Part 2: Biological suitability of potential pine marten reintroduction regions in England

Introduction

Since the Rio Convention, support for biodiversity conservation has increased and in developed countries this has focussed attention on reintroduction of locally extinct species (Anon. 1994; Glowka, Burhenne-Guilmin & Synge, 1994). Many reintroductions have been attempted (Griffith *et al.* 1989; Short *et al.* 1992), mostly with minimal prior assessment of the likelihood of success. This concerns especially the prevailing suitability of release sites, which are generally in altered ecosytems. Perhaps as a consequence, many reintroductions have failed (*eg* Bertram & Moltu, 1986) and remain little known in the grey literature. These represent missed opportunities to learn from what are effectively manipulative field experiments (Bright & Morris, 1994; Caughley, 1994), a waste of resources and individuals of rare species.

The ecology of biological invasions sheds some light on the problem of predicting the suitability of sites for a reintroduction, since both involve the growth of small populations. We suggest that reintroductions, as well as invasions (Williamson, 1996), have two phases: establishment and spread. We postulate that during them largely different factors limit reintroduced populations. Here we define establishment as colonisation and inception of breeding to the point where a population is no more than self sustaining. During establishment when a population is very small, factors operating in a stochastic manner, especially on mortality or sex ratios, are likely to determine success. Spread is when a population grows and increases in distribution, escaping stochastic extinction vortices (Soule, 1987). Factors affecting birth rates, especially food supply, are likely to have a dominant influence on the probability that a reintroduced population will spread.

Beginning from this distinction between establishment and spread, we provide a case study concerning the potential reintroduction of a carnivore rare in Britain, the pine marten *Martes martes*. We aim to determine the likelihood of successful reintroductions to different parts of England and to provide a framework for the biological assessment of regions for reintroductions. We compare habitat for pine martens where they still occur, to relict distribution and regions where they might be reintroduced. The work was part of the national, UK Government supported, Species Recovery Programme which aims to restore the distribution of rare taxa.

In 1800 the pine marten occurred throughout Britain and was common in many regions. Subsequently its distribution contracted to the far north west of Scotland and small areas in north Wales, Cumbria and Yorkshire, reaching a nadir in about 1915 (Langley & Yalden, 1977). The principal cause of decline was persecution concomitant with the rise of gamebird shooting estates, though trapping for their valuable fur and habitat loss in the nineteenth century could have played a minor role in the decline (Langley & Yalden, 1977).

Pine martens are currently slowly recolonising Scotland (Velander, 1983; Balharry *et al.* 1996), following a national reduction in persecution pressure (Tapper, 1992). By contrast relict populations in England and Wales have not spread. The numbers of corpses recovered has declined close to zero (Strachan, Jefferies & Chanin, 1996) and recent surveys suggest that populations in England and Wales are now functionally extinct (see Summary). Against this background reintroductions have been proposed (Whitton, 1990), which we show here and elsewhere to be a viable conservation strategy.

Methods

Selection of regions

Our approach was to seek regions of optimal habitat for pine martens, where risk of violent mortality was low and food availability high. The probability of establishing populations which subsequently spread should be high in such *potential release regions* (PRRs). These were compared to regions of *relict distribution* in England, and sites of *current distribution* in Scotland where pine marten density has been determined (see below). The former were 1-km squares where Strachan *et al.* (1996) recorded pine martens present, grouped by county; they overlapped with potential release regions which had higher woodland cover. The latter were study areas (see *Comparative estimates of pine marten abundance*) plus adjacent 1-km squares of the same land class (Bunce, Barr & Whittaker, 1983) totalling about 200km^2.

Pine martens are woodland animals, reaching greatest density and concentrating their activity in wooded habitat even when this is highly fragmented (Storch, 1988; Brainerd, 1990; Balharry, 1993a). Optimal regions for reintroductions will thus have high woodland cover. Accordingly regions with 25% or more deciduous plus coniferous woodland were selected, these having more than three times the average woodland cover (8.3%) for Britain. Contiguous 1-km gird squares totalling c. 200km^2 or more were chosen as being the minimum area likely to support a potentially viable population, extrapolating from the median known density in Scotland (0.3km^{-2}, see below). Regions were identified from the Institute of Terrestrial Ecology (ITE) Land Cover Map. This is derived from Landsat Thematic Mapper images captured between 1988 and 1991 and packaged in a geographic information system (the Countryside Information System, CIS; Barr *et al.* 1993; Howard *et al.* 1994). Heavily wooded regions in and around the county of Hampshire were not considered as these have high levels of gamebird rearing and would not be suitable for initial releases (see below).

Quantifying ecosystem change

The number of gamekeepers, past principal agents of pine marten decline, recorded in the 1911 population census by county (Tapper, 1992) was compared with gamekeeper numbers in the Game Conservancy gamebag surveys for the 1990s, which cover over 500 shooting estates (S.C. Tapper, *pers. com.*). The Nature Conservancy Council inventory of ancient woodland (Spencer & Kirby, 1992) and Ordnance Survey maps were used to estimate woodland cover in c. 1800 prior to major pine marten decline. This was compared with woodland cover recorded on the ITE Land Cover Map. Most woodland change since 1800 occurred post 1950 (Spencer & Kirby, 1992), after the major pine marten decline in Britain.

There are no data on prey or predator abundance prior to pine marten decline. Since pine martens occurred widely in Britain, motorised road traffic, a potentially important source of violent mortality, has arisen.

Assessing risk of predation

In Britain pine martens are at risk from intra-guild predation by foxes *Vulpes vulpes* and large raptors (eagles *Haliaeetus albicilla*, *Aquila chrysaetos* and possibly goshawks *Accipiter gentilis*; Lindstrom *et al.* 1995); the latter are rare and foxes offer the only significant threat. Fox abundance was assessed by counting distinctive fox scats (faeces, recognised by their pungent odour and morphology; Lawrence & Brown, 1973) on 0.5km transects walked along tracks (mean width 4.8m, SE 0.05) through woodlands (a standard method for estimating carnivore abundance; Wemmer *et al.* 1996). Transects were each in randomly selected 1-km grid squares; 5% of 1-km squares (minimum 30) in a region were sampled.

