Local and landscape-scale impacts of woodland management on wildlife

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The Wild Wood is pretty well populated by now; with all the usual lot, good, bad, and indifferent – I name no names. It takes all sorts to make a world.

12.1 Introduction

The typical 'farmscape' in Britain consists mainly of cropped fields and pastures, but also comprises a diverse range of other habitats, including semi-natural woodlands and hedgerows. Within many landscapes, these wooded elements are the only habitats reminiscent of the original forest ecosystem that developed after the last ice-age (Rackham 2003) and, as a result, many species still found in the wider British countryside depend on them for food (e.g. Merckx et al. 2012), shelter (e.g. Merckx et al. 2008), nesting opportunities (e.g. Macdonald et al. 2004), or dispersal (e.g. Slade et al. 2013). While single trees are sufficient sanctuaries or stepping stones for some species, others (including some invasive species, Box 12.1) need larger woodland patches or hedgerows and woodland corridors to facilitate their dispersal. Mitigation of forest fragmentation and appropriate woodland management are thus key topics in conservation-friendly farming (Buechner 1989; Buesching et al. 2008; Merckx et al. 2012; Slade et al. 2013), and in conservation work globally (Akcakaya et al. 2007; Cushman et al. 2013).

Depending on their mobility and dispersal patterns, the responses of different species and taxa to habitat management practices vary. Whereas some species are very sensitive to localized small-scale changes in their environment, others are affected predominantly by management at a landscape scale. Small mammals, for example, do not regularly traverse distances further than 100 m (Buechner 1989), and thus their local abundances are likely to respond sensitively to changing The Wind in the Willows by Kenneth Graeme

local habitat parameters. They are particularly sensitive to changes in cover from predators and in food availability due to habitat management and grazing pressure (Buesching et al. 2008; Buesching et al. 2011; Bush et al. 2012), making them a suitable model to study the impacts of small-scale habitat management. In Chapter 4, this volume, we have shown how, on farmland, habitat management at the local (i.e. field) scale affects wood mouse *Apodemus sylvaticus* behaviour and population densities. Similarly, the field-scale management of hedgerow trees and field margins has been shown to affect predominantly the abundance and species richness of less mobile moth species, whereas mobile moth species are likely to be more affected at the landscape scale (Chapter 8, this volume).

In this chapter, we will use these same taxonomic groups to look at the effects of different aspects of managing woodlands within the British 'farmscape'. First, we review how the impacts of management of individual woodlands affect small mammal distribution patterns and population densities. Then we investigate how the distribution, extent, and management of woodlands within the landscape influence the diversity, abundance, and movements of macro-moths.

Both taxa are of ecological importance in farmland ecosystems for three major reasons. Firstly, small mammals support a number of larger (and sometimes) endangered carnivores (e.g. stoats *Mustela erminea*, weasels *Mustela nivalis*, red foxes *Vulpes vulpes*, barn owls *Tyto alba*, tawny owls *Strix aluco* (Box 12.3), and buzzards *Buteo buteo* (see Macdonald and Feber 2015): Chapter 10; Harris et al. 2000), while moths are vital prey for bats (see Chapter 9, this volume), and birds (e.g. blue tits *Cyanistes caeruleus* eat a minimum of 35 billion caterpillars each year in Britain alone: Fox et al. 2006). Secondly, both taxa are good indicators for environmental health (small mammals: Harrington and Macdonald 2002; moths: Fox 2013), as well as for general habitat degradation and forest fragmentation (small mammals: Macdonald et al. 1998; moths: Summerville and Crist 2004). Thirdly, both taxa are implicated in woodland regeneration, as small mammals are important seed dispersers for many woodland tree species (e.g. Watts 1968), while some plants rely on moths for pollination (e.g. Devoto et al. 2011). In addition, they are well studied in Wytham (Buesching et al. 2010; Hambler et al. 2010).

Box 12.1 Aliens versus natives: can red and grey squirrels co-exist?

The North American grey squirrel Sciurus carolinensis was introduced into Britain in the late nineteenth century, and since its spread, the native red squirrel Sciurus vulgaris has experienced a dramatic loss of range. In general, when 'greys arrive, reds disappear'; according to the Forestry Commission (2013) there are only 140 000 red squirrels left in Britain, versus 2.5 million grey squirrels. Red squirrels are now restricted to a few island populations in the south of England, pockets in mid and north Wales, northern counties in England, and in Scotland, where an estimated 75% of all British red squirrels are found (Scottish Wildlife Trust 2013). Several factors have been involved in the ecological replacement of red squirrels by greys (Tomkins et al. 2003). The pattern of replacement has indicated that competition for habitats and food resources have played a major role (Usher et al. 1992). In addition, there is growing evidence that the squirrel-specific parapox virus has accelerated rates of competitive replacement in some areas (Rushton et al. 2006).

Interestingly, in the absence of the parapox virus, the native and alien species have been able to co-exist in some areas for prolonged periods. Since habitat composition may be the determinant of short- versus long-term co-existence, Jenny Bryce, leading a WildCRU team, aimed to ascertain similarities in patterns of woodland habitat use by both species. The work focused on the Craigvinean forest in Perthshire, Scotland, a commercial coniferous forest with riparian corridors of mixed broadleaves, where red and grey squirrels had co-existed for over 30 years at the time of our study in the late 1990s.

