Ecology and display behaviour of breeding Eurasian woodcock *Scolopax rusticola*

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ABSTRACT

In Britain, the Eurasian woodcock *Scolopax rusticola* occurs as both a common winter migrant and a resident breeding species. A national Breeding Woodcock Survey, conducted in 2003, provided the first accurate assessment of Britain's resident population size. Here, data from a second national Breeding Woodcock Survey are presented, providing the first opportunity to assess changes in abundance. I estimated Britain's Breeding population to be 55,241 males (95% CL: 41,806–69,004), representing a 29% decline in ten years. Abundance was correlated with the availability of large, well-connected and heterogenous areas of woodland and populations have retracted towards more heavily wooded landscapes. Woodcock site occupancy increases with the availability of certain woodland types, notably birch, and with increasing distance from urban areas.

The 2003 and 2013 Breeding Woodcock Surveys used counts of displaying male woodcock to estimate abundance across a stratified sample of randomly selected sites. Chapters 4 to 7 seek to improve the current understanding of this unique display, known as roding, which underpins national surveys in Britain and elsewhere in Europe. To do this, GPS loggers were used to track the movements of male woodcock during their roding flights. Male woodcock covered roding grounds that were larger in size than most previous estimates, with mean daily roding grounds measuring between 1.11 and 1.29 km^2 depending on the technique employed. Roding activity was reduced if dry periods

preceded roding surveys, and temperature, cloud and moon phase could all influence the timing of display. The woodcock's roding display is targeted towards open space within woodlands and woodland edges, and woodcock showed a preference for permanent clearings during display. These findings are discussed in terms of their potential influence on the interpretation of existing roding survey data and their implications for future assessments of population size and trend.

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1 INTRODUCTION

1.1 Species monitoring

Population monitoring can provide an assessment of a species' abundance and population change over time. Monitoring may be used to justify the division of conservation efforts (Pullin *et al.* 2013; Rodrigues *et al.* 2006; Schmeller *et al.* 2008) or ensure that the chosen actions deliver the desired outcomes (Hockings 2003; Pullin *et al.* 2013; Stem *et al.* 2005). While traditional surveillance modelling may be considered outdated or ineffective by some (Legg & Nagy 2006; Nichols & Williams 2006), alternatives that combine targeted monitoring, adaptive management and population modelling (Nichols & Williams 2006) still require some form of monitoring albeit in a more integrated role.

There are many species whose basic biology prevent a straightforward assessment of their population size or trend. For species exhibiting physical or behavioural crypsis or that provide few obvious field signs, a low probability of detection may result in under-recording (Bellemain *et al.* 2005; Jacob *et al.* 2010; Carbone *et al.* 2001; Durso *et al.* 2011; Sanderson & Trolle 2013). Difficulties distinguishing similar species or their field signs can lead to over- or under-estimation of abundance and the resulting monitoring data are likely to include a high degree of observer error (Broughton 2009; Scott & Hallam 2002; Vodă *et al.* 2015; Williams *et al.* 2018; Miller *et al.* 2011). The practicalities of surveying species in remote regions or on large spatial scales may make monitoring logistically difficult or

prohibitively expensive, although increasingly, automated monitoring techniques are providing alternatives to human fieldworkers (Southwell & Emmerson 2015; Norouzzadeh *et al.* 2018; Zhang *et al.* 2016; Williams *et al.* 2018; Singh & Milner-Gulland 2011; Witczuk *et al.* 2008).

Extremes in population size may be associated with different kinds of errors. False negatives are likely for species occurring at very low densities unless a sufficiently high monitoring effort is employed (MacKenzie *et al.* 2005; Field *et al.* 2005; Gerber *et al.* 2014; Clark & Bjørnstad 2004). For abundant species with large geographic ranges or unspecialised habitat requirements, differences in density or population trend between regions may mean extrapolation from a narrow or unrepresentative sample of sites can amplify errors (Hoffmann & Welk 1999; Cotgreave & Harvey 2017; Marsh-Matthews & Matthews 2000).

Quantifying population trends requires multiple surveys of abundance spread over a defined period of time. The accuracy of an estimated trend increases with the number of temporal data points available (Yoccoz *et al.* 2001; Clark & Bjørnstad 2004), but logistic considerations may limit the frequency that large-scale monitoring can be conducted and, if the monitoring period is too protracted, necessary conservation measures may not be implemented soon enough (Nichols & Williams 2006). Declines that have occurred over long time periods are difficult to monitor as they are reliant on the existence of historical data. For some species, it is difficult to separate natural, cyclical fluctuations in population size from the kind of unsustainable anthropogenic change that require conservation action (Ravier &

Fromentin 2001; Baker *et al.* 2012; Pechmann *et al.* 1991; Fedy & Doherty 2011; Magurran *et al.* 2010).

Effective conservation monitoring requires a complete enough understanding of the species' ecology to ensure accurate interpretation of survey data. Survey method design depends upon an understanding of the focal species' habitat requirements and behaviour (Sutherland 1998; Hayward *et al.* 2015; Witczuk *et al.* 2008; Berger-Tal *et al.* 2016; Burton *et al.* 2015); density estimates may require a measure of mean range size or movement (Anich *et al.* 2009; Burch *et al.* 2005; Sumner *et al.* 2001; Burgman & Fox 2003; Sharma *et al.* 2010; Burgar *et al.* 2018); and the use of population data to model future change requires measures of productivity, mortality and age/sex ratios (Unger *et al.* 2013; Loison *et al.* 2001; Pryde *et al.* 2005; Calvete *et al.* 2005; Grüebler *et al.* 2008; Steifetten & Dale 2006; Rhodes *et al.* 2011; Schaub *et al.* 2010; Hiraldo *et al.* 1996; Anders & Marshall 2005).

1.2 Declines of woodland birds in Britain

Approximately one third of woodland bird species breeding in Britain have experienced population declines since the 1970s (Hewson *et al.* 2007*;* DEFRA 2015) although there is no single, unifying explanation for these declines. Commonly recurring themes include a reduction in understorey density (Amar *et al.* 2006; Hewson *et al.* 2007; Hewson *et al.* 2011; Hopkins & Kirby 2007) and floristic diversity (R. M. Fuller *et al.* 2005), and the loss of open canopy woodland habitats (Fuller *et al.* 2007; Quine *et al.* 2007). While the specific factors responsible vary

between species, these are often the results of the same overarching changes to woodland habitats.

British woodlands have a history of management that spans over 2000 years (Hopkins & Kirby 2007) and this, along with competing land-uses such as agriculture, has shaped the extent and composition of woodland in the British Isles. The early 20th century saw a doubling of woodland coverage from 5% of Britain's land surface to around 12% (Forestry Commission 2011; Rackham 1976), but this net gain masks losses of some specific woodland habitats of high value. In the early 20th century, a greater area was occupied by ancient woodland i.e. land that had been continuously forested for at least 400 years (Rackham 1976) and that was often managed using traditional, low-impact coppice and coppice with standard regimes (Hopkins & Kirby 2007; Rackham 1976). Many ancient woodlands were felled to meet the high timber demands of the First and Second World Wars (Spencer & Kirby 1992) and have since been replaced. Woodland planting was intensified after each of the World Wars to replace depleted stock, meaning a large proportion of Britain's woodland is of a similar age and has matured simultaneously through the latter half of the 20th century.

Increasing woodland age has been implicated in the declines of some woodland species. Local extinctions of common nightingale *Luscinia megarhynchos* have been attributed to a reduction in understory density (Wilson *et al.* 2002), a natural consequence of woodland maturation (Quine *et al.* 2007). Declining woodland bird species are often those associated with open canopy habitats within

deciduous woodlands (Fuller *et al.* 2007) such as Eurasian bullfinch *Pyrrhula pyrrhula* (Carpenter *et al.* 2009) or marsh tit *Poecile palustris* (Hinsley *et al.* 2007) that, like the nightingale, need an open canopy for the sake of a denser understory as well as those like the spotted flycatcher *Muscicapa striata*, which require open spaces in which to feed (Fuller *et al.* 2007). The correct management can maintain structural diversity and preserve a dense understory in woodland where it would otherwise be excluded by a closing canopy, but traditional techniques such as coppicing have declined due to the reduced value of their products and the increasing popularity of more viable alternatives (Mason 2007). Increased browsing pressure from rising deer populations often means that, even where appropriate management is in place, dense understory vegetation is unable to establish (Gill & Fuller 2007).

Some bird species depend on the open habitats that precede these young woodlands with dense understory. The red-listed tree pipit *Anthus trivialis* and amber-listed European nightjar *Caprimulgus europaeus,* for example, prefer very open habitats that possess a low and patchy field layer (Burton 2007; Morris *et al.* 2015; Sharps *et al.* 2015). This may include permanent clearings such as heaths, recently cleared areas or newly planted stands (1-6 years old) (Burton 2007). These features are often created and maintained by human activity and in the absence of grazing/browsing, their persistence relies on a repeated cycle of tree removal and replanting.

At the opposite end of the successional scale, a smaller number of declining species, such as the pied flycatcher *Ficedula hypoleuca,* require old growth woodland in which a mature, closed canopy structure has been reached and, due to the death of individual canopy trees, is succeeded by a varied multi-aged stand (Quine *et al.* 2007). Historic declines of pied flycatchers in Britain are likely to be linked to the loss of ancient woodland, but continuing declines through the latter half of the 20th century (Woodward *et al.* 2018), when the availability of mature oakwoods remained constant (Amar *et al.* 2010), are more likely the effect of poor over-winter survival. In fact, around half of the woodland bird species appearing on the UK Red list, including the pied flycatcher, the tree pipit and the nightingale, are summer visitors (Eaton *et al.* 2015). Declines in trans-Sahelian migrants can also be linked to the loss of wintering habitat (Vickery *et al.* 2014), high mortality during migration (Bairlein 2016) and phenological asynchrony with invertebrate prey species in spring (Both 2010). These additional factors make it difficult to isolate the role that British breeding habitat plays in their declines.

Among resident declining species, some, such as willow tit *Poecile montanus* and lesser spotted woodpecker *Dryobates minor,* appear to be associated with wet woodlands and local extinctions are more common in woods where soil water content is lower (Charman *et al.* 2010; A. J. G. Lewis *et al.* 2007). The decline of the hawfinch *Coccothraustes coccothraustes* has not been extensively studied, but woodland maturation has been proposed as a possible factor (Kirby *et*

al. 2015). Although typically thought of as a bird of ancient semi-natural woodlands, a study in the Netherlands showed that hawfinches colonised woods that were 8-20 years old but that their abundance levelled off thereafter (Bijlsma 1998). Hawfinches appear to select nest-sites close to openings in the woodland canopy (Kirby *et al.* 2015), so the uniformity of age in many 'middle-aged' woods (30-100 years) is likely to be detrimental.

There appears to be some broadscale consistency in the underlying causes of woodland bird declines. The observed trends in mean woodland age and diversity may underpin the declines of other species for which the cause is still unknown. Identifying the exact mechanisms that link habitat change to avian population change, however, can be difficult, especially for species whose basic ecology remain poorly understood.

1.3 Monitoring of Eurasian woodcock populations trends

The Eurasian woodcock *Scolopax rusticola* is a woodland bird for which large-scale estimates of population size and trend can be difficult to attain. The species' cryptic camouflage and nocturnal behaviour mean that detection rates are typically low (Risely *et al.* 2012; Risely *et al.* 2010; Risely *et al.* 2011). Large tracts of the Eurasian woodcock's range are remote and unmonitored, and it is difficult to predict how densities vary in response to latitude, longitude or predominant habitat type. The wide availability of habitat within the species' extensive range

means that extrapolation from localised surveys is likely to magnify any intrinsic error (Yoccoz *et al.* 2001).

As a result, existing global population estimates necessarily have large confidence intervals: the figure is thought to be between 10 and 26 million individuals (Delany & Scott 2006). If accurate, even the lower bound of this estimate would make the Eurasian woodcock one of the world's most abundant waders (Delany & Scott 2006).

An estimate of the European population size and trend is more achievable and serves a practical purpose given that this population receives the highest anthropogenic hunting pressure. Between 13.8 and 17.4 million Eurasian woodcock are believed to breed in Europe, around 12-14 million of which do so in European Russia (Birdlife International 2015a). This figure is a composite of 44 national estimates, which vary in reliability depending upon the way in which they were produced. Many national population assessments are derived from the results of general multi-species bird surveys (e.g. diurnal transects) (Birdlife International 2015a) which are likely to underestimate the abundance of a species that is easily overlooked. For this reason, species-specific woodcock surveys based on counts of displaying males are used to assess site occupancy and population trends in several European countries (Belarus: Mongin *et al.* 2006; Britain: Hoodless *et al.* 2009; France: Ferrand *et al.* 2008; Portugal (the Azores): Machado *et al.* 2008; and parts of Russia: Fokin & Blokhin 2013).

In Britain, a national breeding woodcock survey estimated the size of the breeding population in 2003 (Hoodless *et al.* 2009). Male Eurasian woodcock were counted at a sample of over 800 1x1-km squares, stratified by four woodland area categories and eleven geographic regions.

A preliminary study used sonogram analyses to show that the number of 'registrations' recorded at a site was correlated with the number of males present. Hoodless *et al.* (2008) used a single audio recording of a woodcock from each of 43 separate sites to quantify within- and between-individual variation in the call's repeated 'whistle' element. Five distinguishing call traits were identified and were used to estimate the number of males present at each site. The relationship between registrations and estimated density was consistent enough to allow the derivation of a calibration equation, which was used to estimate mean densities for each of the 44 strata in 2003. By extrapolation, based on the availability of similar squares, the British population was estimated at 78,346 male woodcock (95% CL: 61,717 – 96,493) (Hoodless *et al.* 2009). This was significantly higher than previous estimates derived from general bird surveys. The New Atlas of Breeding Birds in Britain and Ireland (Gibbons *et al.* 1993), for instance, suggested a population of 8,500-21,500 pairs for Britain in 1988-1991 and, based on this, Baker *et al.* (2006) estimated a breeding population of 5,000-12,500 pairs in 2000.

Globally, the Eurasian woodcock is classified as 'least concern' owing to the species' very large population size and range (Birdlife

International 2015a). There is some evidence of a small decline in the breeding populations of European Russia although this may be the result of unusually high counts in the monitoring programme's first year and the relatively short monitoring period of 20 years (Fokin & Blokhin 2013). Populations in Scandinavia, for which trend assessments are believed to be more accurate, show stability (Birdlife International 2015a; Lindström *et al.* 2015).

The British population, on the other hand, was red-listed as a Bird of Conservation Concern in 2015 based on the range contraction recorded in the last 25 years (Eaton *et al.* 2015). Although the Bird Atlas monitoring scheme almost certainly underestimates Eurasian woodcock abundance, the degree of underestimation ought to be constant enough between surveys to give an indication of trend. The atlases shows a marked contraction in the range of the Eurasian woodcock in Britain; while once present in 57% of 10 x 10km squares (1968/72), they occurred in only 30% by 2008/11 (Sharrock 1977; Balmer *et al.* 2013). The British Trust for Ornithology's (BTO) Common Birds Census recorded a 74% decline in the UK during 1968-1999 (95%CL -49% to -88%) (Baillie *et al.* 2002). Similar declines are observed in resident populations in Switzerland (Estoppey 2001). These populations occur at the western edge of the species' range where human populations are denser and where anthropogenic habitat change is greatest.

1.4 Woodcock biology: taxonomy, distribution and non-breeding ecology

The common name ‘woodcock’ is applied to eight species of wading bird belonging to the genus *Scolopax* (Linnaeus, 1758) (IUCN 2018). They make up a small proportion of the *Scolopacidae* family (Sandpipers and their allies) which consists of around 96 species in total (IUCN 2018). Woodcocks possess the long, probing bill that is typical of the scolopacid waders, but compared to other members of the family, are proportionally larger bodied and shorter legged. Woodcocks range in size from 25-31 cm (*S. minor*) to 32-40 cm (*S. rochussenii*) (Piersma *et al.* 1996).

All members of the *Scolopax* genus are adapted to temperate or tropical forests. Five of the eight species inhabit the tropical forests of Southeast Asia and have small non-overlapping island ranges in Indonesia (*S. celebensis, S. rochussenii, S. rosenbergii, S. saturata*), Papua New Guinea (*S. rosenbergii)* and the Philippines (*S. bukidnonensis)* (IUCN 2018). The Amami woodcock *Scolopax mira* is confined to the sub-tropical forests of the Ryukyu Islands in southern Japan (IUCN 2018). Only the Eurasian woodcock and the American woodcock *S. minor* have large continental ranges. The American woodcock is found in temperate forests in eastern North America and breeds between the latitudes of 35° and 51°N (Birdlife International 2018a).

The Eurasian woodcock’s breeding range stretches across the northern Palaearctic from Norway, the British Isles, France and Spain to

Russia's Pacific coast and Japan. This breeding range occurs mostly between the latitudes of 49°N and 64°N, although reaches as far north as 70°N in Fennoscandia (Birdlife International 2018b). Isolated breeding populations exist in mountainous regions south of their core range in northern Italy, the Balkans, the Caucasus and the Himalayas (Birdlife International 2018b). There are small breeding populations in the Canary Islands, the Azores and Madeira and Eurasian woodcock are reported to have colonised Iceland since the turn of the 21st century (Sigurðsson & Magnússon 2005).

Across most of their range, Eurasian woodcock are migratory. Large areas of the core breeding range in Russia and Scandinavia experience average winter temperatures that are too cold for woodcock to tolerate (Cramp *et al.* 1983). In the Western Palaearctic, Eurasian woodcock overwinter in milder western regions, particularly Britain, Ireland and France, and in Mediterranean countries in Southern Europe and North Africa (Birdlife International 2018b). Satellite tracking studies of Eurasian woodcock wintering in Italy, France and Spain have shown that most migrate to the Baltic States and western Russia in spring (Club de Cazadores de Becada 2018; Club National des Becassiers 2018; Federazione Italiana Della Caccia 2018). This was also true of woodcock wintering in the British Isles, although a greater proportion of these woodcock migrated to Finland and Scandinavia (Game & Wildlife Conservation Trust 2018). This roughly corresponds with the results of stable hydrogen isotope analyses, which suggests most woodcock wintering in Spain originate from Central Europe (61%) and the Baltic

regions (30%) (Hobson *et al.* 2013), whereas in the British Isles 39% of woodcock were thought to be of Fennoscandian origin (Hoodless *et al.* 2013). The spring migrations of British wintering woodcock ranged from around 900 km (Denmark and Norway) to 2,000 – 3,000 km (Baltic States and western Russia) and over 6,000 km in the case of three tagged woodcock that returned to Krasnoyarsk Krai, central Russia (Game & Wildlife Conservation Trust 2018). A similar (> 6000 km) Russian migration was made by one of nine wintering woodcock satellite-tagged in Spain (Crespo *et al.* 2016).

In Western Asia, Eurasian woodcock winter in coastal areas such as the Euxine-Colchic forests of Northern Turkey and the Caspian-Hyrcanian forests of Northern Iran (Birdlife International 2018b). Further east, Eurasian woodcock winter in a broad range of temperate, sub-tropical and tropical forests across India, Sri Lanka, southern China, mainland Southeast Asia, South Korea and Japan. Breeding populations confined to mountainous regions, such as those in northern Spain, make altitudinal migrations in autumn. Across their breeding, passage and wintering ranges, Eurasian woodcock regularly occur in at least 77 countries worldwide (IUCN 2018).

Small non-migratory Eurasian woodcock populations exist at the western edge of their range (Birdlife International 2018b), where the Atlantic maritime climate reduces the degree of seasonal variation in temperature. Resident populations can be found in Ireland, Britain, the Netherlands, Belgium, France, Spain, and the Macaronesian islands. In all but Macaronesia, migrant visitors occur alongside resident woodcock

during winter. The species is monotypic across its entire range and even the island populations show no subspeciation (Piersma *et al.* 1996).

The Eurasian woodcock is approximately 33-35 cm long and can weigh between 131g and 420g (Piersma *et al.* 1996). The plumage is predominantly reddish-brown above with a mixture of buff, black and grey markings on the back, scapulars and coverts and broad black bars across the back of the head. The flight feathers are blackish grey with large rufous markings and the breast and belly are buff with fine dark grey bars. The plumage provides very effective visual camouflage which is matched by the species' cryptic behaviour; Eurasian woodcock usually remain motionless until the latest possible moment, then flush with an explosive, zig-zagging escape flight. Like other members of the genus, Eurasian woodcock possess an unusual skull morphology with the ear positioned below the orbit and the cranial cavity rotated so that the cerebellum points downwards and the large eyes sit high in the head (Schäfer & Schmitz 2016). This repositioning of the eyes provides Eurasian woodcock with almost 360° vision (Martin 1994). The Eurasian woodcock's long bill (58-83 mm (Demongin 2016)) is tipped with a remarkably high density of sensory pits, even relative to other Scolopacid waders, which allows woodcock to detect the vibrations of invertebrate prey within leaf-litter or beneath the soil (Cunningham *et al.* 2013).

In winter, Eurasian woodcock feed at night in open habitats such as heathland, arable farmland and pastures (Duriez, Fritz, *et al.* 2005;

Braña *et al.* 2010). This foraging strategy appears to be driven by both food availability and predation risk. Earthworms make up at least 85% of the diet in winter and permanent pastures offered twelve times more worms than woodland (Duriez, Ferrand, *et al.* 2005). Woodcock can travel up to 3-4 km between a daytime roost and nocturnal feeding site (Duriez, Fritz, *et al.* 2005). Feeding during daylight hours is perhaps also avoided because movement compromises the woodcock's camouflage, especially during winter when there is less vegetative cover to offer concealment. At night, when the woodcock's visual camouflage offers little protection against nocturnal predators, feeding in open habitats may improve predator avoidance by providing a greater field of view.

Avian predators include Eurasian sparrowhawk *Accipiter nisus* (Bergman 1961; Selås 2015), northern goshawk *Accipiter gentilis* (Toyne 1993; Verdal & Selås 2010), common buzzard *Buteo buteo* (Reif *et al.* 2001; Swann & Etheridge 2009) and Eurasian eagle owl *Bubo bubo* (Hiraldo *et al.* 1975; Obuch & Karaska 2010; Obuch 2014). Peregrines *Falco peregrinus* are a common predator during the woodcock's migration period (Drewitt & Dixon 2008). Woodcock are at risk of predation when moving between daytime roosts and nocturnal feeding sites, but this is minimised by making such movements when light levels are low (Braña *et al.* 2010). Nevertheless, a risk is still posed by tawny owls *Strix aluco* (Bergman 1961; Hoodless & Coulson 1998; Petty 1999). Mammalian predators of woodcock include red fox *Vulpes vulpes* (Braña *et al.* 2010; Hoodless 1994; Hoodless & Coulson 1998),

raccoon dog *Nyctereutes procyonoides* (Viro & Mikkola 1981), Eurasian lynx *Lynx lynx* (Nystrand 2012), European wildcat *Felis silvestris* (Biró *et al.* 2005), martens *Martes spp.* (Braña *et al.* 2010; Helldin 2000), stoat *Mustela erminea* (Hoodless 1994) and wild boar *Sus scrofa* (Schley & Roper 2003).

Foraging behaviour becomes more varied during the breeding season and moulting period, when woodcock reduce the frequency with which non-woodland habitats are visited. Feeding within woodland becomes more regular, particularly for females who must remain close to their nest and young, and the diet tends to show a greater degree of diversity including more fly larvae, harvestmen, spiders, and beetles (Hoodless & Hirons 2007; Koubek 1986).

The Eurasian woodcock has a long relationship with humans and has been hunted as food since at least Roman times (Cool 2006). Historically, the species was caught using cage-traps, nooses and nets in fields at night. With the advent of modern firearms for hunting, the Eurasian woodcock became a popular gamebird whose erratic escape flight gave it a reputation as a challenging shot. Eurasian woodcock are currently hunted in most European countries in which they occur and the total annual European bag is estimated at around 3-4 million individuals (Duriez, Eraud, *et al.* 2005) (see Section 1.6 for more detail). The Eurasian woodcock features prominently in British folklore. The species is often associated with autumn owing to the large numbers of migrants that arrive in October and November, and it lends its name to November's 'woodcock moon' as well as other autumn migrants such

as the ‘woodcock pilot’ (goldcrest *Regulus regulus*), ‘woodcock owl’ (short-eared owl *Asio flammeus*) and ‘sea-woodcock’ (black-tailed godwit *Limosa limosa)* (Swann 1913). The word woodcock is found in old English as ‘wodecocc’ or ‘wuducoc’ and is at least 950 years old (Bosworth 1898). It was first applied to the Eurasian woodcock, which is still referred to as simply ‘the woodcock’ in British vernacular. This terminology is used hereafter, with the full common name being given for any other woodcock species.

1.5 Breeding ecology of woodcock

Across most of the woodcock’s core breeding range in Northern Europe and Asia, taiga is the predominant habitat. These forests consist mainly of pine (*Pinus sylvestris* and *Pinus sibirica*), spruce (*Picea abies* and *Picea obovata*), fir (*Abies sibirica*) and larch (*Larix gmelinii* and *Larix sibirica*) (World Wildlife Fund 2018). They also contain broadleaf species such as birches *Betula* sp. and common aspen *Populus tremula,* particularly in pre-climax forest (World Wildlife Fund 2018). In Europe, the Himalayas, and parts of central and eastern Russia, woodcock breed in temperate broadleaf and mixed forests. The largest examples are the Central European and Sarmatic mixed forests which collectively cover 1.6 million km² and are dominated by a mix of common oak *Quercus robur*, Norway spruce *Picea abies* and Scot’s pine *Pinus sylvestris* (World Wildlife Fund 2018; IUCN 2018).

A study of woodcock nest sites in western Russia found that 90% of nests were either situated in a glade or clearing, or within forest

that was less than 100 m from a glade, clear-fell or the forest edge (Fokin *et al.* 2013). Nesting woodcock are thought to prefer the early successional forest that occurs during post-fire or post-felling recovery (Etienne *et al.* 2013; Gossmann *et al.* 2017). The same habitat associations are better documented for American woodcock, which are known to favour young forest with dense hardwood stands (Kelley *et al.* 2008).

Non-migratory woodcock populations at the western edge of the range use a broad array of woodland habitats that vary according to climate and human activity. In a lowland English wood, radio-tagged breeding woodcock made greater use of sycamore *Acer psuedoplatanus* stands relative to neighbouring beech *Fagus sylvaticus* and pine, and in Scotland, radio-tagged woodcock favoured young regenerating birch, despite comprising only a small proportion of the available habitat (Hoodless & Hirons 2007). These results, though constrained by the limited range of habitats occurring within each of the study sites, show a tendency to favour woods that are younger, broadleaved and that provide some understory cover.

For resident woodcock, breeding can begin as early as late-February (Hoodless & Coulson 1998). For migrants, breeding follows spring migration, the timing of which appears to depend on the rate of thaw on the breeding grounds and the atmospheric conditions across their route (Game & Wildlife Conservation Trust 2018; Le Rest *et al.* 2019). Breeding typically begins in late-March in Scandinavia and the

Baltic States (European Commission 2008) and early April in Russia (Fokin *et al.* 2013).

At dawn and dusk during the breeding season, male woodcock perform a courtship display known as 'roding'. In the UK, this behaviour can be observed from late February until early July, with activity peaking during May and June (Hirons 1983). The roding call consists of a simple nasal squeak (3-16 kHz) interspersed with 3 - 5 frog-like croaks, which are given during long, roving flights over woodland and neighbouring habitat (Hoodless *et al.* 2008). Based on the assumption that males were patrolling a repeated circuit, and because roding may be interrupted by chasing and aggressive contact calls, it was traditionally believed that this behaviour was territorial (Tester & Watson 1973), and anecdotal accounts of monogamous behaviour, such as the sharing of the incubation duty, exist in older literature (Seigne 1936). A radio-tracking study, however, demonstrated that several males may overlap their display areas, and that males did not accompany females during incubation or brood-rearing, only during laying (Hirons 1980). Woodcock are now thought to be sequential polygamists, with the roding behaviour serving as an indicator of fitness for mate selection by females (Hirons 1980).

There are several similarities between roding and the 'lekking' displays of waders such as great snipe *Gallinago media* (Kålås 2000) and ruff *Calidris pugnax* (Widemo 1998), but the woodcock's display differs in that males do not cluster within a well-defined display area. The display of the American woodcock is more akin to a lek, as each

male restricts his display to a single ‘singing ground’ which may be within a hundred metres or so of the next displaying male (Ellingwood *et al.* 1993). The American woodcock’s display is a hierarchical system whereby certain singing grounds are preferred and males compete for more favourable positions (Ellingwood *et al.* 1993), much like in the true leks of ruff or grouse. In the case of Eurasian woodcock, it has also been proposed that a male’s quality dictates the roding ground that can be accessed as, although they overlap, male-male conflict appears to exclude lower-quality males from areas with higher densities of females (Hirons 1983).

There are practical benefits to understanding the woodcock’s roding display, as the behaviour provide a means of monitoring the species (see Section 1.3). There have been attempts to study roding behaviour using radio-tagged individuals, although the large areas that each male can cover in a single evening have made this difficult. Based purely on field observations, Tester and Watson (1973) estimated that roding areas measured 6 – 13 ha but radio-tracking suggests areas of at least 100 ha are commonly used (Hirons 1980).

The nest is a lightly lined scrape in the ground. A wide variety of nest-sites are reported, ranging from those situated among bare expanses of beech leaf litter, to the more usual reports of nests tucked under dead bracken *Pteridium aquilinum*, bramble *Rubus fruticosus* or at the base of a tree (Morgan & Shorten 1974). The peak nesting period in the UK, based on British Trust for Ornithology (BTO) nest record cards, falls around the end of March (Hoodless & Coulson 1998). A

smaller second peak in late May might support anecdotal evidence of second broods, as most replacement clutches for failed attempts should be laid before this date (Hoodless & Coulson 1998). It is unusual that courtship peaks later than nesting but this probably occurs because, during late March and early April, some successful males are attending laying females rather than engaging in display. Later in the season, a larger proportion of the males present compete for the attention of a limited number of females seeking second matings. Additionally, it seems likely that reports of nest site choice and nesting date are biased by the reduced detectability of later nests owing to denser vegetative cover (Hoodless & Coulson 1998) and a general decline in effort by volunteer nest-recorders over the course of the breeding season (Crick *et al.* 2003).

Woodcock usually lay four eggs (mean = 3.89) which are incubated for 21-23 days (Hoodless & Coulson 1998). During incubation, the female leaves the nest up to four times per day to feed with each foraging trip lasting for about half an hour (des Forges 1975). The woodcock's young are nidifugous and leave the nest within a few hours of hatching (des Forges 1975; Hoodless 1995). The chicks eat a wide variety of surface-dwelling invertebrates, particularly spiders and harvestmen (Hoodless & Hirons 2007). Their ability to probe for food increases with bill length, and earthworms become a larger part of the diet as the chicks grow. Although the young can fly by the age of twenty days and are independent of their mother shortly after, they are not fully grown until at least forty days (Hoodless 1995). Based on nest and

chick survival data for 26 broods in northern England, Hoodless and Coulson (1998) calculated productivity to be 1.80 ± 0.72 chicks per breeding female.

1.6 Woodcock declines in Britain: possible causes

Woodcock declines could be driven by the general tendency towards woodland of an increasing average age, greater homogeneity in structure, and with less understory cover. Existing knowledge of habitat preferences are drawn from relatively small radio-tracking studies but appear to be consistent with the idea that the loss of young woodland habitats might have an impact on breeding woodcock (Hoodless & Hirons 2007). Woodcock may also be affected by the loss of rides and clearings as open spaces appear to be important for the males' aerial displays (Hirons 1983) and as nocturnal feeding sites (Hoodless & Hirons 2007; Hirons 1988). Historic changes in woodland area and management have been attributed to an increase in woodcock abundance in Britain during the first half of the 19th century (Holloway 2002). Continuing changes in the type, age and availability of woodland may be responsible for the national decline observed over the last 40 years.

Isolating woodland change as the key driver of decline, however, is hindered by our incomplete understanding of the species' ecology and there are a number of other, as yet untested, explanations. The woodcock's unique niche as a forest-dwelling wader prevents direct comparisons with other species but, as a ground-nesting woodland

specialist that is widely hunted, there are parallels with several other groups that are also undergoing declines.

The woodcock is one of several species of breeding wader that are declining in Britain. In most instances, these declines can be attributed to changes in moorland management (Pearce-Higgins & Grant 2010; Amar *et al.* 2011) or the loss of certain agricultural habitats due to changing land use (Smart *et al.* 2006; Smart *et al.* 2008; Dallimer *et al.* 2010), increased use of fertilisers (Baines 1988; Donald *et al.* 2001) and increased drainage (Smart *et al.* 2008; Baines 1988; Smart *et al.* 2006).

Woodcock leave woodland at night to forage on meadows, pastures and arable land (Duriez, Ferrand, *et al.* 2005; Braña *et al.* 2010). The drainage of agricultural land may reduce the availability of soil-dwelling invertebrates at these nocturnal feeding sites and in lowland areas, where small patches of woodland are often surrounded by intensive farmland, the effect may extend to woodland soils (see Section 1.5). Global climate change (Leech & Crick 2007) and changes to woodland plant assemblages due to increased browsing by deer (Fuller 2001) also contribute towards drier woodland soils. The same habitats are utilised by migrant visitors in winter, but the impact of drier soils is likely to be most severe in summer when only residents are present.

Drainage, along with a shift in agricultural markets and policy, has driven changes in agricultural land-use (Angus *et al.* 2009) that may further reduce the suitability of nocturnal feeding sites. In lowland

England, large areas of permanent pasture have been lost to more profitable arable agriculture and while the area of grassland in Britain as a whole has remained broadly stable since 1979 (-1%), the widespread decline of dairy farming is likely to have reduced the availability of grazed pasture in the south and west (Angus *et al.* 2009). Eurasian woodcock are not solely reliant on pasture and can forage in a range of arable habitat types, but worm availability is up to five times higher on pastures than cultivated fields (Duriez, Ferrand, *et al.* 2005). Currently, it is not clear whether this difference in food availability could have a population-level impact on woodcock numbers.

High levels of nest (Baines 1990; Macdonald & Bolton 2008) and chick predation (Grant *et al.* 1999) have been attributed to reduced productivity in several species of wading bird. This may particularly affect abundance when operating as a secondary factor alongside the loss of suitable nesting and chick-rearing habitats. The large-scale declines of some wader species, due to habitat change, have left diminished populations more susceptible to the impact of predation and several generalist mesopredators, particularly those that are able to adapt to the disturbed habitats associated with intensive human activity, are increasing in abundance (Gibbons *et al.* 2007). Macdonald and Bolton (2008) state that amongst 544 European studies of wader nest success, 55.3% reported that more than half of nests succumbed to predation and radio-telemetry studies have usually identified predation to be the most common cause of chick mortality (Grant *et al.* 1999). In the cases of both nest and chick predation, mammalian and avian

predators appear to be contributing to low productivity (Wallander *et al.* 2006; Bolton *et al.* 2007; Teunissen *et al.* 2008; Rickenbach *et al.* 2011). As a ground-nester, predation is likely to affect woodcock in a similar way to other waders, but this is not easily studied given the difficulty associated with locating nests.

The woodcock appears on Annex II Part A of the European Union's Birds Directive (species for which hunting is permitted throughout the EU) and the species is hunted in the majority of the EU28 countries (Storch 2018). Woodcock can be hunted from 1st October to 31st January in England, Wales and Northern Ireland and 1st September to 31st January in Scotland (British Association for Shooting and Conservation 2019). The United Kingdom's annual national bag is believed to be about 180,000 individuals (PACEC 2014) with the number of woodcock shot in Britain increasing during the 1970s and stabilising since 1980 (Game & Wildlife Conservation Trust 2019). It is unclear whether this change reflects an increase in the number of migrant woodcock wintering in the UK or an increase in hunting pressure (Hoodless 1994). It is sometimes suggested that hunting is unlikely to explain recent declines in the resident woodcock population given that both migrant and resident woodcock are hunted in winter and yet no decline is observed in the number of migrants wintering in the UK (Balmer *et al.* 2013). Nevertheless, woodcock shooting may have a greater effect on resident birds if they are subjected to a longer hunting season than their migratory counterparts, which typically do not arrive in the UK until mid-November (British Trust for Ornithology *et al.* 2019), or

if migrant populations are more productive and can better withstand the associated increase in mortality. The actual impact of shooting on the UK's resident population is currently unknown and must remain a consideration for future research.

1.7 Scope and aims of this study

The initial aim of this study was to provide an up-to-date assessment of the size of Britain's resident breeding woodcock population. The GWCT/BTO Breeding Woodcock Survey, conducted in 2003 (Hoodless *et al.* 2009), provided the most reliable assessment of the size of Britain's resident woodcock population at that time. A repeat of this survey, conducted in 2013, allows this estimate to be updated, and enables a more accurate means of assessing population change than previously available. This estimate of population trend is compared with longer-running, but less targeted, estimates derived from Bird Atlas (Balmer *et al.* 2013), as well as trends measured at a small sub-sample of sites surveyed on a repeat basis between 2003 and 2013.

The Breeding Woodcock Surveys of 2003 and 2013 provide two large datasets relating to the distribution and relative abundance of breeding woodcock in Britain. Analyses of these data, in relation to national habitat datasets, are used to identify basic habitat associations of breeding woodcock within the UK. The way in which these relationships change over time offers an insight into the factors that may be responsible for observed declines.

The field-based elements of this study focus on the habits of male woodcock during the breeding season and the development of an efficient means of catching male woodcock is described. The small number of existing studies of roding behaviour were limited by the technology available at the time. The advent of satellite-telemetry devices provides a tool that is better-suited to tracking the movements of individual male woodcock during the display period. A better understanding of this behaviour is important given that it underpins our current monitoring method.

2 CURRENT STATUS AND RECENT TREND OF THE EURASIAN WOODCOCK AS A BREEDING BIRD IN BRITAIN

This chapter was published in Bird Study (Heward *et al.* 2015). I was solely responsible for writing the manuscript but made changes in response to comments provided by the five co-authors. Some information has been updated here (e.g. to reflect the woodcock's change in conservation status). I was solely responsible for the analysis except where stated below.

Author Contributions:

Andrew Hoodless: Devised 2003 survey methodology, provided comments on manuscript

Greg Conway: Devised 2003 survey methodology, facilitated collection of volunteer survey data at BTO, provided comments on manuscript

Nicholas Aebischer: Wrote 2003 population estimate script in Genstat, provided comments on manuscript

Simon Gillings: Co-ordinates Bird Atlas data held by BTO, provided comments on use of Bird Atlas data

Rob Fuller: Devised 2003 survey methodology, provided comments on manuscript

2.1 Introduction

An increasing body of research documents recent changes in the composition of woodland bird communities in the UK (Amar *et al.* 2006; Hewson *et al.* 2007; Hopkins & Kirby 2007; Fuller *et al.* 2007), with many species showing declines in range and abundance through the latter half of the twentieth century (R. J. Fuller *et al.* 2005). These may be attributed to a range of hypotheses and their causes are likely to be species-specific (see R. J Fuller *et al.* 2005 for an overview). The declines of several species, however, have been linked to changes in woodland structure and floristic composition, especially reduced understorey density (Amar *et al.* 2006; Hopkins & Kirby 2007; Hewson & Noble 2009; Hewson *et al.* 2011), as well as reduced floristic diversity (R. J. Fuller *et al.* 2005) and the loss of open woodland habitats associated with early successional growth (Fuller *et al.* 2007; Quine *et al.* 2007). An increasing trend in average woodland age since the large-scale post-war afforestation of the late 1940s and 1950s (Hopkins & Kirby 2007; Mason 2007), as well as modification, reduction or cessation of management in many woods (R. J. Fuller *et al.* 2005, Amar *et al.* 2006) are thought to be driving such changes. In many cases, these issues may be compounded by the impact of increased browsing pressure from rising deer populations (Gill & Fuller 2007; Holt *et al.* 2011) and climate change (Leech & Crick 2007).

Although the Eurasian woodcock *Scolopax rusticola* (hereafter woodcock) differs ecologically from most of the woodland birds considered in previous studies, it is likely to be susceptible to some of

the factors thought to be responsible for their declines. R. J. Fuller *et al.* (2005) were unable to identify any strong hypotheses to account for a decline in woodcock but they listed disturbance, reduction of the field layer by deer, increasing dryness of woodland and changes in surrounding land management as potentially relevant. Breeding woodcock are thought to require open rides and clearings for courtship and have specific habitat requirements during incubation and brood-rearing (Hoodless & Hirons 2007). Nesting woodcock typically utilise woodland with open ground layer vegetation and patches of overhead cover (Hirons & Johnson 1987). When feeding, sites where trees are relatively small and close together with a dense shrub or herb layer are preferred (Hirons & Johnson 1987, Hoodless & Hirons 2007). Woodcock feed primarily on earthworms and other soil-dwelling invertebrates (Hoodless & Hirons 2007). During winter, they leave woodland to feed on open fields at night, but this becomes less frequent during the breeding season, when more time is spent foraging within woodland (Hoodless & Hirons 2007). This may make soil moisture and the availability of wet feeding areas within woodland an important consideration, particularly where summers have become drier (Smart *et al.* 2006). Moreover, the woodcock's status as a quarry species may subject it to additional pressure unique to the species.

Until 2015, the woodcock was Amber-listed owing to its 'SPEC 3' classification as a Species of European Conservation concern (Eaton *et al.* 2009). This was the result of moderate, recent declines elsewhere in its European range (Birdlife International 2015b), though for many

regions accurate data are lacking and those used for Britain are probably inaccurate (Hoodless *et al.* 2009). The atlases of breeding birds in Britain and Ireland comprise three comprehensive surveys spanning a forty-year period and provide an important insight into changes in local occupancy. The atlases show a -55% reduction in the breeding range of the woodcock in Britain and Ireland between 1968–72 and 2008–11 (Balmer *et al.* 2013) and because of this, the species was added to Birds of Conservation Concern (BoCC) Red list in 2015 (Eaton *et al.* 2015).

Woodcock are nocturnal, exhibit cryptic behaviour and plumage and occur in comparatively low densities even in the strongholds of their range (Fokin *et al.* 2004; Hoodless *et al.* 2009). Consequently, observations tend to be infrequent and the conventional methods used to survey common birds are inadequate for representative sampling of woodcock (Risely *et al.* 2012). The most suitable alternative relies upon observations of the birds' crepuscular 'roding' display. At dawn and dusk, male woodcock fly looping paths over woodland and intervening habitat advertising their presence to receptive females with a two-part call (Hirons 1980). Woodcock typically rode from late February to mid-July and during the peak of the season (May–June) do so consistently each evening unless inhibited by heavy rain or strong winds (Hoodless *et al.* 2006 although see Chapter 5). This conspicuous display provides an opportunity to reliably observe woodcock at sites where they occur and counts of the number of passes of roding males have been

demonstrated, on the basis of spectrographic validation, to yield a measure of the local abundance of individuals (Hoodless *et al.* 2008).

In 2003, this survey method was employed to estimate woodcock density, based upon the number of encounters recorded in an hour, in the first large-scale survey in Britain. Extrapolation from a stratified sample of 807 randomly selected 1x1 km squares provided regional and national estimates of abundance and the British breeding woodcock population was estimated at 78,346 males (95% CL 61,717–96,493, Hoodless *et al.* 2009). This estimate was far larger than previous British estimates; Gibbons *et al.* (1993) tentatively suggested a population of 8,500–21,500 pairs in 1988–1991, while Baker *et al.* (2006) estimated 5,000–12,500, but both of these sources recognised the difficulty of deriving accurate estimates for the species.

Given the continuing steep decline suggested by the maps in Balmer *et al.* (2013), repeat surveys are important to assess ongoing status and to provide information that may help identify possible drivers of change. We present the results of the second national survey of breeding woodcock in Britain conducted in 2013, enabling an evaluation of recent change in woodcock abundance. We set this in the context of changes in woodcock distribution over the last 40 years based on Bird Atlas data, and alongside the results of annual surveys (2003–2013), which provide short-term trend data and highlight the scale of annual fluctuations.

2.2 Methods

2.2.1 Survey stratification

We used the same survey site stratification and sample of random 1x1-km squares in 2013 as used for the 2003 survey. To find all potential survey squares, every 1x1-km square containing at least 10 ha woodland was identified from the Land Cover Map 2000 (Fuller *et al.* 2002). We specified four woodland size classes (10–30 ha, 31–50 ha, 51–70 ha, 71–100 ha) and, using a GIS (MapInfo 7.5, MapInfo Corporation 2002), determined 11 custom geographic regions (Fig. 2.1) such that each contained similar numbers of squares belonging to the four wood-size classes and, as near as possible, equal numbers of BTO members (potential surveyors). Survey squares were selected using a random number generator, ensuring that the centre of each new square was at least 3 km from the centres of all previously selected squares. Full details of the stratification and justification for our approach are given in Hoodless *et al.* (2009). The total sample of 2677 squares was made available on the BTO online woodcock survey application, where potential observers could view their locations and register to survey a square. The 807 random squares where surveys were conducted in 2003 were flagged as high priority to encourage repeat surveys of these sites in 2013.

