factors for the regions concerned. Consequently in this part of the report, we will use three indirect approaches to assess which factors (ecological and anthropogenic) might most influence the success of a reintroduction: (1) a population simulation model; (2) the responses of countryside and conservation organisations to a questionnaire about marten reintroductions; and (3) a review of the literature on the translocation of martens and other carnivores. In this way we assess whether establishment of new marten populations would be feasible and highlight those factors about which considerably more information is needed prior to translocations. The protocol for a potential release programme is examined in Part 4.

Methods

Population model

Our model was based on data from a sample of 6448 American martens harvested from a population in Ontario, Canada between 1972-1986 (Strickland & Douglas, 1987). This population was subjected to only a low level of trapping and we assumed that the data can therefore provide reliable estimates of population parameters for an reintroduced (unharvested) population. These data were validated by comparison with those for a heavily harvested population from the Yukon, USA (n=839; Archibald & Jessup, 1984) and with the limited data available on pine martens (Corbet & Harris, 1991). This gave a population comprising 58% juveniles (<1 year old) having a survival rate of $0.32/yr^{-1}$. The mean survival rate of adults was $0.60/yr^{-1}$ (Strickland & Douglas, 1987), but we revised this upwards as harvesting, even at a low level, leads to a reduction in adult survival (Table 4). We assumed a maximum longevity of

12 years and a sex ratio of 0.5. Strickland and Douglas (1987) showed that females do not produce young in their first year, that fecundity rates for two year olds are 2.58 and averaged 3.5 for older marten. However data from Scotland (D. Balharry, *pers. comm.*) suggest that females do not breed until their third year and have litters of less than three young. Consequently we revised fecundity rates downwards (Table 4).

Coefficients of variation (CV) in vital rates between years were calculated from Stickland & Douglas (1987) as follows: CV in adult survival: 18%. Adults were >1 year old and the coefficient was calculated across eight age-classes where n>30 and a 12 year period; CV in fecundity: 12%. These were calculated over a 12 year period. No data were available concerning variation in zero age class survival rates, which we assumed to be 30%. In general, all these data represent best-case scenarios and higher between-year variation, in particular, might occur (see below).

These data were used in a stochastic age-structured population model (Ramas/age; Burgman, Ferson & Akcakaya, 1993). We ran 300 simulations for each scenario, all beginning with a population without martens less than one year old, except where we tested the effects of releasing populations of different age-structure. The effects of demographic stochasticity were included in the models, which assumed that there was no density dependence and that extinction had occurred if a population fell below five martens. The distribution of CVs were taken to be log-normal, on the basis that only a small proportion of years will be sufficiently bad (eg low prey availability) to significantly lower vital rates. A sensitivity analysis examined the influence of a 10% decrease in vital rates (or increase in CVs) on quasi-extinction probabilities for a founding population of 20 martens over 10 years.

Questionnaire survey

Countryside and conservation organisations were asked to give their views on the *principle* of reintroducing pine martens to England. The questions asked were:

1. a. Would your organisation support the principle of reintroducing pine martens to England south of the Rivers Humber and Mersey?

   b. If the answer is yes, are there any caveats or qualifications to this support in principle?

   c. If the answer is no, what are your reasons for not supporting the principle of pine marten reintroductions?

2. a. Would you in principle be prepared to allow a pine marten reintroduction project to proceed on land in your control and/or advise your members to co-operate with a pine marten reintroduction to land under their control?

   b. If the answer is yes, are there any caveats or qualifications to this support in principle?

   c. If the answer is no, what are your reasons for not co-operating with the reintroduction?

3. Should a pine marten reintroduction proceed, the highest priority would be given to choosing a site that would minimise the risk of conflicts between pine martens and interests of the local residents. Could you please state:

a. What conflicts, if any, do you foresee between countryside management and pine marten conservation? As much detail as possible would be appreciated.

b. The evidence on which your views in 3a are based.

4. Do you have any other comments that you wish to make on the principle of reintroducing pine martens?

5. Do you have any suggestions as to areas of England that are:

a. Particularly suitable as potential sites to reintroduce pine martens.

b. Particularly unsuitable as potential sites to reintroduce pine martens.

6. Do you wish to comment on the short-list of potential release sites, once they are available?

Results and Discussion

Ecological factors

Founder population age structure

Rates of growth would be very low ($0.038/yr^{-1}$ *per capita*) and probabilities of extinction high (0.12) if a release population had exactly the same age structure as wild populations and included martens below breeding age. If juveniles were not released, but first-time breeders were (here assumed to be two year olds with a fecundity of 2), very substantially higher rates of growth and lower extinction probabilities are predicted (Fig. 5). Population parameters would not be substantially changed if only martens that had reached full breeding maturity (three or more years old with a fecundity of 3) were released (Fig. 5). On this basis, and a consideration of social behaviour (Part 4), releasing martens of two or more years old may be an expeditious strategy. All the following results thus refer to release populations structured in this way.