We radio-tracked 32 red and 34 grey squirrels and found a 77% interspecies dietary niche overlap based on their use of individual tree species, suggesting that the similarity of resources used was likely to preclude their co-existence (Bryce et al. 2002). However, due to the structure of woodlands in the landscape, the habitats within their home ranges overlapped by only 59%. Red squirrels selected home ranges within conifer areas (i.e. favouring Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*), which were avoided by grey squirrels (population densities: 1.63 reds/ha versus 0.08 greys/ha), while grey squirrels used mixed conifer and broad-leaved habitats throughout the year, which red squirrels only used in autumn and winter (0.92 reds/ha and 0.88 greys/ha). Our results suggest that this partitioning of macrohabitats may have reduced interspecific competition between the species, allowing long-term (now 50+ years) coexistence in areas of extensive conifers with isolated patches of broad-leaved woodland. Hence, persistence in a wooded landscape is likely to depend on the extent and productivity of the patches of broadleaved woodland, with red squirrels being predicted to be out-competed at moderate grey squirrel densities (Wauters et al. 2002).

In addition, our studies revealed a near two-fold difference in body weight between the two species (red c. 300 g and grey c. 570 g; Bryce et al. 2001), and this difference in body mass can help to explain the greys' competitive advantage. By examining their relative daily energy expenditure (which increased with body mass), we estimated that one grey squirrel uses 1.65 times the energy of one red squirrel (Bryce et al. 2001). Social dominance in squirrels is driven by body size, hence we would expect grey squirrels to control access to, and consume relatively more of, the available food resources. According to some studies, these competitive advantages manifest through different rates of juvenile recruitment, rather than breeding rates or adult survival (Gurnell et al. 2004). Hence, conifer habitats with little or no broadleaved woodland, which support relatively low densities of squirrels, may provide red squirrels with a refuge from competition with grey squirrels (Bryce et al. 2005). Interestingly, the mix of woodland types in the landscape is also thought to be important in determining disease transmission through habitat connectivity, and via squirrel population densities influencing encounter rates (White et al. 2014).

In conclusion, squirrels are relatively mobile species, but tend to stay close to least-cost corridors (Stevenson et al. 2013). Thus, it is habitat composition and connectivity at a landscape level, rather than overall forest extent, which are likely to be of crucial importance in this ongoing challenge from the introduced congener.

12.2 Local effects of deer browsing on small mammals

Wytham Woods are home to one of the longestrunning small mammal studies in the world. Originated by H.N. Southern in 1943, and inspired by Charles Elton's (1924) on-site research into rodent ecology and population dynamics, small mammals have been livetrapped twice annually (at the end of May/beginning of June, and in December) at the same two sites, located in secondary deciduous woodland in Wytham's Great Wood, for over seventy years (Buesching et al. 2010). Capture-mark-recapture (CMR) techniques allow their numbers to be estimated, and reveal the effects of environmental factors on their population densities. Longterm monitoring of their abundance and distribution has thus contributed to a detailed understanding of their uses of, and preferences for, particular habitats. Such information, in turn, constitutes an important pre-requisite for the design of effective conservation and woodland management strategies.

Over the past 200 years, changes in climate, farming, forestry, and hunting practices, as well as the extinction of their natural predators (e.g. wolves and lynx: Sandom et al. 2013), have resulted in marked increases in deer numbers across the UK (see Box 12.2; Fig. 12.1), mainland Europe (Fuller and Gill 2001), and North America (McCabe and McCabe 1974). These have highlighted a suite of associated conservation issues ranging from intra-guild competition (Bartos et al. 2002), to parasite spread (Bindernagel and Anderson 1972), and human conflict (e.g. zoonotic diseases: Spielman 1994; agricultural damage: Putman and Moore 2002; Road Traffic Accidents: Putman 1997). The impacts of high densities of deer on woodland vegetation can be extreme (Morecroft et al. 2001; Savill et al. 2010). The shrub layer, especially bramble Rubus fruticosa, and many woodland forbs, are reduced by increased browsing pressure (Gill 2000), woodland plants are damaged by trampling (Gill and Beardall 2001), and forest regeneration is arrested (Kirby 2001). Thus, heavy deer grazing can alter the structure of the whole forest, with cascading effects on a wide variety of other species at all trophic levels (Fuller and Gill 2001). Invertebrate communities are affected by changes in forest vegetation; for example, the caterpillars of the peach blossom moth Thyatira batis feed almost exclusively on bramble in late summer (Pollard and Cooke 1994; Stewart 2001; Littlewood 2008; Merckx et al. 2012). The lack of cover from predators can lead to the elimination of ground-nesting birds, such as nightingales (Gosler 1990) and small mammal

populations may become less species diverse (Putman et al. 1989) and less abundant (Smit et al. 2001), resulting in fewer avian and mammalian predators at higher trophic levels (e.g. small mustelids: King 1985; tawny owls: Southern and Lowe 1982; Box 12.3).

Our long-term data set on small mammal populations in Wytham Woods, together with the evolving deer management situation described in Box 12.2, provided a unique opportunity to study not only the effects of high deer population densities on woodland rodents, but also the recovery of woodland ecosystems after the removal of known numbers of deer over a period of several years.