Pine martens escape from predators by taking refuge in trees (Lindstrom *et al.* 1995), so are more vulnerable in regions where woodlands are fragmented (Brainerd, 1990). Balharry (1993a) showed that territories have a minimum of 126ha of woodland. Greater distances between woodlands and woodland areas less than 126ha will therefore increase risk of predation. The areas of woodlands of 2ha or more (ha) and nearest neighbour distances between them (km) were measured from Ordnance Survey 1:25,000 maps using a digitising tablet. Risk of fox predation was then calculated as:-

risk (fox) = mean fox scat count * 1/(mean wood area/126) * *ln*(mean distance between woodlands)

Assessing risk of anthropogenic mortality

Risk of pine marten mortality from captures in traps, shooting incidental to control of other carnivores, or from illegal poisoning was calculated using multiple independent measures. This was to ensure a reliable measure of a very important, but difficult to quantify, source of risk. Measures were calculated for 5000km^2 areas (except (iii) below) centred on regions. This spatial scale was used as the likely minimum area for which the measures, including those predicted from the Countryside Survey 1990 (Barr *et al.* 1993), would be representative. The measures were: (i) number of gamekeepers recorded by the Game Conservancy survey (S.C.Tapper, *pers. com.*); (ii) mean area of woodland (km^{-2}) used for sport shooting predicted from the Countryside Survey 1990 woodland data set (Barr *et al.* 1993); (iii) number of pheasant *Phasianus colchicus* observed within 25m of transects through woodlands (see above); (iv) total relative abundance of game birds (pheasant, partridge *Alectoris rufa, Perdix perdix*) from the British Trust for Ornithology's atlas of breeding birds (Gibbons, Reid & Chapman, 1993); (v) and the number of poisoning incidents of wildlife or domestic animals reported between 1986-1995 to the Ministry of Agriculture or the Scottish Agricultural Science Agency (Anon., 1995a; M. Fletcher pers. com.; K. Hunter, pers. com.).

Pine martens are also vulnerable to road traffic accidents (Velander, 1983) and animals exploring over large distances following release (Davis, 1978) might be especially so. Evidence from another mustelid the badger *Meles meles* (Aaris-Sorensen, 1995) implies that pine martens would be at highest risk where roads pass through woodland. We assumed that higher road and traffic density would also increase risk and calculated it as:-

risk (rta) = (traffic density * mean road density through non-wooded habitat) + 2(traffic density * mean road density through woodland)

Traffic density for 1995 (10^6 vehicle km driven on any road type, by county) was obtained from Department of Transport monitoring statistics (A.J.Arul-anandam, *pers. com.*) Road cover (ha km^{-2}, for 5000km^2 areas centred on regions) was extracted from the Ordnance Survey topographic data set within CIS, for 1-km squares with <25% woodland (roads though non-wooded habitat) and for squares with >=25% woodland (roads though woodland).

Fig. 1. Location of potential release regions (1), regions of relict (2) and current distribution (3). Regions of relict distribution partially overlapped with some potential release regions.

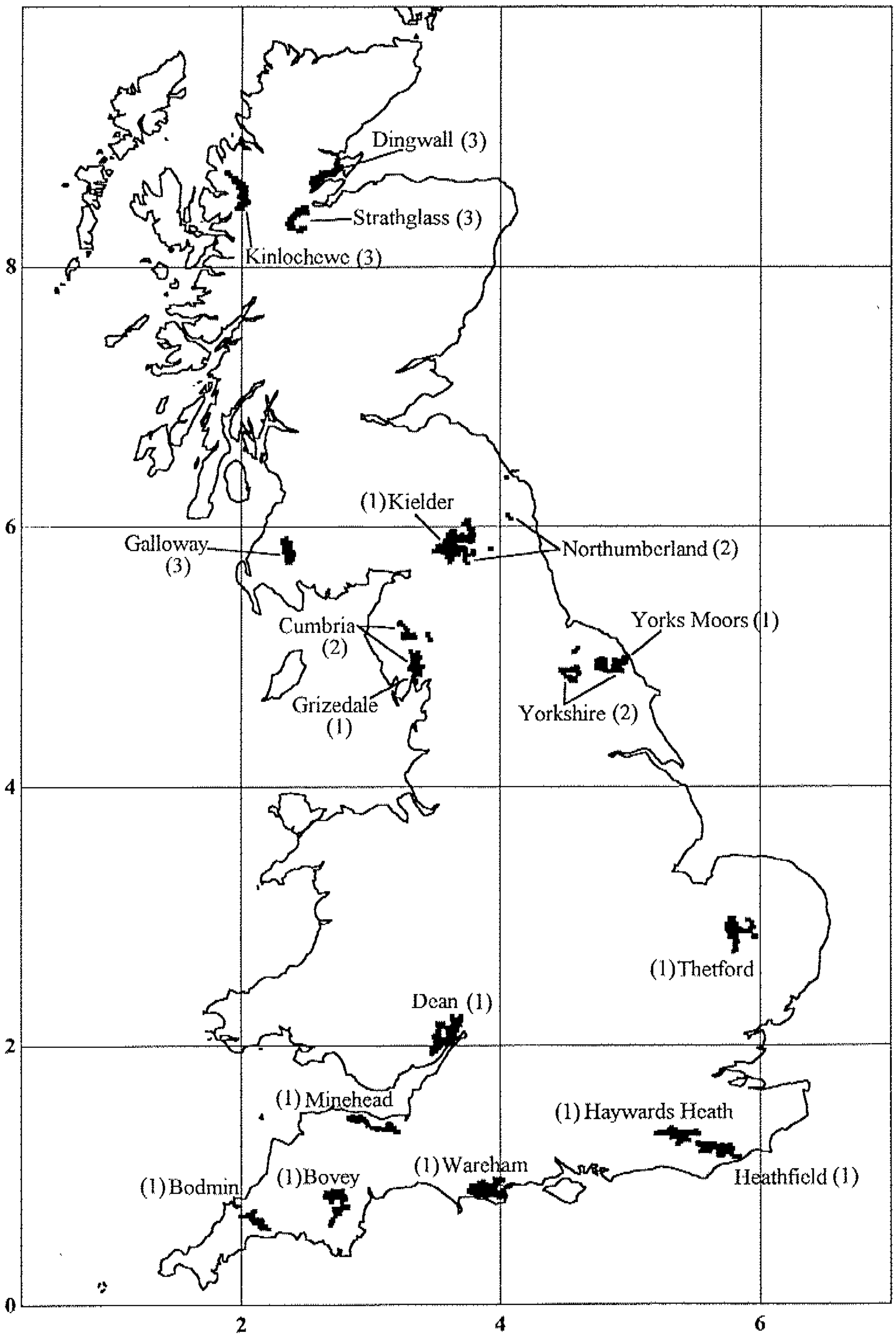


Table 1. Areas and woodland attributes of all potential release regions (PRRs), regions of relict and current distribution. Attributes for regions marked ($^{+}$) refer to study areas where pine marten densities have been determined, which form part of the regions shown in Fig. 1.