2.2.2 Roding woodcock surveys

The survey method employed in 2003 was based on Hoodless *et al.* (2009). A preliminary visit was made in April to find an appropriate

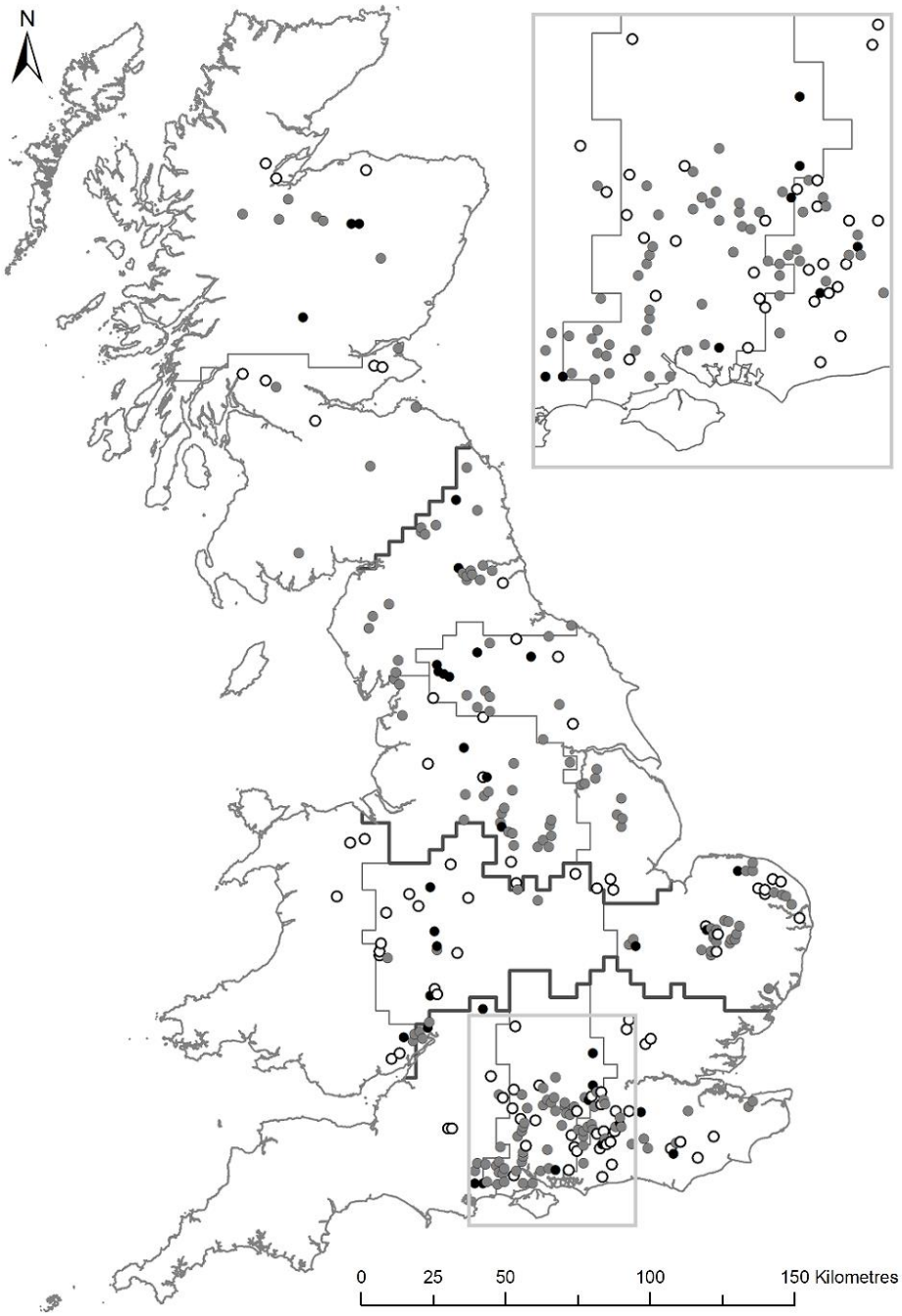


Figure 2.1 Change in occupancy of randomly selected 1x1-km squares where surveys of breeding woodcock were conducted in both 2003 and 2013. Sites are classified as having remained occupied (grey), lost woodcock entirely (white) or been colonized (black). Sites which were unoccupied in both years are not shown. Narrow boundary lines delineate the 11 regions used in the Breeding Woodcock Survey while bold lines delineate the four aggregated regions used in the GLMMs. The inset map shows a densely surveyed part of the Central South region at a larger scale for greater clarity.

survey point within the largest wood in the square, at an open location where the observer's view was not obstructed by the tree canopy. Observers were permitted to select a point up to 400 m outside the allocated square if no other alternative was available. In such cases, the wood-size class was reclassified based on the new 1x1-km square. For sites surveyed in 2003, the same approximate count point was used in 2013 unless changes to the habitat had rendered it unsuitable. This meant 69% of repeated surveys were within 100 m of the original 2003 count point and 82% were within 200 m.

Three surveys were made during May–June 2013, each at least one week apart. Where no woodcock were observed on the preliminary visit and the first two survey visits, the final survey visit was not compulsory. Surveys were not conducted on evenings with continuous rain or wind exceeding Beaufort force 3, so that roding activity and detection of displaying birds were not influenced by weather conditions (Hoodless *et al.* 2006). Surveys began 15 minutes before sunset and lasted for 75 minutes. Surveys in 2013 were 15 minutes longer than those conducted in 2003, as many volunteers reported significant amounts of roding after a 60-minute survey had ended (see Chapter 5). On each occasion that a woodcock was seen or heard, it was recorded as a separate registration and time noted to the nearest minute.

2.2.3 Calculation of population estimates

For each visit, the number of registrations in the first 60 minutes was summed (for compatibility with the 2003 survey). The maximum number

of registrations (R) across visits at each site was used to estimate the number of individual male woodcock (N) using the equation $N = 0.74R^{0.708}$ (Hoodless *et al.* 2008). The maximum count is considered to provide a better representation of the total number of males at a site than the mean count (Hoodless *et al.* 2006, 2008). The density of male woodcock per km² at each survey point (D) was taken to be approximately equivalent to N (Hoodless *et al.* 2009), given that the mean roding area of radio-tracked males was 88 ha (Hirons 1980).

A mean density of woodcock per km² (D_s) was calculated for each of the 44 strata (i.e. the 11 geographic regions subdivided by the 4 wood-size classes). A national (British) population estimate was generated as

$$N_{np} = \sum_{s=1}^{44} (D_s \times G_s)$$

where N_{np} is the national estimate and G_s is the number of 1x1-km grid squares within each stratum (Fig. 2.2). Estimates for each of the 11 regions and for England, Scotland and Wales were obtained in a similar fashion.

Confidence limits were produced by bootstrapping, using the 'SVSTRATIFIED' procedure in Genstat 16.1 (Lawes Agricultural Trust 2006). For each stratum, 1000 boot-strap samples were generated, each with a sample size equal to the number of squares surveyed. From these, confidence limits were calculated via the method described by Sarndal *et al.* (1992) (see Hoodless *et al.* (2009) for a more detailed description).

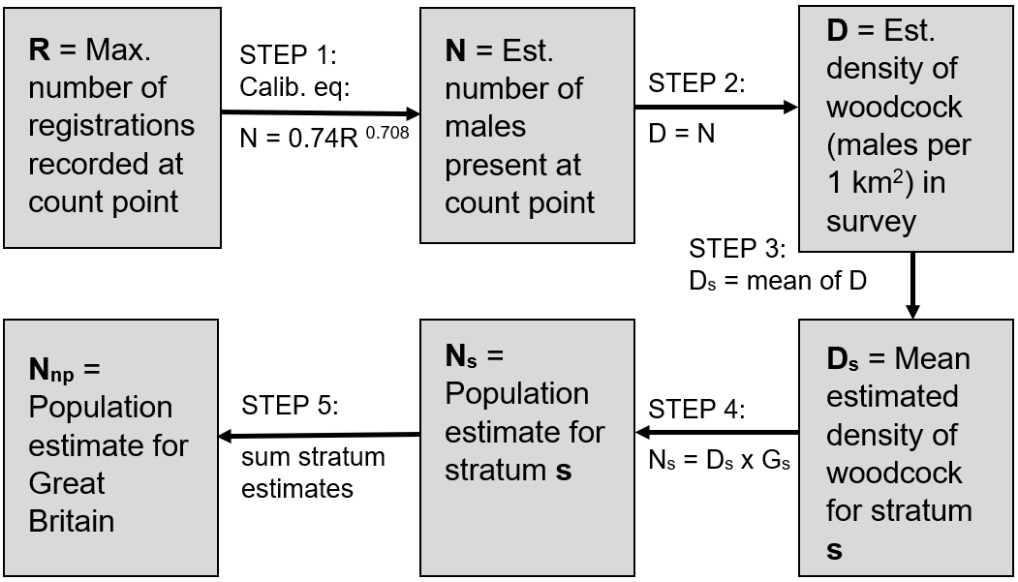


Figure 2.2 Flow chart showing how national population estimates are derived from point counts. G_s is the number of OS grid squares across Britain that match the criteria (region, wood-size class) of stratum s.

The 'SVSTRATIFIED' procedure identifies the ten most influential squares by calculating the potential percentage change in the national population estimate when each square is omitted. To bring the influence of all squares below 5%, we increased the sample size for poorly represented strata by including 11 additional surveys conducted in 2014. These were conducted at sites taken from the original random list that had not been surveyed in 2013. We justified their inclusion on the basis that counts at these sites were not significantly different from those recorded in 2013 for their respective strata. For all 11 regions (r), estimates of presence (P_r) and density in occupied squares (Q_r) were calculated as:

$$P_r = \sum_{s_r=1}^{4} (P_{s_r} \times W_{s_r})$$

and:

$$Q_r = (\sum_{s_r=1}^{4} Q_{s_r} \times P_{s_r} \times W_{s_r}) / P_r$$

where P_{s_r} is the proportion of occupied sites for each stratum in region r; Q_{s_r} is the mean density in occupied squares per stratum and W_{s_r} is the stratum weight calculated as the number of squares per region-wood-size stratum divided by the total number of squares containing at least 10 ha of woodland per region. The standard error of regional density in occupied squares $SE(Q_{s_r})$ was calculated as:

$$SE(Q_r) = \sqrt{\frac{\sum_{s_r=1}^{4}(SE(Q_{s_r}) \times P_{s_r} \times W_{s_r})^2}{{P_r}^2}}$$

where $SE(Q_{s_r})$ is the standard error associated with Q_{s_r}. Mean densities for England, Scotland, Wales and Britain were calculated by multiplying the density in occupied squares by the proportion of occupied squares for each region-wood-size stratum and summing the values of the relevant strata.

We used a generalized linear model (GLM) with binomial errors and a logit link-function to examine whether occupancy at each survey site ('present' vs. 'absent') varied according to the 11 region strata. A second separate model compared occupancy at each survey site to the four wood-size strata. The maximum number of males recorded at each occupied site was examined in relation to region and wood-size class using a Kruskal-Wallis ANOVA.

National and regional population estimates, the proportion of occupied sites per region and the mean number of registrations per region in 2003 and 2013 were compared to provide an indication of

population trend over the ten-year period. Variation in mean woodcock density between 2003 and 2013 was compared at the stratum level using a paired t-test in R (R Development Core Team 2019). More in-depth analysis of population change was confined to sites visited in both survey years, for which there were 544 squares. Change in woodcock abundance based on repeated surveys was analysed using a generalized linear mixed model (GLMM) with a negative binomial distribution and logarithmic link function. The maximum number of registrations recorded in 60 minutes was specified as the response variable, with every site providing a value for 2003 and 2013 as distinct datapoints. Site was included as a random effect, with survey year, wood-class size and region (aggregated as Scotland, Northern England, Central England and Wales, Southern England (Fig. 2.1)) as fixed effects. First and second order interactions between each of these three fixed effects were also considered. The final model was selected by stepwise simplification from the maximal model, testing the effect of each variable's removal using a chi-square test to compare the residual sum of squares. P-values, produced using Wald tests, are reported from the minimal adequate model. Model fit was gauged using plots of Pearson's residuals. GLMMs were conducted in R (R Core Team, 2019) using the glmmADMB package (Skaug *et al.* 2014). A binomial GLM with a logit link function was used to assess whether local extinction at each repeated survey site correlated with the number of woodcock observed during the 2003 count.

2.2.4 Annual counts of roding woodcock

Given that the 2013 Breeding Woodcock Survey was only the second of its kind, a population trend derived from these surveys is limited to two points in time. Surveying sites annually helps validate the trend observed in the main dataset and give an indication of the scale of annual fluctuations.

Annual counts were undertaken between 2003 and 2013 at a selection of random survey squares and additional observer-selected sites. Not all sites were covered for the entire ten-year period; the number visited ranged from 18 to 48 per year and averaged 26. Sites were spread across 24 counties and roding woodcock surveys were conducted using a methodology identical to that used in the 2003 survey. Although these data come from a non-random sample that contains mostly sites with above average woodcock densities, they provide an insight into year-on-year population change.

The results of the annual counts were analysed using a Poisson GLM, with maximum number of woodcock registrations at each site as the dependent variable and year as an explanatory variable. Site was included as a second explanatory variable to account for the fact that not all sites were visited every year. Index values, representing annual change, and standard errors were calculated from the model coefficients. A regression line was fitted in R using the model coefficients to provide an average annual rate of decline.

2.2.5 Bird Atlas data

Three atlases covering Britain and Ireland have mapped the distribution of breeding birds during the periods 1968–1972, 1988–1991 and 2007–2011 (hereafter referred to as '*1970*', '*1990*' and '*2010*' respectively). Full accounts of these are given in *Bird Atlas 2007–11* (Balmer *et al.* 2013). We used atlas data to assess changes in woodcock distribution and examine whether local losses occurred at random or exhibited a geographic pattern; the latter potentially indicating a retraction of the species' range. Not only did the use of atlas data allow analysis of distributional trends over a longer time period than the Breeding Woodcock Survey data, but also presented a more complete picture given that every complete 10x10-km square in mainland Britain was surveyed at least once in each atlas period (Gibbons *et al.* 1993, Balmer *et al.* 2013).

We assessed the presence of woodcock at the 10x10 km square scale from all three atlas periods for England, Wales, the Isle of Man and most of Scotland. Data gathered in the Republic of Ireland and Northern Ireland were excluded, as coverage was not as comprehensive as that achieved for Britain. Shetland and Orkney were excluded as there are no recent records of woodcock breeding in these regions in any of the three atlases (Balmer *et al.* 2013) and the absence of suitable habitat all but eliminates the possibility. Atlas surveys were conducted during the breeding season (April–July). This analysis only included records of woodcock where breeding was categorised as 'probable' or 'confirmed', rejecting records of 'possible' breeding to

avoid inadvertently including observations of non-breeding migrant birds which may remain in the UK as late as mid-April (Hoodless & Coulson 1994).

For each atlas period, Kolmogorov-Smirnov tests and cumulative frequency plots were used to compare the distribution of occupied 10x10 km squares with that of a spatially random pattern on both a South–North and West–East gradient. Kolmogorov-Smirnov tests and plots were produced in R (R Development Core Team 2019) using the spatstat package (Baddeley & Turner 2005).

Changes in distribution between *1970* and *1990,* and between *1990* and *2010,* were examined by classifying occupied 10x10-km squares as ‘persisted’ or ‘lost’ depending on the woodcock’s status in the following atlas. For each inter-atlas period a binomial GLM with a logit link-function was used to determine whether the frequency of local extinctions at the 10x10-km square level (persisted vs. lost) varied according to South–North and West–East gradients. British National Grid X and Y co-ordinates were provided as explanatory variables. GLMs were fitted in R (R Development Core Team 2019) using the lme4 package (Bates *et al.* 2015). Separate binomial GLMs were run to examine relationships between change in status of unoccupied squares and their geographic co-ordinates with squares classed as ‘remaining unoccupied’ or having ‘gained’ woodcock.

2.3 Results

2.3.1 Dataset attributes

In 2013, 823 random squares were surveyed. Eleven extra squares were covered in 2014, giving a grand total of 834 (Table 2.1). Of these, 544 were repeats of squares surveyed in 2003. Discounting the preliminary visit, 88% of squares surveyed received a minimum of two visits. Of those where woodcock were present, 99% received two visits and 89% received the recommended three visits. At occupied sites, the number of visits was independent of wood-size class (Fisher's Exact Test: $P = 0.239$) and region (with regions pooled as Scotland, Northern England, Wales and the Midlands, and Southern England, Fisher's Exact Test: $P = 0.380$).

The 44 strata were not surveyed in the same ratios that they occurred in the randomly selected sample ($\chi^2_{43} = 125.13$, $P < 0.001$). Greater than expected coverage was achieved in the south and east of the Britain; coverage in the Central South and East Anglia regions, in particular, were proportionally greater than anticipated. Generally, the smallest wood-size class (representing 10-30 ha woodland/km^2) was under-represented in the final dataset, with the exception of Northern Scotland.

2.3.2 Woodcock distribution and population estimates

Woodcock were recorded at 273 (33%) of the random survey squares. When weighted by the availability of suitable squares within each of the 44 strata, woodcock presence was estimated at 22% for all 1x1 km=

Table 2.1 Presence of roding woodcock, mean numbers of registrations (based on maximum count per square) and mean densities in occupied squares in 2003 and 2013 (all weighted by the number of available 1-km squares within each region-wood-size class strata)

	Squares Surveyed		Presence (%)		Mean Registrations ± SE		Mean Density (males/km²) ± SE	
Region	2003	2013	2003	2013	2003	2013	2003	2013
North Scotland	27	44	68.50	49.50	5.9 ± 1.65	8.98 ± 1.73	2.39 ± 0.55	3.28 ± 0.47
South Scotland	35	36	35.90	14.06	10.94 ± 5.18	10.31 ± 1.30	3.52 ± 1.28	3.67 ± 0.30
Northern England	55	36	46.20	44.81	8.94 ± 1.51	7.71 ± 3.85	3.32 ± 0.44	2.82 ± 1.11
North Midlands	128	80	27.90	17.24	9.50 ± 1.22	12.48 ± 4.99	3.51 ± 0.33	4.20 ± 1.26
Eastern England	56	48	52.70	32.73	12.05 ± 3.77	13.09 ± 5.26	3.91 ± 0.98	4.22 ± 1.23
East Anglia	80	90	27.30	26.37	12.43 ± 3.11	5.37 ± 0.77	4.10 ± 0.82	2.18 ± 0.22
South Midlands	65	84	10.60	7.12	3.87 ± 0.59	4.67 ± 0.94	1.71 ± 0.18	2.02 ± 0.27
Wales	46	31	21.40	5.16	1.34 ± 0.12	4.05 ± 1.31	0.87 ± 0.04	1.87 ± 0.52
South-west England	53	85	13.20	6.15	4.42 ± 1.70	4.2 ± 1.37	1.81 ± 0.49	1.63 ± 0.34
Central South	110	127	42.10	31.88	8.10 ± 1.08	5.67 ± 0.66	3.07 ± 0.31	2.42 ± 0.22
South-east England	152	173	23.00	11.18	7.01 ± 1.35	7.74 ± 1.70	2.73 ± 0.41	2.95 ± 0.47
Scotland	62	80	53.80	33.59	7.40 ± 1.93	9.23 ± 1.43	2.73 ± 0.54	3.35 ± 0.39
England	699	723	26.90	18.82	8.53 ± 0.74	7.90 ± 1.32	3.11 ± 0.2	2.90 ± 0.36
Wales	46	31	21.40	5.16	1.34 ± 0.12	4.05 ± 1.31	0.87 ± 0.04	1.87 ± 0.52
Britain	807	834	35.20	22.10	7.45 ± 1.03	8.46 ± 0.95	2.76 ± 0.29	3.10 ± 0.26

squares containing ≥10 ha of woodland. Presence varied significantly between regions (Table 2.2). Northern and eastern regions held a greater percentage of occupied squares; the three regions with

Table 2.2 Model output for GLM comparing presence/absence of woodcock across 11 custom regions. P-values are given in relation to the intercept, based on the Central South region.

	Estimate	SE	P-value
(Intercept)	-0.334	0.180	0.0636
North Scotland	0.243	0.351	0.4896
South Scotland	-1.276	0.482	**0.0081**
Northern England	0.947	0.389	**0.0148**
North Midlands	0.031	0.289	0.9132
Eastern England	0.670	0.344	0.0511
East Anglia	0.066	0.279	0.8141
South Midlands	-1.276	0.344	**0.0002**
Wales	-1.576	0.565	**0.0053**
South-west England	-1.128	0.331	**<0.001**
South-east England	-1.074	0.263	**<0.001**

Table 2.3 Model output for GLM comparing presence/absence of woodcock to 4 wood size strata. P-values are given in relation to the intercept, based on the 10–30 ha category.

	Estimate	SE	P-value
(Intercept)	-1.514	0.187	<0.001
31–50 ha	0.527	0.238	**0.0269**
51–70 ha	0.972	0.235	**<0.001**
71–100 ha	1.483	0.235	**<0.001**

highest rates of occupancy were North Scotland (50%), Northern England (44%) and Eastern England (33%). The lowest occupancy was recorded in Wales (5%), with occupancy also low in South-west England (6%) and South Midlands (7%). Likelihood of occupancy differed significantly between the four wood-size classes (Table 2.3). Occupancy increased progressively as woodland area within the 1x1-km square increased, from national averages of 17% (10-30 ha woodland/km^2) up to 36% (71-100 ha woodland/km^2).

In Britain, the mean density of woodcock in occupied squares was 3.1 males/km^2 (Table 2.1). The highest densities were recorded in Eastern England (4.22 ± 1.23) and the Northern Midlands (4.20 ± 1.26) whilst the lowest densities were recorded in South West England (1.63 ± 0.34) and Wales (1.87 ± 0.52). Regional variation was close to statistical significance (Kruskal-Wallis: $\chi^2_{10} = 18.15$, $P = 0.052$). Amongst occupied survey squares, only 19% held densities that exceeded five males/km^2.

The British woodcock population was estimated at 55,241 males (95% CL: 41,806–69,004), comprising 24,229 males in England (95% CL 17,563–32,239), 30,098 males in Scotland (95% CL 19,664–41,015) and 914 males in Wales (95% CL: 119–1900) (Table 2.4). The North Scotland region accounted for the majority of the estimated Scottish population (23,913 males, 95% CL 14,796–33,478). Of the English population, 59% resided within the three northernmost regions.

Table 2.4 Woodcock population size estimates (males) with 95% confidence intervals and percentage change between 2003 (Hoodless et al. 2009) and 2013.

	2003			2013			
Region	Total	Lower 95% CL	Upper 95% CL	Total	Lower 95% CL	Upper 95% CL	% Change
North Scotland	24088	14640	34633	23913	14796	33478	-0.7
South Scotland	15163	6110	28075	6185	2023	11095	-59.2
Northern England	7169	4192	10469	5808	2420	11125	-18.2
North Midlands	5139	2998	7612	3806	1188	7890	-25.9
Eastern England	6811	3011	11712	4562	1771	8148	-33.0
East Anglia	3485	1747	5794	1791	1201	2465	-48.6
South Midlands	1123	520	1820	890	277	1719	-20.8
Wales	1767	541	3259	914	119	1900	-48.3
South-West England	2234	774	4147	939	311	1683	-58.0
Central South	6586	4506	9124	3928	2553	5490	-40.4
South-East England	4782	2480	7785	2507	1046	4396	-47.6
Scotland	39251	24173	56632	30098	19664	41015	-23.3
England	37328	30101	44089	24229	17563	32239	-35.1
Wales	1767	541	3259	914	119	1900	-48.3
Britain	78346	61717	96493	55241	41806	69004	-29.5

2.3.3 Population change

Between 2003 and 2013, the British population estimate dropped from 78,346 males (95% CL 61,717–96,493) to 55,241 males (95% CL 41,806–69,004), representing an overall decline of 29%. Declines were recorded in all 11 regions (Table 2.4), though the scale of decline in North Scotland was less than 1%. Amongst the other regions, declines ranged from -18% in Northern England to -59% in South Scotland. The South-West England, East Anglia, Wales, South-East England and Central South regions all experienced declines greater than 40%. Population estimates for each of the woodland size classes decreased in all but the 71–100 ha class (Fig. 2.3).

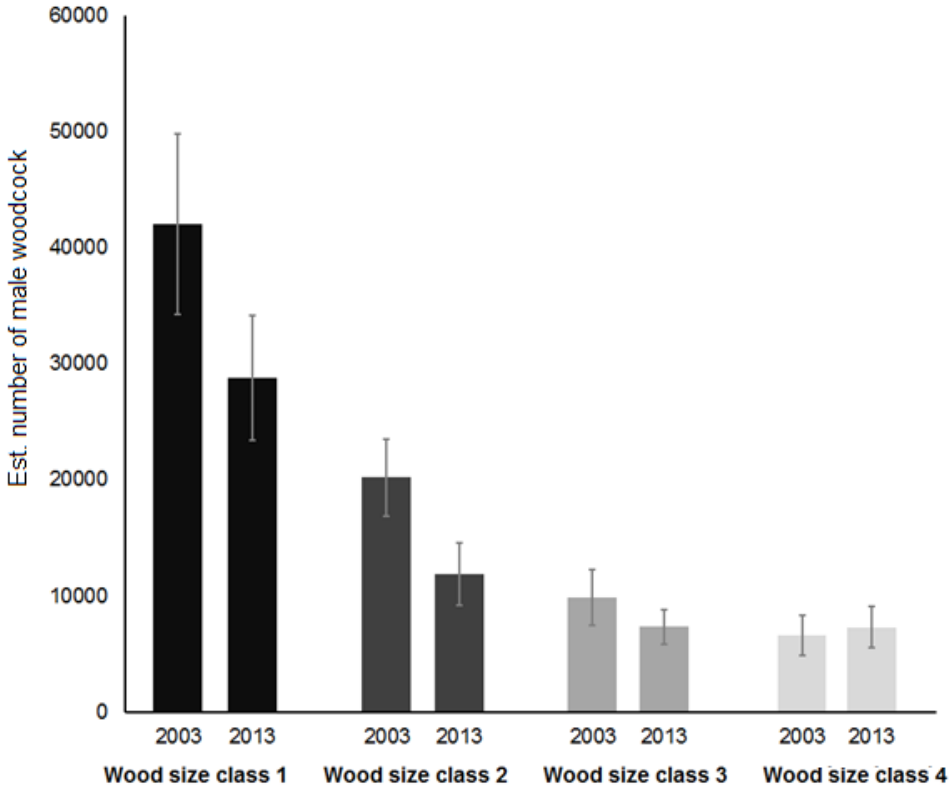


Figure 2.3 Estimates of the British population size in 2003 and 2013 for the four woodland size classes (1 = 10–30 ha, 2 = 31–50 ha, 3 = 51–70 ha, 4 = 71–100 ha) ± 1 SE. Estimates and standard errors were produced by bootstrapping.

The percentage of wooded 1x1 km squares where woodcock were present has declined from 35% to 22%. Considering occupied sites only, and accounting for survey stratification, mean density was 3.1 males per km² in 2013 compared to 2.8 males per km² in 2003. The mean densities of woodcock in each of the 44 strata did not vary significantly between 2003 and 2013 (paired t-test: $t_{43} = 0.57$, $P = 0.570$).

Amongst repeat survey sites, the percentage of sites at which woodcock were seen decreased from 47% in 2003 to 37% by 2013 (Table 2.1). These figures are higher than the averages derived from the entire dataset because a smaller proportion of squares from the smallest wood-size class were included in the repeat surveys. Of the 258 sites occupied in 2003, 86 sites (33%) recorded zero counts in 2013. There were only 34 sites (12% of sites unoccupied in 2003) where gains were recorded. The loss of woodcock from once-occupied squares was significantly more likely where the 2003 survey recorded a lower number of registrations ($\chi^2_1 = 277.70$, $P < 0.001$).

Examination of the change in mean number of registrations revealed the maximal model to be the most appropriate ($\chi^2_9 = 23.42$, $P < 0.005$), suggesting a three-way interaction between year, the four aggregated regions and wood-size class (Suppl. Table 1). The mean number of registrations declined between 2003 and 2013 in all region-wood class strata except in the 10-30 ha category in Scotland, where the maximum number of registrations increased. This was due to large

increases in the maximum number of registrations in the North Scotland region, though this is based on small sample sizes, especially in 2003.

2.3.4 Annual population change

The mean number of registrations for sites visited annually was 14.0 (± 1.5) in 2003 and 9.4 (± 1.8) in 2013, compared to British national survey averages of 4.0 (± 0.2) and 2.7 (± 0.2) respectively. The difference is explained partly by the fact that annual counts were focused on occupied sites (only 9% of sites recorded no woodcock in any year). There was high variation in mean counts between years, with annual trends ranging from +21% (2004-2005) to -27% (2008-2009). However, the overall trend in the mean number of registrations over the ten-year period was a significant decline (GLM year: *Est* = -0.0488 ±0.004, *P* < 0.001). The average annual decline was 4.9%, equivalent to a decline of 39.8% over ten years (Fig. 2.4).

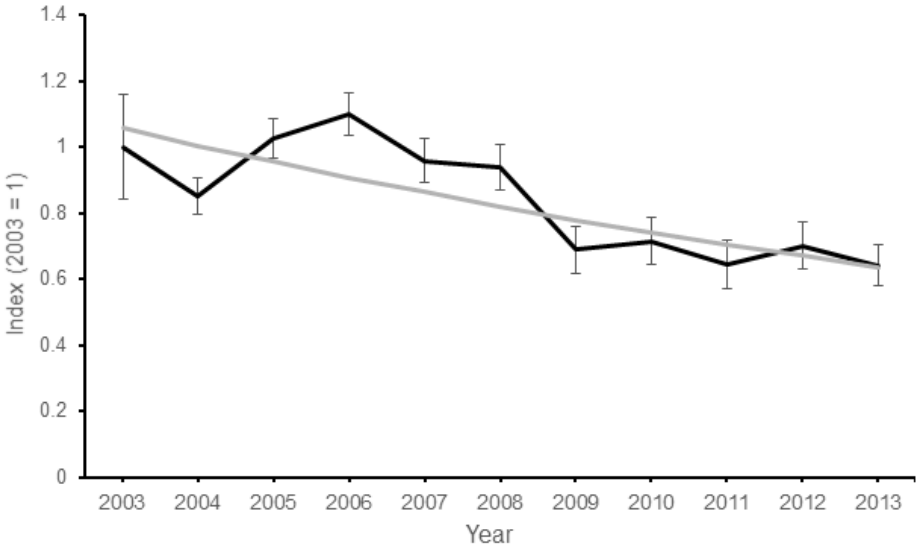


Figure 2.4 Trend in the number of Woodcock registrations at annual survey sites between 2003 and 2013. Index values are based on the mean number of registrations observed in 2003 and are back-transformed year coefficients from a Poisson GLM (error bars ± 1 SE). A regression line is fitted through the index values.

2.3.5 Long-term distributional change

Between *1970* and *1990*, the number of 10x10-km atlas squares where woodcock were present fell from 1439 to 917, a decline of 36%. By *2010*, the number of occupied squares had fallen to 632, a further decline of 31%. Over the whole forty-year period this represents a decline of 56% nationally. The proportion of occupied squares in the west of Britain was lower than would be expected if a completely spatially random distribution existed (Kolmogorov-Smirnov tests *1970*: $D = 0.1369$, $P < 0.001$; *1990*: $D = 0.1595$, $P < 0.001$; *2010*: $D = 0.1889$, $P < 0.001$). On a north-south axis occupancy was lower than expected in the south (Kolmogorov-Smirnov tests *1970*: $D = 0.0985$, $P < 0.001$; *1990*: $D = 0.0776$, $P < 0.001$; *2010*: $D = 0.1451$, $P < 0.001$). These patterns become more pronounced with each subsequent atlas (Fig. 2.5).

In the *1970* atlas, woodcock were generally widespread, with birds absent only from Cornwall, west Devon and the extreme south-west of Wales (Fig. 2.5). Presence was uniformly high in a region that stretches from Derbyshire and Nottinghamshire northwards to central Scotland and there were relatively high concentrations of occupied 10x10 km squares in Northern Scotland, separated from those to the south by the highest peaks of the Cairngorms. West Sussex and Hampshire showed the highest proportion of occupied 10x10-km squares in the south of England, with other clusters of occupied squares in eastern parts of Wales and the Welsh borders (i.e. The Forest of Dean northwards) and East Anglia.

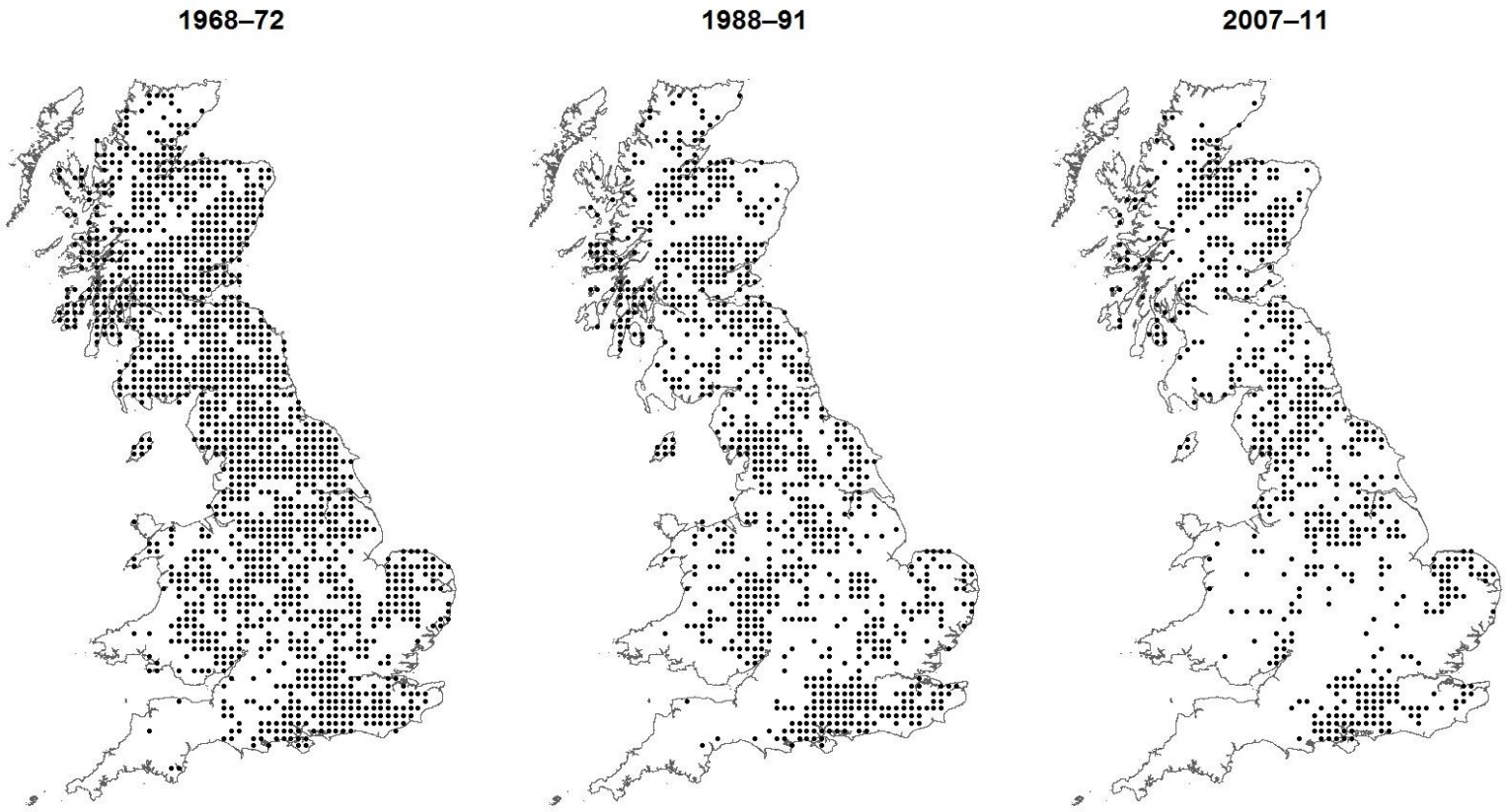


Figure 2.5 Chronological maps of woodcock presence on a 10-km square scale in each of the three atlas periods (1968–72, 1988–91, 2007–11). Where evidence of breeding was only categorised as 'possible', records have been omitted to avoid inadvertent inclusion of migrant woodcock.

Over the course of the next forty years these patterns become more exaggerated and fragmentary (Fig. 2.5). As the number of occupied sites in southern Scotland declined, the populations of Central Scotland and Northern England became more poorly connected and declines in the English Midlands led to the scattered strongholds in the south appearing more distinct. There were large-scale declines in presence in Wales and the South West. Presence in East Anglia declined between *1970* and *1990*, then between *1990* and *2010* the number of occupied squares remained broadly the same, but the East Anglian population became more isolated from those elsewhere in Southern and Central England.

For the period *1970–1990*, there was a significant relationship between the frequency of local extinction (i.e. losses of occupied squares) and longitude (GLM: *Est* = $-1.29 \times 10^{-6} \pm 6.31 \times 10^{-7}$, *P* = 0.042), indicating that woodcock were 'lost' from a higher proportion of 10-km squares in the west of Britain. Over the same period, there was no significant relationship with latitude (GLM: *Est* = $7.53 \times 10^{-8} \pm 3.04 \times 10^{-7}$, *P* = 0.804). For the period *1990–2010*, a similar relationship was observed with longitude (GLM: *Est* = $-3.88 \times 10^{-6} \pm 8.47 \times 10^{-7}$, *P* < 0.001) and a significant latitudinal trend was also detected (GLM: *Est* = $-1.51 \times 10^{-6} \pm 4.00 \times 10^{-7}$, *P* < 0.001) , suggesting that losses were greater in the south of Britain. Amongst squares that were not occupied in *1970*, the proportion of 'gains' by *1990* increased significantly on a west to east gradient (GLM: *Est* = $2.76 \times 10^{-6} \pm 6.74 \times 10^{-7}$, *P* < 0.001) and a south to north gradient (*Est* = $9.23 \times 10^{-7} \pm 3.53 \times 10^{-7}$, *P* <

0.001). These patterns were present and more pronounced in the *1990* to *2010* data (GLM west-east: *Est* =4.60 x 10^{-6} ± 7.06 x 10^{-7}, $P < 0.001$, GLM south-north: *Est* = 2.93 x 10^{-7} ± 3.70 x 10^{-7}, $P < 0.001$)

2.4 Discussion

The two Breeding Woodcock Surveys and three atlases indicate large-scale national declines in site occupancy, ranging from 31% in the atlas (*1990–2010*) to 37% in the Breeding Woodcock Survey (2003–2013). The same broad geographic trends were observed in both surveys, including low levels of occupancy in Wales, South-west England and the South Midlands, and higher than average levels in Northern and Eastern England and Scotland. Changes in regional population estimates demonstrate a decline that is severe but showing regional variation, with woodcock numbers in the north of England and northern Scotland generally declining at a lower rate than those in most of southern England and Wales. Overall, there is clear evidence for a decline that increases in intensity towards the south-west of Britain.

Historical accounts suggest that the woodcock's British range has always exhibited a bias towards the north and east (Holloway 1996). The western boundary of the woodcock's European range lies within the British Isles and abundance appears to increase across Britain, eastwards, with distance from the range edge. Given that breeding woodcock have only rarely been recorded in Cornwall and south-west Wales in the past (Holloway 1996), range is not thought to be physically constrained by the islands' limits but could be determined

by climatic or other geographic factors. This is supported by the fact that the range edge continues through France, and woodcock are absent as a breeding species from Brittany, western Normandy and most of Pays-de-la-Loire (Ferrand *et al.* 2008). Some small sedentary woodcock populations survive much further south and west than this on the Azores, Madeira and the Canary Islands, but these populations are small with restricted distributions largely confined to mountainous regions (Machado *et al.* 2008). The same is true of small breeding populations in Northern Spain (Braña *et al.* 2013). The tendency to favour upland areas, where soils are moister at more southerly latitudes, suggests that climate probably does, in some instances, limit distribution.

As far as Britain is concerned, however, this theory is contradicted by the fact that breeding woodcock are present in south-eastern regions that experience drier summers than most of the South-west. Since spring and summer rainfall is greater in south-west Britain than, for example, East Anglia, where breeding woodcock occur, a simple climatic relationship is not immediately apparent. A more complex explanation that also considers drainage, topography and soil acidity could potentially account for some regional differences in woodcock presence and this may present a possible line of enquiry for future research.

Current declines appear to be exaggerating the woodcock's uneven distribution in Britain and increasing fragmentation may be due to recent climatic changes increasing the extent of unsuitable areas. If

this is so, and British declines are part of a wider change in woodcock abundance at the edges of the species' range, we may expect to see the same pattern in France. Ferrand *et al.* (2008), however, state that the French breeding population for the period 1994–2003 remained stable, with an estimated size of 10,000–30,000 pairs (Birdlife International 2004). This does not eliminate the possibility of wider declines due to changing climate but could suggest that the negative impact is greater in Britain, preceding declines elsewhere in Europe, owing to the additive effect of secondary factors specific to Britain. It may also be that monitoring in France failed to detect localised declines as there was no consideration of regional variations in population trend and woodcock surveys were conducted only at sites where extensive woodland was available (squares in the French survey are approximately 2.8 km² and only those with at least 90% woodland cover are surveyed).

It is important to consider declines at the range edge in relation to trends across the range as a whole (Fuller *et al.* 2007b) and comparison with roding woodcock surveys conducted in Western Russia, thought to be the species' European stronghold, sets British declines in a European context. Trend data from Russia are available only over a short time frame and are based on roding 'intensity' rather than an estimate of true woodcock density. Annual woodcock surveys conducted in Western Russia since 1999 had initially suggested a slight decline (Fokin *et al.* 2004). Continuation of these surveys, however, points towards a Western Russian population trend that exhibits a high

degree of annual variation but is broadly stable between 2000 and 2010 (Fokin & Blokhin 2013). Our annual surveys in Britain also show a large annual variation in abundance, which is likely to be related to environmental conditions and their effects on productivity and adult survival. Given that woodcock feed predominantly on soil invertebrates by probing, extended cold spells with frozen ground in winter and dry summers, that render soil impenetrable, may detrimentally affect woodcock numbers in subsequent years.

Irrespective of other factors, the woodcock's uneven distribution in Britain appears to be partly linked to the availability of large blocks of woodland. Analysis of the paired survey data indicates that 1x1-km squares suffering local extinctions were usually sites with low woodcock densities in 2003, and that this was more common within the smaller wood-size classes. Despite evidence that woodcock persist in some less densely wooded, fragmented areas, recent losses have exaggerated an apparent association with large woods. Several declining woodland specialists, such as pied flycatcher *Ficedula hypoleuca* (Huhta *et al.* 2008), marsh tit *Poecile palustris* (Broughton & Hinsley 2015) and western capercaillie *Tetrao urogallus* (Dolman *et al.* 2007) also show a preference for heavily wooded landscapes with large forested patches and high levels of connectivity.

The specificity of the woodcock's habitat requirements is not fully understood, but the species' once broad range, as shown by the 1968-72 atlas, suggests some adaptability. Moreover, woodcock appear to be less reliant on mature forest than many other woodland specialists

and are thought to require areas with at least some young growth or clearings. Perhaps habitat complementarity is a more important consideration (Dunning *et al.* 1992) as radio-tracking studies suggest habitats associated with nesting and chick-rearing differ (Hirons 1988; Hoodless & Hirons 2007). It may be that larger woods offer a greater diversity of stand type and ages as well as a more diverse range of micro-climates, ensuring the availability of wet feeding areas throughout the summer.

This hypothesis is consistent with recent trends recorded in Wales and Southern Scotland where, despite extensive areas of woodland, woodcock have declined significantly. In these areas, woods exhibit a low diversity of age and stand type despite their large size as they comprise mostly commercial, coniferous forestry which is only utilised by woodcock in its early stages (Shorten 1974). Beyond the thicket stage, reached at 15-20 years, it is no longer suitable and regional declines may be due to an increase in mean woodland age as the large areas of forestry planted during 1935–1985 mature (Hopkins & Kirby 2007).

The respective influences of geographic location, climate, wooded area and woodland diversity are difficult to separate, given that they are so closely linked. There are areas of southern England, for instance, where woodcock have declined in spite of the fact that relatively well-wooded landscapes remain (e.g. south-eastern Weald in Kent and the Chilterns). In such regions, causes of decline are likely to

be complex and could include factors operating on a local scale or interacting at different spatial scales.

Rising deer numbers may affect breeding woodcock by reducing the extent of understorey vegetation, resulting in inferior nesting habitats and drier soils, and in extreme cases, by increasing the likelihood of disturbance and trampling (Gill & Fuller 2007). Although Holt & Fuller (2013) found that intensive deer browsing had no significant effect on the local distribution of woodcock at Bradfield Woods, their study focussed on woodcock abundance during winter when habitat requirements are less specific than those during the breeding season.

The significance of recreational disturbance has been demonstrated for other ground-nesting species such as European nightjars *Caprimulgus europaeus* and woodlarks *Lullula arborea* (Langston, Liley, *et al.* 2007), which also makes the recreational use of woodlands, particularly by dog-walkers, a potential cause for concern. Changes in woodland management have been implicated in the loss of open areas within woodland (Fuller *et al.* 2007a, Quine 2007) and these may be an important requirement of the woodcock's breeding display (see Chapter 7). Hunting may have a local effect on over-winter survival (Duriez, Eraud, *et al.* 2005), but the impact is hard to quantify given that hunting in Britain only occurs in winter when migrant woodcock are also present and outnumber residents by ten to one (Hoodless *et al.* 2013).

2.4.1 Survey accuracy and future considerations

Despite a large sample size overall, several of the 44 strata were poorly represented in both 2003 and 2013, meaning that these stratum estimates are calculated from relatively few surveys. Since survey coverage is dependent on the distribution of potential observers, low survey uptake was expected in less densely populated areas, but this is problematic as coverage is lowest in areas where woodcock densities are thought to be highest. Northern Scotland, which we predict may hold 43% of the national breeding population, has an estimate based on 5% of the completed surveys and Northern England may be similarly, though less acutely, affected. The bias in coverage is greatest in the 2003 Breeding Survey, meaning that the 2013 estimate represents an improvement in accuracy of the population estimate, but comparison of the two figures should be treated with some caution. Particular effort was made to recruit volunteers in regions where low coverage was expected, and this appears to have been effective, but it may be wise for future surveys to pre-empt the shortfall and hire professional fieldworkers to ensure minimum adequate coverage.