In woodlands throughout the UK and most of Europe, the two most common small mammal rodent species are the wood mouse *Apodemus sylvaticus* and the bank vole *Myodes glareolus* (formerly *Clethrionomys glareolus*). They occupy similar ecological niches throughout their range and constitute the prey base for many woodland predators (Flowerdew 1993). In both species, adults typically weigh between 15 and 25 g, and breed mainly between April and October, with



Figure 12.1 Roe deer Capreolus capreolus. ©A.L. Harrington.

Box 12.2 Deer management in Wytham Woods

Wytham Woods (total woodland area 425 ha: for a detailed description of the site see Savill et al. 2010; Buesching et al. 2010) are home to three species of deer: (1) the native roe deer Capreolus capreolus (Fig. 12.1), which, by the mid eighteenth century, had been extirpated from southern England by over-hunting, and only recolonized Oxfordshire in the 1970s (Ward 2005), supplemented by some imports from the continent (Macdonald and Burnham 2010); (2) the fallow deer Cervus dama, which was first introduced into royal hunting grounds by the Normans in the eleventh century and is now considered to be naturalized in England; and (3) the Asian muntjac Muntiacus reevesi, which was introduced from China and Taiwan to Woburn Abbey Park by the Victorians at the end of the nineteenth century, and was dispersed to other collections and menageries across southern England, from where animals escaped and spread widely, colonizing Wytham in the 1960s (Elton 1966).

Deer of all three species rely heavily on forest cover for resting sites but, if given the choice, roe and fallow deer graze preferentially in arable fields. The crop damage on farms adjacent to Wytham Woods forced Oxford University to erect a 2.5 m high deer fence along the 7 km perimeter of the Woods in 1987–1988, effectively fencing in the roe and fallow deer population, although the smaller muntjac could continue to migrate under, or even through, the fence. The absence of any natural predators, and only limited control of their numbers by culling, permitted steady increases in the population densities of deer in Wytham Woods throughout the 1990s until, in 1998, the combination of trampling, overgrazing and browsing, and shading by the dense canopy cover, had eliminated much of the ground cover vegetation (Morecroft et al. 2001), seriously affecting populations of birds (Gosler 1990) and small mammals (Flowerdew and Ellwood 2001), as well as the body condition of the deer themselves (Ellwood 2007). Thus, with the assistance of the British Deer Society, a rigorous culling programme was implemented in the winter of 1998/1999 (Perrins and Overall 2001), which is still in effect.

Empirical deer counts were first conducted in Wytham by Taylor and Morecroft (1997) using dung-count methods. The deer control strategy, however, facilitated the rare opportunity to calibrate different methods to estimate deer numbers by sampling before and after a known number of deer were removed from an effectively closed population (Ellwood 2007; Buesching et al. 2014). Between 1998 and 2003, WildCRU's Stephen Ellwood compared the statistical precision (reliability) and estimate accuracy (using known population size determined by cohort analysis) of two dungcounting methods with observational ('distance') sampling, using a thermal imager at night, and concluded that distance sampling was more precise and accurate than dung counts for all three deer species (Ellwood 2007). However, as distance sampling requires expensive, specialized equipment not available to the average landowner, we also evaluated the accuracy of dropping counts. We found in a large-scale study over ten years that, with appropriate validation and calibration, faecal standing crop counts (Macdonald et al. 1998) can deliver accurate density estimates for larger deer species, such as roe and fallow deer, which can be calibrated against cull figures (Buesching et al. 2014). Faecal pellet group counts are, however, unsuitable for estimating densities of the small, pair-living, and territorial muntjacs, as they deposit their droppings in latrines rather than randomly throughout their range.

In Wytham, winter culling reduced the fallow population from an estimated 440 animals (103.5/100 ha) in 1998 to 35–40 individuals in 2003 (8.5/100 ha), and muntjac from c. 200 (47/100 ha) to 15 (3.5/100 ha). Interestingly, historically, the density of the roe deer population had been comparatively low in Wytham Woods, estimated at 2/100 ha, until the marked decrease in fallow, imposed by culling. This was followed by a sudden significant increase in roe numbers during the reproductive season of 2000 to almost double their previous densities (Savill et al. 2010). Thus, culling of roe commenced over the winter of 2000/2001.

As global warming is predicted to result in warmer and wetter conditions for most parts of the UK, we investigated the effects of population density and weather conditions on deer population dynamics using post-mortem examination of culled fallow and muntjac deer (Ellwood 2007). Our study showed that: (i) in both species, pregnancy rates were unaffected by population density, because most females became pregnant at their earliest opportunity; (ii) fallow fawns were smallest at high densities; and (iii) although fallow fawns and yearlings continued to grow, body condition of individuals of all ages deteriorated over the winter. This effect was exacerbated by high population density, but minimized in warm and wet winters. Muntjac, on the other hand, showed no weather dependency in their body condition (Buesching et al. 2010). Thus, as temperate woodlands are likely to support greater densities of deer in the future, due to predicted changes in weather patterns, present-day forest ecosystems could potentially be altered considerably (Newman and Macdonald 2013).

females establishing mutually exclusive breeding territories. However, their respective survival strategies differ significantly. Whereas the predominantly herbivorous and more sedentary bank vole relies on dense understorey for protection from predators (Fitzgibbon 1997), the wood mouse has well-developed olfactory, visual, and auditory senses, as well as considerable agility. These character traits allow flighty escape from predators (Hansson 1985), affording wood mice the freedom to forage for a more omnivorous diet, including seeds, berries, and up to 15% insects (Watts 1968). Nevertheless, while bank voles are active night and day under the protective shrub layer, wood mice are largely nocturnal, foraging under the cover of darkness (Flowerdew 1993).

