ORIGINS AND NON-BREEDING ECOLOGY OF EURASIAN WOODCOCK

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Abstract

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The Eurasian woodcock *Scolopax rusticola* (hereon woodcock) is a wader adapted to woodland and farmland habitats. It is an important quarry species, widely hunted across Europe, but owing to its cryptic plumage and elusive nature, there exists only poor information concerning its natural history. As such, the conservation status of the woodcock remains uncertain. One area that is particularly lacking is knowledge of its ecology outside the breeding season. Generally, avian ecological studies have focused on breeding season events due to the importance of reproductive success in determining fitness. However, it is now apparent that the non-breeding season represents an equally important period of the annual cycle. For example, recent studies have shown that declines in some migratory bird populations were due to events during the non-breeding season, either during migration, or on the wintering grounds.

In Britain, the non-breeding woodcock population comprises both British breeding and non-British breeding birds, yet the origins and relative distribution of these sub-populations is not fully understood. Nor is it known whether ecological differences exist between them. This thesis addresses these two aspects of woodcock biology, using stable isotope and radio-tracking methods. The former was used to assign birds to their likely origins and determine population-specific distributions across Britain. The latter was used, in conjunction with the former, to determine whether ecological differences exist between locally-breeding and non-locally breeding birds residing in Hampshire in winter.

A large degree of mixing between birds from different breeding populations was apparent for woodcock residing in Britain over winter. Russia and Fennoscandia comprised the most likely origins of migratory birds and regional differences in distributions were apparent. The highest proportions of birds from Russia were found in Norfolk and Wales, whilst the highest proportions of birds from Fennoscandia were found in Scotland. The presence of non-breeding residents in Cornwall and Ireland also provided strong evidence for the short-distance, south-westerly movements of resident birds, which probably originated from Scotland.

Locally, the movements and behaviour of birds were found to vary with age (adult vs. juvenile) and/or predicted migratory status (resident vs. migrant), with adult residents potentially representing the dominant group. Differences in habitat use, commuting flights, home range size and activity patterns were all apparent. As such, these findings might have important consequences for the relative survival rates and breeding success of resident and migrant woodcock.

This work has provided new insights into the non-breeding ecology of woodcock in Britain and contributes significantly to European efforts to better understand this bird species. Given the importance of seasonal interactions, an understanding of events throughout the annual cycle is necessary and this can only be achieved through concerted efforts. Indeed, an integrated approach is imperative to develop the conservation plans necessary to ensure the sustainability of the woodcock.

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I hope I've made you proud.

Love never dies

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Chapter 1

Introduction

Introduction

The Eurasian woodcock *Scolopax rusticola* (hereon woodcock) is a bird species with uncertain conservation status. This is because the scientific knowledge that is required to ascertain an accurate conservation status is lacking for the woodcock, due to its migratory habits and elusive nature. As such, the international conservation status of the woodcock ranges from "stable" (Hoodless & Saari 1997; Wetlands International 2002, 2006) to "unfavourable" (Tucker & Heath 1994; BirdLife International 2004a,b) (Table A1.1), with evidence for declines in abundance on both the breeding and non-breeding grounds being debated (Fadat 1994; Ferrand & Gossmann 2000; Heath *et al.* 2000). Ascertaining an accurate conservation status for the woodcock is imperative, however, since amidst the debate, the species remains legally hunted across most of Europe. It is listed under Annex II Part A of the European Union (EU) Birds Directive (Council Directive 2009/147/EC on the conservation of wild birds) as a quarry species that "may be hunted in the geographical sea and land area" where the Directive applies (The European Parliament and the Council of the European Union 2010). Given that hunting has been shown to have an additive effect on woodcock mortality in Brittany, France (Duriez *et al.* 2005a), combined with the uncertainties surrounding this bird's conservation status, the woodcock represents a conflicted species that necessitates further study. Indeed, the conservation practices necessary to ensure its sustainability, can only be developed through the acquisition of scientific knowledge.

Study species

The Eurasian woodcock *Scolopax rusticola* (Linneaus 1758) belongs to the family Scolopacidae, which comprises 22 genera and 86 species of wading birds, including curlews, sandpipers, godwits, stints and snipe. Despite being the type genus for the family, woodcock are atypical of the family since they rarely occupy coastal habitats, but tend to occur inland, predominantly associated with woodland and farmland areas. Currently, there are seven species of woodcock described within the genus *Scolopax* (Kennedy *et al.* 2001). Of these, *Scolopax rusticola* is the only species found across much of the temperate and boreal Palearctic (Harrison 1982); its distribution extends from east Asia to western Europe and the Macaronesian islands of the Canaries, Madeira and Azores (del Hoyo *et al.* 1996) (Figure 1.1). The main breeding grounds of the woodcock are in Russia, Fennoscandia and the Baltic States, with over 90% of the European population believed to occur in these regions (Hoodless & Saari 1997). Notably, smaller numbers also breed in Denmark, Germany, the Netherlands, Belgium, France, Britain and Ireland (Hoodless & Saari 1997).

Population estimates

Since woodcock are not censused in many countries, it is difficult to determine accurate population estimates. Across its entire range, the woodcock population is estimated at between 10 000 000 and 26 000 000 mature individuals (BirdLife International 2012). The European population of woodcock has been estimated by the European Bird Census Council (EBCC) Atlas at between 1 530 000 and 10 700 000 pairs, with the best estimate at 3 750 000 pairs, including c.350 000

pairs in the European Union (EU) (Hagemeijer & Blair 1997). Similarly, BirdLife International estimates the European population at between 1 800 000 and 6 600 000 pairs, with the European Union population estimated at between 460 000 and 1 500 000 pairs (BirdLife International 2004a).

Survival rates

Woodcock have low annual survival probabilities compared with other shorebirds (Hoodless & Coulson 1994; Piersma *et al.* 1996). The most recent annual adult survival rate (± standard error, SE) for woodcock in Britain and Ireland was estimated at 57.9% (± 1.8 SE), based on 342 rings, recovered during the period 1909-1990 (Hoodless & Coulson 1994). This estimate is lower than those for other wader species such as the black-tailed godwit *Limosa limosa* (90%) (Gill *et al.* 2001), red knot *Calidris canutus* (84%) (Brochard *et al.* 2002) and northern lapwing *Vanellus vanellus* (75-83%) (Roodbergen 2010). The low annual survival rates of woodcock may be due to the fact that they are a hunted species and/or because they utilise different habitat types (Hoodless 1994a).

Conservation status

The International Union for Conservation of Nature (IUCN) Red List of Threatened Species is considered the most authoritative and objective system for classifying and ranking the conservation status of species (Regan *et al.* 2005; de Grammont & Cuaron 2006; Rodrigues *et al.* 2006), with assignments based on data relating to population size, rate of decline, and area of distribution (IUCN 2001, 2005). BirdLife International is the official Red List Authority for birds,

providing the evaluations and documentation for all birds on the IUCN Red List of Threatened Species (BirdLife International 2011).

Globally, the IUCN Red List of Threatened Species has evaluated *S. rusticola* as a species of "least concern", such that it does not approach the thresholds for "vulnerable" under the range size, population trend and/or population size criterions (IUCN 2012). However, the European conservation status of the woodcock ranges from "stable" (Hoodless & Saari 1997; Wetlands International 2002, 2006) to "unfavourable" (Tucker & Heath 1994; BirdLife International 2004a,b) (Table A1.1).

The uncertainties surrounding the conservation status of Eurasian woodcock arise from differing trends between breeding populations. For instance, in Denmark, there have been slight increases in numbers (20-50% increase), whilst breeding populations in Sweden, Finland and Norway have remained stable (< ± 20% change) (Asbirk *et al.* 1997). Recent monitoring in Russia suggests that breeding woodcock numbers have remained stable since 2000 (Fokin *et al.* 2004). This is supported by a stable trend in the numbers of woodcock residing in France during the winter, which constitutes the main non-breeding area for Russian breeders *(*Ferrand *et al.* 2008). The breeding population in France also appears to have remained stable over the past 12 years (Ferrand *et al.* 2008). Conversely, in Britain, there has been an apparent long-term decline in breeding numbers (-76%, 1974-1999) and range (-31%, 1968/72-1988/91) (Gregory *et al.* 2002). This has resulted in the woodcock being amber-listed as a bird of conservation concern, at the national level (Eaton *et al.* 2009). Declines have also been reported for breeding woodcock in some regions of Switzerland (Moyen-

Pays, Pre-Alps, Jura) (Estoppey 2001). Fluctuating trends have been reported for other woodcock populations breeding in western Europe, but often with negative trends being observed locally (Gossmann & Ferrand 2004). As a consequence of these declines or fluctuations, the woodcock is considered, by some, to have an unfavourable conservation status within the EU (Tucker & Heath 1994; BirdLife International 2004a,b). Indeed, BirdLife International has stated that the woodcock represents a "depleted population" (BirdLife International 2004a,b). This is a population that, although does not meet the IUCN Red List Criteria, has not yet recovered from moderate or large historical declines (BirdLife International 2004a). For other countries, the conservation status of breeding populations is unclear owing to sparse (if any) monitoring data (Wetlands International 2006).

Given that woodcock population trends differ between countries, a global or even European threat status does not seem appropriate for this species. Rather, conservation status assignments at the national level are perhaps of more relevance. By considering the conservation status of woodcock breeding populations at the national level, the sustainability of breeding populations within a country can be ensured. The state of each breeding population, however, is heavily influenced by non-breeding season events. Since these typically occur at locations geographically disparate from the breeding grounds, research efforts need to consider trends at the national and international level, such that an integrated approach is required.

Migration

Each stage of the annual cycle is characterised by one or more life processes, with birds in seasonal environments adapting and partitioning their life-history events in accordance with changing conditions (Wingfield 2008). The impetus for migratory movements, whereby birds move between geographically disparate habitats, is considered a response to changes in food availability and/or competition for limited resources (Lack 1968; Alerstam *et al.* 2003).

Although distinct from dispersal or irruptive events, bird migration can be difficult to define, as there are many forms, often with overlapping attributes (Berthold 2001). Migratory movements most commonly correspond to changes in the seasons (seasonal migration) but may alternatively be defined with reference to another characteristic of the migratory behaviour. For example, seasonal migration may be latitudinal in nature, with birds flying north or south in accordance with the changing seasons (Berthold 2001; Newton 2008). The movements of all Nearctic and Neotropical migrants provide examples of latitudinal migration. Nearctic migrants (e.g. ruby-throated hummingbird *Archilochus colubris*, house wren *Troglodytes aedon*, American redstart *Setophaga ruticilla*) breed in North America and migrate southward during the non-breeding season. Neotropical migrants (e.g. American pipit *Anthus rubescens*, cedar waxwing *Bombycilla cedrorum*, swamp sparrow *Melospiza georgiana*) breed in the Neotropics and migrate northward during the non-breeding season (Hayes 1995). Altitudinal migration also tends to occur in accordance with seasonal changes. This is the movement of birds up and down major land features e.g. mountains (Berthold 2001; Newton 2008), which allow

birds to exploit temporal and spatial variation in food resources (Loiselle & Blake 1991; Solorzano *et al.* 2000), reduce the risk of nest predation (Fretwell 1980; Boyle 2008) and/or avoid extreme climatic conditions (Cox 1985). Examples of species that undertake altitudinal migration include the wallcreeper *Tichodroma muraria*, American dipper *Cinclus mexicanus* and resplendent quetzal *Pharomachrus mocinno*.

Migratory bird species are defined as those "where a substantial proportion of the global or a regional population makes regular cyclical movements beyond the breeding range, with predictable timing and destinations" (BirdLife International 2008). Of the world's 9 856 extant bird species, an estimated 1 855 (19%) are considered to be migratory (Kirby *et al.* 2008), and this encompasses true (full), partial and short-distance migrants. The definition of a migratory bird also allows for movements that might be obligate or facultative in nature (Newton 2012). Notably, the non-migratory condition ("not nomadic or migratory"; BirdLife International 2008) is more prevalent amongst the world's bird species, with 81% considered sedentary. Within non-migratory populations, however, some individuals may undertake short (localised) seasonal movements. For example, the British breeding northern lapwing *Vanellus vanellus* population comprises individuals that remain close to their natal areas during the non-breeding season, whilst others undertake short south/south westerly movements in accordance with seasonal changes (Baillie *et al.* 1986).

Partial migration

Partial migration is the pervasive form of bird migration (Berthold 2001). This is the condition whereby some individuals show migratory behaviour, whilst others (within the same species and/or population) remain sedentary (Adriaensen & Dhondt 1990; Berthold 2001). Some species considered partial migrants in Britain include the common kestrel *Falco tinnunculus* (Snow 1968), European robin *Erithacus rubecula* (Snow 1966) and pied wagtail *Motacilla alba* (Davis 1966).

The dichotomy, as to which birds migrate, has received much attention in the literature (reviewed by Dingle 1996), and several control mechanisms have been proposed. In at least some species, there appears to be a strong genetic component to partial migration, as demonstrated by laboratory studies on blackcaps *Sylvia atricapilla* (Berthold 1990) and European robins *Erithacus rubecula* (Biebach 1983). Other studies suggest the influence of environment and body condition (Swingland & Greenwood 1983; Adriaensen & Dhondt 1990), with three hypotheses being proposed to explain intra-population migration patterns: the body-size hypothesis (Belthoff & Gauthreaux 1991), the arrival-time hypothesis (Myers 1981), and the dominance hypothesis (Smith & Nilsson 1987). Across species, the latter is believed to be the major factor determining migratory patterns, typically resulting in the migration of juvenile and female birds (reviewed by Gauthreaux 1982). These hypotheses failed, however, to explain the differential behaviours observed in dark-eyed junco *Junco hyemalis* (Ketterson & Nolan 1983), and so a multi-factorial hypothesis has also been put forward, based on the conceptual framework of Baker (1978) (Ketterson & Nolan 1982, 1983).

Conversely, it has been suggested that partial migration has developed as a mixed evolutionarily stable strategy (ESS) (Maynard Smith 1982; Kaitala *et al.* 1993), whereby the decision to migrate is random, since both the migratory and sedentary condition are equal in terms of fitness (Gauthreaux 1982; Berthold 1984; and references therein). However, field studies have shown that residents tend to have greater fitness than their migratory counterparts (Berthold 1984; Adriaensen & Dhondt 1990), suggesting that migrants are simply "making the best of a bad job" (Lundberg 1988; Adriaensen & Dhondt 1990).

Woodcock migration

Global

Eurasian woodcock are considered partial migrants. Across most of their range, birds show true migratory habits (complete migration) and will typically fly from their eastern breeding grounds in a westerly and southerly direction (Cramp & Simmons 1983; del Hoyo *et al.* 1996). However, sedentary populations also exist, typically occurring in north-western Europe and the Macaronesian islands (Cramp & Simmons 1983; del Hoyo *et al.* 1996) (Figure 1.1).

Like most other migratory bird species, woodcock have long been considered to move on a broad front (Schenk 1925), undertaking long-distance movements without deviating much from the orientation of their original tracks (Berthold 2001). They are able to travel over wide areas and cross all the geo-morphological features (lowlands, mountains, rivers etc.), without being confined to relatively narrow "corridors" (Weaver 1981).

Britain and Ireland

The breeding populations of woodcock in Britain and Ireland are predominantly sedentary in habit (Shorten 1974). During the non-breeding season, these resident populations are supplemented by a large influx of migrants. The British resident population is believed to comprise approximately 157 000 individuals (Hoodless *et al.* 2009), whilst the migratory population is estimated to be between 800 000 (Hirons & Linsley 1989) and 1.4 million birds (The RSPB 2012). This yields a resident to migrant ratio between 1:5 and 1:9. To date, information pertaining to the origins of these migrants has come from ring recoveries. However, because woodcock are not easily caught, only relatively small numbers have been ringed. Information pertaining to the origins of migrants residing in Britain and Ireland during the non-breeding season is currently based on just 226 foreign rings, recovered between 1909 and 1990 (Hoodless & Coulson 1994).

Records from bird observatories suggest that the first migrant woodcock usually arrive in Scotland during the second week of October, with birds reaching southern England and Ireland about ten days later (Williamson 1958). Notably, the earliest ring-recovery for a migrant woodcock was for a bird recovered in Hampshire on 12 October (Hoodless & Coulson 1994). The latest ringing date for a woodcock ringed abroad and recovered in Britain during the same season was for a bird ringed in the Netherlands on 25 December and recovered in Suffolk the following day (Hoodless & Coulson 1994). The variability in arrival dates appears to be a consequence of weather conditions. For instance, changes in air temperature, air pressure and/or wind force, direction and speed, are all likely to affect the migratory impulse of woodcock (Clausager 1974). As a consequence,

birds are often seen arriving in "waves" or "falls", despite migrating as individuals (Shorten 1974).

The majority of British residents appear to remain faithful to their natal or breeding sites during the non-breeding season, with 51% of ring-recoveries found within 10 km of their initial place of ringing and 68% within 30 km (Hoodless & Coulson 1994). However, a proportion of the resident population clearly does make significant movements, with 13% of non-breeding recoveries made at distances of more than 500 km. The common factor among these long distance recoveries is that all the birds originated from Scotland or northern England, and all moved south or south-west to Ireland, France, Spain, Belgium, Portugal or Denmark. Assuming that the recovery rates of ringed woodcock are similar in Britain and mainland Europe, these data suggest that a small proportion (about 4%) of British residents are true (long-distance) migrants that leave their British breeding grounds during the non-breeding season (Hoodless & Coulson 1994).

Ring-recovery records suggest that the majority of migrants depart during late February and early March, although some foreign-ringed birds (4% of all foreign recoveries) have remained in Britain throughout March and into April (up to 15th). Notably, by this time, most resident females would have mated and some would have laid eggs (Hoodless & Coulson 1998). However, there are no records of migrants remaining in Britain to breed.

Non-breeding season

The avian annual cycle is typically separated into breeding and non-breeding periods. The time allocated to each stage can vary between individuals and between species, with factors such as migratory status influencing timings. For instance, long-distance migrants will generally spend three months on the breeding grounds, six months on the non-breeding grounds, and the remaining three months travelling to or from these locations, on spring and autumn migration, respectively (Webster & Marra 2005).

Despite accounting for a substantial portion of the annual cycle, the non-breeding period remains relatively understudied; currently an imbalance exists whereby bird studies have predominantly focused on breeding season events (Vickery & Herkert 1999). When considering evolutionary life-history, the common assumption is that animals maximise their lifetime reproductive success (i.e. their fitness) by investing optimally in reproduction (Hedenstrom 2006). As a consequence, studies tend to be directed toward breeding biology and habitat needs. This issue, however, needs to be re-addressed given that there appears to be an equivalent "non-breeding fitness currency" (Hedenstrom 2006). Indeed, factors operating in the non-breeding season are believed to be playing an important role in the decline of migratory bird species (Rappole & McDonald 1994; Sherry & Holmes 1996; Rappole *et al.* 2003; Keller & Yahner 2006).

Limitation

Bird population changes can be attributed to the influence of extrinsic (environmental) factors upon intrinsic (demographic) features. Of these, the factors that prevent a population from increasing, or cause it to decline, are said to be limiting (Newton 1998). During the non-breeding season, birds may encounter limiting factors that impact individual condition and/or survival, which go on to directly affect population processes (Newton 1998, 2004) (Table A1.2). Since migratory birds do not mate or breed during the non-breeding season, bird behaviour during this time is primarily driven by the need to access resources necessary for self-maintenance and survival (Sherry & Holmes 1996; Studds & Marra 2005; Brown & Sherry 2006). Evidence suggests that the most likely resource for which migratory birds compete during the non-breeding season is food (Sherry & Holmes 1996; Studds & Marra 2005). Indeed, a study of ovenbirds *Seiurus aurocapilla* during the non-breeding season concluded that food abundance was the most important proximate mechanism driving physical condition and thus represented a primary driver for non-breeding season population limitation (Brown & Sherry 2006).

Considering food as the limiting resource on the non-breeding grounds has focused much recent ecological research on intra-specific competition for quality habitats (Sherry & Holmes 1996). Where apparent, studies have shown that non-breeding habitat segregation is often sex biased (Marra *et al.* 1998; Murphy *et al.* 2001; Norris *et al.* 2005), with a trend towards males dominating high-quality, primary forest, whilst females and subordinates are competitively excluded and forced to occupy suboptimal habitats (Gosler 1986; Marra & Holmes 2001;

Bearhop *et al.* 2004; Catry *et al.* 2004). This non-breeding dominance-mediated habitat segregation acts as a key limiting factor, as it not only poses a threat to individual survival but also suggests a mechanism (a "buffer effect") by which density-dependent effects could regulate populations (Newton 2004a). For instance, if non-breeding habitat segregation lowers female survivorship, it may consequently limit the number of females available for reproduction in the following breeding season (Marra & Holmes 2001; Studds & Marra 2005).

Aside from food resources and associated habitats, other forms of non-breeding season limitation are apparent. First, predation can limit populations by reducing breeding numbers below the level that would otherwise occur (Lack 1954; Newton 1993), if acting in an additive manner, compared to other forms of mortality i.e. not simply replacing other causes of death (compensatory) (Newton 1998; Gibbons *et al.* 2007). Notably, levels of predation, and its subsequent impact on individuals and population processes, may vary through time, in response to changes in prey vulnerability, the availability of alternative prey, and/or the prey-predator ratio (Newton 1998). Second, parasites and pathogens, which live within or on the living bodies of birds, can negatively impact individuals and population processes by lowering reproductive success or chances of survival (Gustafsson *et al.* 1994; Hudson *et al.* 1998). It is, however, often difficult to assess the impacts of parasitism on birds, owing to interactions with other potentially limiting factors e.g. individuals weakened by starvation may have increased susceptibility to parasitic disease (Newton 1998). Third, where resources are limiting but shared by more than one species, inter-specific competition may arise and serve as a limiting factor (Madsen 1985; Kristiansen & Jarrett 2002). Finally, extreme weather is known to impact birds (Dobinson &

Richards 1964; Davidson 1982; Clark 1982, 2004), through associations with habitats, food supplies and thermoregulatory demands (Heppleston 1971; Davidson & Evans 1982; Mitchell *et al.* 2000). Weather extremes may go on to cause sudden catastrophic declines in population numbers, which then require several years to recover from. For example, the severe winter of 1962/63 resulted in large declines between the 1962 and 1963 breeding seasons for the common moorhen *Gallinula chloropus*, northern lapwing *Vanellus vanellus*, mistle thrush *Turdus viscivorus*, song thrush *Turdus philomelos*, Eurasian wren *Troglodytes troglodytes* and pied wagtail *Motacilla alba* (Bailey 1967).

In addition to natural limiting factors, human activities may impact birds during the non-breeding season. The most obvious of these is the impact of habitat destruction, which may result in reductions at both the local and wider population level (Dolman & Sutherland 1995). Notably, it is not only the overall loss of habitat that is important, but also its fragmentation. With habitat fragmentation, species become increasingly patchily distributed, making them vulnerable to local extinctions and reduced immigration (Newton 1998). Other impacts imposed by human activities include those from the use of pesticides and/or pollutants (Fry 1995; Mineau 2005), and from hunting, either directly (Thiollay 2005; Sandercock *et al.* 2011), or indirectly through hunting disturbance (Madsen & Fox 1995; Casas *et al.* 2009).

Factors limiting individual condition during the non-breeding season may produce carry-over effects, which go on indirectly to affect population processes (Marra *et al.* 1998; Bearhop *et al.* 2004; Norris *et al.* 2004; Studds & Marra 2005). These can occur at any part of the annual cycle and may alter the timing or

capacity of an individual to migrate, reproduce, or survive at a subsequent stage (Norris 2005; Studds & Marra 2005; Webster & Marra 2005). They are strongest in seasonal environments (Fretwell 1972) and demonstrate the links between different phases of the annual cycle. For instance, the quality of non-breeding habitats have been shown to determine the body condition and spring departure dates of migrants (Marra *et al.* 1998; Bearhop *et al.* 2004), which then carry over to influence arrival schedules (Marra *et al.* 1998; Bearhop *et al.* 2004), body condition (Marra & Holberton 1998; Studds & Marra 2005) and reproductive success (Norris *et al.* 2004) in the breeding season.

Woodcock non-breeding season limitation

During the non-breeding season, woodcock may encounter a number of potentially limiting factors. Of those previously mentioned (see *Limitation*), three are particularly pertinent to woodcock demographics.

Hunting

In accordance with legislation set out in Annex II Part A of the European Union (EU) Birds Directive (Council Directive 2009/147/EEC on the conservation of wild birds), woodcock hunting is permitted in 24 EU countries but is prohibited in Flanders (Belgium), Czech Republic, Netherlands, Canaries (Spain) and Slovenia (Table A1.3). Outside the EU, the woodcock is hunted in five European countries: Azerbaidjan, Norway, Russia, Switzerland and Ukraine (Table A1.4). The woodcock thus represents an important quarry species across much of Europe.

However, the impact of hunting on woodcock mortality may be a major factor affecting woodcock populations.

Most hunting occurs during the non-breeding season, although some countries also permit the shooting of males in spring, during their reproductive display flights ("roding") (Tables A1.3 & A1.4). Hunting pressure is believed to have increased in recent years owing to the scarcity of other game species, such as grey partridges *Perdix perdix* and rabbits *Oryctolagus cuniculus* (Ferrand & Gossmann 2000). However, in order to determine the impact of shooting on woodcock populations, it is necessary to know whether mortality due to hunting is additive or compensatory. Compensation for shooting mortality may arise from reduced competition for limiting resources, as demonstrated for food supplies in the mallard *Anas platyrhynchos* (Hepp *et al.* 1986) and non-breeding territories in male red grouse *Lagopus lagopus scoticus* (Watson & Jenkins 1968; Watson 1985). However, there is clearly a limit to the level of hunting for which populations can compensate through such mechanisms. Duriez *et al.* (2005a) found that hunting over the non-breeding season had an additive effect on woodcock mortality; for birds residing in a hunting area, the mortality probability increased by 23% in adults and 44% in juveniles, compared with birds occupying a hunting-free reserve.

The annual woodcock bag in Europe has been estimated at three to four million birds (Ferrand & Gossmann 2001), yet it is difficult to assess the impact this has on woodcock population dynamics. The collection and quality of harvest data across Europe is highly variable, owing to the different political systems and hunting regulations in place across Europe (Kalchreuter 2000). For instance,

monitoring systems in France are well established. *Club national des bécassiers* (CNB; a French Woodcock Hunter Association) collects detailed information on hunting trips from its members, enabling a hunting index of abundance (ICA) to be calculated (Boidot & Gerard 2011). Furthermore, work carried out by *Office National de la Chasse et de la Faune Sauvage* (ONCFS) has guided the implementation of a national annual bag limit (30 woodcock per hunter), along with the compulsory use of a bag notebook and marking strips (Gossmann *et al.* 2011). Whilst other countries have set bag limits, these tend to be fixed arbitrarily without biological data on population trends (Lutz & Jensen 2006). Typically, limitations refer to quotas (restricted number of birds per hunter per day and/or season) or to a number of hunting days. Currently, a maximum authorised harvest has been applied in five EU countries (France, Greece, Italy, Portugal and Spain). Conversely, in other countries, there is no maximum bag limit and no legal requirement for hunters to submit bag records. In Britain, there is only a voluntary system in place, the National Gamebag Census (NGC), which was established in 1961 by the Game and Wildlife Conservation Trust (GWCT). However, this system has resulted in a bias towards hunters who consistently submit their records on an annual basis, leaving other areas under-represented. The bag data available are also difficult to analyse and interpret, owing to regional changes in hunting pressure and hunter effort.

Weather

Environmental conditions are known to influence the non-breeding survival of woodcock (Tavecchia *et al.* 2002). Stochastic events, such as severe winter conditions, are thought to increase woodcock mortality through associations with

thermoregulation and/or food availability and accessibility (Baillie *et al*. 1986). Declining temperatures place increasing energetic demands on birds, as energy stores need to be sufficiently maintained to buffer against the cold. This increased energy requirement necessitates increased food consumption. However, as temperatures decline, the availability and/or accessibility of food resources also declines. Earthworms comprise 85% of the woodcock diet during the non-breeding season (Granval 1987) but, as temperatures decrease, earthworms become less accessible to woodcock, with ground soil becoming difficult to penetrate and/or earthworms burrowing deeper into the soil (Edwards & Lofty 1972). If birds are unable to find or access sufficient food, then starvation may ensue. Indeed, this was the case during the severe winter of 1962/63, which resulted in increased woodcock mortality (Dobinson & Richards 1964).

Habitat change

The impacts of environmental changes on woodcock populations are likely to be exacerbated by the loss of non-breeding habitat(s) through associations with food availability. Since earthworms are the primary constituent of the woodcock diet during the non-breeding season (Granval 1987) it is likely that earthworm abundance drives woodcock habitat selection and behaviour during this time.

Woodcock utilise a variety of habitats during the non-breeding season, with requirements differing between diurnal and nocturnal sites. For the former, requirements are less specific during the non-breeding season (Shorten 1974; Cramp & Simmons 1983; Kalchreuter 1983), compared to the breeding season (Hirons 1988; Hirons & Johnson 1987; Hoodless & Hirons 2007). However,

woodcock in Brittany, France did show a preference for young forest stands (plantations, followed by coppices and wet forests), with old stands of timber being avoided (Duriez *et al.* 2005b). They also preferred forests with mull humus, which provided a rich food supply, and dense shrub strata, which likely afforded better protection from predators (Duriez *et al.* 2005b). Furthermore, hedges with a high density of trees and shrubs were found to provide important diurnal habitat (Duriez *et al.* 2005b). At night, grass fields have been reported as the preferred habitat of woodcock, despite the increased predation risk (Hirons & Bickford-Smith 1983; Hoodless 1994a; Duriez *et al.* 2005b). These field types are typically rich in earthworms; the biomass of earthworms in grazed meadows was found to be five times higher than those of cultivated fields (Duriez *et al.* 2005b).

Despite their importance for woodcock, suitable diurnal and nocturnal feeding sites are diminishing, owing to European-wide changes in woodland management, agricultural policies, and farming practices. For instance, hedges are threatened with destruction; there was a 60% loss of hedges in France between 1966 and 1996 (Schmutz *et al.* 1996), and this trend is similar across much of Europe. The age and species composition of woodlands have also been changing. In Britain, between 1940 and 1990, there was a 199% increase in coniferous woodland, whilst managed coppice declined by 82% (Forestry Commission 2003). Following changes in agricultural policies and farming practices, ploughing and chemical applications have led to the impoverishment of soil macrofauna (Pain & Pienkowski 1997). Furthermore, ploughing in favour of maize production, for fodder and sale crops, resulted in 12% of natural meadows and pastures disappearing from nine European countries, between 1975 and 1995 (Poiret 1999). Such habitat loss and/or changes across Europe and northern

Asia are believed to have resulted in the pronounced and consistent increase in the woodcock's migration route (in terms of latitude and longitude), documented between 1951 and 1990 (Dobrynina & Kharitonov 2006). Indeed, other bird species reliant on inland water-bodies e.g. the common snipe *Gallinago gallinago* and northern lapwing *Vanellus vanellus*, have shown similar changes in migration route (Dobrynina & Kharitonov 2006).

Mixed populations

Ascertaining the impact of potentially limiting factors on different breeding populations can be problematic during the non-breeding season when there is a mixing of populations. Behavioural studies typically differentiate between the age and sex classes of birds from single populations, but little work has been done to ascertain the differential behaviours between birds from different migratory origins. This issue, however, needs to be addressed, given that differential behaviours between birds of different migratory status may translate into differences in fitness, which then go on to affect overall population dynamics.

The mixing of breeding populations (for birds of the same species) is a common occurrence during the non-breeding season, and is widely encountered across wader species e.g. dunlin *Calidris alpina*, common redshank *Tringa totanus*, European golden plover *Pluvialis apricaria* (Wernham *et al.* 2002). For certain species, morphological differences can be used to distinguish between national breeders (hereon residents) and international breeders (hereon migrants). For example, migratory European blackcaps *Sylvia atricapilla* have longer, more pointed wings, and a smaller body size, compared to residents in Iberia (Telleria

& Carbonell 1999), which enables the two groups to be separated in winter (Perez-tris *et al.* 1999). Similarly, in Spain, the migratory common reed bunting *Emberiza schoeniclus* has larger and more convex wings, compared to residents (Copete *et al.* 1999). Resident and migrant individuals may also vary in their moult schedules, enabling distinction between the two groups (Lundberg & Eriksson 1984). However, for many species, there are often no morphological differences between resident and migrant birds, making distinction difficult, if not impossible, in the field e.g. Eurasian robin *Erithacus rubecula*, common blackbird *Turdus merula* and common starling *Sturnus vulgaris* (Svensson 1992).

In Britain, during the non-breeding season, the national woodcock population comprises a mix of resident (British breeding) and migrant (non-British breeding) birds, with the two groups lacking any morphological distinctions. Whilst early work suggested that variation in plumage coloration was an indicator of woodcock origin, with the "reds" believed to represent residents and the "greys" migrants (Seigne 1930; Bartholomew 1931), it is now accepted that such colour variations are merely a product of individual variation (Stronach *et al.* 1974; Kalchreuter 1983). Other morphological characteristics (Clausager 1973; Rochford & Wilson 1982; Ferrand & Gossmann 2009) have failed to distinguish birds from different breeding populations. Fortunately, for such morphologically indistinct species, the development and application of stable isotope analysis has provided researchers with a means of distinguishing between birds of resident and migratory status.

Application of stable isotopes

In this thesis, stable isotope analyses are applied at two spatial scales: first, to determine the origins of woodcock residing in Britain during the non-breeding season (Chapter 3); second, to determine the predicted migratory status of woodcock residing in Hampshire over winter (Chapters 4 & 5). Neither approach has been applied to the Eurasian woodcock before, thus this thesis represents a unique body of work.

Thesis aims and structure:

This thesis seeks to address four key questions pertaining to the migratory origins and non-breeding ecology of Eurasian woodcock *Scolopax rusticola*.

1. How applicable is the stable isotope approach to the study of woodcock migration? This question is explored in Chapter 2: *Assessing the utility of stable isotope analysis for the study of woodcock migration*, which provides an important methodological foundation to this thesis, since all the questions addressed within necessitate, to an extent, the use of stable isotopes. Given that the stable isotope technique has never before been applied to the study of woodcock, this chapter seeks to assess the utility of the technique, determine where variation exists (if any), and highlight constraints and/or considerations that might serve to guide further work.

2. What is the structural composition of the woodcock population in Britain, during the non-breeding season? From where do birds originate and how are they

distributed across Britain? These questions are investigated in Chapter 3: *Breeding origins and spatial distribution of woodcock in Britain and Ireland during the non-breeding season*, which provides an updated and more accurate assessment of bird origins than those of previous works, and enables patterns of connectivity to be ascertained.

3. What are the preferred habitats of woodcock during the non-breeding season? This question is explored in Chapter 4: *Spatial habitat use of Eurasian woodcock in a British mixed-farming landscape during winter*, which provides insights into the differential habitat use of woodcock according to age (adult vs. juvenile) and predicted migratory status (resident vs. migrant).

4. How do movements and behaviours differ between individual woodcock on the wintering grounds? This question is investigated in Chapter 5: *Behaviour of Eurasian woodcock on the wintering grounds in Britain, in relation to bird age and predicted migratory status*, which provides new insights into the differential movements and behaviours of woodcock according to age (adult vs. juvenile) and predicted migratory status (resident vs. migrant).

Tables & Figures

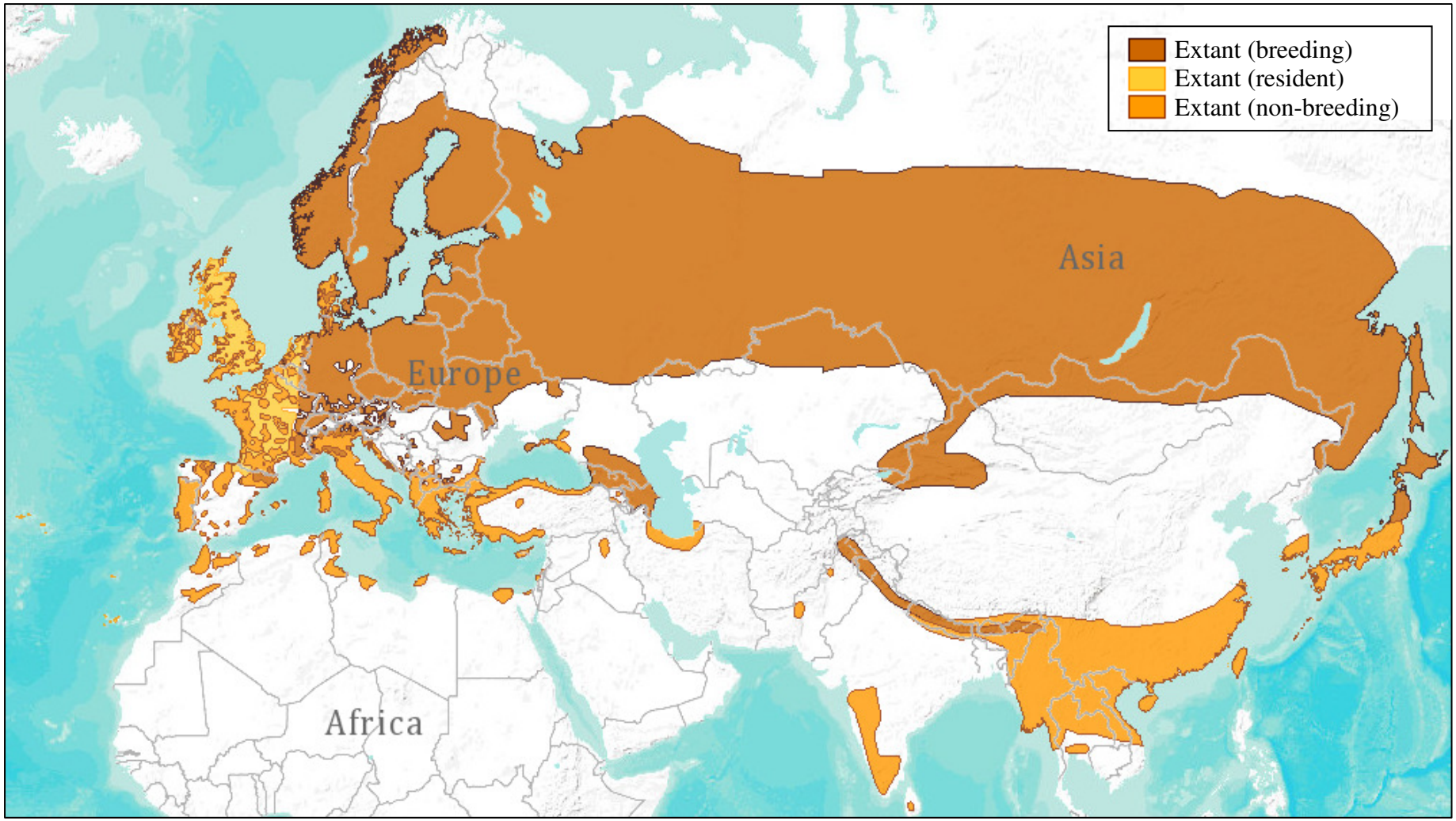


Figure 1.1 The global distribution of Eurasian woodcock (courtesy of BirdLife International & Natureserve 2011).

