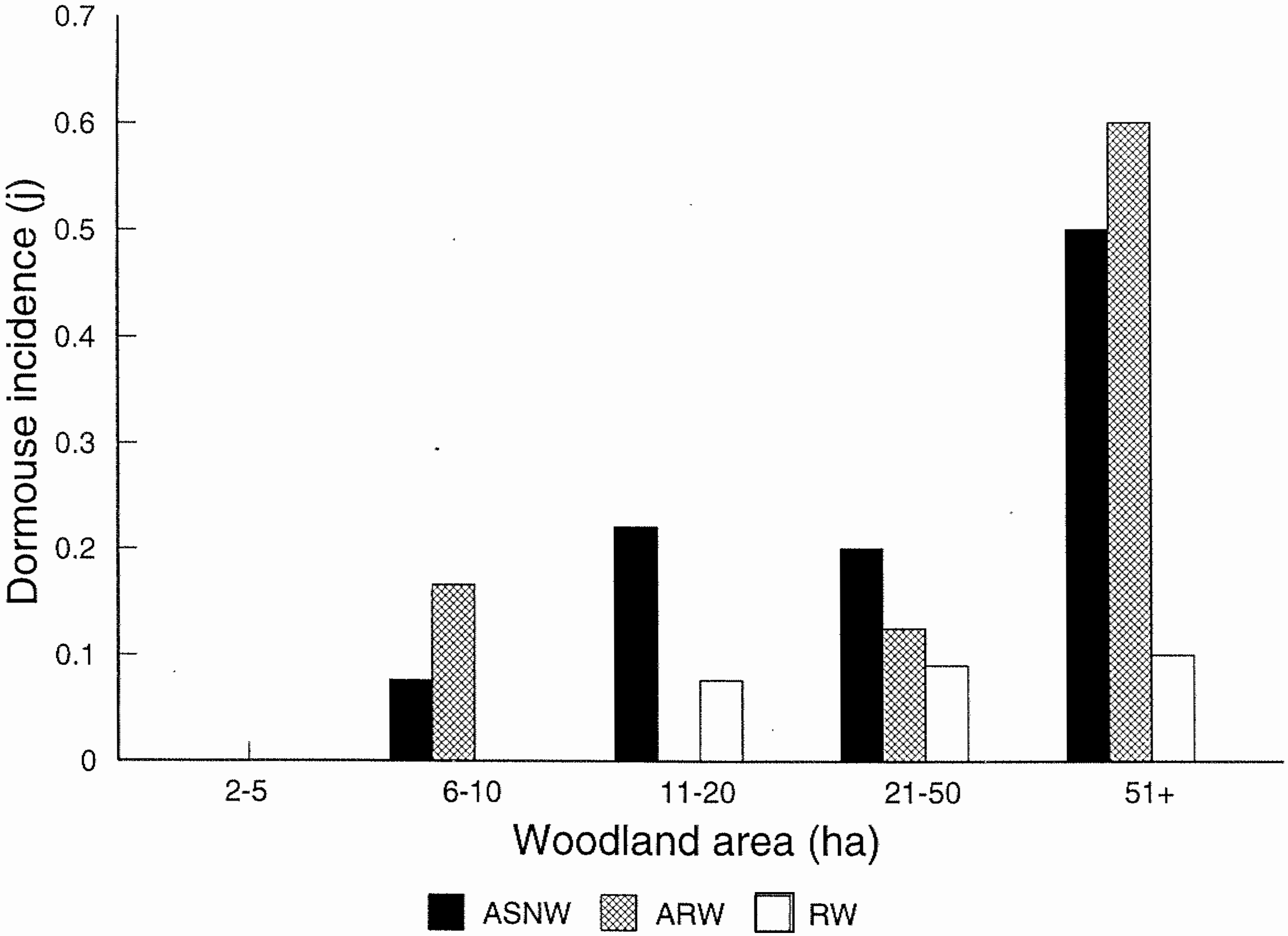
Fig. 2. Incidence of dormice (proportion of sites with dormice present) in relation to woodland site area in the Greater Cotswolds Natural Area. Data for three woodland age classes are shown: ancient semi-natural woodland (ASNW), ancient replanted woodland (ARW) and recent woodland (RW).



Mean site areas were significantly greater in the High Weald than in either the Greater Cotswolds or the Blackdowns. Mean distances to the nearest ancient woodland and mean distances to the nearest 20 ha ancient woodland were significantly different between all regions; in order of increasing magnitude they were: High Weald, Herefordshire, Greater Cotswolds, Blackdowns. The Greater Cotswolds had fewer boundaries per woodland site than any of the other regions and there were also fewer boundaries per site in Herefordshire than in the Blackdowns or the High Weald.

Woodland attributes for each region are summarised in terms of densities per km^2 in Figure 3. This gives an alternative perspective to the site-based statistics, which takes account of the often contagious distribution of woodlands. The Greater Cotswolds were characterised by a low overall density of woodland (all age classes: 6.46 ha/km^2) and of ancient woodland (ASNW and ARW: 3.90 ha/km^2). Woodlands were small (all age classes: mean 16.02 ha) and isolated, especially in terms of the small number of boundaries around them (all age classes: mean 7.05). The Blackdowns had a relatively high density of woodland (all age classes: 8.15 ha/km^2), most of which was of recent origin. A high density of woodland sites and boundaries, reflected the fact the most woodlands were small, but interlinked by many hedgerows. Herefordshire had a density of boundaries and overall density of woodland intermediate between that of the Greater Cotswolds and the Blackdowns, but a much higher proportion of woodland was ancient (ASNW and ARW: mean 5.83 ha/km^2). The High Weald had an exceptionally high density of woodland, most of it ancient, and a high density of boundaries.

Comparison of predicted dormouse distribution between regions

The logistic regressions for each region correctly classified a high proportion of survey woodlands (74-89%; Table 4). The equations were applied to all woodlands in each region that had not been surveyed. Based on a total of 79 woodland sites known to support dormice from previous, independent, surveys, the regressions correctly classified between 72-88% of woodland sites (Table 7). This was on the basis of attributes of woodland site area and isolation alone.

Dormice were predicted to be very rare in the Greater Cotswolds, occupying only 4% of sites; widespread in the High Weald (32% of sites) and Herefordshire (33% of sites); and common in the Blackdowns (46% of sites; Table 7). In the Greater Cotswolds and Herefordshire, most predicted dormouse sites were in ancient woodlands (77% and 92% respectively; the figure for the Greater Cotswolds may be an underestimate, because few RWs were occupied and predictions for this age class alone could consequently not be made; Table 3). By contrast almost half of the predicted sites in the Blackdowns and the High Weald were in recent woodlands (43% and 46% respectively; Table 7).

Maps showing the predicted distribution of dormice and the distribution of woodlands in each region are given in Figures 4 to 11.

Using these predictions, and assuming that occupied sites are randomly distributed (for the purpose of the following crude estimate, they can be assumed to be), the average distance between dormouse sites can be calculated. These are: Greater Cotswolds 4.3 km; Blackdowns 1.1 km; High Weald 1.1 km; Herefordshire 1.6 km.

Table 7. The predicted occupation by dormice of woodland sites in four contrasting regions of England. The percentage of sites in three woodland age classes predicted from logistic regressions to be occupied by dormice are shown, together with the percentage of predicted total sites in each age class. The number of occupied sites found in the same regions by independent surveys and the percentage of these sites that logistic regressions correctly classified are also shown.