Founder population size

Population size is predicted to increase only slowly, with a mean *per capita* growth rate of $0.11/yr^{-1}$ (Fig. 6). At this rate populations are not likely to more than double in size over 10 years. Small founder sizes would thus lead to populations remaining small for several years, during which time they will be acutely vulnerable to stochastic events and any additional mortality (see below; Fig. 6). It is not likely that growth rates could be increased much beyond those used in the model, so larger founder sizes will be essential to population establishment.

Breeding rates

After survival rates, the model was particularly sensitive to changes in fecundity, a 10% decrease in fecundity reducing population growth by 40% and increasing extinction risk by a factor of more than 2.5 (Fig. 7). This emphasises that slow breeding rates would be a central factor acting against population establishment. Clearly, measures to enhance fecundity (eg supplementary feeding, release in prey-rich habitats) would strongly promote the viability of a released population.

Table 4. Vital rates and coefficients of variation (CV) for a population of American marten *Martes americana* and the parameters used in our population model which were derived from them.

Source of data	Adult survival rate/yr^{-1}	Juvenile survival rate/yr^{-1}	Fecundity rate (young/ female/yr^{-1}) 1-2 yr	2+ yr	CV in adult survival (%)	CV in juvenile survival (%)	CV in fecundity (%)
Strickland & Douglas (1987)	0.60	0.32	2.58	3.50	18	-	12
Model parameters	0.75	0.32	2.0	3.0	18	30	12

Fig. 5. Predicted probabilities of extinction and *per capita* population growth rates/yr^{-1} for a founding population of 20 martens. Three different founding age-structures are shown. Closely similar results were obtained for founder populations of other sizes.