Region	Area of region, km^2	% cover of woodland	Mean area of woodlands, km^2 (SE)	Mean inter woodland distance, km (SE)	% cover of woodland in surrounding $5000km^2$
Potential release regions					
Bodmin	193	25.2	0.56 (0.12)	0.88 (0.11)	11.3
Bovey	312	26.1	0.50 (0.09)	0.90 (0.07)	10.4
Dean	439	35.7	2.73 (0.99)	0.38 (0.03)	11.7
Grizedale	205	31.3	1.33 (0.69)	0.49 (0.04)	6.1
Haywards Heath	292	27.3	1.99 (0.83)	0.29 (0.01)	17.5
Heathfield	322	30.5	1.07 (0.39)	0.36 (0.02)	13.0
Kielder	564	51.7	20.82 (11.25)	0.70 (0.11)	14.4
Minehead	256	25.6	0.92 (0.24)	0.91 (0.11)	8.5
Thetford	358	34.1	2.82 (1.28)	0.51 (0.04)	6.2
Wareham	397	27.8	1.60 (0.56)	0.67 (0.11)	15.3
Yorks Moors	249	35.2	5.26 (2.64)	0.46 (0.07)	6.4
Relict distribution					
Cumbria	244	16.4	1.50 (0.70)	0.69 (0.11)	6.1
Northumberland	316	39.3	14.17 (7.42)	0.60 (0.08)	13.0
North Yorkshire	433	29.3	3.38 (1.24)	0.46 (0.07)	6.9
Current distribution					
Dingwall	203	70.0^{+}	3.99 (1.47)	0.33 (0.03)	11.3
Galloway - Minnoch	199	71.0^{+}	21.76 (8.55)	0.33 (0.04)	17.0
Galloway - Trool	“	72.0^{+}	“ “	“ “	“
Kinlochewe	279	3.5^{+}	0.95 (0.24)	0.81 (0.19)	4.5
Strathglass	277	27.0^{+}	5.94 (1.19)	0.25 (0.02)	10.0

Assessing prey availability

The pine marten's prey species show considerable temporal fluctuations of abundance, not necessarily synchronous between habitats/regions (Mallorie & Flowerdew, 1994; Trout & Smith, 1995). Short term surveys may consequently not allow unbiased comparisons of prey abundance between regions. We thus chose to use data from surveys spanning more than one year, or vegetation structure to estimate prey availability.

Field vole *Microtus agrestis* abundance was assessed from the mean length of grass with a tussock growth form (its principal habitat: MacVicar & Trout, 1994) within 25m along either side of transects (see *Assessing risk of predation,* above). Similarly, bank vole *Clethrionomys glareolus* abundance was assessed from the length of dense (non-grass) field layer vegetation (especially bracken *Pteridium aquilinum* and bramble *Rubus fruiticosus*) of 0.5m+ in height. The presence of such vegetation is known to correlate with bank vole abundance (Southern & Lowe, 1968; Hansson, 1971; Flowerdew & Trout, 1995).

Rabbit abundance (km^{-2}) was taken from Ministry of Agriculture surveys of 450 sites in 45 counties between 1980 and 1986, extrapolated by land class (Bunce *et al.* 1983) and incorporated into CIS (R.C. Trout, S. Langton & G.C. Smith, in prep.). The sum of relative abundances of the following birds known to occur in pine marten diets was extracted from abundance maps given in Gibbons *et al.* (1993): wren *Trogoldytes trogoldytes,* robin *Erithacus rubecula,* blue tit *Parus caeruleus,* great tit *P. major,* coal tit *P. ater,* nuthatch *Sitta europaea,* wood pigeon *Columba palumbus,* pied flycatcher *Ficedula hypoleuca,* blackbird *Turdus merula,* song thrush *T. philomelos,* mistle thrush *T. viscivorus.* Availability of carrion was estimated from the numbers of deer (Cervidae) culled (km^{-2} yr^{-1}) by the Forestry Commission and private landowners in different regions (Balharry, 1993a; W.Burlton, C.Critchley, J.Cubby, E. Halliwell, G.Shaw, D. Stocker, pers. com.).

Comparative estimates of pine marten abundance

Potential density of pine martens reintroduced to England was predicted using a relation between characteristics of habitats and current known densities in Scotland. Estimates of current density were based on minimum convex polygon territory areas of breeding animals, determined from radio tracking (Balharry, 1993a; Halliwell, 1997; Part 1).

Results

Distribution of potential release regions

Analysis of woodland cover identified 11 potential release regions (PRRs) in England (Fig. 1). Bodmin, Grizedale, Thetford and Yorks Moors PRRs had small total area, highly fragmented woodlands or little woodland in the surrounding 5000km^2; such factors would limit pine marten spread (Table 1). These PRRs would thus not be optimal places for first releases and will not be considered further here. All remaining PRRs had a spectrum of woodland attributes within the range of those for regions of current distribution (Table 1).

Table 2. Correlations (Spearman rank) between independent potential measures of predator control in potential release regions, regions of current and relict distribution (n=14). Measures were: the number of gamekeepers from the Game Conservancy 1990s gamebag survey (GCT; S.C. Tapper *pers. com.*); total relative abundance of gamebird species from the British Trust for Ornithology's atlas of breeding birds (BTO; Gibbons *et al.* 1993); cover of woodland used for game/sporting purposes from the Countryside Survey 1990 (CS90; Barr *et al.* 1993); the total number of pheasants counted during transect surveys (Field survey; see Methods); and the total number of wildlife poisoning incidents recorded between 1986 and 1995 by MAFF and SASA (Poisoning).

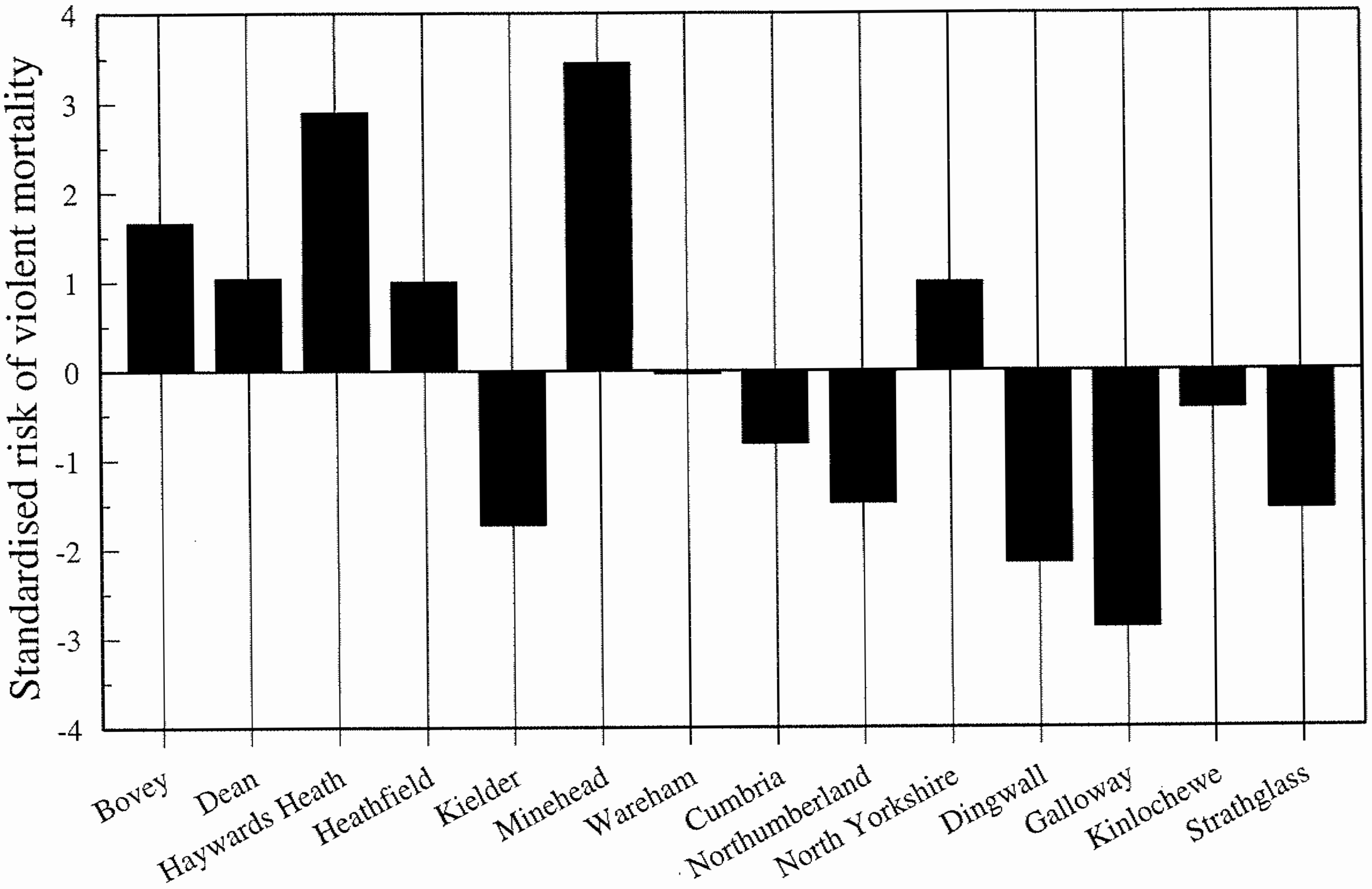
	GCT	BTO	CS90	Field survey
BTO	0.534 **			
CS90	0.710 **	0.369		
Field survey	0.490 *	0.216		
Poisoning	0.317	0.367	-0.853 ***	0.117