Notwithstanding the issue of coverage, this survey illustrates the importance of understanding species-specific behaviour in order to develop effective and accurate survey methodologies for species of conservation concern. Whilst large-scale atlas and multi-species monitoring projects can provide long-term data on general trends and distribution, bespoke methods are required to gather reliable information on densities and fine-scale distribution change.

3 HABITAT CORRELATES OF RESIDENT WOODCOCK ABUNDANCE IN BRITAIN

This chapter was published under the title “Habitat correlates of Eurasian woodcock abundance in a declining resident population” in the Journal of Ornithology (Heward *et al.* 2018). I was solely responsible for writing the manuscript but made changes in response to comments provided by each of the five co-authors. I was solely responsible for the analysis except where stated below.

Author Contributions:

Andrew Hoodless: Devised 2003 survey methodology, provided comments on manuscript

Greg Conway: Devised 2003 survey methodology, facilitated collection of volunteer survey data at BTO, provided comments on manuscript

Nicholas Aebischer: Provided guidance on use of NGC data, provided comments on manuscript

Andrew MacColl: Provided comments on manuscript

Rob Fuller: Devised 2003 survey methodology, provided comments on manuscript

3.1 Introduction

Approximately one third of woodland bird species breeding in Britain have experienced population declines over the past 40 years (Hewson *et al.* 2007; DEFRA 2015). While there have been attempts to link declines to woodland habitat change occurring over the course of the last century (Amar *et al.* 2006; Hewson & Noble 2009), clear evidence of a direct effect remains scarce for most species.

Some declining species are associated with late-stage woodland (e.g. pied flycatcher *Ficedula hypoleuca* (Goodenough 2014), common redstart *Phoenicurus phoenicurus* (Smart *et al.* 2007), wood warbler *Phylloscopus sibilatrix* (Mallord *et al.* 2012)). Others require early successional deciduous woodlands with dense understoreys (e.g. common nightingale *Luscinia megarhynchos* (Fuller & Henderson 1992; Holt *et al.* 2011), willow tit *Poecile montanus* (Lewis *et al.* 2009)). These types of woodland habitat are among those most threatened by changes to woodland management occurring during the last century (Fuller & Warren 1993; Hopkins & Kirby 2007). Isolating a general effect of habitat change, however, is hindered by the fact that many of these species are long-distant migrants, making it difficult to separate the effects of breeding habitat from the unmeasured factors affecting overwinter survival and migration (Mallord *et al.* 2016; Goodenough 2014).

As a British and Irish breeding species, the Eurasian woodcock *Scolopax rusticola* (hereafter woodcock) has experienced a decline since at least 1970 and site occupancy, at the 10x10-km sq scale, has

declined by 56% between 1970 and 2010 (Heward *et al.* 2015). Similar declines have not been observed in the large, migratory populations that breed in northern Europe (Fokin & Blokhin 2013; Lindström *et al.* 2015) and overwinter in Britain and Ireland alongside locally breeding residents (Hoodless *et al.* 2013). This may suggest that the causes of the recent decline in the resident population are taking effect during the breeding season e.g. by reducing productivity or increasing breeding season mortality.

Only a small number of studies have attempted to determine the habitats used by breeding woodcock (Hirons & Johnson 1987; Hoodless & Hirons 2007; Machado, Brito, *et al.* 2008). In the most comprehensive of these, Hoodless and Hirons (2007) used radio-telemetry to study habitat use at two contrasting sites in Derbyshire, central England and Angus, east Scotland. In Derbyshire, young stands of trees with dense ground vegetation were most commonly used for feeding and brood-rearing while more open ground vegetation was preferred for nesting. In Angus, woodcock tended to use sapling-stage birch *Betula* sp. and birch thickets more frequently than older birch or coniferous woodland (Hoodless & Hirons 2007). Such studies offer an insight into the species' selectivity, but their findings vary depending upon the local characteristics of the chosen study area and cannot consider the full range of potential woodcock habitats.

Assessing the potential role of habitat change in a species' decline is difficult for those species whose basic ecology is still poorly understood. A large-scale, multi-site assessment of a species'

abundance in relation to relevant habitat data provides a means of studying basic habitat associations which may be the first step towards identifying causes of decline. Here, we provide this by combining broad measures of woodland area, type and surrounding habitat at multiple spatial scales, with the results of two national, species-specific surveys of breeding woodcock in Britain. We separately model habitat associations in 2003 and 2013 to assess how declines over this period may be shaping correlations with habitat. By identifying the habitat characteristics with which woodcock are most commonly associated, and how these change with time, this study provides a firmer basis for future research into the causes of recent population declines.

3.2 Methods

3.2.1 Woodcock surveys

In 2003, woodcock abundance was assessed at 807 randomly selected 1x1-km British ('Ordnance Survey') national grid squares across Britain (England, Wales and Scotland), using counts of displaying ('roding') males (Hoodless *et al.* 2009). In 2013, identical surveys were conducted at 823 randomly selected 1x1-km survey squares (see below), 544 of which were repeats of survey squares visited in 2003 (Heward *et al.* 2015 and Chapter 2).

All British national grid squares containing > 10 ha of woodland were assigned to one of four woodland-size classes based on their total wooded area (10–30, 31–50, 51–70, 71–100 ha) and one of 11 regions (Fig. 2.1). These regions were delineated so that they each contained

equal proportions of the four woodland-size classes while maintaining logical geographic divisions. Survey squares were then randomly selected using a random number generator, with the number selected per region being based upon the number of potential surveyors (BTO members). Randomly selected squares had to be at least 2 km apart from edge to edge to maintain their independence (roding ranges are typically around 43-132 ha (Hirons *et al.* 1980)). In this way, a list of 2677 random squares was generated, from which volunteer observers, consisting largely of non-professional birdwatchers, were able to select sites to survey. The number of squares available was adjusted for the number of potential observers to ensure regional coverage was not biased towards areas that are densely populated.

Observers were provided with instructions to identify a suitable count point within their chosen square and if sites from the 2003 survey were repeated, the observer was given the grid reference for the original count point and asked to revisit it. Observers were permitted to deviate from the 2003 count point if changes to the surrounding vegetation meant that it no longer met the requirements specified above, or if access to the original count point could not be obtained (see Chapter 2).

Up to three dusk surveys, each 60 minutes in length and at least seven days apart, were conducted in May-June when roding behaviour is at its peak (Hoodless *et al.* 2006). A small number of occupied sites were only visited once (2003: 8%, 2013: < 1%) or twice (2003: 10%, 2013: 11%), and at sites where woodcock were absent on the first two

surveys, the third was not obligatory. Surveys were not conducted during persistent rain or if the wind exceeded Beaufort scale 3. For observers without prior experience of roding woodcock, recordings of typical woodcock calls were provided online (British Trust for Ornithology 2013). Each separate woodcock seen or heard was noted. The survey methodology, interpretation and limitations are covered in greater detail in Hoodless *et al.* (2009) and Chapter 2.

Observers also made a simple assessment of vegetation composition and structure within a 200-m radius of the count point during a visit made between 15th May and 15th June. A recording form, containing clear instructions and a worked example, was provided to yield consistent records. Observers were asked to estimate, with the help of a large-scale map or aerial photograph, the proportion of closed canopy woodland, open space within woodland (tracks/clearings) and non-woodland habitats (arable land/water bodies) within 200 m of their count point (to the nearest 5%). Observers were then asked to divide the area of closed canopy woodland into stands based upon tree age or type, and record:

- the predominant tree type, based on a list of British National Vegetation Classification (NVC) categories (Hall *et al.* 2004)
- the stand age as either establishing (< 2 m height), intermediate (2-5 m) or mature (> 5 m)
- the proportion of the 200-m buffer occupied by each stand as a percentage, to the nearest 5%.

All observers were provided with online web resources for tree identification. A copy of the recording form can be viewed online (British Trust for Ornithology 2013).

3.2.2 Landscape-scale habitat variables

Landscape-scale habitat variables were extracted from a range of sources using ArcGIS 10.6 (ESRI 2019). For each count point, three types of buffer were created: a circular buffer with a 1-km radius (3.1 km^2), a circular buffer with a 2-km radius (12.6 km^2) and a 2-km ring buffer (i.e. the 2-km radius circular buffer with the 1-km buffer removed from its centre, 9.4 km^2). A ring buffer was selected in an attempt to reduce the high levels of collinearity associated with concentric circular buffers and the repetition of their core area (Schneider *et al.* 2011) although the effectiveness of this measure was tested and is presented in the results.

The 1-km radius was selected based on the movements of radio-tagged woodcock described by Hoodless and Hirons (2007); the largest distances travelled in this study were to reach nocturnal foraging sites and averaged 1005 ± 612 m (1 SD). Hirons (1980) found that displaying males roded over areas between 0.34 and 1.32 km^2, around a quarter of the area covered by a 1-km buffer, but these roding areas averaged approximately 2250 m across their longest axis. Roding behaviour and flights to nocturnal foraging sites represent the largest movements made by woodcock during the breeding season (Hirons 1980, Hoodless and Hirons 2007), so most individuals spend the entire breeding

season within a range of these dimensions or smaller. The 2-km ring buffer was used to consider how relationships with habitat occurring within a 1-km buffer, may be reflective of larger landscape-scale patterns. Buffers larger than 2 km could not be used because overlaps with buffers of neighbouring count points became more frequent and greater in area when they exceeded this size. The distribution of count points within selected survey squares meant that no 1-km buffers overlapped in 2003 and only one pair slightly overlapped in 2013. For 2-km ring buffers, 66% of buffers had no overlaps. Among those that did overlap, the average overlap between pairs of neighbours was 11.1 ± 8.3% (1 SD) in 2003 and 11.1 ± 8.2% (1 SD) in 2013. No pair overlapped by more than 26%.

Data relating to woodland area and type were extracted from the Forestry Commission's National Inventory of Woodland and Trees (NIWT) (2003) and the 2013 National Forest Inventory (NFI). At both buffer sizes, the total area of woodland was extracted along with areas of broadleaved, coniferous and mixed woodland and 'open space' within woodland. The latter was a composite of bare ground, felled woodland, land prepared for planting, grass within woodland and 'young' trees i.e. those that are too small to be classified using the NFI's satellite photography classification technique. The area of each woodland habitat was divided by the total wooded area to provide a proportional figure. Other habitat categories recorded by the NFI, such as coppiced woodland or shrubby cover could not be included because of a low rate of occurrence at surveyed sites but were incorporated into

an index of woodland heterogeneity. For both buffer sizes, this measure of heterogeneity was calculated using an index comparable to Simpson's Index of Diversity (D):

$$D = 1 - \sum (a/A)^2$$

where a is the area of each woodland category and A is the total area of woodland within the buffer.

Broad measures of non-woodland land-use were obtained from CEH Land Cover Map (LCM) 2000 (Fuller *et al.* 2002) for the 2003 count points and LCM 2007 (Morton *et al.* 2014) for the 2013 points. The LCM 2000 and LCM 2007 are raster maps that assign each 25x25-m cell a habitat type using satellite imagery.

Total 'urban' area was extracted at both buffer sizes using a combination of the urban and suburban LCM categories. We also measured distance to the nearest continuous 'urban' area greater than 50 ha, which was not confined by the limits of the buffer. The proportion of the buffer occupied by grassland was extracted at both buffer sizes using a composite of the improved, rough, neutral, calcareous and acid grassland LCM categories. The LCM was also used to calculate the area of the individual woodland block in which the survey was conducted (wood block size), by counting the number of contiguous 25x25-m cells containing woodland.

Deer have a significant effect on the structure and floristic composition of woodland habitats (Gill & Fuller 2007). Deer abundance data were obtained from the Game and Wildlife Conservation Trust's (GWCT) National Gamebag Census (NGC) (Aebischer *et al.* 2011). The

NGC provides a measure of relative abundance for a range of mammals that are either hunted as game species or legally controlled as pests. Estimates of abundance are derived from annual bags for each species from 900 sites nationally and provide a reasonable proxy for the relative abundance of live animals (Noble *et al.* 2012).

The relative abundances of three deer species were extracted at each count point from a raster map that provided smoothed values based on all NGC submissions in the surrounding 35-km radius (Noble *et al.* 2012). The species considered were European roe deer *Capreolus capreolus*, fallow deer *Dama dama*, and Reeves' muntjac *Muntiacus reevesi*. In preliminary models, red deer *Cervus elaphus* and sika deer *Cervus nippon* were also initially considered, but because they were completely absent from > 70% and > 85% of squares respectively in 2003, models failed to converge. Deer data averaged over the periods 1995–1999 and 2005–2009 were used for surveys conducted in 2003 and 2013 respectively. More details of the NGC methodology can be found in Noble *et al.* (2012).

3.2.3 Analysis of woodcock abundance in relation to landscape-scale habitat variables

Pearson's correlation tests were used to identify collinearity between the 1-km and 2-km scales for variables measured with both buffer sizes. The 1-km circular buffers were compared to 2-km ring and 2-km circular buffers to assess how effective this measure was at reducing collinearity.

The data were analysed using four generalised linear mixed models (GLMMs), analysing each of the two years and two spatial scales separately. Different models were created for 2003 and 2013 because woodcock declines in the intervening period were expected to affect habitat associations. It was hoped that analysing data from both survey years may reveal something about the causes of decline. Separately analysing each year, rather than directly analysing change in woodcock abundance, was expected to produce results that were easier to interpret; change in habitat areas between surveys was confounded by habitat availability in the initial survey year. The largest proportional changes in woodland area, for instance, were always associated with sites where woodland area was low in 2003. Moreover, only 544 sites (of over 800) were surveyed in both years so an analysis of change would have meant a large reduction in sample size. The 1-km and 2-km scale data were analysed separately with the collinearity tests described above providing the rationale for this approach (see results and Harrison *et al.* 2018). Variables which did not vary with scale, such as the distance from urban area and deer abundance, were included in 1-km buffer and 2-km buffer models.

Woodcock count data were analysed using GLMMs with a Poisson distribution and a logarithmic link function in R (R Development Core Team 2019). The glmmPQL function from the MASS package (Venables & Ripley 2002) was used, which fits GLMMs using penalised quasi-likelihood (PQL) estimation and accounts for overdispersion. Owing to potential spatial autocorrelation arising from the geographic

distribution of woodland within Britain, an exponential correlation structure was specified based on the latitude and longitude of each count point to account for spatial autocorrelation. In preliminary analyses, an exponential structure fitted the woodcock count data more closely than linear or Gaussian correlation structures (Pinheiro *et al.* 2016). A preliminary Pearson's correlation test showed negative collinearity between the proportions of broadleaved and coniferous woodland (r = -0.72 in 2003 and r = -0.91 in 2013 for 1-km buffers and r = -0.73 in 2003 and r = -0.90 in 2013 for 2-km ring buffers) (Fig. 3.1). Because of this, only the proportion of broadleaf was included in the final model, but an equivalent model in which broadleaf was replaced by conifer was trialled and is discussed.The dependent variable was the total number of woodcock registrations recorded across all visits, with the natural logarithm of the number of visits included as an offset to account for sites which did not receive three visits. Twelve fixed effects were considered (Suppl. Table 2) along with three pairwise interactions between the total wooded area, the proportion of broadleaved woodland and of open habitat within woodland. Dependent and independent variables were centred and scaled prior to analysis. Region was included as a random effect and was defined by the 11 regions that are intrinsic to the Breeding Woodcock Survey stratification (Hoodless *et al.* 2009). We present estimates and p-values from 'maximal' models (produced using Wald tests) so that each model, when comparing across the different buffer sizes and years, contained

the same set of variables. Model fit was assessed visually by plotting residuals against fitted values.

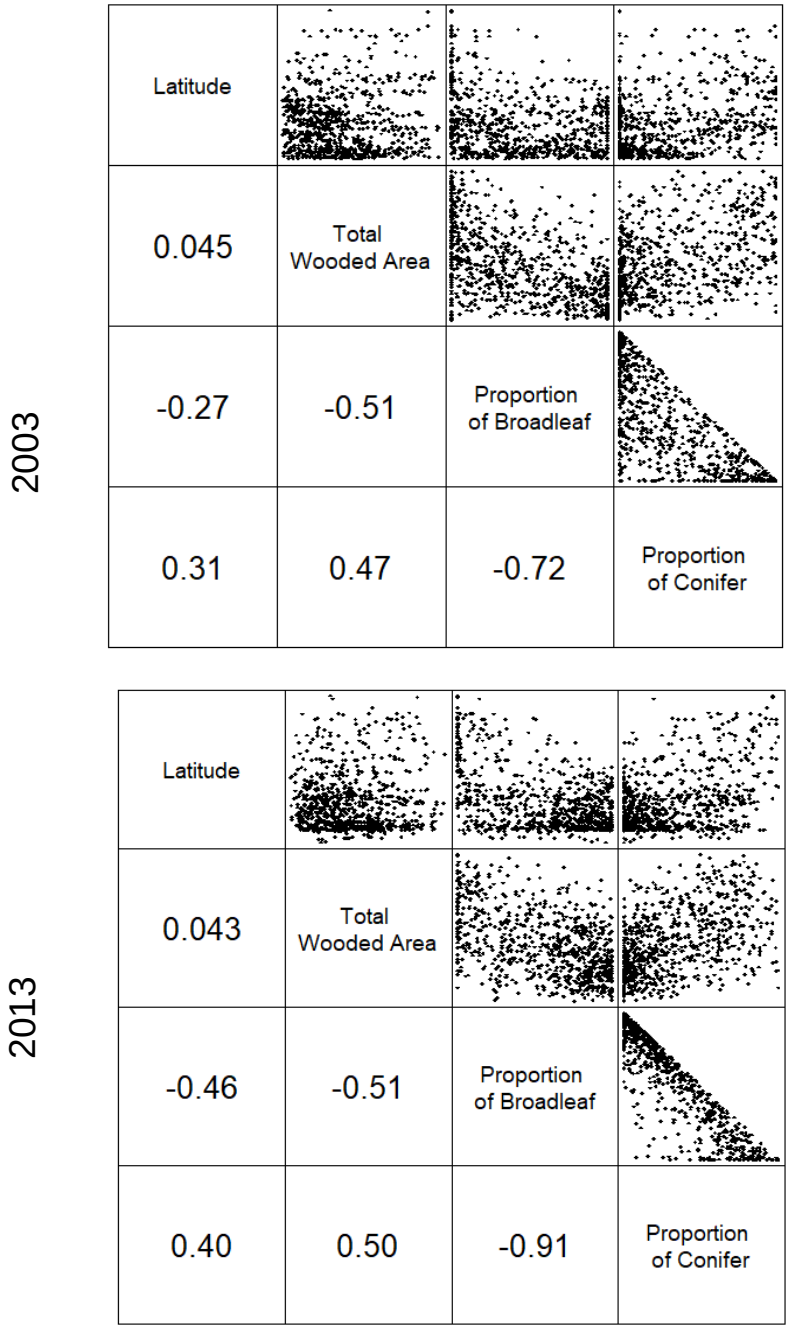


Figure 3.1 Collinearity plots between three model variables measured across Britain at the 1-km buffer scale (total wooded area, proportion of broadleaved woodland, proportion of coniferous woodland and latitude). Pearson's correlation values are provided in the lower panels. Figure produced in R.

3.2.4 Analysis of fine-scale survey site data

Using the habitat data gathered by observers, five explanatory variables were created for each count point: 1.) the proportion of the 200-m buffer occupied by closed canopy woodland, 2.) the proportion of the total wooded area occupied by open woodland habitats c, 3.) the proportion of closed canopy woodland in which stands contained establishing trees (those under 2 m), 4.) a simplified 'predominant tree' type based on seven rudimentary groups and 5.) a binary variable indicating the presence/absence of at least one birch-dominated stand.

Tree categories were created by aggregating similar categories of the NVC (Hall *et al.* 2004). A single tree category was considered predominant if it constituted ≥50% of the closed canopy woodland within the 200-m buffer. Broadleaf woods were classified as either 'beech' (for W12,14,15), 'oak' (for W10,11,16,17), 'wet woodland' (W1-7) or 'other broadleaf' (all other broadleaf categories). Coniferous woods were classified as either 'Sitka spruce' *Picea sitchensis*, which was by far the commonest coniferous category, or 'other coniferous'. A 'mixed' woodland category was used for woodland in which ≥50% of the closed canopy woodland contained an intimate mix of conifer and broadleaf species, with no single species dominating. The 'various' category was used when woods consisted of distinct stands, but no stand type represented >50% of the wooded area.

Birch was identified as a relevant variable when a preliminary of analysis of tree type identified a strong positive association between woodcock and the 'wet woodland' category. True wet woodland, as

defined by the NVC, is relatively rare in the UK but the frequency with which it was recorded suggests that pre-climax birch stands were often classified in the 'birch-dominated' category (W4) usually reserved for birch-*molinia* wet woodlands.

These data were analysed using a binomial GLMM in which woodcock presence was the dependent variable, region was specified as a random effect and the five variables listed above were used as fixed effects. The log number of visits was included as an offset since some sites received fewer than the recommended three visits. The analysis was performed in R using the MASS package.

3.3 Results

3.3.1 Collinearity across spatial scales

The Pearson's correlation tests showed strong collinearity between 1-km and 2-km circular buffers for all habitat variables (r = between 0.81 and 0.94 (Table 3.1)). Using 2-km ring buffers did reduce collinearity (r = between 0.48 and 0.88), particularly for habitat variables that are less common (e.g. open space within woodland). However, this precaution was not effective enough to justify including data for 1-km and 2-km ring buffers in the same GLMMs. In preliminary models where this was attempted, most woodland habitat variables were deemed non-significant at both scales; even those, such as total woodland area, that were highly significant when included singly. When tested in separate 1-km and 2-km ring buffer models, woodland variables showed consistent relationships with woodcock abundance, with the scale that

variables were measured having little effect on correlation strength or standard errors.

Table 3.1 Collinearity between the two spatial scales for eight woodland habitat variables in Britain. The r-values were produced using Pearson's correlation test and compare the area of each variable within 1-km radius buffers to 2-km circular buffers and 2-km ring buffers.

		2003		2013	
		Circular 2-km buffer	Ring 2-km buffer	Circular 2-km buffer	Ring 2-km buffer
Broadleaf	1-km	0.92	0.74	0.94	0.82
Conifer	1-km	0.94	0.81	0.94	0.81
Mixed	1-km	0.85	0.56	0.85	0.48
Open Space	1-km	0.9	0.68	0.85	0.61
Total Woodland	1-km	0.9	0.8	0.88	0.88
Heterogeneity	1-km	0.81	0.81	0.82	0.57
Grassland	1-km	0.9	0.85	0.87	0.81
Urban Area	1-km	0.9	0.84	0.86	0.78

3.3.2 Landscape-scale analysis of habitat data

3.3.2.1 Woodland variables

At the 1-km scale, woodcock abundance was influenced by the interaction between total woodland area and the proportion of broadleaved woodland ($P < 0.001$ in 2003 and $P = 0.026$ in 2013 (Table 3.2)). This meant that woodcock abundance showed a positive correlation with the proportion of broadleaved woodland when the total area of woodland within the buffer was high, but negative when total woodland area was low (Fig. 3.2).

Table 3.2 Results of four GLMMs used to assess the relationship between woodcock abundance in Britain and 15 variables (12 habitat characteristics and 3 interactions). Results are taken from maximal models, but only variables exhibiting a significant relationship with abundance are included in the table. Sections in bold indicate the models in which P < 0.05. The five variables and one interaction in the upper sections of the table were measured at two different spatial scales. Variables which did not vary with scale (lower section) were included in both the 1-km and 2-km ring models.

	2003 1-km buffer			2003 2-km ring buffer			2013 1-km buffer			2013 2-km ring buffer		
	Est.	*SE*	*P*	*Est.*	*SE*	*P*	*Est.*	*SE*	*P*	*Est.*	*SE*	*P*
Intercept												
Total woodland area	**0.5047**	**0.0587**	**<0.001**	**0.5173**	**0.0750**	**<0.001**	**0.5346**	**0.0836**	**<0.001**	**0.5610**	**0.0860**	**<0.001**
Woodland heterogeneity	**0.1780**	**0.0604**	**0.0033**	**0.1406**	**0.0670**	**0.0360**	0.1800	0.0931	0.0537	**0.3443**	**0.1078**	**0.0015**
Mixed woodland	0.0752	0.0524	0.1518	0.0537	0.0586	0.3602	-0.0533	0.0872	0.5410	**-0.2655**	**0.0965**	**0.0061**
Open woodland	-0.2267	0.1326	0.0877	-0.1815	0.1163	0.1189	-0.0960	0.1404	0.4942	**-0.3218**	**0.1353**	**0.0176**
Urban area	-0.0819	0.0621	0.1878	**-0.1972**	**0.0768**	**0.0104**	-0.0643	0.0918	0.4838	-0.1449	0.0947	0.1265
Broadleaf × Total wood	**0.2594**	**0.0578**	**<0.001**	**0.2153**	**0.0675**	**0.0015**	**0.1851**	**0.0832**	**0.0263**	**0.2560**	**0.0853**	**0.0028**
Distance from urban area	**0.1265**	**0.0620**	**0.0418**	0.1036	0.0677	0.1266	**0.2061**	**0.0639**	**0.0013**	**0.1635**	**0.0605**	**0.0070**
Roe deer	**0.2685**	**0.0741**	**0.0003**	**0.2885**	**0.0759**	**0.0002**	0.1418	0.0924	0.1252	0.1549	0.0893	0.0833

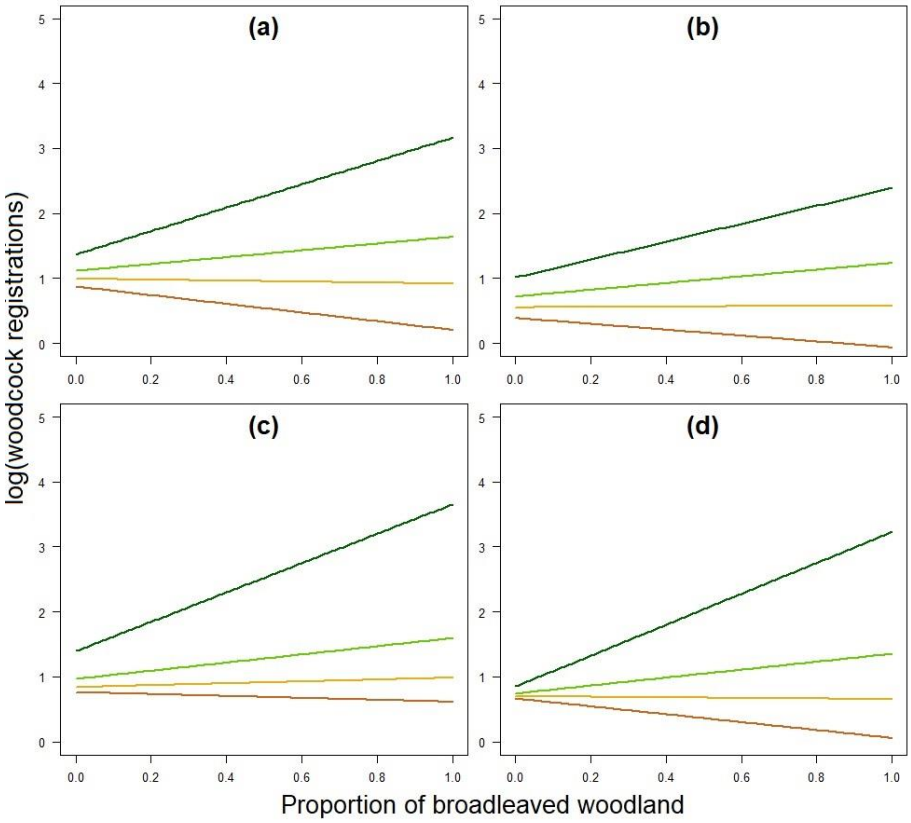


Figure 3.2 The interaction between the proportion of broadleaved woodland and total wooded area in Britain plotted using model coefficients from the (a) 2003 1-km GLMM, (b) 2013 1-km GLMM, (c) 2003 2-km GLMM (d) 2013 2-km GLMM. Woodland area is divided based on sample quartiles (brown = first quartile, gold = second quartile, light green = third quartile, dark green = fourth quartile). Values are rescaled to uncentred axes for ease of interpretation. Woodcock registrations are plotted on a logged scale to reflect the log-link linear predictor of the Poisson models.

There appeared to be a positive association between woodland heterogeneity and woodcock abundance in both years, although this was slightly outside of the 95% confidence interval in 2013 (2003: P = 0.003, 2013 and P = 0.054 (Table 3.2)). Broadly consistent results were recorded at the 2-km ring buffer scale. The same relationship with the interaction between total woodland area and the proportion of broadleaved woodland was observed in both years (P < 0.005 (Table 3.2)) along with a positive relationship with woodland heterogeneity (P = 0.036 in 2003, P = 0.002 in 2013 (Table 3.2)).

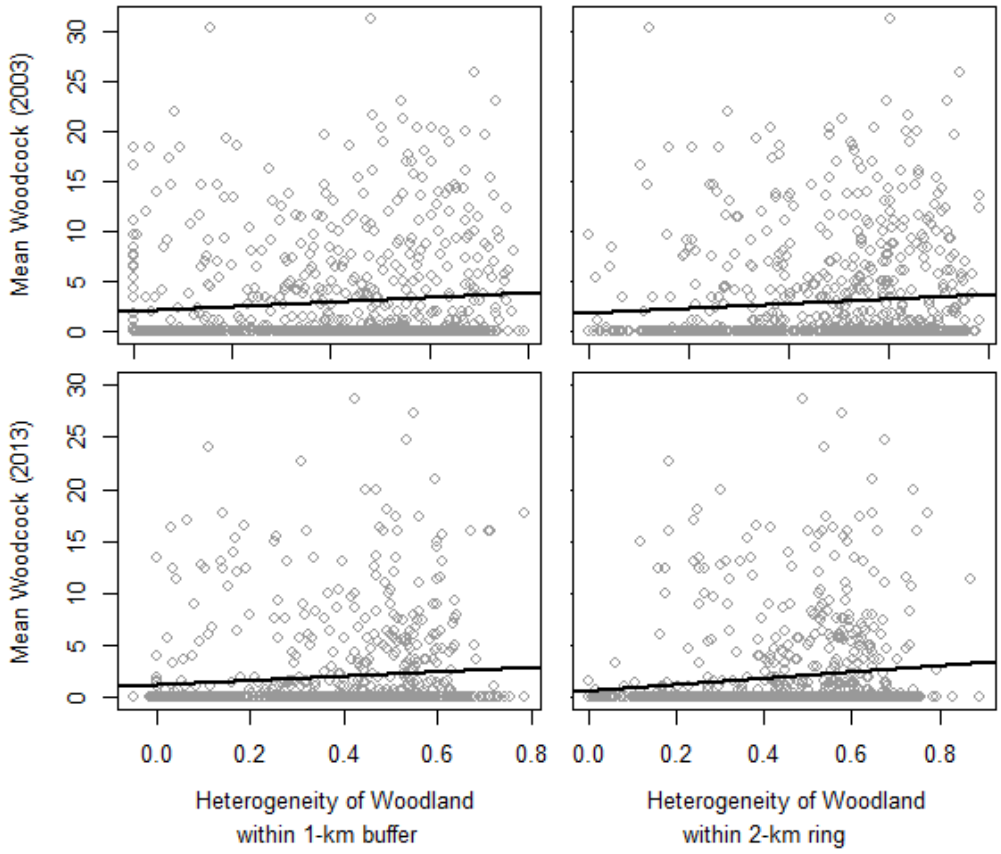


Figure 3.3 The relationship between mean number of woodcock recorded per visit and heterogeneity of woodland within a 1-km buffer (left) and 2-km ring buffer (right). Plots display raw data. Trend lines are produced using a simple linear model correlating these two variables only.

In addition, the 2013 2-km ring buffer model found a negative relationship with the proportion of open habitat within woodland (*Est* = *-0.322 ± 0.135, P* = 0.018) and with the proportion of mixed woodland (*Est = -0.266 ± 0.097, P* = 0.006).

Substituting the broadleaved variable for the collinear coniferous variable made few qualitative differences to the models' outcomes regardless of scale. Similar interactions were observed between conifer and total woodland, but the slopes were mirrored versions of those seen for broadleaf (Fig. 3.3 and Table 3.3).

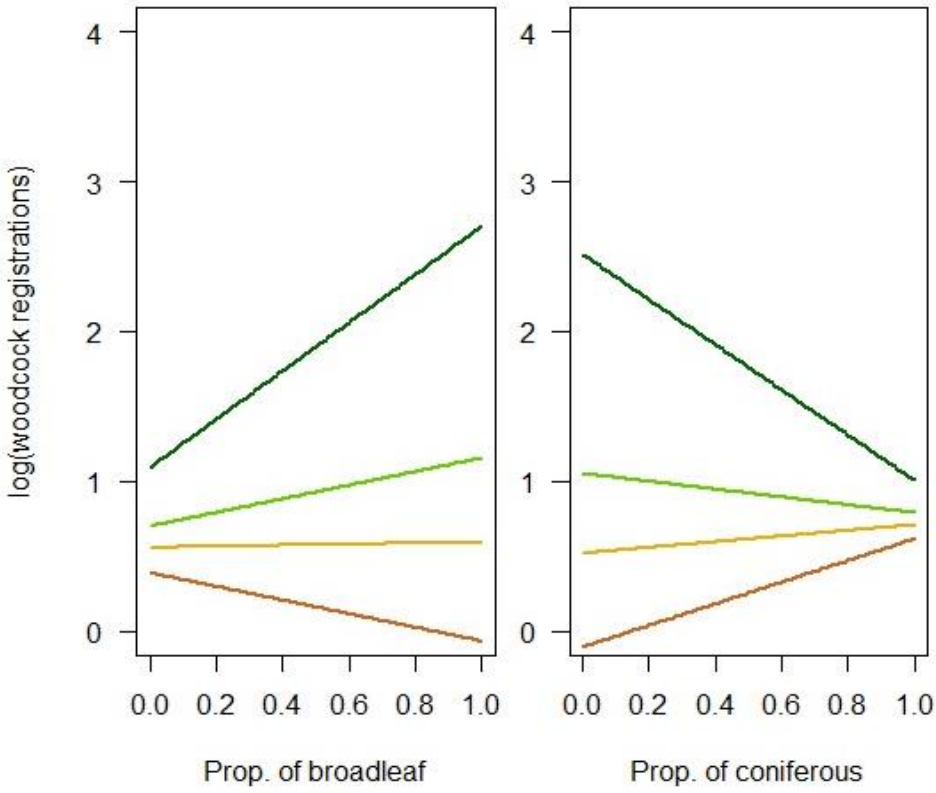


Figure 3.4 The mirrored relationships between broadleaved woodland and coniferous woodland, displaying an interaction with total woodland. Lines are plotted from the model coefficients of the 2013 1-km GLMM. Woodland area is divided based on sample quartiles (brown = first quartile, gold = second quartile, light green = third quartile, dark green = fourth quartile). Values are rescaled to uncentred axes for ease of interpretation. Woodcock registrations are plotted on a logged scale to reflect the log-link linear predictor of the Poisson models.

3.3.2.2 Other habitat variables

In 2003, there was a significant negative relationship between woodcock abundance and the proportion of the buffer occupied by urban habitat at the 2-km scale (*Est = -0.197 ± 0.068, P* = 0.010). In the other three models, woodcock abundance was greater in woods further from urban areas (*P* < 0.05 in all three, Table 3.2). No relationship was observed with the grassland variable at any spatial scale (Suppl. Table 3). Woodcock abundance was positively correlated with roe deer abundance in the 2003 models (*P* < 0.001, Table 3.2) but not the 2013

models. There was no significant relationship with muntjac or fallow in any of the four models (Suppl. Table 3).

Table 3.3 The mirrored relationships between broadleaved woodland and coniferous woodland when conifer is substituted for broadleaf in an otherwise identical model. This example is taken from the 2013 1-km GLMM, but all four models showed the same pattern. "Broad/Con (B/C)" is the variable that differs in the two models.

	Model containing "Prop. of Broadleaf"			Model containing "Prop. of Coniferous"		
	Est	SE	P	Est	SE	P
Total wooded area	**0.535**	**0.084**	**0.000**	**0.513**	**0.087**	**0.000**
Heterogeneity	0.180	0.093	0.054	0.164	0.091	0.072
"Broad/Con"	0.162	0.110	0.140	-0.031	0.090	0.729
Mixed	-0.053	0.087	0.541	-0.069	0.090	0.444
Open	-0.096	0.140	0.494	-0.259	0.118	0.029
Area of Grassland	-0.036	0.072	0.611	-0.027	0.073	0.710
Urban Area	-0.064	0.092	0.484	-0.070	0.092	0.450
"*B/C*" x wood. area	**0.185**	**0.083**	**0.026**	**-0.173**	**0.074**	**0.019**
"*B/C*" x open	0.169	0.114	0.139	0.012	0.106	0.908
open x wood. area	0.080	0.093	0.391	-0.038	0.077	0.620
Dist. urban area	**0.206**	**0.064**	**0.001**	**0.183**	**0.063**	**0.004**
Size of block	-0.105	0.088	0.230	-0.097	0.086	0.257
Muntjac	0.063	0.170	0.711	0.053	0.171	0.755
Roe	0.142	0.092	0.125	0.136	0.093	0.147
Fallow	-0.301	0.164	0.067	-0.291	0.165	0.079

3.3.3 Influence of fine-scale habitat on woodcock occurrence

Among the fine-scale habitat variables measured within a 200-m buffer of the count point, four were identified as significantly related to woodcock occurrence. Woodcock were more likely to be present at

sites where a larger area was occupied by closed canopy woodland (*Est* = 0.021 ± 0.005, *P* < 0.001) and at sites where a proportionally greater area of open space was available within the buffer's woodland (*Est* = 2.051 ± 6.356, *P* = 0.001). There was no relationship between woodcock presence and the occurrence of stands containing establishing trees <2 m (*Est* = -0.045 ± 0.381, *P* = 0.906).

Table 3.4 Percentage of sites occupied by woodcock in Britain (England, Scotland & Wales) in 2013 in relation to dominant tree type. 'Mixed woodland' refers to sites where an intimate mix of broadleaf and conifer dominate. 'Various' refers to sites where no single woodland type makes up ≥50% of the wooded area. Test statistics from the fine-scale vegetation GLMM compare predominant woodland type to beech.

	Surveyed	Occ.(%)	Est.	SE	*P*
Beech (intercept)	37	16.2	-4.822	0.701	0.001
Oak (inc. oak-birch)	158	32.9	1.042	0.521	0.046
Wet woodland	65	52.3	1.532	0.586	0.009
Other broadleaf	117	9.4	0.015	0.584	0.980
Sitka spruce	54	44.4	1.615	0.587	0.006
Other conifer	141	45.4	1.565	0.527	0.003
Mixed woodland	81	29.6	1.286	0.551	0.020
Various	36	41.7	1.383	0.599	0.021
Total	689	33.4			

Predominant tree type showed a significant correlation with woodcock presence (Table 3.4). The lowest site occupancy was recorded in the beech and the 'other broadleaf' categories (16% and 9% respectively), and was highest in wet woodland (52.3%), Sitka spruce (44.4%), other conifer (45.4%) and the 'various' category (41.7%) i.e. woodland in which a single tree type did not predominate. Woodcock occurred more frequently at sites where one or more

woodland stand was dominated by birch (*Est* = 0.916 ± 0.279, *P* = 0.001).

3.4 Discussion

3.4.1 Interactions between woodland type and area

The most consistent correlates of woodcock abundance were the proportion of broadleaf/coniferous woodland and total wooded area, with an interaction between the two variables observed in both years and at both spatial scales. Given that the most heavily wooded landscapes in Britain tend to be dominated by conifer species, the interaction with the proportion of broadleaved woodland might appear to be an artefact of a strong relationship with woodland area. The collinearity plots (Fig. 3.1), however, suggests our sample includes enough heavily wooded areas dominated by broadleaved trees for our models to separate the respective influence of each variable.

The interaction suggests that sites with higher proportions of broadleaf woodland generally supported greater numbers of woodcock, but only when the total wooded area exceeded a certain level. Plots of the interactions (Figure 3.2) appear to show weak negative correlations with broadleaved woodland in less-wooded areas. A possible biological explanation for this might exist if small predominantly coniferous woods in the uplands are surrounded by non-woodland habitats that occasionally support woodcock (such as heather moorland) while lowland, predominantly broadleaf woods are mostly surrounded by farmland. Overall, however, it seems more likely that the significance of

the interaction simply reflects a contrast between a positive correlation and a lack of correlation, rather than positive vs. negative. In the least-wooded areas, where woodland may cover as little as 10% of the survey square, abundance is probably restricted by the availability of woodland regardless of its type and hence no habitat relationship is observed.

At most sites, both coniferous and broadleaved woodland occurred within the 1-km buffer and did so in a broad range of ratios. While many areas with extensive woodland cover are conifer-dominated, it may be that among these, abundances tend to be higher in areas where these conifers are frequently interspersed with stands of broadleaved trees. This observation appears to be supported by the woodcock's association with more heterogenous woodlands and by an existing radio-tracking study (Hoodless and Hirons 2007) which found that woodcock living in predominantly coniferous woods, used home ranges with high proportions of young birch woodland relative to its availability.

The value of broadleaved woodlands likely depends on the exact species in question. Broadleaved species such as beech *Fagus sp.* were associated with low woodcock occurrence in our fine-scale analysis, probably because beech leaves are less palatable to detritivorous invertebrates (Hendriksen 1990), and because beech typically occurs in areas with dry soils and only sparse ground vegetation. Birch woods, on the other hand, provide increased soil penetrability owing to wetter soils and have leaves that decompose

relatively quickly (Cornelissen 1996), potentially resulting in higher earthworm abundance under birch litter particularly compared to coniferous woods. Dense stands of young birch may also provide protection from predators for foraging or roosting woodcock (Hoodless and Hirons 2007).

An underlying relationship with woodland size was to be expected; woodcock declines recorded by Bird Atlas (Balmer *et al.* 2013) show a retraction of the British Breeding population towards more heavily wooded regions. We did not find a significant relationship with the size of the woodland block in which the survey was conducted which suggests wider availability of woodland within the landscape is more important.

Higher numbers of well-connected woodland patches in the landscape may allow male woodcock to access larger or more efficient roding grounds. Woodcock density and roding activity are known to correlate in a non-linear fashion (Hoodless *et al.* 2008) suggesting that social interaction, which would be more common in larger woods, may be a stimulus for display. Ring recoveries of woodcock show that natal dispersal distances are typically short (76% of woodcock ringed as chicks were recovered within 10 km of their natal site (Hoodless and Coulson 1994)) and large inter-wood distances may reduce the ease of movement between isolated but otherwise suitable woods (Tilman & Kareiva 1997).

3.4.2 Landscape-scale woodland heterogeneity

Increased heterogeneity of woodland habitats was generally associated with higher woodcock abundance, despite the very broad woodland categories used to calculate this index. As described above, the association with heterogeneous woods may reflect the relative importance of broadleaf in conifer-dominated landscapes but high heterogeneity should also provide more suitable breeding sites as a range of habitats are required through the different stages of the breeding cycle (Hoodless & Hirons 2007). Changes to woodland management practices over the course of the last century (e.g. reduction of coppicing, monocultural forestry) have reduced the areas of open and young woodland habitats and produced woods that are less heterogenous in terms of tree age and structure (Fuller & Warren 1993; Fuller *et al.* 2007; Hopkins & Kirby 2007). Open areas may be used as nocturnal feeding sites and are visited by roding male woodcock when searching for females, while young woodlands, where trees are smaller and closer together, are used by females foraging with young (Hoodless & Hirons 2007). Young woodlands, with a high density of trees under a 7.6 cm diameter (1400 – 4500 per ha) are important breeding habitat for American woodcock (*Scolopax minor*) (Dessecker & McAuley 2001) which have a similar ecology and diet to their Eurasian counterpart.

Our analysis does not include an accurate measure of young woodland at the landscape-scale but the open space category, which includes areas prepared for planting and freshly planted trees, ought to

indicate that the management required to maintain young woodlands is in place. This variable showed either no correlation, or, in one model, a negative correlation with woodcock abundance. The establishing woodland variable included in the fine-scale analysis, which records the proportion of stands containing trees under 2 m in height, also showed no significant correlation. These findings may contradict what little information we already have about woodcock breeding habitat but are based on crude measures of young and open woodland that may not be sensitive enough to reveal subtle relationships. Confirming any potential relationship with young woodlands will require more accurate measures of woodland age than are currently available on a national scale.

3.4.3 Other factors influencing woodcock abundance

Woodcock abundance showed a negative association with urban area or proximity to human settlements. Assuming this is correlated with human activity, disturbance is likely to be having a negative effect on woodcock breeding success by increasing desertion or the risk of nest predation through more frequent flushing of adults, or directly through predation of nests by domestic pets (Coppes *et al.* 2017; Langston, Liley, *et al.* 2007). It is sensible to assume these factors could affect most ground-nesting species, but the effect of disturbance can be difficult to demonstrate explicitly without monitoring the fate of a large sample of nests.

The relative abundance of roe deer was positively correlated with woodcock abundance in 2003, which seems to be at odds with existing research identifying a negative effect of unnaturally high deer densities upon woodland birds (Gill & Fuller 2007). It seems unlikely that this relationship was directly causal and is more likely to be the product of an underlying geographic covariate. Opposing population trends over the course of the next ten years meant that this pattern was no longer apparent by 2013.