General Methods I

Stable isotope analysis

Stable isotope analysis

The stable isotope approach is commonly used to determine the breeding origins of birds (Hobson *et al.* 2001; Mazerolle *et al.* 2005; Fox *et al.* 2007; Greenberg *et al.* 2007). It is less invasive, less labour intensive and more cost-efficient than alternative methods, and it enables bird origins to be determined from a single tissue sample (Hobson & Wassenaar 2008; Hobson 2011). For these reasons, the stable isotope technique was applied to the study of Eurasian woodcock *Scolopax rusticola* (hereon woodcock).

Stable isotopes

Stable isotopes are different forms of the same chemical element that vary in the number of neutrons they contain and, thus, in their atomic mass. This compositional difference affects their chemical kinetic behaviour, leading to natural isotope separation processes (isotopic fractionation), whereby there is partial separation of light isotopes from heavy isotopes. Amongst biologically important elements (e.g. carbon, nitrogen, hydrogen, oxygen and sulphur), the heavy stable isotopes tend to be discriminated against during fractionation processes, such that they are relatively less abundant than their lighter forms. These differences in abundance can be readily measured by a mass spectrometer and are typically expressed as a ratio of the heavy to light forms (e.g. $^{13}C/^{12}C$, $^{15}N/^{14}N$, $^{2}H/^{1}H$), relative to some international standard(s). Ratios are reported in delta (δ) notation as parts per thousand (‰), according to the equation:

$$\delta X = (R_{sample}/R_{standard} - 1)*1\,000$$

where X is the heavy isotope, R_{sample} is the isotope ratio (heavy to light) of the sample and $R_{standard}$ is the isotope ratio (heavy to light) of the standard. Positive values indicate an enrichment of the heavy isotope, whilst negative values indicate its depletion.

Biological, biogeochemical and/or anthropogenic processes (summarised by Rubenstein & Hobson 2004) affect the magnitude of isotopic fractionation. As a result, each element within a given environment/biome has a distinct "isotopic signature". These signatures can be passed on, through food webs, to higher-order consumers where they are then assimilated into animal tissues (Cormie *et al.* 1994). During this transferral, trophic enrichment (isotopic discrimination) occurs, whereby a calculable difference between the putative diet and the consumer's tissue can be detected. The degree of trophic enrichment varies depending on the element involved (Wada *et al.* 1991; Marshall *et al.* 2007).

Tissue selection

The isotopic signature of an animal's tissue reflects the diet/habitat during the time of tissue synthesis (Hobson & Clark 1992a; Martin *et al.* 2007). By selecting different tissues, with different turnover rates (reviewed by Phillips & Eldridge 2006), isotopic information spanning various temporal scales can be collected. Ultimately, the choice of tissue will depend on the question(s) being asked. Blood and muscle are metabolically active tissues that continuously turn-over (in a matter of weeks) and, since their isotopic signatures vary in accordance with this, such tissues are useful in determining short-term movements, usually within a season (e.g. Norris *et al.* 2005). Conversely, keratinised tissues become

metabolically inert following synthesis; the isotopic signatures within these tissues typically remain unchanged post-synthesis, enabling long-term movements between seasons to be determined (Hobson & Clark 1992a). One notable exception is the hydrogen isotope of keratinised material. Chamberlain *et al.* 1997 documented that a proportion (13%) of non-carbon-bound hydrogen in American redstart *Setophaga ruticilla* feathers was free to exchange with ambient water vapour. This exchange, however, can be corrected for through equilibration techniques (Wassenaar & Hobson 2000a).

For this study, feathers were the tissue of choice. Tissue selection was guided by the questions being asked and the relative ease of feather sampling. Indeed, feathers are often the preferred tissue type, as sampling is non-invasive, less costly, and less labour intensive, compared to those of other tissue types.

Feather isotopes are indicative of moult location. Since woodcock typically moult on the breeding grounds, during the breeding season (Witherby *et al.* 1943; Clausager 1973; Kalchreuter 1983; Ferrand & Gossmann 2009), their moult location becomes synonymous with breeding origin. However, in order to accurately infer information regarding breeding origins from feather stable isotopes, it is necessary to sample the feather type that most accurately reflects this information. An understanding of woodcock plumage cycles and moult was therefore imperative in guiding the feather selection process (Figure GMI.1) (Smith *et al.* 2008; Ferrand & Gossmann 2009).

During the breeding season, juvenile woodcock develop a plumage that is distinctive from their adult counterparts. Aside from a partial post-juvenile

moult, which starts when the birds are approximately two months old and includes the body coverts, usually all lesser and median upper wing coverts, and adjacent marginal coverts, all other feathers are retained (Ferrand & Gossmann 2009). There is no moulting of the primaries, secondaries, tertials, greater primary coverts or under-wing coverts, until after the first breeding season i.e. until after 12 months of age (Witherby *et al.* 1943; Kalchreuter 1983; Ferrand & Gossmann 2009). Moult of body feathers, however, can occasionally be observed in juvenile birds in February/March (Ferrand & Gossmann 2009). Conversely, adults annually undergo a complete moult, which occurs from late June to early October on the breeding grounds (Witherby *et al.* 1943; Clausager 1973; Ferrand & Gossmann 2009). Their remiges and rectrices are moulted between July and September. Notably, the adult post-breeding moult, along with the partial post-juvenile moult, can be suspended by migration departure. However, moult-suspension typically concerns under-wing coverts, only (Ferrand & Gossmann 2009).

The sequences of the various feather-tract moults are not perfectly known for Eurasian woodcock, but comparison can be drawn from their close relative, the American woodcock *Scolopax minor*. The moult process in this species has been well studied, with moult occurring sequentially and descendingly i.e. innermost 1^{st}-10^{th} primary, innermost 1^{st}-10^{th} secondary, 1^{st}-3^{rd} tertial (Owen & Krohn 1973). The few available data on *S. rusticola* (Kozlova 1962) indicate that their feather-tract moult pattern is similar. Since the primary remiges appear to be amongst the first feathers grown for both adult and juvenile birds, feathers from this tract should have an isotopic signature representative of the breeding location. Indeed, work by Clausager (1973) found that adult woodcock in

Denmark generally complete the moult of their primaries by the end of September, with only three out of 600 instances (0.5%) found to have incomplete primary moult between 24 September and 31 December. Given that woodcock moult their feathers sequentially, the first (innermost) primary (P1) should be the first of the primaries grown (i.e. the oldest feather), and should therefore be the feather most representative (of all feathers) of the breeding grounds. As such, P1 was selected (where possible) for sampling.

To ensure retention of an accurate isotopic signature, it is important samples come from metabolically inactive (inert) feathers. However, feathers only reach this state once they are fully grown, specifically when the feather barbs emerge and the follicle blood vessels are reabsorbed (Gill 1990). Therefore, feather samples were only taken from fully-grown birds with fully-grown feathers. Any feathers recorded as "growing" or in "active moult" were excluded from analysis.

For each P1, the distal tip was sampled, as this is the oldest part of the feather and is likely to be most representative of moulting (breeding) locality. Furthermore, following the recommendation of Wassenaar & Hobson 2006, the barbs along the vane of each feather were sampled, whilst the rachis was avoided (Figure GMI.2), owing to its heavy isotopic enrichment. Sampling between feathers was also kept as consistent as possible, since intra-feather variation has been reported between distal and more proximal subsamples (Smith *et al.* 2008).

Age determination

Samples were assigned to one of two age categories: (1) juvenile; defined as a bird hatched that calendar year or a bird hatched the previous calendar year but not yet moulted into adult plumage, (2) adult; defined as a bird hatched before the previous calendar year. Birds were aged on the basis of differential plumage characteristics (Clausager 1973; Ferrand & Gossmann 2009). For birds sampled on their breeding grounds (between April-September), age was determined by the shape and size of the primary tips, coloration and patterning of the primary coverts, and shape of the under-wing coverts (Clausager 1973; Shorten 1974; Ferrand & Gossmann 2009). In addition to these criteria, birds sampled during December and January were aged on the extent of primary wear (Clausager 1973; Ferrand & Gossmann 2009).

Laboratory methods

Laboratory-1: Natural Environment Research Council Life Sciences Mass Spectrometry Facility (NERC LSMSF), East Kilbride, U.K.

Sample preparation

All feather samples were washed in a 2:1 chloroform: methanol solution and air-dried under a fume-hood. Once dry, a distal subsample was clipped from each feather, using surgical scissors. These were weighed into capsules using a self-calibrating microbalance. For δ^2H analysis, 0.1 mg (± 20%) of sample was

measured into silver capsules (4 x 3.2 mm). For $\delta^{13}C$ and $\delta^{15}N$ analysis, 0.7 mg (± 20%) of sample was measured into tin capsules (5 x 3.5 mm).

Hydrogen analysis

Since a proportion of organic hydrogen (mainly that involving N–H and O–H bonds) readily exchanges with ambient water vapour (Schimmelmann 1991), samples were stored, for at least 10 days, alongside a number of keratin standards. This allowed the exchangeable hydrogen in the sample chitin to fully equilibrate with the moisture in the laboratory air. The keratinous standards used were CFS (chicken feather standard), BWB-II (bowhead whale baleen), ISB (Icelandic seabird: black-legged kittiwake *Rissa tridactyla*) (c.f. Wassenaar & Hobson 2003; Fox *et al.* 2007), and WG (willow grouse feathers). Some of these were prepared and measured using an off-line equilibration method at Environment Canada in Saskatoon (Wassenaar & Hobson 2000a), whilst others were prepared using analogous methods (developed by Jason Newton) at the NERC LSMSF.

Samples were reduced at high temperatures, using flash pyrolysis. Stable hydrogen isotope ratios were obtained using Continuous Flow Isotope Ratio Mass Spectrometry (CF-IRMS), employing high-temperature conversion (Thermal Conversion/Elemental Analyser (TC/EA); ThermoFisherScientific, Bremen, Germany) coupled to a Delta V isotope ratio mass spectrometer (ThermoFisherScientific, Bremen, Germany). Ratios were expressed in the standard delta notation i.e. part per mil (‰). Data were corrected using the frequently adopted comparative steam equilibration procedure (Wassenaar &

Hobson 2003). Assuming constant δ^2H of ambient water vapour, during a single six-hour experiment, and a uniform proportion of exchangeable hydrogen in animal keratin (19-20%; Wassenaar & Hobson 2000a), a linear correction equation can be applied to the raw hydrogen isotope data (Wassenaar & Hobson 2003).

Carbon and Nitrogen analysis

Samples were combusted for the simultaneous determination of carbon and nitrogen isotope ratios, using CF-IRMS. A Costech (Milan, Italy) ECS 4010 elemental analyser was used for analyses, interfaced with a Thermo Electron (Bremen, Germany) Delta Plus XP mass spectrometer. Replicate analysis of internal standards tryptophan, gelatine and alanine (^{14}N-alanine and ^{15}N-alanine) were conducted, enabling detection and correction of any instrumental drift. Notably, these standards are cross-checked on a monthly basis with secondary international standards from the International Atomic Energy Agency (IAEA) and National Institute of Standards and Technology (NIST). Stable isotope ratios were expressed in the standard delta notation, i.e. units per mil (‰).

Laboratory-2: IsoAnalytical Ltd., Crewe, U.K.

Sample preparation

Each feather was washed in 0.25M sodium hydroxide solution, followed by two separate washes in purified water. The washed feathers were placed in clean

screw top vials and oven-dried overnight at 50°C. Once dry, the feathers were clipped into fine sections, using surgical scissors.

For δ^2H analysis, 1.0 mg (± 10%) of sample was weighed into silver capsules (8 x 5 mm). The filled capsules were then left open, for a period of no less than 4 days, to allow the exchangeable hydrogen in the sample chitin to fully equilibrate with the moisture in the laboratory air. The capsules were only sealed just prior to analysis. For $\delta^{13}C$ and $\delta^{15}N$ analyses, 1.0 mg (± 10%) of feather sample was weighed into tin capsules (8 x 5 mm).

Hydrogen analysis

The technique used for analysis was EA-IRMS (Elemental Analyser - Isotope Ratio Mass Spectrometry). In this technique, samples and references were loaded into an auto-sampler. They were then dropped into a furnace at 1 080°C and thermally decomposed to H_2 and CO, over glassy carbon. Any traces of water produced were removed by magnesium perchlorate, while any traces of CO_2 formed were removed via a Carbosorb™ trap. H_2 was resolved by a packed column gas chromatograph held at 35°C. The resultant chromatographic peak entered the ion source of the IRMS, where it was ionised and accelerated. Gas species of different mass were separated in a magnetic field, then simultaneously measured on a Faraday cup universal collector array. For H_2, masses two and three were monitored.

The reference material used for δ^2H analysis was IA-R002 (mineral oil, $\delta^2H_{V\text{-}SMOW}$ = -111.2‰). IA-R002 has been calibrated against NBS-22 (mineral oil, $\delta^2H_{V\text{-}SMOW}$

= -118.5‰) and distributed as an isotope reference standard by the IAEA. Samples of IA-R002 and IAEA-CH-7 (polyethylene foil, $\delta^2H_{V\text{-}SMOW}$ = +100.3‰) were analysed along with the feather samples as quality control checks. In addition, samples of BWB-II (whale baleen) and egg shell membrane standards were analysed with feather samples. BWB-II has a known non-exchangeable $\delta^2H_{V\text{-}SMOW}$ value (± standard deviation, SD) of -108‰ (± 4 SD). Egg shell membrane standard has a non-exchangeable $\delta^2H_{V\text{-}SMOW}$ value of -93.8‰ (± 2.3 SD), as independently measured by Len Wassenaar, National Water Research Institute (NWRI), Saskatoon, Canada. By using the measured $\delta^2H_{V\text{-}SMOW}$ value for BWB-II, it was possible to apply a simple correction for exchangeable hydrogen to the $\delta^2H_{V\text{-}SMOW}$ data of the feather samples. The BWB-II adjusted data are quoted in results.

Carbon and Nitrogen analysis

The technique used for analysis was Elemental Analysis Isotope Ratio Mass Spectrometry (EA-IRMS). In this technique, samples and references were loaded into an auto-sampler on a Europa Scientific elemental analyser. They were then dropped in sequence into a furnace held at 1 000°C and combusted in the presence of oxygen. The tin capsules flash combusted, raising the temperature in the region of the sample to ~1 700°C. The combusted gases were swept in a helium stream over a combustion catalyst (chromium oxide - Cr_2O_3), copper oxide wires (to oxidize hydrocarbons), and silver wool, to remove sulphur and halides. The resultant gases, N_2, NO_x, H_2O, O_2, and CO_2 were swept through a reduction stage of pure copper wires held at 600°C. This removed any oxygen and converted NO_x species to N_2. A magnesium perchlorate chemical trap was used to remove

water. Nitrogen and carbon dioxide were separated using a packed column gas chromatograph held at a constant temperature of 65°C. The resultant nitrogen peak entered the ion source of the Europa Scientific 20-20 IRMS first, where it was ionized and accelerated. Nitrogen gas species of different mass were separated in a magnetic field, then simultaneously measured using a Faraday cup collector array to measure the isotopomers of N_2 at m/z 28, 29, and 30. After a delay, the carbon dioxide peak entered the ion source, where it was ionized and accelerated. Carbon dioxide gas species of different mass were separated in a magnetic field, then simultaneously measured using a Faraday cup collector array to measure the isotopomers of N_2 at m/z 44, 45, and 46.

Both references and samples were converted to N_2 and CO_2 and analysed using this method. The analysis proceeded in a batch process, whereby a reference was analysed, followed by a number of samples, and then another reference. The reference material used for $\delta^{13}C$ and $\delta^{15}N$ analysis was NBS-1577B (powdered bovine liver, $\delta^{13}C_{V\text{-}PDB}$ = -21.60‰, $\delta^{15}N_{Air}$ = 7.65‰). NBS-1577B and a mixture of IAEA-CH-6 (sucrose, $\delta^{13}C_{V\text{-}PDB}$ = -10.43‰) and IAEA-N-1 (ammonium sulphate, $\delta^{15}N_{Air}$ = 0.40‰) were run as quality control checks during sample analysis.

Tables & Figures

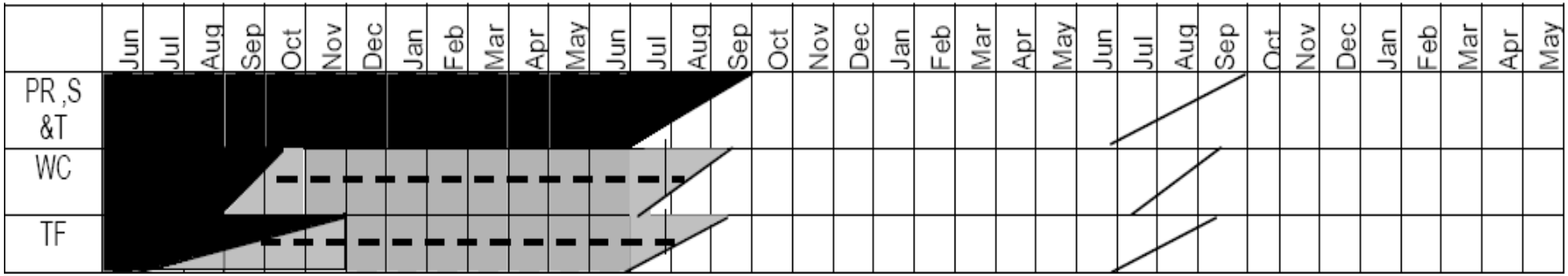


Figure GMI.1 Moult schedule for Eurasian woodcock. PR = primaries, S= secondaries, T = tertials, WC = upper- & under-wing coverts, and TF = tail feathers. Black = juvenile feathers, grey = winter plumage, and white = breeding plumage. Broken line = presence of retained juvenile feathers (after Ferrand & Gossmann 2009).

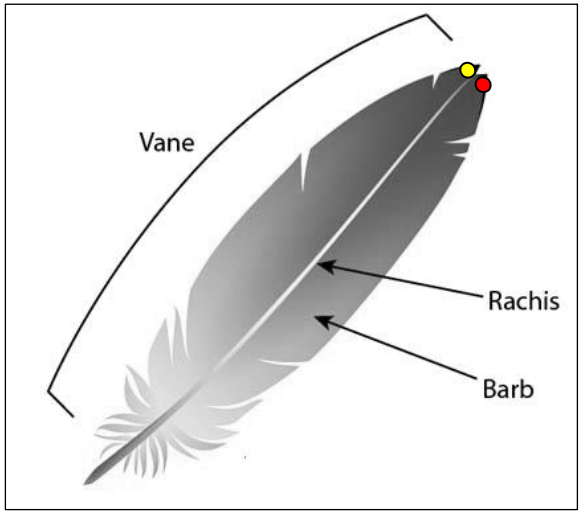


Figure GMI.2 Feather schematic, showing both the sampling region (red circle) and sub-sampling region (yellow circle).

Chapter 2

Assessing the utility of stable isotope analysis for the study of woodcock migration

Assessing the utility of stable isotope analysis for the study of woodcock migration

Abstract

Studying the migratory movements of birds between different phases of the annual cycle is necessary to understand the overall demography and health of bird populations. This area of research, however, has proved challenging for researchers, owing to the often large distances travelled by species, the remoteness of locations occupied, and the limitations of traditional marking techniques. Stable isotope analysis is an innovative method currently being used to determine the geographic origins of migratory birds. This study assessed the values and limitations of the stable isotope approach in relation to Eurasian woodcock *Scolopax rusticola* (hereon woodcock) migration. Known sources of isotopic variation: spatial, temporal, inter-individual, inter-feather, inter-laboratory and intra-laboratory, were assessed for their effects on woodcock feather stable isotopes. The results revealed significant spatial variation for stable hydrogen isotopes (δ^2H), suggesting that δ^2H has potential as a geographic marker for woodcock. Variation in δ^2H was also found between birds of different age class (adult vs. juvenile). All other sources of variation were negligible. The utility of woodcock museum specimens as an additional source of known (breeding) origin sampling material was also assessed. No distinction could be made between the isotope values of museum and contemporary feathers collected on the breeding grounds, lending support to the long-term stability of the hydrogen isoscape and thus validating the use of museum woodcock specimens as an additional sampling source.

Introduction

Tracking the migratory movements of birds has conventionally relied on the use of extrinsic markers, such as individual tags (e.g. leg rings, neck collars or plumage dyes) or remote sensing technology (e.g. radio-transmitters, geolocators or satellite tags). The former can be applied to a broad range of species and offer high spatial resolution, but an initial capture is required and (in most cases) a recapture or re-sighting is also necessary, which typically biases the data toward regions with high mark-recapture efforts (Hobson *et al.* 2004; Hobson & Wassenaar 2008). Whilst remote sensing techniques do not require any form of recapture or re-sighting, sample sizes are often constrained by the expense of such technology. Consequently, remote sensing techniques are unlikely to provide the population-level insights necessary to fully understand the migratory movements of species (Hobson & Wassenaar 2008).

The development of stable isotope analysis has provided a new and powerful tool to trace migratory movements (Hobson 1999). These endogenous markers have a fundamental advantage over existing methods, in that individuals only have to be captured and sampled once. Each capture essentially becomes a recapture because data on previous location can be obtained from a single sampling event. In addition, stable isotopes are relatively inexpensive, compared to remote sensing technology, and they are not species or taxon specific (Hobson & Wassenaar 2008; Hobson 2011).

Application of stable isotopes to migration studies

The potential of the stable isotope technique for tracking bird migration was first highlighted in 1997, with the publication of two pioneering studies: Chamberlain *et al.* (1997) and Hobson & Wassenaar (1997). Since then, stable isotopes have been increasingly used as a tool to improve our understanding of bird migration (Marra *et al.* 1998; Wassenaar & Hobson 2000b; Hobson *et al.* 2004; Mehl *et al.* 2005).

As this area of research has developed, the merits of the stable isotope technique have clearly been demonstrated. For instance, carbon isotope signatures were recently used to elucidate the migration of the globally threatened aquatic warbler *Acrocephalus paludicola*. The wintering grounds of these birds have long been unknown, making flyway conservation efforts impossible. However, the carbon isotope results revealed that discrete breeding populations over-winter in geographically distinct parts of sub-Saharan Africa (Pain *et al.* 2004). These results have since guided conservation efforts to locate the wintering areas of aquatic warblers, with the first of these discovered in 2007 (Walther *et al.* 2007; BirdLife International 2010).

Despite its merits, problems with the stable isotope technique have also been highlighted. Stable isotope data can be highly variable (Wunder *et al.* 2005; Powell & Hobson 2006; Lott & Smith 2006) and, in some situations, this has rendered the technique unsuitable (Kelly *et al.* 2008; Larson & Hobson 2009). Indeed, variation amongst isotope data has led some to question the reliability of isotopes as a tool for geographic assignment (Rocque *et al.* 2006; Farmer *et al.*

2008; Smith *et al.* 2009a). Methods dealing with spatial and analytical error, however, are continually being developed (Wunder & Norris 2008a; Wunder *et al.* 2009). Therefore, despite concerns, stable isotopes remain a useful tool in the study of migratory bird movements. In particular, they are providing new and important insights into previously under-studied and/or under-detected bird species (Hobson *et al.* 2010b; Reichlin *et al.* 2010).

Throughout this thesis, the stable isotope technique is applied to Eurasian woodcock *Scolopax rusticola* (hereon woodcock), a bird species that, owing to its cryptic plumage and elusive nature, has remained relatively under-studied. It is applied in an attempt to better understand the origins and non-breeding ecology of individuals, since data from ringing recoveries (Hoodless & Coulson 1994; Bauthian *et al.* 2007; Guzman *et al.* 2011) and radio-tracking (Hirons & Bickford-Smith 1983; Wilson 1983; Hoodless 1994a; Duriez 2003) are limited. However, before using stable isotopes to explore aspects of migratory behaviour, it is important to first assess the various levels at which isotopic variation might exist, to ensure accurate interpretation of results. Such an assessment of utility is essential given that no previous isotope studies have focussed on this species. If stable isotopes are validated as markers for this species, the application of this approach may serve to greatly improve our understanding of woodcock migratory behaviour.

The woodcock represents a unique and interesting candidate for isotopic study. First, birds migrate along Eurasian flyways that have, as yet, received little attention in the isotope literature (Hobson *et al.* 2004). Second, although other wader species have been the subject of isotope studies (Atkinson *et al.* 2005;

Zockler *et al.* 2006), *S. rusticola* is atypical of this group. Despite sharing a similar morphology and physiology, the woodcock predominantly resides inland and consequently its diet differs considerably from that of other wader species. This marked difference in ecology thus renders isotope studies of woodcock and other waders incomparable.

Assessing sources of isotopic variation

Spatial (geographic) variation

Differences in isotope ratios across various spatial scales enable the creation of isotopic landscapes, or "isoscapes" (Bowen 2010), which can then be used to further explore aspects of migratory behaviour (Hobson *et al.* 2010a). As a first step, the aim here was to ascertain whether isotope ratios from contemporary woodcock feather samples of known origin (see *Methods*) exhibit spatial variation and thus have utility as broad-scale geographical markers. The potential of three elements: carbon, nitrogen and hydrogen, were assessed.

Carbon isotope theory

Stable carbon isotopes ($\delta^{13}C$) arise from photosynthetic processes. The fixation of CO_2 discriminates against the heavy isotope (^{13}C), which results in plants having low $\delta^{13}C$ values relative to other pools in the carbon cycle (Bowen 2010). Notably, $\delta^{13}C$ varies in accordance with the proportion of plants utilising different carbon-fixation methods, within and between environments: the Calvin cycle (C_3), Slack-Hatch cycle (C_4) and Crassulacean acid metabolism (CAM) photosynthetic

pathway (Marshall *et al.* 2007). The magnitude of ^{13}C fractionation varies between these three systems and is most pronounced for C_3 plants (~27‰) (Bowen 2010). However, carbon isotopic discrimination between the diet (environment) and consumer tissues is relatively constant (McCutchan *et al.* 2003), giving $\delta^{13}C$ potential as a local habitat or broad-scale geographic marker (Wada *et al.* 1991; Marra *et al.* 1998; Bearhop *et al.* 2004).

Nitrogen isotope theory

Unlike the carbon isotope system described above, the stable nitrogen isotopes ($\delta^{15}N$) of soil and plants cannot be attributed to a single process; rather, they arise from a suite of processes that result in the removal of ^{15}N (Bowen 2010). Although spatial variation in $\delta^{15}N$ is not well understood, global-scale patterns do exist that allow the protein (amino-acid) pathways from the diet (environment) to be traced. Indeed, measurements have been used to differentiate between waterfowl occupying agricultural areas (enriched in $\delta^{15}N$) and more temperate regions (depleted in $\delta^{15}N$) (Hebert & Wassenaar 2001). Since the woodcock has a propensity to feed in agricultural areas at night, changes in $\delta^{15}N$ may be detectable across broad landscapes.

Hydrogen isotope theory

The stable hydrogen isotope ($\delta^{2}H$), also referred to as deuterium (δD), varies spatially in accordance with continental-scale hydrologic patterns (Hobson 1999; Rubenstein & Hobson 2004; Bowen *et al.* 2005). Altitude, latitude and distance from the coast are considered the three most important parameters influencing

the hydrogen isotope gradient and, owing to Rayleigh's (rainout) distillation process (Gat 1996), δ^2H becomes more depleted as these increase. Since the hydrogen isotopic discrimination between the diet (environment) and consumer tissues is relatively constant (Chamberlain *et al.* 1997; Hobson & Wassenaar 1997), δ^2H has potential as a broad-scale geographic marker (Hobson *et al.* 1999b; Rubenstein *et al.* 2002; Perez & Hobson 2007).

Inter-individual

Despite growing feathers at the same time and at the same location, individuals from a local breeding population can be expected to exhibit isotopic heterogeneity (Wassenaar 2008). The extent of this inter-individual isotopic variation, however, could have serious implications for studies using isotope values to infer origins. The degree of inter-individual variation was therefore assessed between contemporary woodcock samples from similar localities.

Inter-feather

The δ^2H composition of feathers has been shown to vary among generations of feathers (Duxbury *et al.* 2003; Meehan *et al.* 2003; Smith & Dufty 2005; Langin *et al.* 2007) and in some instances among feathers of the same generation (Kelly *et al.* 2002; Smith & Dufty 2005). This has implications for studies using feather stable hydrogen isotopes to infer geographic origins and highlights the importance of appropriate feather selection prior to analysis (Smith *et al.* 2008). Given this, it was important to ascertain whether significant inter-feather variation exists for woodcock. If differences in the isotope values between feather

tracts are apparent, these might provide insights into moulting strategy; for example, pronounced differences might indicate moult suspension.

Inter- and intra- laboratory

The reproducibility of isotope ratio values within laboratories has been strongly debated (Smith *et al.* 2009a,b; Wunder *et al.* 2009). Whilst, ideally, all stable isotope analyses would be conducted in the same laboratory, this is not always feasible. In this study, analyses were conducted in two laboratories, at different facilities. Therefore, to assess for reproducibility between laboratories, a small, random selection of contemporary samples was analysed at both facilities, and the results compared.

Isotopic variation between automated runs within the same laboratory has also been reported (Smith *et al.* 2009a). This is potentially problematic for the majority of studies, as sample sizes will often exceed the batch limit (66 samples), meaning that multiple runs have to be conducted. In an attempt to assess reproducibility between runs, the variation between repeated measures of standards was analysed.

Temporal variation: the utility of museum specimens

Natural history museums often have large collections of bird specimens that can be sampled for scientific purposes. Feathers from appropriate specimens could potentially provide an additional source of known origin sampling material (see *Methods*). However, museum sampling can be problematic for two reasons. First,

museum policy often restricts sampling to just one or two body-contour feathers. Since this may not be the appropriate feather type, it would be necessary to first determine the error, if any, associated with using the museum-dictated feather type. This would require an analysis of contemporary inter-feather variation. If no such variation was apparent, or if there was a constant measurable difference that allowed a correction factor to be applied, then museum specimen sampling could be pursued. The second problem concerning museum specimens is that of age. Museum specimens are often decades old and the isotope values from historic samples may not be representative of isotope values from birds today. Any isotopic study utilising museum specimens should therefore assess the long-term temporal trends in isotope values. Historic changes in isotope values may be present if diet/habitat use has changed over time and, whilst this would render museum specimens unsuitable for a pooled analysis with contemporary samples, it would make for an interesting investigation in its own right. Here, the utility of woodcock museum specimens as an additional source of known origin sampling material was assessed.

Aims

The purpose of this chapter was to ascertain whether the stable isotope approach can be applied successfully to the study of woodcock migration, once known sources of isotopic variation have been accounted for.

Methods

Assessing sources of isotopic variation

Feather isotopes are indicative of moult location. Since woodcock typically moult on the breeding grounds, during the breeding season (Witherby *et al.* 1943; Clausager 1973; Kalchreuter 1983; Ferrand & Gossmann 2009), their moult location becomes synonymous with breeding origin (General Methods I). Feathers collected from woodcock on their breeding grounds, during the breeding season, therefore provide a source of known (breeding) origin sampling material.

Contemporary, known origin feather samples were collected from woodcock across their European breeding grounds, during the breeding season (April-September), between 2002 and 2010. In total, 136 individual samples were collected from 39 different locations (across 10 European countries) (Table A2.1). Samples from Russia and Belarus were taken from birds shot during the spring shooting season (predominantly roding males). The majority of all other European countries, however, have imposed a ban on woodcock hunting in the spring/summer. In these countries, samples were taken from birds caught as by-catch during ringing sessions and from birds killed in car collisions or predation events. Where possible, the distal tip of the first (innermost) primary feather (P1) was sampled. However, four samples from Spain comprised body contour feathers (BC). To allow inclusion of these samples in analyses, it was necessary to reduce any error associated with inter-feather variation. Therefore a correction equation was applied (see *Body contour correction equation*) that enabled the δ^2H values of these body contour feathers to be converted into first primary equivalents.

Samples were then pooled, and assessed for spatial and inter-individual isotopic variation.

To assess inter-feather variation, the δ^2H signatures of P1, the corresponding under-wing covert (U1), and BC were analysed for each of 10 birds, all of unknown breeding origin. Feathers were collected (post-moult) between 2007 and 2009.

In an attempt to assess inter-laboratory variation, P1 samples from birds of unknown breeding origin were randomly selected for replicate analysis (δ^2H: n = 19, $\delta^{13}C$ and $\delta^{15}N$: n = 20). All samples were collected in the winter of 2008/2009. Subsamples were taken from either side of the vane (Figure GMI.2). All samples were analysed in the same automated run.

The mean δ^2H values of laboratory standards were also compared against their accepted (expected) values, in an attempt to assess the reproducibility of δ^2H between automated runs (i.e. intra-laboratory variation). For laboratory-1, all keratinous standards were analysed (i.e. BWB, CFS, ISB and WG), plus IA-R002. For laboratory-2, the reproducibility of IAEA-CH-7 (polyethylene) and eggshell membrane were assessed.

Feather samples from museum specimens were collected from: Biologiezentrum Linz, Austria (n = 2†); Zoology Museum, Copenhagen, Denmark (n = 4†); National Museums Scotland, Edinburgh, UK (n = 4†); Finnish Museum of Natural History, University of Helsinki, Finland (n = 21); Museum of Natural History, Paris, France (n = 11); Museum of Natural History, Stuttgart, Germany (n = 1); Bergen

Museum, University of Bergen, Norway (n = 25†); Tromsø University Museum, Tromsø, Norway (n = 4†); Swedish Museum of Natural History, Stockholm, Sweden (n = 7), and the Natural History Museum, Tring, UK (n = 15). Feather samples came from museum specimens dating from 1885 to 2002 (Table A2.2). For all museum specimens (n = 94, 38 adults, 56 juveniles), a body contour feather, taken from just under the left wing, was analysed for δ^2H. Amongst these, 39 individuals (those marked with †) also had a first primary flight feather analysed.

To reduce any error associated with inter-feather variation, the δ^2H of museum-derived BC was regressed against the δ^2H of museum-derived P1. From this, a correction equation was developed (see *Body contour correction equation*) that enabled the δ^2H values of the remaining museum-BC feathers to be converted into P1 equivalents. Samples were then pooled, and assessed for temporal and spatial isotopic variation.

Body contour correction equation

Reduced major axis (RMA) regression of museum-derived feather samples was used to formulate the predictive equation. This is deemed the most suitable method to use when both variables, measured on the same scale, are characterised by similar levels of uncertainty/error (Sokal & Rholf 1994). Samples from adults (n = 11) and juveniles (n = 28) were regressed separately.

The least squares estimator of the RMA regression slope (m) was calculated as follows:

m = sd(P1)/sd(BC)

where sd(P1) was the standard deviation for P1 δ^2H, and sd(BC) was the standard deviation for BC δ^2H.

The RMA regression slope (m) was then used to calculate the intercept (c).

c = P1_Mean – [sd(P1)/sd(BC)]*BC_Mean

where P1_Mean was the mean δ^2H of P1, and BC_Mean was the mean δ^2H of BC.

The complete RMA regression/conversion equation was derived as follows:

ConvBC = {P1_Mean – [sd(P1)/sd(BC)]*BC_Mean} + [sd(P1)/sd(BC)]*BC

where ConvBC was the converted body contour (P1 equivalent), and BC was the δ^2H of BC.

This yielded the following equation for adults:

ConvBC = (-5.89) + 0.86*BC

and the following for juveniles:

ConvBC = (-15.18) + 0.91*BC

Where necessary, these equations were used to convert the δ^2H values of known origin body contour feathers into first primary feather equivalents.

Sex determination

Woodcock are sexually monomorphic, which makes it difficult, if not impossible, to distinguish between the sexes in the field. Whilst there is a tendency for males to be have longer tails than females (Rochford & Wilson 1982; Ferrand & Gossmann 2009), and for females to have longer bills than males (Clausager 1973; Rochford & Wilson 1982; Ferrand & Gossmann 2009), the overlap between these biometric parameters is considerable (Clausager 1973; Rochford & Wilson 1982; Ferrand & Gossmann 2009), making them unreliable indicators of sex. Consequently, samples could not be assigned to a sex category.

Age determination

Samples were assigned to one of two age categories: (1) juvenile; defined as either a bird hatched that calendar year, or a bird hatched the previous calendar year but not yet moulted into adult plumage, (2) adult; defined as a bird hatched before the previous calendar year. The age of birds was determined from an assessment of differential plumage characteristics (Clausager 1973; Ferrand & Gossmann 2009; General Methods I).

Statistical Analyses

Appropriate statistical tests were determined by assessing the distribution of the dependent variable. The Shapiro-Wilk test and visual inspection of histogram plots were used to achieve this (Figure A2.1). Where the dependent variable was

found to be normally distributed, a parametric test was used. In cases of non-normality, the non-parametric equivalent was used.