* $p<0.05$, ** $p<0.01$, *** $p<0.001$

Table 3. Attributes measuring risk of violent mortality of pine martens and factors that contribute to risks, in potential release regions (PRRs), regions of relict and current distribution. Risk from predator control was the mean rank of independent measures given in Table 2.

Region	Risk from predator control, mean rank	Fox abundance, scats km^{-1} (SE)	Risk of fox predation	Total road length, $\times10^{-3}$ km	Risk of road mortality	Poisoning incidents, 1986-95
Potential release regions						
Bovey	4.7	0.43 (0.14)	3.31	4.20	15.06	15
Dean	8.5	0.94 (0.28)	1.24	2.35	9.50	10
Haywards Heath	12.0	1.74 (0.30)	3.00	2.54	9.97	27
Heathfield	11.5	2.06 (0.36)	6.89	1.51	5.45	16
Kielder	7.7	0.96 (0.20)	0.17	1.41	0.49	15
Minehead	8.2	0.25 (0.12)	1.07	2.68	8.34	25
Wareham	9.2	0.32 (0.12)	0.40	1.73	5.25	11
Relict distribution						
Cumbria	4.7	0.58 (0.15)	1.41	3.09	6.58	27
Northumberland	8.2	0.90 (0.22)	0.23	1.41	0.74	25
North Yorkshire	9.0	2.33 (0.72)	2.46	4.40	6.80	35
Current distribution						
Dingwall	3.5	1.40	1.25	1.50	2.82	***
Galloway	3.5	2.36	0.39	1.41	1.05	***
Kinlochewe	1.7	2.08	8.20	1.50	2.25	***
Strathglass	6.0	1.56	0.91	1.50	2.44	***

Fig. 2. Total standardised risk of violent mortality for potential release regions, regions of relict and current distribution. Risk was calculated as the sum of standardised risks of predation, road mortality and that correlated with gamekeeping. Note that the scale on the abscissa, which may not be linear, is unknown.



Suitability of regions for population establishment

There were significant correlations between all measures of risk from shooting or trapping incidental to the control of other carnivores, but not between these and poisoning incidents (Table 2). Therefore we ranked regions separately by the former measures and calculated the mean of these ranks to quantify risk (Table 3). Risk of mortality associated with predator control in PRRs increased from north west Scotland to south east England. Excepting Bovey, all PRRs had higher risk than regions of current distribution in Scotland. There was no clear trend in poisoning incidents, except that these were not correlated with gamekeeping (Table 3).

Fox abundance was, on average, higher in Scotland than in PRRs except Heathfield and Haywards Heath (Table 3). Risk of predation, calculated as a function of fox abundance and woodland fragmentation, was lowest in Kielder and Wareham.

Risk of road mortality was especially high in Bovey, due to roads with high traffic density passing through woodlands (Table 3). Unsurprisingly, risk of road mortality was higher in PRRs than in regions of current distribution, except in Kielder.

Total risk of violent mortality was calculated by standardising each risk variable to account for different scales of measurement:

$$\text{Total risk} = \text{sum } (\text{risk}_i - \text{mean risk}_i)/S_i^2$$

where risk_i was one of the four measures of violent mortality and S^2 the variance of that risk. Total risk was greater in all PRRs, except Kielder, than in regions of current distribution (Fig. 2). Note that pine martens survive in Kinlochewe even though total risk is only slightly less than the mean. There are no data enabling total risk to be correlated with mortality and its scale of measurement is unknown; it could be linear, curvilinear or (perhaps more likely) have a ratio scale.

Suitability of regions for populations to spread

A different suite of prey was abundant in regions of current distribution compared to most PRRs. There was higher abundance of deer carrion and habitat for field voles in the former, whereas rabbits, bird prey and high quality habitat for bank voles were more abundant in the latter (Table 4). Kielder and to a lesser extent Wareham were exceptional in these respects, having a prey composition similar to regions of current distribution.

Total, standardised, potential prey abundance was calculated as for total risk:

$$\text{Total prey} = \text{sum } (\text{prey}_i - \text{mean prey}_i) / S_i^2$$

where prey_i was one of the five measures of potential prey abundance and S_i^2 the variance of that abundance. Total prey abundance was higher in all PRRs, particularly in Heathfield, Haywards Heath and Dean, than in regions of current distribution (Fig. 3). There was a trend of increasing prey abundance from north west Scotland to south east England

Total standardised prey abundance multiplied by log (e) woodland cover (Table 1) was a significant predictor of known pine marten density in regions of current distribution (Fig. 4; regression, p=0.031). This relation was used to predict pine marten densities that might be realised in PRRs, assuming that risk of violent mortality was the same as in regions of current distribution (it may be higher, Fig. 2; see Discussion). Predicted potential pine marten density in PRRs was in the centre of the range of predicted densities in regions of current

Table 4. Attributes measuring prey abundance for pine martens in potential release regions (PRRs), regions of relict and current distribution.