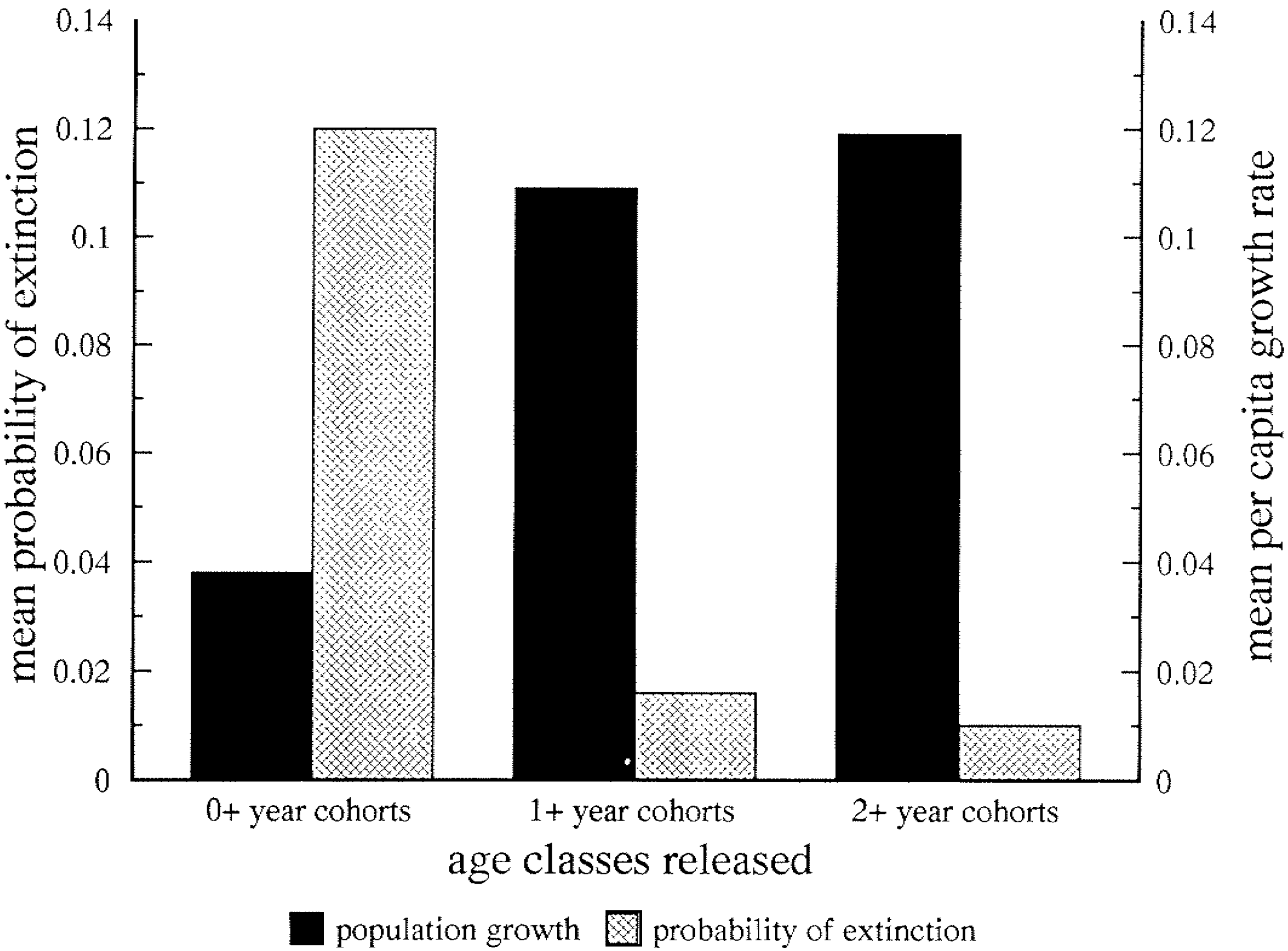


Fig. 6 Predicted increase in marten population sizes over a period of 10 years. Mean population sizes and 95% confidence limits are shown, based on 300 simulations of founder populations of 10, 20, 40 and 60 martens. Note the different scale of the lower two graphs.

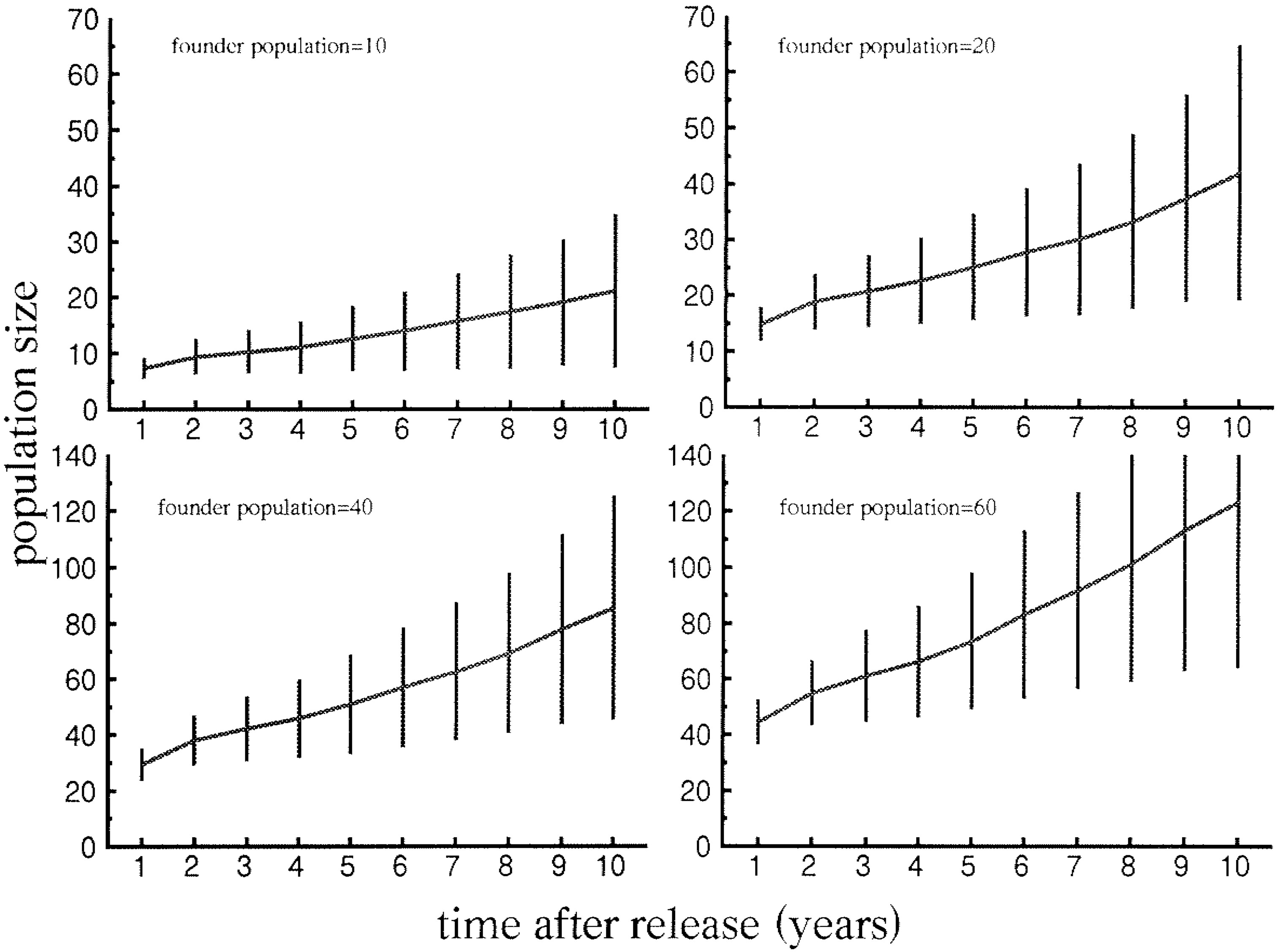


Fig. 7. Relative sensitivity of the marten population model to its constituent parameters (vital rates and coefficients of variation, CV). For each parameter, the analysis is based on 300 simulations of a founding population of 20 martens over 10 years. The factorial (multiplicative) change in extinction probability due to a parameter, while all others are held constant, is shown. Closely similar results were obtained for founder populations of other sizes.