Historically, the numbers of bank voles in Wytham Woods have always exceeded those of wood mice. However, while wood mouse numbers, albeit subject to inter-annual population cycles, stayed within the same density range over the past seven decades, bank voles showed a marked decline in their population density to approximately half their original numbers in the late 1980s, followed by a gradual increase from c. 2002 onwards (Flowerdew and Ellwood 2001; Buesching et al. 2010). While the decrease in bank vole numbers coincided with the substantial increase in deer numbers in the 1990s, after the erection of the deer fence in 1987 (see Box 12.2), their recovery appears to coincide with the regeneration of understorey and forest vegetation after the stringent deer control measures took effect (Buesching et al. 2010; 2014; Bush et al. 2012). Thus, small rodent numbers appear to be linked to the variation in deer-grazing pressure (Flowerdew and Ellwood 2001), and resultant changes in woodland vegetation (Morecroft et al. 2001; Buesching et al. 2011; Bush et al. 2012).

Empirical studies comparing small mammal communities in heavily deer-grazed versus deer-free areas within the same woodland are rare, as they are usually defeated by logistical challenges. In Wytham Woods, we were fortunate that the Environmental Change Network (ECN) established four deer exclosures of approximately 1 ha each in different parts of the Woods in 1998, specifically to study the effects of deer grazing on woodland vegetation (Morecroft et al. 2001). Each exclosure was delimited by a 2.5 m high deer fence, which excluded all deer whilst permitting free access to mice and voles. The absence of grazing pressure has led to a much denser understorey inside the exclosures than in the rest of the woodland, manifesting itself predominantly in increased bramble cover (Morecroft et al. 2001; Buesching et al. 2011).

Between June 2001 and September 2003, we compared the population densities of wood mice and bank voles inside the deer-free exclosures with those recorded in the open woodland subjected to deer grazing (Buesching et al. 2011). With the help of Earthwatch volunteers (see Macdonald and Feber 2015: Chapter 15) we carried out 16 live-trapping sessions, each lasting four days, during which we placed 50 Longworth traps (Fig. 12.2) inside one of the four deer exclosures and 50 traps in the surrounding woodland, rotating between the four different exclosures. Throughout the year, capture-mark-recapture estimates indicated that, on average, there were four times more bank voles than wood mice inside the exclosures, whereas the open woodland supported 1.6 times as many wood mice (Fig. 12.3a) as bank voles (Fig. 12.3b). This result illustrates neatly how strongly bank voles rely on thick vegetation, and how they benefit from reduced browsing pressure by deer. By contrast, wood mice use their acute senses and agility to detect, and evade, predators, allowing them to exploit also resources in the open woodland without jeopardizing their survival.



Figure 12.2 Longworth trap fixed in a tree. Photograph ©Karrie Langdon.



Figure 12.3 Comparison of population densities (\pm STD) of (a) wood mice (As) and (b) bank voles (Mg) in transects (Tr) and exclosures (Ex) in four different exclosures (Marley: ML; Swinford: SF; Lower Ash Hill: LH; Firebreak: FB) trapped in July (07) and September (09) (data from 2003). From Buesching et al. (2011). Reproduced with permission from Elsevier.

In contrast to previous studies (e.g. Yoccoz and Mesnager 1998), we found no difference in the sex ratio or age structure of either species between the open woodland and the exclosures, nor any differences in terms of body weight and/or reproductive status, which would equate to differences in reproductive fitness (Buesching et al. 2011). These results, combined with those of Hansson (1992), who found that in both species smaller females had greater reproductive fitness at high densities than did heavier individuals, provide further evidence that the commonly assumed positive correlation between body weight and reproductive fitness may not apply to cyclic microtine populations.

In the summer of 2010, we repeated this study (Bush et al. 2012). Although the densities of small mammals in different areas of Wytham Woods varied with the overall vegetation cover, our data confirmed that, after a decade of rigorous deer control, bank voles were spreading back into the open woodland, and had reached densities comparable to those inside the exclosures (i.e. between 10 and 30 animals/ha, depending on woodland area), with no significant differences recorded in population structure between grazed and ungrazed areas.

Both of these studies also provide some evidence for the previously suggested inter-specific competition, avoidance, and niche separation between wood mice and bank voles (Gipps 1985). While other studies propose that only bank voles will modify their behaviour to avoid competition with wood mice (Gipps 1985; Gurnell 1985), the results from our research in Wytham Woods suggested that wood mice might also change their behaviour. Wood mouse numbers have been reported to increase if deer are excluded (Smit et al. 2001), or if food resources are increased (Putman et al. 1989). However, under heavy grazing pressure in Wytham, wood mice occurred at approximately three times higher densities $(3.37 \pm 0.71 \text{ SE})$ in the open woodland than inside exclosures (Buesching et al. 2011).