Age class	Total number of sites	% predicted to be occupied	% of predicted sites in each age class	Number of sites surveyed independently	% correct classification
a) Greater Cotswolds Natural Area					
ASNW	286	9.4	50.0		
ARW	103	14.5	27.7		
RW	892	1.3	22.2		
All	1281	4.2	-	17	88.2
b) Blackdowns Natural Area					
ASNW	95	80.0	42.2		
ARW	35	71.4	13.8		
RW	261	30.2	43.8		
All	391	46.0	-	22	72.7
c) High Weald Natural Area					
ASNW	726	21.9	42.6		
ARW	102	38.2	10.4		
RW	337	51.9	46.9		
All	1165	32.0	-	28	85.7
d) Herefordshire					
ASNW	379	34.0	53.7		
ARW	127	73.2	38.7		
RW	203	8.8	7.5		
All	709	33.8	-	12	83.3

Fig. 3. Densities of woodland per kilometre square for four regions of England. The quantities shown are: density of woodland sites, total woodland density, ancient woodland density and density of boundaries around woodlands (equivalent to hedgerows).

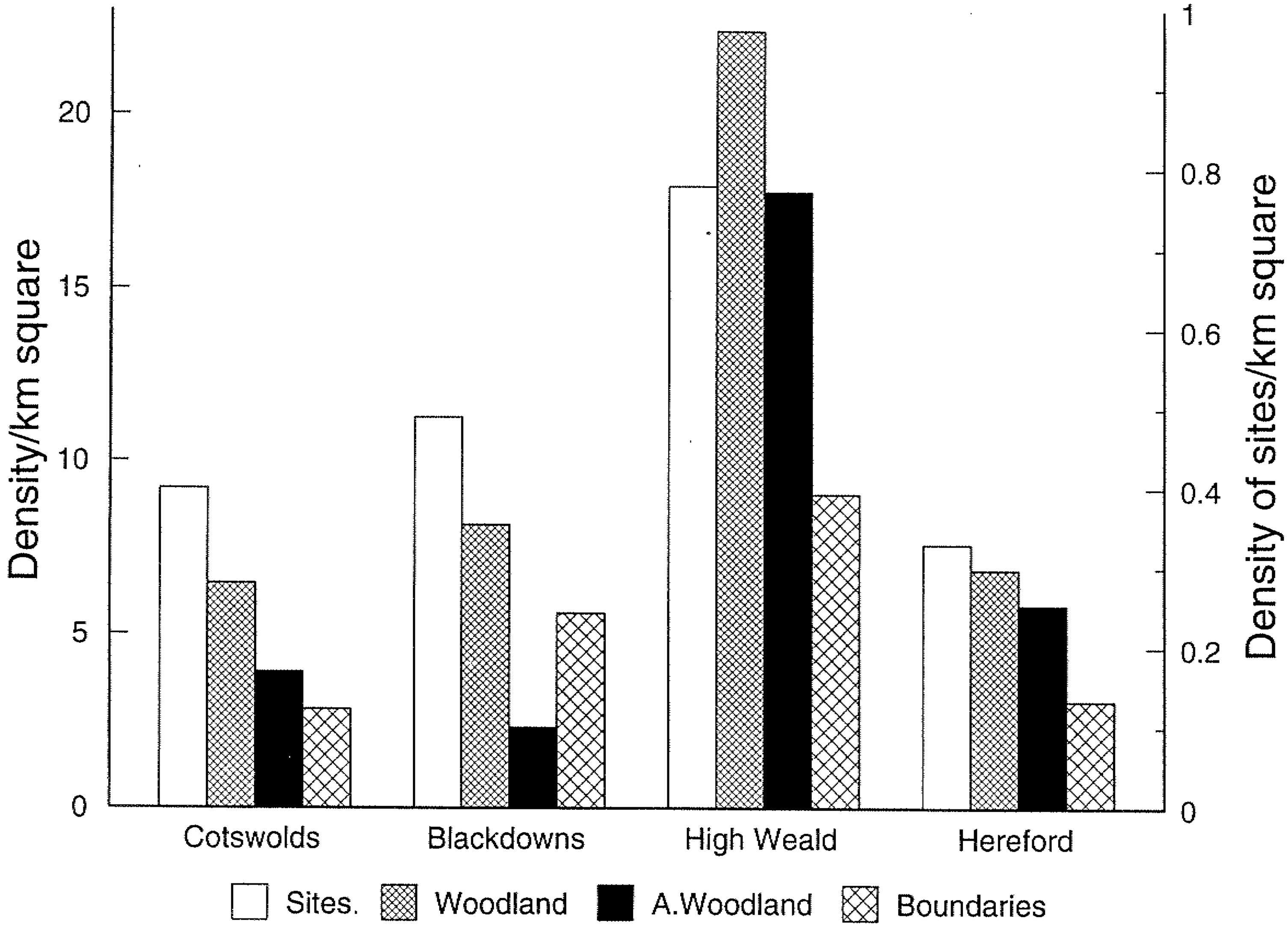


Fig 4. Distribution of woodlands in the **Greater Cotswolds** Natural Area. Three woodland age classes are shown: ancient semi-natural woodland (**black symbols**), ancient replanted woodland (**grey symbols**) and recent woodland (**white symbols**). Larger symbols represent larger woodland site areas. The grid is 10 km.