For regression analysis and restricted maximum likelihood methods, the appropriateness of specified error distributions and link functions were determined from the normality of model residuals. Again, the Shapiro-Wilk test and visual inspection of residual composite plots were used to achieve this.

Linear Mixed Models (LMM) were used for datasets containing repeated measures, so that these could be controlled for. All statistical analyses were conducted using GenStat version 14.0 (VSN International Ltd. 2011). A 5% level of significance was used in all statistical tests/models.

Assessing sources of isotopic variation

Spatial variation

Twenty-nine feather samples from woodcock of known breeding origin were analysed for their $\delta^{13}C$ and $\delta^{15}N$ content. Data were normally distributed (Shapiro-Wilk: $\delta^{13}C$, W = 0.9655, P = 0.444; $\delta^{15}N$, W = 0.9668, P = 0.577). Linear Mixed Models (LMM) were used to test for the effects of age, longitude and latitude on $\delta^{13}C$ and $\delta^{15}N$, separately. Year of feather growth was included in each model as a random factor, with positive constraints applied.

Woodcock feathers from 136 birds of known breeding origin were analysed for their $\delta^{2}H$ content. Data were not normally distributed (Shapiro-Wilk: W = 0.9484,

$P < 0.001$), but rather represented a bi-modal distribution (Figure 2.1). A Mann-Whitney U test was performed to assess for significant differences between age groups. Following this, LMMs were used to test for the effects of longitude and latitude on δ^2H, for adults and juveniles, separately. Year of feather growth was included in each model as a random factor. Non-parametric (Spearman's rank) correlation analyses were also conducted to test the relationships of δ^2H with longitude and latitude.

Inter-individual comparison

Samples from similar latitudes and longitudes were grouped, and allocated to one of 17 broad location categories: 1 = Spain; 2 = Scotland, UK; 3 = England, UK; 4 = Germany; 5 = Norway; 6 = Sweden; 7 = Brest, Belarus; 8 = Estonia/Latvia; 9 = Pskov region, Russia; 10 = Finland; 11 = Vitebsk region, Belarus; 12 = Tver region (NW), Russia; 13 = St Petersburg, Russia; 14 = Tver region (NE), Russia; 15 = Vladimir region, Russia; 16 = Rossosh, Russia; and 17 = Kostroma region, Russia. Notably, increasing location numbers are concurrent with increasing longitudes, representative of a west-east direction.

For each broad location, the standard deviations of samples were calculated to reflect levels of inter-individual variation.

Inter-feather comparison

For 10 individuals, differences in δ^2H content across three feather types (P1, BC and U1) were assessed. Data for each feather type were normally distributed

(Shapiro-Wilk: P1, W = 0.8939, P = 0.188; BC, W = 0.9662, P = 0.854; U1, W = 0.8650, P = 0.087). Two-sample paired t-tests were used to assess differences between the δ^2H of P1 and BC, P1 and U1, and BC and U1.

Inter- and intra-laboratory comparison

The δ^2H values of feathers sampled for replicate analysis (n = 19) were not normally distributed (Shapiro-Wilk: laboratory-1, W = 0.8599, P = 0.008; laboratory-2, W = 0.8858, P = 0.023). A Wilcoxon matched-pairs sign rank test was used to assess differences in δ^2H between replicate samples analysed at laboratory-1 (NERC LSMSF) and laboratory-2 (IsoAnalytical Ltd.).

The δ^2H values of laboratory standards were compared with accepted values. From laboratory-1, the standards tested were BWB, CFS, ISB, WG and IA-R002. Observed δ^2H values were normally distributed for BWB (Shapiro-Wilk: W = 0.9306, P = 0.454), CFS (Shapiro-Wilk: W = 0.9691, P = 0.883), ISB (Shapiro-Wilk: W = 0.9350, P = 0.499) and WG (Shapiro-Wilk: W = 0.9422, P = 0.577), but not for IA-R002 (Shapiro-Wilk: W = 0.5994, $P < 0.001$). Two-sample paired t-tests were used to assess differences between observed and accepted δ^2H values of BWB, CFS, ISB and WG, whilst a Wilcoxon matched-pairs sign rank test was used to assess IA-R002. From laboratory-2, IAEA-CH-7 (polyethylene) and eggshell membrane were the standards tested. Observed δ^2H values were normally distributed for IAEA-CH-7 (Shapiro-Wilk: W = 0.7947, P = 0.053) but not for eggshell membrane (Shapiro-Wilk: W = 0.6138, $P < 0.001$). A two-sample paired t-test was used to assess for differences between observed and accepted

δ^2H values of IAEA-CH-7, whilst a Wilcoxon matched-pairs sign rank test was used to assess eggshell membrane.

Temporal variation: the utility of museum specimens

Woodcock feathers from 94 museum specimens collected on the breeding grounds (representing samples of known origin) were analysed for their δ^2H content. RMA-converted δ^2H values were normally distributed (Shapiro-Wilk: W = 0.9745, $P = 0.063$). An ANOVA test was used to test for differences in δ^2H between adults (n = 38) and juveniles (n = 56). Following this, Linear Models (LM) were used to test for the effects of time, longitude and latitude on δ^2H, for adults and juveniles, separately. Notably, one of two explanatory variables was used (in separate models) to account for temporal effects. The first was a time period factor, which comprised two levels: samples from 1885-1950 (level 1), and 1951-2002 (level 2). The second was a year of feather growth variable, which was continuous.

Data from museum (n = 94) and contemporary (n = 136) samples, all collected on the breeding grounds, were pooled. Data were not normally distributed (Shapiro-Wilk: W = 0.9724, $P < 0.001$). A Mann-Whitney U test was performed to assess for significant differences between age groups. Following this, Linear Models (LM) were used to test for the effects of time, longitude and latitude on δ^2H, for adults and juveniles, separately. Notably, one of two explanatory variables was used (in separate models) to account for temporal effects. The first was a time period factor, which comprised three levels: samples from 1885-1950 (level 1), 1951-2000 (level 2), and 2001-2010 (level 3). The second was a year of feather growth variable, which was continuous.

Results

Assessing sources of isotopic variation

Spatial variation

No significant relationships were found between $\delta^{13}C$ and age (LMM, $F_{1, 25} = 0.12$, $P = 0.735$), longitude (LMM, $F_{1, 26} = 3.04$, $P = 0.093$) or latitude (LMM, $F_{1, 27} = 1.42$, $P = 0.243$). Similarly, no significant relationships were found between $\delta^{15}N$ and age (LMM, $F_{1, 25} = 0.00$, $P = 0.980$), longitude (LMM, $F_{1, 26} = 0.02$, $P = 0.900$), or latitude (LMM, $F_{1, 27} = 3.39$, $P = 0.077$). These results suggest that neither $\delta^{13}C$ nor $\delta^{15}N$ are suitable markers for determining woodcock breeding locations.

For $\delta^{2}H$, the bi-modal distribution of the data-set (Figure 2.1) was explored and attributed to age-related variation. Average $\delta^{2}H$ values (± standard error, SE) for adults (n = 80, mean = -57.0‰ ± 1.97 SE, median = -58.5‰) differed significantly from those of juveniles (n = 56, mean = -92.1‰ ± 1.55 SE, median = -93.4‰) (Mann-Whitney U, U = 237, $P < 0.001$). Given this pronounced age-related variation (Figure 2.2), all further statistical analyses concerning $\delta^{2}H$ were conducted separately for adults and juveniles.

Assessing for spatial variation, adult $\delta^{2}H$ values showed a significant negative correlation with longitude (r = -0.457, Student's t = -4.58, $P < 0.001$) and latitude (r = -0.456, Student's t = -4.57, $P < 0.001$). In addition, a LMM found both longitude (LMM, $F_{1, 74.5} = 10.77$, $P = 0.002$) and latitude (LMM, $F_{1, 74.6} = 7.72$, $P = 0.007$) had a significant effect on adult $\delta^{2}H$ values. Repeating this analysis for

juveniles revealed a significant negative correlation for δ^2H and longitude (r = -0.556, Student's t = -5.00, $P < 0.001$), but a non-significant correlation between δ^2H and latitude (r = -0.195, Student's t = -1.49, $P = 0.143$). However, a LMM found both longitude (LMM, $F_{1, 52.9} = 33.01$, $P < 0.001$) and latitude (LMM, $F_{1, 52} = 9.02$, $P = 0.004$) had a significant effect on juvenile δ^2H values. These results suggest that δ^2H is a suitable marker for determining breeding (moulting) origins of woodcock, with longitudinal (Figure 2.3) and latitudinal (Figure 2.4) trends evident.

Inter-individual comparison

Standard deviations for birds grouped within the same (broad) locations (see *Methods, Inter-individual comparison*) revealed variation in δ^2H for both adult (Table 2.1) and juvenile (Table 2.2) birds. Standard deviations ranged from 3.20 to 15.80 in adults, and from 1.57 to 23.61 in juveniles. Standard errors ranged from 1.07 to 7.82 in adults, and from 0.91 to 16.69 in juveniles. Notably, standard errors were heavily influenced by samples size; the maximum standard errors represent instances where the small sample size was equal to two. For samples sizes greater than two, standard errors ranged from 1.07 to 5.00 in adults, and from 0.91 to 3.44 in juveniles. Figures 2.5-2.6 show the variation in δ^2H within the same (broad) sampling location and within the same moulting year, for adults and juveniles, respectively.

Inter-feather comparison

No significant differences were found between the δ^2H of P1 and BC (t = 0.31, d.f. = 9, $P = 0.766$), P1 and U1 (t = 1.28, d.f. = 9, $P = 0.231$), or BC and U1 (t = 0.89, d.f. = 9, $P = 0.398$) (Table 2.3). Standard errors were 2.31, 1.96 and 2.04, respectively. These results suggest that the feathers of individual birds were all grown at the same breeding location (Figure 2.7).

Inter- and intra-laboratory comparison

Results revealed no significant differences in δ^2H between replicate samples analysed at laboratory-1 (NERC LSMSF) and laboratory-2 (IsoAnalytical Ltd.) (t = 81.0, n = 19, $P = 0.595$). Rather, there was a strong positive correlation in δ^2H between the two laboratories (r = 0.874, $R^2 = 0.76$, Student's t = 7.40, $P < 0.001$) (Figure 2.8).

In laboratory-1, there were no significant differences between the observed δ^2H standard values and the accepted values of BWB (t = -0.93, n = 10, $P = 0.378$), CFS (t = -2.02, n = 10, $P = 0.074$), ISB (t = 0.39, n = 10, $P = 0.707$) or IA-R002 (t = 10.00, n = 6, $P = 1.00$). There was, however, a significant difference between the observed and accepted values for WG (t = 3.76, n = 10, $P = 0.004$). In laboratory-2, there was no significant deviation from the accepted values of δ^2H for IAEA-CH-7 (polyethylene) (t = -2.20, n = 6, $P = 0.079$) or eggshell membrane (t = 5.00, n = 5, $P = 0.625$) standards.

Temporal variation: the utility of museum specimens

Mean δ^2H values (± SE) for adults (n = 38, -54.58‰ ± 3.24 SE) differed significantly from those of juveniles (n = 56, -74.12‰ ± 3.24 SE) (ANOVA, $F_{1, 92} = 36.50$, $P < 0.001$). Given this, adult and juvenile museum samples were analysed separately. For adults, average δ^2H values (± SE) did not differ significantly between the two time periods (time period 1: mean = -52.7‰ ± 3.14 SE, median = -56.3‰; time period 2: mean = -56.7‰ ± 2.27 SE, median = -56.7‰) (Mann-Whitney U, U = 159, $P = 0.553$). Furthermore, a LM revealed no significant relationships between δ^2H and time period (LM, $F_{1, 34} = 0.48$, $P = 0.493$) or latitude (LM, $F_{1, 35} = 1.45$, $P = 0.236$). However, longitude did have a significant effect on δ^2H (LM, $F_{1, 36} = 4.17$, $P = 0.049$). When year of feather growth replaced time period as the fixed temporal effect, these relationships remained the same. In contrast, average δ^2H for juveniles did differ significantly between the two time periods (time period 1: mean = -66.6‰ ± 2.82 SE, median = -67.6‰; time period 2: mean = -81.1‰ ± 3.10 SE, median = -75.8‰) (ANOVA, $F_{1, 54} = 11.84$, $P = 0.001$). Furthermore, a LM for juveniles revealed a non-significant relationship between δ^2H and latitude (LM, $F_{1, 52} = 0.70$, $P = 0.407$) but did reveal significant relationships for time period (LM, $F_{1, 53} = 8.73$, $P = 0.005$) and longitude (LM, $F_{1, 53} = 15.42.$, $P < 0.001$). When year of feather growth replaced time period as the fixed temporal effect, these relationships remained the same. Notably, residuals from the full models showed high variance in δ^2H but no major shifts over time.

Converted museum data were merged with those from contemporary known origin samples, and the analyses repeated. Average δ^2H of adults (n = 118) did not differ significantly between the three time periods (time period 1: mean = -

52.7‰ ± 3.14 SE, median = -56.3‰; time period 2: mean = -57.9‰ ± 2.37 SE, median = -57.5‰; time period 3: mean = -56.7‰ ± 1.93 SE, median = -58.3‰) (Mann-Whitney U, group 2: U = 129, $P = 0.336$; group 3: U = 698, $P = 0.308$). Furthermore, a LM revealed a non-significant relationship between δ^2H and time period (LM, $F_{2, 113} = 1.05$, $P = 0.354$), but did reveal significant relationships for longitude (LM, $F_{1, 115} = 28.01$, $P < 0.001$) and latitude (LM, $F_{1, 115} = 8.36$, $P = 0.005$). When year of feather growth replaced time period as the fixed temporal effect, these relationships remained the same. Conversely, for juveniles (n = 112) average δ^2H did differ significantly between the three time periods (time period 1: mean = -66.6‰ ± 2.82 SE, median = -67.6‰; time period 2: mean = -81.1‰ ± 3.10 SE, median = -75.8‰; time period 3: mean = -92.1‰ ± 1.55 SE, median = -93.4‰) (Mann-Whitney U, group 2: U = 208, $P = 0.002$; group 3: U = 114, $P < 0.001$). Furthermore, a LM for juveniles revealed a non-significant relationship between δ^2H and latitude (LM, $F_{1, 107} = 0.71$, $P = 0.402$) but did reveal significant relationships for time period (LM, $F_{2, 108} = 7.85$, $P < 0.001$) and longitude (LM, $F_{1, 108} = 40.86$, $P < 0.001$). When year of feather growth replaced time period as the fixed temporal effect, these relationships remained the same. Notably, residuals from the full models showed high variance in δ^2H but no major shifts over time.

Discussion

Assessing sources of isotopic variation

Spatial variation

It is apparent from the results that both $\delta^{13}C$ and $\delta^{15}N$ are unsuitable geographic markers for woodcock, as neither of these isotopes showed latitudinal or longitudinal trends. Conversely, analysis of $\delta^{2}H$ revealed a strong negative relationship with longitude and a weaker negative relationship with latitude, such that increases in both latitude and/or longitude result in depletion of deuterium values. This spatial relationship lends support to those studies advocating the use of the European $\delta^{2}H$ isoscape (Hobson *et al.* 2004; Bowen *et al.* 2005), and suggests that $\delta^{2}H$ is a suitable geographic marker for the Eurasian woodcock. Thus, whilst only rudimentary, this analysis validates the further use of feather stable hydrogen isotopes to better investigate woodcock migratory behaviour.

The results of this analysis also revealed the presence of deuterium enrichment in adult tissues relative to juveniles, with isotope values for adults consistently more positive than those of juveniles (mean difference: -35.2‰). Since this trend was apparent for birds sampled at the same localities, it could not be attributed to differences in breeding (moulting) location. Similar age-related variation, however, is well documented within the literature and a number of explanations have been postulated to account for this variation.

Amongst raptors, elevated δ^2H feather values of adults (relative to nestlings) have been attributed to heat stress (Meehan *et al.* 2003; Smith & Dufty 2005). These birds undertake moult during the active phase of the breeding season (Wheeler 2003), and the physiological demands of these concurrent activities are believed to increase the frequency of evaporative cooling, thus leaving the body water pool enriched in the heavier hydrogen isotope (McKechnie *et al.* 2004). This likely occurs in females during incubation and brooding, and in males during food provisioning (Meehan *et al.* 2003). For birds that undergo a post-breeding moult, and/or a moult before migration, however, evaporative cooling is less likely to play a significant role in the deuterium enrichment of tissues (Smith & Dufty 2005), as birds do not experience the same physiological demands.

Alternatively, the variation in δ^2H values between nestlings and their fully-grown counterparts has been attributed to differences in diet. In their study of known origin American redstarts *Setophaga ruticilla*, Langin *et al.* (2007) noted that first year and adult birds had access to hydrogen derived from both food items and drinking water (Hobson *et al.* 1999a), whereas nestlings only had access to food-derived sources. Since food items produce more negative δ^2H values than drinking water, the variation in δ^2H values between the two age-classes was thus explained. The authors postulated that once the nestlings fledge (and have access to drinking water), the isotopic composition of their tissues will then likely change. Indeed, through diet manipulation experiments, Duxbury *et al.* (2003) found that the hydrogen isotope ratios of Japanese quail *Coturnix japonica* and peregrine falcon *Falco peregrinus anatum* nestlings reflected those of the female/mother (through the input of endogenous resources into egg development), but that these values shifted once chicks were older and able to incorporate

exogenous food resources into their diet. However, since woodcock feathers were only sampled from fully-grown juveniles or adults, when both age-classes would have access to the same dietary resources, this diet-hypothesis cannot account for the δ^2H variation observed between adult and juvenile woodcock.

A more plausible explanation comes from Hobson & Wassenaar (1997), who attributed the age-related variation in δ^2H values amongst least flycatchers *Empidonax minimus* to differential timings of moult. Isotopic signatures vary not only across spatial scales, but also across temporal scales, producing inter-and intra-annual variation across the isotope data (Bowen 2008; Bowen & West 2008; West *et al.* 2010). Seasonal changes, within a given year, can be particularly pronounced (especially in the northern hemisphere) (Figure 2.9) as isotopic fractionation responds to local environmental conditions (Bowen & West 2008). Given this, differences in the timing of moult are likely to be reflected in isotopic signatures. For woodcock, moult occurs on the breeding grounds, yet juveniles and adults are known to moult at different times (General Methods I; Ferrand & Gossmann 2009). Thus, the observed variation in δ^2H between adults and juveniles may be attributable to temporal (seasonal) isotopic variation that coincides with moult phenology.

Inter-individual comparison

Accounting for temporal (age-related) effects, variation in δ^2H is evident amongst woodcock from (broadly) the same moulting locality. Such variation is likely to result from slight differences in feeding location, diet, metabolism (Wassenaar & Hobson 2006), and the contribution of water-derived hydrogen (Langin *et al.*

2007). Whilst a degree of inter-sample isotopic heterogeneity is expected (Wassenaar 2008), its extent is important because large variation between individuals could have serious implications for studies using isotope values to infer origins. For instance, in their study of mountain plover *Charadrius montanus* chicks, Wunder *et al.* (2005) reported δ^2H values ranging from 7‰ to nearly 60‰ in a given year, which could result in seriously inaccurate assignments. Fortunately, the extent of variation in the δ^2H of woodcock feathers was not of this magnitude and can be dealt with using improved statistical methods (Wunder & Norris 2008a).

Inter-feather comparison

Variation in isotope values between feather tracts is well documented in the literature (Kelly *et al.* 2002; Smith & Dufty 2005; Langin *et al.* 2007; Smith *et al.* 2008), with the general consensus that body contour feathers are more enriched in δ^2H than primary wing feathers. This inter-feather variation can be accounted for, and might even be expected, amongst birds that moult different feathers/feather tracts at isotopically disparate sites. In such instances, stable isotope analyses can be used to be better understand moult strategies (Neto *et al.* 2006). However, this does not explain the inter-variation present amongst birds, such as the woodcock (Ferrand & Gossmann 2009), that moult in one location.

Two explanations for the observed inter-feather variation in feather deuterium composition have been put forward for birds undertaking moult at a single location: (1) hydrogen isotope fractionation associated with feather growth rate, and (2) the incorporation of temporal variation in δ^2H into growing feathers

(Smith *et al.* 2008). However, systematic differences in feather δ^2H appear to vary according to the species under study. For instance, raptors and passerines seemingly differ in their incorporation of deuterium into feathers (Mazerolle *et al.* 2005; Wassenaar & Hobson 2006; Smith *et al.* 2008). In this study, there were no significant differences in the δ^2H values between primaries, body contours and under-wing coverts. This finding supports the assumption that woodcock moult on their breeding grounds and are faithful to this site throughout the moulting period (Ferrand & Gossmann 2009).

Inter- and intra-laboratory comparison

The issue of poor reproducibility within and between laboratories was highlighted by Smith *et al.* (2009a), who reported average isotopic shifts from 15.6‰ to 27.5‰ (with standard deviations of 6.0 to 12.4) for repeat δ^2H measures of raptor feathers. The reasons for poor reproducibility remain largely unknown, but subtleties in the preparation and subsequent analysis of feather samples often exist between laboratories that may be responsible for (some) error in the isotope data. For instance, differences in cleaning regime were found to affect the stable isotope ratios of Japanese quail *Coturnix japonica* feathers (Paritte & Kelly 2009); a 2:1 chloroform: methanol solution resulted in enrichment of δ^2H values, compared to other treatments. In this study, despite the differences in sample preparation and analysis between the two laboratories (highlighted in General Methods I), there were no significant effects on reproducibility.

Since isotopic variation between automated runs within the same laboratory has also been reported (Smith *et al.* 2009a), it has been suggested that all automated

runs within a single study should contain several sample replicates (Jardine & Cunjak 2005), to ensure that results can justifiably be pooled. However, this in itself is problematic when dealing with feather samples owing to intra-feather variation. For example, in an analysis of raptor contour feathers, proximal sub-samples were found to be enriched in δ^2H relative to their more distal sub-sample (Smith *et al.* 2008). To reliably assess within-lab variation reliably, repeat measures of standards were analysed. This yielded no significant effects, suggesting good reproducibility.

Until the source(s) of poor reproducibility can be determined, it has been suggested that, as a precautionary measure, researchers handle and prepare all feather samples as similarly as possible, including having the same person prepping all samples in the same laboratory, and that samples be analysed in as few sequential automated runs as possible (Smith *et al.* 2009a). Where possible, these suggestions were adhered to within this study.

Temporal variation: the utility of museum specimens

Statistical analyses from both the stand-alone museum dataset and the merged museum-contemporary samples suggest that sampling year (time period) does not significantly affect the δ^2H of adult feathers, but does affect the δ^2H of juvenile feathers. The latter result, however, needs to be interpreted with caution. Sampling across locations and time periods was unequal (Figure 2.10), therefore this result might represent an artefact of poor sampling distribution rather than an ecological trend. Indeed, residuals from the full models showed high variance in the δ^2H of feathers but no major shifts over time. This high

variance could be attributed to poor description of the provenance of museum samples (low geographic resolution on museum tags) or to inter-annual variation (Bowen & West 2008; West *et al.* 2010). The former is more likely, given that isomaps (based on climatological averages) reflect the relative stability of isoscapes between years, suggesting that the baseline isotopic surface has not changed appreciably over time. Furthermore, other isotopic studies using museum specimens have reported no long-term temporal changes in isotope values (Kelly *et al.* 2002; Lott & Smith 2006; Hobson *et al.* 2010b). Whilst the high variance in the δ^2H of museum feather samples does suggest that museum specimens may be of a lower quality than contemporary samples (which show low variance, in comparison), it is apparent that they still represent a valid source of sampling material.

Acknowledgements

Many thanks to those who provided feather samples: the landowners, hunters, gamekeepers, bird-ringers, and the following museum curators: Jürgen Plass (Austria), Jan Bolding Kristensen (Copenhagen, Denmark), Bob McGowan (Edinburgh, UK), Martti Hildén (Helsinki, Finland), Marie Portas (Paris, France), Dr. Friederike Woog (Stuttgart, Germany), Ingvar Byrkjedal (Bergen, Norway), Robert T. Barrett (Tromsø, Norway), Ulf Johansson (Stockholm, Sweden), and Mark Adams (Tring, UK). Thanks also to Dr. Jason Newton (NERC LSMSF) and Dr. Ian Begley (IsoAnalytical Ltd) for assistance with the stable isotope analyses. This work was funded by the Game and Wildlife Conservation Trust (GWCT), Countryside Alliance Foundation, and Natural Environment Research Council (NERC).

Tables & Figures

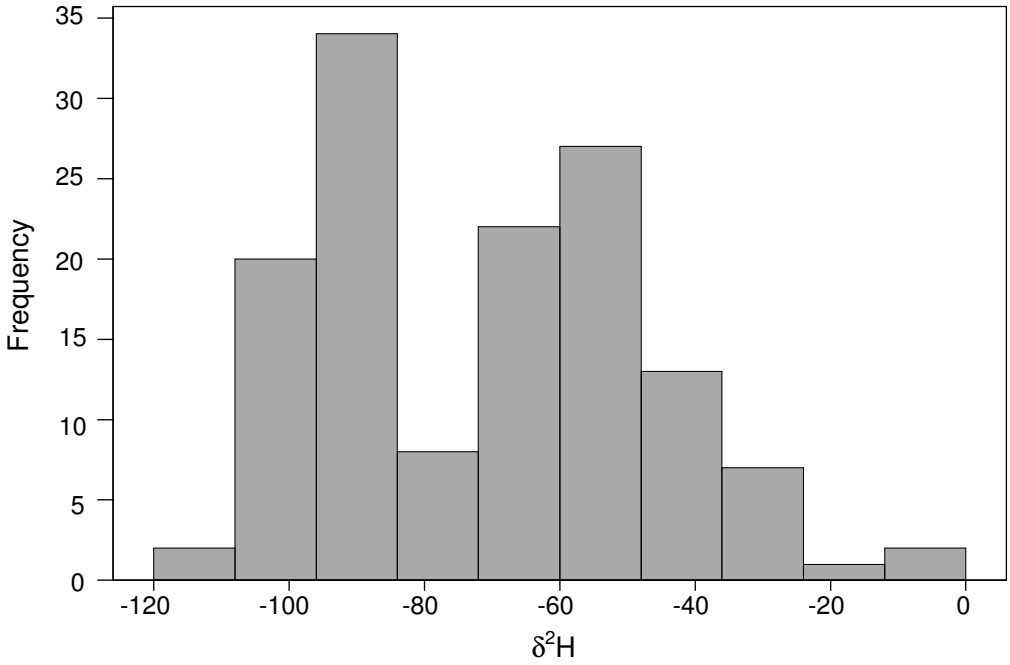


Figure 2.1 Frequency of feather δ^2H values for Eurasian woodcock (n = 136) sampled on the breeding grounds. Data are for adults and juveniles, combined.

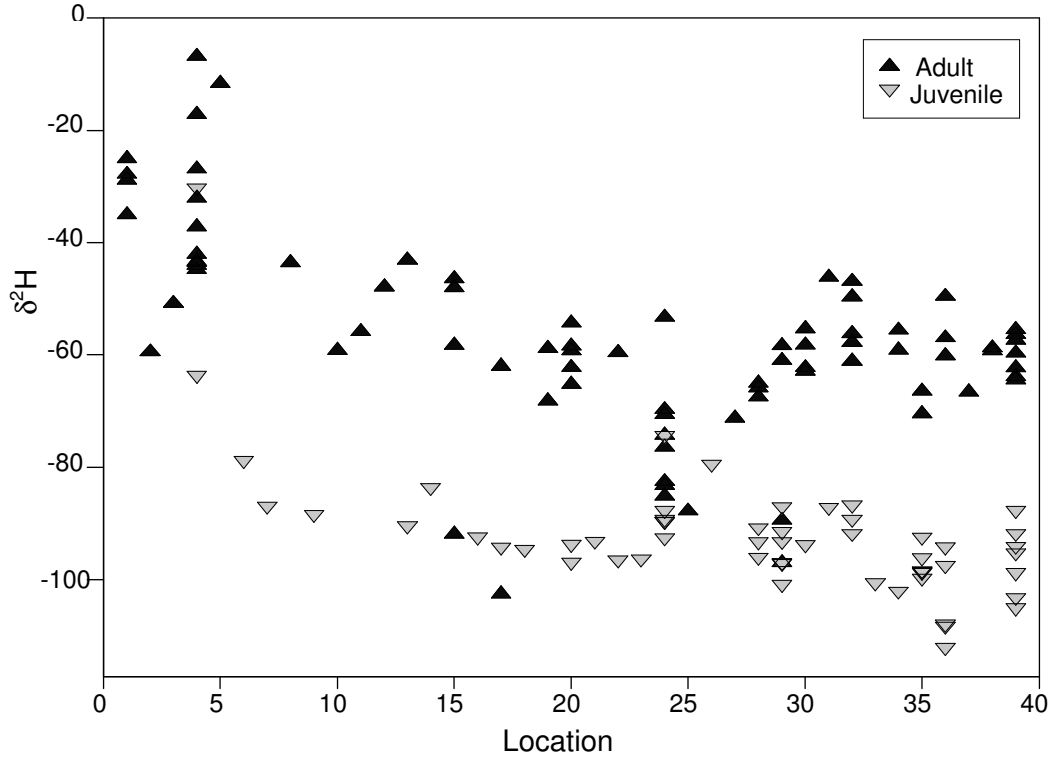


Figure 2.2 Feather δ^2H for Eurasian woodcock sampled across breeding locations (n = 39). Data are stratified by age: adult (n = 80) and juvenile (n = 56). Each location number represents a unique latitude and longitude. Increasing location numbers are concurrent with increasing longitudes, representative of a west-east direction.

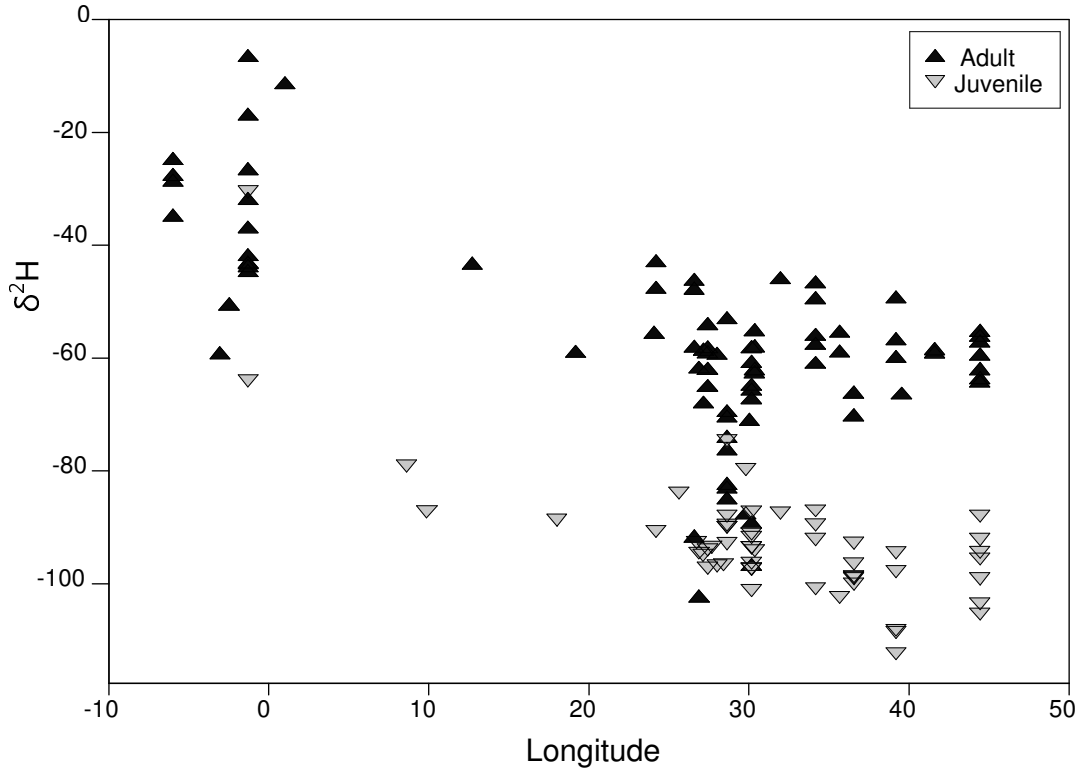


Figure 2.3 Feather δ^2H for Eurasian woodcock sampled at different longitudes on the breeding grounds. Data are stratified by age: adult (n = 80) and juvenile (n = 56).

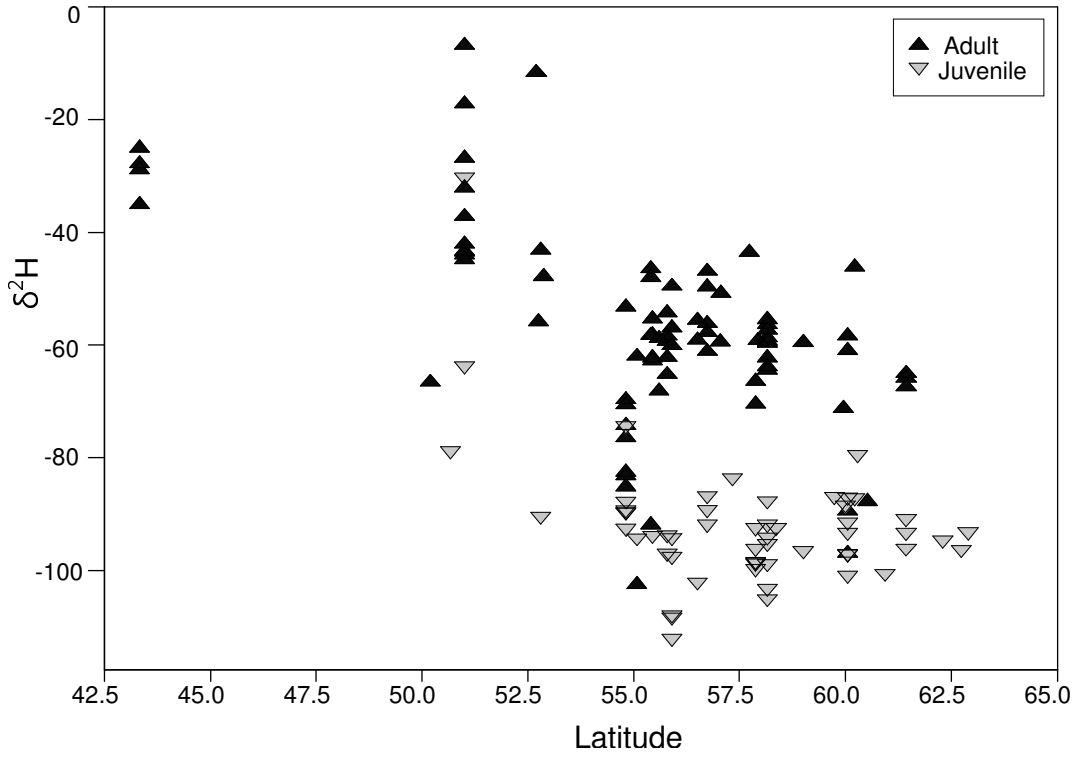


Figure 2.4 Feather δ^2H for Eurasian woodcock sampled at different latitudes on the breeding grounds. Data are stratified by age: adult (n = 80) and juvenile (n = 56).

Table 2.1 Mean δ^2H, standard errors (SE), and standard deviations (SD) for adult Eurasian woodcock (n = 80) sampled across broad breeding locations. Each location number represents a grouping of similar latitudes and longitudes (1 = Spain; 2 = Scotland, UK; 3 = England, UK; 4 = Germany; 5 = Norway; 6 = Sweden; 7 = Brest, Belarus; 8 = Estonia/Latvia; 9 = Pskov region, Russia; 10 = Finland; 11 = Vitebsk region, Belarus; 12 = Tver region (NW), Russia; 13 = St Petersburg, Russia; 14 = Tver region (NE), Russia; 15 = Vladimir region, Russia; 16 = Rossosh, Russia; and 17 = Kostroma region, Russia). Increasing location numbers are concurrent with increasing longitudes, representative of a west-east direction. Standard deviations show the extent of inter-individual variation within each locality, except where the location sample size was equal to one; in these instances a standard deviation could not be calculated.

Location	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
Sample size	4	2	11	x	x	2	3	x	1	x	25	5	10	4	3	1	9
Mean δ^2H	-29.2	-55.1	-31.8	x	x	-51.4	-48.9	x	-59.6	x	-66.7	-54.3	-70.9	-62.9	-55.5	-66.6	-59.7
SE	2.11	4.32	4.25	x	x	7.82	3.70	x	-	x	2.76	2.63	5.00	3.38	3.13	-	1.07
SD	4.22	6.10	14.10	x	x	11.05	6.41	x	-	x	13.82	5.88	15.80	6.76	5.42	-	3.20

Table 2.2 Mean δ^2H, standard errors (SE), and standard deviations (SD) for juvenile Eurasian woodcock (n = 56) sampled across breeding locations. Each location number represents a grouping of similar latitudes and longitudes (1 = Spain; 2 = Scotland, UK; 3 = England, UK; 4 = Germany; 5 = Norway; 6 = Sweden; 7 = Brest, Belarus; 8 = Estonia/Latvia; 9 = Pskov region, Russia; 10 = Finland; 11 = Vitebsk region, Belarus; 12 = Tver region (NW), Russia; 13 = St Petersburg, Russia; 14 = Tver region (NE), Russia; 15 = Vladimir region, Russia; 16 = Rossosh, Russia; and 17 = Kostroma region, Russia). Increasing location numbers are concurrent with increasing longitudes, representative of a west-east direction. Standard deviations show the extent of inter-individual variation within locality, except where the location sample size was equal to one; in these instances a standard deviation could not be calculated.