3.4.4 Suggestions for future research

Our analysis shows that the current distribution of breeding woodcock in Britain correlates with several woodland habitat variables; chiefly the availability of large, well-connected and heterogeneous woods. The once widespread British distribution of the woodcock shows that there is no inherent dependency upon large woods or particular woodland types, but that many smaller, particularly lowland, sites have apparently become unsuitable over the latter half of the twentieth century (Sharrock 1977; Balmer *et al.* 2013).

It is possible that there are underlying links between these variables and woodland management, whether it be the decline of active management in lowland deciduous woods or the management strategies associated with commercial forestry in the uplands. Investigating the role of management in the maintenance or creation of suitable habitat seems a logical next step. This should not only compare between areas where active management is present and

absent, but also between different management techniques and stages within the timber rotation period. This line of enquiry should clarify whether young woodland is important to breeding woodcock.

Changes to woodland habitats are not the only factors associated with woodcock abundance and other variables may be having an equally large influence on recent declines: disturbance, nest and chick predation and increased severity of wet summers could all reduce breeding success while hunting and severe winter weather may affect overwinter survival. A comprehensive study that considers these additional factors alongside the habitat variables highlighted here would be required to fully understand the causes of recent woodcock declines. This could be complemented by radio-tracking studies of resident British woodcock that compare productivity and adult survival in woods supporting high and low woodcock densities.

4 A METHOD FOR MIST-NETTING BREEDING WOODCOCK

This chapter was published under the title “A method for mist-netting breeding Eurasian woodcock: use of visual and audio lures increases capture rate” in Ringing and Migration (Heward *et al.* 2017). The text and content are completely unchanged except for formatting and the addition of Figure 4.1. I was solely responsible for writing the manuscript except for Section 4.2.2 and the corresponding paragraph in the results section (see below).

Author Contributions:

Andrew Hoodless: Wrote description of existing method (4.2.2) and final paragraph of results section

Andrew Lowe: Helped devise the capture technique, provided comments on manuscript

4.1 Introduction

Ringing has provided a means of studying chick survival, winter dispersal and philopatry in the Eurasian woodcock *Scolopax rusticola* as well as a rudimentary understanding of the species' migration (Hoodless & Coulson 1994; Hoodless & Coulson 1998). The number of woodcock ringed in the British Isles has increased dramatically in recent years, with an average of 65 ringed per year during 2000-2005 rising to over 1,300 individuals each year during 2010-2015 (Robinson *et al.* 2016). This is largely due to the increased use of dazzling to catch woodcock following a concerted effort to promote the method (Williams 2015). Dazzling is conducted at night during the winter months, when woodcock leave woodland to feed on arable fields and grassland.

Woodcock caught in winter may belong to Britain's small breeding population (c. 55,240 males (Heward *et al.* 2015)) or to one of the larger Russian, Baltic or Fennoscandian populations which overwinter in Western Europe (c. 800,000 to 1.5 million individuals winter in Britain each year (Musgrove *et al.* 2011)). Trends differ between these populations, with most continental migrant populations appearing stable (Birdlife International 2015b; Lindström *et al.* 2015) compared to the marked decline of British residents (Heward *et al.* 2015). These populations cannot be separated morphometrically. Lower woodcock densities and seasonal changes in their nocturnal behaviour make dazzling unproductive during spring and summer (Hoodless & Hirons 2007), but an alternative method for capturing woodcock during the breeding season, when only residents are present, would be beneficial.

An approach similar to the BTO's Retrapping Adults for Survival (RAS) scheme, at a variety of sites, would be a useful start towards better understanding the demographic drivers of decline providing sufficient birds could be captured.

A number of studies have used mist-nets to catch woodcock (Sheldon 1957; Hirons 1980; McAuley & Longcore 1993; Hoodless & Hirons 2007), but a comprehensive guide to catching woodcock using this technique has never been published. Literature regarding catching techniques for American woodcock *Scolopax minor* during the breeding season is not directly applicable to the Eurasian woodcock given the differences in their breeding displays (McAuley & Longcore 1993). Older studies of Eurasian woodcock have relied on the use of a live bantam decoy, as described by Hirons (1980). There are animal welfare considerations associated with this method and, in the UK, a live decoy cannot be used without the prior consent of the ringing unit (Redfern & Clark 2001). Some researchers have caught small numbers of woodcock in spring and summer using walk-in traps in woodland (Hoodless & Hirons 2007) or by locating incubating females or broods using pointing dogs (McAuley & Longcore 1993). Here, we summarise an efficient technique for mist-netting woodcock in the breeding season.

4.2 Method

4.2.1 Capture technique

During this study, we captured woodcock in three large (> 100 ha) woodlands in Nottinghamshire, UK, managed by the Forestry

Commission, in 2015 and 2016. Mist-netting was conducted at dusk, from mid-April to mid-July, when male woodcock perform their breeding displays (known as ‘roding’). Capture sites were usually selected based on preliminary counts of roding woodcock and were located in clearings and wide rides. Catching was most successful at sites where ground vegetation was low or patchy. Catching sites included heaths, mown areas such as car parks and picnic sites, clearfells, permanent clearings covered with low vegetation or dead bracken and woodland rides. The sizes of clearings used varied from 0.5 to 4 ha.

Mist-nets were erected 30 min before sunset and sessions were run until 60 to 90 min after sunset. We used Ecotone 45x45-mm mesh nylon nets (110 denier/2 ply) with four shelves. Up to four nets were used, with a maximum combined length of 60 m (2 x 12 m, 2 x 18 m). Nets were most commonly arranged as a four-sided ‘box’ or an open three-sided ‘box’, often using a woodland edge to form the fourth side. Occasionally nets were set in a continuous line dog-legged across the clearing. On forest tracks and rides, we set three separate nets perpendicular to the ride (Fig. 4.1).

Woodcock were attracted to nets using a playback lure and a decoy. The playback lure was placed near to the centre of the ‘box’ of nets or, where parallel rows were used, to one side of the central net.

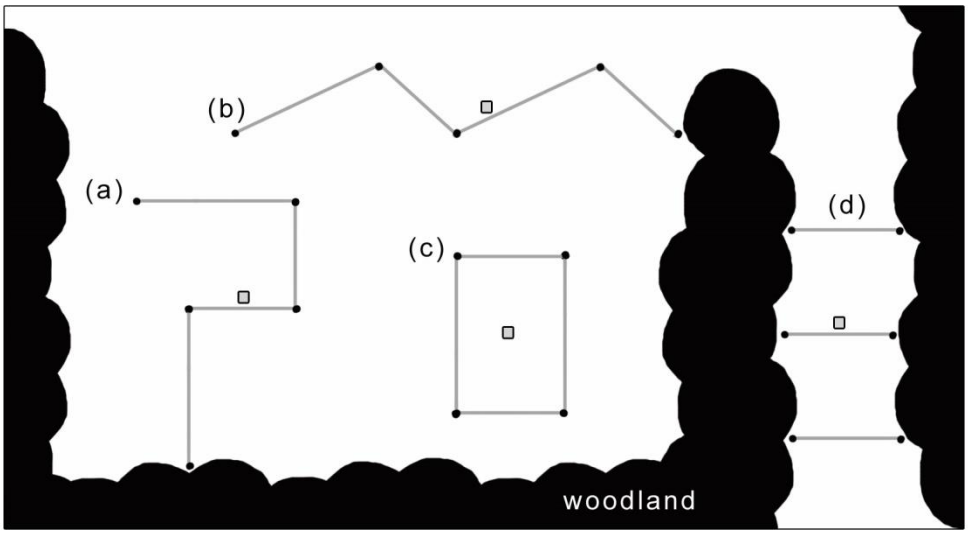


Figure 4.1 Four possible mist-net arrangements using a combination of 12m and 18m nets: (a) a 'question-mark' or open box, (b) a 'dog leg', (c) a box and (d) parallel nets. The grey box shows the approximate location that the playback lure was placed.

Three types of decoy have been used, each separately: a taxidermied woodcock, a papier-mâché model with a real woodcock tail and a motorised 'weasel' cat toy, the latter providing a moving stimulus. The importance and relative effectiveness of these three decoys has not yet been quantified. An observer hid in nearby vegetation, usually within 8-15 m of the nets, and used a remote control to select between different calls stored on the playback lure. Any UK ringer wishing to use playback lures during the breeding season will need a specific endorsement on their ringing permit.

When a roding woodcock was seen or heard it was drawn close to the nets using the high frequency 'whistle' element of the roding call (a recording with the low frequency grunt component removed). When a bird was seen to alter its flight towards the call, the playback was

switched to a ‘chasing’ contact call. This chasing vocalisation, a rapid series of whistles, is usually used during male-male confrontation and can elicit a noticeable change in behaviour. The playback lure was most effective when its use was restricted to the latter half of the roding period, generally between 30 and 60 minutes after sunset. Nets were watched by the lure operator whenever the playback was in use and birds were extracted from the nets as soon as they were caught. When nets were set in a ‘box’ arrangement, this observer positioned themselves so that any woodcock landing in the centre of the box without becoming caught might be flushed towards the nets.

4.2.2 Comparison with existing technique

We compared our capture rate using this new technique with that recorded by Hoodless & Hirons (2007) at Whitwell Wood, Derbyshire, during April-June 1991-92. At Whitwell Wood, woodcock were captured in mist-nets without use of playback or a decoy. Whitwell Wood lies within 15 km of our current study sites and the number of registrations of roding woodcock in 1991-92 was similar to recent counts at our current sites (15-25 per evening roding period). Typically, 126 m of mist-net (one 18-m and nine 12-m nets) was opened for 75-90 min, with 51 dawn sessions and 49 dusk sessions over the two years. Nets were North Ronaldsay 32x32-mm mesh (75 denier/3 ply), except one 12 m net with 38x38-mm mesh. Observations of woodcock hitting various Ecotone and North Ronaldsay mist-nets with mesh sizes varying from 30–45 mm suggest similar likelihoods of capture; certainly, woodcock

were never observed to ‘bounce’ out of any of these mist nets. At smaller mesh sizes (e.g. 16-19 mm square mesh), however, this is more likely to occur.

Capture rate was analysed using a generalized linear model (GLM) with captures per session as the dependent variable (range = 0 – 3). A Poisson error distribution was specified and $\log_e$(length of net) used as an offset. Two explanatory variables were specified: 1. a combination of method and time of day (i.e. net only at dawn; net only at dusk; net and lure at dusk) and 2. time of year (summarised as two-week periods corresponding to the first and second half of each month). P-values calculated from F-statistics are produced in Genstat (VSN International 2005) by alternately removing each of the two variables.

4.3 Results

We caught 15 woodcock in 2015 and 19 new woodcock in 2016. In 2015 we recaptured three birds. In 2016, we made one same-year recapture and recaptured three birds originally caught in 2015. We recorded no mortalities and no injuries to woodcock as a result of mist-nets or during handling. After experimenting with the technique in 2015, the method outlined above was consistently repeated for 39 sessions in 2016, with birds caught between 19 April and 13 July. Birds were captured, on average, 54 ± 19 min (1 SD) after sunset. Of the 22 woodcock caught in 2016 (19 new and three recaptures), 19 (86%) were confirmed as male. Fifteen were sexed based on display behaviour immediately prior to capture. The remaining four birds were

sexed based upon their bill: tail length ratio (about 45% of adult birds can be sexed in this way (Ferrand & Gossmann 2009)) and/or their subsequent behaviour (woodcock were fitted with radio-tags). Two birds were unsexed and one was confirmed as female by the remnants of a brood patch. A strong sex bias is unsurprising given that the playback method uses a recording of a vocalisation usually used between males.

There was no difference in capture rate with mist-nets between 1991 and 1992, so data were pooled for further analysis (GLM year $F_{1,97} = 0.10$, $P = 0.753$, time of day $F_{1,97} = 8.77$, $P = 0.004$, year x time of day $F_{1,96} = 0.55$, $P = 0.462$). There was a consistent difference in capture rate between methods, and between dawn and dusk sessions, during April to mid-July (GLM method-time $F_{2,130} = 22.18$, $P < 0.001$, two-week period $F_{6,130} = 1.25$, $P = 0.285$, method-time x period $F_{9,121} = 1.46$, $P = 0.169$). At Whitwell, capture rate was almost three times higher at dawn than dusk when using mist-nets alone (mist-net only at dawn 0.157 ± 0.030 capture/50 m net; mist-net only at dusk 0.055 ± 0.018). Comparing between methods, capture rate at dusk was over nine times higher when using the playback lure (playback lure 0.527 ± 0.098). Results based on captures per session, ignoring the difference in number of nets used between methods, were similar (GLM method-time $F_{2,130} = 8.60$, $P < 0.001$, two-week period $F_{6,130} = 1.37$, $P = 0.231$, method-time x period $F_{9,121} = 1.58$, $P = 0.128$; playback lure 0.590 ± 0.110 capture/session; mist-net only at dawn 0.412 ± 0.080; mist-net only at dusk 0.143 ± 0.047).

4.4 Discussion

Our new method of capturing woodcock in the breeding season appears to be more efficient than mist-netting alone and requires the use of fewer nets. Because comparisons are made between two different studies, conducted at different sites and times, it is possible that these confounding factors partially account for some of the observed difference in capture rates. However, given the nine-fold increase in capture rate associated with the use of our remote-control lure, it seems unlikely that any more than a small proportion of this difference is attributable to site and timing effects. It might be possible to improve the capture rate further by employing the technique at dawn. The capture method described here is not without its limitations; chiefly that the skewed sex ratio of birds caught means females are poorly represented. Nevertheless, ringing woodcock during the breeding season using this method over several years could generate valuable data on annual survival rates of resident breeders and help in determining the drivers of their decline provided any potential sex-specific effects are considered. The combination of mist-netting during the breeding season and dazzling on nearby fields in winter could be used to provide additional recaptures and hence possible seasonal estimates of survival. Monitoring over-winter survival at a sample of sites would be valuable given that the impacts of hunting and harsh winter weather are poorly understood.

5 FACTORS AFFECTING THE TIMING AND INTENSITY OF WOODCOCK DISPLAY BEHAVIOUR AND THE IMPLICATIONS FOR RODING SURVEY DESIGN

5.1 Introduction

Male Eurasian woodcock *Scolopax rusticola* perform a distinctive breeding display known as 'roding', which consists of a simple repeated call given in flight. Male woodcock roam over large areas while displaying and, based on field observations alone, it is difficult to follow the movements of a single male since the roding ranges of several birds may overlap (Hirons 1980). The display period usually begins shortly before sunset and continues for an hour or more after (Hirons 1983), with a shorter display period occurring just before sunrise (Hirons 1983). The behaviour appears to be a signal for female mate selection rather than male-male territoriality (Hirons 1980) and can be observed from February to July, with display peaking during May and June (Hoodless *et al.* 2006).

The roding display provides a practical means of surveying woodcock and counts of roding males are used to assess population trends in a number of European regions, such as France, the Azores and Western Russia (Ferrand *et al.* 2008; Machado, Ferrand, *et al.* 2008; Fokin & Blokhin 2013). In some regions, such as Britain, roding surveys are also used to estimate regional and national population size (Hoodless *et al.* 2009; Heward *et al.* 2015). In Britain, roding surveys

are the only effective way of detecting breeding population trends as alternative methods, such as hunting bag analyses (e.g. Seamans and Rau 2017), are confounded by the large numbers of migrant woodcock that winter alongside British breeders (Hoodless *et al.* 2013).

The British Breeding Woodcock Survey was conducted at over 800 randomly selected sites in 2003 and 2013 (Heward *et al.* 2015, Chapter 2). Although the 2003 survey revealed that the British breeding woodcock population was far larger than any previous estimates had suggested, the 2013 survey confirmed that the population was undergoing large scale declines (-29% in ten years). Following the first national survey, a small non-random sub-sample of occupied sites continued to be surveyed on a repeated basis. Overall, these counts saw a mean yearly decline of 4.9% (Heward *et al.* 2015) but were characterised by a high degree of annual variation with population trends ranging from +21% to -27% (Heward *et al.* 2015, see Chapter 2).

Weather may be one potential source of annual variation in survey results. Weather could have a direct impact on the number of woodcock present if long-term weather patterns influence over-winter survival or productivity in the previous breeding season. Weather may also affect survey results by influencing the amount of effort that each male invests in display. This may occur if weather reduces food availability and individual fitness, preventing woodcock from meeting the high energetic costs of display. Woodcock may be less willing to engage in display during unsuitable weather conditions if they affect the efficiency of display behaviour by reducing signal transmission (e.g. by

providing extra background noise) or increase the energetic costs (e.g. the increased cost of maintaining steady flight during wind or rain). Additionally, weather during the survey period may reduce detectability by surveyors, which would affect survey results even if woodcock activity was unchanged. There is already some evidence that roding activity can be reduced by poor weather during the display period but Hoodless *et al.* (2006) suggest that this must be relatively severe before it has a noticeable effect. No previous studies have considered the broader effect of prevailing weather in the period prior to the roding survey and there may be more subtle effects of weather during the survey period than are currently documented.

The timing of the survey period, in relation to woodcock display, is an aspect of the methodology which has been subject to change and one for which a greater understanding of the interaction between weather and woodcock behaviour would be informative. In 2003, survey visits had a duration of 60 minutes and began 15 minutes before sunset which reportedly ensures 'detection of 83% of woodcock passes' (Hoodless 2006). Following the 2003 survey there were concerns that, at some survey sites, woodcock continued to display far beyond the limits of the original 60-minute period and in 2013, the survey duration was extended to 75 minutes (Heward *et al.* 2015). Providing it is consistent, surveying only part of the display period should not affect survey results *per se*, but if weather influences the timing of roding it may mean the portion of the display period falling within the fixed survey period varies.

Here, I investigate the potential benefit of continuing to employ the extended survey duration of 75 minutes as a buffer against such variation. I do this by using the 2013 national survey data to analyse how detection rates change as a result of the additional 15 minutes and measure the effect of time of year and weather. Since these survey data say little about the birds that remain unrecorded outside of the 75-minute survey period, I also include tracking data relating to the roding activity of a sample of male woodcock tagged with GPS-loggers. I consider the wider relationship between roding survey results and weather, using repeat woodcock survey data collected over a 12-year period. The improved understanding of roding behaviour that this provides will allow the refinement of future survey methodology design and the collection of more representative data both in Britain and elsewhere in Europe.

5.2 Methods

5.2.1 2013 Breeding Woodcock Survey: timing of roding and weather

The methodology of the 2013 Breeding Woodcock Survey, and the 2003 survey on which it is based, are described in more detail in Chapters 2 and 3 and Hoodless *et al.* (2009).

A random sample of 823 survey squares across England Scotland and Wales were visited by volunteer surveyors. Survey squares were visited three times, at least one week apart, between the start of May and the end of June. Visits started 15 minutes before

sunset and were 75 minutes in length. Surveyors were provided with instructions to allow them to select a suitable site where roding could be observed; generally, a woodland clearing or the intersection of two wide rides (British Trust for Ornithology 2013). Surveyors recorded each separate occasion that a woodcock was seen or heard as a distinct 'registration' with the corresponding time to the nearest minute.

Surveyors assigned cloud cover to one of three broad categories: 0 – 33%, 34 – 66%, 67 – 100%. Wind strength was rated as calm, light or moderate (equivalent to 0-1, 2 and 3, respectively on the Beaufort scale). Rainfall was categorised as 'no rain', 'drizzle' (very light, continuous rain) or 'showers' (moderate, intermittent rain). Surveys were not conducted if rain was persistent, or if the wind exceeded Beaufort Scale 3. Moon phase data were sourced from a moon phase generator available online (somacon.com 2011). This gives the date of each full moon during the study period, which was used to calculate the number of days between the survey and the nearest full moon (a number between 0 and 14 days).

The times of the first and last woodcock registration were expressed in relation to sunset time (accurate to the nearest whole minute) for each survey visit at each site. Sites were classified into one of four aggregated regions, following a latitudinal gradient, based on the boundaries of the eleven custom regions intrinsic to the Breeding Woodcock Survey (Scotland, Northern England, Central England and Wales, Southern England (Fig. 5.1 and Fig. 2.1)). The date on which

the survey was conducted was converted to a day number in which 1st January was classified as day 1.

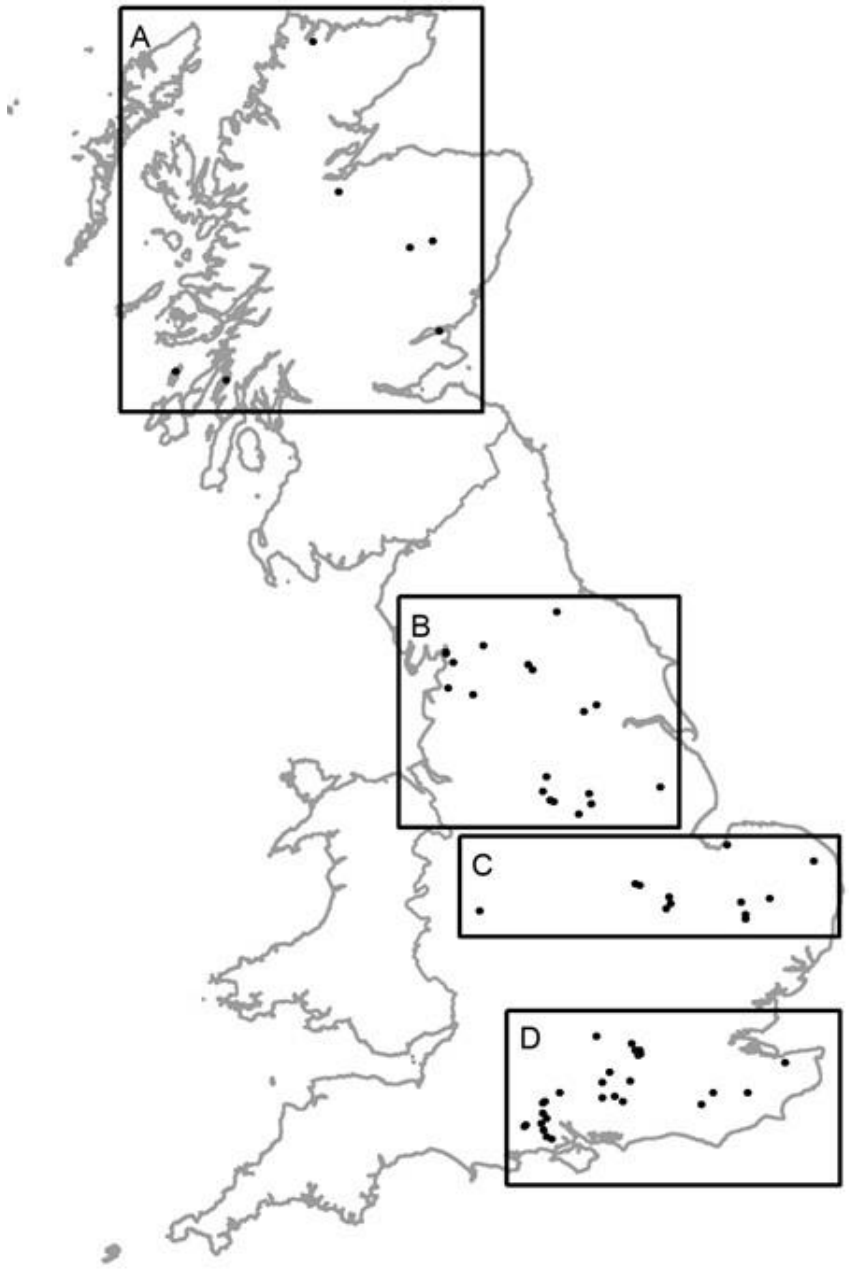


Figure 5.1 Map showing the 65 survey sites and the boundaries of the 4 regions used in our analysis: A = Scotland (n = 7), B = Northern England (n = 19), C = East Anglia and the Midlands (n = 12), D = South-east England (n = 27).

Analysis of start time and end time at occupied sites was confined to visits on which five or more woodcock registrations per visit were recorded. This five-registration threshold was designed to keep the sample size large enough for statistical analysis whilst removing the bias associated with low counts. Sites where fewer than five registrations were recorded are likely to introduce bias if they originate from poorly selected count points, or from sites where woodcock densities are very low and activity is therefore limited. The effect of using ten registration and fifteen registration thresholds was explored (see results). The five-registration threshold resulted in a final dataset containing 472 woodcock survey visits conducted across 213 sites.

A generalised linear mixed model (GLMM) with a Poisson distribution and logarithmic link function was run in R (R Development Core Team 2019) using the lme4 package (Bates *et al.* 2015). The time of the first woodcock registration was specified as the dependent variable, with cloud cover, wind, moon phase and day number as explanatory variables, and site nested within region as a random effect. A similar GLMM, with identical distributions, explanatory variables and random effects was run, replacing the dependent variable with the time of the last woodcock registration. Rain was not included as an explanatory variable as most surveys (n = 455/470) were conducted in dry conditions. The models were simplified using a backward stepwise method where the least significant explanatory variables were successively removed until a significant change in the model's explanatory power was detected by a chi-square test. The fit of the final

model was gauged using a Pearson's residuals plot. The starting maximal models did not always converge if they included an interaction between cloud and moon, but the effect of adding this interaction to the simpler final model was considered. GLMMs in the lme4 package provide P-values produced using Wald tests (Bates *et al.* 2015).

To demonstrate that a longer roding period was analogous to more roding activity, and could therefore influence interpretation of roding survey results, a GLMM with a Poisson distribution and logarithmic link function was created. The total number of woodcock registrations was specified as the dependent variable, and the length of the roding period, i.e. the window of time in which all roding occurred, was the sole explanatory variable. Site was included as a random factor. Model fit was assessed graphically using a plot of Pearson residuals. Two additional versions of this model were run, using a subset of the data in which total registrations ≥10 and ≥15, to check that any observed relationship was not influenced by the arbitrary five registration threshold.

For each visit to each site, the number of additional registrations recorded in the last fifteen minutes of the survey period was extracted. A GLMM with a binomial distribution and logit link function was used to compare variation in the proportion of observations in the last fifteen minutes to four explanatory variables: day number, cloud cover, moon phase and wind. I reduced the model size by removing the least significant variables in turn, monitoring the effect of each variable's removal using chi-square tests. P-values are presented from the

minimum adequate model and produced using a Wald test. Survey site, nested within region, was included as a random factor.

Table 5.1 The analysis of three principal datasets to explore the potential influence of weather on roding behaviour/surveys. See methods for details of random effect structures.

	Model	Dependent variable	Explanatory variables	Source of exp. variable
2013 BREEDING WOODCOCK SURVEY	Start time ~ short term weather	Time of first woodcock registration	Cloud cover	Surveyor
			Wind	Surveyor
			Moon phase	Somacon.com
			Day of year	
	End time ~ weather	Time of last woodcock registration	Cloud cover	Surveyor
			Wind	Surveyor
			Moon phase	Somacon.com
			Day of year	
	No. of woodcock ~ duration of roding period	Total number of woodcock registrations	Length of roding period (minutes)	
	Registrations in final 15 minutes ~ weather	Proportion of registrations occurring in last 15 minutes	Cloud cover	Surveyor
			Wind	Surveyor
			Moon phase	Somacon.com
			Day of year	
REPEAT BREEDING WOODCOCK	No. of woodcock ~ short- and long-term weather	Total number of woodcock registrations	Cloud cover	Surveyor
			Wind	Surveyor
			Moon phase	Somacon.com
			Min. temp (day)	Met Office
			Min. temp (14 days)	Met Office
			Total rain (day)	CEH-GEAR
WOODCOCK TRACKING DATA	Roding behaviour ~ short term weather	Binary 'roding' vs. 'non-roding' variable based on tracking data	Cloud cover	Met Office
			Wind	Met Office
			Min. temp	Met Office
			Rain	Met Office
			Moon phase	Somacon.com
	Start time ~ short term weather	Time that tagged individuals began roding	Cloud cover	Met Office
			Wind	Met Office
			Min. temp	Met Office
			Rain	Met Office
			Moon phase	Somacon.com
	End time ~ short term weather	Time that tagged individuals finished roding	Cloud cover	Met Office
			Wind	Met Office
			Min. temp	Met Office
			Rain	Met Office
			Moon phase	Somacon.com

5.2.2 Repeat breeding woodcock surveys: the broader influence of weather

To look at broader relationships with weather, I analysed repeat roding survey data which monitor a sub-sample of sites over several years, capturing greater variation in weather conditions for each site than a single-year dataset can. Surveyors taking part in the 2003 GWCT/BTO Breeding Woodcock Survey were encouraged to continue their counts, resulting in 65 sites (Fig. 5.1), all of which were occupied by woodcock, receiving repeat visits (Heward *et al.* 2015). Sites were not visited annually, but each was visited in at least three different years between 2004 and 2015 and most received multiple visits per year. On average, each site received 13.6 visits (range = 4 – 32) across 5.0 different years (range = 3 – 11). Ideally, these repeat surveys would have been conducted at an entirely random selection of sites on a strictly annual basis, but this was not possible without increasing the risk of reduced uptake or poor continuity of surveys.

The survey methodology followed that of the 2003 survey, which is similar to the 2013 national survey described above, but each visit was for a duration of 60, rather than 75, minutes. Surveyors recorded the same basic weather variables (cloud cover, wind and rainfall) as described for the 2013 national survey and moon phase data were acquired and categorised in the same manner.

Additional weather variables were obtained from national-scale datasets. Daily rainfall data were obtained from the Centre for Ecology and Hydrology's (CEH) CEH-GEAR dataset (Tanguy *et al.* 2016) and,

for each survey, used to calculate the total rainfall on the day of the survey and total rainfall for the two weeks preceding the day of the survey. For the same time periods, minimum temperature was extracted from the Met Office's UKCP09 dataset (Met Office 2017). Both datasets are interpolated raster maps based on observations from national Met Office weather stations. Collinearity between these variables and 'date' (day number) was assessed using Pearson's correlation tests and scatter plots.

Data were analysed using a GLMM with a Poisson distribution and a logarithmic link function. The analysis was conducted in R (R Development Core Team 2019) using the lme4 package (Bates *et al.* 2015). The number of woodcock registrations recorded on each survey was specified as the dependent variable. The fixed effects were log(minimum temperature) on the survey day and during the preceding two weeks, the total rainfall in the two weeks preceding the survey, moon phase on the evening of the survey, and cloud cover and wind during the survey as recorded by the surveyor. Site, nested within year (with year as a categorical variable), was specified as a random effect.

Logged temperature values were chosen because earlier versions of the GLMM demonstrated a positive but weak relationship between roding activity and the two week temperature variable. There were ecological reasons to expect a non-linear relationship here, as both unusually warm and unusually cool weather could inhibit roding. Rain recorded during the survey period by surveyors and daily rainfall variables were not included because of the very heavy bias towards

surveys experiencing no rain at all (n = 838/886) which prevented earlier models from converging.

A maximal model was simplified in a backward stepwise manner with the effect of each term's removal gauged using chi-square tests. P-values are presented from the minimum adequate model and produced by the *glmer* function using a Wald's test (Bates *et al.* 2015).

5.2.3 Tracking roding male woodcock using GPS-loggers

Male woodcock were caught in mist-nets during April-June 2015-2017 (Heward *et al.* 2017), at three large woodland sites in Nottinghamshire (See Section 7.2.1 for more details of site characteristics). These sites are located at the southern end of the 'Northern England' region (Fig. 5.1). Woodcock were sexed based on behaviour; those observed roding immediately prior to their capture could be confirmed as males. When roding behaviour was not observed, individuals were sexed based upon the appearance of the cloacal protuberance or presence of a brood patch, and using biometric data according to Ferrand & Gossmann (2009). Male woodcock were tagged with a 7.5g GPS-logger/VHF radio-tag (PinPoint 50 GPS (Biotrack Ltd, Wareham, UK) + 5.0g radio-tag (Perdix Wildlife Supplies, Stratford-upon-Avon, UK) which was attached to a small patch of skin on the rump using cyanoacrylate glue and secured to a small number of surrounding feathers with a gauze mount. These GPS-loggers were programmed to begin recording five days after birds were tagged and then to record 90 locations per evening at one-minute intervals commencing 15 minutes

before sunset. The number of days for which this schedule could be repeated varied between one and six days depending upon the time taken to acquire position fixes and, consequently, the rate of battery depletion. Tags were recovered by recapturing tagged birds or, as was more commonly the case, using the VHF-signal to locate tags once shed. For each evening recorded, tagged individuals were classified as 'roding' or 'non-roding' based on the tracking data from the first 75 minutes of the 90-minute recording period. If birds were in flight for ≥20 minutes of the first 75, or if they flew long wandering paths indicative of display behaviour, they were classified as roding (Cramp *et al.* 1983). Males classified as non-roding clearly differed from this; they moved only for a small portion of the recording period, if at all, and this was always a direct flight between two locations (Fig. 5.2).

Classification and analysis based on the first 75 minutes of the recording period excludes post-roding commuting flights to nocturnal foraging sites; the only other long-distance movements made during the tag's 90-minute recording period. Male woodcock may produce their roding call whilst making these commuting flights (Cramp *et al.* 1983) but they typically occur after the end of a standard 75-minute roding survey visit. Commuting flights are usually long, direct flights to arable fields, heaths or pastures outside of the bird's typical display area and are unlikely to account for a significant proportion of observations made by surveyors.

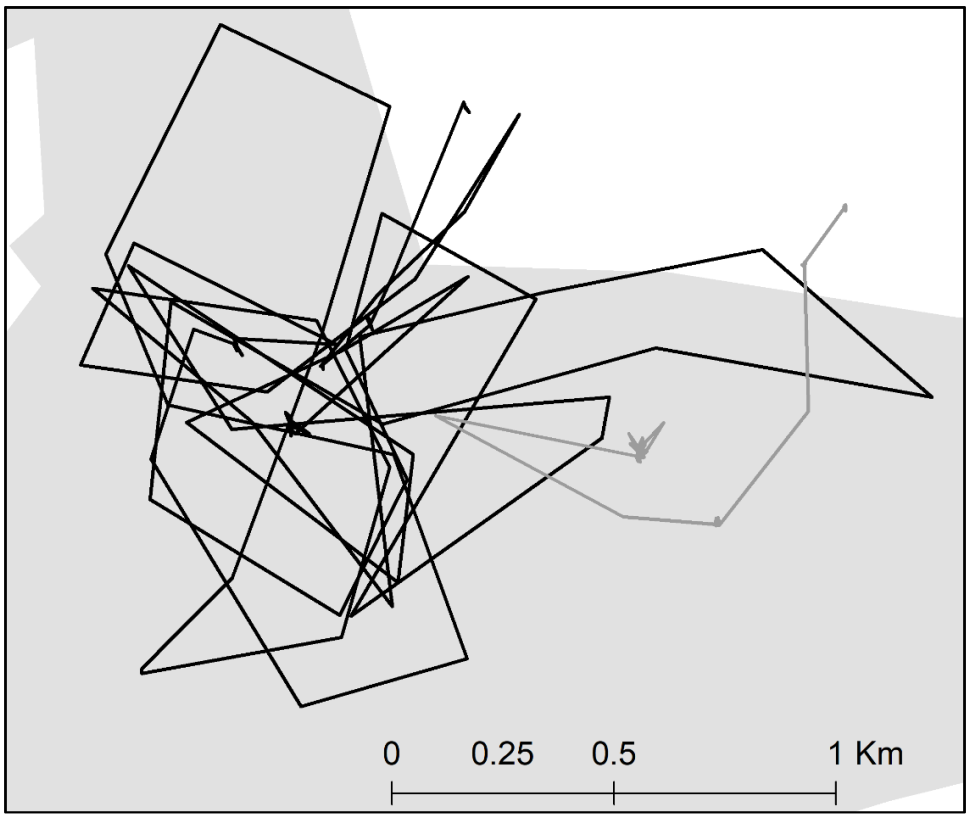


Figure 5.2 Map showing typical 'roding' (black) and 'non-roding' (grey) location data from two woodcock tagged with GPS-loggers. Each example shows one 90-minute tracking period. The grey shaded area shows the extent of woodland.

Weather data were obtained from the UK Met Office's observation station at Watnall, UK (Lat: 53.005N Long: 1.250W) approximately 20 km from the tracking locations (the locations of weather stations are selected to be representative 'of an area up to several tens of km from the station' (Met Office 2018)). From hourly weather observation data (Met Office 2006b), I calculated minimum temperature, mean wind speed and mean cloud cover (oktas) for a four-hour period around sunset. Weather measurements are taken on the hour, and the period was set so that the start of the fourth hour began at the time closest to sunset (i.e. 2100h or 2200h). From hourly rainfall data (Met Office 2006a), I calculated total rainfall for a 12-hour

period, with the twelfth hour beginning as close as possible to sunset. A 12-hour period was chosen for rainfall to maximise variation within this variable, repeating the same four-hour period used for temperature, wind and cloud would have meant a large majority of rainfall values were zero. A ‘moon’ variable recorded the number of days between the evening in question and the nearest full moon using data from an online moon phase calculator (Somacon.com 2011). Collinearity between these five variables and ‘date’ (day number) was assessed using Pearson’s correlation tests and scatter plots.

The correlates of ‘roding’ and ‘non-roding’ behaviour were assessed using a binomial GLMM with a logit link function in R’s lme4 package. Each males’s status as ‘roding’ or ‘non-roding’, on each evening it was tracked, was used as the depdent variable with individual (ring number) specified as a random effect. A maximal model containing minimum temperature, rainfall, wind, cloud and moonlight was run, including an interaction between cloud and moon phase.

For woodcock that roded, the time at which roding began and ended was extracted for each evening they were tracked. If the start or end of roding was not recorded i.e. it fell outside of the 90-minute recording period, the limits of the recorded period were used and, hence, the values presented here represent minimum estimates. While this may truncate extreme start and end times, it was deemed more representative than removing these data, as this would selectively remove data relating to more active individuals. These results are presented as averages of each individual’s average, meaning that each

bird has equal influence on the result, regardless of the number of nights it was tracked for.

A GLMM with a Poisson distribution and logarithmic link compared the relationship between the time that roding began and the same five explanatory variables: cloud cover, minimum temperature, rainfall, windspeed and moon phase (including an interaction between moon phase and cloud). The bird's identity (ring number) was a random effect. In an otherwise identical GLMM, end time replaced start time as the dependent variable.

GLMMs were simplified by sequentially removing non-significant variables, selecting the most appropriate model using chi-square tests. Model fit was assessed visually using Pearson residual plots. P-values are taken from the most appropriate model and produced by the *glmer* function using a Wald test (Bates *et al.* 2015).

5.3 Results

5.3.1 2013 Breeding Woodcock Survey: timing of roding behaviour

Of the 823 randomly selected sites surveyed in 2013, 273 (33%) were occupied by woodcock (≥1 registration). There were no sites classified as occupied by a 75-minute survey visit that would have been classified as unoccupied by a 60-minute survey visit.

On average, the first registration was recorded 4.1 ± 12.1 minutes (1 SD) after sunset. The time of first registration was affected by visit day number (*Est* = -0.775 ± 0.089, $P < 0.001$), wind (Beaufort

scale 0-1 vs 2 *Est* = 0.164 ± 0.067, *P* = 0.015) and cloud cover (0-33% vs 67-100% cloud cover *Est* = -0.441 ± 0.039, *P* < 0.001). The first registration was recorded, on average, 7 minutes earlier on evenings when cloud cover was between 66 and 100% (1.0 ± 9.9 minute before sunset) compared to 0-33% (6.0 ± 12.0 minutes after sunset) (Fig 5.3). Only moon phase was dropped from the initial GLMM (Table 5.3). The relationship between start time and cloud did not interact with moon (X^2_1 =0.568, *P* = 0.451), and this interaction was also omitted from the final model.

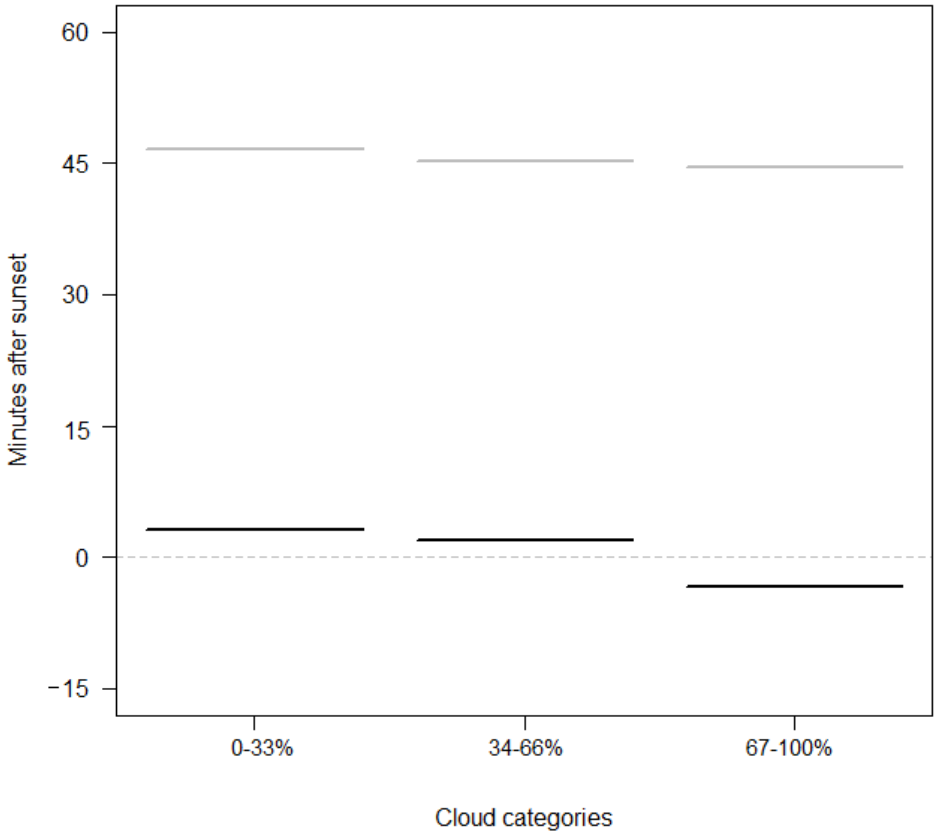


Figure 5.3 The effect of cloud cover on the time at which the first woodcock registration was recorded (black) and last woodcock registration was recorded (grey). The values are plotted from back-transformed model coefficients, fixing all other variables at their mean values (wind, day number). The graph is plotted using R package 'visreg' (Breheny & Burchett 2015) *which does not produce error bars for models containing random effects.*

Table 5.2 Time of the first woodcock registration was compared to four variables using a GLMM. The maximal model (left half of the table) suggested there was a significant relationship with all variables other than moon. This was supported by stepwise regression. Removal of the moon variable had no significant effect on the model's explanatory power, but removal of the next least significant term, wind, did.

	Maximal GLMM			Stepwise model selection and effect of variable removal		
	Est	SE	*P*	Order	X^2	*P*
Intercept	3.167	0.068	<0.001			
Moon	-0.032	0.035	0.362	1st	0.82	0.364
Day number	-0.754	0.092	<0.001			
Wind 1	0.168	0.674	0.013	(2nd)	9.19	0.010
Wind 2	-0.038	0.034	0.264			
Cloud 1	0.060	0.040	0.132			
Cloud 2	-0.438	0.040	<0.001			

Table 5.3 Time of the first woodcock registration was significantly correlated with three variables. This final model was produced using the stepwise simplification of the starting model described in Table 5.2

	Est	SE	*P*
Intercept	3.200	0.058	<0.001
Day number	-0.775	0.089	<0.001
Wind 1	0.164	0.672	0.014
Wind 2	-0.042	0.034	0.206
Cloud 1	0.063	0.040	0.111
Cloud 2	-0.441	0.039	<0.001

The last bird was observed, on average, 46.5 ± 10.0 minutes (1 SD) after sunset and the timing of this final registration did not appear to vary with weather or day number (Table 5.4). In the maximal model, there appeared to be a significant effect of wind speed (Beaufort scale 0-1 vs 2 *Est* = 0.068 ± 0.034, *P* = 0.043), but this was not supported in the final model.

Table 5.4 Time of the last woodcock registration was compared to four variables using a GLMM. The maximal model (left half of the table) suggested a possible relationship with wind, but stepwise removal of variables (right half of table) found that no model was significantly different to the null model.

	Maximal GLMM			Stepwise model selection and effect of variable removal		
	Est	SE	*P*	Order	X^2	*P*
Intercept	4.127	0.027	<0.001			
Moon	-0.021	0.019	0.249	1st	0.26	0.6
Day number	-0.032	0.018	0.075	2nd	0.758	0.384
Wind 1 Wind 2	0.068 -0.003	0.034 0.016	0.043 0.869	3rd	4.274	0.118
Cloud 1 Cloud 2	0.009 -0.033	0.018 0.045	0.609 0.466	4th	3.658	0.16

Duration of roding ranged from 36.8 ± 13.7 minutes in early May to 44.2 ± 12.7 minutes (1 SD) in late May (Fig. 5.4). Roding period duration in June was similar to late May (early June: 43.4 minutes, late June: 42.7 minutes) but may have been truncated by the limits of the survey period. The total number of woodcock registrations was higher when the duration of the roding period was longer (n = 470, *Est* = 0.15 ± 0.01, $p < 0.001$) and this remained true when the five-registration threshold was raised to ten (n = 262, *Est* = 0.10 ± 0.02, $p < 0.001$) and 15 registrations (n = 133, *Est* = 0.06 ± 0.02, $p = 0.004$). The number of woodcock registrations recorded in the final 15 minutes of the count period varied between zero and nine registrations.