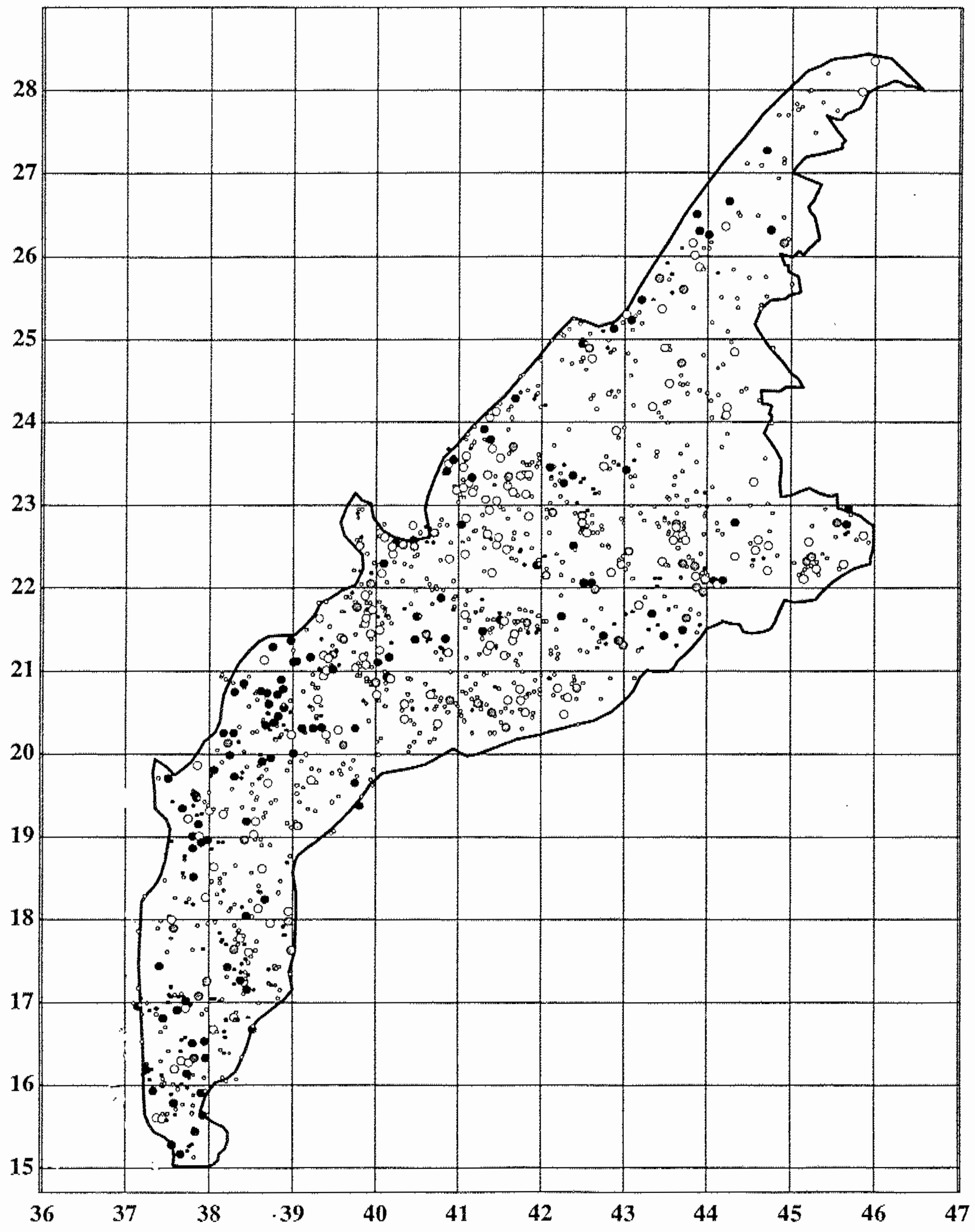


Fig. 5. Known and predicted distribution of dormice in the **Greater Cotswolds** Natural Area. Black symbols represent dormouse presence, white symbols dormouse absence. The grid is 10 km.

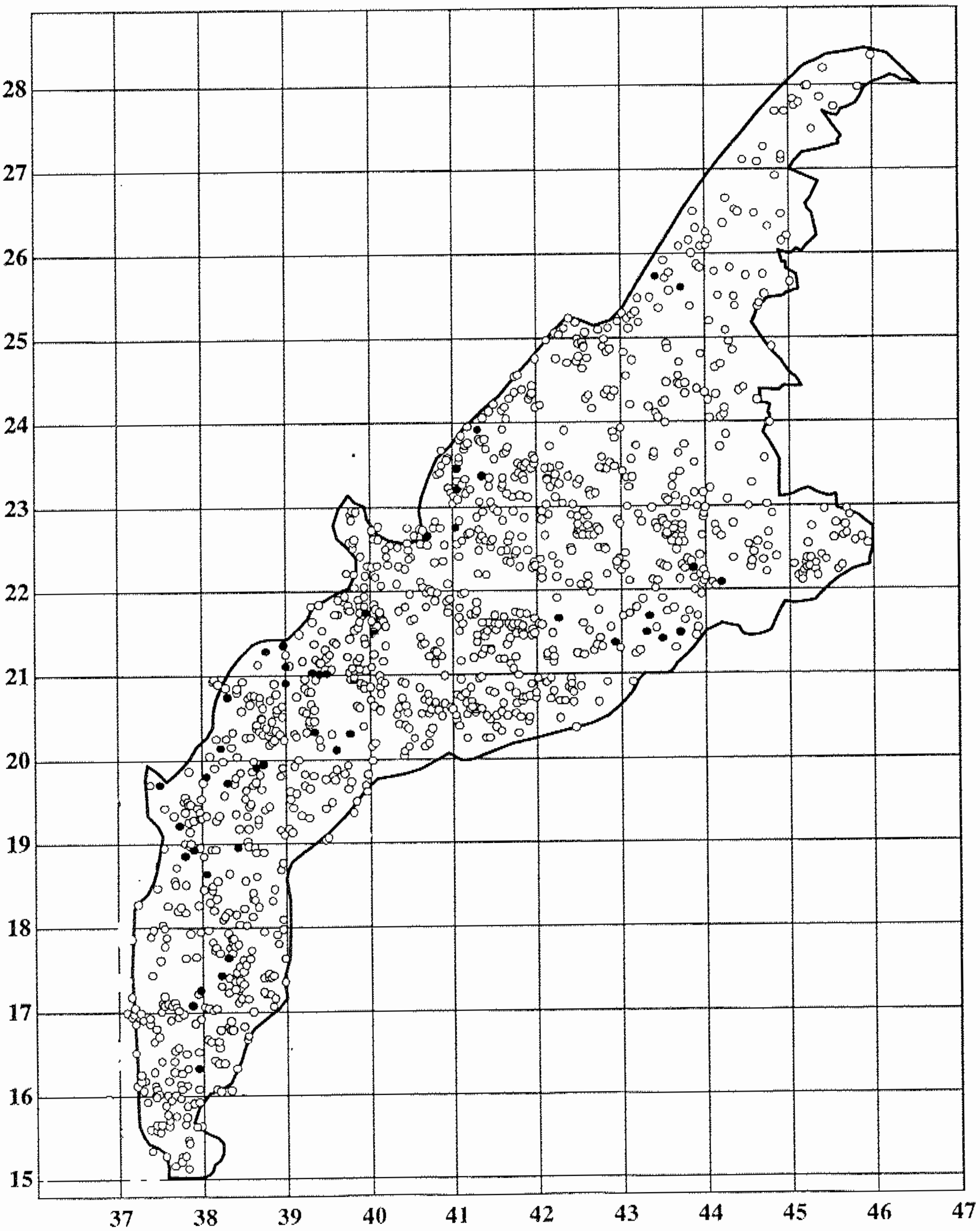


Fig 6. Distribution of woodlands in the **Blackdowns** Natural Area. Three woodland age classes are shown: ancient semi-natural woodland (**black symbols**), ancient replanted woodland (**grey symbols**) and recent woodland (**white symbols**). Larger symbols represent larger woodland site areas. The grid is 10 km.

