Part 2: Climatic and Habitat Correlates of Large Scale Dormouse Distribution

Introduction

Several species of small mammalian hibernator reach the limits of their distributional range in Britain. The species have a mainly southern distribution (Corbet & Harris, 1991). During adverse weather conditions in summer they employ diurnal torpor as a compensatory mechanism to maintain energy balance (Bright, *in preparation*). The timing of births and other population events in these species are closely correlated with climatic conditions (Ransome & McOwat, 1994). In winter, warm weather may stimulate excess arousals from hibernation and so regulate over winter survival (Bright, *in preparation*). Furthermore, the distribution of one species, the dormouse *Muscardinus avellanarius*, has contracted by more than half from north to south in Britain this century (Hurrell & MacIntosh, 1994; Bright, Morris & Mitchell-Jones, 1996).

There is thus a broad spectrum of evidence implying that the national scale (100s to 1000s of kilometres) distribution of small hibernators, including several bats and the dormouse, is directly limited by climate. This an attractive hypothesis, because it offers hope that distribution can be predicted from simple measures of the physical environment. However, it also raises important questions about the conservation of these protected species in regions of Britain the may be climatically unsuitable. Distribution maps suggest that dormice are more common in the south and west of England and this might be associated with milder climates in the south and west.

This part of the report deals with correlates of dormouse distribution on a national scale. It examines dormouse incidence on west-east and south-north axes, attempting to control for variation in incidence due to regional differences in habitat fragmentation (see Part 1). Two hypotheses are examined about distribution on a national scale:

1) That distribution is controlled by habitat quality (excluding fragmentation effects), especially habitat structure and tree species diversity. These factors are important because they determine the amount of food available to dormice (Bright & Morris, 1990).

2) That distribution is controlled by climate. This might occur through the direct effect of ambient air temperature and rainfall on foraging (Bright, Morris & Wiles, 1996) and on intra-hibernal arousals (Bright, *in preparation*). It might also occur indirectly though the influence of weather on the productivity and timing of maturation of tree flowers and fruits (Bright & Morris, 1993).

There is no evidence to suggest that national scale distribution is controlled by other agents, such as predators, parasites or pathogens (Bright & Morris, 1996).

The following analysis shows that there are strong correlations between dormouse incidence and climate. These can be used to improve comparisons of incidence between regions (Part 1), where regions have significantly different climates. They provide the first quantified basis for predicting whether sites or regions are climatically suitable for dormice and thus for targetting reintroductions and habitat management. The results imply that the south-north distribution of dormice and perhaps other small hibernators, is likely to be controlled by climate and that the performance of their populations will be a good indicator of climate change.

Methods

Selection of survey sites

Samples of woodlands were surveyed along a 350 km west-east transect from Devon to Kent and along a 250 south-north transect from Dorset to Shropshire (Fig. 1). Transects were 20 km wide and followed national grid east and north respectively. Transect routes were selected to maximise the distance past through current dormouse distribution, while, for logistical reasons, following the national grid axes. Each transect was divided into segments that were 50 km long and exactly 12 woodlands were surveyed in each.

In an attempt to control for regional differences in habitat fragmentation (Part 1), all survey woodlands belonged to the same woodland age class, area classes and isolation classes (measured as the distance to the nearest ancient woodland). Accordingly, they were all ancient semi-natural woodlands (ASNW) *ie* woodlands with a natural or semi-natural growth form on sites thought to have supported woodland continuously or at least since AD 1600. These were identified from the NCC ancient woodland inventory (Spencer & Kirby, 1992). Six woodlands in each transect segment were 11-20 ha in area and isolated by <500 m. The six remaining woodlands were 21-50 ha in area and isolated by <500 m (there were insufficient ASNWs within transect segments to sample a single area class). Aside from this stratification, all survey woodlands were chosen randomly from Ordnance Survey 1:25,000 maps.