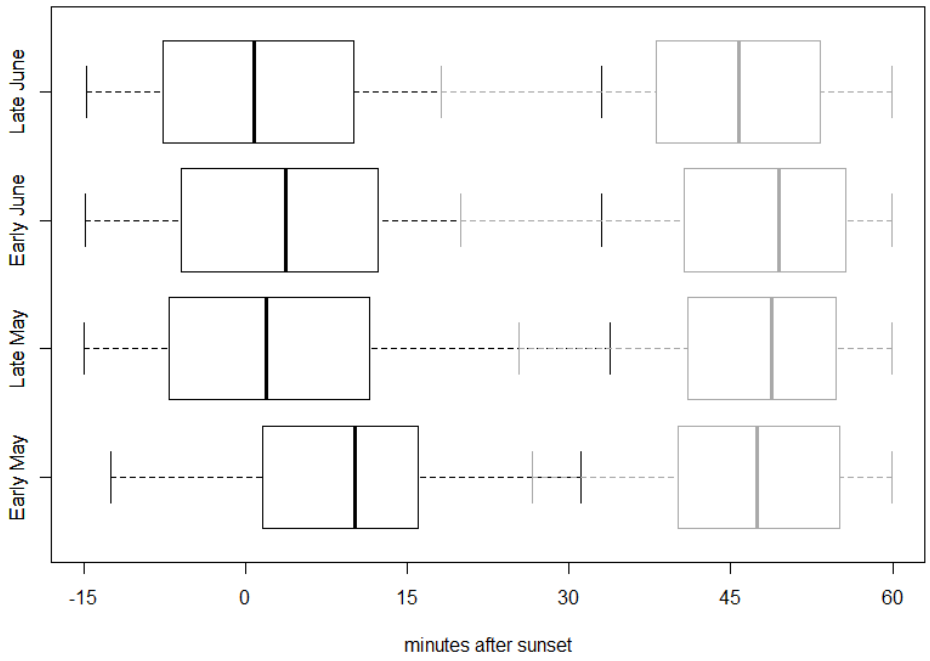


Figure 5.4 Variation in the time of first registration (black) and last registration (grey) during 75-minute roding woodcock surveys. Each boxplot displays the mean (bold central bar) ± 1 SD (box limits) and the minimum and maximum values (capped dashed lines). The four date categories (1st May–15th May, 16th May–31st May, 1st June–15th June, 16th June–30th June) are used to illustrate seasonal variation but a continuous 'day number' variable was used in analyses.

On average, these accounted for 12.6 % of registrations per survey (range = 0 - 80%). Woodcock were recorded in the final 15 minutes on 59.7 % of survey visits. There was a significant relationship between the proportion of registrations made in the final 15 minutes and cloud cover (33-66% cloud: *Est* = -0.29, *p* = 0.029, 67-100% cloud: *Est* = -0.29 ± 0.13, *p* = 0.028), with the proportion of observations decreasing on cloudy evenings. Stepwise regression from a maximal model successively removed the non-significant variables of moon (X^2_1 =0.0132, *P* = 0.909), day number (X^2_1 =0.187, *P* = 0.665), and wind (X^2_1 =4.541, *P* = 0.103).

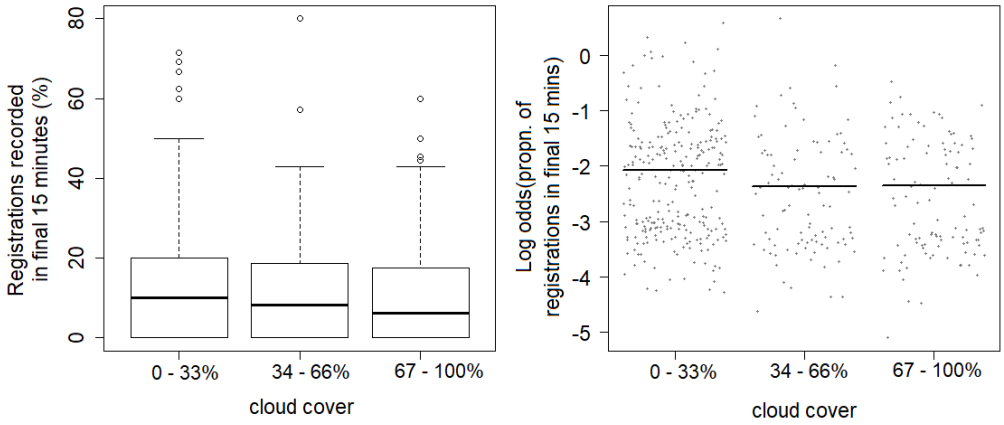


Figure 5.5 The relationship between the three cloud categories and the proportion of woodcock registrations that were recorded in the final 15 minutes of the survey. The proportion of registrations are expressed as raw percentages (left) and using model coefficients from a binomial GLMM that accounts for differences between sites (right).

5.3.2 Repeat breeding woodcock surveys: the broader influence of weather

Only one of the weather variables, minimum temperature in the two-week period preceding the survey, showed a high degree of collinearity with date (r = 0.67). Date is not included in the model, but it is possible that minimum temperature is collinear with other unmeasured variables that vary on a temporal scale (e.g. stage of breeding). The cloud, wind, rain and temperature variables showed no strong collinearity with one another but there was moderate collinearity between the two measures of minimum temperature (daily and in the two weeks preceding the survey) (r = 0.68) (Table 5.5).

The number of woodcock registrations recorded during repeat breeding woodcock surveys correlated with four weather variables: log(minimum temperature) in the two weeks preceding the survey, total

Table 5.5 Collinearity of weather variables used in repeat breeding woodcock survey GLMM. Cloud and wind variables were classified by surveyors, whereas rain and temperature measures were taken from Met Office datasets for a given period preceding the survey.

	Year	Day of the year	Wind (3 categories)	Cloud (3 categories)	Total Rain (preceding 2 weeks)	Min. temp (preceding 2 weeks)
Log min. temp (on survey day)	-0.12	**0.52**	-0.14	-0.058	-0.22	**0.68**
Log min. temp (preceding 2 weeks)	-0.14	**0.67**	-0.15	-0.067	-0.20	
Total Rain (preceding 2 weeks)	0.043	-0.005	0.01	0.057		
Cloud (3 categories)	0.039	0.006	0.000			
Wind (3 categories)	0.47	-0.089				
Day of the year	0.013					

rainfall in the two weeks preceding the survey, and the wind speed and cloud variables recorded by surveyors. Stepwise simplification from the starting model removed daily temperature, followed by moon (Table 5.6). The relationship with logged temperature in the two weeks preceding the survey was positive (*Est* = 0.24 ± 0.084, $p = 0.004$) (Fig 5.6). The relationship with rainfall in the two weeks preceding the survey was also positive (*Est* = 0.03 ± 0.005, $p < 0.001$) (Fig 5.6). The number of woodcock registrations was lower when wind was classified as 'light' (*Est* = -0.15 ± 0.04, $p < 0.001$) or 'moderate' (*Est* = -0.16 ±

0.04, $p < 0.001$) compared to 'still'. The relationship with cloud was also negative; counts were lower when cloud cover was categorised as '67-100%' compared to '0-33%' (*Est* = 0.08 ± 0.03, $p = 0.018$) (Fig 5.7).

Table 5.6 The number of woodcock registrations was compared to six variables using a GLMM. The maximal model (left half of the table) suggested that daily minimum temperature and moon were the only variables that did not significantly correlate with the number of woodcock registrations. This was supported by stepwise simplification of the model (right half of the table).

	Maximal GLMM			Stepwise model selection and effect of variable removal		
	Est	SE	*P*	Order	X^2	*P*
Intercept	1.838	0.093	0.000			
Moon	0.018	0.030	0.554	2nd	0.31	0.578
Log(temp daily)	0.040	0.063	0.524	1st	0.40	0.527
Log(temp 14 days)	0.208	0.098	0.034	(3rd)	8.28	0.004
Rainfall 14 days	0.033	0.005	0.000			
Wind 1	-0.147	0.037	0.000			
Wind 2	-0.151	0.041	0.000			
Cloud 1	0.020	0.037	0.591			
Cloud 2	-0.094	0.035	0.006			

Table 5.7 The number of woodcock registrations was significantly correlated with four variables. This final model was produced using the stepwise simplification of the starting model described in Table 5.6.

	Est	SE	*P*
Intercept	0.244	0.084	0.004
Log(temp 14 days)	0.032	0.005	0.000
Rainfall 14 days	-0.152	0.036	0.000
Wind 1	-0.153	0.040	0.000
Wind 2	0.020	0.037	0.588
Cloud 1	-0.094	0.035	0.007
Cloud 2	0.244	0.084	0.004

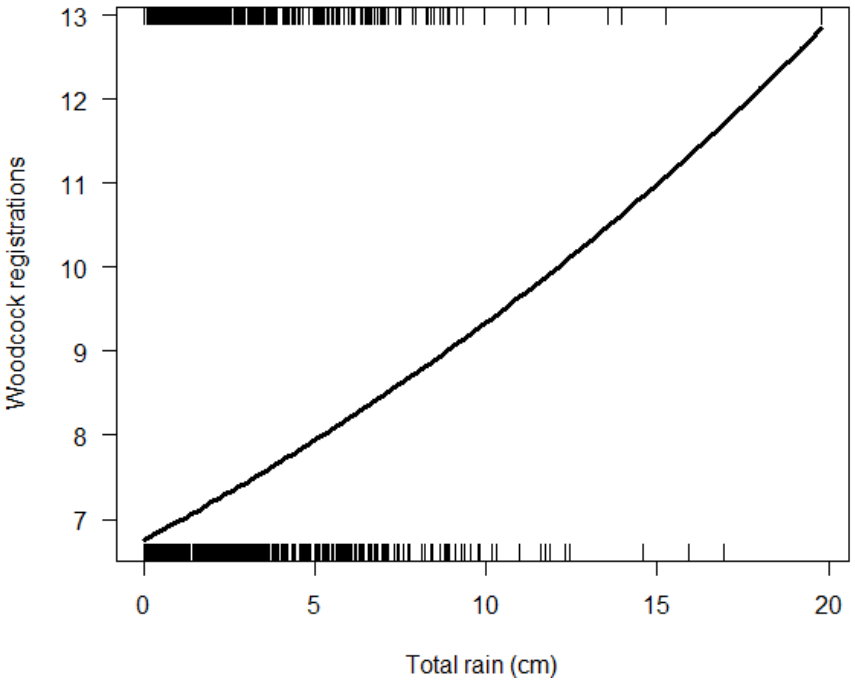


Figure 5.6 The relationship between total rainfall in the fortnight preceding a survey and the number of woodcock registrations, expressed on the original scale of the response variable. The graph is plotted from model coefficients and all other variables within the final model (log min temperature, cloud cover and wind) are fixed at their mean values.

5.3.3 Tracking roding male woodcock using GPS-loggers

GPS-loggers recorded usable data from 27 individual male woodcock, producing 69 'bird-days' of roding data. Of these, 16 individuals were tracked while roding, producing 47 bird-days of roding data. There were three occasions when roding began before the tag started recording, with each instance associated with a different individual. On four occasions, involving four different birds, woodcock were still roding when the tag reached the end of its recording period. There was no occasion where both the start and end of roding was outside of the 90-minute roding period on the same bird-day.

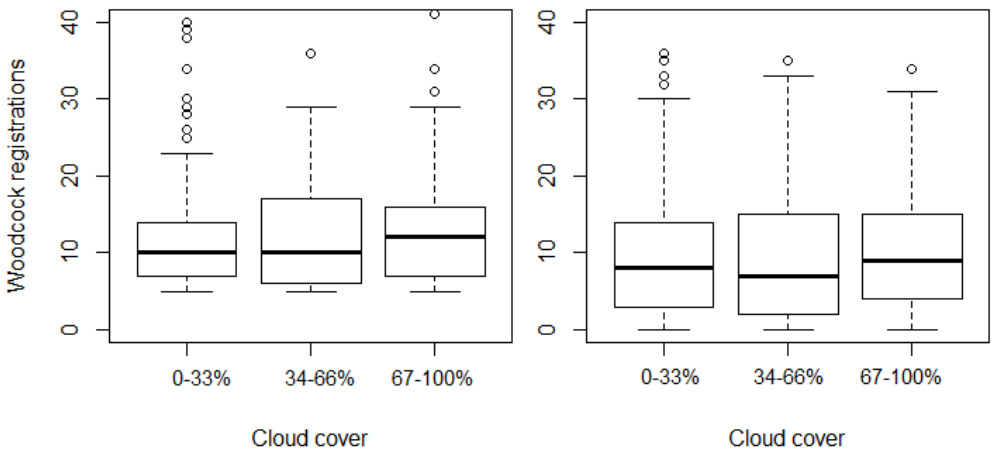


Figure 5.7 Relationship between the number of woodcock registrations and the three cloud categories. The graphs are plotted from the raw Breeding Woodcock Survey 2013 data (left) and the raw repeat breeding woodcock survey data (right). When included in the respective GLMMs, cloud data showed significant correlations with woodcock registrations but with opposing trends. In the 2013 data, cloudier evenings were associated with longer roding periods, which in turn was related to more woodcock activity. In the repeat survey data fewer woodcock were recorded on cloudier nights.

On average, each individual male woodcock started roding 5.3 ± 12.7 minutes (1 SD) after sunset and ceased roding 61.7 ± 9.1 minutes (1 SD) minutes after sunset. The mean duration of the roding period, across all individuals was 56.2 ± 16.2 minutes. The latest that any woodcock began roding was 28 minutes after sunset. On 38 of the 43 nights for which the end of roding was recorded (88%), roding finished later than 45 minutes after sunset i.e. after the end of a 60-minute count period. On 25 of these 43 nights (58%), tagged birds continued roding beyond 60 minutes after sunset i.e. the end of a 75-minute survey.

The likelihood that woodcock exhibited display behaviour ("roding" vs. "not roding") did not correlate with any of the five weather variables tested (Table 5.8). There were, however, several variables that showed correlations with the timing of their display activity.

Table 5.8 The likelihood that tagged woodcock engaged in roding behaviour was compared to five weather variables using a GLMM. The maximal model (left half of the table) showed that none of the factors had any correlation with the likelihood of roding, which was borne out by stepwise regression of this model (right half of the table).

	Maximal GLMM			Stepwise model selection and effect of variable removal		
	Est	SE	*P*	Order	X^2	*P*
Intercept	14.702	11.299	0.193			
Cloud cover	-0.010	0.538	0.985	1st	0	1
Rain	-0.119	1.131	0.928	2nd	0.009	0.925
Min. temp	-0.300	0.564	0.595	3rd	0.319	0.572
Wind	-0.332	0.550	0.547	4th	0.231	0.630
Moon phase	0.245	0.474	0.604	5th	0.248	0.168

Table 5.9 The time that tagged woodcock started displaying compared to five environmental variables. The maximal model (left half of the table) informed the order in which variables were removed during model simplification (right half of the table).

	Maximal GLMM			Stepwise model selection and effect of variable removal		
	Est	SE	*P*	Order	X^2	*P*
Intercept	3.868	0.282	<0.001			
Cloud cover	-0.088	0.411	0.831			
Rain	-0.030	0.013	0.022			
Min. temp	-0.693	0.205	0.001	(4th)	6.135	0.013
Wind	-0.015	0.019	0.405	3rd	0.717	0.397
Moon phase	0.246	0.302	0.415	2nd	0.002	0.968
Cloud:moon	-0.525	0.463	0.257	1st	1.276	0.259

Table 5.10 The time that tagged woodcock started displaying correlated with three variables. This final model was produced using the stepwise simplification of the starting model described in Table 5.9.

	Est	SE	*P*
Intercept	3.941	0.234	<0.001
Cloud cover	-0.515	0.139	0.000
Rain	-0.031	0.013	0.015
Min. temp	-0.643	0.173	0.000

Stepwise simplification of the 'start time' model removed the cloud:moon interaction, followed by moon phase and then windspeed (Table 5.9). Three significant variables were retained. Roding began earlier on evenings with greater cloud cover (*Est* = -0.52 ± 0.13, $p < 0.001$) and following days with greater rainfall (*Est* = -0.03 ± 0.01, $p = 0.015$). Roding also appeared to begin later when the minimum temperature was lower (*Est* = -0.64 ± 0.17, $p < 0.001$), although this is the one weather variable for which there was collinearity with date (r = 0.53). Stepwise simplification of the 'end time' model removed the wind speed, rain, then temperature variables (Table 5.11) retaining only the interaction between moon phase and cloud. This significant interaction (*Est* = -0.44 ± 0.22, $p = 0.030$) suggest that roding finishes later on evenings closer to the full moon, but only when cloud cover is low. On cloudy nights, there is no strong relationship with moon (Fig 5.8).

Table 5.11 The time that tagged woodcock finished displaying compared to five environmental variables. The maximal model (left half of the table) informed the order in which variables were removed during model simplification (right half of the table).

	Maximal GLMM			Stepwise model selection and effect of variable removal		
	Est	SE	*P*	Order	X^2	*P*
Intercept	4.505	0.134	<0.001			
Cloud cover	-0.392	0.183	0.032			
Rain	0.006	0.004	0.151	2nd	0.170	0.192
Min. temp	0.111	0.067	0.096	3rd	0.980	0.322
Wind	0.003	0.006	0.628	1st	0.231	0.631
Moon phase	-0.342	0.114	0.003			
Cloud:moon	0.417	0.202	0.039	(4th)	5.206	0.023

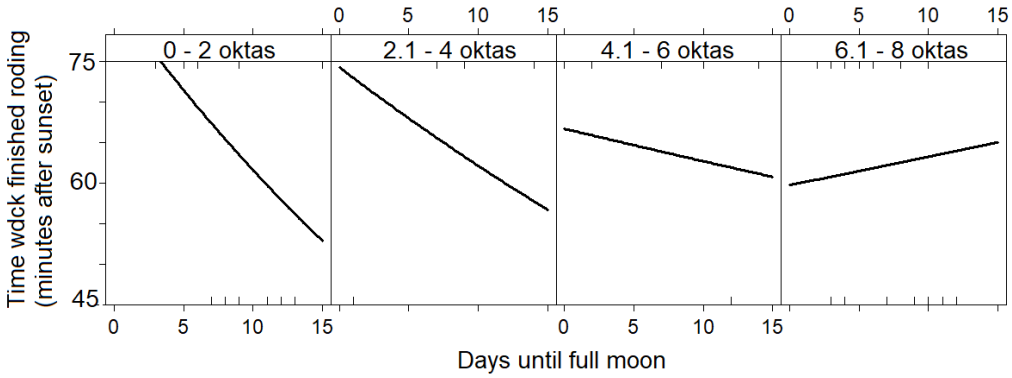


Figure 5.8 The interaction between the time that tagged woodcock finished roding (minutes after sunset), moon phase and cloud. Male woodcock roded later on nights nearer the full moon, but not on cloudy nights.

Table 5.12 Summary of the output of seven GLMMs. Only statistically significant results are given an estimated trend symbol. The abbreviations 'n.s.' = non-significant and 'NA' = not assessed.

		Wind	Cloud	min. temp (day)	min. temp (14 days)	Total rain (day)	Total rain (day)	Moon
2013 BREEDING WDCK SURVEY	Start time	+	-	NA	NA	NA	NA	n.s.
	End time	n.s.	n.s.	NA	NA	NA	NA	n.s.
	Registrations final 15 mins	n.s.	-	NA	NA	NA	NA	n.s.
REPEAT BREEDING WDCK SURVEYS	Number of registrations	-	-	n.s.	+	NA	+	n.s.
WDCK TRACKING DATA	Roding vs. non-roding	n.s.	n.s.	n.s.	NA	n.s.	NA	n.s.
	Start time	n.s.	-	-	NA	-	NA	ns
	End time	n.s.	interacts w. moon	n.s.	NA	n.s.	NA	interacts w. cloud

5.4 Discussion

More than half of sites recorded additional registrations when a 75-minute, rather than a 60-minute, survey period was employed. This was to be expected, as the 60-minute survey period was designed to

capture the peak of roding only (on average, 83% of woodcock passes (Hoodless *et al.* 2006)). Its ability to do this consistently, however, may be undermined by the fact that the period during which woodcock rode is not fixed in relation to sunset and as such, the actual percentage of roding woodcock passes detected appears to vary in relation to weather.

Both the 2013 survey data and the GPS-tracking data suggested some correlation between cloud cover and the timing of roding although the latter suggested this interacts with moon phase. This is likely to be linked to dusk light levels. Certain light levels may be selected for roding because they reduce the risk posed by aerial predators (Mougeot & Bretagnolle 2000; Prugh & Golden 2014) or because the woodcock, as a nocturnal species, is able to reduce acoustic competition with other bird species by displaying during darker conditions (Cuthill *et al.* 2002). Light levels were found to be an important cue for display in the closely-related American woodcock *Scolopax minor* (Bergh 2011). The proportion of registrations made in a visit's final 15 minutes increased significantly on clear nights, supporting a shift in the peak of display behaviour.

The analysis of the repeat survey data, however, appears to contradict the conclusions drawn from the other two datasets. If greater cloud cover encourages woodcock to begin roding earlier, as suggested by the analyses of roding timings, we should expect to record a greater number of registrations on cloudier nights. This is not because woodcock rode more intensely on cloudy nights, but because

on clear nights, a larger proportion of the evening's roding occurs after the survey has finished. The repeat survey data did not support this. In fact, the analysis of the repeat woodcock surveys found that woodcock counts tended to be lower on cloudy nights. One potential cause of this may be that on very cloudy nights some roding occurs before surveys begin and early passes of roding birds go unregistered. Another possible explanation may be that the repeat count survey dataset, which refers to surveys conducted 2003-2015, capture a greater degree of variation than the 2013 Breeding Woodcock Survey and GPS-logger data which only refer to one and two years respectively.

Total rainfall during the day preceding a dusk roding survey did not correlate with the number of woodcock registrations recorded. This is probably because surveyors were instructed not to conduct roding surveys during heavy or persistent rain, and suitable survey conditions were more likely to follow dry days, reducing the degree of variation in the model. This requirement of the survey method is based on prior studies that found heavy rain inhibited roding, which seems plausible given that rainfall is likely to reduce signal transmission (Lengagne & Slater 2002). Nevertheless, the GPS-tracking data only shows a relationship between roding timing and rainfall on the survey day, not with the overall likelihood that woodcock displayed.

Over longer time periods there was a clear positive relationship between the number of woodcock registrations and rainfall during the two weeks prior to the survey. Lower rainfall in spring or summer is likely to drive the soil-dwelling invertebrates on which woodcock feed

deeper into the soil (Gerard 1967; Hoodless & Hirons 2007) and poorer foraging conditions may leave woodcock with less energy to expend on display during dry spells.

During roding surveys in which the wind was recorded as a light or moderate breeze, fewer woodcock were encountered than those that were still. The GPS-tracking data did not show that tagged woodcock were any less likely to rode on windier nights, which may imply environmental noise is impeding detection by surveyors (Alldredge *et al.* 2007). In the North American Singing Ground Surveys however, reduced American woodcock activity during stronger winds was attributed to a change in bird behaviour (Blankenship 1957; Goudy 1960; Bergh 2011) rather than just detectability. The study presented here only considers the likelihood of roding occurring and the timing that it takes place but does not attempt to measure more subtle changes in behavior. It could be that woodcock fly lower when displaying in strong winds, limit themselves to more sheltered areas, or take longer breaks during displaying.

Minimum daily temperature correlated with the time that GPS-tagged woodcock started roding, but not the time that they finished, suggesting that the roding period is shorter on colder evenings. There are several possible explanations as to how temperature may influence roding behaviour, but given the collinearity between temperature and date, it is just as likely to be the result of an underlying seasonal relationship unrelated to weather (as observed in Hirons 1983). Hirons (1983) suggests that temperature only has a strong influence on roding

behaviour during March. Temperature is a cue for breeding behavior in other birds (Visser *et al.* 2009), so may determine the period of display on a seasonal basis by prompting the development of breeding physiology, but not on a daily basis once breeding condition is reached. This is unlikely to have a strong influence on the tracking data presented here as they relate to the months of April, May, June after this development is already complete.

5.4.1 Implications for roding surveys

The national Breeding Woodcock Survey uses a calibration equation to estimate male woodcock density at each survey site. These values contribute towards estimates of regional and national population size. The calibration equation is based on Hoodless (2008), in which analysis of vocal individuality found a consistent relationship between the number of registrations recorded in a 60-minute survey and the actual number of displaying males. The study presented here confirms that all displaying males will be active during part of the standard 60-minute survey and thus, are accounted for by this method. But my study also suggests that subtle changes in some weather variables can cause a shift in the period of woodcock activity, which is likely to have an influence on the relationship between the number of registrations and the number of individuals present. Changing to a 75-minute survey window would mean a larger proportion of the display activity at a site is captured, regardless of the weather, and by doing so the calibration equation would include a smaller amount of error. It would, however,

mean that the equation must be recalculated for the extended survey period. While this would take a considerable amount of effort, the process could be used to gather more data on the influence of weather variation and other factors, such as region or woodland extent.

As well as the weather during the survey period, there appears to be an impact of long-term weather conditions prior to the survey, particularly extended dry spells. Another existing measure that may help counter this is the requirement for three visits per site to be completed. Estimates of local density are derived from the maximum count, rather than the mean, which should counter the effects of sub-optimal weather providing at least one visit is conducted during ideal conditions. Our findings reiterate the need for all three visits to be completed and the exclusion of sites that do not receive them all. This has not always been the case previously (Heward *et al.* 2015). Ensuring three visits are always completed at these remote sites may require visits from paid fieldworkers rather than relying on volunteers.

At present, it is specified that the three visits must be completed one week apart. Extending this interval to ten days or two weeks would distribute the three visits more broadly through the survey season and perhaps lessen the influence of long-term weather events, but again, the practical implications of more restrictive survey methodology must be considered.

When unfavorable weather conditions become particularly protracted or severe, an effect on survey results may be driven by population change as well as a reduction in display behaviour. This

would most likely occur because of reduced breeding success (Guzmán & Arroyo 2015; Selås 2006) rather than an impact upon adult survival, and would probably therefore manifest in the following year. It would be possible to shed more light on these types of weather events by reanalysing annual data to include weather variables based on the entire breeding season and by incorporating measures of conditions experienced in the previous breeding season and the intervening winter (Sánchez-García *et al.* 2018). This would probably require even longer-term data than are currently available as such severe weather events are rare.

There have only been two large-scale national surveys of breeding woodcock in the UK to date and these could be biased by the prevailing weather in the years they were conducted. All evidence points towards a decline in the British breeding woodcock population that is real and long-term (Heward *et al.* 2015; Balmer *et al.* 2013; Hewson & Noble 2009), but its true scale will become clearer with each repeat of the national survey as the longer time-series reduces the influence of weather in any single year. In the meantime, the complementary data provided by conducting repeat surveys at a subsample of the national survey's sites, such as those analyzed here, give some impression of annual variability in roding counts in response to weather. Continuing to account for weather in survey methodology and improving the way in which this is done will help strengthen the results of future surveys and management policies based upon them.

6 EXPLORING THE POTENTIAL EFFECT OF GPS-TRACKING DATA ON POPULATION ESTIMATES: A CASE STUDY OF THE EURASIAN WOODCOCK

6.1 Introduction

To accurately assess a species' population size, certain aspects of its basic biology must be quantified. Estimates of population size often require a measure of mean home range size or density and are improved by an understanding of how these parameters vary with habitat. Animal tracking can directly inform conservation by improving our understanding of a species' resource requirements (Quigley 1992; Kramer & Chapman 1999; Linnell *et al.* 2001), but less attention has been given to the ways in which tracking data can be used to improve monitoring through better estimates of population size and trend.

Calculating seemingly simple statistics such as home range size from spatial point data is complicated by the diverse array of methods that are available (Worton 1989; Larkin & Halkin 1994; Jennrich & Turner 1969; Calenge 2015), each of which come with their own set of specific parameters to be selected, often without clear objective starting points (Laver & Kelly 2008; Worton 1989). These decisions can have a large influence on final estimates of home range, but the effect of this on the interpretations of survey data and calculation of population estimates is rarely acknowledged.

The interdependence of individual range size and population estimates is exemplified by current monitoring of the Eurasian

woodcock *Scolopax rusticola.* The species' cryptic behaviour and typically low breeding densities mean that traditional diurnal bird surveys do not accurately reflect breeding woodcock abundance (Hoodless *et al.* 2009) but an established species-specific method, based on counts of displaying males, yields more representative results (Chapter 2). During their roding displays, male woodcock compete to attract the attention of females on the ground by flying long, overlapping routes while producing a distinctive two-part call (Hoodless 1995). The behaviour is believed to be non-territorial and is similar to a very dispersed form of lek (Hirons 1980). The areas of their display grounds are not necessarily analogous to home-ranges (Hirons 1983), but their size and arrangement are relevant to estimates of abundance given that this behaviour is the basis of the survey method (Ferrand 1993; Hoodless *et al.* 2006).

Estimates of roding ground size could potentially influence population estimates in two ways: they are relevant when selecting a minimum distance between sites to prevent double-counting (Hoodless *et al.* 2006); and they inform the way in which density is calculated based on count data from a static point (Hoodless *et al.* 2009). Both require some quantification of the individuals' movements during the display period to relate a measure of abundance at a single geographic location to an estimate of density across a sample unit of a given area.

Woodcock are one of many bird species for which species-specific census methods are the only viable means of accurately assessing population size and trend (Kålås 2000; Aldridge & Brigham

2003; Alonso *et al.* 2003; Conway *et al.* 2010; Hayhow *et al.* 2015; Seamans & Rau 2017; Worthington-Hill & Conway 2017). As is often the case, existing field studies have informed survey design and interpretation (Hoodless *et al.* 2009), but the number and scale of relevant studies are limited (Hirons 1980; Ferrand 1983).

Comprehensive biological data do not exist for every species and it is often justifiable to make reasonable assumptions based on what little information is available. Ideally these assumptions should be reassessed, especially when new technology allows their refinement. Unless it casts serious doubt over integral aspects of the original survey design, new information does not necessarily preclude the use of existing survey data but may allow for more accurate re-interpretation.

GPS-telemetry allows more accurate, more targeted and less biased forms of tracking than long-established techniques such as radio-telemetry (Tomkiewicz *et al.* 2010). This chapter uses GPS-telemetry to provide more accurate measures of roding ground size and the consistency of the roding ground covered. Different methods for deriving roding range size from spatial point data are explored, using three well-known methods: minimum convex polygons (e.g. Mohr 1947), localised convex hulls (Getz *et al.* 2007) and Brownian bridge kernels (Horne *et al.* 2007). I calculate the potential effect that these tracking data, and the different methods of analysing them, have on existing population estimates and describe the implications for future survey design.

6.2 Methods

6.2.1 Tracking male woodcock

Roding woodcock were tracked in three woods in Nottinghamshire, UK: Birklands Forest (8.4 km^2), Sherwood Pines (13.3 km^2) and Park Forest (1.6 km^2). All three contain a mixture of woodland types in varying proportions, including mature oak *Quercus robur* – birch *Betula pendula* woodland; young birch thicket; Scots pine *Pinus sylvestris* and Corsican pine *P. nigra* plantation; and diverse mixed-species stands containing a combination of the species mentioned above, alongside sweet chestnut *Castanea sativa*, common beech *Fagus sylvaticus*, red oak *Quercus rubra* and sycamore *Acer psuedoplatanus*. All sites are subject to active management and contain permanent and rotational clearings.

Woodcock were caught in woodland clearings at dusk, between late April and mid-July in 2015, 2016 and 2017 using the vocal lure method described in Chapter 4 (Heward *et al.* 2017). A total of 45 different individuals were caught over the three years, three of which were subsequently recaptured and tagged in a second breeding season.

Because it employs a vocal lure, our capture method produced a biased sex ratio and most tagged woodcock could be positively identified as male. For 63% of birds this was evident from observations of display behaviour immediately prior to capture. Most remaining individuals were sexed based on the appearance of the cloaca, as suggested for other waders (Giunchi & Pollonara 2007), or bill: tail ratio (Ferrand & Gossmann 2009). Seven individuals, for which sex could not

be definitively determined, were assumed to be male because they lacked a brood patch. Woodcock which could be identified as female (n = 3) were not tagged. Woodcock were aged as first-year (birds in their first-breeding season) or adult (≥ 2 breeding seasons) according to Ferrand and Gossmann (2009).

Woodcock were marked with a British Trust for Ornithology (BTO) ring and tagged with a 7.5g combined GPS-logger/VHF radio-tag (PinPoint 50 GPS (Biotrack Ltd, Wareham, UK) + 5.0g radio-tag (Perdix Wildlife Supplies, Stratford-upon-Avon, UK)) attached to the synsacrum using a gauze mount and cyanoacrylate glue. The tag is 2.5 - 3% of a male woodcock's bodyweight during the breeding season (250-300g). Mist-netting, use of a vocal-lure and tagging were conducted by the author under a BTO licence.

GPS-loggers were programmed to allow birds a five-day acclimatisation period from the day of capture. Locations were then recorded at one-minute intervals for 90 minutes during the dusk display period, beginning 15 minutes before sunset. This schedule was repeated each day thereafter, allowing one to six days of recording depending on the rate of battery depletion. Tags were recovered by recapturing the bird, or by locating shed tags using the VHF radio signal. Once recovered, stored data were downloaded.

For each evening recorded, tagged woodcock were classified as 'roding' or 'non-roding' based on their tracking data. This followed the same criteria as described in Section 5.2.3. Classification and analysis were based on the first 75 minutes of the tracking period as commuting

flights to nocturnal foraging sites typically occur after the roding period has finished and their inclusion would result in overestimates of roding ground size.

6.2.2 Calculation of daily roding ground size

Daily roding ground sizes were calculated using three different methods: minimum convex polygons (MCPs), local convex hulls (LoCoHs) (Getz *et al.* 2007) and Brownian bridge (BB) kernels (Horne *et al.* 2007). The term ‘roding ground’ is used here to describe the geographic area within which an individual male woodcock’s display flights occur and is synonymous with ‘roding range’ or ‘display area’. Daily roding ground is the area covered in a single evening, while total roding ground refers to the area covered in the entire period the bird was tracked. ‘Roding path’ is used to describe the route taken by the woodcock on a given night and is estimated by drawing straight lines between consecutive points.

Prior to roding ground size estimation, tracking data were filtered based upon dilution of precision (DOP). DOP does not directly measure the accuracy of a GPS location, but measures the potential for error based upon the satellite geometry. As such, filtering based on DOP reduces the chance of inaccurate points being included in the dataset, but at the potential cost of removing some accurate points in the process. Using recommendations of Lewis *et al.* (2007) as a starting point, I removed locations with DOP values greater than eight, which

retained, on average, 95% of locations per bird-day and resulted in a mean interval between locations of 1.08 minutes ± 0.20 (1 SD).

MCPs are a common method for estimating home range size from geographical point data. An MCP is the smallest possible polygon, with no interior angles exceeding 180°, in which the recorded locations can be contained. They have become a widely accepted standard for home range assessments because they are simple to compute and interpret, but MCPs can be biased if home ranges are irregular or concave shapes e.g. when constrained by habitat extent or boundary features. MCPs were used to estimate daily roding ground size using the adehabitatHR package (Calenge 2006) in R (R Development Core Team 2019). For all roding ground size estimates, analysis was restricted to woodcock classified as 'roding'.

LoCoHs, like MCPs, are based on convex hulls, but create a separate polygon for each point using a specified number of neighbours (k). Smaller polygons populate areas in which the animal spends the most time. The home range can be defined by the total area covered by this array of polygons or by ordering polygons from smallest to largest and combining them until a given percentage of points are contained. Additional forms of LoCoH (not explored here) can be based on fixed search radii, rather than a number of neighbours, or more complex adaptive methods. LoCoH estimates of daily roding ground size were implemented using the package adehabitatHR in R based on nine and 22 neighbours per point (i.e. k = 9 and k = 22). A k value of nine was based on suggestions made by Getz *et al.* (2007) who recommended

trialling an initial value equal to the square root of the number of points, whereas 22 was the lowest value of k at which every daily roding ground was a single continuous area. For both LoCoH and MCP, roding range estimates were based upon 100% of the data available per bird-day after DOP filtering. The exclusion of a certain proportion of outlying points may be used to prevent atypical exploratory movements from influencing range size, but in this instance the data apply to a 75-minute period in which all movements are relevant and spurious fixes are already removed via filtering.

The BB kernel method uses the rate of movement and the time between fixes to produce a utilization distribution (UD) (i.e. a probability density that provides the frequency with which the animal is expected to occur at a given location (Van Winkle 1975)), and is based not only on the location of each point, but also the possible paths used to move between them. This probabilistic method does not provide a definitive home range boundary, but one may be drawn from a user-specified isopleth. Börger *et al.* (2006) recommends using the 90% contour (the area within which there is a 90% chance of the animal occurring) to define home ranges and caution against the use of higher values. BB kernels were created using adehabitatHR following a method similar to that described by Calenge (2015) and Bullard (1999) to estimate home range size. On three occasions where a tag was unable to record its position accurately for an extended period (> 20 minutes), data for the entire bird-day were excluded from analysis, as the Brownian bridge method cannot handle such uneven intervals between locations

(Calenge 2015), and to maintain comparability, these birds were also excluded from MCP and LoCoH estimates.

The Brownian bridge kernel function requires a measure of the tag's precision (sig2). This was estimated using data from three static GPS-loggers recording in representative woodland locations and programmed (i.e. 90 locations per evening at 1-minute intervals) and filtered in the same way as deployed tags. The standard deviation of the distance of the first 200 points from their centroid was calculated for each tag, and the mean value of 22.1 m was specified as sig2. The value of sig1, a parameter controlling the width of the bridges, was calculated using the adehabitatHR package's *liker* function and set at the optimal value of 27.7. Daily roding grounds were measured using the 70%, 80% and 90% isopleths. For each method, an average daily roding ground size was calculated for each individual, which were used to produce an overall mean and standard deviation. This prevents woodcock that were tracked for longer time periods having a greater influence on the final averages.

6.2.3 Correlates of daily roding ground size

I compared daily roding ground size to bird age and environmental factors using two measures of roding ground size: LoCoH (k = 9) and BB kernels (90% isopleth). These methods produced estimates of daily roding ground size that were fairly similar to one another, moderate in size and appeared most realistic when plotted. Using average areas of daily roding grounds produced using each of these methods, a

Wilcoxon rank-sum test was used to test for a correlation between roding ground size and age (first-year vs. adult). A pair of linear mixed model (LMM) was used to test whether daily roding ground size estimates varied according to date, repeating the following method for the LoCoH and BB kernel estimates. Daily roding ground size was specified as a dependent variable, with the Julian day of year as an explanatory variable. Measures of cloud cover and minimum temperature, identical to those used in Chapter 5, were also included as explanatory variables as known correlates of display duration (see Chapter 5). The bird's identity (i.e. ring number) was specified as a random factor. The model was produced in lme4 (Bates *et al.* 2015), and p-values are reported from the maximal model.

6.2.4 Total roding ground size and consistency

For individuals in which roding was recorded for ≥2 days, total roding ground size was calculated for the individual by overlaying the daily roding grounds and measuring the total area covered. Total roding grounds are calculated from daily roding ground sizes produced using LoCoH (k = 9) and BB kernels (90% isopleth. The consistency of roding ground size over successive days was assessed by calculating the coefficient of variation for roding ground size (CV) for each bird:

$$CV = \left(\frac{\sigma_x}{\bar{x}}\right) \times 100$$

where σ_x is the standard deviation of roding ground size and $\bar{x}$ is the mean daily roding ground size. A linear model (R Development Core Team 2019) was used to test for a correlation between total roding

ground size (from BB kernels) and the number of nights that each bird was tracked for. A similar model tested CV of roding ground size against nights tracked. Both tests were repeated using the LoCoH (k = 9) total roding ranges.

6.2.5 Independence of survey squares

The 2003 and 2013 GWCT/BTO Breeding Woodcock Surveys gathered count data which were used to estimate Britain's resident woodcock population size (see Chapter 2 for a more detailed description of the methodology). Point count surveys were conducted within 807 1x1-km squares in 2003 and 834 1x1-km squares in 2013/14 across Great Britain. Survey squares were chosen by volunteer surveyors from a randomly selected pool of 2677 squares, stratified according to four wood-size classes (10–30, 31–50, 51–70, 71–100 ha of woodland) and 11 regions. To avoid bias towards more densely populated areas, the number of squares available per region reflected the number of potential surveyors (BTO members).

Squares within the initial randomly selected list maintained a minimum distance of 2 km from edge to edge. If male woodcock rode over greater areas than this, the 2 km rule may not be sufficient to guarantee independence. To test this, GPS-logger data from displaying male woodcock were compared to hypothetical randomly selected samples of survey squares.

Five hundred hypothetical random samples of survey squares were generated for the 'North Midlands' region; the region that the

GPS-tracking study sites fall within. Random samples were produced using the subsample.distance function from R's spatialEco package (Evans 2018). Wooded squares (≥10% woodland) were selected at random, maintaining a minimum distance of 2 km between neighbours, until all possible squares were selected. This resulted in a mean sample size of 824.0 squares (range = 797 to 853). The study site at which woodcock were GPS-tracked was defined as a 9x19-km rectangle and contained 122 wooded squares; the smallest rectangle of grid-squares within which all GPS locations could be contained (except those of the single bird tracked in Park Forest, which was excluded from this analysis). In any given random sample, eight to fifteen of these 122 wooded squares were selected.

For each hypothetical random sample, daily roding paths that passed through more than one survey square (i.e. paths for which double-counting would be possible) were identified. A linear model was used to test whether the number of iterations in which a daily roding path included > 1 survey square was correlated with a) the total number of 1-km squares the path passed through and b) the total length of the daily path. To improve model fit, the cube-root of the number of iterations was used as the dependent variable. For each iteration, I identified which squares within the study site were selected and which of these were involved in hypothetical incidences of 'double-counting'.

The random sampling process was repeated and the same statistics calculated for 500 samples maintaining a minimum of 3 km and 4 km between chosen squares. In this case, the samples averaged

546.3 squares (range = 525 to 566) and 368.9 squares (range = 387 to 349), respectively. A 3 km separation rule resulted in between four and eleven squares within the 122-square study site being selected, a 4 km separation meant between two and eight.

The hypothetical random samples represent maximal densities of random squares which, although they do not occur uniformly through the real survey sample, do occur in some parts of the country (Fig. 6.1). To show how this reflects the real survey sample, I calculated the proportion of survey squares, within the pool of 2677 randomly selected squares, that had at least one, two or three neighbours within 2 km. I calculated the same statistics for the sample of 823 squares that were surveyed in 2013. A logistic regression (R Development Core Team 2019) was used to test whether occupied squares were more likely to have one or more neighbours within 2 km. This would likely be the case if the requirements of random squares mean that they are more likely to clustered in heavily wooded areas.

6.2.6 Potential effect on assessments of population size

The analysis of GPS-tracking data presented here suggests that survey squares separated by 2 km cannot always be assumed to be independent. A minimum of 3 km did not eliminate the possibility of double-counting but reduced the risk significantly, and a minimum of 4 km reduced this further (see results for more details).

The potential effects of this new information were tested by reanalysing the 2003 Breeding Woodcock Survey data. Sites were

removed from the dataset to create a subset in which all squares were at least 3 km from their nearest neighbour. Squares were removed by making the smallest possible number of exclusions necessary to meet this requirement. If this still meant a choice had to be made between squares, the square belonging to the more poorly represented woodland-size-class within the region was retained. If the two squares were of the same wood-size class, one was removed at random. The process was repeated with the 2013 survey data.

In 2003 and 2013, volunteers made up to three visits to survey squares during May-June. Roding woodcock counts, which were conducted from a single count point within the square, recorded the total number of woodcock registrations (seen or heard) in a 60-minute period at dusk. The maximum number of registrations recorded was converted to an estimated number of males present using a calibration equation. The equation is derived from a study of vocal individuality in which males were distinguished by vocal characteristics and a non-linear correlation between the number of registrations and the number of males was identified (Hoodless *et al.* 2008).

To estimate population size, the number of male woodcock encountered at a count point must be converted to an estimate of local density. These density estimates are then used to calculate a mean density for each of the 44 strata (4 wood-size classes x 11 regions). Stratum densities are extrapolated to form stratum population estimates and these are summed to create a national population estimate.