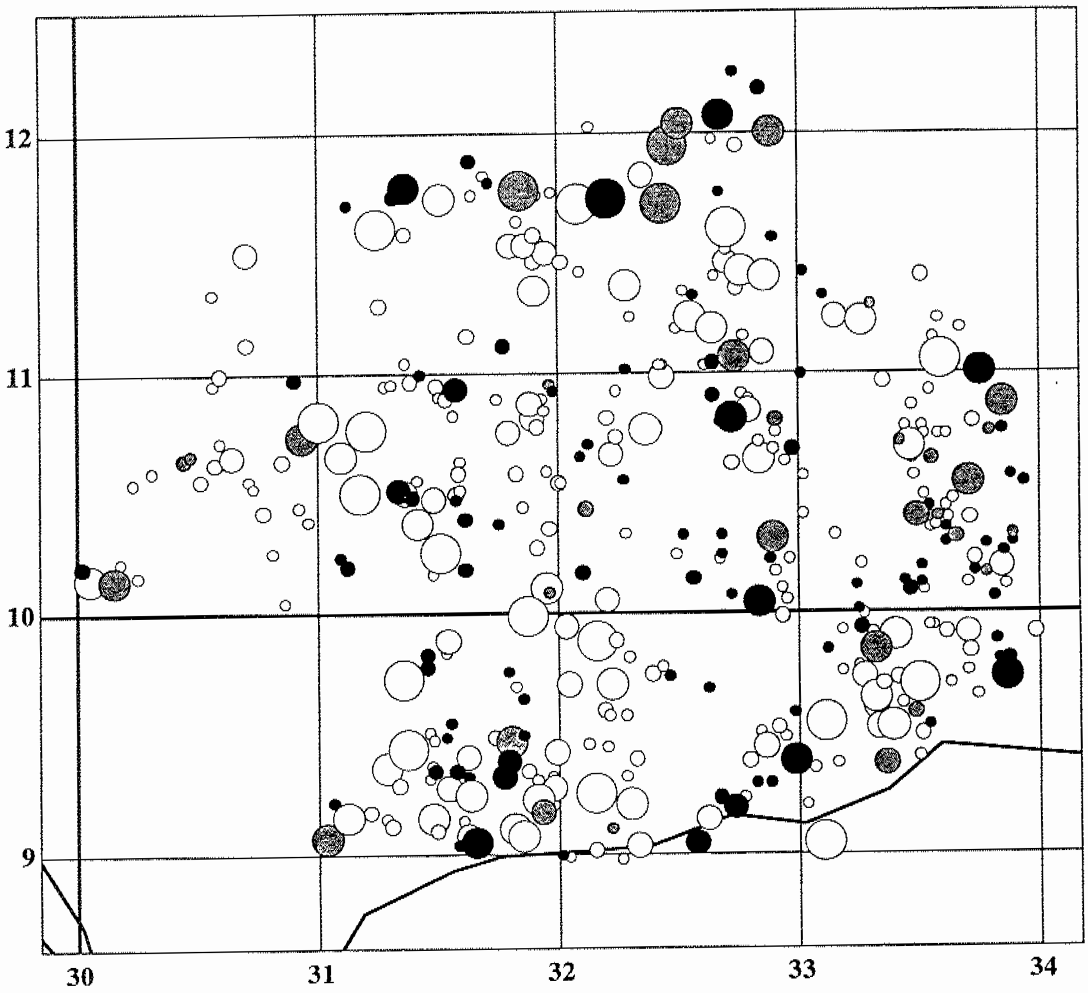


Fig. 7. Known and predicted distribution of dormice in the **Blackdowns** Natural Area. Black symbols represent dormouse presence, white symbols dormouse absence. The grid is 10 km.

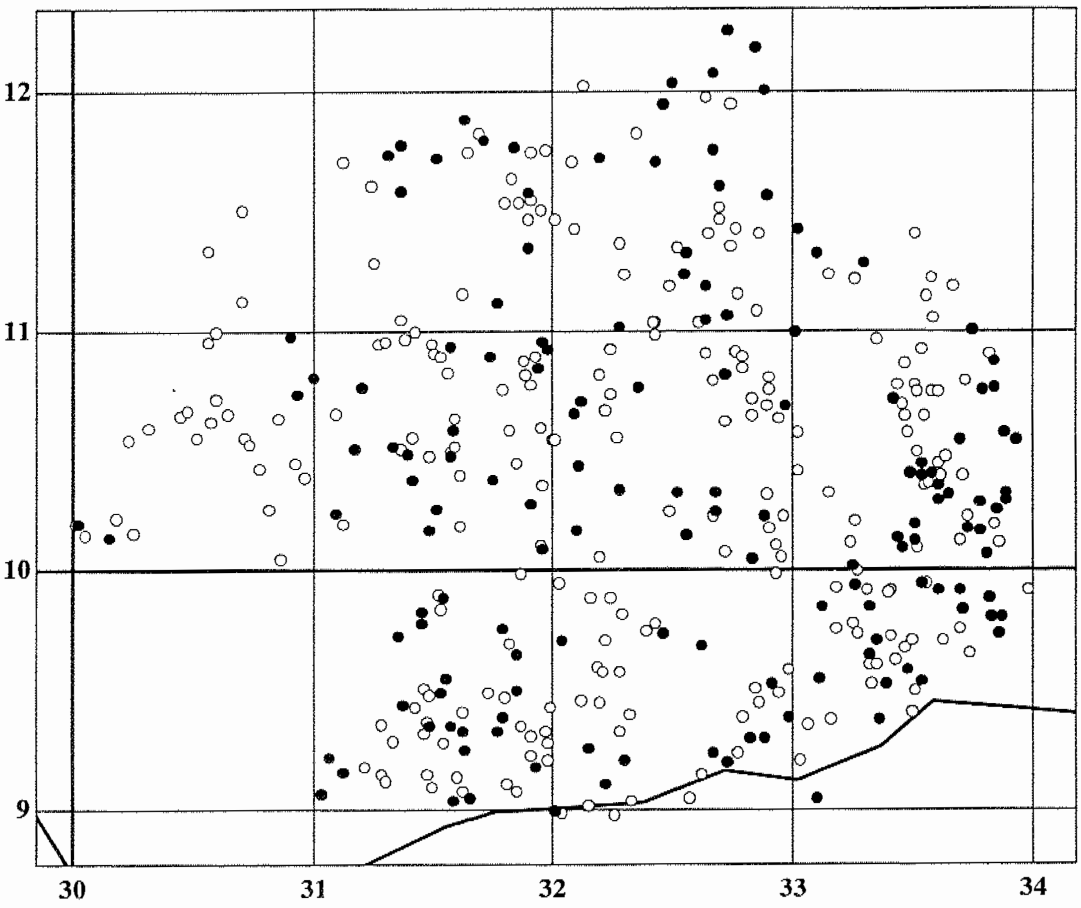


Fig 8. Distribution of woodlands in the **High Weald** Natural Area. Three woodland age classes are shown: ancient semi-natural woodland (**black symbols**), ancient replanted woodland (**grey symbols**) and recent woodland (**white symbols**). Larger symbols represent larger woodland site areas. The grid is 10 km.

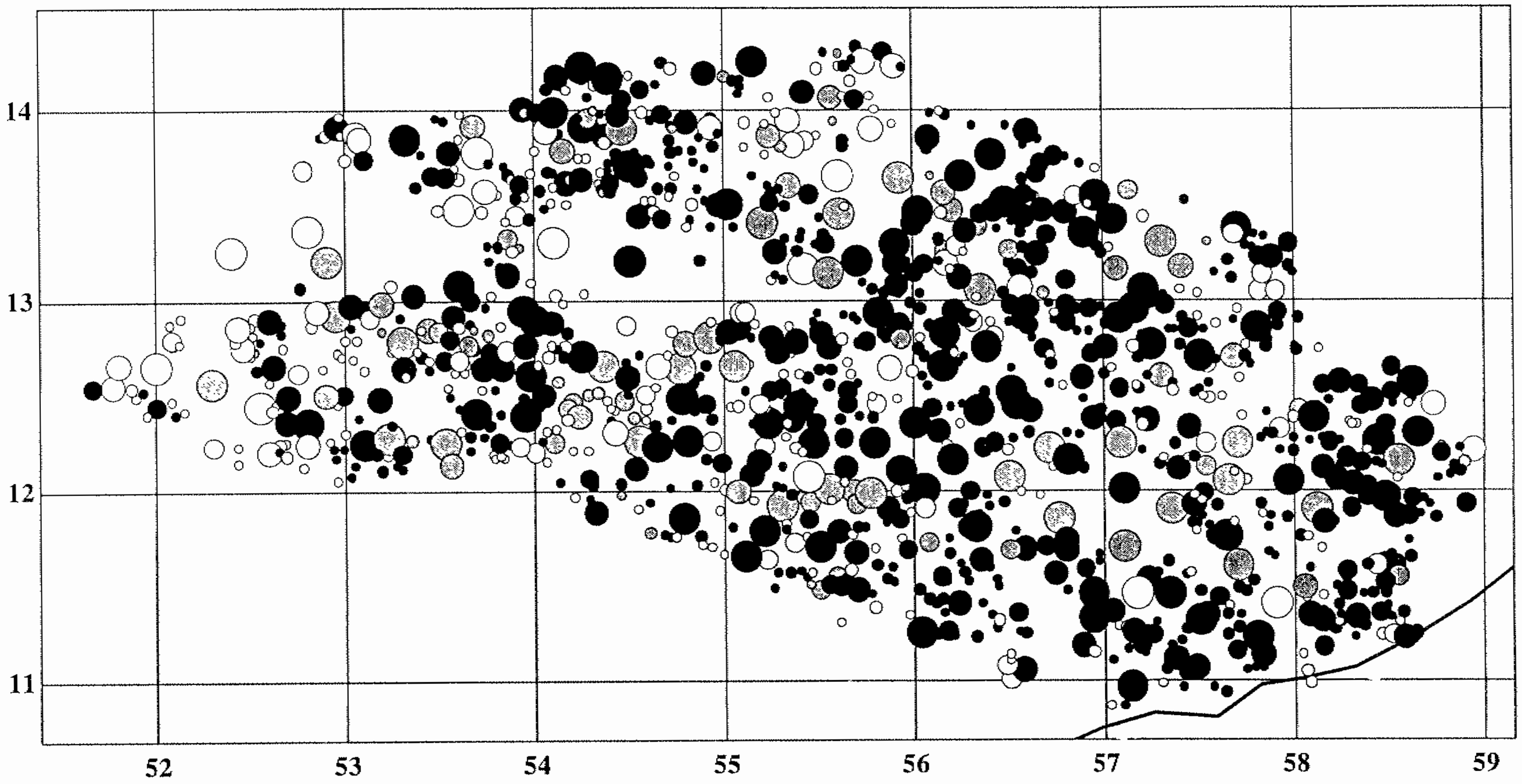


Fig. 9. Known and predicted distribution of dormice in the **High Weald** Natural Area. Black symbols represent dormouse presence, white symbols dormouse absence. The grid is 10 km.