Location	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
Sample size	x	x	2	1	1	1	1	2	1	3	10	3	12	7	5	x	7
Mean δ^2H	x	x	-47.0	-78.8	-86.9	-88.4	-90.4	-88.0	-96.5	-94.7	-90.1	-89.2	-92.8	-98.0	-103.9	x	-96.5
SE	x	x	16.69	-	-	-	-	4.41	-	0.91	1.98	1.46	1.79	1.14	3.44	x	2.34
SD	x	x	23.61	-	-	-	-	6.24	-	1.57	6.25	2.53	6.19	3.02	7.70	x	6.19

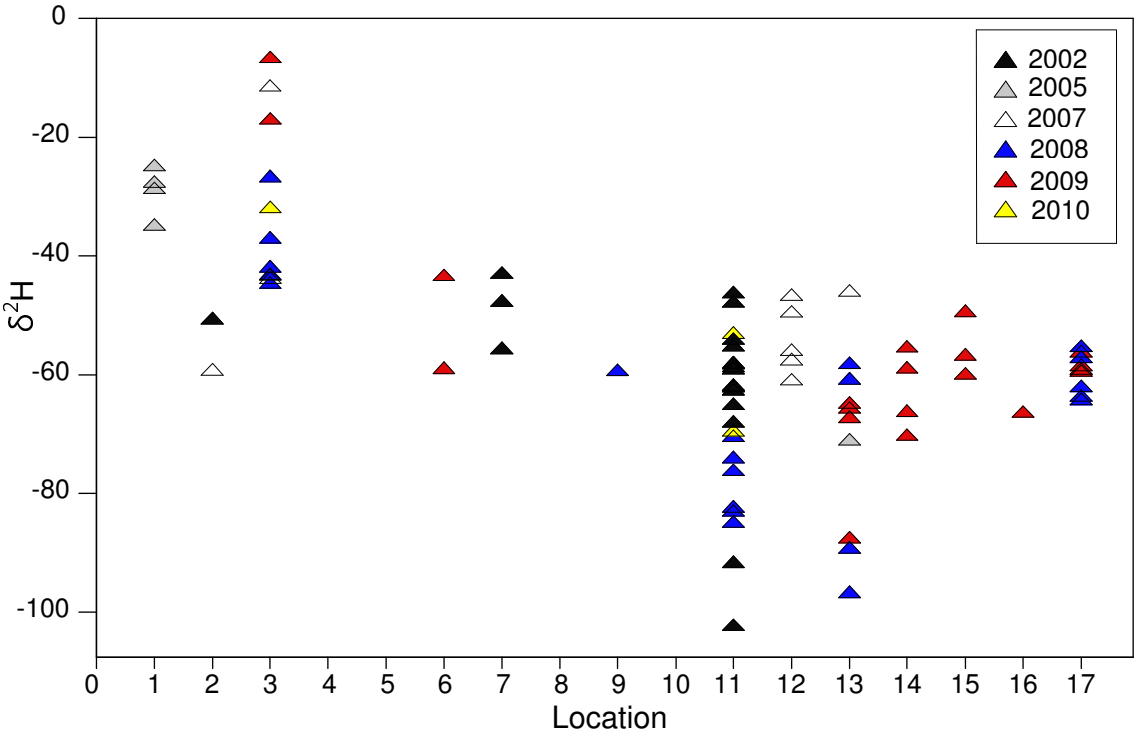


Figure 2.5 Feather δ^2H for adult Eurasian woodcock (n = 80) sampled across broad breeding locations. Data are stratified according to moulting year. Each location number represents a grouping of similar latitudes and longitudes (1 = Spain; 2 = Scotland, UK; 3 = England, UK; 4 = Germany; 5 = Norway; 6 = Sweden; 7 = Brest, Belarus; 8 = Estonia/Latvia; 9 = Pskov region, Russia; 10 = Finland; 11 = Vitebsk region, Belarus; 12 = Tver region (NW), Russia; 13 = St Petersburg, Russia; 14 = Tver region (NE), Russia; 15 = Vladimir region, Russia; 16 = Rossosh, Russia; and 17 = Kostroma region, Russia). Increasing location numbers are concurrent with increasing longitudes, representative of a west-east direction.

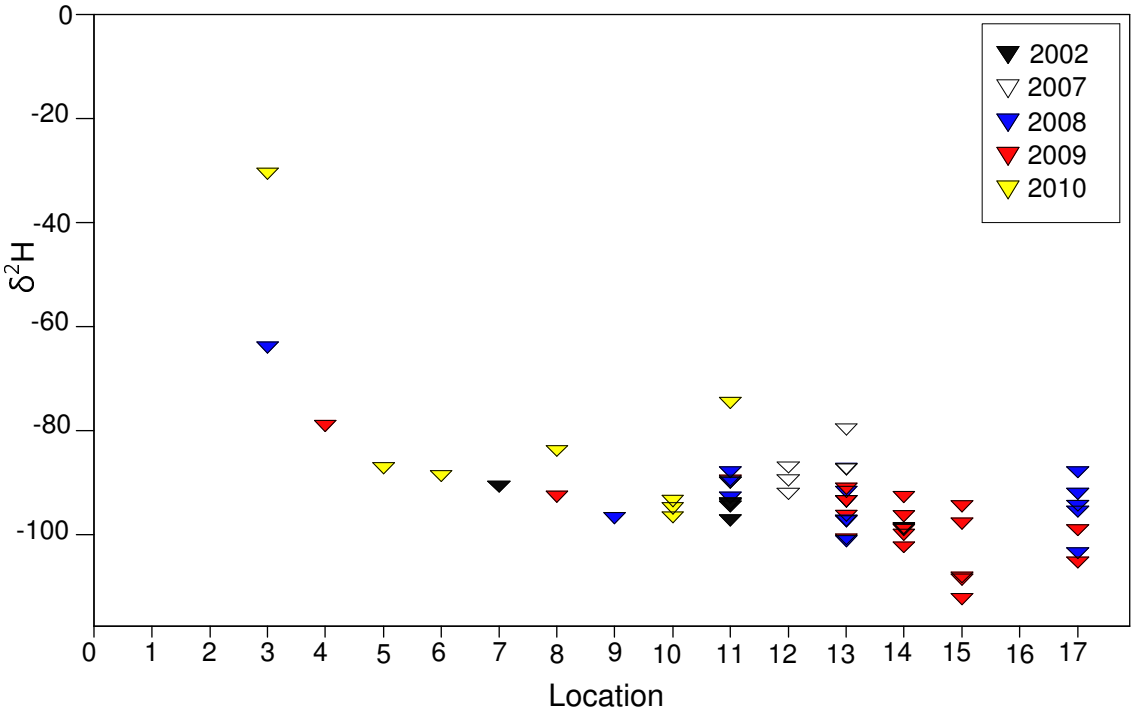


Figure 2.6 Feather δ^2H for juvenile Eurasian woodcock (n = 56) sampled across broad breeding locations. Data are stratified according to moulting year. Each location number represents a grouping of similar latitudes and longitudes (1 = Spain; 2 = Scotland, UK; 3 = England, UK; 4 = Germany; 5 = Norway; 6 = Sweden; 7 = Brest, Belarus; 8 = Estonia/Latvia; 9 = Pskov region, Russia; 10 = Finland; 11 = Vitebsk region, Belarus; 12 = Tver region (NW), Russia; 13 = St Petersburg, Russia; 14 = Tver region (NE), Russia; 15 = Vladimir region, Russia; 16 = Rossosh, Russia; and 17 = Kostroma region, Russia). Increasing location numbers are concurrent with increasing longitudes, representative of a west-east direction.

Table 2.3 Results of parametric paired t.tests comparing the δ^2H of Eurasian woodcock feathers from difference feather tracts. P1 = first primary, BC = body contour, U1 = first under-wing covert (corresponding to P1). Standard deviations (SD) show the extent of inter-feather variation within individuals. SE = standard error, d.f. = degrees of freedom.

Variables	Number of birds sampled	Mean	Variance	SD	SE	95% Confidence interval	Test statistic	d.f.	Probability
P1 vs BC	10	0.7	53.3	7.30	2.31	-4.51, 5.93	0.31	9	0.77
P1 vs U1	10	2.5	38.5	6.21	1.96	-1.92, 6.96	1.28	9	0.23
BC vs U1	10	1.8	41.7	6.46	2.04	-2.81, 6.43	0.89	9	0.40

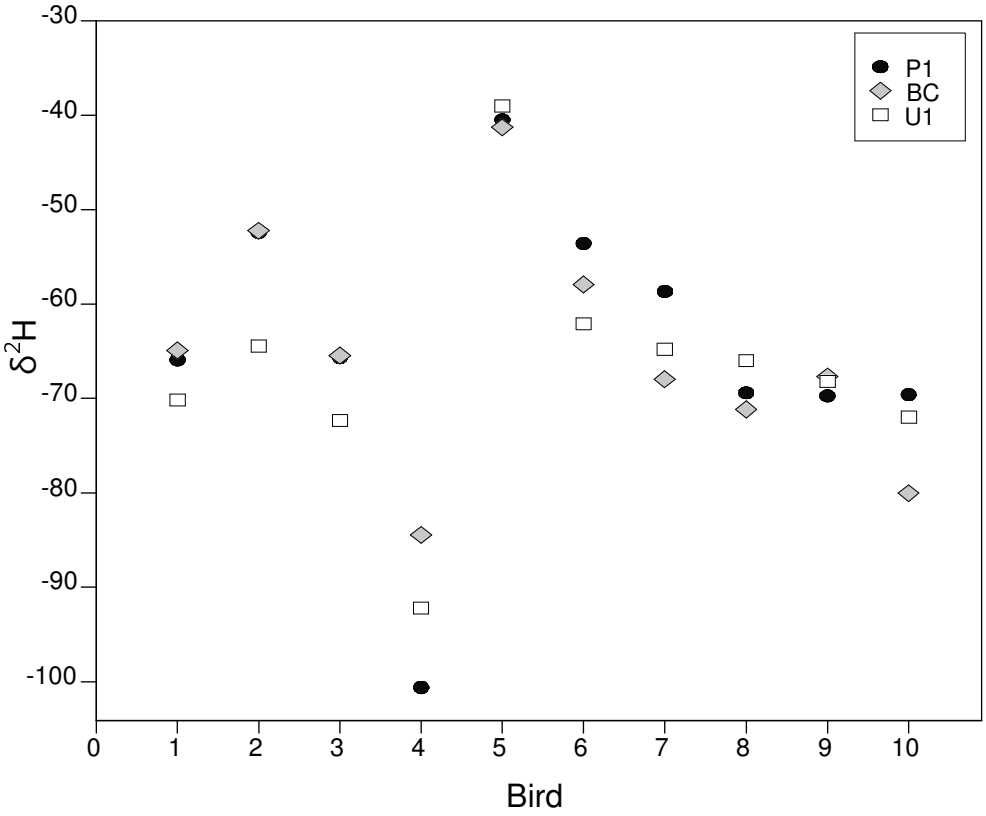


Figure 2.7 Inter-feather δ^2H for Eurasian woodcock (n = 10). Data are stratified by feather type: first primaries (P1), body contours (BC), and under-wing coverts (U1).

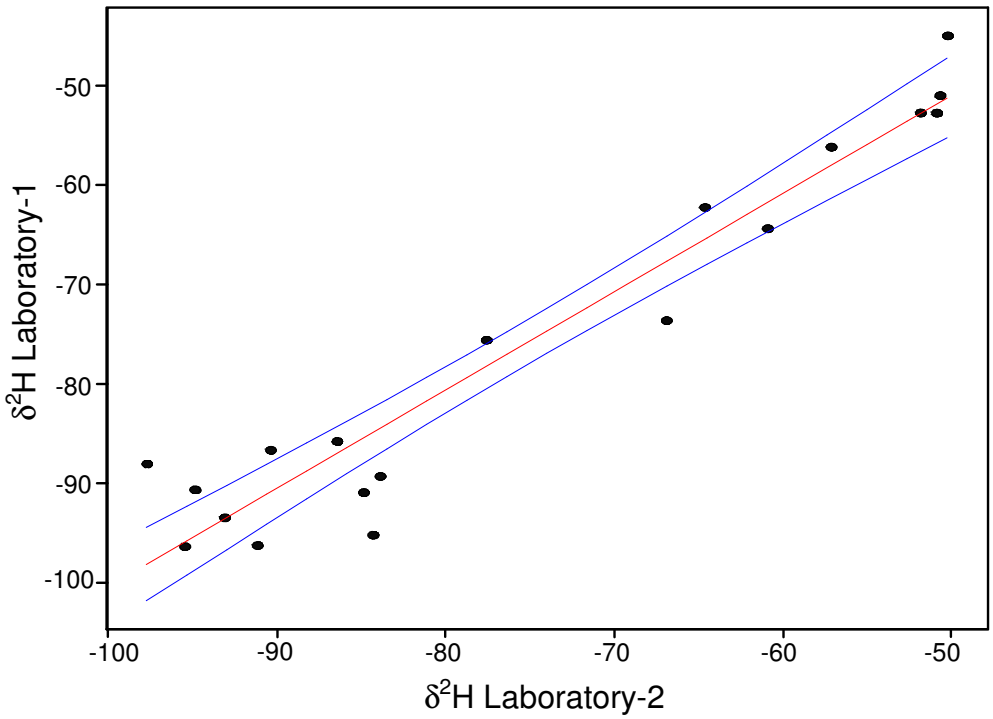


Figure 2.8 Linear regression showing the reproducibility of δ^2H for Eurasian woodcock feathers (n = 19) analysed at laboratory-1 (NERC LSMSF) and laboratory-2. (IsoAnalytical Ltd.). The red line represents the line of best fit. The blue lines show the 95% confidence limits for the fitted line.

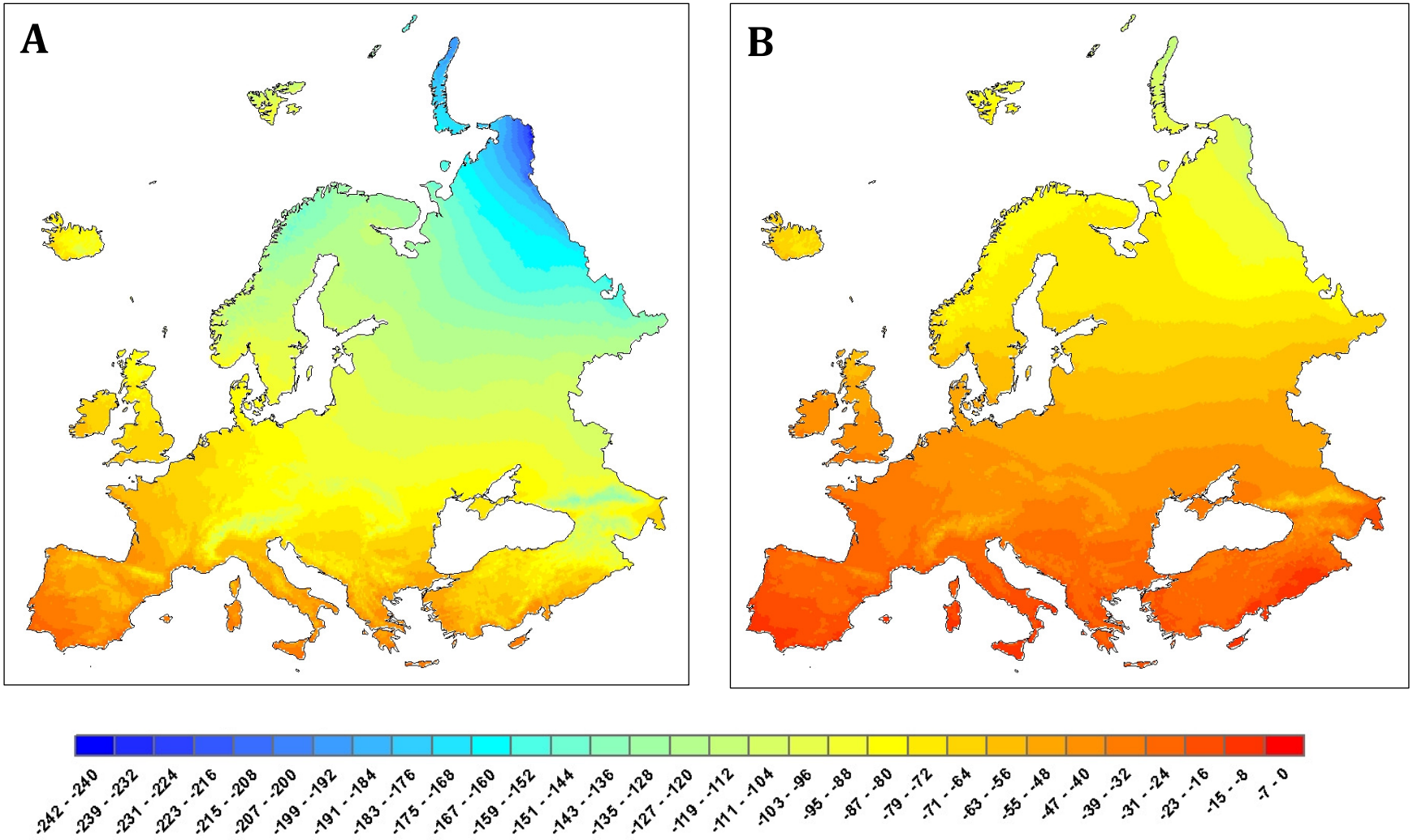


Figure 2.9 European isoscape(s) showing mean δ^2H precipitation in a) January and b) August (using data from 1960-2003) (after Bowen *et al.* 2005).

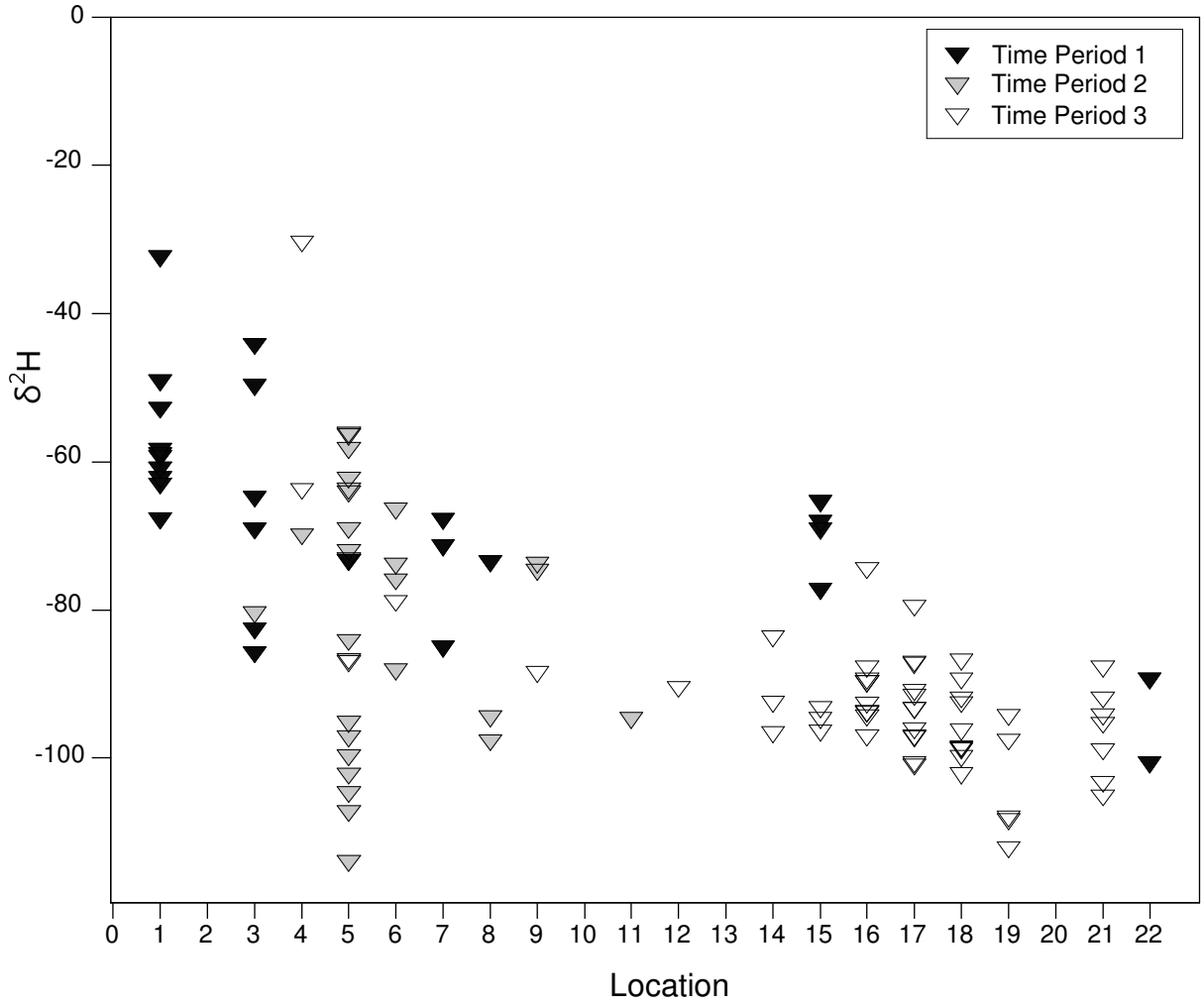


Figure 2.10 Feather δ^2H for juvenile Eurasian woodcock (n = 112) sampled across broad breeding locations. Data are stratified according to the period of feather growth (time period 1: 1885-1950, time period 2: 1951-2000, time period 3: 2000-2010). Each location number represents a grouping of similar latitudes and longitudes (1 = Azores; 2 = Spain; 3 = Scottish border, UK; 4 = England, UK; 5 = Norway (SE); 6 = German/Austrian/French border; 7 = Sweden (SW); 8 = Norway (N); 9 = Sweden (SE); 10 = Aland islands, Finland; 11 = Swedish/Finnish border; 12 = Brest, Belarus; 13 = Poland; 14 = Estonian/Latvian/Russian border; 15 = Finland; 16 = Vitebsk region, Belarus; 17 = St Petersburg, Russia; 18 = Tver region (NW), Russia; 19 = Vladimir region, Russia; 20 = Rossosh, Russia; 21 = Kostroma region, Russia; and 22 = Western Siberia). Increasing location numbers are concurrent with increasing longitudes, representative of a west-east direction.

Chapter 3

Breeding origins and spatial distribution of woodcock in Britain and Ireland during the non-breeding season

Breeding origins and spatial distribution of woodcock in Britain and Ireland during the non-breeding season

Abstract

The stable isotope technique is increasingly being used to determine the large-scale movements of birds and it was applied here to the study of Eurasian woodcock *Scolopax rusticola* (hereon woodcock). Owing to the elusive nature of this species and a paucity of ringing data, there exists a dearth of information regarding woodcock migration and non-breeding ecology. Using a spatially explicit assignment approach within a Bayesian framework, the breeding origins and composition of the non-breeding woodcock population in Britain and Ireland were successfully determined. Results indicated the occurrence of both broad-front and leap-frog migratory strategies, with Russia and Fennoscandia found to comprise the most likely breeding origins. A large degree of interchange between breeding populations within Britain and Ireland was also apparent during the non-breeding season, suggestive of weak connectivity.

Introduction

To better understand the overall demography of wild bird populations, it is important to first determine the links between different phases of the annual cycle. Following the identification of seasonal interactions or carry-over effects, whereby events at one stage of the annual cycle interact and influence events at subsequent stages (Marra *et al.* 1998; Norris 2005), the need for a wider, inter-seasonal approach has become increasingly apparent. For example, it is increasingly reported that the breeding and non-breeding sites utilised by a

species can have a profound effect on the fitness of both the individual and the population as a whole (Marra *et al.* 1998; Studds & Marra 2005; Norris & Marra 2007). Birds often spend different phases of the annual cycle in widely separated and ecologically disparate locations, exposing them to changes in climate and habitat structure. Long-distance migrants may also cross geopolitical borders, which expose them to different conservation regimes. At the individual level, these differences in exposure to environment and risk may directly influence mortality or may produce non-lethal, residual effects that carry over to influence individuals indirectly in the following season (Bety *et al.* 2003; Norris *et al.* 2004; Studds & Marra 2005). These individual-level interactions may then go on to have wider reaching effects at the population level (Gill *et al.* 2001; Hobson & Norris 2008). It is therefore important to identify the key sites utilised by individuals across the annual cycle, to better understand the population demographics of a species. Such knowledge is of particular importance for declining bird species and/or species of conservation concern.

The Eurasian woodcock *Scolopax rusticola* (hereon woodcock) is a game species with uncertain conservation status; evidence for declines in abundance on both the breeding and non-breeding grounds continue to be debated (Fadat 1994; Tucker & Heath 1994; Hagemeijer & Blair 1997; Ferrand & Gossmann 2000; Heath *et al.* 2000). Consequently, the international conservation status of the woodcock ranges from "stable" (Wetlands International 2002) to "unfavourable" (Tucker & Heath 1994; BirdLife International 2004a). Since the woodcock is relatively understudied, owing to its cryptic plumage and elusive nature, the information necessary to establish an accurate conservation status remains lacking for this species.

Historically, there have been few studies on woodcock in Britain and Ireland (Alexander 1939; Wilson 1982; Wilson 1983; Hoodless & Coulson 1994; Summers & Buckland 1996), whilst more recent works have focused on woodcock breeding ecology (Hoodless & Coulson 1998; Hoodless & Hirons 2007; Hoodless *et al.* 2009). Consequently, there still exists a dearth of information regarding non-breeding woodcock in Britain and Ireland. It is known that, from October to mid-April, the non-breeding population in Britain and Ireland comprises both resident birds (British and Irish breeders) and foreign migrants, with the latter likely comprising c.84-91% of the total (Hoodless 1994a; Hoodless & Coulson 1994). However, the migratory origins and movements of these birds remain poorly understood, with the little information that is available coming solely from ring-recovery analyses.

As is typical of game species, the ring-recovery rate of woodcock is relatively high, compared to that of other birds, since the majority of ring recoveries come from shot birds (Hoodless & Coulson 1994; Hobson 2003). Yet despite this, years of data collection are still required in order to make strong inferences (Hobson 2003). Hoodless & Coulson (1994) used British ring-recovery records, collected from 1909-1990, to show the origins of woodcock residing in Britain during the non-breeding season. Furthermore, they went on to estimate the approximate proportions of foreign migrants arriving in Britain, taking into consideration likely biases caused by historical changes in woodcock shooting seasons, and the fact that some countries permitted the shooting of roding males in spring (i.e. males shot during their reproductive display flights). They found that the British non-breeding population comprised approximately 47% of birds from Fennoscandia (Norway, Sweden, and Finland), 36% from Russia (former USSR)

and 3% from other European countries, although the latter probably represented birds ringed on migration. The remaining 14% comprised British residents. Despite uncertainties in the breeding population estimates used to derive results, these remain the only published data pertaining to the origins and relative proportions of the British non-breeding woodcock population.

Once on the non-breeding grounds, there is often a degree of mixing and dispersal amongst migratory populations (Rubenstein *et al.* 2002; Boulet *et al.* 2006; Norris *et al.* 2006). The degree of interchange between different breeding and non-breeding populations can have important effects on levels of connectivity. Migratory connectivity (weak vs. strong) describes the extent to which individuals from the same breeding grounds migrate to the same non-breeding grounds (and vice-versa). The patterns of connectivity across the non-breeding grounds have important consequences for the ecology, evolution and conservation of migratory bird species, due to effects associated with gene flow (Webster & Marra 2005). For example, migratory connectivity is likely to affect the degree to which birds adapt to local conditions on the non-breeding grounds, the rate of non-breeding range expansion, and the ability to adapt to gradually changing selective pressures, such as climate and habitat (Webster *et al.* 2002; Webster & Marra 2005).

To ascertain levels of migratory connectivity, it is necessary to know the geographical origins of birds sampled at particular non-breeding sites (Webster *et al.* 2002). Although Hoodless & Coulson (1994) did examine the temporal and spatial distribution of non-breeding ring-recoveries within Britain, the origins of foreign-migrants were not specified. Consequently, patterns of connectivity could

not be deduced. As such, levels of migratory connectivity remain unknown for the non-breeding woodcock population in Britain and Ireland.

Application of stable isotopes to migration studies

Whilst analyses from ring-recoveries have proven useful (Reichlin *et al.* 2009; Clark *et al.* 2010), the stable isotope approach is revolutionising the field of migration ecology, by providing a substitute or complementary technique to ring-recovery analysis.

Stable hydrogen isotopes in precipitation (δ^2H_p) vary spatially in accordance with continental-scale hydrological patterns (Hobson 1999; Graves *et al.* 2002; Rubenstein *et al.* 2002; Hobson *et al.* 2003; Bowen *et al.* 2005), becoming progressively more depleted with increasing altitude, latitude and distance from the coast, in accordance with Rayleigh's (rainout) distillation process (Gat 1996). These geographically predictable trends have proven useful in assigning birds of unknown provenance to their hatching or moulting origin (often synonymous with breeding location). The potential of δ^2H_p was first highlighted in two pioneering studies: Hobson & Wassenaar (1997) showed that the hydrogen isotope values of feathers (δ^2H_f) were strongly correlated with δ^2H_p for the regions in which they were grown and, from this, went on to demonstrate that the origins of non-breeding migrants could be inferred from their δ^2H_f. Adopting the same approach, Chamberlain *et al.* (1997) were able to determine the origins of migratory black-throated blue warblers *Dendroica caerulescens* residing on their non-breeding grounds.

Both these studies adopted the "map lookup" approach, which remains the most commonly used method to assign birds of unknown provenance to their hatching or moulting origin (Bearhop *et al.* 2005; Mazerolle *et al.* 2005; Boulet *et al.* 2006; Hobson *et al.* 2006; Lott & Smith 2006). Based on amount-weighted mean annual deuterium (MAD) or amount-weighted growing season average deuterium (GSD) (Bowen *et al.* 2005), geospatial models that reflect the δ^2H_p isotopic landscape (isoscape) are incorporated into a regression analysis that enables the δ^2H_p isoscape to be re-calibrated into a δ^2H_f isoscape. From this, δ^2H_f values of birds from unknown hatching or moulting origin can be assigned to their corresponding values within the δ^2H_f isoscape. To date, useful δ^2H_p isoscapes have been established for North America and Europe (Hobson *et al.* 2004; Bowen *et al.* 2005), with the latter so far used to infer the origins of butterflies (Brattström *et al.* 2008; Brattström *et al.* 2010), migratory passerines (Hobson *et al.* 2004; Bearhop *et al.* 2005; Newton *et al.* 2006; Marquiss *et al.* 2008) and a European game species (Hobson *et al.* 2009a).

Whilst the "map lookup" approach is favoured for its ease of implementation, it does not incorporate spatial variability or other known sources of error inherent in the assignment process (Wunder & Norris 2008a,b). Therefore, more robust approaches that incorporate estimates of error have been established. Amongst these, application likelihood based methods, which assess the probability that a given sample could have come from a given location, have proven to be particularly flexible, and are readily adaptable to spatially explicit assignment tests (Wunder & Norris 2008b; Wunder 2010; Van Wilgenburg & Hobson 2011).

Combining stable isotopes and ring-recovery data

Given that longitudinal resolution is often limited within δ^2H_p isoscapes (Bowen *et al.* 2005), the spatial resolution of assignments for birds with broad longitudinal distributions may be relatively coarse. Fortunately, it is possible to overcome this limitation, by incorporating sources of prior information, such as abundance data (Royle & Rubenstein 2004), or ringing data (Hobson *et al.* 2009b; Van Wilgenburg & Hobson 2011), which help to further constrain assignments. Despite the aforementioned shortcomings of the latter, their application as a source of prior information has proven particularly useful in refining the longitudinal resolution of geospatial assignments of migratory birds to δ^2H_f isoscapes (Hobson *et al.* 2009b; Van Wilgenburg & Hobson 2011).

Aims

The purpose of this chapter was to determine the breeding origins and spatial distribution of the non-breeding woodcock population in Britain and Ireland, through an analysis of stable isotope data. To achieve this, a spatially explicit assignment approach was employed, incorporating sources of error and prior information from ring-recovery data. The stable isotope approach has never before been applied to the study of Eurasian woodcock and, although other wader species have been the subject of such studies (Atkinson *et al.* 2005; Zockler *et al.* 2006), *S. rusticola* is atypical of this group. Therefore the woodcock makes an interesting addition to the list of species already established in isotopic studies (Lott & Smith 2006). Data derived using this technique will enhance knowledge

of woodcock migratory behaviour during the non-breeding season and may assist in the conservation of this species.

Methods

Sample collection

Known (breeding) origin

Feather isotopes are indicative of moult location. Since woodcock typically moult on the breeding grounds, during the breeding season (Witherby *et al.* 1943; Clausager 1973; Kalchreuter 1983; Ferrand & Gossmann 2009), their moult location becomes synonymous with breeding origin (General Methods I). Feathers collected from woodcock on their breeding grounds, during the breeding season, therefore provide a source of known (breeding) origin sampling material.

Feather samples were collected from birds across their European breeding grounds, during the breeding season (April-September), providing a source of known origin sampling material. In total, 230 samples were collected. Of these, 136 represented contemporary samples collected between 2002 and 2010. The remainder (n = 94) were derived from museum-specimens dated between 1885 and 2002 (for full details see Chapter 2).

Unknown (breeding) origin

Feather samples were collected from shot birds of unknown breeding origins. The Eurasian woodcock is listed under Schedule 2 Part 1 of the Wildlife & Countryside Act 1981 as one of the species that can be legally taken from the wild, without a licence, during the open season. The woodcock shooting season opens on 1 September in Scotland, on 1 October in England, Wales and Northern Ireland, and on 1 November in Ireland, with all woodcock hunting (in Britain and Ireland) closing on 31 January (Wildlife & Countryside Act 1981). Wings/feathers were collected from birds shot in December and January across four shooting seasons (2004/05: n = 280, 2008/09: n = 287, 2009/10: n = 279 and 2010/11: n = 283) (Table A3.1). In all instances, the distal tip of the first (innermost) primary feather was sampled, as this is likely to be the most representative of moulting (breeding) locality.

Samples were collected from five geographical regions in Britain, representing the North (Scotland, latitude: 55.74; longitude: -2.75), East (Norfolk, latitude: 53.03; longitude: 0.24), South (Cornwall, latitude: 50.30; longitude: -5.51) and West (Wales, latitude: 52.13; longitude: -4.19), with an additional fifth sampling region in Hampshire (latitude: 51.20; longitude: -1.38). These designated sampling regions were selected on the basis of geographical spread and the availability of samples, and were subsequently defined by their national grid codes (Figure 3.1). Samples were also collected from Ireland (latitude: 53.78; longitude: -8.25). Since the grid coding system is not applicable here, samples were taken from a number of sites clustered around County Roscommon (Figure 3.1).

Sex determination

Woodcock are sexually monomorphic, which makes it difficult, if not impossible, to distinguish between the sexes in the field. Whilst there is a tendency for males to be have longer tails than females (Rochford & Wilson 1982; Ferrand & Gossmann 2009), and for females to have longer bills than males (Clausager 1973; Rochford & Wilson 1982; Ferrand & Gossmann 2009), the overlap between these biometric parameters is considerable (Clausager 1973; Rochford & Wilson 1982; Ferrand & Gossmann 2009), making them unreliable indicators of sex. Consequently, samples could not be assigned to a sex category.

Age determination

Samples were assigned to one of two age categories: (1) juvenile; defined as either a bird hatched that calendar year, or a bird hatched the previous calendar year but not yet moulted into adult plumage, (2) adult; defined as a bird hatched before the previous calendar year. This was determined from an assessment of differential plumage characteristics (Clausager 1973; Ferrand & Gossmann 2009; General Methods I).

Stable isotope analysis

All feather samples (from birds of known and unknown origins) were analysed for δ^2H_f, using the techniques described in General Methods I.

Creating a woodcock-specific δ^2H_f isoscape

Having established that woodcock δ^2H_f has utility as a broad-scale geographical marker (Chapter 2), the correlation between woodcock δ^2H_f and δ^2H_p (for both MAD and GSD) was examined. This was necessary to determine how closely the isotope signatures of known origin feathers reflect those of their local environment. Using R 2.13.2 (R Development Core Team 2011), General Linear Models (GLM) were run to examine the relationship between δ^2H_f and δ^2H_p, with respect to bird age (juvenile vs. adult) and sample source (contemporary vs. museum). The most parsimonious model was selected, based on AIC*c* (Akaike's Information Criterion adjusted for small sample size) and AIC model weights (Burnham & Anderson 2002). From this, woodcock-specific calibration equations were derived, using a regression analysis of observed versus predicted values. Notably, plotting observed (y-axis) against predicted (x-axis) values, as opposed to predicted versus observed, avoids spurious effects being added to the regression parameters (Pineiro *et al.* 2008), which improves the accuracy of the regression equations. The derivation of these equations allowed δ^2H_p to be calibrated into a woodcock-specific δ^2H_f surface (isoscape).

Ring recovery analysis

In order to apply similar approaches to those of Van Wilgenburg & Hobson (2011), woodcock ring recovery records were obtained from the British Trust for Ornithology (BTO). The dataset contained 1 237 ring-recoveries dating from 1909-2010. Of these, only ring recoveries for birds ringed during the breeding season (April-Sept) and recovered in the non-breeding season (Figure A3.1a), or

ringed during the non-breeding season and recovered in the breeding season (Figure A3.1b), were selected for analysis. In addition, birds recovered less than 30 km from their initial point of capture were removed from the database, to exclude localised movements (Hoodless & Coulson 1994). In total, the screened dataset yielded 372 useable ring recoveries. These were imported into a Geographic Information System (GIS) (ArcGIS version 9.1; ESRI 2005), enabling all ring recoveries with vectors (lines connecting ring and recovery locations) passing within 300 km of the six geographic sampling regions to be selected. This distance represented a compromise between keeping the analysis local (to sampling region) and achieving sufficient sample sizes. Numerous vectors fell within 300 km of more than one locality, resulting in the following sample sizes: Scotland, n = 192; Norfolk, n = 140; Cornwall, n = 33; Wales, n = 95; Hampshire, n = 95 and Ireland, n = 124 (Table A3.2). Since the movement directions (0-360°) in the ring recovery database represented movements both to and from the breeding grounds, the movement directions were transformed to fall within the range of 270 to 90° (through 360°) i.e. the direction data for birds ringed on the breeding grounds were transformed by adding 180 degrees and taking the remainder if the result was greater than 360 (modulo operation). The 'circular' package (Lund & Agostinelli 2011), within R 2.13.2 (R Development Core Team 2011), was then used to estimate probability densities. Since the recovery directions for some sites were bimodal, this was achieved via kernel density estimation (as opposed to maximum likelihood estimation), given a von Mises's smoothing function. The results enabled prior probability surfaces to be created, for use in the spatially explicit assignment of birds from unknown breeding origin.