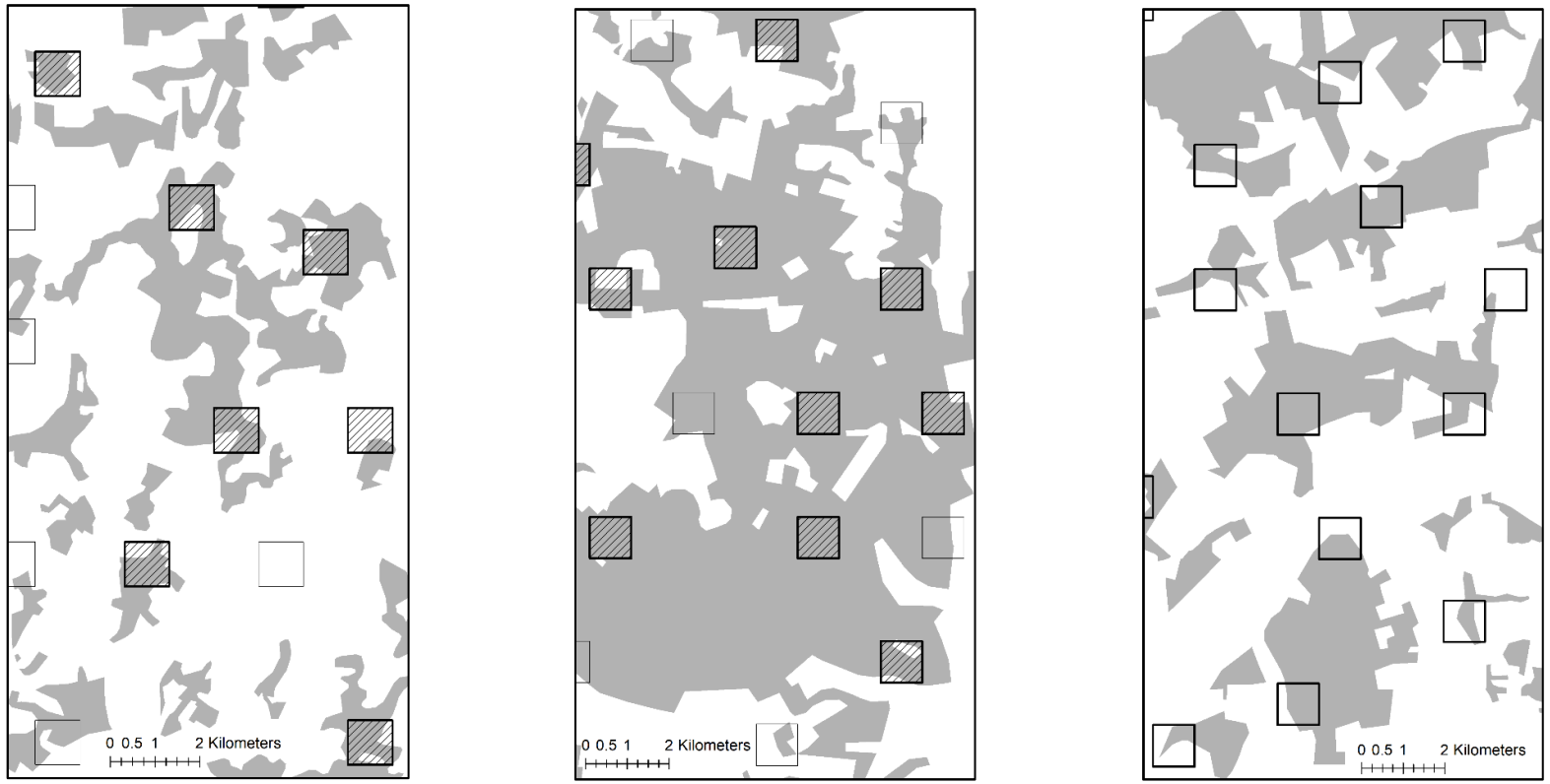


Figure 6.1 Examples of high-density survey square selection in the 2013 Breeding Woodcock Survey: (a) along the Surrey-West Sussex county border and (b) in Thetford Forest, Norfolk. Bold hatched squares are those that received survey visits in 2013. Figure 6.1(c) is an example of a randomly generated sample within the Sherwood study site using the same 2-km separation (edge to edge) rule. Grey shading = woodland.

Understanding the geographic area sampled by the static count point is necessary to infer density per sample unit from point count data. Because a previous study (Hirons 1980) suggested that daily roding grounds were approximately similar in size to the 1x1-km sample unit (mean roding ground = 0.88 km^2), a 1:1 conversion rate was employed whereby the number of males encountered was considered equivalent to the density per km^2.

The results presented here indicate that roding ground sizes may be larger than previously expected, meaning that this 1:1 relationship may no longer be valid. Instead, males per count point must be converted to males per km^2 using an appropriate correction factor, the value of which depends upon the method used to calculate roding ground size. I measured the potential effect that three methods of roding range size estimation have on population estimates: MCP, LoCoH (k = 9) and BB kernels (90% isopleth). Correction factors are derived from the 1x1-km sample unit expressed as a proportion of the mean daily roding ground size, giving N x 0.50, N x 0.78 and N x 0.90 for MCP, LoCoH and BB kernels respectively, where N is the estimated number of males encountered at the count point (representing Step 2 in Fig. 2.2).

The tracking study is based upon a small sample within a single geographic area, so population estimates are only calculated for the 'North Midlands' region that the tracking study site falls within ('North Midlands' approximately corresponds to Nottinghamshire, Derbyshire, Cheshire, Lancashire, West Yorkshire, South Yorkshire, Manchester

and Merseyside). Correction factors are applied to the original dataset and the subset of data within which nearest neighbours closer than 3 km have been removed. Population for the North Midlands region is also estimated from this subset of data with no correction factor, to establish the degree of influence this step alone has. The estimation process, including bootstrapping for confidence intervals, is otherwise identical to the established method (see Chapter 2).

6.3 Results

6.3.1 Daily roding ground size and comparison of methods

Of the 45 GPS/radio-tags deployed, 37 tags (82.2%) were recovered. Of these, 27 recorded analysable data on at least one evening and 16 individuals were recorded roding at least once (Table 6.1). The ten tags which did not produce useable data either failed to find satellites for extended periods (n = 8) or were shed before recording started (n = 2).

Mean daily roding ground sizes varied greatly according to the method of range size estimation employed (Fig. 6.2 and Table 6.2). Generally, MCPs produced the largest estimates: mean daily roding ground size was 2.00 ± 2.17 km^2 (1 SD) (Table 6.2). LoCoH estimates of mean daily roding ground size were 1.29 ± 1.40 km^2 (when k = 9) and 1.78 ± 2.06 km^2 (k = 22). For most individuals, BB kernel estimates were considerably smaller: mean daily roding ground size ranged from 0.41 ± 0.22 km^2 to 1.11 ± 0.66 km^2 (70% to 90% isopleth). Using the 70% or 80% isopleth as the roding range boundary produced fragmented roding ranges, whereas the 90% isopleth tended to

*Table 6.1 Sixteen woodcock for which roding data were acquired including the number of evenings and dates tracked (Age when ringed: Ad = adult, FY = first-year). * individuals recaptured and tagged in subsequent years*

	Age	Capture Loc.	Ringed	No. Evenings	Tracking periods
F	Ad	S. Pines	22/05/2015	2	*12-13 June 2016**
G	FY	Birklands	23/05/2015	1	*30 May 2015*
H	Ad	Birklands	23/05/2015	2	*6-7 May 2017**
J	FY	Park	03/06/2015	1	*10 June 2015*
K	Ad	S. Pines	15/06/2015	3	*22 June '15, 11-12 May '16**
L	FY	S. Pines	24/04/2016	6	*29 April - 4 May 2016*
M	FY	Birklands	30/04/2016	4	*5-8 May 2016*
N	Ad	S. Pines	07/05/2016	6	*12-17 May 2016*
P	FY	S. Pines	16/05/2016	1	*23 May 2016*
Q	Ad	S. Pines	22/05/2016	4	*27-30 May 2016*
R	Ad	S. Pines	08/06/2016	6	*13-18 June 2016*
S	FY	S. Pines	20/06/2016	2	*25-26 June 2016*
T	FY	S. Pines	23/05/2017	3	*28-30 May 2017*
V	Ad	S. Pines	01/06/2017	1	*05 June 2017*
X	FY	S. Pines	03/06/2017	1	*08 June 2017*
Y	Ad	Birklands	13/06/2017	1	*18 June 2017*

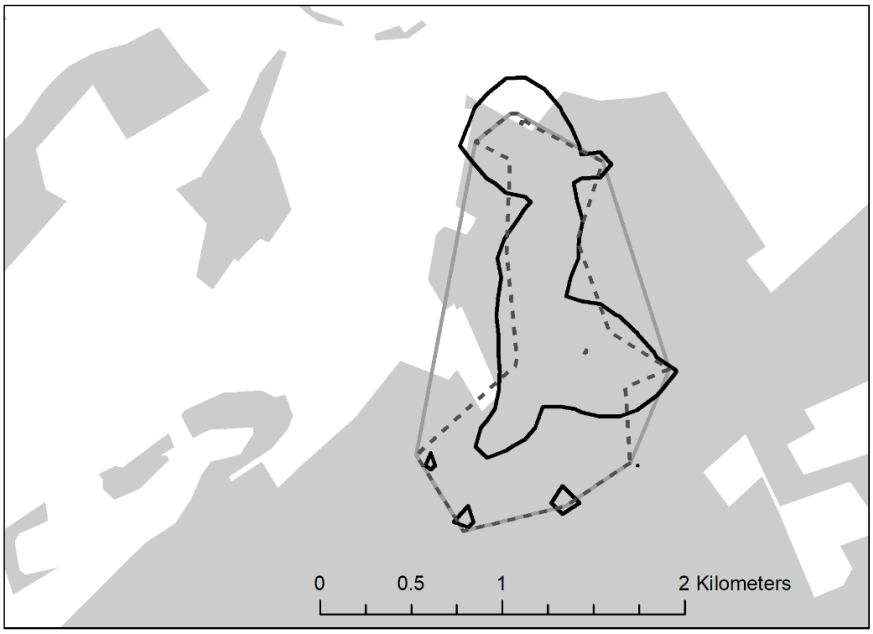


Figure 6.2 Comparison of the three methods of daily roding ground estimation for a typical evening's roding (Bird "L" on the 3rd May 2016). Black = Brownian bridge (90% isopleth), grey = minimum convex polygon, dark grey dashed = localised convex hull (k = 9). Light grey shading = woodland

Table 6.2 Six estimates of mean daily roding range size using three methods: Brownian bridge kernels, Localised convex hulls and minimum convex polygons. Figures given in km^2 to 4 d.p.

	BB 70%	BB 80%	BB 90%	LoCoH k = 9	LoCoH k = 22	MCP 100
F	0.5866	1.2636	2.6308	5.6958	8.6273	9.0225
G	0.5061	0.763	1.2161	1.3653	1.523	1.5232
H	0.2205	0.3332	0.5652	0.0905	0.1213	0.2223
J	0.2341	0.3964	0.6376	0.2951	0.5285	0.6119
K	0.4681	0.8727	1.8638	2.5532	3.0515	3.4627
L	0.4454	0.7704	1.3323	1.4841	1.9985	2.2739
M	0.3124	0.5101	0.9061	1.6578	2.2675	2.351
N	0.1573	0.2284	0.3645	0.3809	0.438	0.5338
P	0.2841	0.4555	0.7598	0.1846	0.4622	1.1251
Q	0.2104	0.325	0.5575	0.6063	0.7412	0.7929
R	0.7011	1.0723	1.7064	2.0143	3.0598	3.918
S	1.0316	1.5415	2.1933	1.9861	2.5808	2.795
T	0.3371	0.528	0.8437	0.6823	0.9076	1.1452
V	0.2695	0.3842	0.5539	0.3447	0.5404	0.5404
X	0.4681	0.6464	0.9853	0.8458	0.9343	0.9927
Y	0.3312	0.4605	0.6767	0.4215	0.7183	0.746
Mean	0.4102	0.6595	1.1121	1.288	1.7813	2.0036
SD	0.2231	0.3699	0.6633	1.3989	2.0689	2.1771

produce ‘bulges’ around any areas where birds remained static (Fig. 6.3).

For one bird-day in particular (“F” on the 12th June 2016), MCP and LoCoH seem to greatly overestimate daily roding ground size; with estimates of 14.61 km^2 (MCP) and 8.1 km^2 (LoCoH k = 9) compared to 4.11 km^2 for the 90% isopleth of the BB kernel UD (Fig. 6.4). This was a woodcock whose roding flight covered arable land as well as woodland and travelled large distances between unconnected woodland blocks. The MCP and LoCoH roding ranges for this bird-day are 6.6 and 7.2 times larger than the respective means, compared to only 3.6 times for the 90% BB kernel, and this single night’s roding has a strong influence

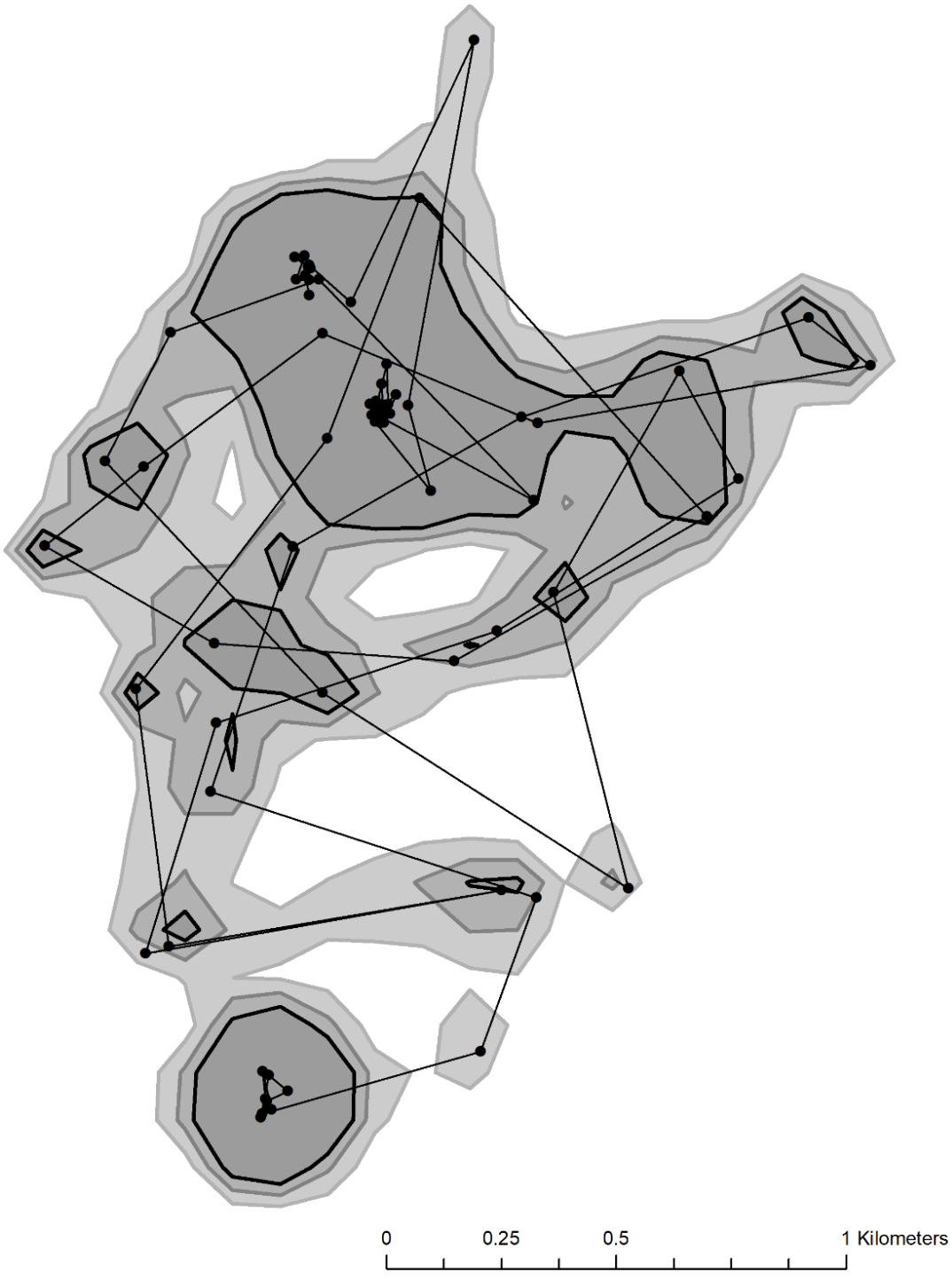


Figure 6.3 Brownian bridge roding grounds for Bird "S" on the 25th June 2016. The shaded areas represent the area within the 70%, 80% and 90% isopleths (darkest to lightest). Black dots show the location of each GPS location and the connecting lines represent the roding path (straight lines between consecutive points).

on the high standard deviations associated with the convex hull methods. Excluding this bird produces means and standard deviations of 1.53 ± 1.15 km^2 (MCP), 0.99 ± 0.79 km^2 (LoCoH k = 9) and 1.32 ± 1.01 km^2 (LoCoH k = 22).

There was no correlation between the size of BB (90%) roding grounds and the day of the year (*Est* = 1.16 ± 0.921, *P* = 0.219), cloud (*Est* = 3.70 ± 3.466, *P* = 0.292), or temperature (*Est* = 1.08 ± 4.056, *P* = 0.792), suggesting that there is no significant change in roding ground size over the course of the breeding season. This was also true when comparing the sizes of LoCoH (k=9) roding grounds (day of the year: *Est* = 1.48 ± 2.000, *P* = 0.466, cloud: *Est* = 6.92 ± 3.466, *P* = 7.520, temperature: *Est* = 4.56 ± 8.797, *P* = 0.607).

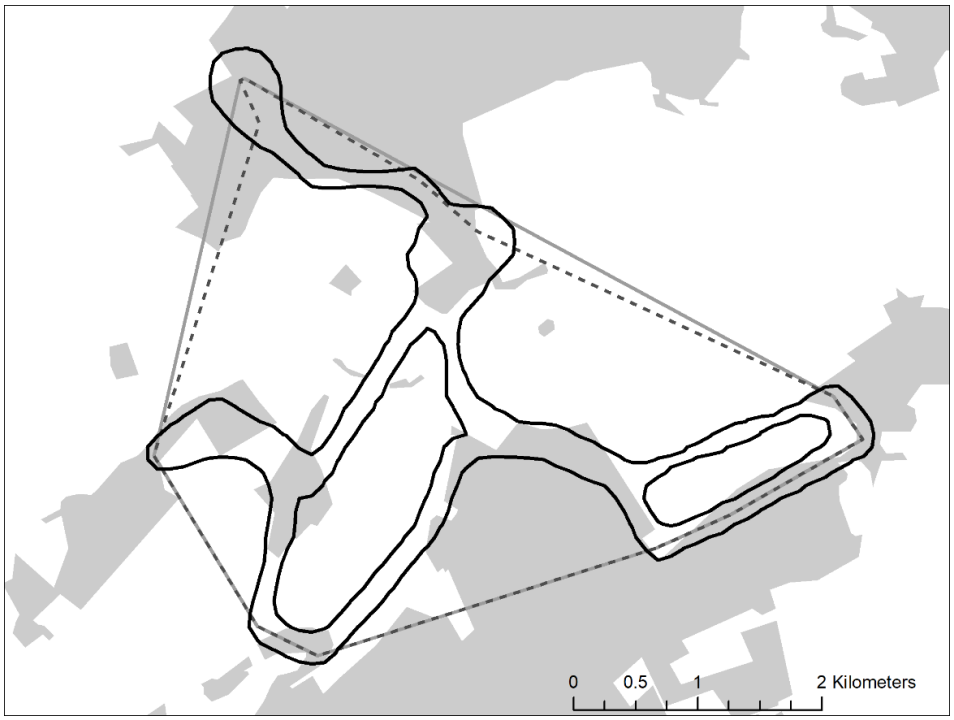


Figure 6.4 Comparison of the three methods of daily roding ground estimation for Bird "F" on the 12th May 2016; an individual that flew long distances over non-woodland habitat. Black = Brownian bridge (90% isopleth), grey = minimum convex polygon, dark grey dashed = localised convex hull (k = 9). Light grey shading = woodland.

	Nights	Mean BB	Total BB	CV BB	Mean LoCoH	Total LoCoH	CV LoCoH
F	2	263.08	445.36	80.03	569.58	911.53	60.17
H	2	56.52	73.20	21.02	9.05	17.08	17.17
S	2	219.33	276.02	15.20	198.61	239.83	5.86
T	3	84.37	144.67	20.60	68.23	109.45	25.39
K	3	186.38	434.50	23.25	255.32	411.60	22.94
Q	4	55.75	93.63	16.40	60.63	128.57	49.61
M	4	90.61	249.93	48.97	165.78	559.93	129.08
L	6	133.23	334.45	33.76	148.41	397.93	57.65
N	6	36.45	53.98	12.23	38.09	75.90	32.67
R	6	170.64	376.71	32.33	201.43	543.10	64.92
	mean	129.64	248.25	30.38	171.51	339.49	46.55

Table 6.3 Total roding ground sizes (ha) for all woodcock tracked for > 1 evening. Estimations of total roding ground size are given for the Brownian bridge method (90% isopleth) and the localised convex hull (k = 9).

There was no relationship between mean daily roding ground size and age (BB 90% W = 41, df = 15, P = 0.382, *LoCoH* (k=9), W = 32, df = 15, P = 0.31).

6.3.2 Total roding ground size and consistency

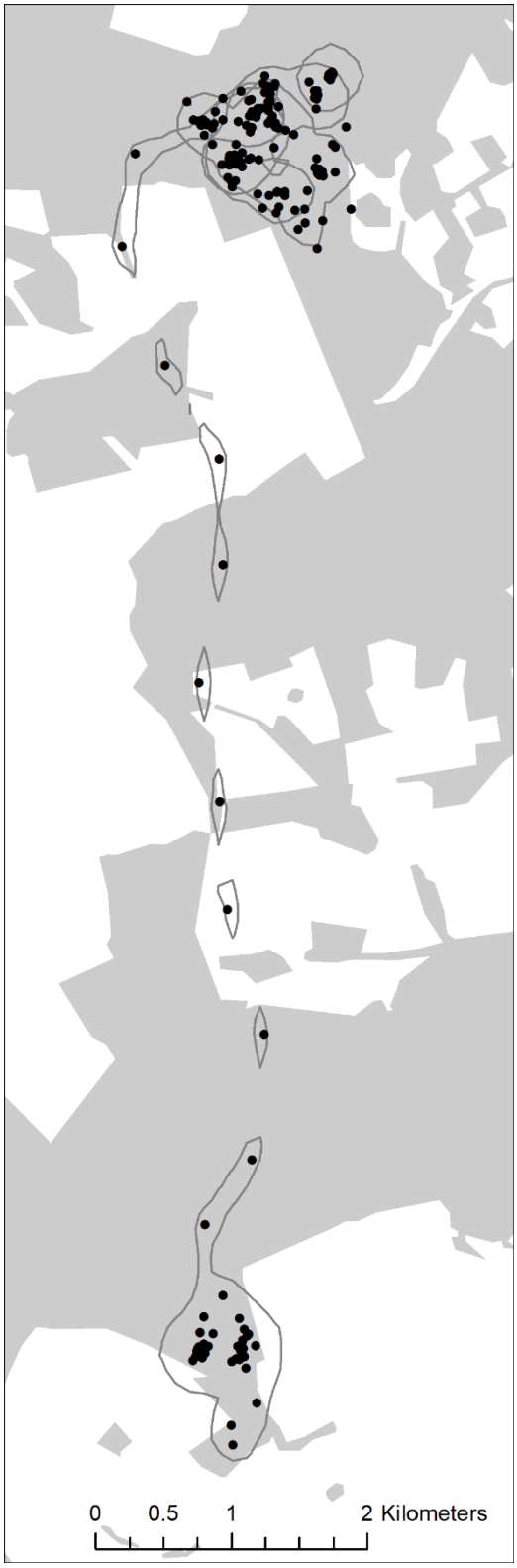
Total roding ground sizes are given in Table 6.3. Most woodcock covered roding grounds that were reasonably consistent in size and shape (Figure 6.5). Their routes did not adhere to the traditionally held view of roding as a series of repeated circuits. Instead, the paths taken were often far more varied, but the areas covered by each individual over consecutive nights were broadly similar. The mean coefficient of variation (CV) for daily roding range size was 46.5% (based on LoCoH) and 30.3% (based on the BB method). One woodcock (bird “M”)

appeared to use two completely separate roding grounds over the six days it was tracked (Figure 6.6).



Figure 6.5 Four daily roding grounds recorded over four consecutive days (Bird "L", early May 2016). Boundaries drawn using the BB 90% isopleth. Grey shading = woodland.

Bird "M" began roding over a typical roding ground close to its capture site but flew 10 km north and settled in a new patch of woodland at the end of the first evening's recording period. For the next three nights it roded at the new site, utilising a smaller than average roding ground



(daily mean 0.69 km^2). At the end of the fourth night, it returned to the wood in which it was caught.

Total roding ground size was not influenced by the number of days tracked (*Est* = 29.45 ± 18.45, *P* = 0.13), and neither was CV (*Est* = -2.30 ± 42.39, *P* = 0.60). The same was true when the analysis was based on figures derived from LoCoH home range estimates. This, along with the generally low values of CV, might appear to suggest that roding ground size is reasonably consistent, but it is impossible to draw firm conclusions without tracking roding males over a longer portion of the breeding season.

Figure 6.6 The roding grounds of Bird "M" recorded for four days in early May in 2016. Boundaries are delineated using the Brownian bridge 90% contour, which does not form a continuous joined range during the transition between the two sites.

6.3.3 Independence of survey squares

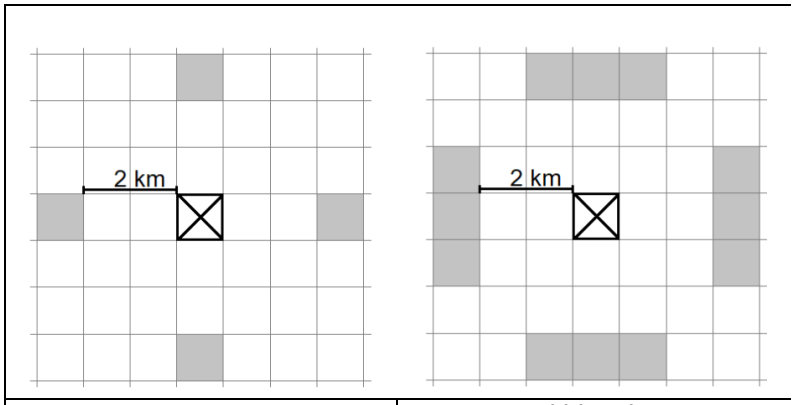
Among the 500 random samples where survey squares were separated by a minimum of 2 km, nine out of 43 daily roding paths (20.9%) passed through more than one survey square (relating to 5 out of 15 individuals). The frequency with which this was observed varied between paths: ranging from 3 out of 500 iterations (0.6%) to 144 out of 500 iterations (28.8%). Unsurprisingly, the likelihood of a path passing through multiple survey squares was strongly correlated to the total number of 1x1-km grid squares travelled through (*Est* = 0.444 ± 0.041, $P < 0.001$) but not the total distance travelled by the individual that night (*Est* = 0.083 ± 0.041, $P = 0.054$).

All wooded squares within the 9 x 19-km study site were selected in at least 20 out of 500 iterations (average = 47.8). Of the 43 squares within which a GPS-tagged woodcock was recorded, all but seven were involved in hypothetical ‘double-counting’ in at least a fifth of the samples they were selected.

When squares within the 500 random samples were separated by a minimum of 3 km, seven of 43 daily paths (16.3%) still passed through > 1 survey square, but for each, incidence rates were much lower: ranging from three out of 500 iterations (0.6%) to 37 out of 500 (7.4%). Extending the minimum separating distance to 4 km reduced the number of paths affected to two out of 43, and double counting was only possible in 2% of random samples for each of the two paths.

Of the 2677 random squares actually selected for the 2013 survey, 409 had at least one neighbour within 2 km, 36 had at least two

neighbours within 2 km and one had three. This only considers 2 km separation in cardinal directions (e.g. those that are 3 km apart centre to centre). When also including those that were 2 km apart corner to corner, 975 had at least one neighbour within 2 km, 239 had at least two neighbours within 2 km and 28 had three or more (Fig 6.7).



	Within 2 km edge to edge		Within 2 km edge to edge OR corner to corner	
	randomly selected	surveyed	randomly selected	surveyed
At least 1 neighbour	409 (15%)	70 (8%)	975 (36%)	183 (22%)
At least 2 neighbours	36 (1.3%)	0	239 (9%)	0
3 neighbours	1 (0.04%)	0	28 (1.0%)	0

Figure 6.7 The number of squares within the randomly selected sample (n = 2677) and the surveyed sample (n = 834) that have one or more neighbour within 2 km. Sketches show possible conflicts shaded in grey based upon an 'edge to edge' rule (left) and a 'corner to corner' rule (right) for a given square (X).

Of the 834 that were surveyed, 70 had at least one neighbour within 2 km (edge to edge) and 183 had at least one neighbour within 2 km (edge to edge or corner to corner). Such squares were more common in the south and east of England where the high number of potential surveyors resulted in both a larger initial sample and greater

coverage, and the more limited distribution of woodland meant squares were more likely to be clustered. A logistic regression found that squares with a nearest neighbour within 2 km (including corner to corner) were more likely to be occupied by woodcock (*Est* = 0.562 0.173, *P* = 0.001), presumably because higher square densities were generated in heavily wooded regions where woodcock were more abundant (See Chapter 3).

6.3.4 Possible effect on assessments of population size

A distance of 3 km between randomly selected survey squares was expected to reduce the likelihood of double-counting. Meeting this requirement in the North Midlands region meant the removal of 13 squares in 2003 (10.2%) and 6 squares in 2013 (7.6%). Overall, this meant the recalculated population estimates for this region were drawn from 115 squares in 2003 and 74 squares in 2013. The percentages removed are similar to those that would be required nationally (83 squares (10.3%) in 2003 and 83 squares (9.9%) in 2013) but this varies between regions in relation to square density and survey uptake.

The original population estimate for the North Midlands region was 5,139 males (95% CL: 2,998 – 7,612) in 2003 and 3,806 males (95% CL: 1,188–7,890) in 2013 (Chapter 2). Based upon the subset of squares separated by 3-km edge to edge, but using an otherwise identical method, these population estimates are 4,604 males (95% CL: 2,623–7,003) in 2003 and 2,198 males (95% CL: 1,036–3,779) in 2013. The associated estimate of population trend was -52.2% between 2003

and 2013, compared to the original estimate of -25.9% (Heward *et al.* 2015). Much of this change can be attributed to the removal of a single square in the lowest wood-size class in 2013, where a count of 22 registrations was recorded (stratum mean = 1.69 registrations in original sample). The influence of a single square can be expressed as the percentage change in the population estimate when this square is omitted, and the square in question featured in the top ten most-influential squares nationally (its omission would result in a 3.1% reduction in the national estimate).

Table 6.4 Estimates of woodcock population size (no. of males) for the North Midlands region recalculated to account for (a) 3-km separation between survey squares and (b) different methods of estimating density at the 1-km scale from point count data. The latter vary according to the 'sample unit:mean roding ground size' relationship and are compared to the original estimate that assumed a 1:1 relationship. The 95% CLs are provided beneath each estimate. Each estimate is also given in brackets as a percentage of the original estimate.

		1:1	MCP 0.5 : 1	LoCoH (k=9) 0.78 : 1	BB (90%) 0.9 : 1
2003	**2 km**	**5139** 3000 - 7374	**2570** *(50%)* 1500 - 3687	**4008** *(78%)* 2340 - 5752	**4625** *(90%)* 2700 - 6637
2003	**3 km**	**4604** *(89.6%)* 2623 - 7003	**2302** *(44.8%)* 1311- 3502)	**3591** *(69.9%)* 2046 - 5462	**4144** *(80.6%)* 2360 - 6303
2013	**2 km**	**3806** 1188 -7890	**1903** *(50%)* 594 - 3945	**2969** *(78%)* 927- 6154	**3425** *(90%)* 1069 - 7101
2013	**3 km**	**2198** (57.7%) 1036 - 3779	**1099** *(28.9%)* 518 - 1890	**1714** *(45.0%)* 808 - 2948	**1978** *(52.0%)* 932 - 3401

When also including the potential effect of daily roding ground size, population estimates for the North Midlands region would be calculated as 10–71% lower (Table 6.4). This is based on roding

ranges calculated using MCPs, LoCoH and BB kernels, some of which appear to overestimate roding ground size. As such, these population estimates ought not be seen as improved versions; rather an illustration of the potential effect inaccurate home-range estimates can have.

6.4 Discussion

6.4.1 Roding behaviour

GPS-loggers have provided a new insight into the woodcock's breeding display. Although they are not directly comparable to previous estimates, the data presented here suggest that roding ranges are probably larger than previously thought. Hirons *et al.* (1980) proposed that the average total roding ground, for males radio-tracked for up to 100 days, was 88 ha in size, whereas 9 of 16 males within this study displayed over areas larger than this in a single night. Radio-telemetry is poorly suited to recording large-scale movements over such short time periods as it is biased by the detectability of transmitters and the placement of receivers, the latter being based upon prior assumptions regarding the birds' expected behaviour.

A larger sample of tagged males would be required to understand what determines the size of an individual's roding ground, but the data analysed here do not appear to support a simple relationship with age (adult vs. first-year). Roding ground size could plausibly reflect male quality, for instance if higher-quality males can cover larger roding areas and therefore access a greater number of females. But the largest daily roding ranges in this study were those

that contained a high proportion of non-woodland habitat where females are unlikely to be encountered. Although roding behaviour is not thought to be territorial, lower quality individuals may be forced to use less suitable roding grounds if they are outcompeted by rivals at preferred sites. In American woodcock *Scolopax minor*, residency at singing grounds is hierarchical, with central, more prominent display areas being held by higher quality males (Ellingwood *et al.* 1993). Any future attempts to explain variation in roding ground size should also consider roding ground quality, e.g. the proportion of suitable breeding habitat and the distribution of clearings, both of which may influence the availability of females (Hirons 1983).

Woodland extent appears to influence roding circuit size and shape in more fundamental ways. The boundaries of a wood are clearly not a barrier to roding, but movement between neighbouring woods is likely to be influenced by habitat connectivity. The data analysed here include several instances of males moving between discrete woodland blocks via connecting features such as shelter belts, and in one instance, overhead power lines. This could also explain Hirons' lower estimates as they refer to a single wood with limited connectivity (Whitwell Wood, Derbyshire, UK), where roding may be constrained by the lack of neighbouring habitat (Hirons 1980; Hoodless & Hirons 2007).

6.4.2 Home-range methods for fine-scale temporal data

Deciding how to define the boundaries of a roding range from spatial point data is complicated. Existing radio-telemetry studies have done so subjectively (Hirons 1980), by recording the direction of movement of the radio-tagged woodcock at each receiving station and using these paths to approximately sketch the bird's inferred range. A more objective method would improve roding range estimates, but all approaches include some element of subjectivity.

A number of existing studies have compared methods of home-range estimation (Stark *et al.* 2017; Getz *et al.* 2007; Laver & Kelly 2008), but few have considered tracking data characterised by such short time intervals and high mobility. Existing methods are designed to define ranges utilised over a period weeks or months, rather than the geographic areas associated with a specific and relatively brief behaviour. The example presented here may be unique to the woodcock's unusual display, but there are parallels in other species with highly mobile displays or, more broadly, in species where the areas covered during individual foraging trips are of interest (e.g. seabirds (Mcleay *et al.* 2010; Awkerman *et al.* 2005) or pinnipeds (Nordstrom *et al.* 2013)).

MCP roding grounds clearly overestimated roding ground size and incorporated large areas that were fully or partially surrounded by GPS fixes but were never crossed or entered by the bird. LoCoH was better at addressing this problem if a low k-value was specified, but still tended to include some unused areas if they were completely

surrounded by GPS fixes. Occasionally ‘holes’ were cut from unused central parts of LoCoH roding ranges, but this was rarer than for BB kernels (Fig. 6.5)).

The BB kernel approach produced the smallest roding ranges and, visually, appeared to fit the point data most closely. If roding paths included large loops where the central area was not crossed, these usually appeared as cut-out ‘holes’ in the final roding ranges. The two most obvious weaknesses of this approach were that a) roding ranges were disjointed when the boundary was based upon lower isopleths (≥80%), and b) ‘bulges’ in the range boundary were drawn around locations where tagged woodcock remained static for several minutes (Fig. 6.4).

The former is generally not considered problematic for typical home-range estimates, where the areas used for resting, feeding and reproduction are of the greatest interest and the intervening areas, that are only crossed when moving between these resources, are not. In this instance, however, the path, as well as the points, are of direct interest and it was hoped that BB ranges would indicate the approximate routes taken between points. Because certainty decreases with distance from a known location the likelihood that consecutive fixes appear as continuous paths depends on the isopleth used to draw the range’s boundary, as well as the distance between fixes and the value of $sig1^2$ (the Brownian motion variance parameter (Horne *et al.* 2007)).

Ranges drawn using higher isopleths are more likely to show continuous paths between consecutive fixes but are more likely to

encounter the second problem: a ‘bulge’ in the range boundary that surrounds clusters of GPS fixes in a single location. Although the woodcock was apparently static, it is theoretically possible that it could have flown a given distance from the location and returned to it during the interval between fixes. The excess surrounding a static location represents the area that the animal could have moved within and increases with the isopleth used to draw the boundary, the number of fixes at this location, and the interval between each fix (which vary because the filtering process removed some inaccurate fixes).

The size of these ‘bulges’ can be reduced by lowering the value of $sig1^2$ which relates indirectly to the speed of movement, although this becomes a subjective process when gauged by eye. Nevertheless, it might be possible to adapt the BB method so that the period of time between consecutive points is binarily distinguished as ‘static’ (not roding) or ‘mobile’ (roding) based on the distance between points, and then uses one of two different Brownian motion variance parameters accordingly (Horne *et al.* 2007; Jonsen *et al.* 2005; Morales *et al.* 2004).

Despite these issues, LoCoH estimates (k = 9) and the BB estimates (90% isopleth) appear to be the most realistic roding ranges based on visual comparisons with the raw point data. Even though attempts were made to choose parameters based on a predefined rule (e.g. k value selection) or, in its absence, trialled multiple parameters to visualise their effect (BB kernel isopleths), deciding which method is most appropriate still requires a subjective judgment. These approaches produce size estimates that are, for the most part,

reasonably consistent with one another. The greatest divergence with regards to both size and shape was for birds that covered very large areas and moved between multiple woods, but these individuals were atypical. These methods would tentatively suggest the 'true' mean daily roding range realistically lie within the bounds of 1.11 and 1.29 km^2.

6.4.3 Interactions between roding movements and population estimates

GPS-tracking data suggest that the existing rule, stipulating that at least 2 km should separate survey squares, meant around a third of male woodcock could be encountered in more than one square if maximal sampling densities were applied to the study site. Inspection of the actual random sample showed there were several areas where this maximal sampling occurred. Removing squares from the current random sample illustrates the potential effect of this, but redrawing the sample based on a new rule would be preferable for future surveys in order to reduce bias. It is important to remember that increasing the minimum distance between squares reduces the overall sample size and could affect comparability and survey participation, so the between-square distance must not be increased further than necessary simply as a precaution.

Doing so may also have an effect on the structure of the random sample. The process of removing squares inadvertently demonstrated how single sites can have a large effect on population estimates. The removal of 6 squares in 2013 resulted in a 42% reduction in the

population estimate for the North Midlands region, most of which can be attributed to a single square. This is not just a consequence of a low sample size for this stratum, but of a site with a particularly high count occurring in the lowest wood-size class (10-30% wooded). Here, it was removed because it was within 2 km of a survey square in the highest wood-size class (71-100% wooded) and it seems likely that the count was influenced by the availability of woodland outside of the square. In the absence of double-counting, this is not a problem; rather it captures some of the real variation observed within the stratum. But squares like this (i.e. low woodland coverage but occurring in heavily wooded areas), should be represented within the stratum sample in the same proportions that they naturally occur. If the sampling process stipulates a set distance between squares, while trying to maximise representation of the four wood-size classes, the selection of those within the lower wood-size classes will be biased away from heavily wooded landscapes. In heavily wooded areas, the necessary selection of squares in the higher wood-size classes prevents nearby squares in lower wood-size classes being selected. The specified distance between squares could therefore influence the structure of the stratified sample so it is no longer a fair representation of the wider ‘population’ of squares. This issue may already occur within the existing dataset but would be more pronounced if the specified distance between squares were increased. One solution would be to freely select wooded squares irrespective of their wood-size class and without any attempt to maximise representation of the four wood-size strata, but this would

result in very small numbers of the highest wood-size class being selected.

Looking beyond the limits of this study and the existing data, a better way of drawing random samples might be to use a larger sampling unit, particularly if this could classify woodland area on a more biologically appropriate scale (Chapter 3). The 1x1-km British National Grid (BNG) could easily be incorporated into a 3x3-km sampling unit where roding counts are conducted in the central 1x1-km square, but woodland is classified according to the surrounding 9 km^2 square. Specifying that the central square should be surveyed means part of the sampling unit itself is a buffer to double-counting. A 3x3 method was previously mentioned in Hoodless *et al.* (2008), but any changes to the existing method now come at a cost if they reduce comparability with the two previous surveys.

The correction factors applied to survey data crudely gauge how the relationship between a static point count and the sample unit can influence final population estimates. It is unsafe to assume that a count point accurately censuses the entire area of the sample unit without some biological justification of this and GPS-loggers appear to be able to provide relevant information in this regard. If we accept that the LoCoH (k = 9) and BB kernel (90% isopleth) methods offered the most realistic roding ranges, then their estimated sizes of 1.11 to 1.29 km are reasonably similar in size to the 1 km^2 sample unit. Although each woodcock does not confine itself to the arbitrary 1x1-km square, registered birds that cross into neighbouring squares should be

balanced by unregistered birds within the selected square. The only risk to this assumption is that by surveying from an open clearing, the count point coincides with a location that draws roding males from a larger surrounding area. Even though each woodcock's roding range is equivalent to the sampling unit, the count point could be sampling woodcock from a wider geographic area.

With increasing scrutiny, it becomes harder to precisely define what is meant by a roding range, much as it is for a home range more generally. The definition may be strengthened by a particular biological qualifier e.g. the area within which a male woodcock is detectable to potential mates. Alternatively, the definition might be tailored to the practical application e.g. the area within which the male is detectable to the average human observer. In both cases, the delineation of roding range boundaries depends not only on the male's movements but also some understanding of detectability. In the case of woodcock, the use of remote sound recorders could enhance interpretation of logger data. Male woodcock can be distinguished using sonogram analysis (Hoodless *et al.* 2008) and measuring the frequency of detection for individual males at an array of points within the survey square and its neighbours would allow better quantification of the actual area censused by a single count point.

7 THE ROLE OF HABITAT IN THE WOODCOCK'S BREEDING DISPLAY

7.1 Introduction

The habitat requirements of breeding birds usually include specific habitat features associated with nest-sites and areas used for foraging while rearing chicks (Clark & Shutler 1999; Helzer & Jelinski 1999; Jedlikowski *et al.* 2016; Zarnowitz & Manuwal 2012). For some species, however, there are additional habitat requirements associated with courtship or territorial displays e.g. song posts (Barg *et al.* 2006; Beck & George 1999). These features may influence where breeding sites are situated but, given that they are usually inseparably linked with broader breeding habitat requirements, it is difficult to isolate their individual effect on site-use.

For species with non-territorial courtship displays, the relationship between display and breeding habitat is less well understood. Lekking is a non-resource based mating system where females select mates based only upon physical or behavioural characteristics of males demonstrated during aggregated displays (Widemo & Owens 1995; Morales *et al.* 2001). These aggregations are usually associated with specific geographic areas but there are different hypotheses to explain the development of lek locations, only some of which relate to habitat (Alonso & Jose 2012; Beehler & Foster 1988; Gjerde *et al.* 2000; Ryder *et al.* 2006; Widemo & Owens 1995). The hotspot hypothesis proposes that males gather to display where female

densities are highest (Bradbury *et al.* 1989; Schroeder & White 1993), which may reflect the surrounding habitat's suitability for nesting or brood-rearing (Ryder *et al.* 2006; Schroeder & White 1993). It may be that the specific location of the lek site within this area is influenced by how habitat improves the visibility of the male's display e.g. exposed branches or raised ground (Alonso & Jose 2012; Aspbury & Gibson 2004; Bradbury *et al.* 1989; Heindl & Winkler 2003; Hunt & Best 2010).

The Eurasian woodcock *Scolopax rusticola* has a unique courtship display flight, known as roding, which is thought to be non-territorial and has been described as an 'aerial lek' (Hirons 1980). But there are several characteristics of the woodcock's display that differ from those of typical lekking species, including the fact that the display is not confined to a single location (Morales *et al.* 2001). Male woodcock often cover areas > 1 km^2 while performing their display flights (Chapter 6). It is widely accepted that the woodcock's roding display is associated with rides and clearings within woodland (Nethersole-Thompson & Nethersole-Thompson 1986; Tester & Watson 1973), however this is currently only known from field observations. Many previous assumptions concerning the woodcock's display, such as the once-common view that roding areas did not overlap (Tester & Watson 1973), have since been disproven using radio-telemetry (Hirons 1980). Human observations of roding displays are inevitably biased towards clearings since the males' display flights occur above tree canopy height (Hirons & Owen 1982) and are more easily viewed from these locations.

The improved visibility of roding woodcock from clearings does provide a logical explanation as to why open areas might be important. The roding display of the male is used to attract the attention of potential mates that assess multiple displaying males from a static location on the ground (Hirons 1980). It is unknown whether females base their choice of mate on vocal or visual cues, but it is thought that receptive females signal to their preferred male using their tail (Hoodless 1995), which provides at least one reason why visual contact between individuals is required.

It is not known whether specific characteristics of the clearings have an effect on their use. Clearings will vary in their size, age, permanence and location within the woodland, all of which could conceivably affect their relative use by roding males. In addition, differences in vegetative structure, such as height or patchiness of cover (Cramp *et al.* 1983), might further influence a clearing's suitability. As well as influencing the effectiveness of visual and vocal signalling between males and females, habitat may influence predation risk during the display period and foraging opportunities, with anecdotal evidence suggesting male woodcock may feed during or immediately after roding (Hirons 1983).

The first step to understanding how habitat influences display behaviour is to ascertain whether some habitat features are in fact visited more frequently during display flights. Doing so could validate the assumption that roding requires open areas and identify which types of clearing are most frequently used. This information may have

practical benefits if it ensures effective selection of count points for censuses of roding males. It may also help identify any links that exist between habitats associated with roding and those associated with nest-sites and females (something previously postulated in Hirons 1983). It is unlikely that long-term declines in breeding woodcock populations are driven purely by the loss of habitats associated with display but, if these habitats have a broader significance, roding activity may be a practical indicator of breeding habitat suitability.

GPS-loggers present an opportunity to study fine-scale habitat associations during a period of very high mobility, something that was not previously possible with older forms of telemetry (Cagnacci *et al.* 2010). Here, I present a compositional analysis of habitat use derived from GPS-logger data to establish which habitat types are most frequently visited by roding woodcock.