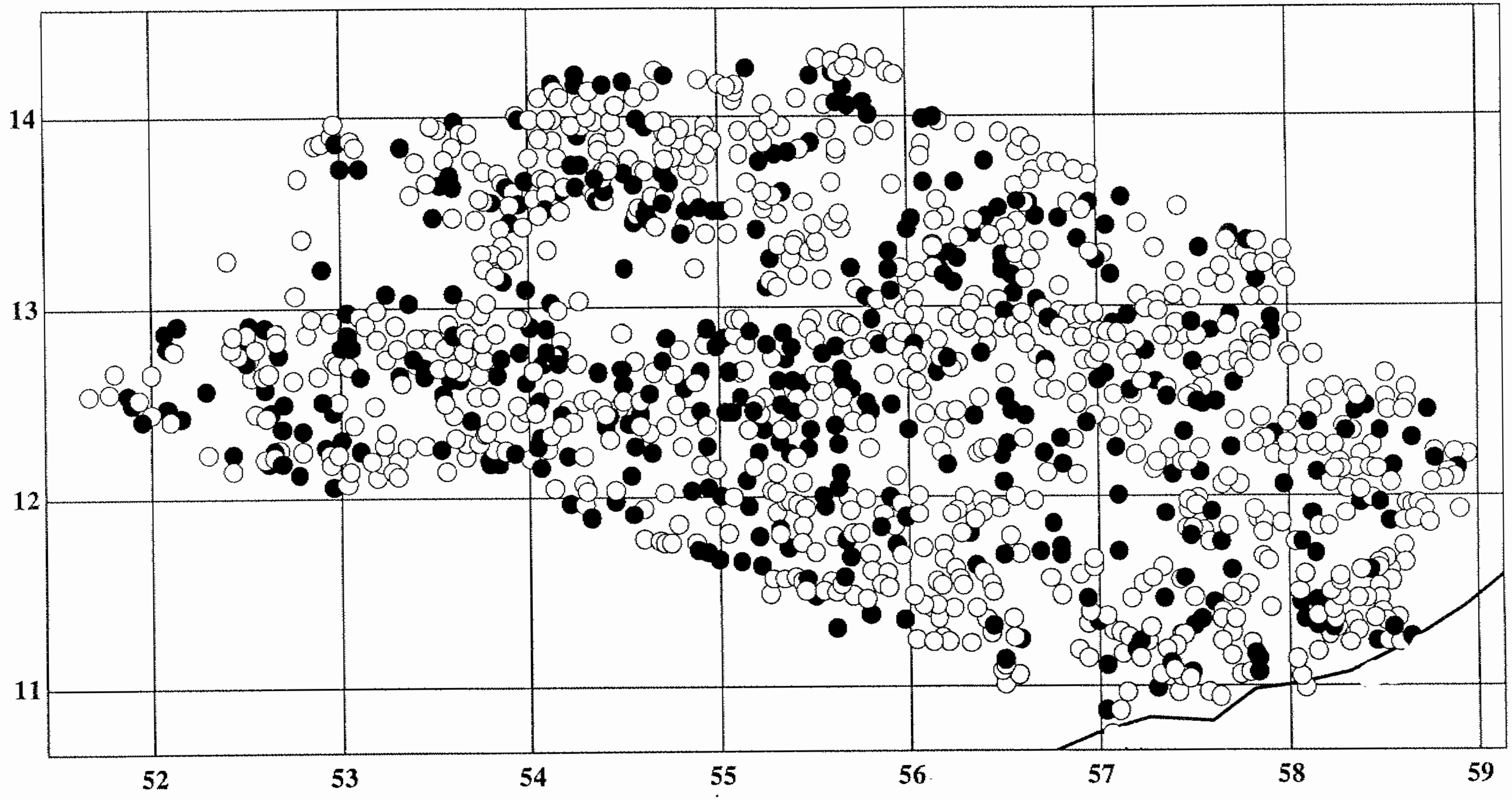


Fig 10. Distribution of woodlands in the **Herefordshire** survey area. Three woodland age classes are shown: ancient semi-natural woodland (**black symbols**), ancient replanted woodland (**grey symbols**) and recent woodland (**white symbols**). Larger symbols represent larger woodland site areas. Data for recent woodlands from: Bright, Mitchell & Morris, 1994. The grid is 10 km.