Spatially explicit assignment of woodcock to geographic origins, using stable isotope and ring-recovery data

Following Van Wilgenburg & Hobson (2011), a likelihood-based assignment was used that incorporated estimates of uncertainty, combined with prior probabilities generated from the ring recovery analysis (*Methods, Ring recovery analysis*). The first step in this assignment approach was to estimate the likelihood that any given cell, within the appropriate woodcock-specific (adult or juvenile) δ^2H_f isoscape, represented the origin of a given individual in the sample. This was achieved using a normal probability density function to assess the likelihoods (Eq. 1).

$$f(y^* \mid \mu_c, \sigma_c) = \left(\frac{1}{\sqrt{2\pi}\sigma_c}\right)\exp\left[-\frac{1}{2\pi\sigma_c^{\,2}}(y^* - \mu_c)^2\right] \qquad \text{(Eq. 1)}$$

In equation 1, $f(y^* \mid \mu_c, \sigma_c)$ represents the likelihood that a given cell, within the δ^2H_f isoscape (c), represents a potential origin for an individual of unknown provenance, given the observed value of δ^2H_f (y^*), the expected mean δ^2H_f for that cell (μ_c), and the expected standard deviation of δ^2H_f (σ_c) between individuals growing their feathers at the same locality. The latter was estimated using the standard deviation of the residuals from the following general linear model: δ^2H_f ~ MAD + Age (*Methods, Creating a woodcock-specific δ^2H_f isoscape*). This resulted in a separate surface of spatially explicit probability densities for each bird in the sample. Kernel densities (estimated in *Methods, Ring-recovery analysis*) were incorporated as prior probabilities in assessing posterior probabilities (f_x or "probability of origin") by applying Bayes' Rule (Eq. 2).

$$f_x = \frac{f(y^* \mid \mu_c, \sigma_c) f_{vm}}{\sum_i f(y^* \mid \mu_c, \sigma_c) f_{vm}} \qquad \text{(Eq. 2)}$$

Equation 2 takes the form of likelihood prior probabilities divided by the sum of these results, across each cell in the isoscape. The likelihood (f ($y^* \mid$ μ_c, σ_c)) is estimated as per equation 1, and f_{vm} represents the spatially explicit prior probabilities of woodcock origins, as estimated from the movement direction model. Division by the sum of the posterior probability densities ensures that there is a 100% probability that the sample originates from somewhere within the range, and thus the estimate for each cell is an approximation that it represents a potential origin for the sample.

To depict likely origins across all samples, the probabilities of individual posterior probability maps were reclassified into likely (value of 1) versus unlikely (value of 0) origins, based on a threshold cumulative probability. This resulted in one binary map per assigned individual. A 3:1 odds ratio was selected, representing a 75% probability of correctly assigning a bird to its origin. This provided a reasonable compromise in the trade-off between incorrect assignment and geographic resolution; higher odds result in birds being assigned to increasingly large areas but with lower risk of misclassification (Van Wilgenburg & Hobson 2011). The results of the individual assignments were then summed over all individuals, which resulted in a surface similar in interpretation to a kernel density estimate. This enabled stronger inferences to be made than if single assignments had been used (Wunder & Norris 2008b). Functions within R 2.13.2 (R Development Core Team 2011) were used to make assignments and plot the respective assignment maps, using the "raster", "rgdal" and "maps" packages.

Distribution maps were standardised relative to the maximum number of assignments for ease of interpretation and to allow for qualitative comparisons between plots. The scale of each map represents the probability distribution of assignment likelihood, such that a cell on the map reflects the likelihood probability of it being a potential origin. For example, the maximum number of assignments allocated to cells for adult woodcock sampled across all regions and all years was 474. All cells within the distribution map that correspond to this value represent a potential origin with the highest likelihood probability (P = 1.0). Cells that were not allocated an assignment (i.e. 0%) were coloured white on the maps, so as to be synonymous with null areas that represent areas outside the likely woodcock breeding distribution. In total, up to 34 countries encapsulated assigned cells. For ease of interpretation and discussion of results, these were grouped into four broad potential breeding areas: (1) Russia (& bordering countries), comprising Azerbaijan, Belarus, Estonia, Georgia, Kazakhstan, Latvia, Lithuania, Russia and Ukraine; (2) Fennoscandia, comprising Finland, Norway and Sweden; (3) Europe (mainland), comprising: Andorra, Austria, Belgium, Bosnia and Herzegovina, Bulgaria, Czech Republic, Denmark, France, Germany, Hungary, Italy, Luxembourg, Netherlands, Poland, Romania, Serbia, Montenegro, Slovakia, Spain and Switzerland; and (4) Britain and Ireland.

For each posterior probability surface, it was possible to extract the longitude, latitude and number of assignments to each cell. This was achieved using the "SDMTools" package, and the "cbind" and "extract" functions within R 2.13.2 (R Development Core Team 2011). The extracted data for each distribution were imported into Microsoft Office Excel 2003 (Microsoft Corporation 2003). Here, the

relative proportions of assignments to potential breeding origins were calculated using pivot tables. Centres of gravity were also calculated; the SUMPRODUCT function was used to determine weighted mean longitudes/latitudes, whilst standard errors were derived from the variance of weighted averages equation (Eq. 3):

$$\sigma_{wav} = \frac{1}{\sqrt{\sum w_i}} \qquad \text{(Eq. 3)}$$

Ascertaining levels of connectivity, through examination of cell overlap

Extracted data for each distribution were imported into GenStat version 14.0 (VSN International Ltd. 2011), where a numerical coding system was applied that enabled identification and selection of overlapping cells. From this, it was possible to calculate relative proportions of overlap, thus enabling levels of connectivity to be ascertained.

Results

Preliminary analyses: Raw isotope data

Preliminary analyses were conducted in GenStat version 14.0 (VSN International Ltd. 2011). The residuals of all statistical models were assessed for normality using the Shapiro-Wilk test and/or the residual composite plots (Figure A2.1). A 5% level of significance was used in all statistical tests/models.

The δ^2H_f values obtained from woodcock feathers of unknown origin (n = 1 129) were not normally distributed (W = 0.9705, $P < 0.001$), but rather represented a bi-modal distribution. Given findings in Chapter 2, this was attributed to age-related variation. Indeed, a Mann-Whitney U test revealed that average δ^2H_f (± standard error, SE) for adults (n = 581, mean = -60.7‰ ± 0.54 SE, median = -61.5) differed significantly from δ^2H_f of juveniles (n = 548, mean = -87.3‰ ± 0.47 SE, median = -88.9) (Mann-Whitney U, U = 19328.5, $P < 0.001$). Therefore, all further analyses were conducted separately for adults and juveniles.

General Linear Models (GLM) found no significant effect of sampling year (2004/05, 2008/09, 2009/10, 2010/11) on the δ^2H_f of adults (GLM, $F_{3, 572} = 1.04$, $P = 0.374$), or juveniles (GLM, $F_{3, 539} = 0.87$, $P = 0.459$). However, δ^2H_f values did vary significantly between sampling regions (Scotland, Norfolk, Cornwall, Wales, Hampshire, Ireland), for both adults (GLM, $F_{5, 572} = 7.17$, $P < 0.001$) and juveniles (GLM, $F_{5, 539} = 4.49$, $P < 0.001$) (Figure 3.2). Therefore, where applicable, further analyses and/or mapping were pooled across sampling years but stratified according to sampling region.

Creating a woodcock-specific δ^2H_f isoscape

Using δ^2H_p isoscapes provided by Bowen *et al.* (2005), the correlation between δ^2H_f and MAD was found to be marginally better than the correlation with GSD (Pearson's product moments: 0.49, $P < 0.001$ and 0.44, $P < 0.001$, respectively). Thus all subsequent modelling was done using MAD as a predictor variable.

The top three models from 11 *a priori* candidate GLM models (see *Methods, Creation of a woodcock-specific δ^2H_f isoscape*) received 100% of the support, and all included the factor for source. Parameter estimates from the top three models, and inspection of scatterplots of δ^2H_f against MAD, suggested that museum samples provided a less reliable source for calibrating the δ^2H_f isoscape. The data-set was therefore restricted to contemporary samples for subsequent analyses.

Using the subset of 136 contemporary samples, four candidate models were considered to explain the variance in δ^2H_f. This was modelled as a function of 1) an intercept only model; 2) MAD; 3) MAD and age; and 4) MAD, age, and their interaction. The top model (δ^2H_f = MAD + age) received 74% of the support, whilst the second best model (δ^2H_f = MAD + age + MAD*age) received 26% of the support, and these were separated by 2.08 AIC*c* units. An Analysis of Variance (ANOVA) test was used to further compare the top model two models, to determine if the addition of the interaction term provided any improvement upon the less parameterized model. The addition of the interaction term, however, provided no substantive improvement ($F_{1, 132}$ = 0.07, P = 0.78). Given this, the parameter estimates from the less parameterized model (Table 3.1 & Figure 3.3) were used to calibrate the MAD isoscape into an age-specific δ^2H_f surface (isoscape) (Figure 3.4). The selected model explained 75% of the variance in δ^2H_f (R^2 = 0.75), and had a residual standard error of 11.76‰. Calibration equations were derived for adults (Eq. 4) and juveniles (Eq. 5).

δ^2H_f (adult) = 4.51 (± 6.34 SE) + 0.80 (± 0.08 SE) * MAD

(Eq. 4)

δ^2H_f (juvenile) = 4.51 (± 6.34 SE) + 0.80 (± 0.08 SE) * MAD - 28.73 (± 2.15 SE)

(Eq. 5)

Ringing recovery analysis

Movement direction models were derived from an analysis of woodcock ringing recoveries (Figure A3.1), for each of the six geographical sampling areas (Table A3.2). These predicted the likely compass bearings from which woodcock could have originated. Results were reported at various percentiles of the probability distribution (Table 3.2) and were also presented as probability density "wedge" maps (Figure 3.5). For each sampling region, circular plots showed that the greatest frequency of observations lay between 0° and 90°. More specifically, all bearings within 75-100% of the probability density lay between 1.5° north (N) and 81.5° east by north (EbN), based on the 32-point compass rose. For birds caught in Scotland and Norfolk, the distribution of these data was uni-modal, with birds most likely originating from Fennoscandia or Russia. In contrast, birds caught in Cornwall, Wales and Ireland showed a bimodal distribution, with potential origins located in Fennoscandia or Russia, or alternatively from bearings representative of British locales, specifically more eastern (e.g. Norfolk) and northern (e.g. Scotland) regions. Notably, this bimodal distribution was most pronounced for birds caught in Cornwall. The probability density for birds caught in Hampshire was unimodal, and suggested that birds most likely originated from more eastern regions of Britain.

Spatially explicit assignment of woodcock to geographic origins, using stable isotope and ring-recovery data

Distribution maps depicting the likely origins of adult and juvenile woodcock were created for birds sampled across all regions (Scotland, Norfolk, Cornwall, Wales, Hampshire and Ireland) and all years (2004/05, 2008/09, 2009/10, and 2010/11) (Figure 3.6). These showed that Russia and Fennoscandia comprised the most likely origins of migratory birds sampled. Considering the entire adult probability distribution, the relative proportions of assignments allocated to each potential breeding area were as follows: 51.4% of assignments allocated to Russia (& bordering countries), 39.2% to Fennoscandia, 7.9% to Europe (mainland) and 1.5% to Britain and Ireland. Similarly, for juveniles, 50.5% of assignments were allocated to Russia (& bordering countries), 39.9% to Fennoscandia, 7.9% to Europe (mainland) and 1.7% to Britain and Ireland (Table 3.3). Notably, when considering 50-100% and 75-100% of the probability distribution, Fennoscandia comprised the most likely origins, for both adult and juvenile birds.

For each sampling region, the weighted mean longitude (x) and latitude (y) of assignments was calculated, enabling its centre of gravity to be determined. For adult birds sampled in each region, the weighted mean (x, y) values (± SE) were as follows: Scotland (25.7 ± 0.00003 SE, 60.9 ± 0.00003 SE), Norfolk (28.1 ± 0.00003 SE, 58.3 ± 0.00003 SE), Cornwall (22.6 ± 0.00003 SE, 58.4 ± 0.00003 SE), Wales (28.5 ± 0.00003 SE, 59.5 ± 0.00003 SE), Hampshire (25.9 ± 0.00003 SE, 57.1 ± 0.00003 SE), and Ireland (25.5 ± 0.00003 SE, 59.8 ± 0.00003 SE). For juvenile birds sampled in each region, the weighted (x, y) values were: Scotland (24.6 ± 0.00003 SE, 60.6 ± 0.00003 SE), Norfolk (27.5 ± 0.00003 SE, 58.2 ±

0.00003 SE), Cornwall (22.6 ± 0.00002 SE, 58.9 ± 0.00002 SE), Wales (26.8 ± 0.00003 SE, 58.4 ± 0.00003 SE), Hampshire (24.9 ± 0.00004 SE, 57.2 ± 0.00004 SE), and Ireland (24.3 ± 0.00003 SE, 59.1 ± 0.00003 SE). The weighted means were plotted separately, for adults and juveniles, to allow the centres of gravity to be compared qualitatively (Figure 3.7).

For adults and juveniles sampled in each region, distribution maps were plotted (adults: Figure 3.8, juveniles: Figure 3.9), and the relative proportions of assignments to each of the four (aforementioned) potential breeding areas calculated (Figure 3.10). Results revealed regional differences. For birds sampled in Scotland and Norfolk, assignments to British origins were only present at the lowest proportions of the probability density (0-10%). In contrast, birds sampled in Cornwall and Ireland had the highest proportions of British assignments (Table 3.4), with Scotland found to be the most likely origin of these assignments. Birds sampled in Wales and Hampshire also showed a small proportion of assignments allocated to British origins. For the former, assignments were located in north-eastern regions of Britain, whilst the latter were located in more eastern regions.

Considering the entire probability distribution, the highest proportions of birds from Russia were found in Norfolk (adults: 60.1%, juveniles: 60.2%) and Wales (adults: 59.0%, juveniles: 58.1%), whilst the highest proportions of birds from Fennoscandia were found in Scotland (adults: 52.1%, juveniles: 54.1%). For mainland Europe, proportions were low across all sampling regions (adults: 2.3-19.44%, juveniles: 1.7-17.78%), but of these the largest proportions were found in

Hampshire (adults: 19.4%, juveniles: 17.8%) and Cornwall (adults: 13.5%, juveniles: 10.1%)

Ascertaining levels of connectivity, through examination of cell overlap

Qualitatively comparing distribution maps depicting spatially explicit assignments of geographic origins revealed overlap in cell occupancy. The extent of this overlap was explored further, by considering the relative probabilities of assignment likelihood for overlapping cells.

To uncover any age-related differences, adult and juvenile distributions were plotted on the same maps and stratified according to sampling region, with all sampling years combined. In these plots, the probability distribution of assignment likelihood was considered at two levels: 1-49% and 50-100%, enabling easy comparison of overlapping and non-overlapping cells, whilst retaining information regarding the relative probabilities of assignment likelihood (Figure 3.11). The overall percentages of cell overlap for adults and juveniles from the same sampling regions indicated that, in most cases, the juvenile distribution was completely contained within the adult distribution, with 1-15% of the adult distribution extending further than that of juveniles (Table 3.5).

To ascertain which cells were common to all sampling distributions, overlapping cells were plotted for all sampling regions and all sampling years (combined), but separately for adults and juveniles (Figure 3.12). Further to this, cells unique to each sampling region were identified for adults (Figure 3.13) and juveniles

(Figure 3.14). Notably, all unique cells occurred at the 1-49% level of assignment likelihood; there were no unique cells at the 50-100% level.

Discussion

Preliminary analyses: Raw isotope data

Age-related differences in woodcock δ^2H_f values were apparent, with adult δ^2H_f values enriched, compared to those of juveniles. Whilst a number of explanations have been put forward to account for age-related variation in δ^2H_f (Meehan *et al.* 2003; Smith & Dufty 2005; Langin *et al.* 2007), for woodcock, it is most likely attributable to temporal (seasonal) isotopic variation that coincides with moult phenology (Hobson & Wassenaar 1997; Chapter 2).

Creating a woodcock-specific δ^2H_f isoscape

Woodcock δ^2H_f was found to better reflect amount-weighted mean annual δ^2H_p (MAD), as opposed to the amount-weighted growing season average (GSD). GSD relates to the growing season of plant matter and is restricted to those months where the average monthly temperature is > 0°C (Bowen *et al.* 2005). Whilst this is likely to be a good predictor for bird species incorporating large proportions of plant material in their diet (directly and/or through higher trophic levels), this may not be the case for all bird species. MAD is dissociated from the growing season and, for woodcock, with a diet typically comprising earthworms (Hoodless & Hirons 2007), it seems intuitive that δ^2H_f values should correspond more closely to MAD than GSD. Indeed, MAD may be the best predictor of δ^2H_f for

other soil-probing species. Given this, it is advised that the choice of predictor be made on a species-specific basis, taking into consideration foraging ecology.

Typically, isotope studies rely on generic calibration equations derived from a suite of bird species to determine origins (Hobson & Wassenaar 1997; Hobson *et al.* 2004; Clark *et al.* 2006). However, the non-specific nature of these equations is likely to introduce error and, in turn, reduce the accuracy of results. It is therefore advised, where possible, to derive species-specific calibration equations (Hobson *et al.* 2004). The woodcock calibration developed here represents the first for this species. Compared to the generic equation (Eq. 6) developed for European birds (Hobson *et al.* 2004):

$$\delta^2H_f = 29.4 + 1.13*MAD \qquad \text{(Eq. 6)}$$

the woodcock calibration revealed an important age effect, with juvenile δ^2H_f values depleted by approximately 28.7‰ (± 2.15 SE). This necessitated the development of age-specific woodcock calibration equations i.e. one for adults and one for juveniles. If this age effect had not been considered, then birds would have been incorrectly assigned to place of origin. Furthermore, the R^2 value obtained for the woodcock calibration (0.75) accounts for more of the variation in δ^2H_f than that of the generic equation (0.66). This supports the notion that species-specific calibrations have stronger power and ultimately result in more reliable assignments.

Ring-recovery analysis

Woodcock ring recoveries were used to calculate prior probabilities within a Bayesian framework, primarily because this can increase the geographic precision to which birds are assigned (Van Wilgenburg & Hobson 2011). Although ring-recoveries may suffer spatial and temporal bias depending on ringing and hunting effort (Perdeck 1977), prior probabilities from other data sources e.g. abundance data (Royle & Rubenstein 2004; Wunder *et al.* 2005) are scant available for woodcock. Using ring recoveries as prior probabilities enabled migration direction models to be generated, which provided a simplified approach to those of Van Wilgenburg & Hobson (2011), where Spherically Projected Multivariate Linear (SPML) models were used to model migration direction.

Considered in isolation, migration direction models represent an alternative approach to analysing ring-recovery data and, here, provide an updated picture of work initially carried out by Hoodless & Coulson (1994). Indeed, the wedge maps revealed a more expansive range of potential origins than those obtained by Hoodless & Coulson (1994), and they provided more substantial evidence that Russia and Fennoscandia comprise the most likely origins for birds in Britain, during the non-breeding season. Furthermore, although the majority of British woodcock remain faithful to their natal or breeding sites during the non-breeding season (Hoodless & Coulson 1994), it is clear that a proportion of resident birds appear to relocate to alternative non-breeding sites (within Britain). These relocation events appear to occur along a southwards and/or westwards trajectory, supporting the suggestion for cold-weather movements during the winter, whereby resident birds leave their breeding grounds to occupy sites that

are typically milder in climate (Spencer 1982). Such movements are believed to be driven by the accessibility and availability of food resources. The woodcock diet comprises mostly earthworms in winter (Granval 1987), yet the accessibility and availability of these decline as environmental conditions deteriorate over the winter (Edwards & Lofty 1972). By relocating to more south/south-westerly regions, which tend to be warmer and wetter than more north/north easterly regions (Met Office 2010a), conditions for feeding are likely to be improved.

Spatially explicit assignment of woodcock to geographic origins, using stable isotope and ring-recovery data

Probability distributions depicting the spatially explicit assignment of geographic origins, for combined sampling regions and sampling years, revealed similar patterns for adults and juveniles. This suggests that adults and juveniles have similar migratory origins. At the level of the entire probability distribution (i.e. 1-100% of assignments), Russia and Fennoscandia were found to comprise the main breeding grounds for migratory birds. Whilst previous works have suggested that over 90% of the European population occurs in these regions (Tucker & Heath 1994; Hagemeijer & Blair 1997), this was based on scant information, and stronger evidence has been required to substantiate it. The results here provide strong support that this estimation is correct. When considering 75-100% of the probability distribution, Fennoscandia was found to comprise the most likely origins for both adult and juvenile birds. Since woodcock from north-eastern populations migrate, in parallel, to more south-western non-breeding grounds (Ferrand & Gossmann 2001), a larger proportion of woodcock originating from Fennoscandia would be expected in Britain, compared to birds

from Russia, and this is evidenced here. In accordance with these general migratory trends, the converse appears to be true for birds residing in France during the non-breeding season (Ferrand & Gossmann 2001; Bauthian *et al.* 2007).

Distribution plots for each sampling region revealed a large degree of interchange between birds from different breeding populations. However, across sampling regions, centres of gravity were similar. All points were clustered around Estonia, Latvia, the Russian/Estonia border, the Russian/Latvia border, and southern Finland, highlighting the high degree of overlap in breeding origins between the wintering areas sampled. Notably, subtle differences in the compositions of birds from the same breeding grounds were apparent across sampling regions, suggestive of differential spatial distributions. These differences were mirrored in both adult and juvenile distributions.

Only small proportions of British assignments were found across sampling regions (adults: 0.01-4.88%, juveniles: 0.04-5.70%). Although these may seem to suggest lower abundance of resident birds in comparison to migrants, abundance data are required for further interpretation. Notably, the proportions of British assignments obtained here are much lower than those derived by Hoodless & Coulson (1994), who found British residents comprised approximately 13% of recaptures. However, in accordance with their work, the highest proportions of British assignments were found in south/south-westerly locales. These are likely to be attributable to cold-weather movements (previously discussed). In this study, Cornwall and Ireland were found to have the highest proportions of British assignments. These regions tend to be warmer and wetter than more

north/north easterly areas (Met Office 2010a), and so likely offer improved feeding conditions.

The finding that Russia and Fennoscandia comprised the most likely origins of migratory birds, across all sampling regions, suggests the occurrence of broad-front migration (Berthold 2001). However, subtle regional differences were apparent. The highest proportions of birds from Russia were found in Norfolk and Wales, whilst the highest proportions of birds from Fennoscandia were found in Scotland. These regional differences were probably attributable to differences in the migratory flyways of birds arriving from Russia and Fennoscandia. Indeed, the identification of two such flyways for birds residing in France during the non-breeding season provides support for this notion (Bauthian *et al.* 2007). Notably, Russian and Fennoscandian proportions were almost equal for birds sampled in Cornwall and in Ireland, a finding that may be attributable to cold-weather movements. As previously described for resident birds, foreign migrants may move from the harsh climes of more northerly regions, to occupy milder areas in the south and/or west that offer improved feeding conditions.

For birds sampled in Ireland, Russian and Fennoscandian assignments may be indicative of leap-frog migration. This typically occurs when northern breeding populations leap-frog southern populations, to occupy non-breeding areas that lie further south (Berthold 2001). However, eastward to westward movements have also been described (Berthold 2001). Migrant woodcock may therefore leap-frog Britain to occupy Irish sites, during the non-breeding season.

Low proportions of foreign migrants from likely European origins were found across all sampling regions, thus supporting the suggestion that European countries comprise only a small proportion (< 10%) of the Eurasian woodcock breeding population (Tucker & Heath 1994; Hagemeijer & Blair 1997). The largest proportions of foreign migrants assigned to European origins were found in Hampshire and Cornwall. The higher prevalence of birds from European origins in these regions may be due to the fact that they are located on a similar latitudinal plane to many European countries.

Ascertaining levels of connectivity, through examination of cell overlap

Across the six winter sampling regions, a large degree of overlap was found between woodcock breeding distributions. By examining the overlap of these distributions, it was possible to discern two forms of connectivity. First, for cells outside Britain and Ireland, the extent of overlap determined the strength of migratory connectivity. This describes the extent to which individuals from the same non-breeding grounds migrate to the same breeding grounds (and vice-versa). It operates at large spatial scales and is, by definition, cross-seasonal (Webster *et al.* 2002). In contrast, the extent of overlap for British and Irish cells determined the strength of landscape connectivity, which involves the regional (small-scale) movements of individuals within a season (Webster *et al.* 2002).

The strength of connectivity was determined by the proportion of overlapping/non-overlapping assignments. If birds from the same non-breeding population occupy the same breeding area then they are considered to show strong connectivity. Conversely, if individuals from the same non-breeding

population disperse widely across the breeding grounds then they are considered to show weak connectivity (Hobson & Wassenaar 2008). Here, a large degree of interchange between woodcock from different breeding populations was prevalent across sampling regions, indicative of weak connectivity. The weakest levels of connectivity were found amongst birds, of both age groups, that likely originated from Fennoscandia and the Baltic States. Only a few unique cells, indicative of the strongest levels of connectivity, were apparent across sampling regions. The highest prevalence of these occurred amongst juvenile birds sampled in Ireland, with unique origins likely in Russia (east of Moscow) and northern Norway. Adult and juvenile birds sampled in Norfolk and Wales, also revealed a few unique cells in Russia (east of Moscow).

Determining levels of connectivity are important due to their relationship with population dynamics. Populations exhibiting weak connectivity, such as those of woodcock, are believed to be less vulnerable to changing selective pressures than those exhibiting strong connectivity (Webster *et al.* 2002; Webster & Marra 2005). This is because populations showing weak connectivity typically have high genetic variation, which may improve their ability to evolve an adaptive response.

Acknowledgements

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Tables & Figures

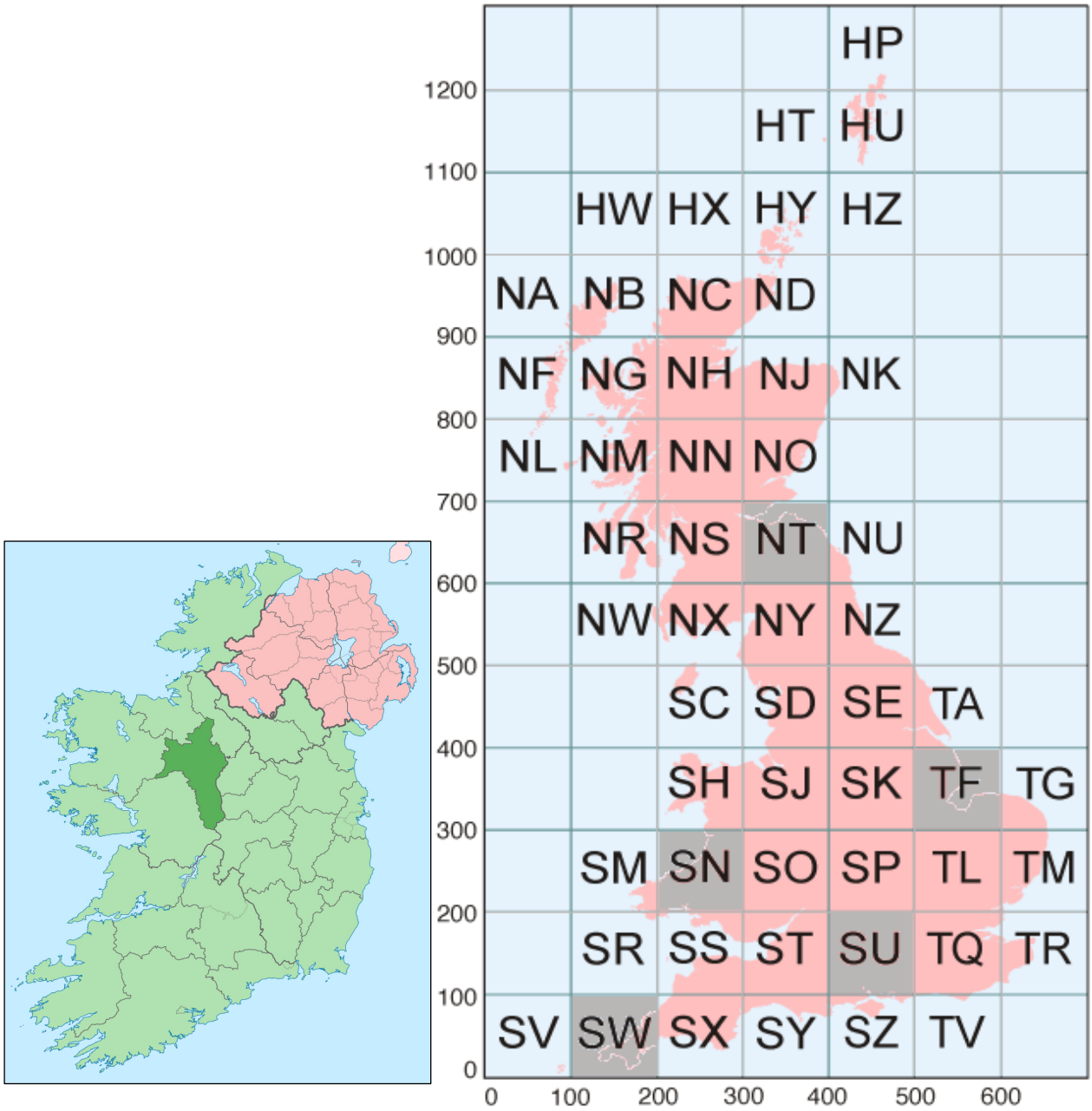


Figure 3.1 Map of Britain (right) depicting the national grid coding system. Highlighted squares indicate sampling regions. These represent the north (Scotland - NT), south (Cornwall - SW), east (Norfolk - TF), and west (Wales - SN), with an additional fifth sampling region in Hampshire (SU). To the left is a map of Ireland (green) and Northern Ireland (pink). The highlighted region (dark green) indicates the sampling region (County Roscommon).

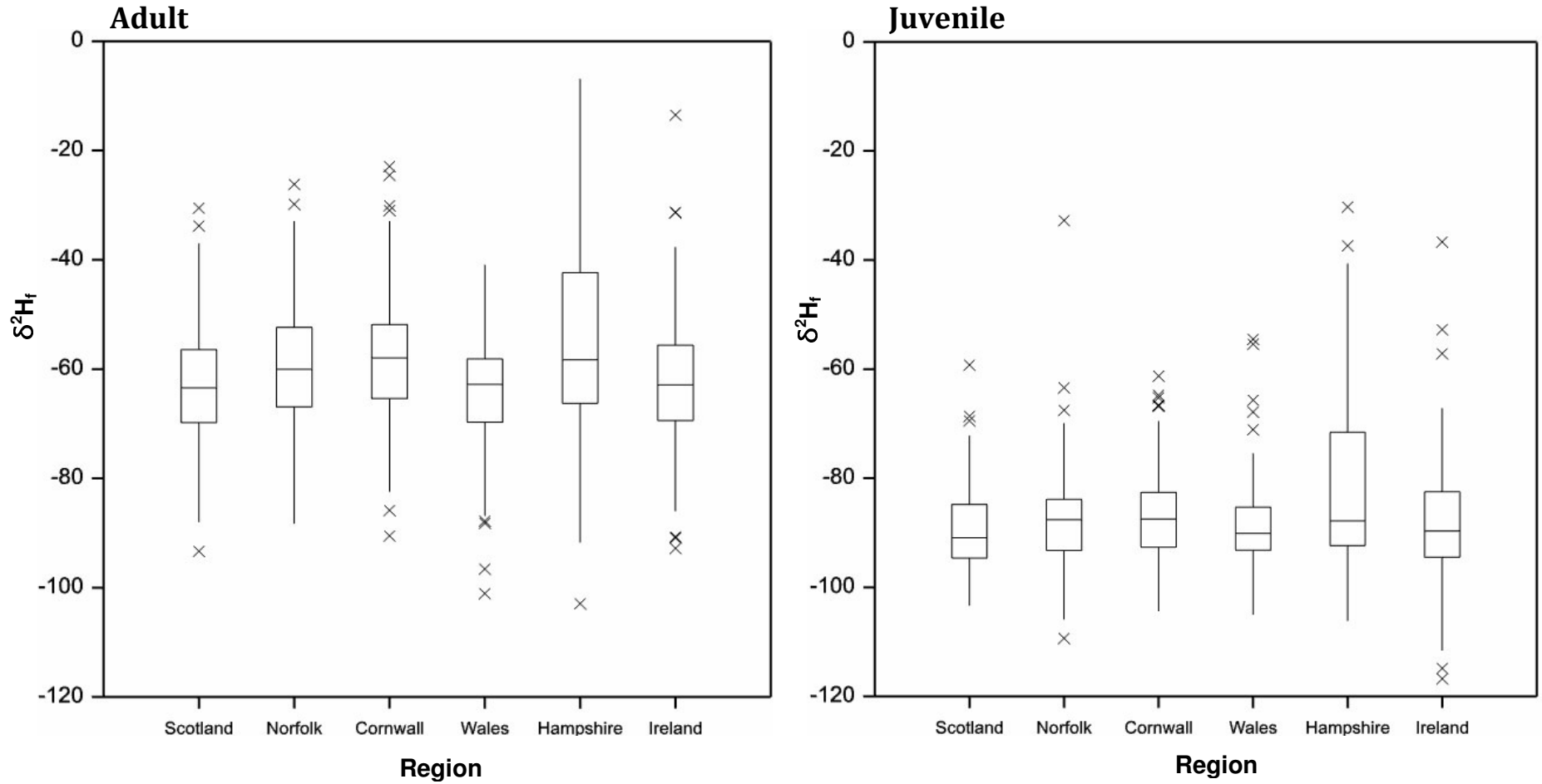


Figure 3.2 Feather δ^2H for adult and juvenile Eurasian woodcock, sampled across six geographic regions within Britain and Ireland, over the winter period. Plots are for combined sampling years (winters: 2004/05, 2008/09, 2009/10, and 2010/11). Samples sizes for adults were: Scotland, n = 109; Norfolk, n = 102; Cornwall, n = 98; Wales, n = 109; Hampshire, n = 59; and Ireland, n = 104. Sample sizes for juveniles were: Scotland, n = 94; Norfolk, n = 100; Cornwall, n = 116; Wales, n = 82; Hampshire, n = 57; and Ireland, n = 99. Each box spans the interquartile range of values. The middle 50% of the data lie within the box, with the intersecting line representing the median. Whiskers extend as far as the minimum and maximum values. Crosses represent outliers.

Table 3.1 Parameter estimates from a minimum adequate model, testing the effects of amount-weighted mean annual deuterium (MAD), and bird age (adult, juvenile), on the feather δ^2H (δ^2H_f) of Eurasian woodcock sampled on the breeding grounds. 1Q = first quartile, 3Q = third quartile, SE = standard error.

Model: δ^2H_f ~ MAD + Age				
Residuals				
Minimum	**1Q**	**Median**	**3Q**	**Maximum**
-45.149	-5.376	0.767	6.254	35.694
Coefficients				
	Estimate	**SE**	**t value**	**Pr(>|t|)**
(Intercept)	4.50799	6.34005	0.711	0.478
MAD	0.79760	0.08049	9.909	<0.001
Age[T.J]	-28.73077	2.14900	-13.369	<0.001

Residual standard error: 11.76 on 133 degrees of freedom
Multiple R-squared: 0.747, Adjusted R-squared: 0.7432
F-statistic: 196.4 on 2 and 133 DF, $P < 0.001$

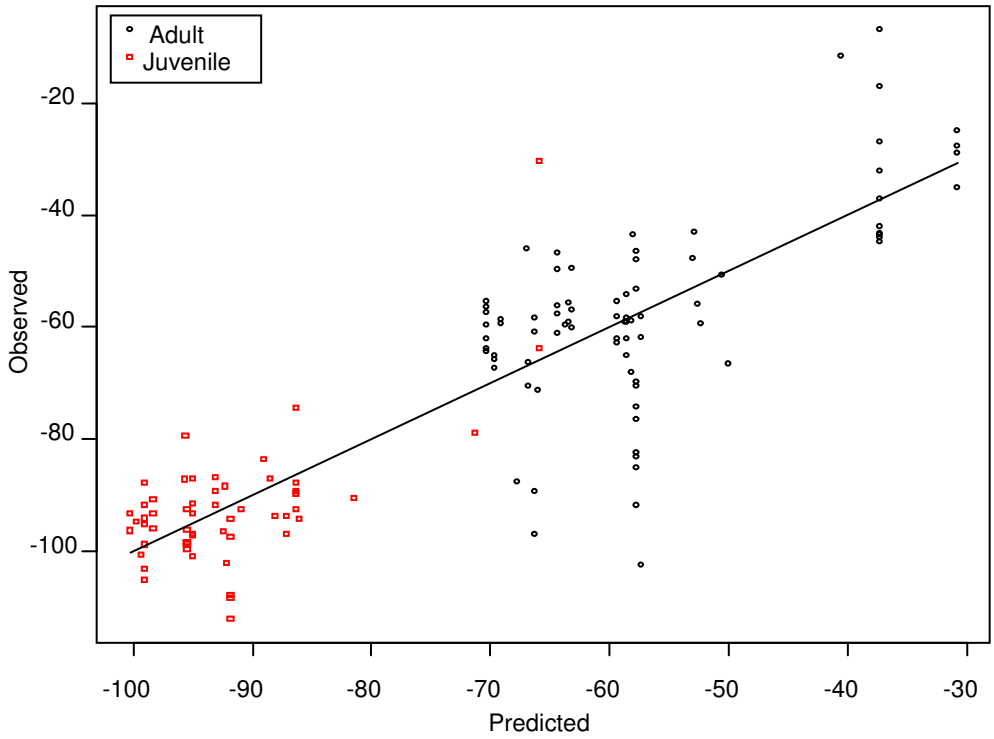


Figure 3.3 Predicted against observed feather δ^2H for Eurasian woodcock sampled on the breeding grounds (adult: n = 80, juvenile: n = 56). Predicted values were calculated using parameter estimates from the model: δ^2H_f ~ MAD + Age (see Table 3.1).