Region	Field vole habitat, m km^{-1} (SE)	High quality bank vole habitat, m km^{-1} (SE)	Rabbit abundance, numbers, km^{-2}	Relative abundance of bird prey	Deer carrion, numbers culled, km^{-2} yr^{-1}
Potential release regions					
Bovey	94 (18)	92 (22)	31	8.6	0.67
Dean	63 (12)	175 (30)	34	9.3	0.64
Haywards Heath	76 (16)	230 (35)	40	9.6	0.21
Heathfield	71 (18)	317 (35)	39	9.3	0.14
Kielder	199 (23)	17 (8)	21	6.9	2.12
Minehead	67 (17)	72 (19)	31	8.8	0.65
Wareham	230 (35)	38 (10)	32	7.1	0.41
Relict distribution					
Cumbria	146 (41)	95 (20)	21	7.1	2.18
Northumberland	213 (24)	17 (8)	21	7.1	1.80
North Yorkshire	163 (36)	189 (39)	21	7.5	1.14
Current distribution					
Dingwall	242 (21)	121 (22)	30	5.8	2.50
Galloway - Minnoch	137 (26)	17 (8)	0	6.1	1.67
Galloway - Trool	172 (27)	26 (10)	5	6.7	2.43
Kinlochewe	287 (48)	70 (28)	0	2.9	0.85
Strathglass	248 (22)	129 (26)	5	6.4	2.08

Fig. 3. Total standardised prey abundance for potential release regions, regions of relict and current distribution. Abundance was calculated as the sum of standardised abundances of field vole habitat, bank vole habitat, rabbit abundance, relative abundance of bird prey and deer carrion. As with Fig. 2, the scale on the abscissa is unknown.

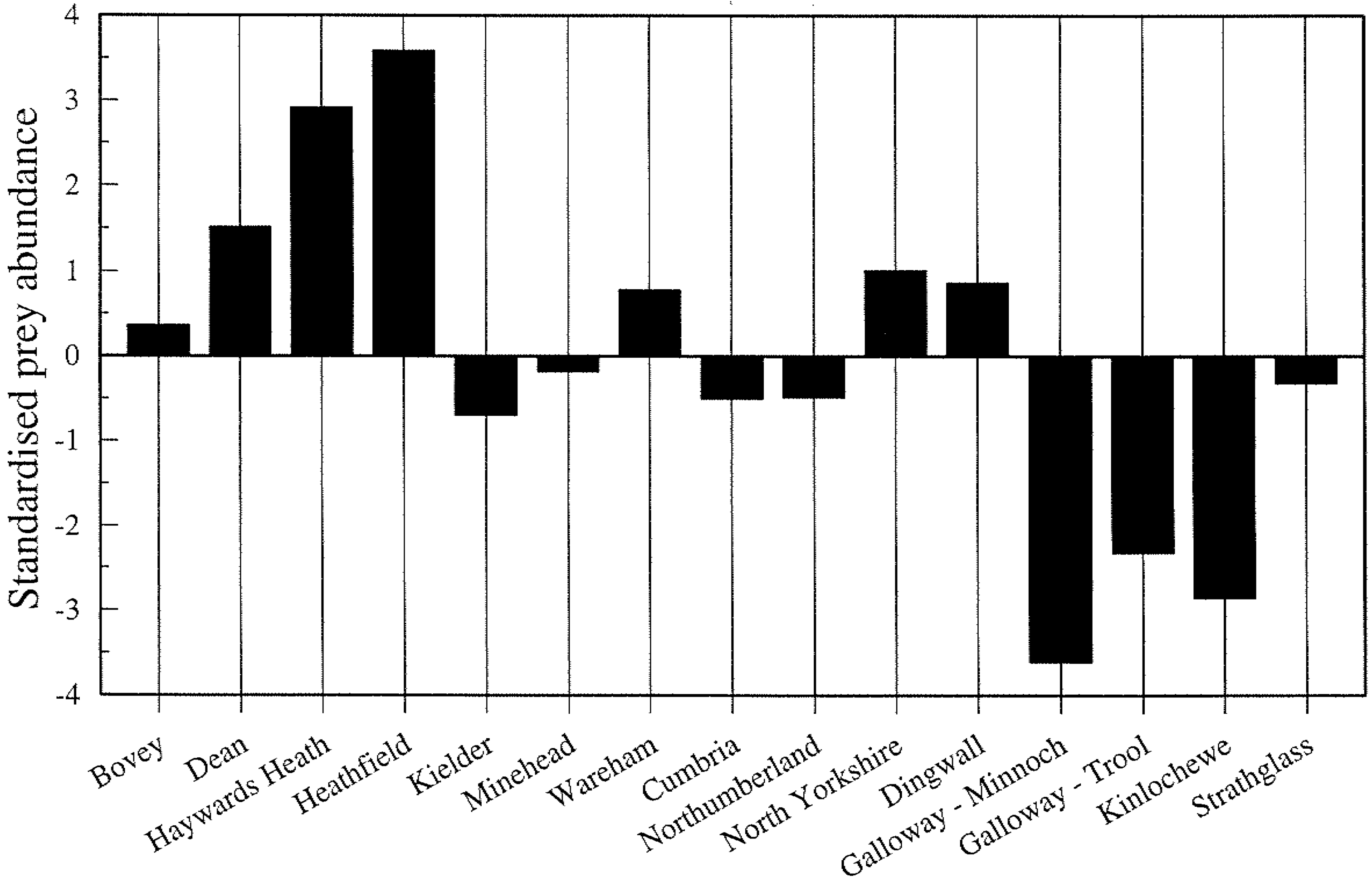


Table 5. Comparative woodland cover and gamekeeper density before and after the major decline of pine martens in Britain, for potential release regions, regions of relict and current distribution. No data on past woodland cover were available for regions of current distribution.

Region	Woodland cover in c.1800, %	Change in woodland cover: c.1800 to 1990s, %	Gamekeeper density in 1911, $\times 10^1$ km^{-2}	Change in gamekeeper density: 1911 to 1990s, %
Potential release regions				
Bodmin	2.05	8.62	0.6	-95
Bovey	2.81	8.73	0.6	-100
Dean	16.37	2.84	1.2	-26
Grizedale	4.00	3.67	0.6	-95
Haywards Heath	16.42	3.03	2.4	-92
Heathfield	17.94	2.80	2.4	-91
Kielder	0.90	13.47	0.9	-91
Minehead	3.55	7.02	1.2	-95
Thetford	0.24	17.47	1.2	-84
Wareham	2.58	20.47	1.2	-98
Yorks Moors	4.33	9.43	1.2	-87
Relict distribution				
Cumbria	4.00	3.67	0.6	-26
Northumberland	0.90	13.47	0.9	-91
North Yorkshire	4.33	9.43	1.2	-87
Current distribution				
Dingwall	-	-	0.6	-90
Galloway	-	-	1.2	-95
Kinlochewe	-	-	0.6	-94
Strathglass	-	-	0.6	-89

distribution (1990s; Fig. 5). All PRRs, except Minehead, had predicted densities close to that currently in Strathglass, which offers high quality habitat for pine martens (Balharry, 1993a).

Change in woodland and gamkeepers in potential release regions

Using the regression equation above (Fig. 4), pine marten densities were predicted for PRRs in 1911. As above, these are only *potential* densities which show capability of regions to support pine martens; actual densities would have been lower due to gamekeeping pressure. They are based on woodland cover at the time, but *current* estimates of prey abundance (which probably under estimate prey abundance in 1911; see Discussion). Woodland cover in PRRs increased by a mean of 137% between c.1800, but especially between 1950, and the present (Table 5; Wilcoxon test: T_{11}=66, p=0.003). Consequently predicted densities in all PRRs in the 1990s were greater than in any PRR in 1911 (Fig. 5). Conversely, the numbers of gamekeepers in PRRs decreased significantly by a mean of 86% between 1911 and the 1990s (Table 5; Fig. 5; Wilcoxon test: T_{11}=66, p=0.003). Except in Dean, gamekeeper densities are currently lower than in any PRR in 1911 (Fig. 5). Thus the principal habitat of pine martens has increased, while the agents of their past decline have greatly decreased.