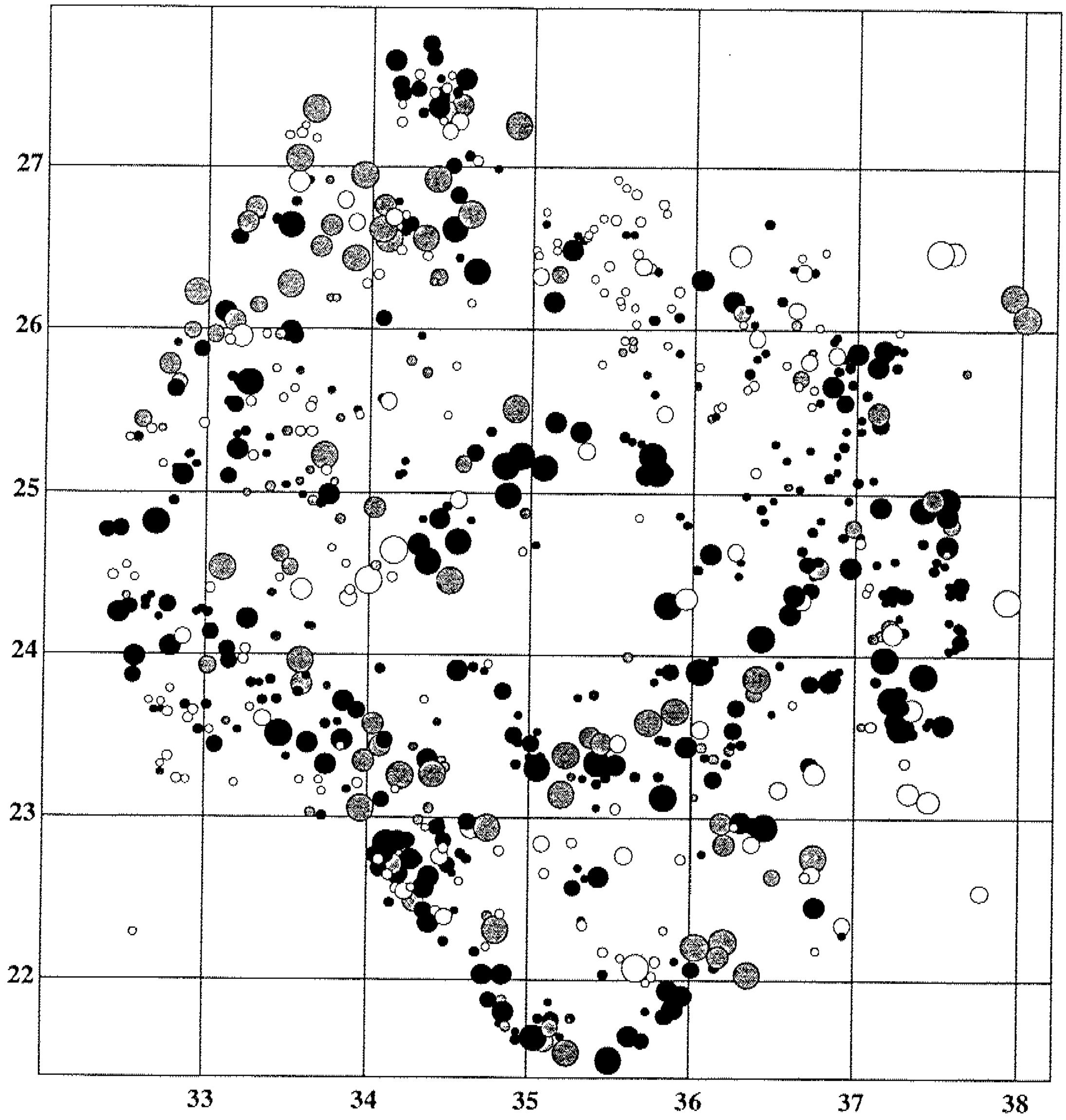
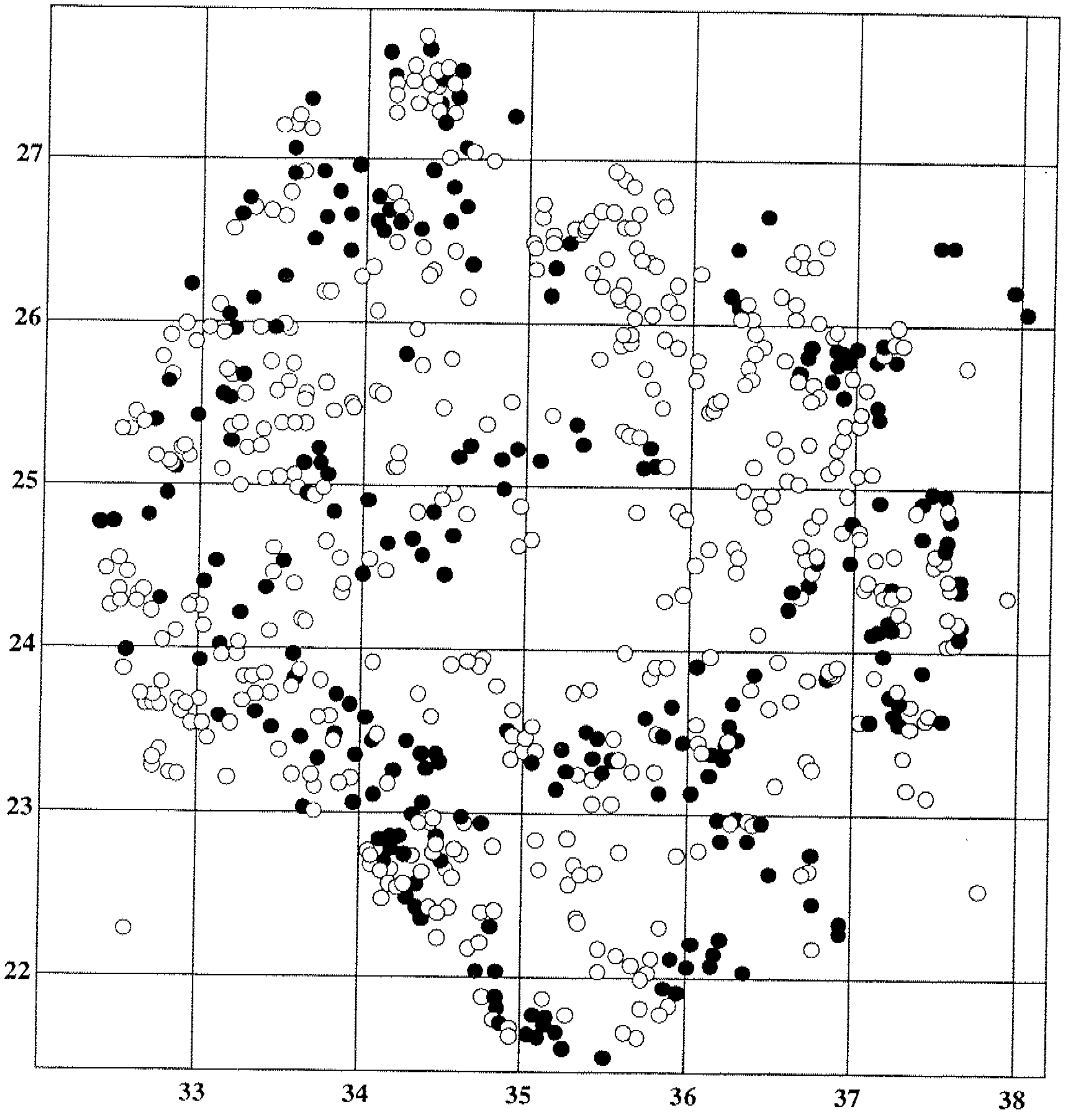


Fig. 11. Known and predicted distribution of dormice in the **Herefordshire** survey area. Black symbols represent dormouse presence, white symbols dormouse absence. Data from: Bright, Mitchell & Morris, 1994. The grid is 10 km.



Discussion

Limitations of the survey and predictive techniques

The survey was designed to resolve the broad patterns of dormouse distribution, based on predictions from simple map-derived attributes. This it did very successfully, correctly classifying a large proportion of independently surveyed sites. However it is important to appreciate that the predictions take no direct account of habitat quality, woodland management history or climate, which are likely to be important local determinants of site occupancy by dormice. The survey thus provides a sound basis for understanding the factors that control large scale distribution and planning conservation management accordingly; it does not provide a substitute for further detailed local surveys, especially in regions not covered by the current study.

Limitations of the field survey technique were discussed by Bright *et al.* (1994). In statistical terms, a large proportion of woodlands were surveyed in each region (12% to 33%), which together with stratified sampling should have produced robust estimates of dormouse incidence. As in the Herefordshire survey (Bright *et al.* 1994), some woodlands could not be surveyed because they lacked heavily fruiting hazel (they were replaced by others with the same attributes). Woodlands in extreme area or isolation classes were also very infrequent in some regions, so that the target of 12 woodlands per survey stratum was not always met. However, as in the Herefordshire survey, it is clear that these factors did not influence the results.

Incidence was used as a measure of dormouse status. It represents the density of populations, a more appropriate measure of status for a regional-scale study than population density *per se*. Incidence should closely reflect total regional population size (though measuring this was not an objective), unless there is large systematic variation between regions in population density or population size at individual sites. Existing data from over 30 sites suggests that population density is not likely to vary systematically between the regions surveyed; instead it is closely correlated with site-specific habitat quality (Bright, unpublished; see also Part 2 of this report). However, mean woodland areas were significantly larger in the High Weald than in the Greater Cotswolds or the Blackdowns (Herefordshire did not differ). Therefore incidence may under-index total population size in the High Weald by a factor of 1.38 (the ratio of the mean site area in the High Weald: mean site area for all regions). In the present context, this would only be important if regional persistence was mainly correlated with the size of individual populations (woodland areas), which it is not (see below).