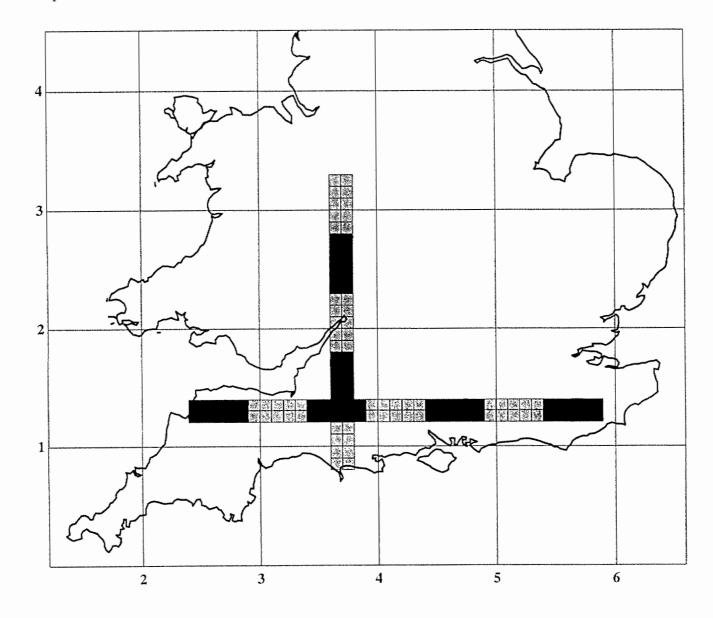
Field methods

Methods used to determine dormouse presence or absence were the same as those described in Part 1. To assess habitat structure, tree species composition and diversity (and find suitable places to survey for hazel nut shells), the survey woodland was quartered and a representative area of 50 m by 100 m (0.5 ha) identified. The total number of canopy-forming trees within this area were counted (DEN). The maximum diameter of the canopies of 25 of these trees was then estimated (DIA). These measurements yielded an index of tree canopy overlap (m^2):

Tree canopy overlap = $DEN/(1/pi(0.5 DIA)^2)$

This complex variable measures the amount of shade cast on the understorey by canopy trees and is a powerful discriminant of habitat quality for dormice (Bright & Morris, 1990). The higher the overlap, the lower the habitat quality because understorey shrubs are more shaded and produce fewer flowers and fruits, which are principal dormouse foods (Richards *et al.* 1984; Bright & Morris, 1993). Within the 50 m by 100 m area previously identified, the relative percentage cover of trees and shrubs was estimated in 15, 10 m by 10 m quadrats. This allowed estimation of the percentage cover of different woody species for a representative area of each woodland and calculation of a Shannon diversity index (Magurran, 1988). Woody species diversity is another powerful discriminant of habitat quality for dormice (Bright & Morris, 1990); higher diversity represents the availability of a more continuous succession of arboreal food resources. Oak abundance and hazel abundance (% cover) are also discriminants of habitat quality, because they are very important sources of food at most sites (Bright & Morris, 1993; Bright & Morris, unpublished).

Fig. 1. Routes of transects across England used to examine national scale changes in dormouse incidence. Transects were 20 km wide. The west-east transect was 350 km long and ran from Devon to Kent. The south-north transect was 250 km long and ran from Dorset to Shropshire.



Climate data and analytical approach

Measures of ambient temperature, rainfall and bright sunshine for each survey woodland were interpolated using the multiple regression equations provided by White & Smith (1982). Eleven topographical variables, describing such features as elevation and direction of slope, were measured for each survey woodland from Ordnance Survey 1:25,000 maps, following the methods given in White & Smith (1982). These were used as independent variables in regressions which predict micro-climatic variables for each quarter of the year. This method has been subject to some criticism, but a recent analysis confirmed that the regressions had high explanatory power (Lennon & Turner, 1995). PWB has micro-climatic data from several woodlands that could be used to help validate the predictions from White and Smith's (1982) regressions, but doing so was not part of the present contract. It can however be assumed that the regression equations at least provide reliable *relative* (between woodlands) measures of micro-climate.

The relationships between habitat and climate and dormouse incidence were analysed using multiple logistic regression in the manner described in Part 1. The climatic variables were autocorrelated and therefore could have been exchangeable in the logistic regressions. This potential problem was addressed by examining the regression between incidence and each variable individually. Variables that, individually, were related to incidence were entered into a multiple regression. Subsequently, terms describing first-order interactions between these variables were added to the model; they were retained if they significantly increased the deviance explained by the model. In this way parsimonious models were generated, while accounting for autocorrelation between independent variables. This approach was preferred to reducing the suite of independent variables to principle components, because it generated results that were more readily interpretable and likely to represent real functional relationships.