Comparison with regions of relict distribution

Potential pine marten densities in regions of relict distribution were calculated as above, for 1911, the 1990s and 1950, the latter being before most afforestation but after the major decline of gamekeepers (Avery & Leslie, 1990; Tapper, 1992). Predicted potential pine marten densities in 1911 were amongst the lowest for any region. Gamekeeper densities were similar to the majority of other regions (PRRs) from which pine martens were extirpated (Fig. 5). Potential pine marten densities in c. 1950 were very close to the lowest known current density in Scotland (Kinlochewe; Fig. 5). Thus, the capability of regions of relict distribution to support pine martens was low until significant afforestation took place after 1950.

Current risk of violent mortality and prey abundance in regions of relict distribution were close to the mean risks and abundances for all regions. Predicted pine marten densities are in the centre and lower tail of predicted densities for PRRs (Fig. 5).

Discussion

Establishment and spread

Recently reintroduced populations face the same stochastic risks and consequent high extinction probabilities of all small populations (Lande, 1988; Caughley, 1994). The majority of reintroductions probably fail in their early stages because of high mortality amongst a usually small number of propagules (Griffith *et al.* 1989; Short *et al.* 1992; *eg* Bertrum and Moltu, 1986). It thus seems clear that stochastic mortality is an over-riding constraint during establishment of reintroduced populations. Food availability should not limit establishment, as food suppliments are usually provided to reintroduced populations (*eg* Bright & Morris, 1994).

What constrains spread following reintroduction is much less clear, not least as reintroductions are a recent phenomena and spread a long term one. Some, though by no means all (Williamson, 1996), instances of spread by mammals and birds seem correlated with high abundance of food or suitable habitat. Short *et al.* (1992) found that

Fig. 4. The relation between woodland cover (proportion of land cover), total standardised prey abundance and known pine marten density in regions of current distribution, which took the form: known density = 0.0792 + 0.5053 * (woodland cover * *ln* standardised prey abundance). Regression: r^2=83%, p=0.031.

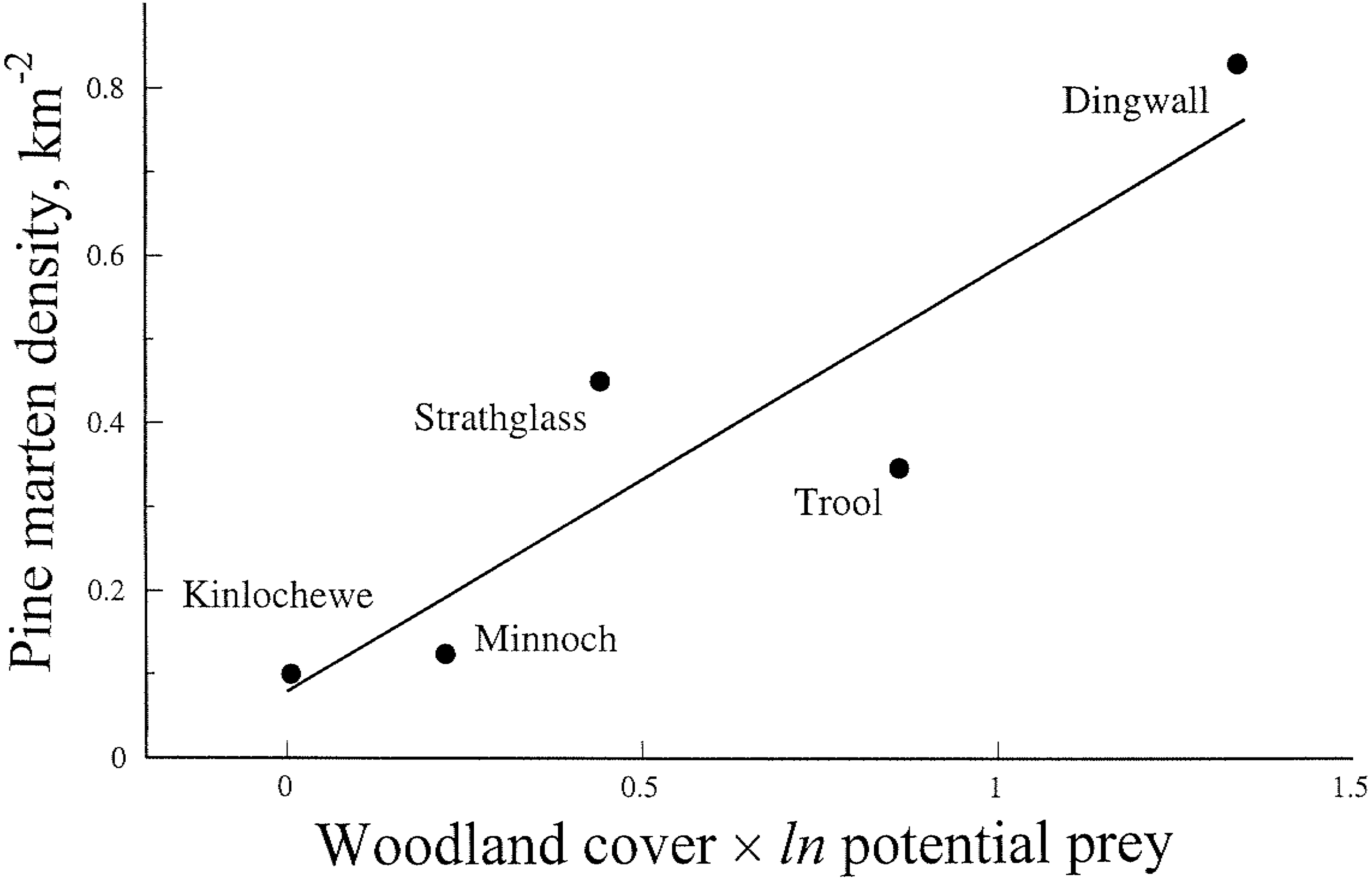
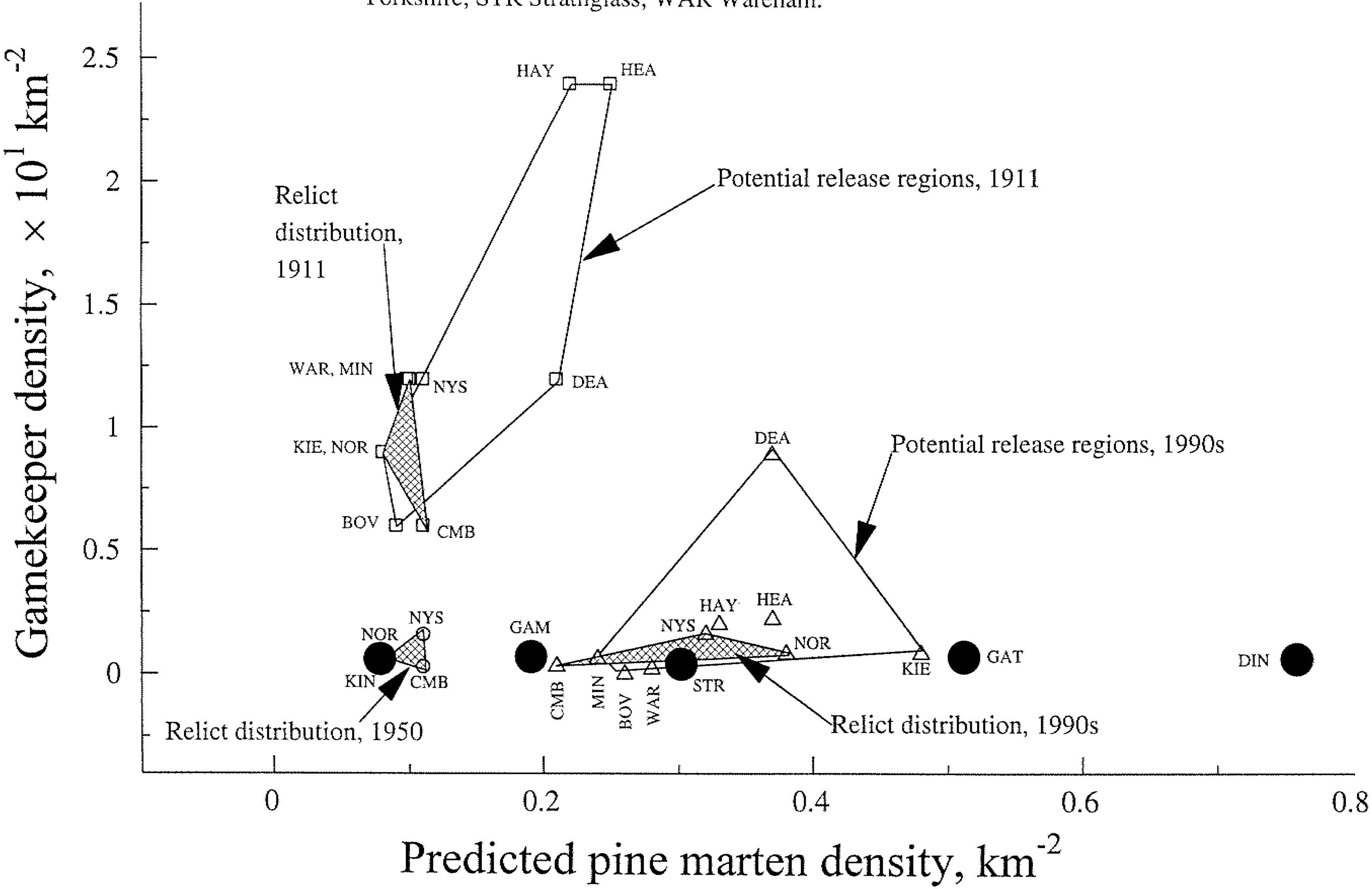