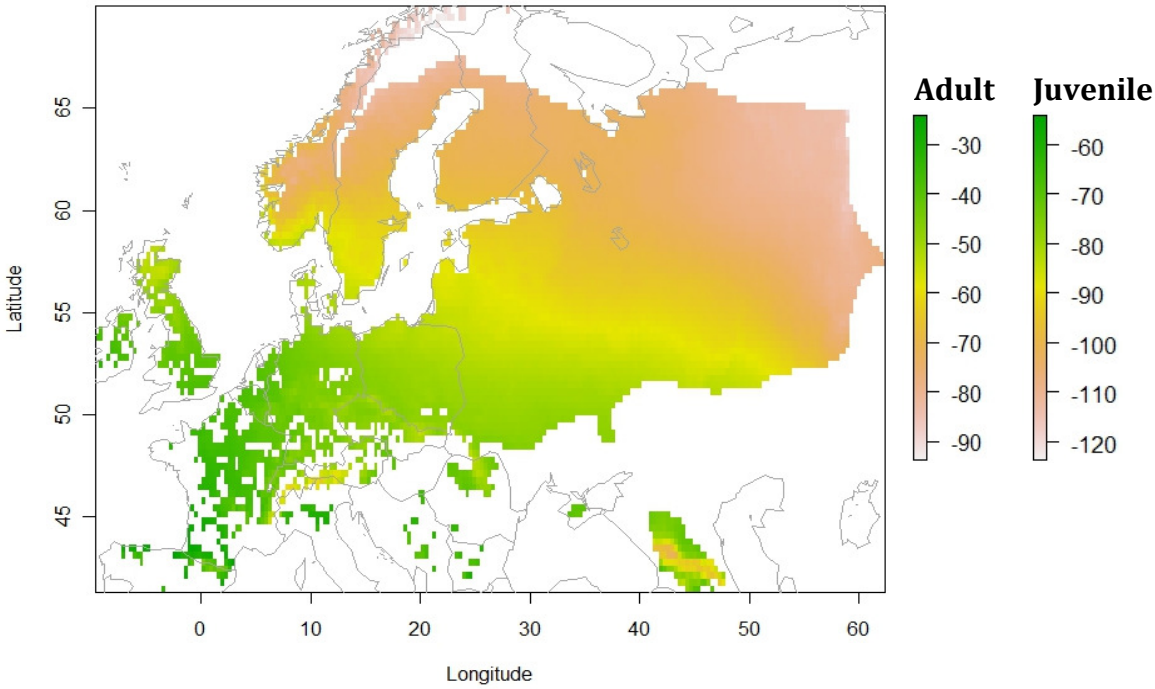
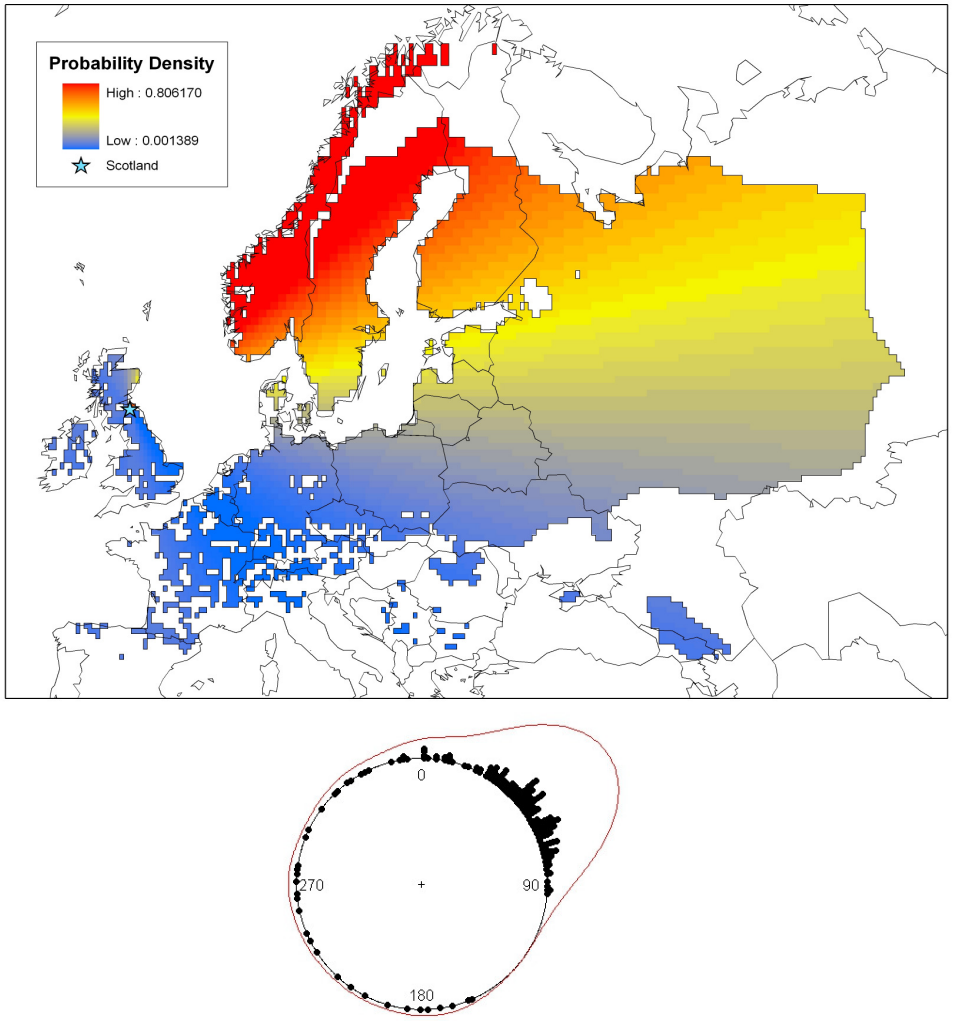


Figure 3.4 Isoscape depicting the likely δ^2H_f values for Eurasian woodcock from a given cell (origin). This is a calibrated version of the MAD isoscape (provided by Bowen *et al.* 2005). It represents an age-specific δ^2H_f surface, such that adults and juveniles have different δ^2H_f values for any given cell (origin).

Table 3.2 The bearing ranges from which Eurasian woodcock most likely originated, for birds ringed/recovered across six geographic regions within Britain and Ireland (Scotland: n = 192, Norfolk: n = 140, Cornwall: n = 33, Wales: n = 95, Hampshire: n = 95, and Ireland: n = 124). Bearing ranges are considered at different proportions of the probability density. Bearings in parentheses represent polar bearings. Directions are based on the 32-wind compass rose.

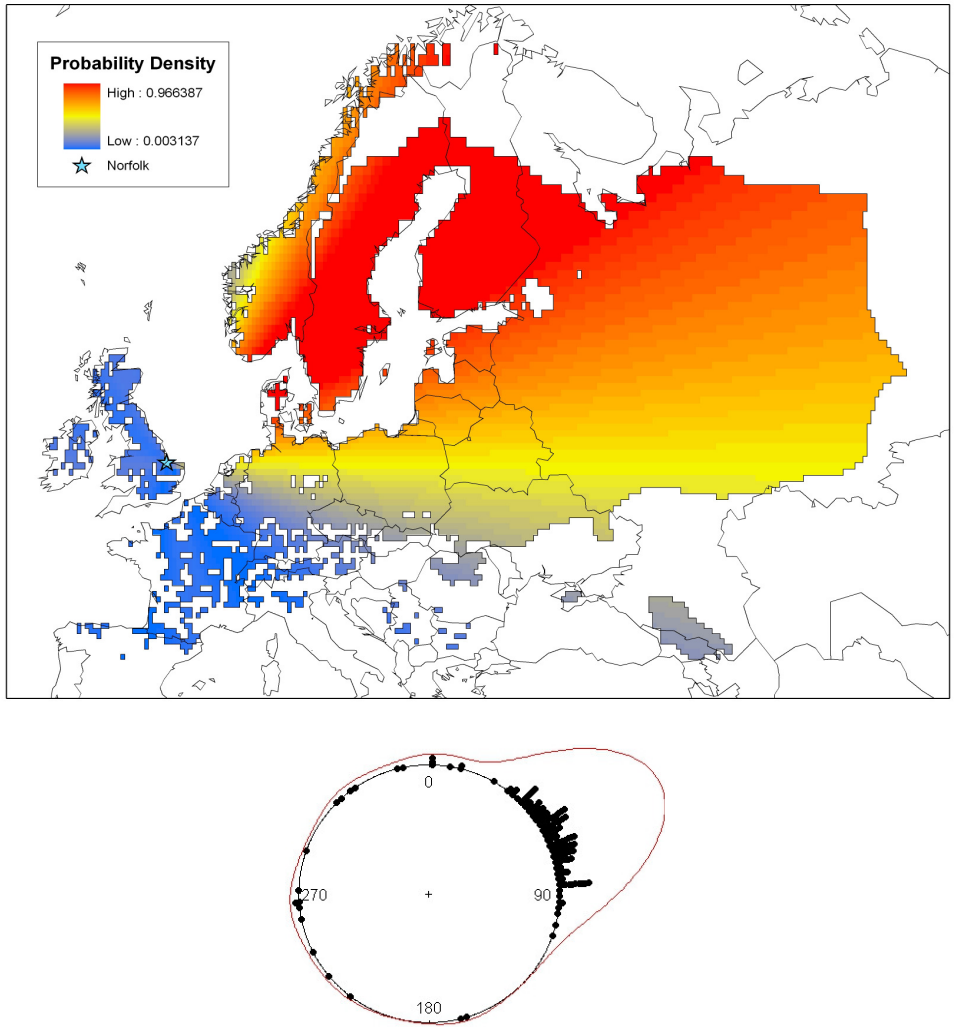
	Bearing range (°)							
Region	**1-100%**		**25-100%**		**50-100%**		**75-100%**	
Scotland	0.5 N	(-0.5 N)	13.5 NbE	(-269.5 W)	29.5 NEbN	80.5 EbN	38.5 NEbN	71.5 ENE
Norfolk	0.5 N	(-0.5 N)	33.5 NEbN	(-261.5 WbS)	42.5 NE	88.5 E	49.5 NE	79.5 EbN
Cornwall	0.5 N	(-0.5 N)	0.5 N	(-0.5 N)	0.5 N	(-0.5 N)	1.5 N	72.5 ENE
Wales	0.5 N	(-0.5 N)	0.5 N	(-0.5 N)	42.5 NE	89.5 E	51.5 NEbE	81.5 EbN
Hampshire	0.5 N	(-0.5 N)	0.5 N	(-0.5 N)	40.5 NE	84.5 E	47.5 NE	76.5 EbN
Ireland	0.5 N	(-0.5 N)	21.5 NNE	(-266.5 W)	29.5 NEbN	83.5 EbN	38.5 NEbN	74.5 EbN

A


Probability Density
High : 0.806170
Low : 0.001389
Scotland

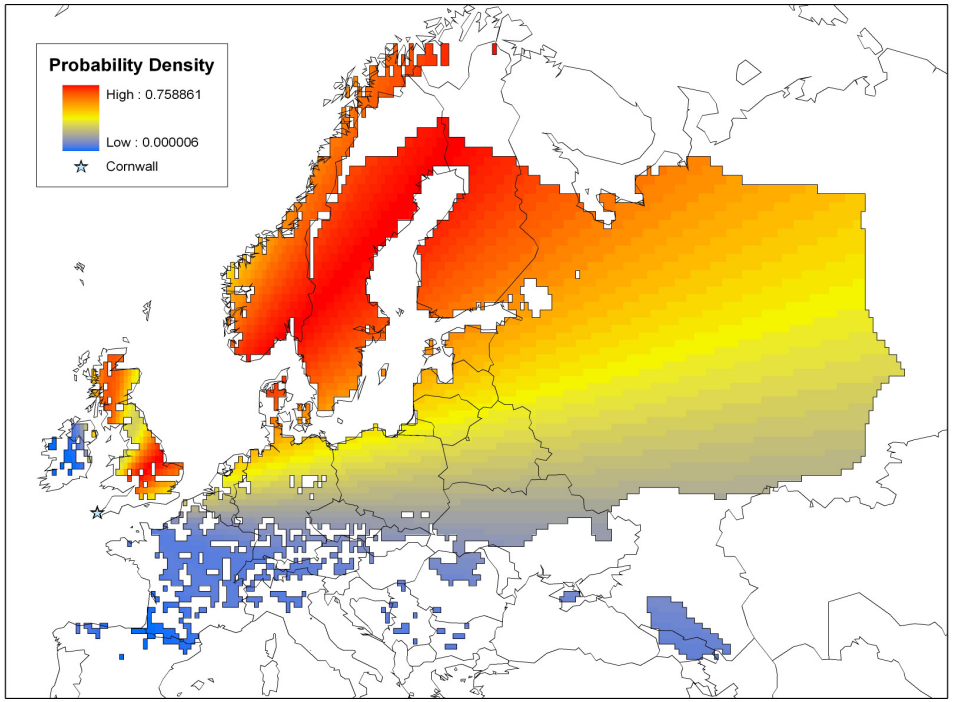
0
90
180
270

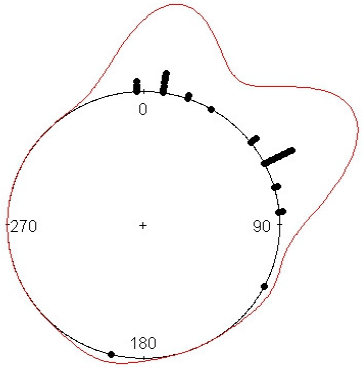
B


Probability Density
High : 0.966387
Low : 0.003137
Norfolk

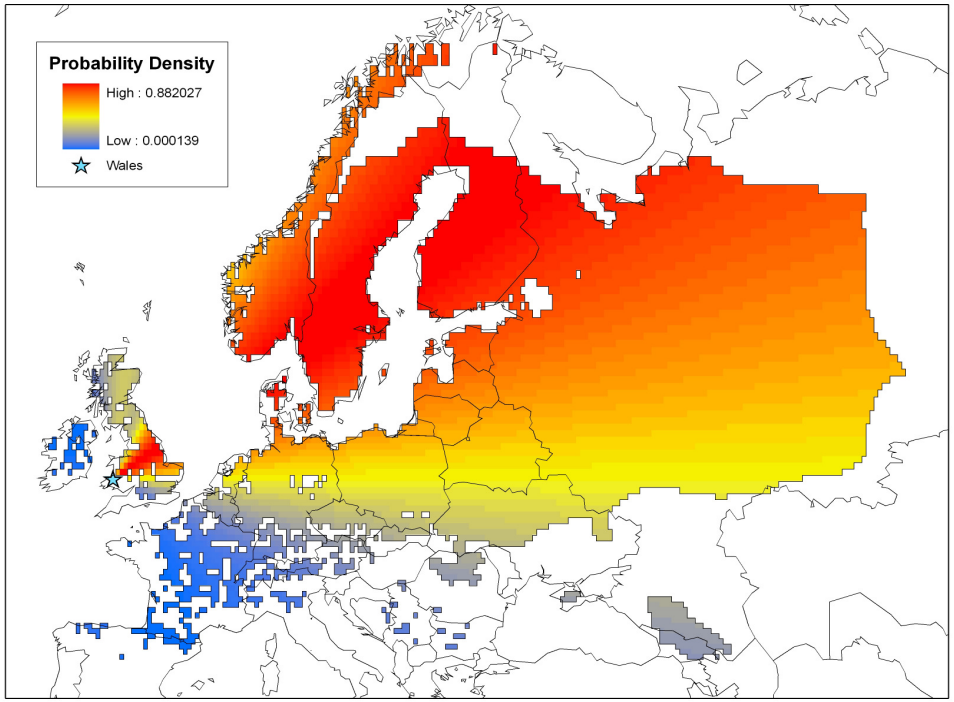
0
90
180
270

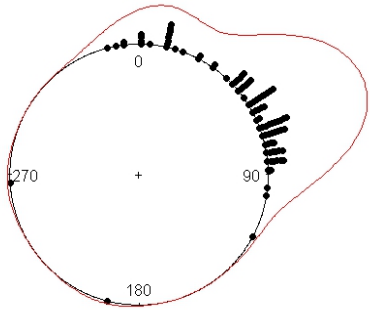
C


Probability Density
High : 0.758861
Low : 0.000006
Cornwall


0
90
180
270

D


Probability Density
High : 0.882027
Low : 0.000139
Wales


0
90
180
270

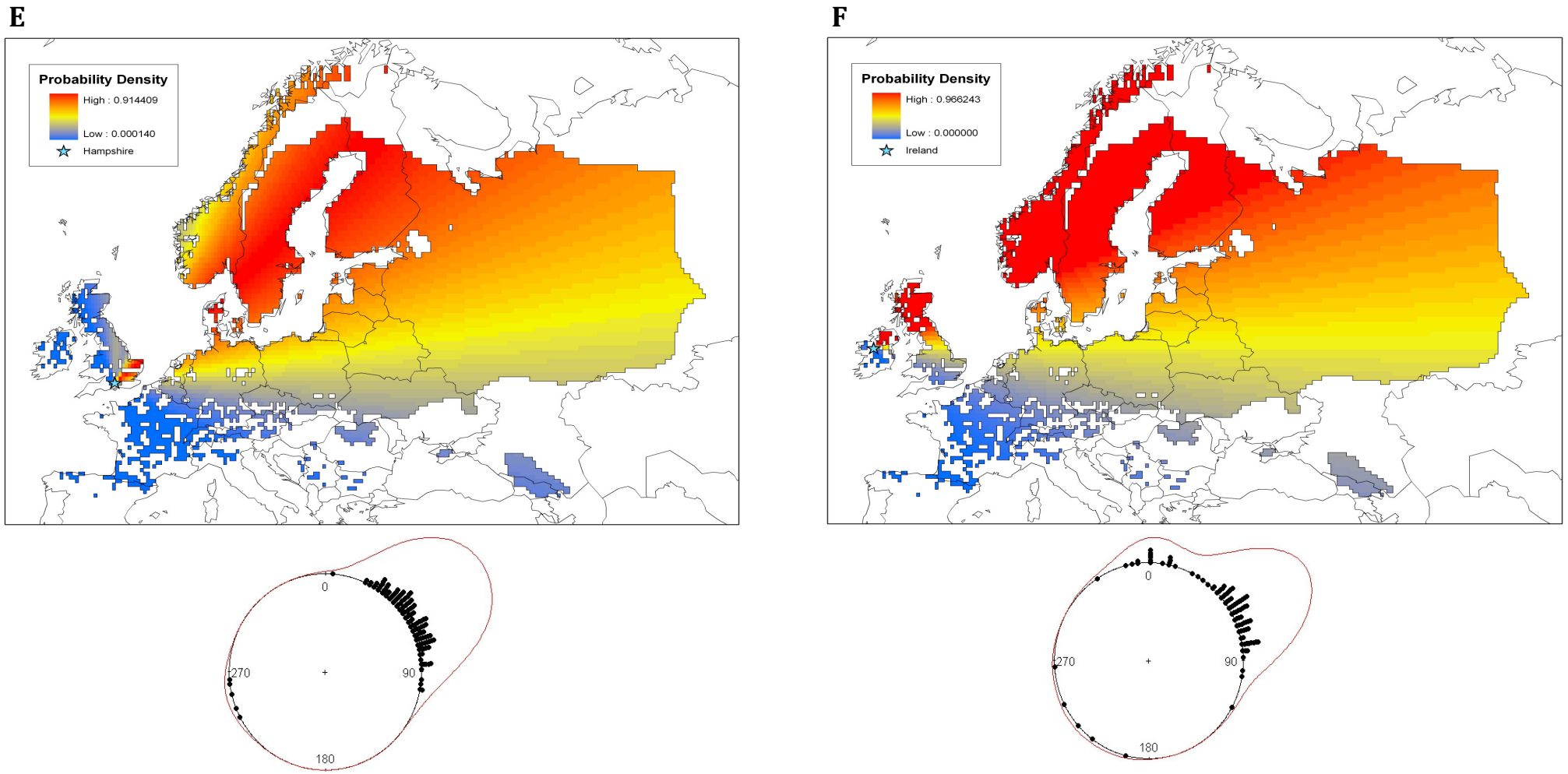


Figure 3.5 Density maps depicting estimated probabilities that Eurasian woodcock (adults and juveniles, combined) caught in a) Scotland (n = 192), b) Norfolk (n = 140), c) Cornwall (n = 33), d) Wales (n = 95), e) Hampshire (n = 95), and f) Ireland (n = 124) (locations denoted by star), could come from a given direction. Probabilities were estimated using a kernel density estimator (allowing for bimodal distribution), and were standardised relative to the maximum value for ease of interpretation. Below the density maps are the respective circular plots of observed data, showing the bearings of likely breeding origins. Stacked points represent the frequencies. Red lines represent the probability density function.

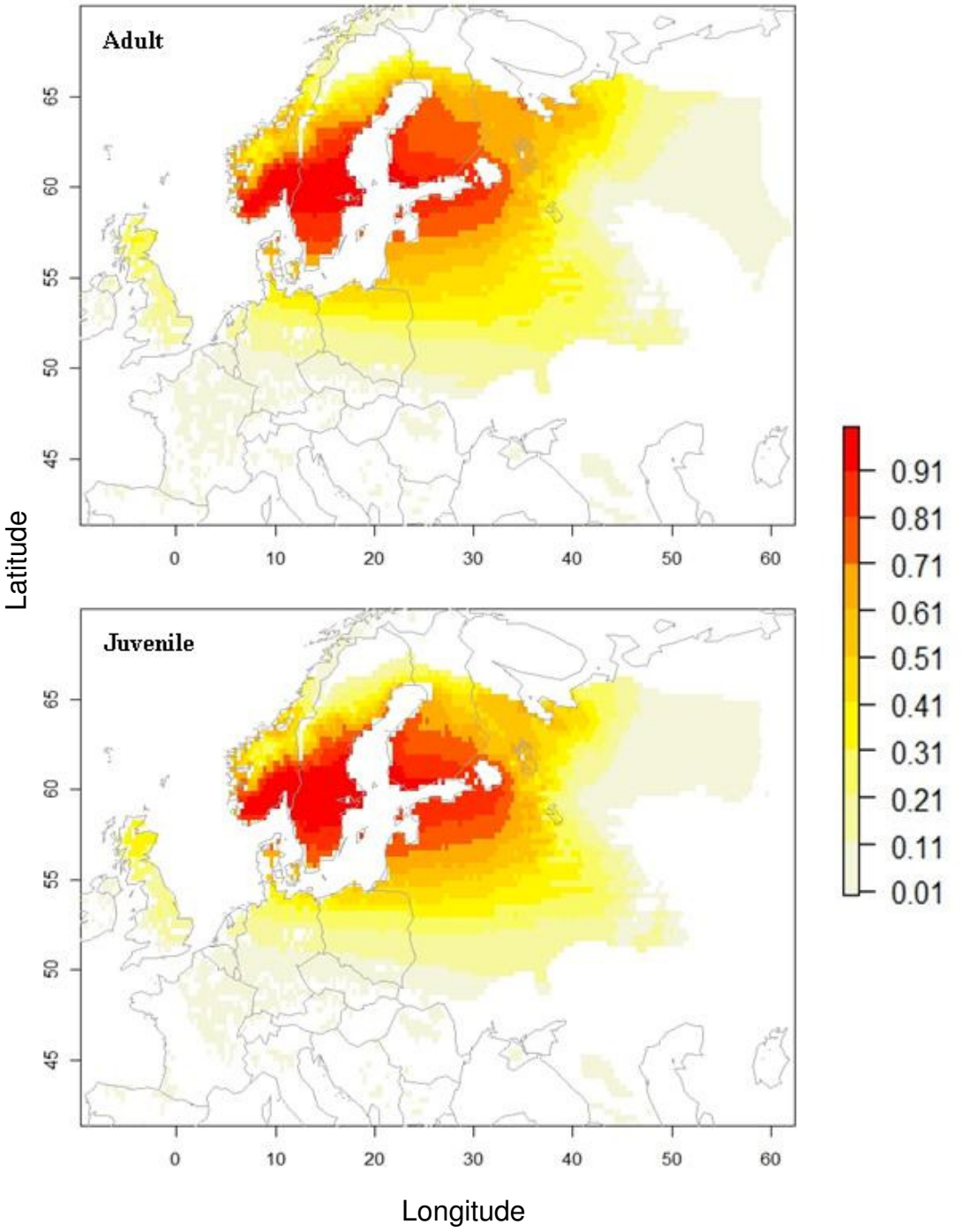


Figure 3.6 Probability distribution maps depicting predicted breeding origins and the likelihood of assignments, for adult (n = 581) and juvenile (n = 548) Eurasian woodcock of unknown breeding origins. Probabilities were standardised relative to the maximum number of assignments for ease of interpretation. Maps are based on data from birds sampled across six combined geographic regions within Britain and Ireland (Scotland, Norfolk, Cornwall, Wales, Hampshire, and Ireland), and across combined sampling years (winters: 2004/05, 2008/09, 2009/10, and 2010/11).

Table 3.3 Proportions of likelihood assignments allocated to each of four predicted breeding areas, for adult (n = 581) and juvenile (n = 548) Eurasian woodcock of unknown breeding origins. Assignments are considered at different proportions of the probability distribution. Data are from birds sampled across six combined geographic regions within Britain and Ireland (Scotland, Norfolk, Cornwall, Wales, Hampshire, and Ireland), and across combined sampling years (winters: 2004/05, 2008/09, 2009/10, and 2010/11). Potential breeding areas (areas of assignment) comprise the following countries: Russia & bordering countries = Azerbaijan, Belarus, Estonia, Georgia, Kazakhstan, Latvia, Lithuania, Russia, and Ukraine; Fennoscandia = Finland, Norway, and Sweden; Europe (mainland) = Andorra, Austria, Belgium, Bosnia and Herzegovina, Bulgaria, Czech Republic, Denmark, France, Germany, Hungary, Italy, Luxembourg, Netherlands, Poland, Romania, Serbia, Montenegro, Slovakia, Spain, and Switzerland; and Britain & Ireland = England, Scotland, Wales, and Ireland.

	Assignments (%)							
	1-100%		**25-100%**		**50-100%**		**75-100%**	
Area of assignment	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
Russia (& bordering countries)	51.40	50.45	48.26	48.28	41.35	43.57	18.09	27.40
Fennoscandia	39.19	39.92	46.06	46.30	57.88	55.46	81.91	72.49
Europe (mainland)	7.89	7.87	5.06	4.48	0.77	0.96	0.00	0.11
Britain & Ireland	1.52	1.74	0.63	0.95	0.00	0.00	0.00	0.00

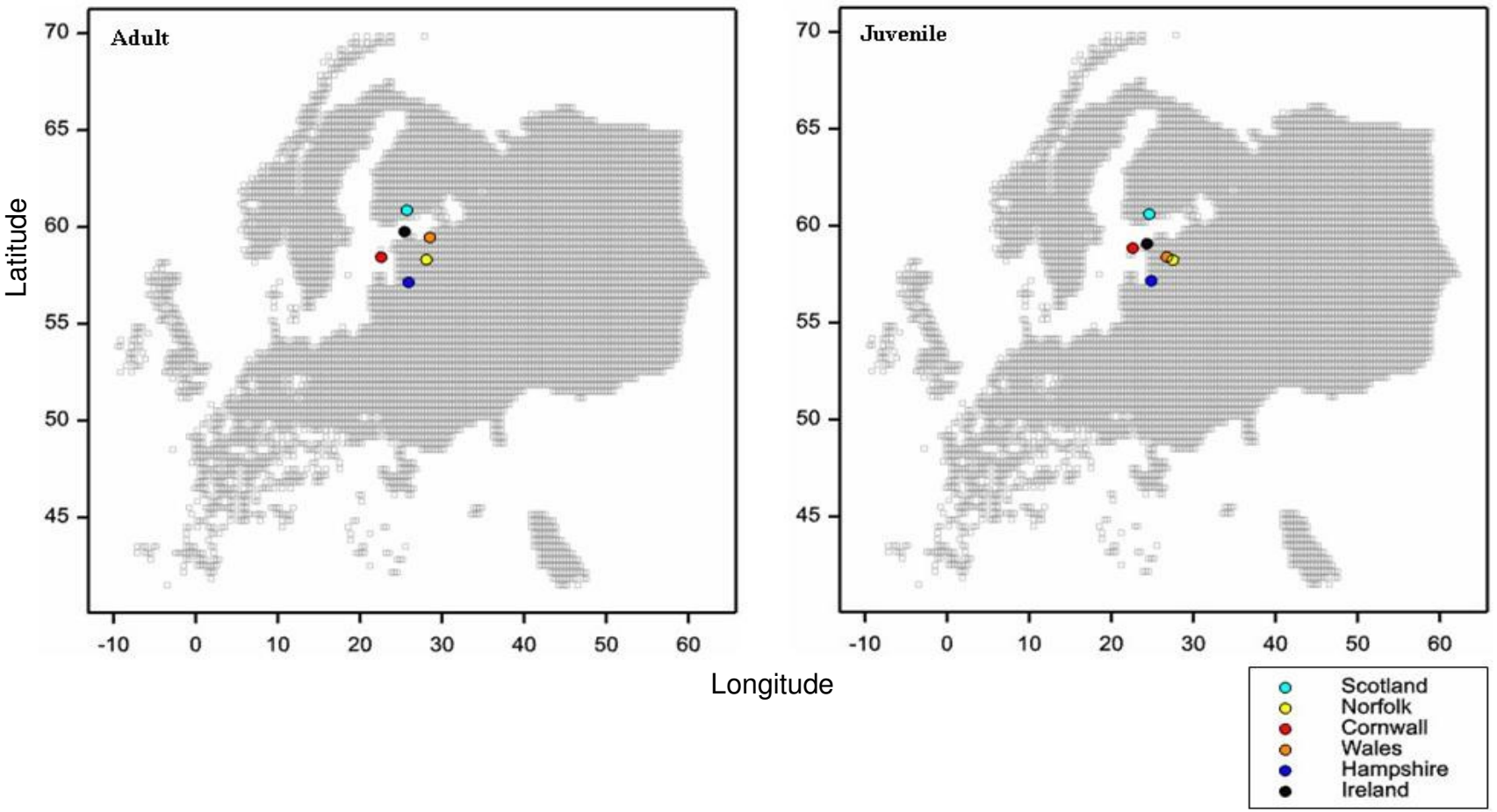
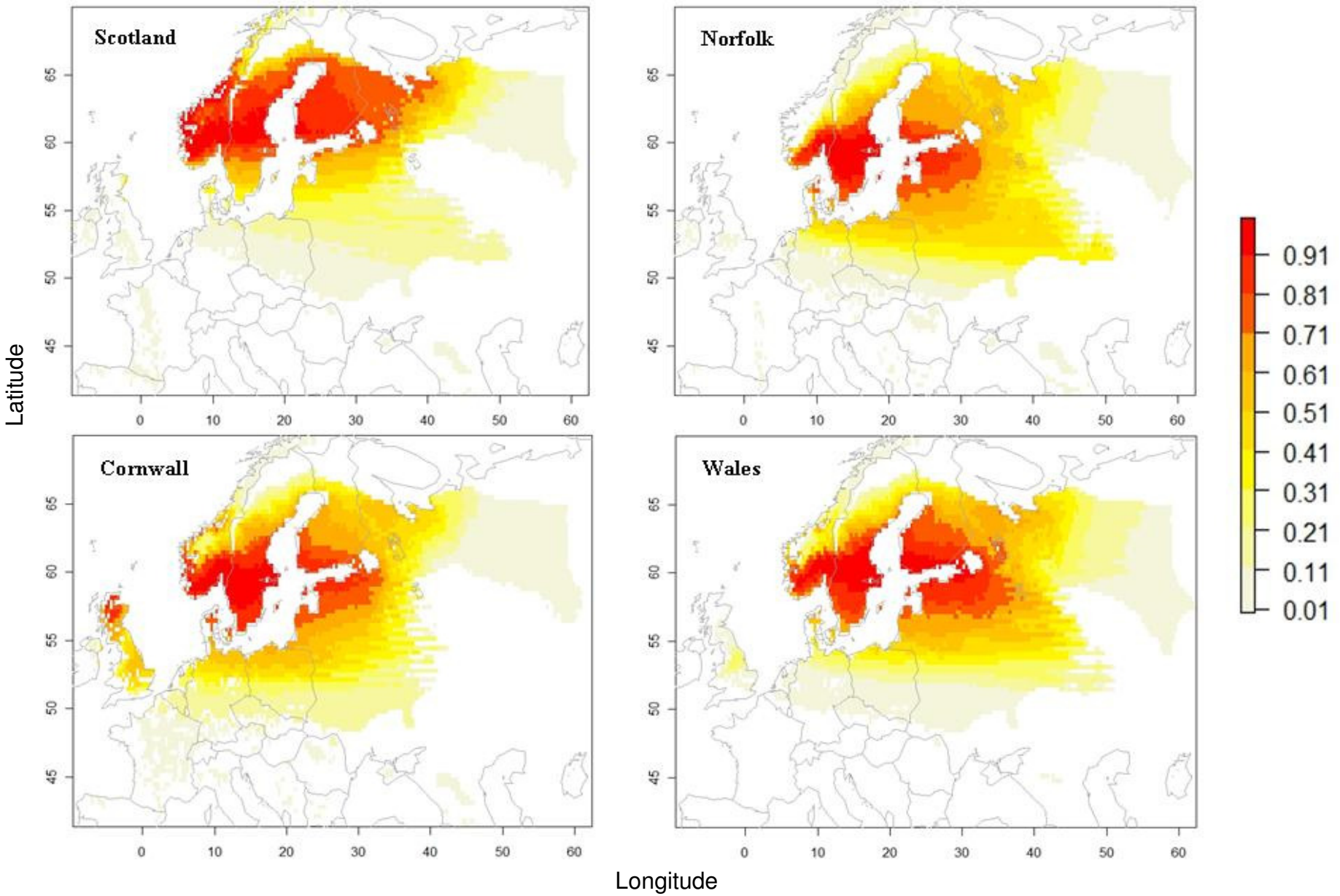


Figure 3.7 Centres of gravity (weighted mean longitudes and latitudes) derived from assignments of predicted origins, for adult and juvenile Eurasian woodcock of unknown breeding origins. These are based on data from birds sampled across six geographic regions within Britain and Ireland, and across combined sampling years (winters: 2004/05, 2008/09, 2009/10, and 2010/11). Sample sizes for adult birds were: Scotland, n = 109; Norfolk, n = 102; Cornwall, n = 98; Wales, n = 109; Hampshire, n = 59; and Ireland, n = 104. Sample sizes for juvenile birds were: Scotland, n = 94; Norfolk, n = 100; Cornwall, n = 116; Wales, n = 82; Hampshire, n = 57; and Ireland, n = 99.