Theoretical framework

The woodland attributes measured in this study were chosen because they were likely to correlate with two of the principle processes influencing large scale distribution: population colonisation and extinction. Less isolated woodlands should have a higher probability of being colonised. On average, woodlands of greater area should support larger dormouse populations, with a congruent lower probability of extinction. Alternatively, larger woodlands may be more likely to contain the micro-habitat that dormice need and thus more likely to support them. However, preliminary analysis of vegetation data collected during the survey shows that this was not the case: within age classes, there were no differences between area strata in tree and shrub diversity or woodland structure.

This emphasis on site area and isolation should not be taken to imply that dormice are distributed as metapopulations *ie* a population of discrete local populations, persisting through dispersal of individuals between suitable habitat patches (Hanski

& Gilpin, 1991). Dormice certainly also occur as isolated, relict, populations (non-equilibrium metapopulations). A correlation between incidence and woodland area, but not woodland isolation, would be suggestive of relict populations. By contrast, a correlation between dormouse incidence and woodland isolation would provide partial evidence for a metapopulation structure. It is likely that dormouse populations are structured in both these ways, depending on woodland and hedgerow fragmentation.

It should also be appreciated that dormice are unlikely to fit the traditional Levins metapopulation model, in which individual populations are transient, the metapopulation persisting by frequent colonisation and extinction (Hanski & Gilpin, 1991). Such turnover probably does occur in dormouse populations, but its frequency needs to be measured over decades, not annually. Dormouse populations probably thus have higher temporal stability than that implied by the Levins model, and their dynamics need to be viewed on ecological, not human, time scales.

Processes controlling regional distribution

Dormouse incidence was related to attributes of woodland area and/or isolation in all regions. These relationships could have been genuinely causal or purely statistical, area and isolation being autocorrelated with other variables. In particular, site area and isolation might have been autocorrelated with habitat quality or climate. It is clear, however, that habitat quality did not affect the relationships because: a) samples were selected on the basis of map-derived attributes, not habitat - woods of differing quality should therefore have been randomly distributed among survey strata; and b) preliminary analysis of vegetation data collected during the survey shows that within age classes there were no differences in habitat quality between area and isolation classes. There *were* differences in habitat quality between age classes, indeed this was the reason for stratifying the samples by woodland age. However, within age classes habitat quality did not appear to differ between regions.

Part 2 of this report describes the influence of climate on dormouse incidence. It shows that climate is related to incidence on a south-north, but not a west-east axis. Thus incidence in the Greater Cotswolds and Herefordshire (further north) might be lower due to climate than in the Blackdowns or the High Weald (further south). A logistic regression showed that the mean incidence at the same distance north as the Greater Cotswolds was 0.19. The corresponding figure for the Blackdowns was 0.25. Thus incidence declined by only 0.06 (but decreased very rapidly north of the Greater Cotswolds; Part 2). Within the regions surveyed, incidence thus appears to change little as a result of climate.

It is thus clear that the relationships between incidence and site area and isolation are not unduly confounded by other factors. Furthermore, it is here postulated that these relationships are in fact also causal.

In the Blackdowns and the High Weald where the number of boundaries (equivalent to hedgerows) around woodlands were high and the density of woodland sites (per km^2) were also high, dormice frequently occurred in recent as well as ancient woodlands. Logistic regressions showed that incidence in the Blackdowns and the High Weald was strongly correlated with measures of woodland isolation, especially the number of boundaries. These results clearly imply that low isolation between sites in some regions has permitted dormice to colonise recent woodlands.

Furthermore, dormice occurred frequently in very small woodlands in the Blackdowns, whereas they were very scarce in small woodlands in other regions where woodlands were isolated (Greater Cotswolds, Herefordshire). Evidence from

Herefordshire (Bright *et al.* 1994) and the Greater Cotswolds (see below) suggests that dormice are unlikely to persist in such woodlands if these are isolated. This further supports the contention that dispersal between sites may be an important process supporting the maintenance of dormouse distribution in the Blackdowns and the High Weald.

By contrast, dormouse incidence in recent woodlands in the Greater Cotswolds and Herefordshire was very low. Woodlands in these regions, especially the Greater Cotswolds, were very isolated, both in terms of the number of boundaries and the density of woodland sites per square kilometre. Logistic regressions showed that woodland area was the major correlate of incidence in the Cotswolds; this was also the case for recent and ancient semi-natural woodlands in Herefordshire (Bright *et al.* 1994). These results imply that the dominant process controlling distribution in these regions was extinction in smaller woodlands (dormice were rare in small woodlands in both regions).

Dormouse woodland requirements

Woodland ages

This study showed that dormice frequently occur in recent woodlands in some regions. Recent woodlands can provide excellent habitats for dormice as suggested by Bright *et al.* (1994). However, in many regions of Britain, like the Greater Cotswolds and Herefordshire, woodlands are probably too isolated to have allowed dormice to colonise most recent woodlands. Thus the majority of the dormouse population in Britain probably occurs within ancient woodlands, but recent woodlands can be equally useful provided the arboreal integrity of landscapes is maintained so that they can be colonised.

This study also confirmed that dormice frequently occur in ancient replanted woodlands. The majority of these sites are likely to provide sub-optimal habitats for dormice eg if they are planted with coniferous monocultures. However, most ancient replanted woodlands are large and often occur in clusters so that their mutual isolation is low. Logistic regressions showed that dormouse incidence in ARWs was correlated with measures of isolation, rather than site area, in all regions except the Greater Cotswolds. This implies that dispersal between sites is an important process controlling distribution in ancient replanted woodlands. This may be because populations in ancient replanted woodlands are relatively small (due to low habitat quality) and are often disrupted (by felling and planting), precipitating local extinctions, which dispersal from nearby woodlands could counteract. Thus, as suggested for Herefordshire (Bright *et al.* 1994), survival of dormice in ancient replanted woodlands may crucially depend on the maintenance of high woodland and hedgerow density.

Minimum woodland areas

Bright *et al.* (1994) suggested that 20 ha might represent a critical minimum area of *isolated* woodland to support viable dormouse populations, based on an incidence function. They stressed, however, that this estimate might well be specific to Herefordshire where surveys had been conducted. Estimates were needed for other regions where woodlands were totally isolated and dormouse populations within them could therefore be assumed to be self-sustaining.

Dormouse incidence in the Blackdowns and the Weald was related to woodland isolation rather than woodland area, so estimation of minimum area requirements based on these regions was not possible.

In the Greater Cotswolds dormouse incidence for all woodland age classes was low in woodlands of up to 50 ha. Above this size incidence increased sharply, implying that 50 ha represents a critical minimum area for dormouse populations in the Greater Cotswolds. This estimate of minimum area requirements is higher than that for Herefordshire, but not because of differences in climate (the regions are the same distance north) or habitat. The difference is probably due to isolation: woodlands in the Greater Cotswolds were isolated by a mean of 2486m from the nearest 20 ha ancient woodland, much greater than the distance surveys of Herefordshire suggested that dormice could disperse (1700m). Dormouse populations in the Greater Cotswolds were thus probably completely isolated, whereas those in Herefordshire may interact to some extent by dispersal of individuals. Therefore the Greater Cotswolds may provide a more precise estimate of area requirements in totally isolated woodlands, which may be in excess of 50 ha not 20 ha.

It must be emphasised that such large woodlands are not essential to the persistence of dormouse populations, even in the longer term: dormice were, for example, present in many much smaller woodland in the Blackdowns. However, these sites were significantly less isolated (more boundaries and higher site density). An increase in their mutual isolation, eg by removal of hedgerows, might result in the eventual extinction of the populations they currently support.

Given the very large size of woodlands in the High Weald, and their very low isolation, dormouse incidence might have been expected to be higher than it was (dormice were predicted to occur in only one third of woodlands). The reason for this is unclear, but it does not seem to be the result of lower quality habitats in the High Weald.