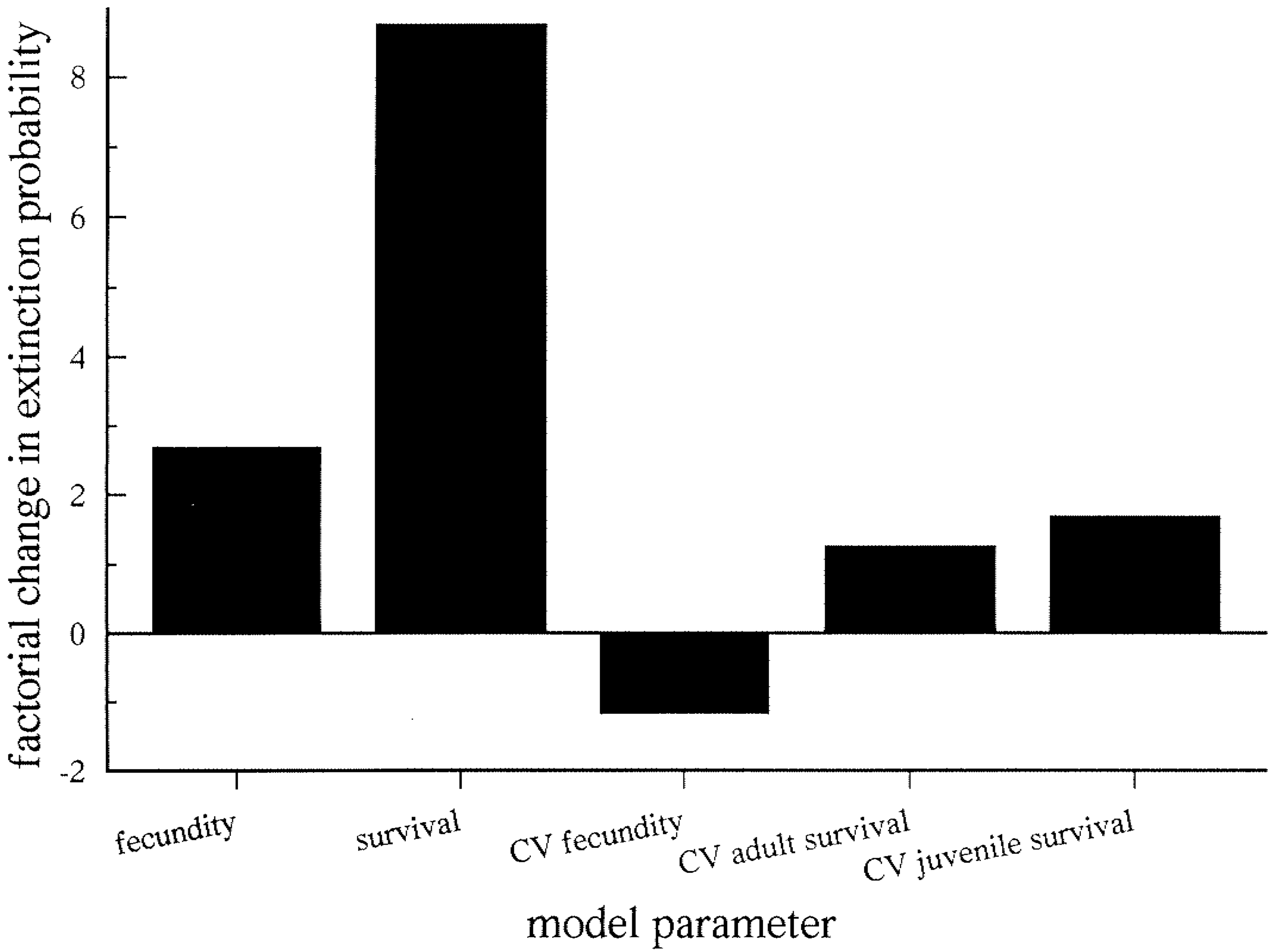


Fig. 8. Predicted probability of population extinction in relation to the percentage rate of mortality/yr^{-1}, additional to that operating on an undisturbed wild marten population. Probabilities are based on 300 simulations for a 10 year period and founder populations of 10, 20, 40 and 60 martens.