Aside from predators, small mammal population densities are also heavily affected by food availability. The Habitat Saturation Hypothesis (Selander 1964) postulates that their populations are regulated by available resources in a density-dependent way (Plesner-Jensen 1996). Using behavioural observations and radio-tracking, our research at Wytham established that wood mice are not only capable of detecting and remembering rich food patches (Macdonald et al. 2006), but that the size of their territories correlates negatively with the richness of food resources. We also found that wood mice and bank voles show a further degree of niche separation in their use of the three-dimensional forest structure (Buesching et al. 2008). In this study, half of the traps were placed on the ground and half were fixed in shrubs and trees between heights of 30 cm and 2.5 m (Fig. 12.2). The study confirmed that arboreality is common in small mammals: an average of one in five wood mice, and one in ten bank voles, were caught in trees. Although almost 90% of these arboreal animals were caught at heights of 50–100 cm above the ground, some reached heights of up to 2.2 m. While the majority (68%) of mice caught in trees were male, in bank voles, most arboreal individuals (72%) were female.

In both species, arboreality was correlated positively with population density. However, whilst bank voles were found to be arboreal only in July and August, wood mice were found above ground throughout the reproductive season, with males being caught in trees approximately twice as often as females. Dense intertwining vegetation, for instance provided by bramble, hawthorn *Crataegus monogyna*, hazel *Corylus avellana*, and elder *Sambucus nigra*, increased arboreality in both species, probably since these plants provide good branch networks for runways at the preferred vegetation height.

Although many hypotheses have been suggested to explain arboreality in small mammals (for review, see Buesching et al. 2008), we concluded that it can best be explained by a combination of factors. It is likely that only wood mice can afford to be truly arboreal, exploiting food resources (e.g. insects, berries) above ground, because only mice are sufficiently swift and agile to escape predators whilst running along thin branches. As the mating system of wood mice involves one male territory overlapping that of several females (femaledefence polygyny: Tew and Macdonald 1994), it is likely that male territory holders use trees, not only during foraging trips, but also as direct routes and over-passes between different, and not necessarily contiguous, female territories. Bank voles, on the other hand, may be driven to arboreality only in times of high population densities and little food availability on the ground (i.e. in summer) to exploit (unripe) seeds and flowers above ground. Even then, they are unlikely to climb as high as wood mice due to their lack of agility and their reliance on dense vegetation for protection from predators (Buesching et al. 2008). Thus, reduction in the understorey layer, either through over-grazing by deer, or through well-established forest management practices, such as large-scale felling operations and brush cutting, has the potential to alter small mammal

Box 12.3 The effects of fluctuations in field vole populations on tawny owls Strix aluco

Fluctuations in prey populations affect abundance and population dynamics of their predators. For example, tawny owls *Strix aluco* predate small mammals (Southern and Lowe 1982) such as bank voles, wood mice, and field voles *Microtus agrestis* (see Chapter 4, this volume), as well as eating earthworms *Lumbricus terrestris*. Small mammal densities follow cyclical abundance patterns, and thus vary in their availability as prey for tawny owls on a seasonal as well as on an inter-annual basis, while earthworm distribution depends on soil micro-climate, and thus varies in availability as prey for tawny owls on a nightly basis (Macdonald 1976).

Studying tawny owls in Kielder Forest, Northumberland, in 1994 and 1995, a team led by WildCRU's Bridget Appleby investigated how changes in the abundance of field voles can affect the survival and parasite loads of tawny owls, and how parents can maximize their fitness by adjusting the sex ratio of their offspring in response to differences in resource availability (Appleby et al. 1997; 1999). During these two years, Appleby et al. determined the sex (through DNA fingerprinting of microsatellites in blood samples) of chicks from nests where all eggs hatched. Field vole abundance was estimated for each owl territory, based on the presence of fresh grass clippings in vole runs in March and June at 20 survey sites distributed throughout the study area. Although local field vole abundance fluctuates inter-annually following a three- to four-year cycle, these cycles can be asynchronous between neighbouring populations (Petty 1992), and indeed, during the research period at Kielder, field vole abundance increased in some parts of the forest, but simultaneously decreased in others. In 1994, vole abundance (and thus owl food) increased in all study territories, resulting in a low chick mortality between hatching and fledging of only 15% (N = 116). However, 1995 was a year of much lower vole abundance, and chick mortality increased to 31% (N = 70) (Appleby et al. 1997). Interestingly, female reproductive success (i.e. number of fledglings) was correlated with vole abundance in their respective territories only in 1995 (Appleby et al. 1997). The results therefore suggest

population structure, behaviour, and inter-specific interactions. As small mammals are important seed dispersers, forest regeneration may be impaired if rodent populations drop below a minimum level (Watts 1968), causing cascade effects throughout the ecosystem, and repressing population densities of many avian and mammalian predators (e.g. weasels, see Box 4.8 in Chapter 4, this volume; owls, Box 12.3). that, in general, high abundance of prey (in 1994) allows even poorer individuals to breed successfully, while only high-quality individuals breed successfully when vole numbers are low (as in 1995).

As tawny owls are sexually dimorphic, with females weighing 20% more than males (Snow and Perrins 1998), rearing females implies a larger parental investment in acquiring food resources. Parents should thus produce more of the heavier sex when resources are most plentiful. Indeed, during both years, territories with higher abundances of field voles in June (when chicks fledge) supported a larger proportion of female chicks within a brood (Appleby et al. 1997). This appeared to be a flexible response to the prevailing supply of field voles in the territory in that year, rather than being a consequence of sex-biased mortality in eggs or nestlings. So, are owls able to predict future food supplies? Since tawny owls lay eggs in March, the results indicate that owls might be able to predict the future abundance of field voles, and respond by laying female-biased clutches, which are most likely to gain a long-term benefit when resources are good (Appleby et al. 1997). Possible explanations for this 'predictive ability' are the detection of pregnant and lactating vole females, the size of voles, which are larger on the increasing phase of multi-annual population cycles, and/or the detection of the voles' reproductive hormones (Appleby et al. 1997).