Landscape structure

Dormouse incidence was correlated with woodland site area and/or isolation in all regions. Habitat fragmentation, a decrease in the area of habitat patches and an increase in their mutual isolation, is therefore confirmed as a major process affecting dormouse distribution (Bright *et al.* 1994). In the Greater Cotswolds woodlands and hedgerows were highly fragmented (woodland site density 0.40/km^2, mean number of boundaries 7.05) and dormice were rare as a consequence - even in larger (20-50 ha) woodlands. By contrast in the Blackdowns woodlands and hedgerows were little fragmented (woodland site density 0.51/km^2, mean number of boundaries 11.27) and dormice were common. This was despite ancient woodlands being isolated and mean site areas being small in the Blackdowns. These results clearly suggest that the integrity of the arboreal landscape (woodlands and hedgerows) is of paramount importance for the maintenance of dormouse distribution on a regional scale.

In the Greater Cotswolds the integrity of the arboreal landscape has been lost and dormouse distribution seems consequently to have contracted to a few sites. These sites are isolated from one another by a mean of 4.3 km, a distance over which dormice are unlikely to disperse (Bright *et al.* 1994) especially as there are few hedgerows to use as dispersal corridors. In the Greater Cotswolds dormice probably thus occur as isolated, non-interacting, relict populations (non-equilibrium metapopulation).

In the Blackdowns, the High Weald and some parts of Herefordshire, the arboreal landscape is more-or-less intact and dormice are an order of magnitude more frequent than in the Greater Cotswolds. Mean distances between sites where dormice are predicted to occur in these regions were no more than 1.6 km, a distance over which dormice are probably able to disperse (Bright *et al.* 1994; Bright, *in preparation*). In the Blackdowns, the High Weald and some parts of Herefordshire, dormice thus probably occur as metapopulations. This assertion cannot be proven without evidence of dispersal or turnover *ie* extinction and recolonisation of sites, which may be difficult to detect as it is likely to occur mainly over long time scales (decades). However, woodland site areas in the Blackdowns are so small (and presumably extinction rates in them commensurately relatively high) that it seems unlikely that dormice could be common in the region unless distributed as a metapopulation.

Conservation Management Guidelines

1. Management strategies for dormouse populations should be on a large-scale and be region-specific: they should depend on the degree of woodland and hedgerow fragmentation. Natural Areas provide an excellent basis for region-scale management, because they constitute relatively homogeneous landscape types within which uniform management strategies can be applied.

2. In Natural Areas such as the Blackdowns and the High Weald, the strategy should be to preserve the existing arboreal integrity of the landscape, rather than concentrate on habitat management within individual sites. In Natural Areas with similar attributes to the Blackdowns, where woodland site areas are small, preservation of landscape arboreal integrity will probably be vital to the maintenance of dormouse distribution. Removal or change in management of hedgerows is likely to result in the collapse of potential dormouse metapopulations over a time-span of decades.

3. Dormouse conservation should be given highest priority in Natural Areas, like the Blackdowns and High Weald, where the arboreal integrity of the landscape is relatively intact and dormice are still widespread. These areas are strongholds for the species. The landscape-level approach that will be required for dormouse conservation in such areas (see 2 above) may be no more logistically or financially challenging than instigating appropriate habitat management at numerous individual sites.

4. In Natural Areas like the Greater Cotswolds the long term objective should be to restore hedgerows and woodlands where these have been lost in the last 100 years. This is especially important in the Natural Areas where reintroductions are currently being attempted. However, such measures may not be practical in the majority of such Natural Areas.

5. Instead, the management strategy should be to improve habitat quality (by eg appropriate coppicing; Bright & Morris, 1990) at sites where dormice are already present and likely to be able to maintain viable populations. This means that management (including reintroductions and grant-in-aid) should be targeted in ancient woodlands that are at least 20 ha, but preferably 50 ha in extent. In the longer term, where woodlands are totally isolated, it will probably be fruitless to deploy limited resources in smaller woodlands.

6. In Natural Areas like the Greater Cotswolds, large sites where habitat management effort should be targeted are frequently ancient replanted woodlands. Existing habitat management in ancient replanted woodlands will generally be inimical to dormouse needs. Every effort should be made to safeguard dormouse populations in these important sites, but this will require greater understanding of dormouse habitat requirements and dynamics in replanted, often conifer-dominated, woodlands.

Future Work

1. This study and recent experimental translocations at Briddlesford supported by PTES (Bright, *in preparation*), have reconfirmed the likely pivotal importance of hedgerows to the maintenance of dormice distribution in many regions. We know that dormouse presence is correlated with the prevalence of hedgerows around a woodland and can infer that hedgerows are important for dispersal between sites. We also know that dormice are behaviourally very reluctant to cross gaps in hedgerows and have difficulty crossing open fields. However, despite efforts at Briddlesford, virtually nothing is known about the autecology of dormice *resident* in hedgerows. This means that fully informed advice on hedgerow management to benefit dormice cannot be given - a great lacuna in our existing armoury of knowledge. Thus a full scale study to determine range sizes, densities, habitat requirements and population dynamics of dormice resident in hedgerows (they are not at Briddlesford) is needed. There are several potential study sites, including one in Wales where nestboxes are already in place. It would be important to make comparisons between two or more sites.

2. There is now a large database which could be used to make predictions about the prevalence (and perhaps distribution) of dormice in Natural Areas that have not so far been surveyed. This would be easily accomplished and allow management strategies to be formulated for all Natural Areas. Such a project would clearly provide extremely valuable information and should be combined with 3 and 4 below.

3. The regional-scale habitat requirements of the dormouse, for networks of hedgerows and a high density of woodland sites, identified in this study, are shared with a host of other species of great conservation concern. These are insular species of ancient woodlands and ancient hedgerows, which are highly vulnerable to habitat fragmentation. Conservation of this *ancient landscape community* should be integrated and guidelines provided for each appropriate Natural Area. An unrivalled opportunity now exists to combine the extensive, high quality data on dormouse distribution just collected with that for other less well known members of its ancient landscape community. This would be a relatively large undertaking, but would be extremely worthwhile. It would provide management guidelines for a wide range of species at a landscape (Natural Areas) scale. Such an integrated approach is clearly needed 'on the ground' and would enable a host of species to be covered in a highly cost-effect way.

4. Reversing the fragmentation of woodlands and hedgerows would be of great benefit to dormice and many other taxa. Two experimental trials to test the efficacy of such measures are suggested: a) in an area where dormice are resident, the effect of reduced hedgerow cutting should be monitored to determine at what rate hedgerows are colonised; and b) colonisation rates of newly planted (farm) woodlands should be determined. Without such trials it will not be possible to assess whether reverse fragmentation measures actually work.

5. The existing large data set on dormouse distribution can also be used to predict the effects of habitat destruction in surveyed areas. Metapopulation or epidemiological models could be used to predict critical levels of habitat destruction or fragmentation that would precipitate the loss of dormouse populations. PWB will pursue some of this work as soon as time allows.

6. An extensive, high quality data set now exists, identifying both positive and negative sites, which can be used as a baseline for future dormouse surveillance. Such work should be integrated with national mammal monitoring and begin around five years hence. It would be especially important to revisit sites where dormice are likely to have become locally extinct. In particular it would be valuable to compare rates of extinction in woodlands of different sizes and compare small woodlands that are isolated with small woodlands that are not.

7. As suggested for dormouse sites in Wales (Bright, 1995), understanding of dormouse requirements in replanted ancient woodlands (especially coniferous monocultures) is a high conservation priority. Two sites already exist where this work could be done. As for hedgerow studies it would be important to make comparisons at two or more sites.

8. Much of the data interpretation in this section of the report rests on the assumption that dormice disperse between woodlands. Monitoring of dispersal rates has begun at Briddlesford on the Isle of Wight, supported by PTES. It is very important that this continues and, if possible is extended to another site where woodlands are more isolated.