Fig. 5. Pine marten densities, predicted from the relation in Fig. 4, plotted against gamekeeper density. Data are for potential release regions in 1911 and the 1990s (open polygons); for regions of relict distribution in 1911, c. 1950 and the 1990s (shaded polygons); and regions of current distribution (solid circles). Region abbreviations: BOV Bovey, CMB Cumbria, DEA Dean, DIN Dingwall, GAM Galloway-Minnoch, GAT Galloway-Trool, HAY Haywards Heath, HEA Heathfield, KIE Kielder, KIN Kinlochewe, MIN Minehead, NOR Northumberland, NYS North Yorkshire, STR Strathglass, WAR Wareham.



most macropod (re)introductions leading to established populations were subsequently habitat limited. Grey squirrel *Sciurus carolinensis* spread in the British Isles appears correlated with woodland cover (Reynolds, 1985). Intuitively, it seems unlikely that a reintroduced population established in the face of stochastic mortality would subsequently experience mortality as the main constraint on spread, assuming that areas to which a population spreads offer similar risks to release sites. Spread should be more a product of population productivity (natality) and will not be likely from unproductive habitats. Though obviously a simplification of complex reality, these intuitive ideas have an important practical implication: suitability assessments of reintroduction regions need to consider two sets of different factors, those promoting establishment and those promoting spread.

These incomplete observations give some credence to the postulated dominant influence of mortality and natality during establishment and spread respectively (there will, of course, be a trade-off between births and deaths during both phases). Viewing reintroductions in this way encourages simple comparative evaluation of regional suitability from the standpoint of population processes (*eg* risk of mortality), rather than relying on more abstract but widely used habitat suitability indices (HSI; *eg* Cole & Smith, 1983) Such an approach should foster greater insight into the usually little known population biology of the rare species (Caughley, 1994) that are candidates for reintroduction.

Assessing regional suitability for establishment

Risks to animals reintroduced in altered ecosystems will often originate from novel sources of mortality (O'Bryan & McCullough, 1985). Consequently we quantified all known or likely sources of violent mortality for pine martens, but there are no data from which to determine the partial contribution of these to absolute mortality rates. Thus mortality risk can currently be expressed only in relative terms on a standardised scale which is probably non linear; a large difference in standardised risk may not equate to a large difference in reality. This approach will, however, readily permit evaluation of risks in different regions once data on mortality from trial reintroductions are available (see below).

The high concordance between different indices of mortality arising from gamekeeping demonstrates that we have a reliable measure of this difficult to quantify risk. This measure was not correlated with poisoning incidents, suggesting that poisoning represents a less spatially predictable threat, not the result of gamekeeping. Note however that data on poisoning are collected through reactive survey (Anon., 1995a), so can give only an indication of 'hot spots' but no measure of absence of risk. The poisoning data show which regions should be avoided, at least initially, such as North Yorkshire which has an alarmingly high level of reported incidents, potentially responsible for the absence of some predatory birds from the region (Gibbons *et al.* 1995).

Our surveys provide some of the first indices of rural fox abundance in multiple regions in Britain (cf Macdonald, Bunce & Bacon, 1981). Current distribution of pine martens in Kinlochewe (albeit at low density; Balharry, 1993a) where risk of fox predation was highest, suggests that fox predation might not constrain establishment of pine martens in PRRs of relatively high predation risk. However, recently reintroduced animals and younger cohorts might be more vulnerable to predation (McCallum, Timmers & Hoyle, 1995; Scheepers & Venzke, 1995) and significant pine marten mortality due to intra-guild predation has been documented (Lindstrom *et al.* 1995). Thus reintroductions need to avoid regions of higher predation risk.

Pine martens are killed on roads (Velander, 1983), but there are no data on absolute mortality rates, so again our measure of risk provides only a comparative index, of unknown scale. Pine martens survive in areas of continental Europe where road density is similar to southern England (cf Labrid, 1986; Muskens, & Broekhuizen, 1986; Anon, 1995b) and other mustelid populations are thought to withstand high levels of violent mortality (Kruuk & Conroy, 1991). As with predation, it would clearly be prudent to avoid PRRs with higher risk until data on sources of mortality are available.