Furthermore, Appleby et al. (1999) also measured the prevalence of blood parasites in parent birds as well as chicks. They found that field vole availability had both a short-term effect on owls, in which birds suffering a decline in food abundance in their territories between the two study years showed an increase in parasite load, and a long-term effect, which was reflected in higher parasite burdens of adult owls that had experienced poorer food supply as chicks (Appleby et al. 1999). In conclusion, the results show that fluctuations in small mammal populations affect the quantity, quality, and sex of birds at higher trophic levels.

12.3 Effects of woodland management on moths

English semi-natural, broad-leaved lowland woodlands, such as Wytham Woods, are often sheltered biotopes contained within highly exposed agricultural landscapes. Woodlands provide Lepidoptera (i.e. butterflies and moths) with habitat resources, including larval foodplants, nectar sources, and shelter (Usher and Keiller 1998; Summerville and Crist 2004; Dennis 2010). Nevertheless, many of these resources have been lost during the last half of the twentieth century, with the replacement of traditional coppicing through intensive forest management (Warren and Key 1991; Gorissen et al. 2004). This has led to losses of a significant proportion of butterflies from woodlands (van Swaay et al. 2006), including both woodland specialists and species of open woodland (Gorissen et al. 2004).

Our recent macro-moth conservation research has concentrated on farmscapes (see Chapter 8, this volume). However, populations of widespread macromoth species are declining and the causes are likely to include factors other than management of farmland (Fox 2013). An estimated 60% of widespread moth species depend on semi-natural woodlands (Young 1997). Some species are exclusively restricted to dense woodland (e.g. the lobster moth Stauropus fagi, Fig. 12.6a, which received its English name from the remarkable crustacean-like appearance of the caterpillar), while others (e.g. rosy marbled *Elaphria venustula*) depend on open woodland complexes such as rides, heaths, glades, and scallops (Waring and Townsend 2009). However, these latter associations have rarely been quantified (see Merckx et al. 2012). The impacts of contrasting woodland management are only well understood for butterflies (Warren and Thomas 1992; Hodgson et al. 2009), with studies on moths being scarce and limited in terms of scale and re-sampling (Broome et al. 2011).

We conducted a large-scale study to explore whether woodland management, at the scale of the woodland patch, had the potential to halt and/or reverse macro-moth declines within woodlands for both rare and localized species of conservation concern and for widespread, yet declining species (Merckx et al. 2012). First, the study aimed to test how macro-moth abundance and species richness were affected by two common woodland conservation management practices, coppicing and ride management. Second, we assessed whether species groups of different conservation status reacted differently to these management practices, and if such variations depended on group/species ecology. Finally, we suggested clear recommendations for woodland conservation management that allowed for management practices that simultaneously catered for different ecological and conservation status groups of Lepidoptera.

The light-trap experiment was conducted in the Tytherley woodland landscape, a landscape of *c*. 17 000 ha, containing 98 woodland patches totalling 2500 ha of ancient semi-natural woodland, near Salisbury, UK. We compared the presence/absence, abundance, and species richness of macro-moths at 36 fixed trap sites located within the woodland. Trap sites were set within six experimental 'woodland management' treatments: hazel coppice (young: 1–2 yrs; medium: 3–6 yrs; old: 7–9 yrs), ride widths (wide: > 20 m; standard: < 10 m), and 'standard woodland' of non-coppiced, sheltered, high deciduous oak forest (at least 60 yrs old with some 300 yr-old individual trees). A total of 11 670 individuals from 265 macro-moth species were recorded, including 15 'Scarce/Red Data Book (RDB)' species (249 individuals), 38 'Common Severely Declining' species (891 individuals), and 90 'Common Declining' species (3564 individuals)¹.

Overall, numbers of both individuals and species of macro-moth were higher in the late-successional high deciduous forest biotope of 'standard woodland', which is characterized by higher levels of shelter, darkness, and humidity, compared to coppiced sites (Fig. 12.4). Shelter affects levels of convective cooling (Merckx et al. 2008), aiding the capacity of these endothermic insects to increase their temperature, and, as a consequence, their activity level, which may in part explain the higher overall abundance and species richness within sheltered woodland. Sheltered woodland habitats were especially important for scarce/ RDB species (Fig. 12.5) such as the UK BAP species light crimson underwing Catocala promissa, and the nationally scarce great oak beauty Hypomecis roboraria, which was mirrored by the observation that 60% of species in this group (N = 15) were strict woodland species.

At the same time, we showed that coppicing and ride widening (> 20 m), which open up dense forest structures and which are practices often employed for butterfly conservation, are also indispensable woodland management tools to conserve other sets of macro-moth species. For instance, 18% (i.e. 49 species) of all our recorded species were fully restricted to sites with coppice/wide ride management.

The study also demonstrated that the mechanism behind the pattern of increased species richness at the woodland scale involved an increase in structural heterogeneity of plant species (e.g. in wide rides) and, hence, an increased micro-climatic and resource diversity for species with an affinity for more open biotopes. This increased habitat diversity especially benefited

¹ 'Common Severely Declining' and 'Common Declining' species show national declines > 69% and 0–69%, respectively, over a 35-year period (Conrad et al. 2006).