Scotland
Norfolk
Cornwall
Wales
Latitude
Longitude
0.91
0.81
0.71
0.61
0.51
0.41
0.31
0.21
0.11
0.01

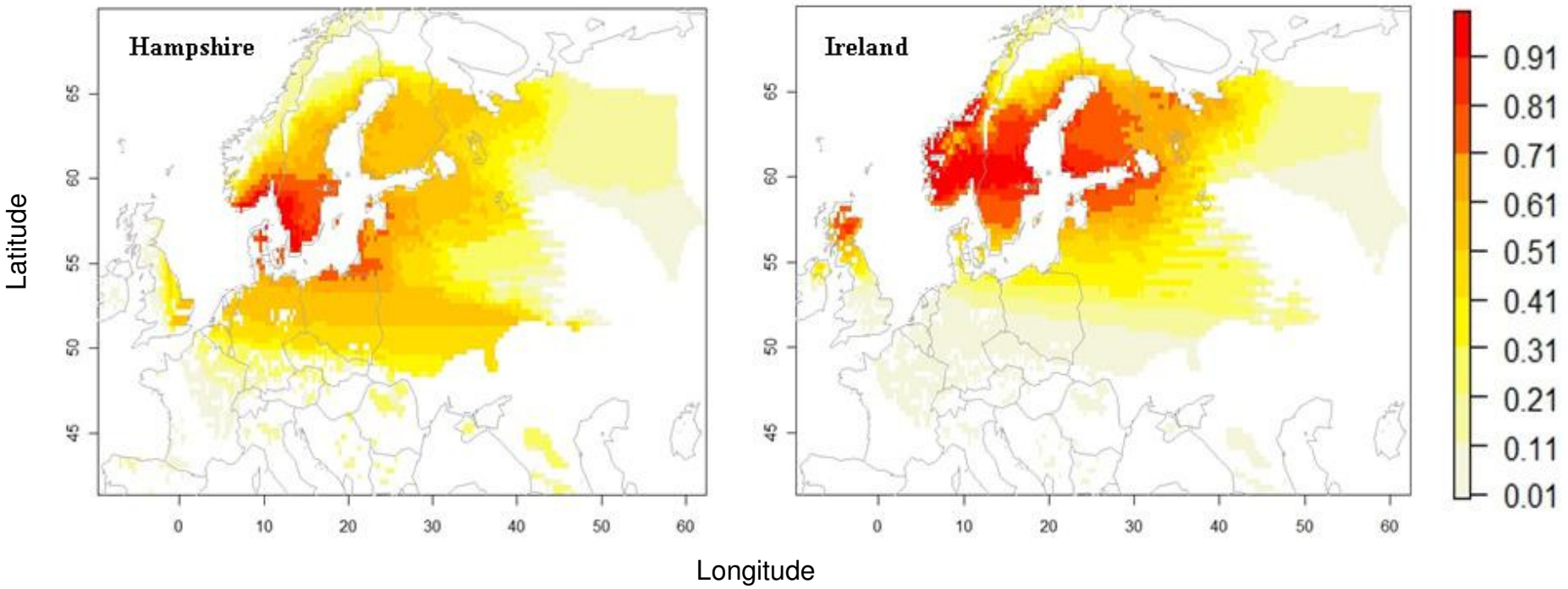
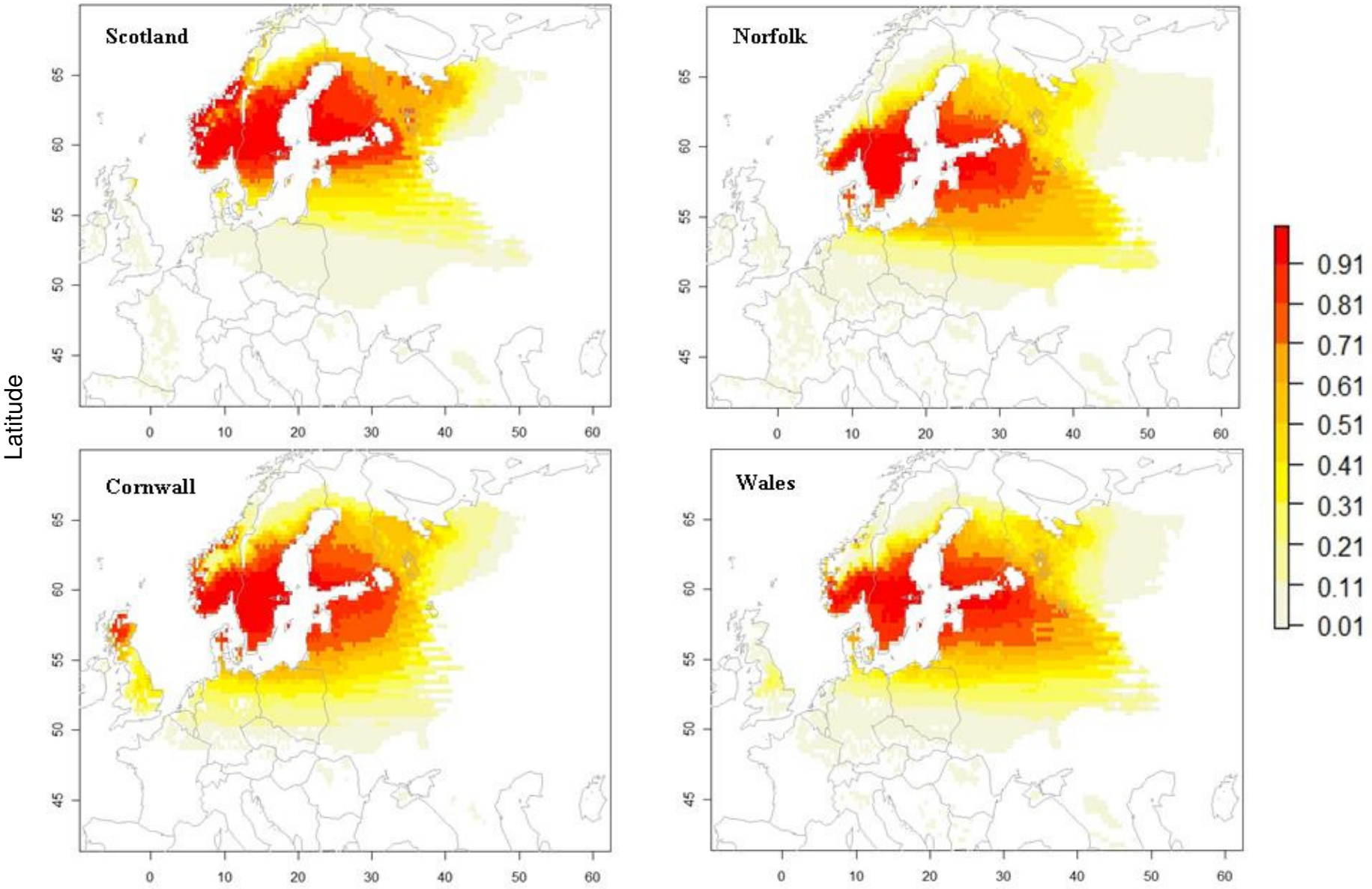


Figure 3.8 Probability distribution maps depicting predicted breeding origins and the likelihood of assignments, for adult Eurasian woodcock of unknown breeding origin, stratified according to sampling region. Probabilities were standardised relative to the maximum number of assignments for ease of interpretation. Maps are based on data from birds sampled in Scotland (n = 109), Norfolk (n = 102), Cornwall (n = 98), Wales (n = 109), Hampshire (n = 59), and Ireland (n = 104). Maps are for combined sampling years (winters: 2004/05, 2008/09, 2009/10, and 2010/11).


Scotland
Norfolk
Cornwall
Wales
Latitude
Longitude
0
10
20
30
40
50
60
45
50
55
60
65
0.91
0.81
0.71
0.61
0.51
0.41
0.31
0.21
0.11
0.01

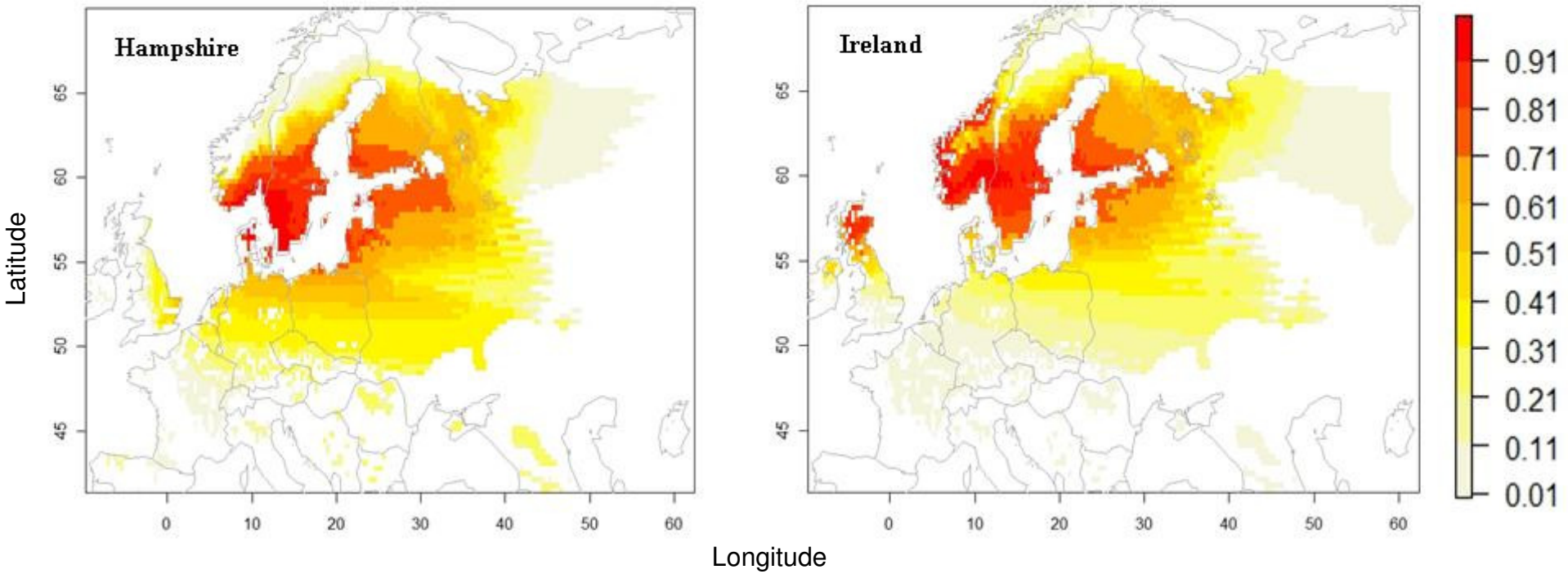


Figure 3.9 Probability distribution maps depicting predicted breeding origins and the likelihood of assignments, for juvenile Eurasian woodcock of unknown breeding origin, stratified according to sampling region. Probabilities were standardised relative to the maximum number of assignments for ease of interpretation. Maps are based on data from birds sampled in Scotland (n = 94), Norfolk (n = 100), Cornwall (n = 116), Wales (n = 82), Hampshire (n = 57), and Ireland (n = 99). Maps are for combined sampling years (winters: 2004/05, 2008/09, 2009/10, and 2010/11).

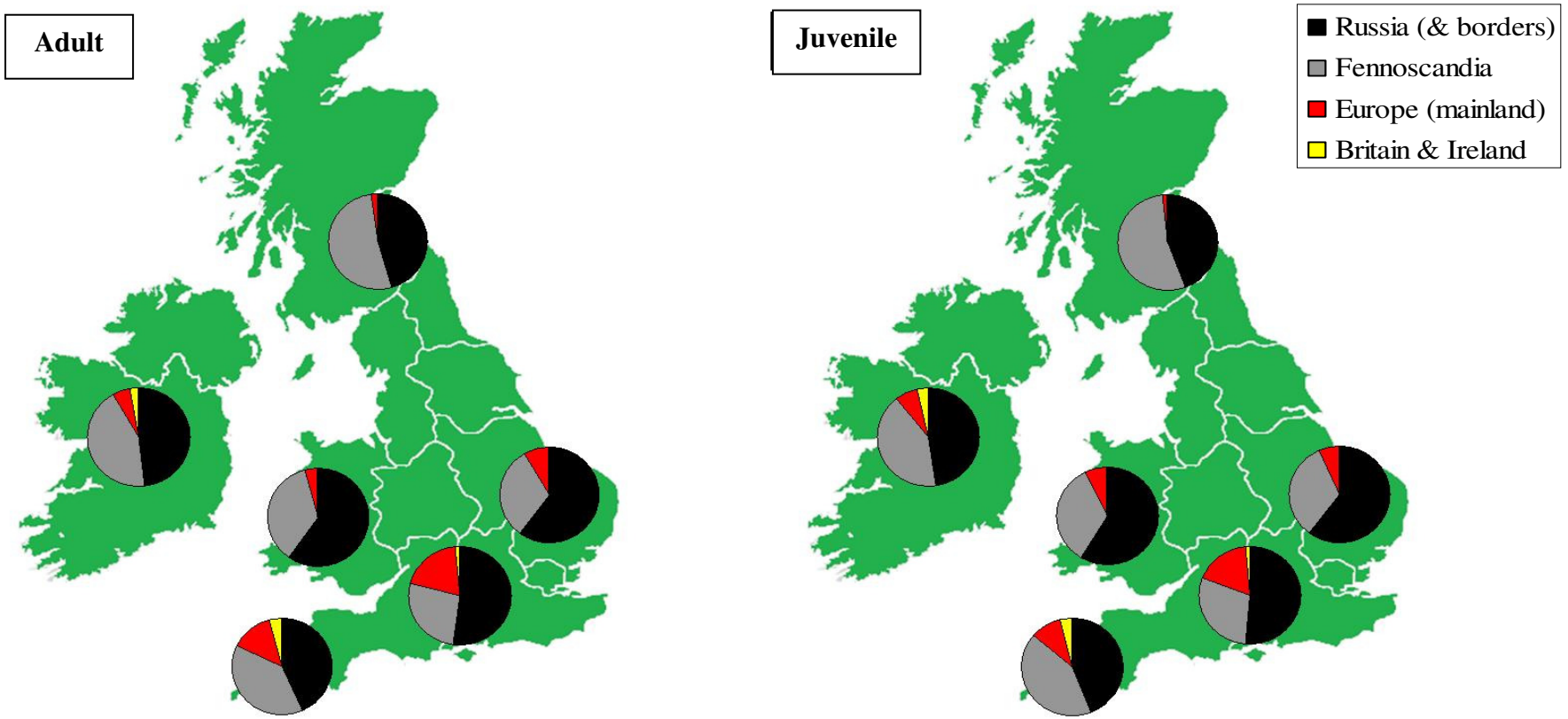
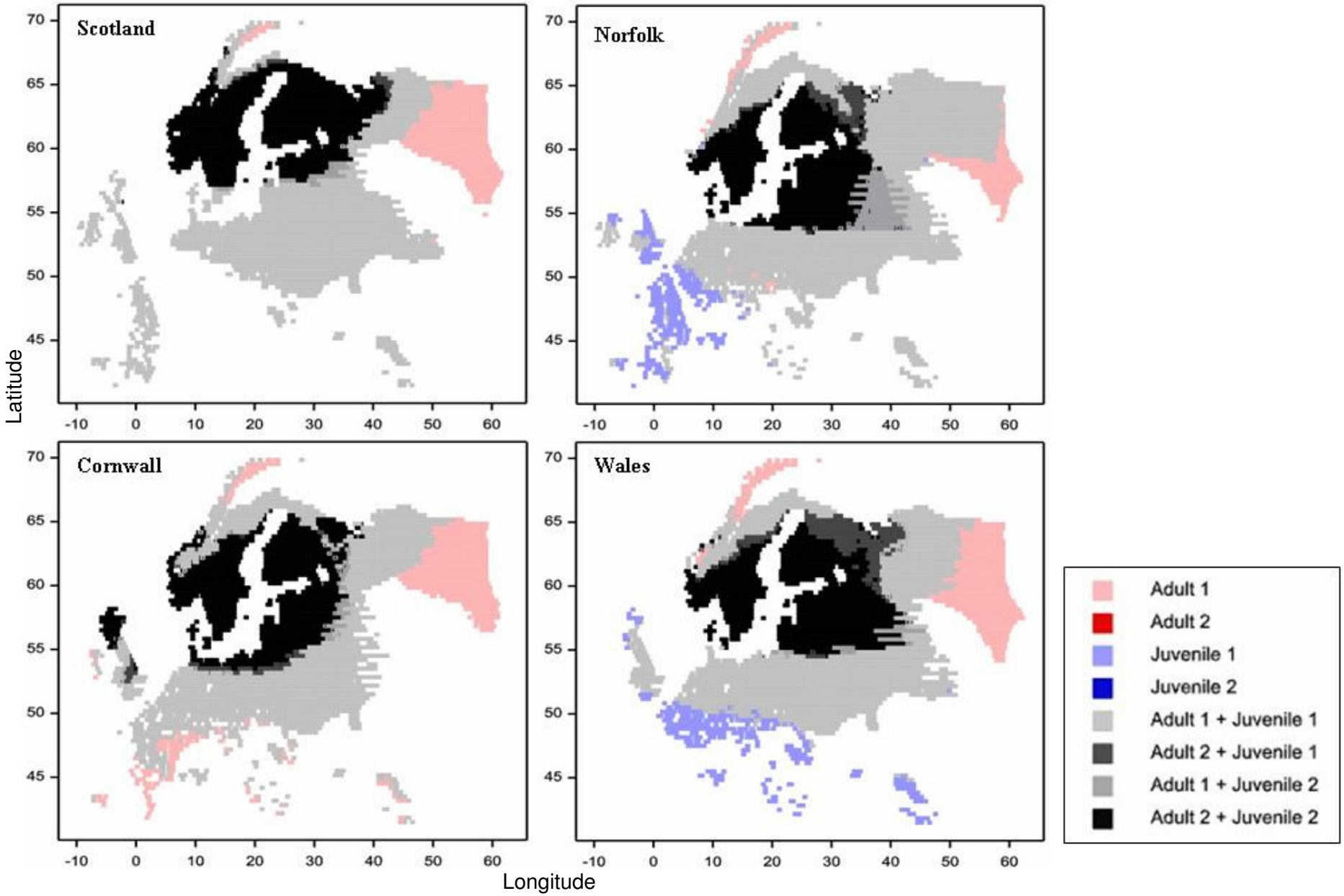


Figure 3.10 Pie charts depicting the proportions of likelihood assignments allocated to each of four predicted breeding areas, for adult and juvenile Eurasian woodcock of unknown breeding origins. Plots are based on data from birds sampled in six geographic regions within Britain and Ireland, across combined sampling years (winters: 2004/05, 2008/09, 2009/10, and 2010/11). Assignments were considered at the level of the entire probability distribution (i.e. 1-100%). Sample sizes for adults were: Scotland, n = 109; Norfolk, n = 102; Cornwall, n = 98; Wales, n = 109; Hampshire, n = 59; and Ireland, n = 104. Sample sizes for juveniles were: Scotland, n = 94; Norfolk, n = 100; Cornwall, n = 116; Wales, n = 82; Hampshire, n = 57; and Ireland, n = 99. Potential breeding areas (areas of assignment) comprise the following countries: Russia (& borders) = Azerbaijan, Belarus, Estonia, Georgia, Kazakhstan, Latvia, Lithuania, Russia, and Ukraine; Fennoscandia = Finland, Norway, and Sweden; Europe (mainland) = Andorra, Austria, Belgium, Bosnia and Herzegovina, Bulgaria, Czech Republic, Denmark, France, Germany, Hungary, Italy, Luxembourg, Netherlands, Poland, Romania, Serbia, Montenegro, Slovakia, Spain, and Switzerland; and Britain & Ireland = England, Scotland, Wales, and Ireland.

Table 3.4 Proportions of likelihood assignments allocated to Britain and Ireland (latter in parentheses), for adult and juvenile Eurasian woodcock of unknown breeding origins. Proportions are considered at different levels of the probability distribution, and are stratified according to sampling region. Data are for combined sampling years (winters: 2004/05, 2008/09, 2009/10, and 2010/11). Sample sizes for adults were: Scotland, n = 109; Norfolk, n = 102; Cornwall, n = 98; Wales, n = 109; Hampshire, n = 59; and Ireland, n = 104. Sample sizes for juveniles were: Scotland, n = 94; Norfolk, n = 100; Cornwall, n = 116; Wales, n = 82; Hampshire, n = 57; and Ireland, n = 99.

	Assignments (%)							
	1-100%		**25-100%**		**50-100%**		**75-100%**	
Region	**Adult**	**Juvenile**	**Adult**	**Juvenile**	**Adult**	**Juvenile**	**Adult**	**Juvenile**
Scotland	0.21 (0.03)	0.18 (0.02)	0.08	0.08	0.04	0.04	0.00	0.00
Norfolk	0.03 (0.02)	0.05 (0.01)	0.00	0.00	0.00	0.00	0.00	0.00
Cornwall	4.28 (0.03)	3.85 (0.01)	4.88	4.05	4.33	3.17	3.15	2.73
Wales	0.49	0.82	0.01	0.29	0.00	0.00	0.00	0.00
Hampshire	1.44 (0.02)	1.28 (0.03)	1.39	1.15	0.82	0.20	0.00	0.00
Ireland	2.75 (0.06)	3.33 (0.08)	2.89 (0.03)	3.53 (0.05)	2.95	3.92	2.50	5.70


Scotland
Norfolk
Cornwall
Wales
Latitude
Longitude
70
65
60
55
50
45
-10
0
10
20
30
40
50
60
Adult 1
Adult 2
Juvenile 1
Juvenile 2
Adult 1 + Juvenile 1
Adult 2 + Juvenile 1
Adult 1 + Juvenile 2
Adult 2 + Juvenile 2

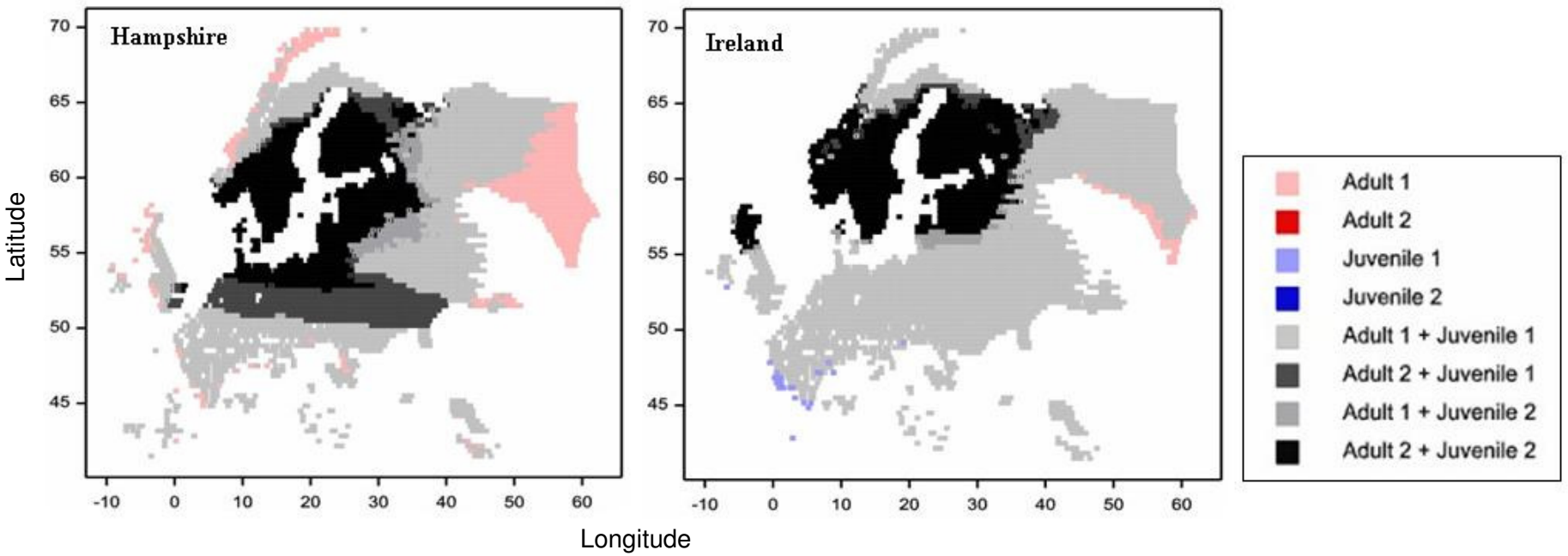


Figure 3.11 Non-overlapping and overlapping likelihood assignments for Eurasian woodcock of unknown breeding origin (adults and juveniles, combined). Plots depict the likelihood of assignment at two levels of the probability distribution; (1) 1-49% and (2) 50-100%. Unique (non-overlapping) cells are depicted in red shades for adults and blue shades for juveniles. Overlapping cells are depicted in grey/black shades. Plots are stratified according to sampling region. Combined samples sizes were: Scotland, n = 203; Norfolk, n = 202; Cornwall, n = 214; Wales, n = 191; Hampshire, n = 116; and Ireland, n = 203. Data are for combined sampling years (winters: 2004/05, 2008/09, 2009/10, and 2010/11).

Table 3.5 Proportions of overlap between predicted breeding distributions of adult and juvenile Eurasian woodcock. Proportions are standardised relative to the maximum number of assigned cells for ease of interpretation. Proportions are stratified according to sampling region. Combined samples sizes were: Scotland, n = 203; Norfolk, n = 202; Cornwall, n = 214; Wales, n = 191; Hampshire, n = 116; and Ireland, n = 203. Data are for combined sampling years (winters: 2004/05, 2008/09, 2009/10, and 2010/11).

	Overlap (%)	
Region	**Adult vs. Juvenile**	**Juvenile vs. Adult**
Scotland	86	100
Norfolk	95	94
Cornwall	85	100
Wales	87	93
Hampshire	88	100
Ireland	99	100

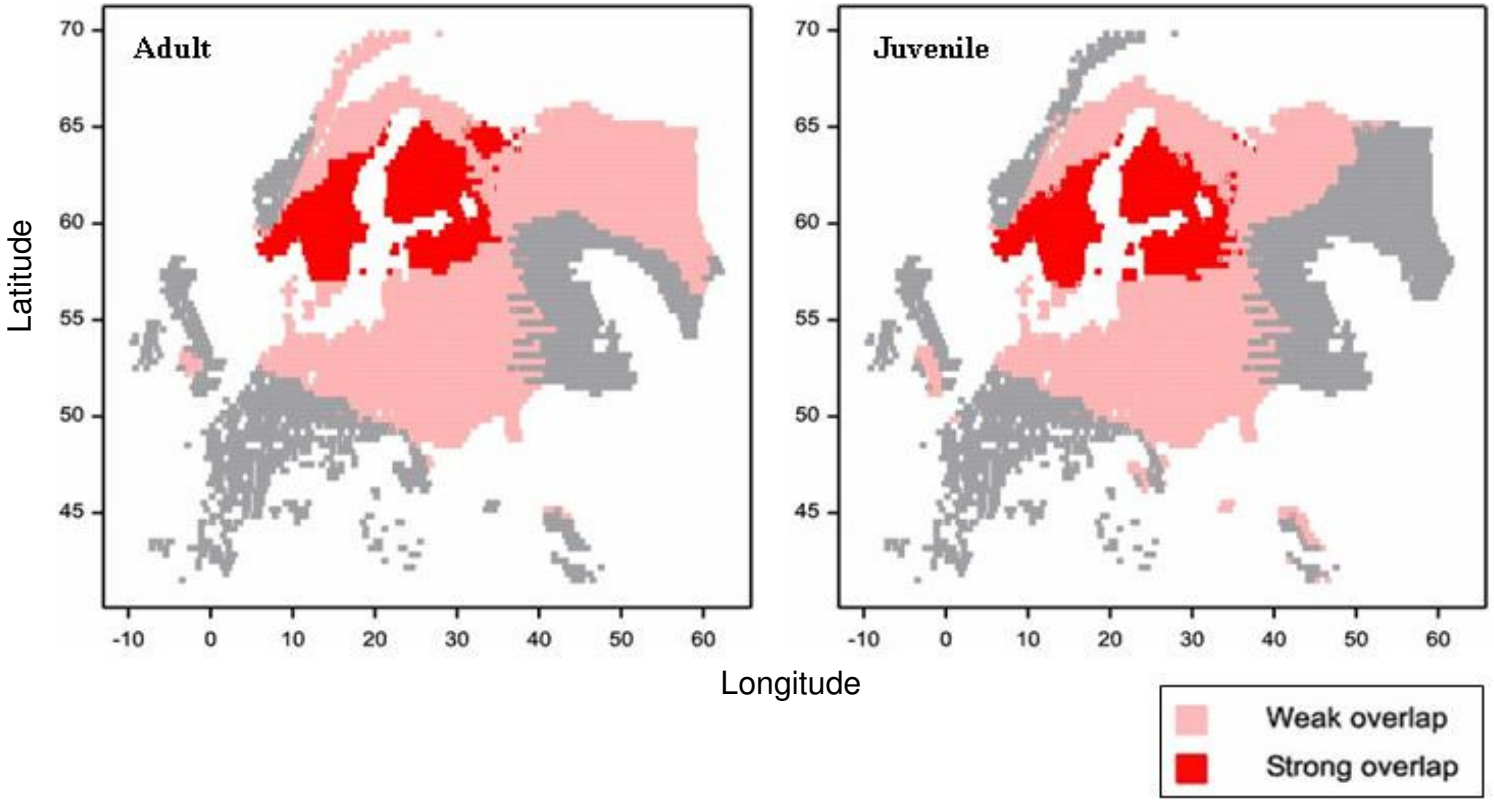


Figure 3.12 Overlapping likelihood assignments for adult (n = 581) and juvenile (n = 548) Eurasian woodcock of unknown breeding origins. Red cells show overlap at 50-100% of the probability distribution. Pink cells show overlap across at various levels of the probability distribution. Grey cells represent a mixture of overlap and non-overlap. Plots are based on data from birds sampled across six combined geographic regions within Britain and Ireland (Scotland, Norfolk, Cornwall, Wales, Hampshire, and Ireland), and across combined sampling years (winters: 2004/05, 2008/09, 2009/10, and 2010/11).

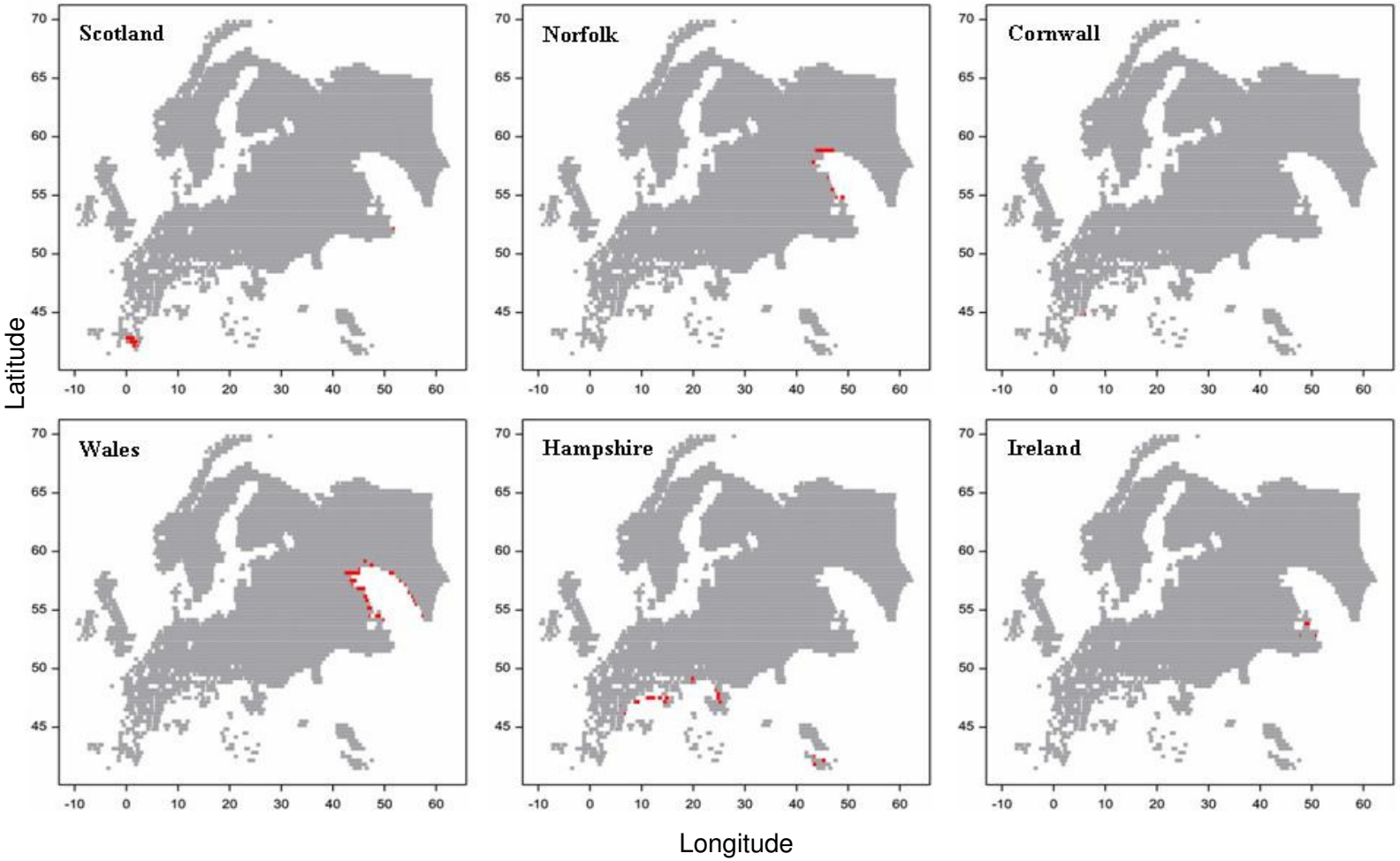


Figure 3.13 Non-overlapping (unique) likelihood assignments (red cells) for adult Eurasian woodcock of unknown breeding origins. All unique cells occurred within 1-49% of the probability distribution. Grey cells represent overlapping cells between two or more sampling regions. Plots are stratified according to sampling region. Samples sizes were: Scotland, n = 109; Norfolk, n = 102; Cornwall, n = 98; Wales, n = 109; Hampshire, n = 59; and Ireland, n = 104. Maps are based on data from combined sampling years (winters: 2004/05, 2008/09, 2009/10, and 2010/11).

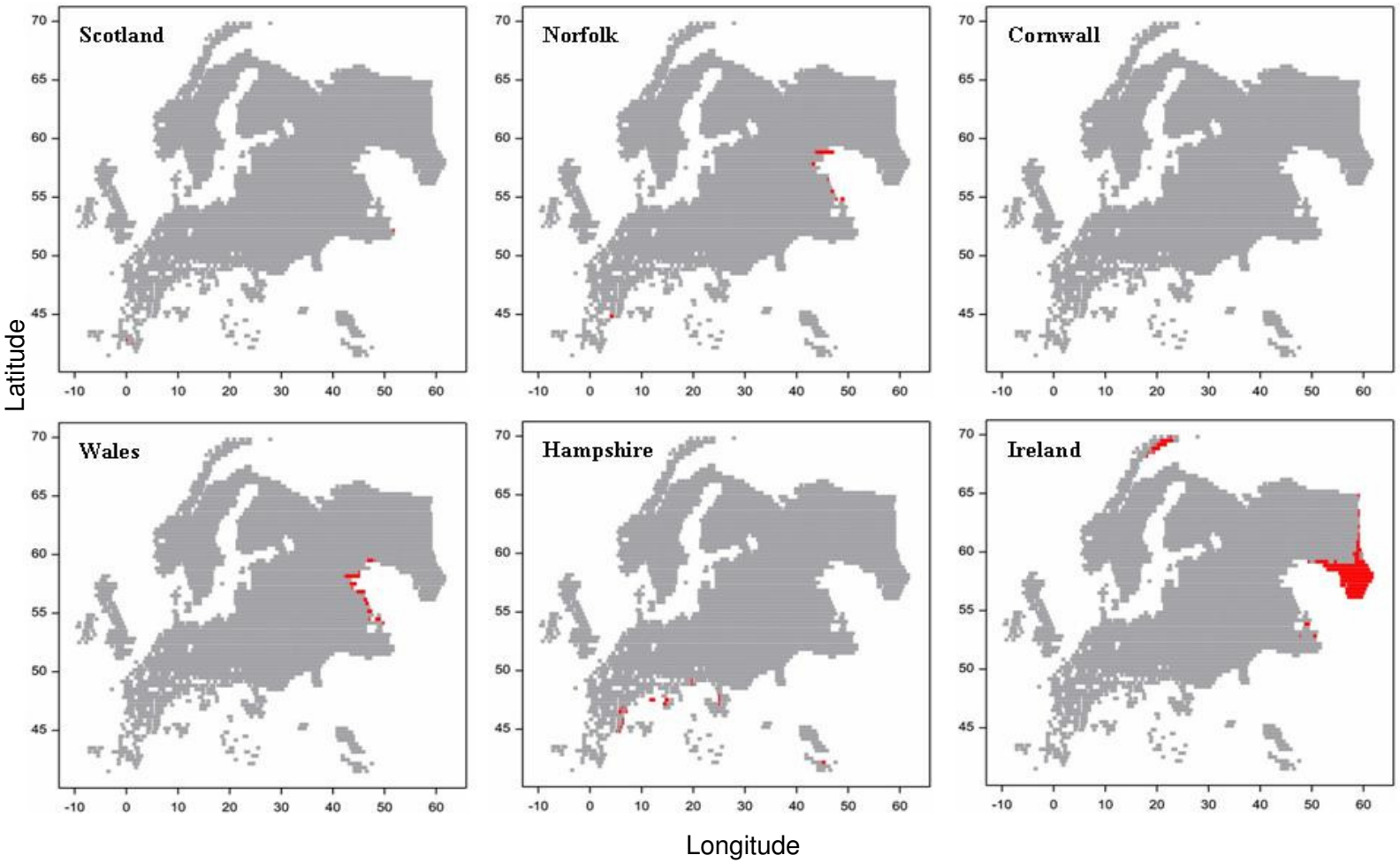


Figure 3.14 Non-overlapping (unique) likelihood assignments (red cells) for juvenile Eurasian woodcock of unknown breeding origins. All unique cells occurred within 1-49% of the probability distribution. Grey cells represent overlapping cells between two or more sampling regions. Plots are stratified according to sampling region. Sample sizes were: Scotland, n = 94; Norfolk, n = 100; Cornwall, n = 116; Wales, n = 82; Hampshire, n = 57; and Ireland, n = 99. Maps are based on data from combined sampling years (winters: 2004/05, 2008/09, 2009/10, and 2010/11).

General Methods II

Radio-tracking

Radio-tracking

The development of radio-tracking technology has aided the study of cryptic and elusive species, such as the Eurasian woodcock *Scolopax rusticola* (hereon woodcock), that are difficult to observe directly (Hirons & Owen 1982). Radio-tracking provides a reliable means of detection, enables the quantification of an animal's movements, and allows behavioural strategies between individuals to be compared (Kenward 2001). For these reasons, a radio-tracking programme was undertaken in Hampshire, to assess the non-breeding ecology of a mixed woodcock population, comprising birds from different breeding origins.

Study area

The study was conducted around Longparish (Hampshire, UK) (latitude: 51.2°N; longitude: -1.4°W), covering an area of c.3 800 hectares and comprising land owned by Middleton Estate, Testbourne Estate, Wherwell Estate and Manor Farm, Newton Stacey. The area was known to have a regionally (Hampshire) breeding (hereon resident) woodcock population, and to receive influxes of migrants (i.e. birds from outside Hampshire), during the non-breeding season (Oct-March) (Andrew Hoodless, pers. comm). The study area comprised field (62%) and woodland (28%) habitats (Figure GMII.1). The principal block of woodland was the Harewood Forest complex (c.311 hectares) located in the north-west half of the study area, but several smaller woods were interspersed throughout, including small copses of wet woodland near the River Test.