7.2 Methods

7.2.1 Study site and woodcock tagging

Woodcock were caught and tagged in three woods near Mansfield, Nottinghamshire: Birklands Forest (lat: 53.20, lon: -1.10), Sherwood Pines (lat: 53.15, lon: -1.09) and Park Forest (lat: 53.05, lon: -1.25). All three woods contain a mixture of coniferous and deciduous woodland interspersed with open clearings and rides. Sherwood Pines (13.3 km^2) is dominated by conifers (70.3% of its area), predominantly Scots pine *Pinus sylvestris* and Corsican pine *P. nigra* plantation, with smaller stands of deciduous trees such as birch *Betula pendula* and sweet

chestnut *Castanea sativa*. Park Forest comprises similar habitat but is much smaller in area (1.6 km^2). Birklands Forest (8.4 km^2) has a higher proportion of mixed and deciduous stands and includes a 1.51 km^2 block of ancient oak woodland (17.9%) on its eastern side. The commonest habitat surrounding these woods is arable farmland, followed by human settlements (villages and small towns). Other significant non-woodland habitats include scrubby or grassy wasteland associated with colliery spoil and, in the case of Birklands Forest, a 1.35 km^2 lowland heath (Budby Common).

Capture sites included permanent clearings, clearfells, rides and woodland edges and were visited between late April and mid-July in 2015, 2016 and 2017. We attempted to catch woodcock at a wide-range of sites to avoid bias towards particular areas or habitat types although, given the method employed, it is not possible to catch woodcock within closed stands of woodland (Figs. 7.1 and 7.2). Woodcock were caught using the method described in Heward *et al.* (2017) and processed and tagged as described in Section 6.2.1. The 7.5g GPS-logger/VHF radio-tag (Biotrack, Wareham, UK/Perdix Wildlife Supplies, Stratford-upon-Avon, UK) was programmed to record the woodcock's location at one-minute intervals, for 90 minutes, beginning 15 minutes before sunset. This schedule was repeated for one to six consecutive days, depending upon battery-use, then recovered by recapturing the individual or retrieving the tag once shed.

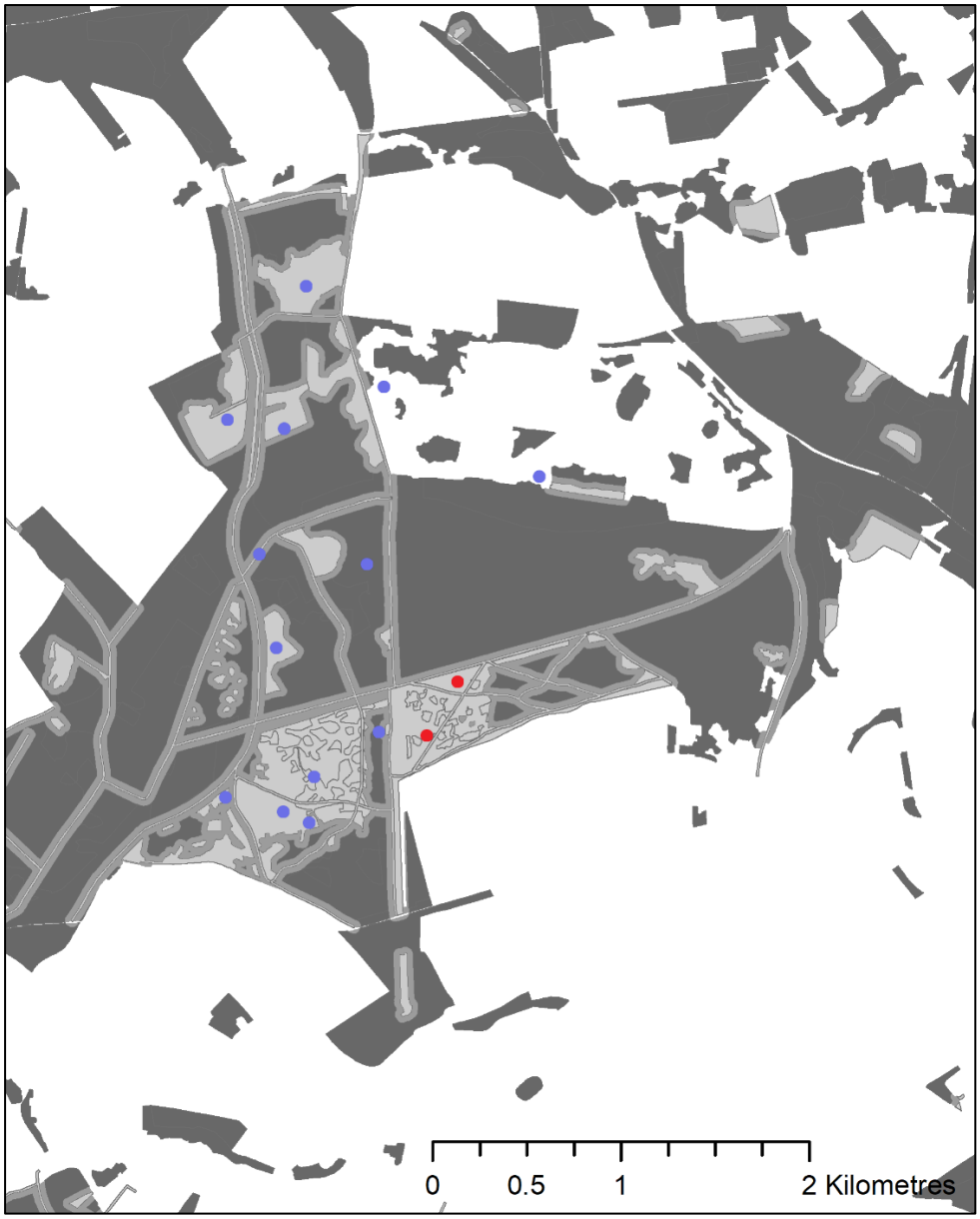


Figure 7.1 Sites in Birklands Forest at which catching was attempted. Blue dots show sites where at least one woodcock was successfully caught. Red dots show sites at which woodcock were never caught (unsuccessful sites were attempted at least twice).

7.2.2 Classification of behaviour

The movements of male woodcock, for each given night, were classified as roding or non-roding based on the criteria outlined in Section 6.2.2, and only bird-days on which roding occurred are analysed here.

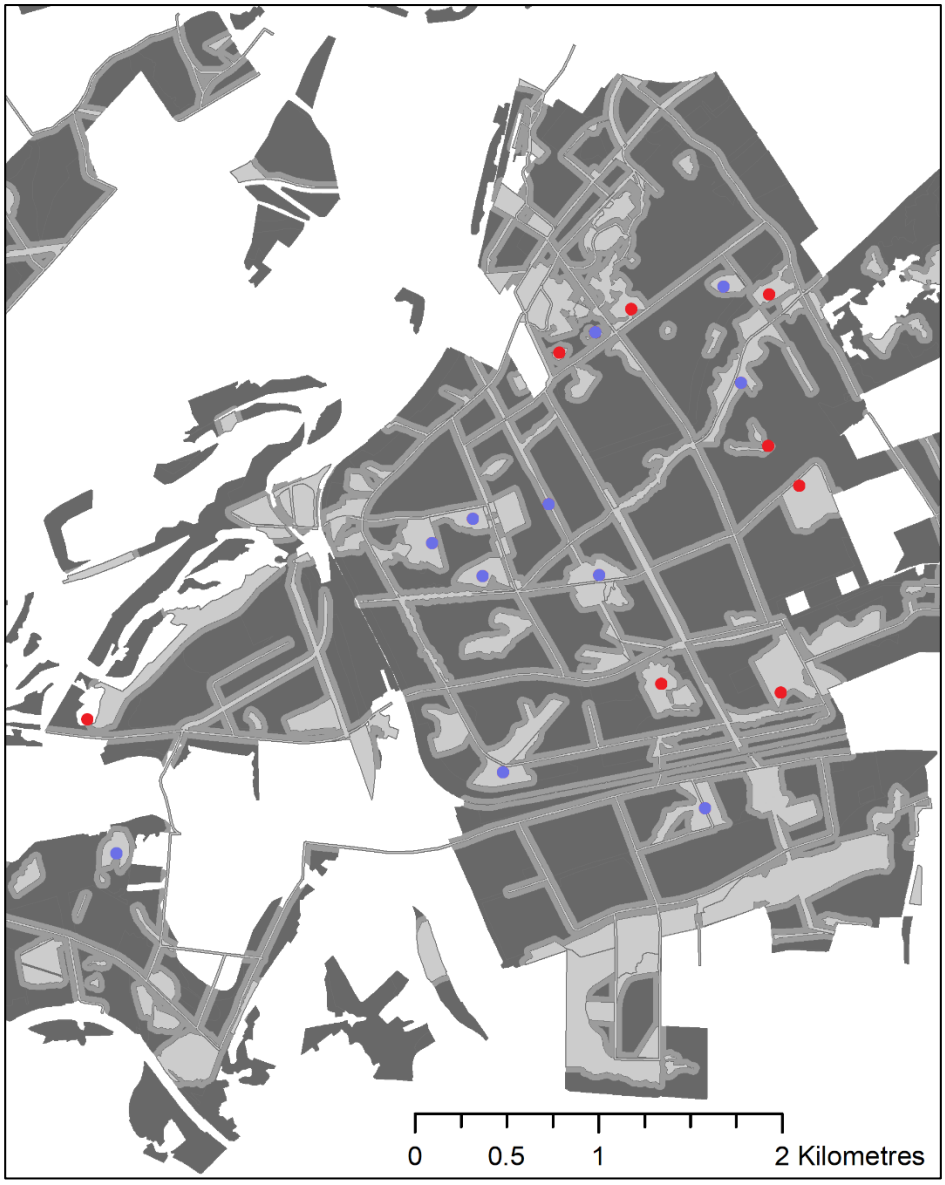


Figure 7.2 Sites in Sherwood Pine at which catching was attempted. Blue dots show sites where at least one woodcock was successfully caught. Red dots show sites at which woodcock were never caught (unsuccessful sites were attempted at least twice).

Movement data were filtered and those with dilution of precision values > 8 were excluded (Section 6.2.3). Remaining points were classified as one of four types. Points were classified as 'mobile' if both the preceding and following points were greater than 100 m away. Points where the preceding or following fix was within 100m were classified as 'stationary', although it is not known whether the bird was truly

stationary (i.e. on the ground) or restricting its movement to a small area. The first cluster of stationary points for each evening were classified as the ‘start location’ (i.e. all points until the first movement > 100 m was made). The final cluster of stationary points was classified as the ‘finish location’. If the bird was already moving when the logger started recording, or was still moving when recording ended, the first single fix or last single fix were classed as the ‘start’ or ‘finish’ location. Points classified as ‘start’ or ‘finish’ locations were excluded from analyses, as these are likely to reflect roosting habitat and nocturnal feeding habitat respectively, rather than habitat associated with roding. Fixes for which the preceding or following fix was separated by an interval ≥ 2 minutes were excluded (this occurred if the tag failed to successfully take a fix or if 2 consecutive points were removed during filtering).

Compositional analysis of habitat use compares the habitats observed at animal-tracking locations to those available within a wider area, usually an estimated home-range (Aebischer *et al.* 1993). The intention here is to compare locations at which a tagged woodcock was recorded during the roding period, to the broader habitat available to the bird within an equivalent range. The latter, hereafter termed ‘potential roding range’, was estimated by drawing a circular buffer around the individual’s first location with a radius equal to the straight-line distance between the start location and the furthest subsequent point recorded that evening (*f*) (Fig. 7.3). This meant that the size of the circle varied from one bird-day to the next but was constrained by the

mobility of the tagged individual on that day. This method was chosen over a fixed radius based on pooled data from all tagged woodcock as a) extent of movement may be constrained by factors that vary between individuals and b) some tagged woodcock covered very large roding areas, which would inflate the potential roding ranges for other birds.

7.2.3 Woodland data

Woodland habitat data were compiled by combining two different Forestry Commission (FC) datasets: the National Forest Estate dataset (Forestry Commission 2019a) and the National Forest Inventory (Forestry Commission 2019b). The National Forest Estate (NFE) dataset provides comprehensive woodland data, relating to habitat type, tree species and planting date of forested sub-compartments within FC-managed woodland as well as additional information relating to within-wood open areas. Within-wood service roads are mapped as spatial lines in a separate data file. The National Forest Inventory (NFI) provides lower levels of detail but features data for all woods, including those that are not managed by the FC. NFI habitats are classified using satellite imagery to distinguish between broad differences in types of closed canopy woodland (e.g. broadleaved, coniferous) and open areas (e.g. grass, heathland, felled etc) (Forestry Commission 2018). NFE data are available for the majority of the study site including all of Sherwood Pines and Park Forest, and 70.7 % of Birklands Forest. NFE data are not available for the Sherwood Forest NNR within Birklands

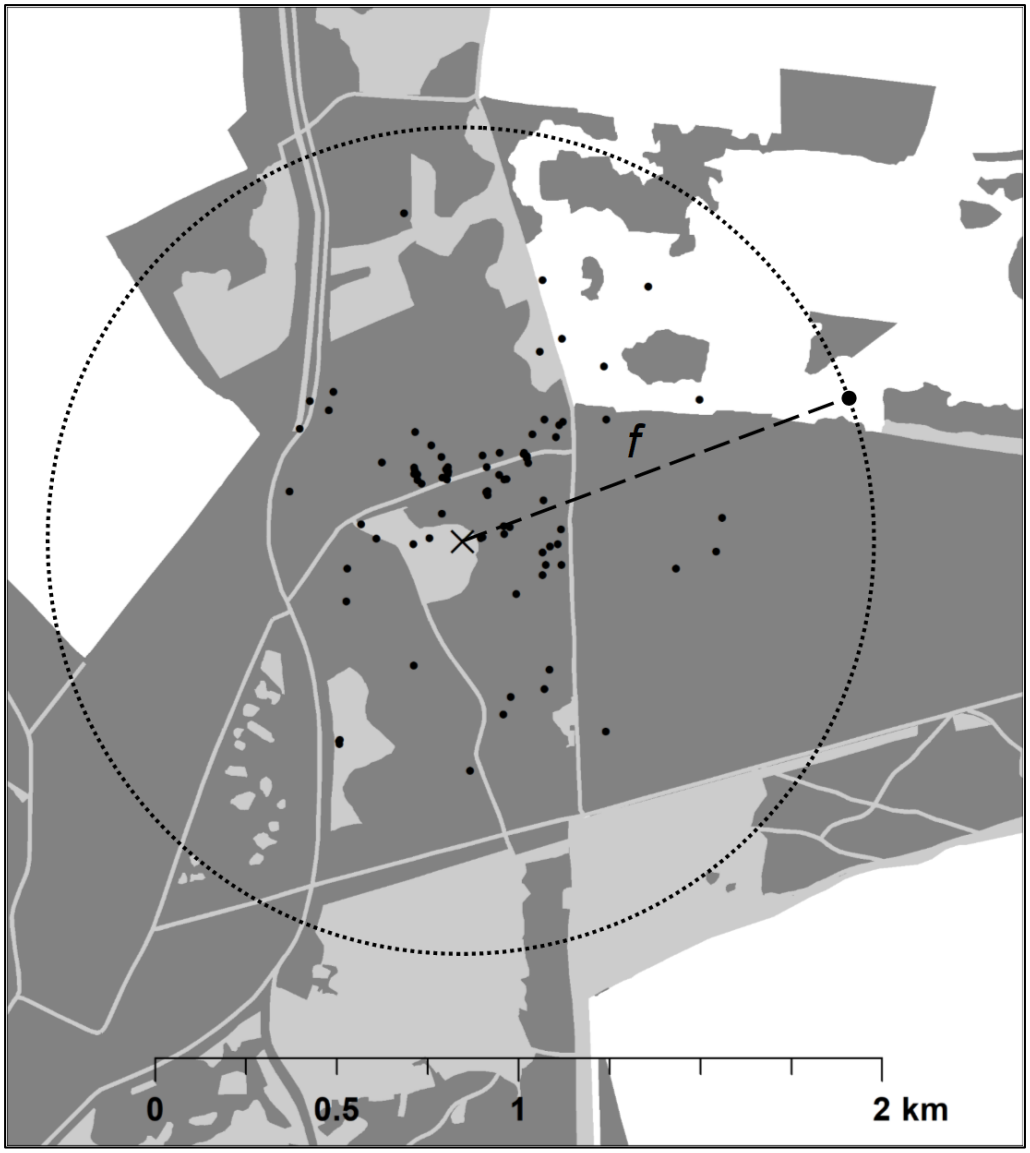


Figure 7.3 Calculation of the 'potential roding range' i.e. a circular buffer with a radius of f (dotted line). f = the distance between the starting location and the furthest subsequent point (dashed line). Shading represents three main habitat groupings: closed canopy woodland (dark grey), open space within woodland (light grey), non-woodland (white).

Forest, but this consists almost entirely of closed canopy ancient oak woodland except for a few open areas which are mapped by the NFI.

The NFE and NFI were used to categorise all within-wood sub-compartments (i.e. ‘stands’) into one of three closed woodland categories (broadleaf, conifer and unknown) or three open woodland categories (permanent open spaces; clearfells and young restocks; and

other open). Categorisation was based upon the primary habitat data provided by the NFE dataset or, if this was not available, the land-use categories given in the NFI.

The NFI's 'mixed mainly broadleaved' and 'mixed mainly conifer' categories were classified as 'broadleaf' and 'conifer' respectively. The 'permanent open' category includes all areas classified as grassland or heathland as well as grassy mown public amenities such as car parks, picnic areas, verges and tracks. Tracks and verges were incorporated by using the NFE roads dataset (Forestry Commission 2019c) and buffering the spatial lines with a flat-ended 6-m radius buffer (Forestry Commission tracks are approximately 12 m wide when measured on Google Earth (Google 2019)). The 'clearfell and young restocks' category includes most temporary open habitats within woodland such as those classified as felled, burnt or bare as well as areas that have been prepared for replanting or replanted during the period 2010-2018. This designation combines sites that are structurally similar; both clearfells and replanted sites tend to have patchy vegetation (bracken/herbs) and areas of bare earth or brash. The 'other open' category consists of other open features not covered by the three other categories; within this study site this mostly means establishing trees that have not yet reached the mature, closed canopy stage.

For GPS locations recorded within woodland, 87% were in areas classified according to the NFE rather than the NFI. Within potential roding ranges, 73.1% of woodland habitats were classified based upon the NFE. The NFI tended to be required more often for birds which

roded over larger areas and moved further from the core study site. Although the NFE is generally more reliable, the origin of the source data are unlikely to produce large discrepancies in the classification here given the broad woodland categories used.

A seventh woodland category, ‘edge woodland’, was created for areas classified as ‘closed broadleaf’, ‘closed conifer’ or ‘closed unknown’, that were within 30 m of an open woodland habitat. It was not applied to closed woodlands within 30m of a non-woodland habitat (i.e. the outer perimeter of the woodland block). The 30 m buffer was chosen to slightly exceed the 22 m standard deviation in distance from tag locations and their centroid based on static locations (see Section 6.2.3).

Non-woodland habitats were divided into three categories: ‘urban’, ‘farmland’ and ‘other’. Urban areas (villages and towns) within buffer areas were manually digitised using a 1:25000 Ordnance Survey map (Ordnance Survey 2018) as a base. Non-farmland features were also manually digitised in the same manner, and included colliery spoil areas, golf courses, parkland, large lakes and the lowland heath of Budby Common. All remaining intervening space was then classified as ‘farmland’, by far the commonest non-woodland habitat, although this does in reality include some non-farmland habitats such as public roads, isolated buildings and some industrial areas outside of conurbations. Habitat classification was performed in ArcGIS 10.6 (ESRI 2019) (union of polygons, addition of stand-edge woodland,

manual checking) and R 3.5.2 (R Development Core Team 2019) (automated classification based on source data).

7.2.4 Analysis

The total distance flown during the display period was calculated by summing all straight-line paths between consecutive points > 100 m. Those less than 100 m, i.e. that occur during stationary periods, are unlikely to represent display behaviour and may be exaggerated by tag error (static locations often appear as a spiky cluster of back-and-forth movements, even for test data where the tag has remained completely stationary). The duration of each continuous period of movement was calculated and used to produce a mean value for each bird. I also calculated the mean number of stationary periods per bird-day and the mean duration of each stationary period or 'break' from roding.

Compositional analysis was used to compare GPS-locations to potential roding ranges. Points classified as mobile and stationary were analysed separately to account for possible differences between display and mid-display breaks. For each bird-day, I calculated the percentage of the mobile points that intersected each of the ten habitats and the percentage of the potential roding range occupied by each habitat. These percentages were averaged for each bird to ensure individuals tracked for longer periods of time did not have a greater influence in the analysis (i.e. each bird represented a row of data, rather than each bird-day). If a bird was not recorded within a given habitat, or the habitat did not occur within the potential roding range

buffer, the percentage was set to 0.01 (for comparison, the lowest non-zero percentage recorded for any habitat was 0.1%).

I followed the method for compositional analysis outlined in Aebischer *et al.* (1993) to test whether the habitats occurring at GPS-locations differed in their proportions from those available within the potential roding range. For each bird, the proportion of points recorded within each habitat were transformed to log-ratios using the proportion of closed conifer as the denominator. The same was done for the proportions in which the habitats occurred within the corresponding potential roding range. The differences between pairs of utilised and available habitat log-ratios were calculated. These differences were used to calculate a matrix of raw sums of squares and cross products (R_2), and a matrix of mean-corrected sums of squares and cross-products (R_1). A generalised likelihood ratio statistic (Λ) was calculated by dividing the determinant of R_1 by the determinant of R_2. A chi-square test statistic was calculated as the natural log of Λ multiplied by the sample size and was used to estimate *P*-values (Aebischer *et al.*1993).

The process described above provides a statistical means of distinguishing 'non-random' habitat use but does not indicate specifically which habitats are more or less favoured. To do this, habitat use is ranked. For a given pair of habitats, X_i and X_j, d_{ij} was calculated as:

$$d_{ij} = \ln\left(\frac{X_{Uj}}{X_{Ui}}\right) - \left(\frac{X_{Aj}}{X_{Ai}}\right)$$

where U denotes the proportions of X_i and X_j utilised by the bird and A denotes the proportions available. The value d_{ij} is calculated for every

pairwise combination of the ten habitats and used to populate a matrix for each bird. In these matrices, more frequently used habitats will have a higher number of positive values per row and can be used to rank the habitat in order of its relative use. A table of ratio means and standard errors was produced by combining the tables of all individuals. Ratio means provide *t*-values to indicate where non-random habitat use occurs and estimate *P*-values (Aebischer *et al.* 1993).

This process was applied to roding and stationary GPS locations separately. In each case, the process was repeated with non-woodland habitats excluded and percentages corrected to reflect the proportion of the wooded area represented by each of the seven woodland categories.

I used a linear mixed model (LMM) to test whether the availability of open habitats influenced how widely each tagged woodcock ranged. Given the difficulties associated with calculating unbiased estimates of roding ground size (Chapter 6), I used the natural log of *f*, the distance between the start point and the furthest subsequent point, as the dependent variable. Logging brought the values of f closer to a normal distribution. The proportion of the potential roding range occupied by open woodland habitats was specified as the explanatory variable. The bird's identity (ring number) was provided as a random effect.

7.3 Results

In total, 45 male woodcock were tagged during the three study years. Thirty-seven of these tags were recovered, 27 completed at least one

full 90-minute recording period and 16 performed roding behaviour on at least one evening.

Catching 45 males required 94 catching sessions. The habitats in which these capture attempts were carried out, and those that were successful, are summarised in Table 7.1. Four of these birds were caught and retagged in subsequent years, and in three cases these were on different clearing types.

Table 7.1 Table summarising the habitats within which catching was attempted and those in which catching attempts were successful. Usable data was only acquired from a subsample of the birds caught, details of which are provided in the third column, but the likelihood of roding data being recorded is unlikely to be influenced by the habitat at the initial capture site.

	attempted catching sites	successful catching sites	capture sites of males providing roding data
Temporary clearfells or newly planted areas	56.3%	58.0%	31.3%
Permanent clearings e.g. heaths and grassy areas	32.9%	28.0%	56.3%
Tracks or rides	7.4%	10.0%	12.5%
Outside woodland	3.1%	4.0%	0%

Roding woodcock flew an average of 13.3 ± 6.14 km (1 SD) per evening split over one to seven flights. Each display included one, or occasionally two, long continuous flights greater than 15 minutes. Excluding short flights (< 3 minutes) typically occurring at the start and end of the roding period, the average period of continuous movement lasted 13.5 minutes but could be up to 49 minutes. Woodcock took up

to six breaks during roding which lasted between 1 and 39 minutes each (mean = 10.3 ± 8.2 minutes (1 SD)). On average, 35% of stationary locations per bird were recorded in open spaces within woodland, rising to 62% when edge woodland (i.e. within 30m of a clearing) was also included (Figs. 7.4 and 7.5).

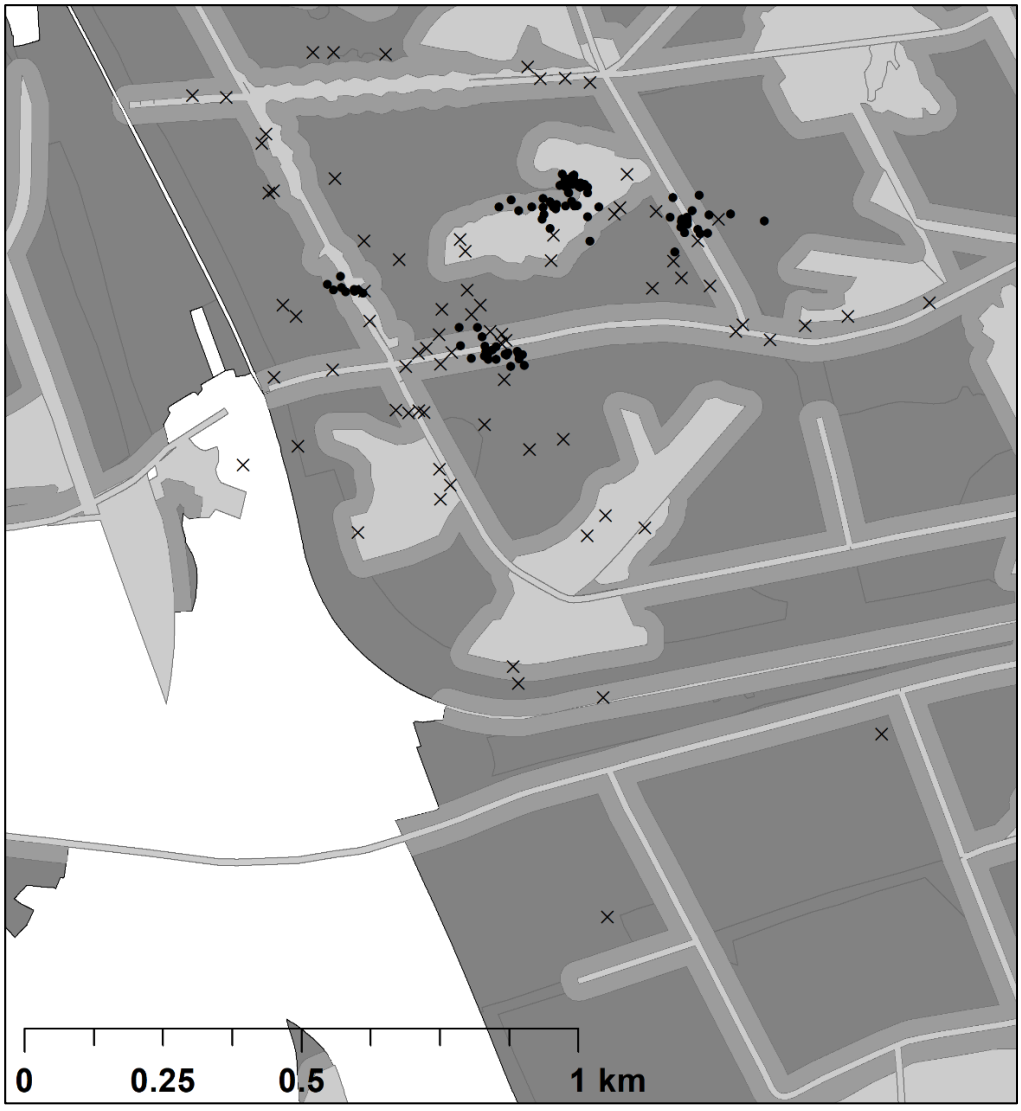


Figure 7.4 GPS-tracking data for a single woodcock recorded over one 90-minute roding period. Black circles represent locations where the woodcock stopped during roding. This excludes the first cluster of locations, most likely the birds diurnal roost, and the final cluster of locations, usually a feeding site or nocturnal roost. Crosses represent GPS locations recorded during periods of movement. Shading represents four habitat types: closed canopy woodland (dark grey), edge woodland (mid grey), open habitats within woodland (light grey) and non-woodland (white).



Figure 7.5 GPS-tracking data for a single woodcock recorded over two 90-minute roding periods in two consecutive evenings. Black circles represent locations where the woodcock stopped during roding. Crosses represent GPS locations recorded during periods of movement. Shading represents four habitat types: closed canopy woodland (dark grey), edge woodland (mid grey), open habitats within woodland (light grey) and non-woodland (white).

The maximum distance from start point, used to calculate the radii of potential roding ranges (*f)*, ranged from 0.59 – 9.15 km with a mean of 1.95 ± 1.72 km (1 SD). The value of *f* was negatively correlated to the amount of open woodland habitats occurring within the bird's potential roding range (*Est* = - 0.036 ± 0.015*, P* = 0.023).

Simplified habitat rankings are shown in Tables 7.2a and 7.2b and the mean t-values and standard errors from which they derived are found in Supplementary Tables 4 and 5. Habitat use was non-random during active periods of roding (Λ = 0.07, χ^2_9 = 42.647 p < 0.001) and during stationary periods (Λ = 0.11, χ^2_9 = 33.357, p < 0.001). This was significant even when non-woodland habitats were excluded, suggesting a preference for some woodland habitats over others (mobile: Λ = 0.236, χ^2_6 = 23.092 p < 0.001, stationary: Λ = 0.109, χ^2_6 = 33.872, p < 0.001). Woodcock were more likely to move over 'permanent open spaces', 'stand-edge woodland' and 'closed conifer' than any of the non-woodland habitats (Table 7.2a and Suppl. Table 4). 'Permanent open spaces' and 'edge woodland' were also significantly more likely to be roded over than 'clearfell and young restocks' and 'other open' areas, but 'closed conifer' was not (Table 7.2a and Suppl. Table 4).

Woodcock were significantly more likely to spend stationary periods of time in 'permanent open spaces' or 'edge woodland' than in 'closed broadleaf', 'closed conifer', 'closed unknown' or any non-woodland categories (Table 7.2b and Suppl. Table 5). 'Permanent open' and 'edge woodland' were the two highest-ranking categories

although there was no significant difference between one another (t_{15} = 0.63 ± 0.33, P = 0.072). 'Permanent open spaces' were significantly favoured over 'clearfell and young restocks' t_{15} = 2.03 ± 0.88, *P* = 0.036), but 'stand-edge woodland' was not (t_{15} = 1.40 ± 0.98, *P* = 0.174).

Table 7.2 Ranking matrices showing pairwise comparison of habitats used during (a) periods of roding movement and (b) mid-roding stationary periods (overleaf). Every pairwise combination of habitats is compared following the method outlined in Section 7.2.2. Symbols demonstrate the use of the habitats listed in horizontal rows in relation to those in the columns e.g. 'Permanent open' was used more, relative to its availability, than all other habitats. The use of a triple sign denotes those that were statistically significant at P < 0.05 based on the t-values provided in Supplementary Tables 4 and 5.

(a)	**NON WOODLAND**			**OPEN WOODLAND**			**CLOSED WOODLAND**				
	Agricultural	**Urban**	**Other non-woodland**	**Permanent open**	**Clearfell and young restock**	**Other open woodland**	**Closed Broadleaf**	**Closed Conifer**	**Closed Unknown**	**Edge Woodland**	**RANK**
Agri.		+	-	---	-	-	-	---	---	---	9
Urban	-		-	---	-	-	-	---	---	---	10
O. non	+	+		---	-	-	-	---	-	---	8
Perm.	**+++**	**+++**	**+++**		**+++**	**+++**	**+++**	+	+	+	1
C & Y R	+	+	+	---		+	-	-	-	---	6
O. open	+	+	+	---	-		-	-	-	---	7
Broad	+	+	+	---	+	+		-	-	-	5
Conifer	**+++**	**+++**	**+++**	-	+	+	+		+	-	3
Cl. Un.	**+++**	**+++**	+	-	+	+	+	-		-	4
Edge	**+++**	**+++**	**+++**	-	**+++**	**+++**	+	+	+		2

Table 7.2 contd.

(b)	NON WOODLAND			OPEN WOODLAND			CLOSED WOODLAND				
	Agricultural	**Urban**	**Other non-woodland**	**Permanent open**	**Clearfell and young restock**	**Other open woodland**	**Closed Broadleaf**	**Closed Conifer**	**Closed Unknown**	**Edge Woodland**	**RANK**
Agri.		-	-	---	-	+	-	---	---	---	9
Urban	+		-	---	-	+	-	---	---	---	8
O. non	+	+		---	-	+	-	---	---	---	7
Perm.	**+++**	**+++**	**+++**		**+++**	**+++**	**+++**	**+++**	**+++**	+	1
C & Y R	+	+	+	---		**+++**	+	-	-	-	5
O. open	-	-	-	---	---		-	---	---	---	10
Broad	+	+	+	---	-	+		-	-	---	6
Conifer	**+++**	**+++**	**+++**	---	+	**+++**	+		-	---	4
Cl. Un.	**+++**	**+++**	**+++**	---	+	**+++**	+	+		---	3
Edge	**+++**	**+++**	**+++**	-	+	**+++**	**+++**	**+++**	**+++**		2

7.4 Discussion

It is often stated that woodcock prefer to display over woodland clearings and rides but, until now, there has been little evidence of this beyond field observations (Tester & Watson 1973; Nethersole-Thompson & Nethersole-Thompson 1986). The telemetry data analysed here, however, generally support existing ideas regarding roding and habitat use. The observed preference for permanent open areas and edge woodland is consistent with the prevailing understanding of roding behaviour as a means of sexual selection similar to a lek (Hirons 1980; Hoodless 1995). Female woodcock assess male quality based on their roding call and/or flight and open

areas, given the lack of physical obstructions, make it easier for females to see and hear potential mates and for males to see the signals of receptive females (Hoodless 1995). By focussing their display behaviour towards these areas, males should be more likely to encounter females.

This is clearest in the analysis of ‘stationary’ locations which tend to be well-defined clusters of GPS points spanning the edges of permanent clearings and the adjacent woodland. Male woodcock may be vulnerable to predators (Hoodless & Coulson 1994; Selås 2015; Verdal & Selås 2010; Bergman 1961), especially when on the ground, and it is possible that they remain close to the edge of closed canopy woodland to improve their chance of escape. Almost all roding sessions include one or more stationary periods lasting several minutes and it seems likely that most are spent resting or feeding rather than interacting with females. This behaviour was observed during a preliminary visit to a catch site when a roding woodcock landed in a clearing and fed intensely until disturbed (also observed by Hirons 1983). Clearings may provide better foraging opportunities as grassy glades or verges are likely to support higher earthworm densities than neighbouring closed-canopy woodland (Duriez, Ferrand, *et al.* 2005). If edges of clearings are safer for male woodcock, the same ought to be true for females too, and males may be favouring edges both to reduce their own predation risk and increase the likelihood of encountering females. The tendency to remain close to the edges of clearings may also support the theory proposed by Hirons (1983) that roding activity is

greatest around suitable nesting habitat, as it is suggested that woodcock prefer to nest in edge woodland (Fokin *et al.* 2013).

The observed preference for permanent, rather than temporary, clearings may be driven by their spatial arrangement rather than the habitat itself. Permanent clearings were mostly narrow rides and small glades, meaning that each was associated with a proportionally greater area of edge habitat and were distributed more widely than clearfells which tended to occur in a small number of larger blocks. Grassy permanent clearings may offer better feeding opportunities than clearfells, but the preference is unlikely to be purely driven by food availability, as woodcock were observed feeding on clearfells during this study (field observations with thermal-imaging equipment/unpublished radio-telemetry data).

The analysis of the habitats passed over during display flights showed a weaker association with open habitats and there was no significant preference for permanent open spaces or woodland edge over closed conifer wood. The tracking data sometimes show male woodcock following linear open features while moving between clearings, but only loosely, and given that rides and tracks tend to be narrow, woodcock following them are as likely to be recorded over neighbouring edge woodland, or closed conifer when cutting corners, as they are the track itself. This is likely to be exaggerated by the small errors associated with the GPS-loggers. Effective display behaviour may be a compromise between covering suitable habitat patches (i.e. clearings) and covering large enough areas of woodland to access

multiple patches. This may be supported by the fact that males roding in areas containing a higher proportion of permanent woodland clearings tended to display over more confined areas. All tagged male woodcock incorporated multiple clearings into their roding flights, so such wide-ranging movements do not appear to be caused solely by displacement during male-male interactions.

The high degree of mobility is the main characteristic of the woodcock's display that diverges from the traditional view of a lek (Morales *et al.* 2001); males do not aggregate or display within a restricted location. This is in contrast to the American woodcock *Scolopax minor*, which displays in loose aggregations at established singing grounds (Ellingwood *et al.* 1993). The hotspot hypothesis suggests that leks develop in areas where higher female densities already occur (Bradbury *et al.* 1989; Schroeder & White 1993). Assuming their display does constitute an atypical lek, these explanations may be consistent with the Eurasian woodcock's display but, owing to low female densities or higher male-male competition, males visit multiple 'hotspots' (i.e. clearings) per evening to increase their chance of mating.

The woodcock tracked during this study were mostly caught in clearings and it is logical to suggest that this might bias its findings, but all were highly mobile when roding and included a wide range of habitats within their roding ground. Woodcock were attracted to mist-nets with an audible decoy which could be detected by individuals flying over nearby closed canopy woodland as well as the clearing itself.

Catching effort was spread across different clearing types and our tagged cohort includes birds caught on clearfells and non-woodland habitats as well as permanent clearings. While this is an important consideration of any study of habitat choice, the habitat in which a bird was captured is unlikely to have a large effect on the findings presented here.

Although woodcock appear to favour permanent clearings and woodland edges while roding, it is currently unclear whether these habitats are an essential component of woodcock home ranges and whether woodcock cease to breed in woods where these features are no longer present. The analysis of habitat associations presented in Chapter 3 found no relationship between roding count results and the area of open woodland habitats within a 1-km or 2-km buffer of the count point. The survey's methodology, however, stipulates that counts must be conducted from 'a clearing or the intersection of two rides' (British Trust for Ornithology 2013) and, although survey squares are selected at random, count points necessarily target the most suitable area within those squares to provide accurate presence/absence data at the 1-km square level. The analysis in Chapter 3 did not distinguish between clearfells and permanent open features, and sites with very high proportions of open space are probably those containing extensive clearfells rather than the network of permanent rides and clearings that are more likely to be favoured. A more sensitive approach is required to tease out whether the relationship with open space identified on the

individual level has a broader effect on site use or local population change.

Examples of birds whose declines are driven purely by the loss of display habitat are hard to find, but this is largely because display habitat is intrinsically linked to broader breeding habitat requirements, with display and nesting often occurring in close proximity (Hirons 1983). This could be the case for woodcock and roding activity may provide an indication of general breeding habitat suitability on a localised within-wood scale. Woodland management that provides more permanent clearings might benefit breeding woodcock by creating display sites, feeding sites (clearings) and brood-rearing sites (edge woodland/young woodland) (Hoodless & Hirons 2007; Fokin *et al.* 2013) with roding activity acting as an overall indicator of the effectiveness of such measures.

7.4.1 Suggestions for further research

Further research into habitat use during display should focus on the aspects with the greatest practical benefit. Firstly, it would be beneficial to know how habitat use varies at sites with differing amounts of open space and whether woodcock cease to breed at sites where the proportion of open space passes beneath a certain threshold. To help understand this, roding activity could be measured over time in areas where open features are maintained or created alongside those where they have been lost. With the corresponding habitat data, this could be a future application for the national survey data.

Secondly, it would be beneficial to know whether there are particular characteristics of permanent clearings that may make them more or less attractive. One hypothesis might be that clearings are of greater benefit when the vegetation is shorter assuming that this allows clearer visual signalling between males and females and provide easier foraging than those dominated by bracken *Pteridium aquilinum* or other tall vegetation. Cramp *et al.* (1983) proposes that courtship requires sites where woodcock can easily move on the ground. Understanding habitat preferences more clearly would require some indication of woodcock behaviour. GPS-loggers combined with accelerometers (Bouten *et al.* 2013) or other movement-sensitive tags (Hirons & Owen 1982) would allow flight periods to be distinguished from time spent on the ground and may even be able to distinguish specific behaviours e.g. feeding vs resting, roding vs. non-roding flight.

Finally, our understanding of habitat use, and the woodcock's mating system more generally, would be improved by a comprehensive study of female behaviour using similar GPS-tracking techniques as those employed here. Any future research into breeding females is more likely to focus on nest-site selection and brood-rearing than mate choice and pre-breeding habitat use, but this may be beneficial nevertheless if it provides more conclusive evidence to explain the link between nesting habitat and display sites.

8 DISCUSSION

8.1 Size, trend, and distribution of Britain's resident population

Following an established method, Britain's woodcock population was estimated at 55,241 males (95% CL: 41,806 – 69,004). Although Chapter 5 identifies the method's sensitivity to certain assumptions, it currently provides the best available estimate of trend. Between 2003 and 2013, woodcock abundance declined by 29%, supporting previous suggestions (Noble *et al.* 2007), based on changes in occupancy (Gibbons *et al.* 1993), that woodcock populations are undergoing significant declines. The scale of change varies according to differences in the way declines have been measured (occupancy vs. abundance, variation in spatial scale) or the exact periods considered. Comparisons between declines in occupancy are fairer as earlier estimates of abundance are less reliable. These include a 56% decline in occupied 10x10-km squares between 1970 and 2010 (Chapter 2, Bird Atlas data); a 31% decline in occupied 10x10-km squares between 1990 and 2010 (Chapter 2, Bird Atlas data); and an estimated 37% decline in occupied 1x1-km squares between 2003 and 2013 (Chapter 2, Breeding Woodcock Survey data and Heward *et al.* 2015).

Assessments of population trends prior to 1970 are only available from anecdotal sources but generally suggest very infrequent breeding in Britain prior to c. 1820, with marked population increases thereafter (Holloway 2002). By the end of the 19th Century woodcock were thought to breed in almost all counties in England and Scotland,

including Cornwall and Devon (Holloway 2002; Alexander 1945). This expansion is usually attributed to the planting of new woodland and widespread removal of many of the species' predators during this period (Holloway 2002; More 1865), but it is possible that climate also played a role (Gibbons *et al.* 1993). In some areas these increases continued through the early 20th Century (Alexander 1945) and it is likely that declines captured from 1968 onwards began only shortly before the start of the atlas monitoring period (Cramp *et al.* 1983).

By the start of the national Breeding Woodcock Survey in 2003, woodcock were already absent from most of South-west Britain. Continuing declines have seen the population retract further eastward, with very few occupied 10x10-km squares remaining in Wales and the Midlands. This pattern of decline is a mirror image of their expansion in the 19th Century (Alexander 1945; Holloway 2002; Chapter 2), showing a retraction to core areas in Northern England and parts of Scotland. The rapid historic expansion of the woodcock population following periods of forestry planting suggests a relationship with young woodland, but this has been difficult to demonstrate.

8.2 Woodcock and habitat

The present study adds to existing knowledge regarding the woodcock's breeding habitat (Ferrand 1983; Hirons 1988; Hoodless & Hirons 2007; Machado, Brito, *et al.* 2008) and is the first assessment of habitat associations on a national scale in Britain. Where previous studies have focussed on individual-based habitat use (Hirons &

Johnson 1987; Hirons 1988) the breadth of sites included here have allowed a broader assessment of landscape-scale habitat characteristics.

Woodcock abundance displayed strong correlations with total woodland area over large landscape scales. For any species, population size inevitably depends on the available area of suitable habitat, but here this relationship is skewed towards the most heavily wooded regions. Many less wooded sites, although historically occupied (Holloway 2002), no longer support breeding woodcock (Balmer *et al.* 2013). The retraction to heavily wooded regions may simply be the first sign of a universal decline, with smaller populations in isolated habitat patches being more susceptible to local extinctions (Fahrig & Merriam 1985; Verboom *et al.* 2009). Alternatively, it may reflect the fact that some important habitat features are more likely to have been retained in large woods.

There was an interaction between woodcock abundance, the area of broadleaf woodland and total woodland area, implying that woodland area does not act in isolation as a driver of higher abundance. Some of the most heavily wooded landscapes in Britain are dominated by conifer (Mason 2007; Morton *et al.* 2014) but this finding implies that these are more commonly used by woodcock if they also contain broadleaf stands; something that may also be reflected in the observed relationship with heterogeneity. It would be useful to study in greater detail the relationship between woodland area, patch connectivity and structural heterogeneity. The frequency and type of

forestry management practised are likely to interact with all three as felling and replanting are more likely to occur in large woods and provide a source of habitat heterogeneity.