Figure 12.4 Overall macro-moth abundance (number of individuals) and species richness (number of species) (log₁₀-transformed mean (SE)) for six experimental woodland management treatments. From Merckx et al. (2012). Reproduced with permission from Elsevier.



Figure 12.5 Abundance (log₁₀-transformed mean (SE)) of two high profile conservation status species groups, for six experimental woodland management treatments. 'Scarce/RDB' species followed the overall trend with overall macro-moth abundance highest in standard rides and standard woodland and lowest in coppice and wide rides, while the 'Common Severely Declining' species, by contrast, were relatively abundant at wide woodland rides, while showing the smallest difference in abundance between the woodland management treatments. From Merckx et al. (2012). Reproduced with permission from Elsevier.

Common Severely Declining species, with ten (of 38) species of this group only found at open sites (e.g. figure of eight *Diloba caeruleocephala*). Wide woodland rides specifically benefited this group in terms of abundance (Fig. 12.5).

Based on these findings, we recommend a two-tier approach of zoning woodland conservation, which involves a combination of management practices that enlarge existing dense forest cores, while buffering those cores with lighter woodland zones (containing coppicing and wide woodland rides). This would allow for the differential value of successional stages for different ecological groups of Lepidoptera, and would hence be beneficial for both woodland specialists and species of open habitats.

Importantly, this study also demonstrated that the size of the woodland patch surrounding coppiced plots was a key factor that positively affected abundance and species richness of nationally declining and severely declining species of moths in coppiced plots (Merckx et al. 2012). Thus, the woodland size/ scale where the coppice management effort takes place matters to achieve maximum conservation outputs for moths. Our results suggested that larger woodlands offer more cost-effective opportunities to increase biodiversity through active coppice management.

12.4 Landscape-scale effects of woodland fragmentation on moths

Habitat connectivity, and in particular hedgerows and hedgerow trees, have been shown to be important for moth mobility at the field and farm scale (Merckx et al. 2010; Chapter 8, this volume). At the landscape scale, movement patterns of moth species associated with woodland are often restricted by forest fragmentation and the lack of functional corridors in agricultural landscapes. However, the impacts of fragmentation may also depend on the mobility of individual moth species (Merckx et al. 2010; Slade et al. 2013). We conducted the first investigation into the movement patterns of multiple species of moths on a landscape scale, by means of a large-scale capture-mark-recapture (CMR) study (Slade et al. 2013; see Macdonald and Feber 2015: Chapter 15). We examined how both lifehistory traits and landscape characteristics can be used to predict macro-moth responses to forest fragmentation, and the importance of woodland patch size, hedgerows, and single trees for movements of forestassociated moths within agricultural landscapes.

Enlisting the help of volunteers (Macdonald and Feber 2015: Chapter 15), we placed 44 six-watt actinic light traps across Wytham Woods, the surrounding forest fragments, and the landscape matrix in between, covering a 2 km radius from the centre of Wytham Woods. Captured moths from 89 species were individually marked on the hindwing with a unique identifying number using a permanent marker pen (Fig. 12.6a), and then released. This CMR experiment ran every night throughout most of June and July 2009. Nearly 15 000 moths were marked during the study, including several rare and UK BAP species, such as a healthy population of the nationally declining garden tiger *Arctia caja*, a species thought to be affected by climate change (Conrad et al. 2002).

Previous studies have shown that many moth species move at scales larger than the field scale (Merckx et al. 2009; 2010; Chapter 8, this volume), with individuals able to cover several kilometres a night. The longest movement distance we recorded was for a broad-bordered yellow underwing *Noctua fimbriata*, which was recaptured outside the study area, having moved 13.7 km in two months. However, the majority of species were predicted to move less than 500 m in a week, with the range increasing with wingspan. Wingspan, wing shape, adult feeding, and larval feeding guild all predicted macro-moth mobility. For moths with weak or strong forest affinity, those species with pointed wings moved further than those with broad wings. Moreover, the most mobile species were those with pointed wings, rather than those with the largest wingspan (e.g. the weekly movement rate of green arches Anaplectoides prasina-48 mm wingspan, pointed wings-was 1207 m, whereas that of the garden tiger Arctia caja-70 mm wingspan, rounded wings-was 297 m). The three species with the largest predicted movement rate, i.e. lobster moth Stauropus fagi (Fig. 12.6a), green arches Anaplectoides prasina (Fig. 12.6b), and scarce silver-lines Bena bicolorana (Fig. 12.6c), were all forest species with pointed wings. Moths that fed as adults, and moths with shrub/treefeeding larvae, had larger predicted movement rates than those that did not feed as adults or with grass/ herb-feeding larvae. This pattern was similar for both forest specialists and ubiquitous species.

In terms of landscape structure, we found that both forest size and connectivity were important (Slade et al. 2013). Solitary trees and small fragments functioned as 'stepping stones', especially when their landscape connectivity was increased by being positioned within hedgerows or within a favourable matrix. Mobile forest specialists, such as the lobster moth, were most affected by forest fragmentation despite their high intrinsic dispersal capability. These species were confined mostly to the largest of the forest patches due to their strong affinity for the forest habitat, and thus were also heavily dependent on forest connectivity in order to cross the agricultural matrix. The majority of species with a strong forest affinity were first captured in the large fragments (> 5 ha) (94% of individuals and 89% of species), and were then only recaptured in the largest fragments, or rarely at hedgerow trees, and never in smaller fragments or at isolated trees (Fig. 12.7 a,c). Moreover, the results of this study suggest that forest fragments need to be larger than 5 ha, and need to have interior forest more than 100 m from the edge, in order to sustain populations of these forest specialists (Fig. 12.7).