Results

In total 144 woodlands were surveyed, 84 for the west-east transect and 60 for the south-north transect. The sample was stratified by woodland site area and isolation from the nearest ancient woodland. Logistic regressions were run to check that woodland isolation measured in other ways (namely distance to the nearest 20 ha ancient woodland, number of boundaries around a site and total area of ancient woodland in nine 1-km squares) did not confound relationships with dormouse incidence. None of these measures were related to incidence (p > 0.45 for all variables).

Trends in habitat and climate along the south-north transect

There were no relationships between distance north and any of the measures of habitat quality for dormice, except tree canopy overlap (Table 1). The latter showed a strongly significant decrease with distance north, implying that canopies were more open so there was less shade on the understorey and habitats were more suitable for dormice. Ambient temperature showed the expected decrease with distance north during all quarters of the year, but the relationship was much stronger (p smaller and r^2 larger) during the winter (January-March and October-December). The mean difference in temperature between the ends of the transect ranged between 1.5°C in October-December and 0.7 °C in July-September.

During July-September there was a significant increase in rainfall with distance north. Sunshine showed a strongly significant decrease with distance north at all times of the year (Table 1).

Variable	r^2	Slope	Intercept	р
a) South-north transect, Dorset to S	Shropshire, 2	250 km (df 59).	
Tree & shrub diversity	0.03	0.00001	1.22	NS
Canopy overlap	0.22	-0.007	3.24	0.001
Hazel abundance	0.05	0.044	11.44	NS
Oak abundance	0.03	-0.043	41.15	NS
January-March temperature	0.19	-0.002	4.32	0.001
April-June temperature	0.07	-0.001	11.97	0.036
July-September temperature	0.13	-0.003	15.68	0.036
October-December temperature	0.69	-0.006	7.94	0.001
January-March rain	0.09	0.00002	0.18	NS
April-June rain	0.00	0.00001	0.19	NS
July-September rain	0.10	0.00006	0.24	0.012
October-December rain	0.00	0.000009	0.26	NS
January-March sunshine	0.94	-0.002	4.36	0.003
April-June sunshine	0.92	-0.003	6.51	0.001
July-September sunshine	0.90	0.002	5.95	0.003
October-December sunshine	0.95	-0.002	2.70	0.001
b) West-east transect, Devon to Ker	nt, 350 km (o	lf 83)		
Tree & shrub diversity	0.09	-0.0005	1.54	0.004
Canopy overlap	0.00	0.00001	1.89	NS
Hazel abundance	0.02	0.0069	15.11	NS
Oak abundance	0.08	-0.044	49.01	0.006
January-March temperature	0.07	-0.0011	4.57	0.01
April-June temperature	0.44	0.0031	10.63	0.00
July-September temperature	0.35	0.0042	13.76	0.00
October-December temperature	0.01	0.00004	7.04	NS
January-March rain	0.75	-0.00003	0.34	0.00
April-June rain	0.61	-0.00002	0.30	0.00
July-September rain	0.75	-0.00002	0.35	0.00
October-December rain	0.75	-0.00005	0.46	0.00
January-March sunshine	0.99	0.0036	2.63	0.00
April-June sunshine	0.21	0.00005	5.84	0.00
	0.78	0.00009	5.95	0.00
July-September sunshine	0.70	0.00002	0.00	0.00

Table 1. Linear regression of variables describing habitat quality and climate on: **a**) northing (south-north transect) and **b**) easting (west-east transect).

Table 2. Logistic regression analysis of factors related to national scale trends in dormouse incidence along **a**) a south-north and **b**) a west-east transect of England. Dormouse incidence was measured in a sample of ancient semi-natural woodlands, which were stratified by woodland site area and isolation in an attempt to control for regional differences in these factors. Incidence was regressed against quarterly measures of climate (temperature, rainfall, bright sunshine), tree diversity, hazel abundance, oak abundance and tree canopy overlap (a measure of woodland structure).

Variable	Coefficient	Wald χ^2	R [*]	р
April-June temperature	41.366	4.99	0.19	0.020
January-March rainfall	474.672	9.19	0.30	0.002
April-June rainfall	2023.219	4.21	0.17	0.040
October-December rainfall	-256.255	6.20	0.23	0.012
April-June temperature × April-June rainfall interaction	-167.161	4.07	0.16	0.043
Constant	-525.468	5.23	-	0.022

a) South-north transect, from Dorset to Shropshire totalling 250 km. The regression correctly classified 80.0% of 60 survey sites. χ^2 goodness-of-fit, p=0.94.

b) West-east transect, from Devon to Kent totalling 350 km. Neither habitat quality nor climate variables were correlated with dormouse incidence and thus no regression was generated.