For the most part, the findings of the landscape-scale analyses correspond to those of the smaller-scale analysis and of existing individual-based studies using radio-telemetry. Radio-telemetry studies have found associations with particular types of woodland, such as stands of young dense sycamores *Acer pseudoplatanus* or birch *Betula pendula* thickets (Hoodless & Hirons 2007), which vary according to the study site. It is likely that associations of this kind are driven by the woodland structure (e.g. tree density or ground cover density), or an underlying relationship with soil type or moisture, rather than specific plant species. This is probably the case for the observed relationship with birch stands in the analysis of survey sites presented here as birch is the commonest species in dense early successional stands in upland woods (Spracklen *et al.* 2013).

A direct relationship with young stands and open space within woodland was not borne out by the analysis of National Forest Inventory data, but the requirement for some young woodland and open areas may be another potential explanation for the observed significance of woodland heterogeneity (which is based on the relative availability of mature conifer, mature deciduous, mature mixed, young, open and coppice). A targeted analysis of young woodland and open space would require more detailed habitat mapping since the satellite mapping method of the NFI is unable to identify small open spaces or

distinguish subtle differences in woodland age. This analysis should take the view that the relationship is likely to be non-linear, assuming that open space needs to be balanced by large areas of adjacent closed woodland.

Open space was visited frequently during the roding displays of GPS-tagged woodcock. Given that the display requires contact between a male in the air and a female on the ground (Cramp *et al.* 1983), the preference for clearings and open rides might seem self-explanatory. But it is not known whether this habitat association is a product of their aerial display or whether a pre-existing preference for clearings has driven the display's evolution. If females are patchily distributed, owing to a preference for clearings or woodland edges, the male's wandering display may have developed to search for females over a network of suitable patches (see section 8.3 and Ostermeyer & Ferrand 1979). Open spaces or the woodland around them may offer more profitable feeding sites during the breeding season (Edwards & Bohlen 1996) or edge woodland may have more suitable tree densities or ground flora composition for nest concealment (Nemetschek 1977; Gossmann *et al.* 2017).

Apart from urban area, which is likely a proxy for human disturbance (Liley & Clarke 2003), surrounding non-woodland habitats did not correlate with breeding woodcock abundance. Grasslands are widely used as nocturnal feeding sites during winter (Duriez, Ferrand, *et al.* 2005), but this is reduced in summer (Hoodless & Hirons 2007), probably because breeding woodcock with chicks are less mobile;

because grasslands are less suitable owing to taller vegetation; or because earthworms are less readily available here in summer (Edwards & Bohlen 1996). The only habitat of potential importance, which was not considered, is heather moorland and heathland which some sources suggest are the only non-woodland habitat regularly used by nesting females and those with broods (Hoodless 1995; Morgan & Shorten 1974).

Woodcock habitat use in Britain ought to be framed by a wider understanding of habitat use across the rest of the species' Eurasian range. It is unknown whether British-breeding woodcock favour woodlands that resemble those at the core of the species' range or have different habitat preferences in Britain. Woodcock breeding on Atlantic islands, such as the Azores and the Canary Islands, breed in laurisilva forests and tree-heath *Erica arborea* scrub (Bannerman 1963; Machado, Brito, *et al.* 2008) demonstrating the ability to adapt to regions that are very different to their core range. The observations made here, regarding the woodcock's association for large heterogenous woods, could feasibly apply to woodcock at the core of the range. In Russia, for example, industrial timber removal is widespread across the woodcock's range, and mature forest blocks are often interspersed with regenerating cleared areas, even in more remote regions (Food and Agriculture Organization of the United Nations 2012). This has resulted in an increase in the proportion of woodland occupied by birch and aspen *Populus tremula* (Food and Agriculture Organization of the United Nations 2012) which, although

potentially detrimental to species associated with undisturbed interior boreal forest, may benefit woodcock. In a more natural system, open space is created by fire and the death of individual trees (Angelstam & Kuuluvainen 2004), and maintained by large herbivores such as elk *Alces alces* and roe deer *Capreolus capreolus* (Abaturov & Smirnov 2002; Angelstam *et al.* 2000; Linder *et al.* 1997), promoting the diversity of structure and age that is thought to be important.

The habitat associations explored in this study help explain woodcock distributions at two points in time, but future studies should focus specifically on how changes to the habitats identified as important directly influence abundance over time. The ten-year interval between the 2003 and 2013 national surveys may not be long enough to demonstrate clear links between woodland age, structure and declining population trends, but if a third national survey is completed in 2023 this will provide a long-term dataset that is better suited to such an analysis.

8.2.1 Woodland management for woodcock and other species

The evidence presented here and in earlier sources (Hoodless & Hirons 2007) suggests several mechanisms by woodcock habitat may be influenced by woodland management. The next step is to explicitly test for causal links and separate the anthropogenic factors that have direct effects on woodcock populations from those which correlate as the result of underlying relationships with region, woodland type and wooded area.

The eventual aim of a study like this would be to propose a suite of management recommendations that promote the maintenance of suitable woodcock breeding habitat. The intention would be to tailor current management techniques to maximise their benefit and encourage the uptake of some management at sites where it has completely ceased. As a popular quarry species (PACEC 2014), the woodcock has a cultural value to many landowners, which might provide an incentive to adopt woodland management techniques with wider benefits.

Most of the possible management options are currently too speculative to recommend, but the present study, and those before it (Hoodless & Hirons 2007), highlight areas worth exploring further. Maintaining open rides or a well-connected network of clearings would encourage roding behaviour, but at a population-level, the benefits to females and their broods ought to be quantified to test this recommendation's value. Allowing the natural regeneration of some felled stands will create areas of young dense woodland. Combining these options, woodland management recommendations for woodcock might include providing both permanent and temporary clearings in close proximity, with the latter being allowed to naturally regenerate from the open clearings used for display and nocturnal feeding (this study and Hirons and Johnson 1987), towards the dense thickets preferred for roosting and brood rearing (Hoodless & Hirons 2007). An important topic for future research, assuming such suggestions are proven to be beneficial, would be to investigate the optimum size of

clearings and the optimum proportion of open and young woodland within a given site.

Such recommendations may offer benefits to other woodland species. Most British woodland butterflies favour open glades/adjacent woodland e.g. silver-washed fritillary *Argynnis paphia*, small pearl-bordered fritillary *Boloria selene*, wood white *Leptidea sinapis* (Robertson *et al.* 1995) and some species require young growth woodland e.g. high brown fritillary *Argynnis adippe*, pearl-bordered fritillary *Boloria euphrosyne*, heath fritillary *Melitaea athalia* (Robertson *et al.* 1995). Birds associated with open space within woodlands, particularly European nightjar *Caprimulgus europaeus* (Langston, Wotton, *et al.* 2007; Sharps *et al.* 2015), tree pipit *Anthus trivialis* (Burton 2007) and woodlark *Lullula arborea* (Langston, Wotton, *et al.* 2007) use recently cleared areas as nest sites (Hewson *et al.* 2011).

8.3 Roding behaviour

The study presented here shows that daily roding ranges are large with means likely to be in the region of 1.11 km^2 to 1.29 km^2 depending on the method of measurement. The sixteen woodcock for which roding data were recorded displayed a high degree of variation between individuals (range = 0.36 – 2.63 km^2, SD = 66.3, based on the Brownian bridge method). One roding male alternated between two roding grounds 10 km apart, moving between these sites in a single night.

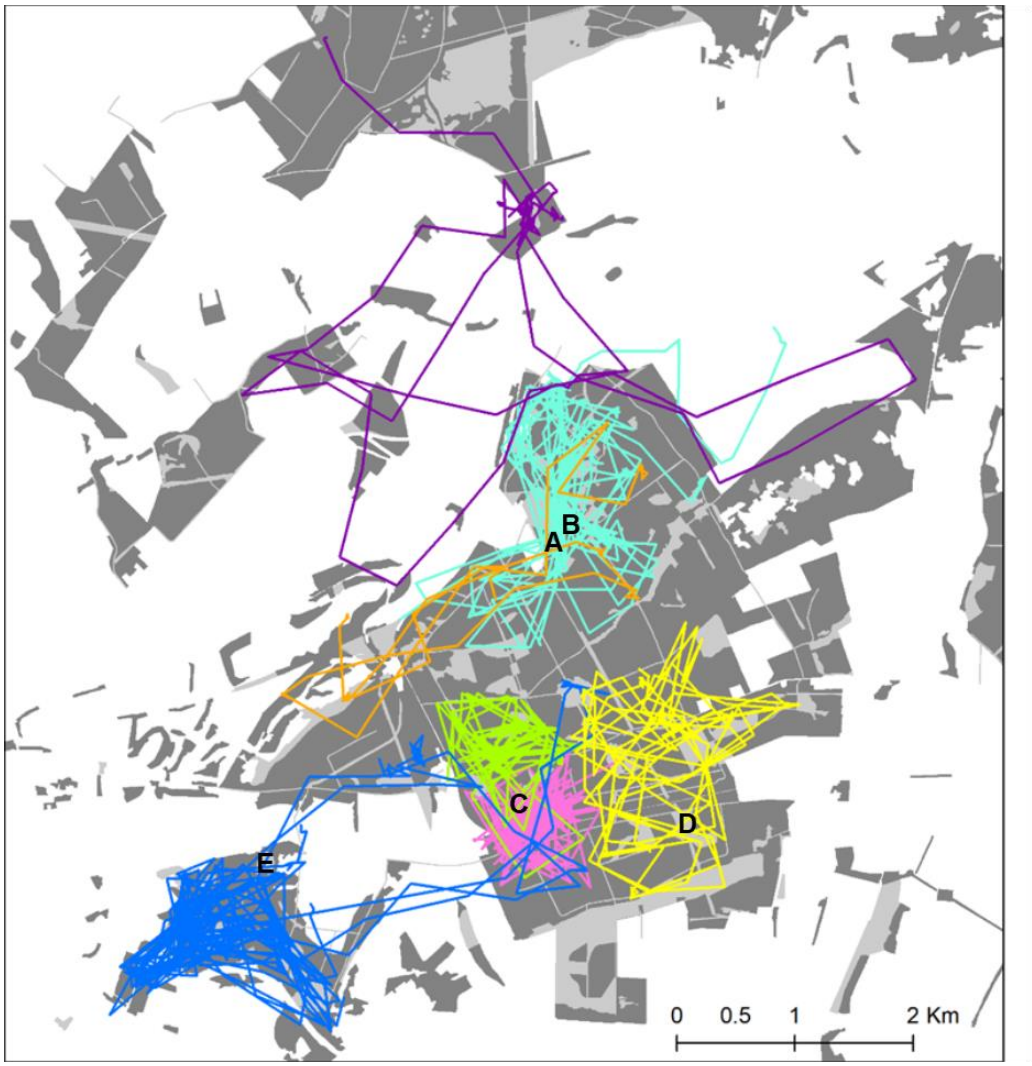
It is easy to see why roding behaviour has traditionally been interpreted as territorial. Roding woodcock appear to follow repeated

paths and often interact aggressively with one another, leading some authors to conclude that males defensively patrolled the perimeter of their territory (Tester & Watson 1973). There had been some suggestions that this interpretation was incorrect (Steinfatt 1938; Nemetschek 1977) and the first evidence came when Hirons (1980) showed that diurnal home ranges and roding grounds of competing males often overlapped, sometimes almost entirely; on a number of occasions marked birds were found feeding within around 30 m of one another (Hirons 1980). The apparently unrestricted movement of woodcock within the study site does not provide any evidence of exclusive, defended areas within any individual's core range. Moreover, roding paths varied too greatly and too frequently to suggest that they represent a territorial boundary. The GPS-tracking data presented here support the findings of Hirons (1980), as do diurnal radio-telemetry data recorded during this study using the tags' VHF beacons (unpublished).

Hirons (1980) suggests that his estimates of roding ground size are likely to be minima which is confirmed by the larger mean range recorded here (total roding ranges were at least 2.1 times large in this study). In part, the estimates of Hirons (1980) may be constrained by the radio-telemetry method, which is less well-suited to tracking wide-ranging individuals (Hirons & Owen 1982), but also by the extent of woodland at his study site. The larger roding grounds found in this study may be reflective of the large interconnected woods present within the Sherwood study site and may more accurately reflect current woodcock populations which have retracted to more heavily wooded

landscapes during recent declines. It is also conceivable that declines could cause larger roding grounds if males are forced to travel further in search of females when densities are lower.

There was large variation in size between the roding grounds of different males in this study. The lower suitability of the habitat covered by larger roding grounds (e.g. large areas of non-woodland habitat) might suggest that they belong to less-dominant males as this search strategy is undoubtedly less effective. It is likely that females gauge male quality using the male's vocal elements as cues, but male-male chasing is common during display and could also play a role. Quality may be demonstrated by a male's ability to display in more favourable areas, like in great snipe *Gallinago media* (Hoglund & Lundberg 1987) and American woodcock *Scolopax minor* (Ellingwood *et al.* 1993), where males holding more prominent central lek sites mate most frequently. Although the behaviour appears to be non-territorial, GPS-logger data might imply that roding woodcock attempt to exclude competitors (Fig. 8.1). Currently the sample of woodcock tracked in each year is too small to test this, but often roding ranges in this study only overlapped with those of neighbouring birds at their edges, unlike those radio-tracked by Hirons (1980). This is in contrast to daytime radio-tag locations, which overlapped freely and offer no indication of permanent territories. The idea that dominant males attempt to exclude rivals is supported by an experiment in which two dominant males were removed from a site and within a period of a few days roding activity



	Age	Colour	Capture Loc.	No. Evenings	Tracking periods
F	Ad	Purple	A	2	*12-13 June 2016**
K	Ad	Orange	A	3	*11-12 May 2016**
L	FY	Cyan	B	6	*29 April - 4 May 2016*
N	Ad	Pink	C	6	*12-17 May 2016*
Q	Ad	Green	C	4	*27-30 May 2016*
R	Ad	Blue	D	6	*13-18 June 2016*
S	FY	Yellow	E	2	*25-26 June 2016*

Figure 8.1 The roding movements of seven woodcock tracked in Sherwood Pines in 2016. Woodcock were not tracked concurrently, and these tagged males only represent a small proportion of those present. Nevertheless, it may suggest some partial exclusivity of roding grounds or hierarchy. A more specialised method, sampling the movements of males during exactly the same time periods, would need to be employed to understand this fully.

recovered to the levels observed prior to their removal (Hirons 1983). Hirons (1980; 1983) and Hoodless *et al.* (2008) suggest that roding behaviour is hierarchical, with 'one or two dominant males roding for longest' (Hoodless *et al.* 2008). It may be that the subdominant males rode for equal lengths of time but are recorded less frequently because they are partially excluded from prime sites. Exclusive roding grounds and a dominance hierarchy amongst males does not necessarily imply territoriality, especially given that it appears to only be maintained during roding, but it consistent with the kind of male-male interactions observed in classic lekking species (Robel & Ballard 1974; Magaña *et al.* 2011; Beehler & Foster 1988). These interpretations are currently speculative, but a slightly modified method could be employed to look at the role of male-male chasing, male hierarchy and roding ground exclusivity.

The calibration equation of Hoodless *et al.* (2008) reports a non-linear relationship between the number of registrations and the true number of males. It is assumed that high densities stimulate more display per individual as the increase in competition demands a greater effort from each bird, but there may be alternative explanations. If males attempt to exclude one another from their roding grounds, this would be more difficult when woodcock occur at higher densities; allowing each rival to spend more time within a dominant rival's roding ground and increasing activity at a single count point within his range. At low densities, females may be more widely spaced meaning each

male must cover a larger area and would be seen less frequently at a static location.

One aspect of roding that remains unknown is the prevalence of non-roding males. Hirons (1983) speculated that these exist and it seems likely that, in a monomorphic species with an elaborate display, some males will to try to cheat the conventions of the mating system (Vervoort & Kempenaers 2020; Plaistow *et al.* 2004; Lanctot *et al.* 1997). The GPS-logger data analysed here offer no strong evidence either way; many of the tagged woodcock did not display at all, but each was recorded for only 1 – 6 days. Nevertheless, the absence of display behaviour did not correlate with weather, and a lack of roding behaviour was often observed for males that were not roding when caught. The vocal lure was only used intermittently during the catching period and some seemingly less responsive males were caught investigating the capture site while the lure was silent. Despite this, the technique probably favours more dominant males.

8.3.1 Roding as a model for studying lek behaviour

Lek evolution has been a popular research topic because it has implications for our broader understanding of mate choice and sexual selection. A wide-range of lekking birds have been studied including grouse such as the greater prairie chicken *Tympanuchus cupido* (Schroeder & White 1993), black grouse *Lyrurus tetrix* (Borecha *et al.* 2017) and greater sage-grouse *Centrocercus urophasianus* (Aspbury & Gibson 2004; Bradbury *et al.* 1989); waders such as the Ruff *Calidris*

pugnax (Widemo 1998); and some passerines, mainly manakins *Pipradae* (Heindl & Winkler 2003; Ryder *et al.* 2006). Some species that are closely related to the Eurasian woodcock perform true lek displays, such as the great snipe (Hoglund & Lundberg 1987) and the American woodcock (Ellingwood *et al.* 1993), both of which have exploded leks where males display around 100m apart.

It is not entirely clear whether the Eurasian woodcock's roding display really constitutes a lek but their polygynous mating system meets several of the key criteria, particularly that there is no male parental care and no resource provision to females (des Forges 1975; Hirons 1980). In a lek mating system, and apparently in the case of the Eurasian woodcock (Hirons 1983), the only benefit received by the female is the male's genetic contribution to her offspring. The roding display also resembles a lek in the sense that it offers females a high degree of mate choice (Hirons 1983) but, unlike a typical lek, each male is not associated with a small discrete display ground. As shown here, males cover roding areas over which constant visual or auditory communication with all neighbouring rivals cannot be maintained. As an atypical example of a lek or 'lek-like' behaviour, the woodcock may provide an informative study species in which to expand our current understanding of the behaviour.

There are several different hypotheses to explain the development of lek behaviour. The preference hypothesis suggests that females prefer to select males at communal display sites because it offers some advantage over isolated display e.g. it aids comparison of

males or reduces search time (Bradbury & Gibson 1983). The hotspot hypothesis proposes that displays becomes aggregated because males gather in areas where female concentrations are naturally higher (Ryder *et al.* 2006). The hotshot hypothesis suggests that lower-quality males choose to display close to higher-quality individuals in order to benefit from the female attention that they attract (Beehler & Foster 1988). These theories are not necessarily mutually exclusive and may interact.

Several studies have compared the size and arrangement of female home-ranges to lek sites in order to test the hotspot hypothesis (Beehler & Foster 1988). The woodcock presents an unusual example because each male covers a roding ground far larger than any single female home-range (Hoodless & Hirons 2007), but when doing so appears to favour areas where females are more likely to be encountered. This may imply that males must visit multiple hotspots per display session, as a consequence of some aspect of their ecology such as low female density or mobility. The Eurasian woodcock's display may partly support a female preference model despite the lack of male aggregations, as females are provided the opportunity to sample a large number of males without travelling between them. For American woodcock and great snipe, a hotshot model could be applicable because attractive males are more likely to hold central positions within the lek site (Hoglund & Lundberg 1987; Ellingwood *et al.* 1993), giving the impression that lower-quality males assemble around them. Although it is possible that there is some hierarchical

element to the Eurasian woodcock's display, it is difficult to see how this would fully explain the adoption of the current mating system, but it might influence the spatial arrangement of individuals.

Around a quarter of lekking species are, like the woodcock, monomorphic. Trail (1990) suggests that, for monomorphic species in which both male and female possess non-cryptic plumage (e.g. red-ruffed fruitcrow *Pyroderus scutatus*, capuchinbird *Perissocephalus tricolor*), monomorphism could be driven by intense intrasexual competition, with females benefiting from a male-like appearance because it deters female-female aggression at the lek. For woodcock and snipe, however, where neither sex is brightly coloured, it seems more likely that monomorphism is the result of a strong and equal selection pressure on both sexes to remain camouflaged. Visual ornamentation may come at too great a cost in a species where crypsis is important year-round (Hartley 2007).

It is unclear why the woodcock's display differs from a traditional lek; should it be seen as a more basal form of lek or an atypical example arising from the woodcock's ecology? This study provides new information regarding the male woodcock's display, but there are several key aspects of the behaviour which need to be understood before the Eurasian woodcock can contribute further to lek research. Understanding the movements of females would demonstrate whether the high mobility of males during display compensates for low mobility of females and whether male display is focussed towards areas where females are more likely to occur. It would also be useful to know which

male traits females select for, as this would allow human observers to derive some indication of the attractiveness of individual males. The two-part call produced throughout their roding display seems the most likely signal. A large degree of inter-individual variation is already known to exist in the whistle element of the call (Hoodless *et al.* 2008) and small variations in the grunt element of the call are perceptible to the human ear. Other traits of the display, such as the slow flight and male-male chasing may simply be means of accentuating the vocal elements of the display and reducing competing noise. Often studies of lekking species compare physical or behavioural traits to mating success between different males, but practically, it seems unlikely that field observations or genetic techniques will ever allow this for a species as difficult to observe as woodcock.

8.4 Considerations for roding surveys

Roding surveys remain the only reliable means of counting male woodcock. They can be used to estimate local population densities, can be extrapolated to form regional and national population estimates and can quantify local and regional population trends. Comparisons on smaller geographic scales (i.e. within-site) may also be able to provide an indication of habitat suitability if roding intensity and the distribution of nesting females are interlinked (Hirons 1998). This study identifies several potential improvements to roding survey design and the derivation of population estimates from them.

In the 2003 and 2013 Breeding Woodcock Surveys, occupancy levels were highest in the north and east of Britain where survey participation was low. This finding was supported by the atlases (Sharrock 1977; Gibbons *et al.* 1993; Balmer *et al.* 2013) and there are several biological explanations such as greater woodland coverage, a more favourable climate or lower human population density. But it is also possible that this pattern was exaggerated by the small number of surveyors, who may have tended to select sites that they knew were occupied. Presently, this is difficult to examine, but in future versions of the national survey it would be informative to record the order in which survey squares were selected by volunteers and compare this to areas in the south where surveyors are more readily available and coverage is practically complete.

Roding activity varies according to a range of meteorological conditions, including those that occur on the evening of the survey and those that occur in the weeks prior to it. Trying to avoid this variation in survey weather is difficult; any attempts to confine roding surveys to 'optimal' conditions would lead to an impractically restrictive set of specifications that would be difficult to predict. A better way to deal with this might be to ensure that the 'three-visit' requirement is always adhered to. Taking the maximum of three counts selects the visit on which the weather is closest to the optimum and, if each visit is separated by at least a week, reduces the impact of longer-term patterns in temperature and rainfall. While this recommendation should help ensure that maximum counts are as representative as possible, it

is unlikely to have a large effect at most sites. In the 2013 Breeding Woodcock Survey, 11% of surveys at occupied sites were incomplete but maximum counts did not significantly differ from those that received all three visits. The analysis of weather considered data from 12 different years, however, and the effect could be larger in years in which unfavourable weather is more frequent. Improving count accuracy at even a small number of sites is desirable as single sites can hold a high degree of influence but removing incomplete sites could have a negative effect on final estimates if it inflates the influence of those that remain. To minimise the number of exclusions required, the value of multiple visits should be emphasised to surveyors.

Single sites can have a large influence on population estimates, as demonstrated when the North Midlands survey data were reanalysed with a small number of sites removed. Sites with the strongest influence on the final estimate are those whose counts are substantially higher than the stratum's average and are consequently more likely to occur in strata with small sample sizes. The national survey's sample size is reasonably large for a single species survey (> 800 sites) but is split unevenly into 44 strata (4 wood-size classes x 11 regions). It would be inadvisable to consolidate strata given that woodcock abundance varies significantly between region and wooded area, but in future surveys, more effort should be made to improve survey coverage in poorly represented strata. Greater coverage is especially required in Wales, northern and eastern England and Scotland. Restricted numbers of squares were offered in these areas

because the numbers of potential surveyors were lower, and it was feared that this would otherwise lead to a sample skewed towards ‘easier’ counts e.g. those close to human settlements. This precaution was justified, but the restricted sample may have inadvertently reduced survey participation if surveyors were unwilling to travel long distances to reach random count points. The employment of paid fieldworkers was recommended following the first national survey to improve coverage (Hoodless *et al.* 2009). This advice was not followed in 2013, but a number of additional targeted counts were completed the following year to ensure no site had more than a 5% influence on the national estimate. For future surveys, professional fieldworkers should be enlisted.

In 2013, surveys were 75 minutes long, although to ensure comparability with the 2003 method, only registrations recorded during the first hour could be used to calculate woodcock densities. The 75-minute surveys offer a small advantage, as it reduces the impact of environmental conditions that affect the onset of roding. Switching to a 75-minute survey would require the calculation of a new calibration equation.

GPS-logger data suggests that woodcock favour permanent woodland clearings and woodland edges while displaying. This means that the current recommendations advising observers to select the intersection of two rides, a glade or felled area are apt, but it may be advisable to recommend permanent clearings over temporary ones where available. Not only do rides and permanent clearings appear to

be more frequently visited, temporary clearings may become less suitable over time as their size or openness reduces. It is not necessarily true that revisiting the same count point within a wood ensures comparability; providing the same wood within the random square is visited, it is probably more important to choose the most suitable count point and maximise detectability. Current survey instructions advise observers to choose a new count point if an existing one becomes unsuitable, but the need to do this is probably only apparent once a reduction in the number of registrations has been observed.

The tracking data also reveal that the movements of male woodcock during the roding period provide a moderate risk of double counting in regions with denser survey coverage. The same random sample of survey squares was used in both 2003 and 2013, but it will have to be redrawn for any future incarnations of the national survey as changes over the intervening 20 years will mean that some of the original wood-size classifications are no longer applicable. When doing so, it may be advisable to increase the minimum distance between randomly selected squares. There are potential implications for the structure of the random sample if the minimum distance is greater than necessary, but a separation of 3 km should reduce the risk while maintaining a large enough sample. It is important to understand whether this change could affect comparability with previous surveys. The lower woodland size classes (e.g. 10-30 ha of woodland per 1x1-km) should represent squares that cover the edges of large woods, as

well as small isolated woods. A greater degree of separation will skew the lower wood-size classes towards the latter, as the minimum distance from nearby squares in higher wood-size classes is increased.

Another way of dealing with this could be to increase the size of the sample unit as suggested in Chapter 6.4. Using a 3 x 3-km square sample unit, in which the central square 1x1-km is surveyed, would provide a larger buffer against double counting while potentially improving the representativity of wood-size class strata since woodcock abundance was seen to correlate with woodland coverage measured over large spatial scales. The most obvious cost of a 3x3-km square national grid is that it will greatly reduce comparability with previous national surveys and, where surveyor density is very high, may reduce the total number of available squares. It would also be necessary to measure how the results of a single central count point relate to density across a 3x3-km square sample unit, although a greater understanding of this would also improve interpretation of the current 1x1-km square sample unit.

Hoodless *et al.* (2008) considered whether the relationship between the number of registrations and the number of males varied according to wooded area and this was reasonably close to significant ($P = 0.122$ for woodland within 3x3 km^2). Mulhauser & Zimmermann (2010) also found that calibration equations were not consistent between sites. Anecdotal observations from the GPS-logger data presented here support the idea that woodland coverage and connectivity influences the way woodcock rode and perhaps, in doing

so, the frequency with which a single bird is recorded at a static point. Although an ambitious undertaking, the ideal study of this would be to take a 3x3-km square based on the British National Grid and a) quantify the relationship between the number of registrations at the central count point and the number of males this relates to (as in Hoodless 2008) b) repeat this in each of the eight surrounding squares to assess how the number of registrations recorded at the central count point reflects the number of males across the 3x3-km square and c) how these factors vary in relation to woodland cover.

The calibration equation itself has not been discussed or investigated here. The established method was used for the 2003 national survey data and used consistently throughout my study. It may be informative to reassess the calibration equation before undertaking future national surveys. Trying to capture data from a wider range of sites than the 2008 study would improve the calibration, especially given that wooded area might be playing an unidentified role.

Remote sound recorders could aid future national surveys or preceding studies. Using remote recorders to conduct a certain proportion of counts during the national survey would efficiently improve coverage in remote areas and the data could be used test whether the calibration equation is universally applicable. If not, it would enable the calibration equation to be tailored to specific regions or wood-size strata. Prior to this, it would be necessary to check that remote recorders exhibit similar detection rates as the average human observer and produce sound recordings of high enough quality to discriminate

between individuals. An array of recorders could be deployed at various points within a survey square, or across a grid of adjoining squares, to quantify the relationship between the number of males encountered at a single point and the broader density of woodcock across the sample unit. Sound-recorders, twinned with radio-logging stations, could validate the calibration method using a sample of radio-tagged males, as proposed in Hoodless (2008).

These recommendations for improvement are only likely to have small effects on survey results and current methods ought to be considered adequate. The declines these surveys have identified should not be played down by any suggestion that the method is inappropriate, particularly since the widespread declines in site occupancy are supported by other sources. The estimate of population size is more likely to change as a result of methodological improvements, especially given the high degree of influence held by single sites. The estimate should always be considered in relation to their confidence limits (95% CL: 41,806 – 69,004), and the true population size likely lies well within these bounds.

8.5 Summary of recommendations for future research

The recommendations for future research on woodcock breeding ecology, which are discussed in detail above, can be summarised in five main points: 1) nest site selection and brood rearing habitat selection in relation to open space and the activity of roding males; 2) the role of forest management in the creation and maintenance of

favourable breeding habitat; 3) the life-history stage(s) (e.g. nesting success, chick survival, adult survival) having the greatest influence on current declines; and 4) ways of integrating suggested improvements to national roding surveys without reducing comparability with previous surveys. These four points are directly relevant to woodcock conservation and its monitoring. Finally, 5) a more comprehensive study of mate-choice and the woodcock's mating system, has a more theoretical application concerning the evolution of lek behaviour. Except for point 4, the consistent thread across these recommendations, is the need for a more detailed understanding of female woodcock ecology, something that remains difficult to obtain.

APPENDICES

Supplementary Table 1 Estimates, standard errors and p-values from a GLMM assessing the effects of year, wood size class and region on the maximum number of male woodcock encountered. The analysis is based on 544 sites that were in both 2003 and 2013. Site was specified as a random effect. There was a significant three-way interaction between year, wood size class and region.

	Est.	*SE*	*P*
(Intercept)	-2.656	1.137	**0.020**
year 2013	2.044	0.943	**0.030**
31–50 ha	3.649	1.363	**0.007**
51–70 ha	2.518	1.466	**0.086**
71–100 ha	2.254	1.418	0.112
Northern England	2.080	1.271	0.102
Central England and Wales	0.636	1.290	0.622
Southern England	1.378	1.218	0.258
Year 2013: 31–50 ha	-2.959	1.127	**0.009**
Year 2013: 51–70 ha	-2.638	1.157	**0.023**
Year 2013: 71–100 ha	-2.114	1.157	0.068
year 2013: Northern England	-2.795	1.072	**0.009**
year 2013: Central England and Wales	-4.631	1.273	**0.000**
year 2013: Southern England	-2.735	1.015	**0.007**
31–50 ha: Northern England	-2.487	1.532	0.105
51–70 ha: Northern England	-1.091	1.631	0.504
71–100 ha: Northern England	0.081	1.619	0.960
31–50 ha: Central England and Wales	-2.756	1.564	0.078
51–70 ha: Central England and Wales	0.141	1.657	0.932
71–100 ha: Central England and Wales	0.492	1.627	0.762
31–50 ha: Southern England	-2.956	1.483	**0.046**
51–70 ha: Southern England	-1.701	1.584	0.283
71–100 ha: Southern England	0.111	1.521	0.942
year 2013: 31–50 ha: Northern England	3.302	1.273	**0.009**
year 2013: 51–70 ha: Northern England	3.248	1.298	**0.012**
year 2013: 71–100 ha: Northern England	2.618	1.319	**0.047**
year 2013: 31–50 ha: Central England and Wales	5.242	1.469	**0.000**
year 2013: 51–70 ha: Central England and Wales	3.975	1.486	**0.007**
year 2013: 71–100 ha: Central England and Wales	4.226	1.489	**0.005**
year 2013: 31–50 ha: Southern England	2.031	1.234	0.100
year 2013: 51–70 ha: Southern England	3.076	1.255	**0.014**
year 2013: 71–100 ha: Southern England	2.293	1.237	0.064

*Supplementary Table 2 The variables considered in the two analyses (LS = landscape scale, FS = fine scale, Exc.= excluded from analysis due to high collinearity with another variable/low occurrence). * Scale is abbreviated as: (a) within a 200-m radius buffer of the count point, (b) within a 1-km radius buffer of the count point, (c) within a 2 km ring buffer centred upon the count point (d) an estimate for the count point derived from smoothed raster maps (see method for details). Continued overleaf.*

Variable		Source	Scale					An.
			a	b	c	d	n/a	
Total urban area	Area of urban and suburban habitat within buffer	LCM		✓	✓			LS
Dist. to urban area > 50 ha	Distance to nearest urban area over 50 ha in size	LCM					✓	LS
Total area of grassland	Area of grassland habitat within buffer	LCM		✓	✓			LS
Wood block size	Size of contiguous woodland block	LCM					✓	LS
Total woodland area	Total area of woodland habitat within buffer	NIWT & NFI		✓	✓			LS
Woodland heterogeneity	Diversity index based on categories of NIWT / NFI	NIWT & NFI		✓	✓			LS

Variable		Source	Scale					An.
			a	b	c	d	n/a	
Prop. of mature broadleaf	Proportion of wooded area occ. by mature broadleaf	NIWT & NFI		✓	✓			LS
Prop. of mature conifer	Proportion of wooded area occ. by mature conifer	NIWT & NFI		✓	✓			Exc.
Prop. of mature mixed	Proportion of wooded area occ. by mature mixed	NIWT & NFI		✓	✓			LS
Prop. of open space	Proportion of wooded area occ. by open woodland (bare ground, felled woodland, land prepared for planting, grass within woodland and ‘young’ trees)	NIWT & NFI		✓	✓			LS
Prop. of coppice	Proportion of wooded area occ. by coppiced woodland	NIWT & NFI		✓	✓			Exc.
Prop. of shrub	Proportion of wooded area occ. by shrub	NIWT & NFI		✓	✓			Exc.
Muntjac	Relative abundance of muntjac deer	GWCT NGC				✓		LS

Variable		Source	Scale					An.
			a	b	c	d	n/a	
Fallow	Relative abundance of fallow deer	GWCT NGC				✓		LS
Roe	Relative abundance of roe deer	GWCT NGC				✓		LS
Red	Relative abundance of red deer	GWCT NGC				✓		Exc.
Sika	Relative abundance of sika deer	GWCT NGC				✓		Exc.
Prop. of closed canopy	% of buffer occ. by closed canopy woodland	Wdck Surveys	✓					FS
Prop. of open canopy	% of wooded area occ. by open canopy habitats	Wdck Surveys	✓					FS
Establishing trees	Prop. of woodland containing young (< 2 m) trees	Wdck Surveys	✓					FS
Dominant tree type (see Table 3.4)	Tree type making up greater than 50% of the wooded area	Wdck Surveys	✓					FS
Presence of birch	Presence of one or more birch-dominated stand	Wdck Surveys	✓					FS

Supplementary Table 3. Results of four GLMMs used to assess the relationship between woodcock abundance in Britain and 12 habitat variables (outlined in Suppl. Table 2). P-values are taken from maximal models produced using glmmPQL in the MASS package (Venables & Ripley 2002)*. Variables in bold were statistically significant (P < 0.05) in at least one model*

	2003 1-km buffer			**2003 2-km ring buffer**			**2013 1-km buffer**			**2013 2-km ring buffer**		
	Est.	**SE**	**P**	**Est.**	**SE**	**P**	**Est.**	**SE**	**P**	**Est.**	**SE**	**P**
(Intercept)	1.2262	0.1795	<0.001	1.2237	0.1938	0.0000	0.7702	0.1854	<0.001	0.7336	0.2077	0.0004
Measured on different scales												
Total woodland area	**0.5047**	**0.0587**	**<0.001**	**0.5173**	**0.0750**	**<0.001**	**0.5346**	**0.0836**	**<0.001**	**0.5610**	**0.0860**	**<0.001**
Heterogeneity	**0.1780**	**0.0604**	**0.0033**	**0.1406**	**0.0670**	**0.0360**	**0.1800**	**0.0931**	**0.0537**	**0.3443**	**0.1078**	**0.0015**
Mixed woodland	**0.0752**	**0.0524**	**0.1518**	**0.0537**	**0.0586**	**0.3602**	**-0.0533**	**0.0872**	**0.5410**	**-0.2655**	**0.0965**	**0.0061**
Open woodland	**-0.2267**	**0.1326**	**0.0877**	**-0.1815**	**0.1163**	**0.1189**	**-0.0960**	**0.1404**	**0.4942**	**-0.3218**	**0.1353**	**0.0176**
Urban area	**-0.0819**	**0.0621**	**0.1878**	**-0.1972**	**0.0768**	**0.0104**	**-0.0643**	**0.0918**	**0.4838**	**-0.1449**	**0.0947**	**0.1265**
Prop. broadleaf	0.1296	0.0811	0.1107	0.1497	0.0827	0.0708	0.1623	0.1100	0.1403	0.1475	0.1196	0.2180
Total grassland area	-0.0263	0.0490	0.5924	-0.0994	0.0548	0.0698	-0.0365	0.0716	0.6109	-0.0484	0.0710	0.4958
Interactions												
Broadleaf x total wood	**0.2594**	**0.0578**	**0.0000**	**0.2153**	**0.0675**	**0.0015**	**0.1851**	**0.0832**	**0.0263**	**0.2560**	**0.0853**	**0.0028**
Open x total wood	0.0907	0.0657	0.1678	-0.0195	0.0566	0.7301	0.0801	0.0934	0.3910	-0.0985	0.0817	0.2286
Broadleaf x open	0.0359	0.1246	0.7736	-0.0748	0.1019	0.4631	0.1690	0.1140	0.1386	-0.0777	0.0985	0.4306
Does not change with scale												
Distance from urban	**0.1265**	**0.0620**	**0.0418**	**0.1036**	**0.0677**	**0.1266**	**0.2061**	**0.0639**	**0.0013**	**0.1635**	**0.0605**	**0.0070**
Roe	**0.2685**	**0.0741**	**0.0003**	**0.2885**	**0.0759**	**0.0002**	**0.1418**	**0.0924**	**0.1252**	**0.1549**	**0.0893**	**0.0833**
Muntjac	0.0374	0.0731	0.6094	0.0837	0.0713	0.2407	0.0631	0.1704	0.7114	0.0608	0.1649	0.7123
Fallow	-0.0946	0.0699	0.1768	-0.0687	0.0712	0.3350	-0.3010	0.1643	0.0674	-0.2039	0.1589	0.1998
Size of wood	-0.0638	0.0539	0.2364	-0.1118	0.0601	0.0634	-0.1055	0.0877	0.2295	-0.0594	0.0937	0.5261

Supplementary Table 4 Ranking matrix showing pairwise comparison of habitats used during periods of roding movement. Every pairwise combination of habitats, for every individual, is compared following the method outlined in Section 7.2.2. Here we provide mean values of d for 16 individuals and SEs to 2 d.p. Values demonstrate the relative use of habitats listed in horizontal rows when compared to the corresponding columns. Habitats are ranked by the number of positive values in each row. Values in bold represent a significant difference between the pair of habitats ($P < 0.05$).

(a)	**NON WOODLAND**			**OPEN WOODLAND**			**CLOSED WOODLAND**			
	Agricultural	**Urban**	**Other non-woodland**	**Permanent open**	**Clearfell and young restock**	**Other open woodland**	**Closed Broadleaf**	**Closed Conifer**	**Closed Unknown**	**Edge Woodland**
Agri.		0.03 ± 1.15	-0.8±1.01	-3.03 ± 0.75	-0.99 ± 1.03	-0.89 ± 1	-1.32 ± 0.92	-2.34 ± 0.75	-2.3 ± 0.82	-2.81 ± 0.92
Urban	-0.03 ± 1.15		-0.83 ± 0.99	-3.06 ± 0.96	-1.03 ± 1.33	-0.92 ± 0.88	-1.35 ± 1.26	-2.38 ± 0.85	-2.33 ± 0.65	-2.85 ± 1.03
O. non	0.8 ± 1.01	0.83 ± 0.99		-2.23 ± 0.72	-0.2 ± 1.02	-0.09 ± 0.94	-0.52 ± 1.02	-1.55 ± 0.63	-1.5 ± 0.75	-2.02 ± 0.75
Perm.	**3.03 ± 0.75**	**3.06 ± 0.96**	**2.23 ± 0.72**		**2.03 ± 0.66**	**2.14 ± 0.69**	**1.71 ± 0.68**	0.68 ± 0.67	0.73 ± 0.6	0.21 ± 0.76
C & Y R	0.99 ± 1.03	1.03 ± 1.33	0.2 ± 1.02	-2.03 ± 0.66		0.1 ± 1.02	-0.32 ± 0.74	-1.35 ± 0.95	-1.3 ± 0.94	-1.82 ± 0.74
O. open	0.89 ± 1	0.92 ± 0.88	0.09 ± 0.94	-2.14 ± 0.69	-0.1 ± 1.02		-0.43 ± 0.84	-1.46 ± 0.98	-1.41 ± 0.7	-1.93 ± 0.88
Broad	1.32 ± 0.92	1.35 ± 1.26	0.52 ± 1.02	-1.71 ± 0.68	0.32 ± 0.74	0.43 ± 0.84		-1.03 ± 0.97	-0.98 ± 0.92	-1.5 ± 0.76
Conifer	**2.34 ± 0.75**	**2.38 ± 0.85**	**1.55 ± 0.63**	-0.68 ± 0.67	1.35 ± 0.95	1.46 ± 0.98	1.03 ± 0.97		0.05 ± 0.57	-0.47 ± 0.74
Cl. Un.	**2.3 ± 0.82**	**2.33 ± 0.65**	1.5 ± 0.75	-0.73 ± 0.6	1.3 ± 0.94	1.41 ± 0.7	0.98 ± 0.92	-0.05 ± 0.57		-0.52 ± 0.68
Edge	**2.81 ± 0.92**	**2.85 ± 1.03**	**2.02 ± 0.75**	-0.21 ± 0.76	**1.82 ± 0.74**	**1.93 ± 0.88**	1.5 ± 0.76	0.47 ± 0.74	0.52 ± 0.68	

Supplementary Table 5 Ranking matrix showing pairwise comparison of habitats used during mid-roding breaks. Every pairwise combination of habitats, for every individual, is compared following the method outlined in Section 7.2.2. Here we provide mean values of d for 16 individuals and SEs to 2 d.p. Values demonstrate the relative use of habitats listed in horizontal rows when compared to the corresponding columns. Habitats are ranked by the number of positive values in each row. Values in bold represent a significant difference between the pair of habitats ($P < 0.05$).

(b)	**NON WOODLAND**			**OPEN WOODLAND**			**CLOSED WOODLAND**			
	Agricultural	**Urban**	**Other non-woodland**	**Permanent open**	**Clearfell and young restock**	**Other open woodland**	**Closed Broadleaf**	**Closed Conifer**	**Closed Unknown**	**Edge Woodland**
Agri.		-0.36 ± 1.33	-0.96 ± 1.24	-4.42 ± 0.89	-2.39 ± 1.27	0.23 ± 0.93	-1.19 ± 0.96	-2.57 ± 0.95	-3.05 ± 0.97	-3.79 ± 0.98
Urban	0.36 ± 1.33		-0.6 ± 0.97	-4.06 ± 0.87	-2.03 ± 1.24	0.6 ± 0.76	-0.82 ± 1.3	-2.2 ± 0.94	-2.69 ± 0.66	-3.42 ± 0.7
O. non	0.96 ± 1.24	0.6 ± 0.97		-3.46 ± 0.65	-1.43 ± 0.9	1.2 ± 0.68	-0.22 ± 1.13	-1.6 ± 0.55	-2.09 ± 0.78	-2.82 ± 0.72
Perm.	**4.42 ± 0.89**	**4.06 ± 0.87**	**3.46 ± 0.65**		**2.03 ± 0.88**	**4.65 ± 0.55**	**3.23 ± 0.84**	**1.86 ± 0.48**	**1.37 ± 0.43**	0.63 ± 0.33
C & Y R	2.39 ± 1.27	2.03 ± 1.24	1.43 ± 0.9	-2.03 ± 0.88		**2.62 ± 1.1**	1.2 ± 1.33	-0.18 ± 0.84	-0.67 ± 1.01	-1.4 ± 0.98
O. open	-0.23 ± 0.93	-0.6 ± 0.76	-1.2 ± 0.68	-4.65 ± 0.55	-2.62 ± 1.1		-1.42 ± 1.02	-2.8 ± 0.62	-3.29 ± 0.57	-4.02 ± 0.56
Broad	1.19 ± 0.96	0.82 ± 1.3	0.22 ± 1.13	-3.23 ± 0.84	-1.2 ± 1.33	1.42 ± 1.02		-1.38 ± 0.97	-1.87 ± 0.93	-2.6 ± 0.86
Conifer	**2.57 ± 0.95**	**2.2 ± 0.94**	**1.6 ± 0.55**	-1.86 ± 0.48	0.18 ± 0.84	**2.8 ± 0.62**	1.38 ± 0.97		-0.49 ± 0.63	-1.22 ± 0.52
Cl. Un.	**3.05 ± 0.97**	**2.69 ± 0.66**	**2.09 ± 0.78**	-1.37 ± 0.43	0.67 ± 1.01	**3.29 ± 0.57**	1.87 ± 0.93	0.49 ± 0.63		-0.73 ± 0.34
Edge	**3.79 ± 0.98**	**3.42 ± 0.7**	**2.82 ± 0.72**	-0.63 ± 0.33	1.4 ± 0.98	**4.02 ± 0.56**	**2.6 ± 0.86**	**1.22 ± 0.52**	**0.73 ± 0.34**	

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