The land use of the surrounding matrix was also found to have an effect on the number of both ubiquitous and forest specialist species using oak trees. Tall sward pastures were associated with higher moth numbers than short pastures and intensively managed arable crops. Reduced vegetation structure, fewer nectar sources, and reduced shelter, in grazed and arable fields, have been shown to be detrimental to many moth species (Littlewood 2008). Ubiquitous species, such as the nationally declining bright-line brown-eye *Lacanobia oleracea*, heart and dart *Agrotis exclamationis*, flame shoulder *Ochropleura plecta*, and flame *Axylia putris*, were relatively abundant at hedgerow oak trees in



Figure 12.6 Mobile—note the pointed forewings—macro-moth species typical of forests: (a) lobster moth *Stauropus fagi* marked on the wing, the larvae feed on beech *Fagus*, oak *Quercus*, and several other trees. Photograph © E. Slade; (b) green arches *Anaplectoides prasina*, larvae feed on a number of plants, including bilberry *Vaccinium myrtillus*, honeysuckle *Lonicera*, and knotgrass *Polygonium*. Photograph © Maarten Jacobs; and (c) scarce silver-lines *Bena bicolorana* the larvae are typically found on oak. Photograph © Maarten Jacobs.

particular, suggesting that they are using hedgerows as corridors when crossing the agricultural landscape. In fact, hedgerow oaks approached small fragments in terms of abundance and species richness of species with weak to medium forest affinity (Fig. 12.7 a,c). Species with weak to medium forest affinity were also frequently captured at isolated oaks, and low recapture rates at the same tree suggest that they were being used as 'stepping stones', enabling movement across the landscape. Small forest fragments also seemed to be acting as 'stepping stones', and as a key habitat for many species with a medium forest affinity, such as blood-vein Timandra comae, lackey Malacosoma neustria, and pretty chalk carpet Melanthia procellata, all of which are severely declining in Britain (Conrad et al. 2006). Many farm woodland schemes conserve small

patches of forest (i.e. < 2 ha) within the agricultural landscape. Thus, while such schemes may not benefit true forest specialists, our results suggest that small forest fragments may provide key habitat resources for many other moth species.

Our study thus highlighted that both forest size and forest connectivity are important when considering how to conserve moth diversity in fragmented agricultural landscapes (Slade et al. 2013). Physical links in the landscape, such as hedgerows, may be important both for forest specialists and generalists, and such connectivity will become increasingly important in the light of climate change, as species try to move in order to stay within their climatic envelopes (Devictor et al. 2012). We suggest that increasing the landscape connectivity between patches of remaining forest should be a key



Figure 12.7 Model-predicted abundance and a species richness measure (PropS) of moths for three forest affinity classes (weak, medium, and strong), in relation to (a) and (c) forest area (hedgerow and isolated oaks were given a value of 0.0015 ha and 0.001 ha respectively) and (b) and (d) distance from forest edge. Note that in (a) and (b), the y-axis has a different range for the strong forest affinity class. In (b) and (d), positive values are the distance from within (i.e. trap is placed inside the forest) and negative values are the distance from outside (i.e. trap is outside the forest at solitary oak trees). Redrawn from Slade et al. (2013).

priority (e.g. for national agri-environment schemes, AES). The extent of forest cover in the UK, although very small, is now increasing (Mason 2007) and AES, combined with farm business models that include sustainable forest revenue streams, have the potential to be used to increase connectivity and create forest networks at the landscape level, leading to ecologically functional landscapes. However, in order to maintain the full complement of species within the landscape, and in particular forest specialists, it is necessary to maintain both connectivity and large patches of suitable forest habitat.

12.5 Forest management in the 'farmscape'

Our small mammal and moth research portfolios highlight some key conservation issues for the management of woodlands and the intervening matrix in the 'farmscape'. To maintain forest ecosystem functionality within smaller woodland patches, grazing pressure on forest regeneration needs to be controlled through rigorous deer population management, thus benefiting forest flora and ground cover. Encouraging a well-developed three-dimensional forest structure with sufficient bramble and hawthorn cover provides small mammals and ground-nesting birds with cover from avian and mammalian predators, while simultaneously providing food and nesting opportunities for a variety of species (Buesching et al. 2008).

Pure forest specialists can be accommodated through the implementation of a two-tier management approach for larger woodlands (Merckx et al. 2012), which serves to create core areas of dark, sheltered, and humid forest, while the buffering of these core areas with lighter zones of more open woodland helps to provide a variety of resources to those species which cannot satisfy all their requirements of food, shelter, and nesting opportunities in our increasingly intensified countryside. However, caution must be exercised in establishing too many rides through contiguous woodlands, as there is strong evidence that they may act as movement and dispersal barriers for small mammals (Buesching et al. unpublished data)

At the landscape scale, maintaining sufficient functional connectivity between woodland patches (e.g. through hedgerows, hedgerow trees, solitary field trees, small woodlots, and favourable ground cover; Slade et al. 2013) facilitates species dispersal—and thus re-population of those areas in the 'farmscape', which, due to land use and agricultural practices, have become depauperate.

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