* The R statistics can be interpreted as the partial contribution of a variable to the regression model.

Trends in habitat and climate along the west-east transect

Tree and shrub diversity showed a significant decrease from west to east, but by a small amount (Shannon index from 1.54 to 1.36) and the regression explained only a small percentage of the variation (9%; Table 1). Oak abundance showed a similar significant trend, but also changed by only a small amount from west to east (49% to 33%) and the regression explained little of the variance. Thus there were no biologically significant trends in habitat quality for dormice along the west-east transect.

During the summer months (April-June and July-September), ambient temperatures showed a strongly significant increase with distance east; the mean difference in temperature between the ends of the transect was about $1^{\text{O}\text{C}}$. The direction of the relationship was reversed in January-March, but the regression relationships was much weaker (r² smaller and p larger). The dominant difference in temperature was thus in summer, not winter. As expected there was a strongly significant gradient in rainfall, decreasing from west to east, at all times of the year. This was mirrored by a gradient in sunshine which strongly significantly increased from west to east (Table 1).

Relationships between dormouse incidence, habitat and climate

Along the south-north transect, there were no relationships between dormouse incidence and variables describing habitat quality for dormice. Incidence was, however, strongly correlated with climatic variables: April-June temperature, rainfall in January-March, April-June and October-December. There was a significant interaction between temperature and rainfall in April-June. Correlations were positive, except for the latter interaction and October-December rainfall. The logistic regression correctly classified a large proportion (80%) of survey woodlands (Table 2).

Along the west-east transect none of the variables describing habitat quality or climate were correlated with dormouse incidence (Table 2).

Discussion

Limitations of the survey and analysis

The survey sought to partition the influence of regional differences in woodland fragmentation from national scale trends in climate and habitat quality. Rigourous stratification of samples clearly achieved this to a large extent, as evidenced from the fact that: a) measures of woodland isolation not used to stratify the samples were not significant predictors of dormouse incidence; and b) individual transect segments spanned two or more landscape types (eg Natural Areas), so they reflected dormouse incidence on a larger scale than the regional one examined in Part 1. However, it would be naive to suggest that the sampling protocol completely removed effects due to woodland fragmentation. Rather, it should have allowed resolution of national-scale trends that would otherwise have been masked by regional differences in woodland fragmentation.

Variables were selected for inclusion in the regression models according to the strength of their individual correlation with dormouse incidence. The regressions should thus not have been unduly influenced by autocorrelation between the independent variables, as they might have been if stepwise variable selection had been used. The close correlation between some variables, eg rainfall and

temperature, was reflected in interaction terms included in the models. Nevertheless, weather variables are clearly interdependent, so it is likely that in part the regressions represent purely statistical rather than functional relationships. However, autecological studies provide direct evidence that dormice are influenced by weather conditions (Bright *et al.* 1996), so many of the relationships are likely to be functional.

Correlates of national scale distribution

Dormouse incidence was strongly correlated with climatic variables along the southnorth transect, as expected from distribution maps (Hurrell & MacIntosh, 1984; Bright, Morris, Mitchell-Jones, 1996). Incidence decreased from 0.41 at the south end of the transect to 0.08 at the northern end, despite an increase in habitat quality (decrease in canopy overlap) with distance north. Lower temperatures and rainfall are known to retard the activity of dormice in summer (Bright *et al.* 1996), and probably compromise survival and reproductive output. Therefore the south-north distribution of dormice is probably controlled by climate, rather that habitat quality or fragmentation.

Dormouse incidence was positively related to rainfall during January-March, whereas rainfall is known to decrease dormouse activity (Bright, *et al.* 1996). This anomalous finding may imply that the relationship is purely statistical rather than functional, but equally may reflect use of different rainfall statistics. Bright *et al.* (1996) used total nightly rainfall which is likely to closely reflect the nocturnal conditions dormice experience. The present study used mean daily rainfall, which may not correlate with dormouse activity. It does, however, reflect soil moisture deficit, an important predictor of plant growth, which, in turn, will be correlated with food availability for dormice. Whatever the explanation, it is clear that dormouse incidence is strongly related to the south-north climatic gradient.