Assessing regional suitability for spread

Although microtine voles can be a dominant item in the pine martens diet (*eg* Lockie 1961; Balharry, 1993a), it is clear that other small rodents, especially *Clethrionomys* spp. may be staple prey (Jedrzejewski, Zalweski & Jedrzejewska, 1993). The pine marten is clearly a generalist predator, flexible enough to rely heavily on fruits and insects as food in Mediterranean habitats (Clevenger, 1994). Thus the different suite of prey available in most PRRs compared with regions of current distribution should not be an impediment to spread.

Our estimates of small rodent (*Microtus, Clethrionomys*) abundance were based on documented associations with vegetation structure (Southern & Lowe, 1968; Hansson, 1971; MacVicar & Trout, 1994; Flowerdew & Trout, 1995). Given the considerable spatio-temporal variation in rodent abundance (*eg* Mallorie & Flowerdew, 1994) and the coarse (regional) scale at which estimates were needed, these should be robust comparative measures. We were not able to quantify the abundance of shrews *Sorex* spp., fruits or invertebrates (particularly Coleoptera). These can be seasonally frequent, but generally contribute relatively little to biomass of prey consumed (Balharry, 1993a; Clevenger, 1994).

Rabbits occur in pine marten diets (Halliwell, 1997) and might be highly economic prey. Although their abundance also shows considerable spatio-temporal unpredictably (R.C. Trout, S. Langton & G.C. Smith, *in prep.*), higher abundance in PRRs than in regions of current distribution, is likely to favour spread. The decreasing trend in deer carrion abundance from the north and west of Britain to south-east England, may under represent the availability of this winter food source (Balharry, 1993a) in southern England; carrion biomass from rabbits and road mortality of birds and mammals, including deer, is clearly higher in southern England (personal observation). Pine martens are known to feed on road-killed carrion (D. Balharry, pers. com.).

Potential release regions

Numerous studies have demonstrated that pine martens and (probably conspecific; Anderson, 1970) American martens *Martes americana* reach greatest densities where woodland cover and prey abundance, or both are high (Grakov, 1972; Brainerd, 1990; Storch *et al.* 1990; Balharry, 1993a; Strickland, 1994; Buskirk & Powell, 1994). Our relation between woodland, prey and pine marten density (Fig. 4) is thus founded on considerable previous knowledge. From this it is clear that all PRRs may have the *capability* to support medium to high densities of pine martens (c. 0.2 to 0.5km^{-2}). However, this prediction extrapolates from conditions in regions of current distribution which have lower risk of violent mortality; pine martens might not attain such high density in all PRRs. In practise this means that reintroductions should be first to PRRs with lower risk, even if these have lower predicted density or suitability for spread. They should be undertaken as trials, in part to quantify mortality and inform choice of subsequent release regions.

The biologically most suitable PRR for trial reintroductions would thus be Kielder (lowest risk of violent mortality), followed by Wareham, Heathfield, Dean and Bovey. Kielder has also the advantage of being closely similar to the Galloway forest, where the ecology of pine martens is now known (Parts 3 & 4). Ultimate selection of regions will, however, need to take full account of local acceptability of pine martens and their potential impacts on native fauna and game; we shall address these matters elsewhere.

Our necessarily broad brush approach omits some features of pine marten ecology, such as dens and the role of coarse wood debris (Brainerd, 1990) in foraging habitat quality. These could be important factors in local habitat suitability, but are probably not significant on the scale of our regions, nor in comparison with sources of mortality and prey availability. As with mortality, their importance in altered ecosystems needs to be determined from trial reintroductions.

Our results show that habitat availability in all PRRs has increased since the nadir in pine marten distribution in c. 1915, as a result of afforestation (Fig. 5; Avery & Leslie, 1990). This may have been tempered by a decrease in prey biomass following the decline of coppice woodland management (Peterken, 1981) and agricultural intensification, but only partially since woodland cover appears to be a more important predictor of density (there are no comparative data on prey abundance for earlier this century). Since 1911 the past principal agent of pine marten decline (gamekeeping) has been greatly reduced. Prevalence of gamekeeping in all PRRs except Dean, now appears close to that in regions of current distribution. It is also important to note that gamekeeping practise has improved considerably this century, being now closely targetted on a few pest species, while the rarer carnivores have been given legal protection. Two pre-eminent pre-conditions for reintroductions, suitability of release regions and reduction of the agent of decline (Anon., 1987), are thus clearly fulfilled (though note the above caveats concerning new sources of violent mortality).

PRRs are surrounded by landscapes with a mean woodland cover of 12.7% (Table 1), substantially more than the national average (8.3%). Habitat availability *per se* should thus not initially limit spread; all PRRs plus surrounding regions have the potential habitat cover to support long term viable populations.

Suitability of relict regions

Pine marten densities were predicted to have been low in regions of relict distribution until significant afforestation post 1950. The implication is that woodland cover would have constrained recovery of relict populations despite exponential reduction of gamekeeping in the 1920s to 1950s (Tapper, 1992). By 1915 pine marten populations in England and Wales were confined to small areas (Langley & Yalden, 1977). These were thus isolated, small populations, probably entrapped by stochastic extinction vortices and social dysfunction (cf Balharry, 1993b) which have likely prevented their expansion this century (Strachan *et al.* 1996; P.W. Bright, R. McDonald & S. Harris, unpublished report). By contrast the contiguous relict population in Scotland was distributed over a much larger region (Langley & Yalden, 1977), suggesting sufficient size to escape stochastic extinction.

Current predicted densities within the lower half of those for PRRs therefore mask the impoverished habitat and demographic history of relict regions. They graphically illustrate the common fallacy of assuming that regions of relict distribution equate to optimal habitats (Caughley, 1994). As for a wide range of birds, relict regions are where the ultimate agents driving extinction are weak, and not necessarily good habitats (Kear & Berger, 1980; Miller & Mullette, 1985; Jones, 1987). Consequently, inferring habitat requirements for pine martens from relict regions (cf Strachan *et al.* 1996) may lead to erroneous conclusions.

North Yorkshire remains unsuitable for initial reintroductions, having high predator control, illegal poisoning and low cover of woodland in surrounding regions. The significance of a single pine marten skull unearthed there in 1994 is impossible to judge (Jefferies & Critchley, 1994). Northumberland and Cumbria (partially overlapping with PRRs Kielder and Grizedale) offer more promise.

General implications for reintroductions

Our study suggests a framework for the biological assessment of reintroduction regions. Firstly, suitability should be considered separately in terms of establishment and spread, because different constraints will generally operate on these processes. Variables likely to closely correlate with birth and death rates should be quantified, as these can yield information on causation of population change. Assessments should also be structured to allow refinement using data from trial reintroductions. Finally, assessments should not extrapolate suitability solely from regions of relict distribution, which may be far from optimal. Since reintroductions of threatened species are about 60% more likely to succeed in high quality compared to low quality habitat (Griffith *et al.* 1989), such assessments may be highly cost effective in increasing rates of successful reintroduction.

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