Dormouse incidence was not correlated with climate or habitat quality along the west-east transect, nor did it show any significant trend with distance east. By contrast, distribution maps show that there are more *known* dormouse *sites* in southwest rather than south-east England (Hurrell & MacIntosh, 1994; Bright *et al.* 1996). Evidence from the Blackdowns and the High Weald (Part 1) confirms that this is the case, at least for these Natural Areas. This apparent contradiction arises because woodlands are more fragmented in the west of England where there are many small woodland sites; there are fewer, larger sites in the east. Such confounding affects of woodland fragmentation were controlled for, at least in part, by the sampling protocol used in the present study (see above). Therefore the west-east distribution of dormice is not controlled by climate or habitat quality. There are no trends in west-east dormouse incidence, at least along the transect route, that cannot be explained by regional differences in woodland fragmentation.

The lack of difference in incidence between the west and east end of the transect is perhaps surprising, given the strong west-east climatic gradients and the strong correlation between incidence and similar climatic gradients on the south-north transect. The lack of difference may be due to a threshold effect: climatic conditions along the entire west-east transect may be within bounds of tolerance by dormice, while parts of the south-north transect lie beyond a threshold at which climate begins to influence the animals.

Implications for Conservation

1. This study provides the first quantified evidence that the south-north distribution of dormice is related to climate. With current data, it is difficult to define at what distance north in Britain climate begins to significantly compromise dormouse populations. However, there was a very rapid fall in dormouse incidence along the south-north transect in Shropshire. A reasonable estimate would thus be that populations north of Shropshire are likely to be directly limited by climate. Populations this far north may thus be in jeopardy, unless local habitat or micoclimate conditions are especially favourable.

2. Conservation management of dormice in northern England (north of Shropshire) should thus concentrate on maintaining high habitat quality, to buffer populations against an unfavourable climate. Existing evidence from nestbox monitoring shows that northern populations occur at low density and are unlikely to be productive. In all probability they are therefore likely to be closed, relict populations. Landscape scale management for them will thus be pointless.

3. Dormice are known from only three areas in northern England (the River Allen valley in Northumberland, Roudsea Wood NNR and the Duddon valley in west Cumbria). The Great Nut Hunt failed to locate any new sites in the north. It is thus clear that dormice have not simply been under recorded in northern England and that the populations occurring there are especially precious. Habitat management for and monitoring of these populations should be a high conservation priority, because their extinction would mean the contraction of the dormouse's range by over 200 km.

4. The findings that the west-east distribution of dormice is not correlated with climate and that dormice are not more numerous in the west of England after the effects of woodland fragmentation are accounted for, were unexpected. They are important because it has been assumed that the west of England was more favourable for dormice. This is not the case, and conservation management (including grant-in-aid) should not therefore be biased towards western England.

5. Confirmation that the south-north distribution of dormice is controlled by climate, raises the longer term question of the response of dormouse populations to predicted climate change. Most climate change scenarios suggest an increase in rainfall as well as temperature for Britain. Current understanding of dormouse ecology suggests that higher rainfall would adversely affect dormouse populations, but that higher temperatures (at least in summer) might benefit them. It is thus uncertain how dormouse populations would respond. There is a need to understand more about these likely responses to help plan future conservation strategies, because recent extinction of dormice from the northern half of their range may well have been precipitated by climatic flux. Future climatic change may have commensurately large and possibly detrimental affects on dormouse distribution in Britain.

Future work

1. The results in Part 2 of this report need to be integrated with data on the density and performance of dormouse populations which is already available from National Dormouse Nestbox Monitoring sites. This would allow a synthesis of the factors and mechanisms controlling distribution on local scales (nestbox data), and the large scales examined in this report. PWB will undertake this work as soon as time allows.

2. The relict distribution of dormice at a few sites in northern England is paralleled by the distribution of several species of lepidoptera and probably a host of other invertebrates and plants. These species may be climate-sensitive like the dormouse. An understanding of the climatic factors that have allowed relict dormouse populations to survive at certain favoured sites in the north should thus provide invaluable information pertinent to a whole group of other climate-sensitive species. A study is needed to: a) examine critical aspects of the population ecology of dormice at northern sites and compare these with populations in the south; b) identify special features of the micro-climate of northern sites; c) to compare the distribution of past and present relict dormouse populations in the north with the distribution of similar populations of other climate-sensitive species.

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