Woodcock hunting

The Eurasian woodcock is listed under Schedule 2 Part 1 of the Wildlife and Countryside Act 1981 as a species that can be legally taken from the wild, without a licence, during the open season. In England, this season commences on the 1 October and finishes on 31 January (Wildlife and Countryside Act 1981). Across the study area, woodcock shooting was minimal. On Manor Farm, woodcock were never the target species on shoots; rather, they were incidental quarry taken when shooting pheasant *Phasianus colchicus* and/or red-legged partridge *Alectoris rufa*. On land owned by Middleton and Wherwell Estates, woodcock shooting was restricted to just one or two species-specific shoot days in January, whilst on Testbourne Estate it was entirely prohibited.

Capture methods and radio-tracking

Woodcock were captured using one of two techniques. First, by lamping (dazzling) birds in fields at night, using a spotlight and landing net. This has become a recognized technique for catching woodcock in the non-breeding season (Gossmann *et al.* 1986) and is generally conducted during the two week period that coincides with a new moon, as the birds tend to be more settled and easier to dazzle around this time (Gossmann *et al.* 1986; Hoodless 1994a,b). The second catching method employed was mist-netting at dawn, using 12 metre mist-nets erected across woodland rides.

Upon capture, birds were fitted with a British Trust for Ornithology (BTO) metal leg ring and aged according to non-breeding season plumage characteristics

(Clausager 1973; Ferrand & Gossmann 2009) (General Methods I). Samples were assigned to one of two age categories: (1) juvenile; defined as either a bird hatched that calendar year, or a bird hatched the previous calendar year but not yet moulted into adult plumage, (2) adult; defined as a bird hatched before the previous calendar year. Tarsus and bill lengths were measured (to the nearest 0.1 mm) with calipers, wing chord was measured (to the nearest mm) using a wing-rule, and body mass was measured (to the nearest gram) using a Pesola spring balance. For each bird, the distal tip of the first (innermost) primary feather was also clipped (using a pair of small surgical scissors) so that its migratory status could be determined using stable isotope analysis (see *Assigning migratory status*).

Lastly, birds were fitted with a radio-transmitter (Biotrack Ltd., Wareham, UK), weighing four, six or 12 grams. Tag weight varied according to the battery size and presence of an activity tilt-switch, but all fell within the recommended range (2–4% of body mass; Kenward 2001). The 12 gram radio-tags were attached to the bird's back between the wings, using Kamar hypoallergenic livestock glue and a single loop wire harness (Duriez 2003). The four and six gram tags were mounted on the synsacrum (Figure GMII.2), using cyanoacrylate adhesive. To minimise any potential negative influences caused by the presence of tags, all were made as inconspicuous and unobtrusive as possible. For instance, both the attachment gauze and the antenna were darkened using a permanent marker, and tags were positioned in such a way to allow the bird's feathers to cover/hide the tag. On average, bird processing/handling time was 20 minutes and birds were released at their place of capture.

After release, each bird was tracked (on foot) three to five times per week, during the day and the night, using a three-element flexible Yagi antenna and SIKA radio-tracking receiver (Biotrack, Wareham, UK). In flat, open country, transmitters had a range of approximately one km. However, the topography of the land meant radio-waves were subject to attenuation (gradual loss of intensity through a medium, such as dense vegetation, and/or increasing distance), reflection ("bounce" off surfaces) and diffraction (bending around small objects and spreading out past small openings) (Cresswell 2000). Given this, birds were tracked within close proximity to ensure an accurate radio-location (commonly referred to as a "fix") was obtained. On average, detection distances were 10 metres in woodland and 20-40 metres in open fields, with care being taken not to disturb or flush birds. When no movement was detected for two consecutive days and/or nights, birds were flushed to check they were still alive. Tags were retrieved in instances where the bird had been predated or the tag had become detached. Birds were tracked throughout the non-breeding season until the tag was shed or the signal was lost (due to battery failure or departure events). In total, 79 birds were tagged across three consecutive winters (2008/09: n = 22, 2009/10: n = 20, 2010/11: n = 37), however, not all of these were included in analyses, owing to a paucity of radio-tracking data. Notably, two individuals were re-caught in succeeding field-seasons and were re-tagged. For details of birds caught and tagged see Tables GMII.1-GMII.3.

Assigning migratory status

Stable isotope data were used to ascertain the predicted migratory status of non-breeding woodcock caught and sampled on the study site. Here, residency was

considered at the regional level, with residents defined as birds from the regional (Hampshire) population and migrants as all non-regional birds (i.e. those from outside Hampshire). For purposes of this work, it was not necessary to determine the specific origins of migrants, and so British birds from outside Hampshire were synonymous with birds from other countries.

It was possible to determine the expected isotope values of feathers grown locally in a specific year, using isotope data from known residents (Tables GMII.1-GMII.3). Notably, the resident status of these birds was confirmed through re-trapping, re-sampling and additional tracking events. Where more than one bird was retrapped in a given year (i.e. 2009), the mean δ^2H_f was used as the 'best' estimate of local δ^2H_f. Since all retraps were adults birds, the expected local δ^2H_f for juveniles was calculated by applying an arithmetic correction of -28.73‰, which was taken from the parameter estimates of the known-source calibration (Chapter 3). Expected δ^2H_f values for local birds (presumed to have grown their feathers within the study area) were as follows: in 2008, adults = -37.2‰, juveniles = -65.9‰; in 2009, adults = -11.5‰, juveniles = -40.2‰; and in 2010, adults = -30.1‰, juveniles = -58.8‰.

The expected δ^2H_f values for locally grown feathers within a given year were used to devise an assignment test that accounted for assignment error (sensu Van Wilgenburg *et al. in press*). For each combination of year and age class, 10 000 data values were simulated from a normal distribution, assuming means as per the expected δ^2H_f values and a standard deviation of 11.76‰ (derived from residuals of the known-source calibration equation, see Chapter 3). Percentiles of these simulated distributions were then estimated to find proportions of the area

under the curve corresponding to a specific odds ratio of being correct versus incorrect (Van Wilgenburg *et al. in press*). Three odds ratios were considered: 2:1 (i.e. 67% of being correct), 3:1 (i.e. 75% of being correct) and 19:1 (i.e. 95% of being correct). For 2:1 odds, the values of the simulated data corresponded to the 0.167 and 0.833 percentiles, for 3:1 odds, these values corresponded to the 0.125 and 0.875 percentiles, and for 19:1 odds they corresponded to the 0.025 and 0.975 percentiles. Finally, observed values of δ^2H_f from radio-tracked birds were compared to the cut-off values determined from the percentiles at the specified odds ratio. If the observed δ^2H_f fell within the percentiles, it was classified as a resident bird (and a migrant otherwise). For example, an adult woodcock would have been considered a resident in 2008 if δ^2H_f fell between -48.4‰ and -26.1‰ at 2:1 odds, between -50.6‰ and -23.8‰ at 3:1 odds, or between -60.5‰ and -13.9‰ at 19:1 odds. Considering all three odds ratios, final assignments were based on 3:1 odds. This seemed an appropriate compromise, given that higher odds were more conservative towards the resident condition. Notably, final assignments were based on results from one-tailed tests; this assumed that birds were not from areas further south of Hampshire, such that enriched values of δ^2H_f were still representative of feathers grown in the local area.

Whilst residents were defined by stable isotope analysis at the regional level, it should be noted that these birds are likely to be local to the study site. British-breeding woodcock are considered to be highly site-faithful throughout the year (Hoodless & Coulson 1994), such that birds do not travel far between their breeding and non-breeding locations. Indeed, in this study, a number of resident-defined birds were tracked into the breeding season and found to remain on the study site, close to their non-breeding locations.

The described methodology was successfully used to assign a predicted migratory status to all birds with a δ^2H_f value. However, in one instance (tag frequency 797) these data were missing, as a feather sample was not collected during the processing procedure. Given that this bird was tracked up until the 24th March, and then recorded as departing the field-site, a migrant status was assigned.

Radio-tracking data

Post-tagging, birds often exhibit chronic short-term effects, such as reduced foraging activity or increased levels of preening (Kenward 2001). This behaviour may be a response to the tag itself, or a latent result of the capture/handling process, but adverse effects usually diminish within a 24-hour period (Broekhuizen *et al.* 1980). Considering this, radio-tracking data collected within the initial 36-hours of a bird's release were excluded from analyses, to allow for a conservative tag adjustment period.

Radio-tracking data were entered into Microsoft Office Excel 2003 (Microsoft Corporation 2003) and then imported into MapInfo Professional version 11.0.3 (Pitney Bowes Software Inc. 2009). A vector-style map of the field-site (Digimap, UK) was also imported into MapInfo Professional version 11.0.3 (Pitney Bowes Software Inc. 2009). These were all set to the same projection (category: British co-ordinate system; category member: British National Grid (EPSG: 27700)).

Tables & Figures

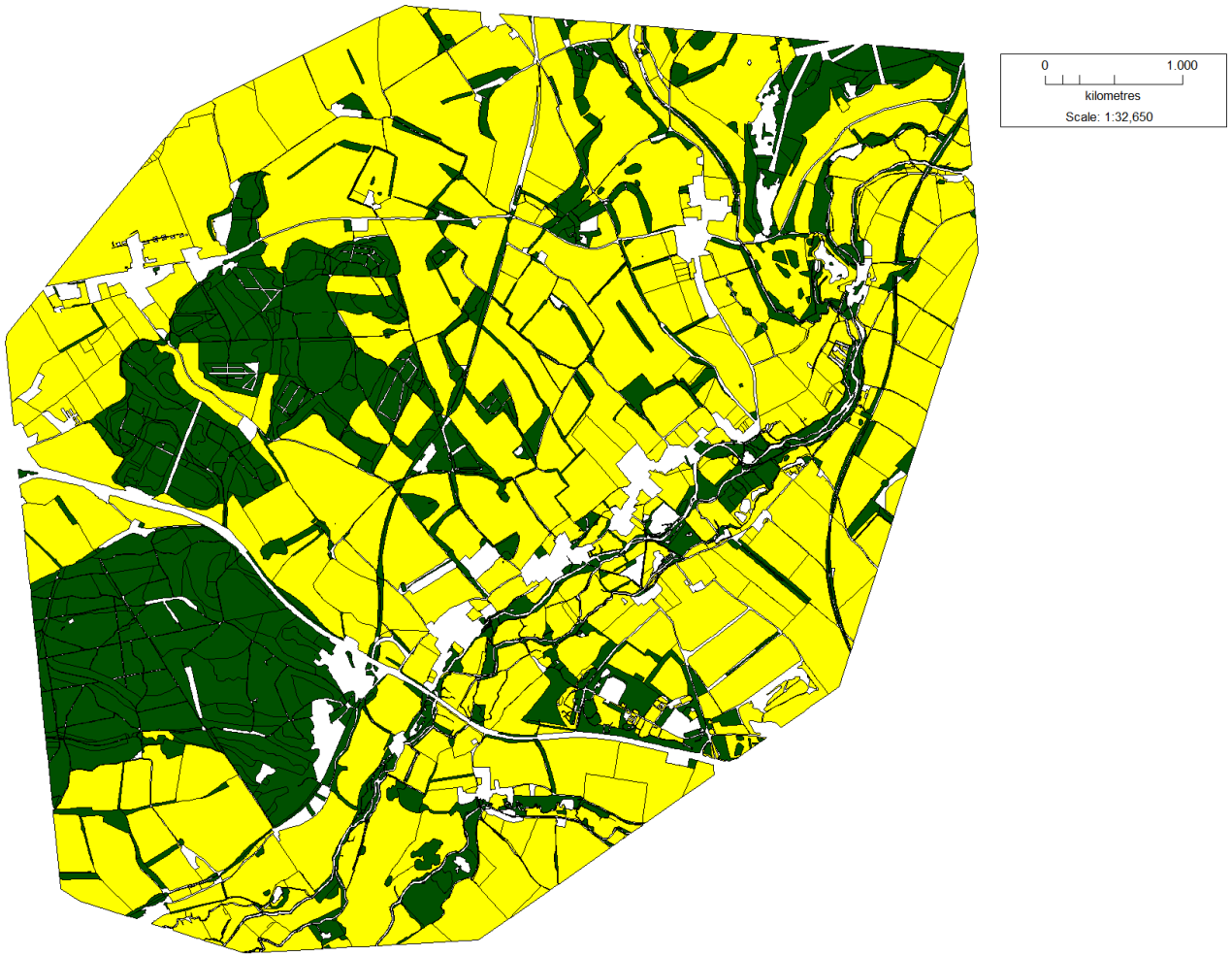


Figure GMII.2 Map of the study area, as defined by a composite Minimum Convex Polygon (MCP), encompassing the combined diurnal and nocturnal fixes of 55 birds, collected over three winters (2008/09, 2009/10, and 2010/11) (total fixes = 4 011). Polygons in yellow represent field habitats, polygons in green represent woodland habitats. White areas represent unsuitable/unavailable habitat e.g. roads, buildings, rivers.



Figure GMII.2 Eurasian woodcock with radio-tag attached to the synsacrum (photograph by Andrew Hoodless).

Table GMII.1 Details of Eurasian woodcock radio-tracked in Hampshire during the winter of 2008/09. Residents marked with an asterisk (*) indicate those with confirmed status. Twelve gram tags denoted with the letters "AS" indicate those containing an activity tilt-switch. The last encounter date refers to the last date the tag was detected. Total fixes refers to the sum of day and night fixes (excluding those obtained during the tag adjustment period and additional fixes obtained during the 24-hour analysis). Tag status refers to the fate of the tag (bird) at the last encounter. For tags with a "lost" status, tracking did continue after the last encounter date (until mid-April), but remained undetected.

Tagging date	Bird ID (Tag freq)	Migratory status	Tag weight (g)	Bird age	Tracking start date	Last encounter	Total fixes	Tag status
16/12/2008	246	Migrant	12	Juvenile	11/01/2009	26/02/2009	52	Tag shed
22/01/2009	255	Migrant	12	Adult	23/01/2009	16/03/2009	50	Lost
21/11/2008	265	Resident*	12	Adult	23/11/2008	27/03/2009	94	Active
23/12/2008	285	Migrant	12	Juvenile	24/12/2008	27/03/2009	72	Active
05/10/2008	307	Resident	12	Adult	06/10/2008	27/03/2009	104	Active
17/11/2008	317	Migrant	6	Adult	19/11/2008	09/12/2008	10	Predated
12/12/2008	327	Migrant	6	Juvenile	18/12/2008	26/01/2009	10	Tag shed
16/12/2008	336	Migrant	6	Juvenile	18/12/2008	09/03/2009	60	Lost
21/11/2008	346	Resident	6	Adult	23/11/2008	27/03/2009	88	Active
14/01/2009	538	Migrant	12 AS	Adult	16/01/2009	27/03/2009	68	Active
27/11/2008	635	Migrant	12 AS	Adult	28/11/2008	27/03/2009	83	Active
28/02/2009	701	Migrant	6	Juvenile	02/03/2009	16/03/2009	9	Lost
04/12/2008	783	Migrant	6	Adult	05/12/2008	26/03/2009	67	Predated
29/01/2009	797	Migrant	6	Adult	29/01/2009	24/03/2009	50	Lost
16/01/2009	819	Resident	6	Adult	20/01/2009	28/01/2009	10	Tag shed
22/01/2009	847	Migrant	6	Juvenile	22/01/2009	03/03/2009	40	Predated
22/01/2009	897	Resident	6	Juvenile	22/01/2009	06/02/2009	12	Tag shed
09/12/2008	907	Migrant	6	Juvenile	11/12/2008	27/03/2009	79	Active
23/11/2008	917	Migrant	6	Juvenile	25/11/2008	30/01/2009	36	Tag shed
28/02/2009	918	Resident	6	Adult	02/03/2009	27/03/2009	17	Active
28/01/2009	937	Migrant	6	Juvenile	28/01/2009	27/03/2009	55	Predated
22/01/2009	949	Migrant	6	Juvenile	22/01/2009	27/03/2009	65	Active

Table GMII.2 Details of Eurasian woodcock radio-tracked in Hampshire during the winter of 2009/10. Where bird ID is denoted by the letter "R", this refers to a retrap, with the value in parentheses indicating the original tag frequency (refer to GMII.1). Residents marked with an asterisk (*) indicate those with confirmed status. Twelve gram tags denoted with the letters "AS" indicate those containing an activity tilt-switch. The last encounter date refers to the last date the tag was detected. Total fixes refers to the sum of day and night fixes (excluding those obtained during the tag adjustment period and additional fixes obtained during the 24-hour analysis). Tag status refers to the fate of the tag (bird) at the last encounter. For tags with a "lost" status, tracking did continue after the last encounter date (until mid-April), but remained undetected.

Tagging date	Bird ID (Tag freq)	Migratory status	Tag weight (g)	Bird age	Tracking start date	Last encounter	Total fixes	Tag status
14/12/2009	35	-	6	Juvenile	-	-	-	-
21/01/2010	74	Migrant	6	Adult	22/01/2010	19/03/2010	61	Lost
22/01/2010	108	Migrant	6	Juvenile	22/01/2010	16/02/2010	26	Tag shed
21/01/2010	125	-	6	Adult	-	-	-	-
17/12/2009	149	Migrant	6	Adult	17/12/2009	11/01/2010	3	Lost
12/02/2010	206	Migrant	12	Adult	15/02/2010	07/04/2010	46	Lost
05/12/2009	217	Migrant	12	Adult	07/12/2009	12/03/2010	12	Lost
13/11/2009	236	Migrant	12	Juvenile	16/11/2009	21/12/2009	36	Shot (off study site)
22/01/2010	278	Migrant	12	Adult	22/01/2010	26/03/2010	69	Lost
13/11/2009	297	Resident	12	Adult	16/11/2009	12/01/2010	14	Shot (off study site)
20/10/2009	447	Migrant	12 AS	Juvenile	26/10/2009	05/01/2010	53	Lost
22/01/2010	457	Resident	12 AS	Adult	22/01/2010	02/02/2010	11	Tag shed
08/02/2010	458	Resident	12 AS	Juvenile	09/02/2010	22/03/2010	45	Lost
17/12/2009	477	Migrant	12 AS	Adult	17/12/2009	09/02/2010	44	Predated
14/12/2009	587	Migrant	12 AS	Juvenile	15/12/2009	19/01/2010	22	Tag shed
21/10/2009	665	Resident	12 AS	Adult	26/10/2009	07/04/2010	116	Active
15/02/2010	686	Migrant	12 AS	Adult	16/02/2010	22/03/2010	34	Lost
18/11/2009	808	Resident*	6	Adult	19/11/2009	24/03/2010	89	Lost
19/01/2010	967	Migrant	4	Adult	20/01/2010	01/03/2010	31	Lost
19/11/2009	988R (265)	Resident*	4	Adult	19/11/2009	04/02/2010	62	Lost

Table GMII.3 Details of Eurasian woodcock radio-tracked in Hampshire during the winter of 2010/11. Where bird ID is denoted by the letter "R", this refers to a retrap, with the value in parentheses indicating the original tag frequency (refer to GM11.2). Residents marked with an asterisk (*) indicate those with confirmed status. Twelve gram tags denoted with the letters "AS" indicate those containing an activity tilt-switch. The last encounter date refers to the last date the tag was detected. Total fixes refers to the sum of day and night fixes (excluding those obtained during the tag adjustment period and additional fixes obtained during the 24-hour analysis). Tag status refers to the fate of the tag (bird) at the last encounter. For tags with a "lost" status, tracking did continue after the last encounter date (until mid-April), but remained undetected.

Tagging date	Bird ID (Tag freq)	Migratory status	Tag weight (g)	Bird age	Tracking start date	Last encounter	Total fixes	Tag status
07/01/2011	15	Resident	6	Adult	10/01/2011	01/04/2011	113	Active
05/01/2011	53.6	Migrant	6	Adult	06/01/2011	13/01/2011	12	Lost
11/12/2010	68	Migrant	6	Adult	13/12/2010	05/01/2011	21	Predated
13/01/2011	69	Migrant	6	Juvenile	14/01/2011	17/03/2011	85	Lost
08/12/2010	86	Resident	6	Juvenile	09/12/2010	25/03/2011	128	Lost
08/12/2010	141	Migrant	6	Adult	09/12/2010	25/03/2011	128	Lost
04/02/2011	163.5R (808)	Resident*	6	Adult	07/02/2011	30/03/2011	69	Tag shed
11/12/2010	174	Resident	6	Juvenile	13/12/2010	04/01/2011	17	Tag shed
13/01/2011	175	Resident	6	Juvenile	14/01/2011	25/03/2011	96	Lost
08/01/2011	188	Resident	6	Juvenile	10/01/2011	04/02/2011	40	Lost
17/11/2010	196	Migrant	6	Juvenile	19/11/2010	25/03/2011	151	Lost
12/12/2010	216	Migrant	6	Adult	13/12/2010	01/03/2011	88	Lost
05/02/2011	292	-	6	Juvenile	-	-	-	-
05/02/2011	454	-	6	Adult	-	-	-	-
01/12/2010	476	Migrant	12 AS	Juvenile	03/12/2010	12/01/2011	40	Shot (on study site)
28/01/2011	478	Resident	12 AS	Juvenile	31/01/2011	08/02/2011	14	Tag shed
11/02/2011	479	Migrant	12 AS	Juvenile	14/02/2011	18/03/2011	47	Lost
07/01/2011	537	Migrant	12 AS	Juvenile	10/01/2011	28/03/2011	107	Lost
18/11/2010	567	Resident	12 AS	Juvenile	22/11/2010	01/04/2011	156	Active
07/12/2010	586	Migrant	12 AS	Adult	09/12/2010	30/03/2011	139	Lost

08/01/2011	634	Migrant	12 AS	Juvenile	10/01/2011	11/03/2011	86	Lost
29/11/2010	647	-	12 AS	Juvenile	-	-	-	-
08/12/2010	755	Resident	6	Juvenile	09/12/2010	18/03/2011	117	Lost
03/02/2011	785	-	6	Adult	-	-	-	-
10/02/2011	784.5	Resident	6	Adult	14/02/2011	01/04/2011	62	Active
12/11/2010	816	Migrant	12 AS	Adult	15/11/2010	25/03/2011	164	Tag shed
04/02/2011	824.4	Migrant	12 AS	Adult	07/02/2011	25/03/2011	66	Lost
08/12/2010	848	Resident	6	Juvenile	09/12/2010	18/01/2011	43	Tag shed
28/01/2011	849	Migrant	6	Juvenile	31/01/2011	08/02/2011	14	Tag shed
11/02/2011	848.1	Migrant	6	Juvenile	14/02/2011	18/03/2011	47	Lost
06/11/2010	908	Resident	12 AS	Juvenile	08/11/2010	06/01/2011	45	Tag shed
13/01/2011	909	Migrant	12 AS	Juvenile	14/01/2011	11/02/2011	41	Lost
04/01/2011	916	Migrant	12 AS	Juvenile	06/01/2011	17/03/2011	98	Tag shed
08/01/2011	938.7	Migrant	4	Adult	11/01/2011	22/02/2011	60	Lost
18/11/2010	957	Migrant	12 AS	Adult	22/11/2010	05/01/2011	40	Predated
13/01/2011	958	Migrant	12 AS	Adult	14/01/2011	31/03/2011	103	Lost
12/01/2011	976.5	Migrant	4	Adult	14/01/2011	24/01/2011	13	Lost

Chapter 4

Spatial habitat use of Eurasian woodcock in a British mixed-farming landscape during winter

Spatial habitat use of Eurasian woodcock in a British mixed-farming landscape during winter

Abstract

The distribution of birds across winter habitats can have important consequences for population dynamics through associations with food accessibility and/or availability. For the Eurasian woodcock *Scolopax rusticola* (hereon woodcock), a bird species with uncertain conservation status, understanding spatial habitat use during the winter is therefore of fundamental importance. In this study, habitat selections were determined for woodcock residing in a mixed-farming landscape, during the winter. Wet woodlands were the most frequently used diurnal habitat. At night, woodcock most commonly used grazed permanent pasture, grazed and ungrazed leys, and un-grazed permanent pasture. Since food resources are believed to drive habitat occupancy during this phase of the annual cycle, woodcock habitat selections were considered in relation to earthworm availability and accessibility. Both diurnal and nocturnal habitat use were found to vary across winters. There were no effects of predicted migratory status (resident vs. migrant) on habitat selections. However, age (adult vs. juvenile) was found to have a significant effect at night, with adults showing greater use of grazed permanent pastures, compared to juveniles. These differences might have important consequences for birds at the individual and population level.

Introduction

During the winter, habitats are utilized by birds primarily to access resources needed for self-maintenance and survival, with food being the most likely

resource for which birds compete (Sherry & Holmes 1996; Studds & Marra 2005). Indeed, in their study of ovenbirds *Seiurus aurocapilla*, Brown & Sherry (2006) concluded that food abundance was the most important proximate mechanism driving physical condition outside the breeding season, and represented a primary driver for population limitation. As such, habitat selection, through its association with food resources, may have important consequences for population processes. For instance, birds occupying food-poor sites may be unable to maintain body condition, which results in reduced survival, either directly through starvation or indirectly through increased sensitivity to predation and/or hunting pressure (Tavecchia *et al.* 2002). The survival of individuals may then go on to influence the mortality rates of the population by, for example, density-dependent mechanisms ("buffer effects") (Newton 2004a). Alternatively, birds in poor body condition during the winter may incur carry-over effects, which then go on to affect population processes (Gill *et al.* 2001; Hobson & Norris 2008). These are seasonal interactions that occur when ecological factors, such as poor habitat quality, limit individual condition in one part of the annual cycle, and thereby alter the timing or capacity of an individual to migrate, reproduce, or survive at a subsequent stage (Norris 2005; Studds & Marra 2005).

The Eurasian woodcock *Scolopax rusticola* (hereon woodcock) is a bird of uncertain conservation status; evidence for declines in abundance on both the breeding and non-breeding grounds are debated (Fadat 1994; Tucker & Heath 1994; Hagemeijer & Blair 1997; Ferrand & Gossmann 2000; Heath *et al.* 2000). Whilst concerns for this species sustainability have focussed primarily on the impacts of hunting, little consideration has been given to ecological issues. Since events during the winter are believed to contribute to the decline of many

migratory bird species (Rappole & McDonald 1994; Sherry & Holmes 1996; Rappole *et al.* 2003; Keller & Yahner 2006), it is important to improve our understanding of the movements and behaviour of woodcock during this period. As established, habitat occupancy during the winter can have important consequences for birds, and these are likely to be exacerbated as natural habitats continue to be changed and developed (Dolman & Sutherland 1995). Therefore, determining the spatial habitat use of woodcock during the winter is important in estimating woodcock habitat needs and the likely impact of habitat changes.

Woodcock are known to exhibit differential patterns of habitat use during the winter, typically occupying woodlands and hedges by day, then flying out to fields at night (Cramp & Simmons 1983; Hirons & Bickford-Smith 1983; Wilson 1983; Gossmann *et al.* 1986; Granval & Bouche 1993). However, more detailed information on woodcock habitat use has proved difficult to obtain, owing to the cryptic plumage and elusive nature of this species. Previous attempts have relied on pointing dogs, bag statistics (Imbert 1988), or habitats documented during ringing events (Ferrand & Gossmann 1986; Granval & Bouche 1993). Unfortunately, the data collected using such methods tend to be of limited use, as biases are often introduced by the behaviours of the dog, the hunter, or the ringer. The development of radio-tracking technology, however, has provided a more reliable means of collecting location data. This method enables rigorous and detailed information to be collected, whilst avoiding human biases (Kenward 2001). It provides a reliable means of detection and can assist in identifying key habitat types used by a species (Kenward 2001). Furthermore, it allows comparisons to be made between individuals. Although it is costly, labour intensive and it is not (usually) possible to compare data with untagged controls

(Kenward 2001), radio-tagging is often the only realistic option for studying species, such as the woodcock, that would otherwise be difficult to observe (Hirons & Owen 1982).

In Britain and Ireland, only three small-scale studies focussing on the habitat selections of woodcock during winter have been carried out to date. These were based on just three (Wilson 1983), five (Hirons & Bickford-Smith 1983) and 13 (Hoodless 1994a) individuals, and all were conducted across largely pastoral landscapes. Contrary to these previous works, this study aimed to determine the habitat use of woodcock residing in a mixed farming landscape during winter, and was carried out on a scale comparable to similar works in France (Duriez *et al.* 2005b).

Non-breeding habitat selections often reveal patterns of segregation between groups of individuals. For instance, sex biases are commonly reported in forest systems (Marra *et al.* 1998; Murphy *et al.* 2001; Norris *et al.* 2005), with a trend towards males dominating high-quality forest, whilst females and subordinates are competitively excluded and forced to occupy suboptimal habitats (Gosler 1987; Marra & Holmes 2001; Bearhop *et al.* 2004; Catry *et al.* 2004). It is important to consider patterns indicative of non-breeding habitat segregation, as this could act as a key limiting factor, posing a threat to individual survival and also suggesting a mechanism (a "buffer effect") by which density-dependent effects could regulate populations (Newton 2004a). The habitat selections of woodcock were therefore considered in relation to bird age and predicted migratory status (hereon status).

Across much of Britain, woodcock populations during the winter comprise British breeding and non-British breeding birds. Discerning ecological differences between these two groups, however, has proved difficult, since they are morphologically indistinguishable (Clausager 1973; Rochford & Wilson 1982; Ferrand & Gossmann 2009). Whilst early work suggested that variation in plumage coloration was an indicator of origin, with the "reds" believed to represent resident birds and the "greys" migrants (Seigne 1930; Bartholomew 1931), it is now accepted that such colour aberrations are merely a product of individual variation (Stronach *et al.* 1974; Kalchreuter 1983). Other morphological characteristics (Clausager 1973; Rochford & Wilson 1982; Ferrand & Gossmann 2009) have also, so far, failed to distinguish birds from different breeding populations. Fortunately, the development of genetic and biogeochemical techniques now offers a means of obtaining this information (Clegg *et al.* 2003; Kelly *et al.* 2005; Smith *et al.* 2005; Boulet *et al.* 2006).

In this study, woodcock considered to be Hampshire breeders (hereon residents) were distinguished from those breeding outside of Hampshire (hereon migrants), using the discriminatory ability provided by stable isotopes (General Method II). Used in this way, the stable isotope approach enabled differential winter habitat use across individuals to be assessed in terms of status.

Since comparisons between woodcock of different migratory status have never been made before, this work provides a unique insight into the behaviours of these two groups, and might have important conservation consequences for both (McGregor & Peake 1998; Kenward 2001). If resident-defined birds are indeed considered to be local to the study area (General Method II), then they might be

expected to have fitness advantages and increased survival, relative to migrants. This is because local birds are more likely to be familiar with the area, and therefore able to use their experience and spatial knowledge to optimise their exploitation of food-rich patches. As a consequence, residents may be able to satisfy their daily energy requirements more efficiently than their migratory counterparts, which lack familiarity with the site. For similar reasoning, differential habitat use between adults and juveniles was also explored, as knowledge pertaining to optimal habitat types may be improved with age and experience.

Woodcock habitat selections were determined using compositional analysis. This is deemed the most appropriate technique for analysing habitat use (Aebischer *et al.* 1993), as alternative approaches (reviewed by White & Garrott 1990) suffer from at least one of four shortcomings: inappropriate levels of sampling and sampling size, non-independence of habitat proportions, differential habitat use by groups of individuals, and arbitrary definitions of habitat availability (Aebischer *et al.* 1993). The habitat-analysis approach used here was based on the log-ratio analysis of compositions. This enabled habitats to be ranked according to relative use, and for significant between-rank differences to be located (Aitchison 1986; Aebischer *et al.* 1993).

Aims

The aim of this chapter was to determine the diurnal and nocturnal habitat selections of a woodcock population residing in a mixed farming landscape, in winter. The habitat selections of individuals were considered in relation to bird

age (adult vs. juvenile) and status (resident vs. migrant), in an attempt to discern differences between groups.

Methods

Study site details, and information pertaining to capture methods, radio-tracking, and the assignment of status can be found in General Methods II.

Habitat mapping

Rather than defining arbitrary study area boundaries, the study area was defined as the composite Minimum Convex Polygon (MCP) encompassing combined diurnal and nocturnal radio-locations (hereon fixes) of woodcock (n = 55), radio-tracked over the three winters of study (2008/09, 2009/10, and 2010/11) (total fixes = 4 011). From this, a base-map of the study area was created in a Geographic Information System (GIS) (MapInfo Professional version 11.0.3, Pitney Bowes Software Inc. 2009). Three fixes for one bird (tag I.D. 336) were omitted because they lay a long distance outside the bird's usual area of activity; if retained, these would have resulted in the addition of a relatively large area of fields not used by any other birds.

Habitat maps detailing the tree and shrub species composition in woodland stands, at the 1:10 000 scale, were obtained from the estates and farms comprising the study area. In addition, details pertaining to crop types and the presence of livestock were obtained for all fields across the study area. Using this information, habitat maps were created as layers in MapInfo Professional version

11.0.3 (Pitney Bowes Software Inc. 2009). Woodland (Figure 4.1) and field (Figures 4.2-4.4) habitat-types were coded in accordance with pre-defined categories (see *Woodland*, *Fields*). Notably, the number of habitat categories was kept to a minimum, as compositional analysis is sensitive to the number of habitats tested (Aebischer *et al.* 1993).

Woodland

Woodland habitats were categorised according to stand-type. Since stand-types did not change over the study period (winters 2008/09, 2009/10, and 2010/11), woodland habitats were assigned the same codes across winters. Woodland habitats were categorised as: 1) wet woodland, characterised by willows *Salix* sp., alders *Alnus glutinosa* and poplars *Populus* sp., and the presence of wetland plants, such as greater tussock sedges *Carex paniculata* and common rushes *Juncus conglomeratus*, 2) coniferous stands, comprising species such as Scots pine *Pinus sylvestris*, Douglas fir *Pseudotsuga menziesii*, and yew *Taxus baccata*, 3) strips, comprising tree belts and/or hedges, spanning a width of 10-40 m, 4) young woodland e.g. common beech *Fagus sylvatica*, sitka spruce *Picea sitchensis*, and Douglas fir, which included trees over young conifer plantations and trees over young mixed plantations, 5) oak (pedunculate *Quercus robur* and sessile *Quercus petraea*) mixed with hazel *Corylus avellana*, 6) oak (pedunculate and sessile) mixed with birch *Betula* sp., and 7) mixed woodland, comprising species such as common ash *Fraxinus excelsior*, maple *Acer* species, and hazel. Harewood forest (spanning Middleton and Wherwell Estates) accounted for the largest block of continuous woodland habitat (311 hectares).

Fields

Fields were categorised according to crop-type. Since crop-types typically change on an annual basis (in accordance with crop rotation schemes), field codes were changed to reflect the crop-types during the winters of 2008/09, 2009/10, and 2010/11. Fields were categorised as: 1) winter-drilled wheat *Triticum* species, barley *Hordeum vulgare*, and rye *Secale cereale*, 2) winter-drilled oilseed rape *Brassica napus*, and beans (of the family Fabaceae/Leguminosae), 3) stubbles (for spring-drilled crops), 4) grazed permanent pasture, 5) un-grazed permanent pasture, 6) grazed leys, and 7) un-grazed leys. A field was characterised as "grazed" if livestock were present, or if there were signs of recent grazing, as indicated by the presence of dung, footprints, and short vegetation. Tall grass and the absence of livestock identified "un-grazed" fields.

Compositional analysis

In compositional analysis, the proportions of habitats used by each individual are compared to the proportions of habitats available. Since woodcock undertake commuting flights, defined as flights performed at twilight between diurnal and nocturnal habitats (Duriez *et al.* 2005d), this results in large areas of unused (yet available) habitat being incorporated into home ranges. As such, analysis of habitat selections on the basis of home ranges was deemed inappropriate for the woodcock. Rather, radio-tracking fixes were considered the most appropriate unit for quantifying each individual's habitat use. Only birds with at least 20 fixes (10 day and 10 night) were included in analyses (adults: n = 26, juveniles: n = 29), with data from re-trapped birds excluded.

Across the three winters, compositional analysis was used to determine the diurnal and nocturnal habitat use of woodcock by comparing the proportions of fixes in each habitat with the availability of habitats in the study area (Aebischer *et al.* 1993) (Figures 4.5-4.10). As day fixes were only found in woodland habitats, results only relate to the seven woodland categories (see *Woodland*). Conversely, night fixes were located in both woodland and field habitats. Since only a small proportion (12%) of night fixes were found in the former, a single generic woodland category was created, representing an amalgamation of the seven woodland categories specified above.

Compositional analysis can result in inflated Type I errors when habitats with small proportional availability and/or 0% use are included in analysis (Bingham & Brennan 2004). To avoid problems associated with the former, a check was made to ensure that none of the habitat categories within the study area were present in very small proportions (i.e. > 2%). Whilst, this was apparent for two field categories, grazed (~1%) and un-grazed leys (~1%), both of these represented temporary grass, and so the problem was easily overcome by amalgamating the two categories. To avoid problems associated with 0% use, null proportions were replaced with a small, non-zero value (Aebischer *et al.* 1993). It has been assumed that the smaller the substitution value the better, with authors arbitrarily using values such as 0.001 (Miller *et al.* 1999), or 0.00001 (Hartke & Hepp 2004), to replace 0% use of habitat categories. However, it has been found that, the smaller the substitution value, the more likely Type I errors (Bingham & Brennan 2004) and misclassifications (Bingham *et al.* 2007) are to occur. Considering this, a substitution value of 0.006 was used in this study. This

represents the mid-point of the range of suitable values suggested by Bingham & Brennan (2004).

Using SYSTAT version 13.1 (SYSTAT Software Inc. 2011), an overall Multivariate Analysis of Variance (MANOVA) was conducted, on log-ratio differences, to test whether habitat use was significantly non-random. As fixes were compared with availability of habitats in the study area, the situation never arose where a habitat was not available to a bird. As such, it was not necessary to conduct randomizations to estimate p-values. Where habitat use was non-random (as indicated by a significant p-value), a ranking matrix was constructed based on the signs of mean log-ratio differences across all birds. The significance of differences between habitats was assessed using t-tests comparing the mean log-ratio differences to zero. The MANOVA was then repeated to test for the effects of winter, bird age, bird status, and all two-way interactions, on woodcock habitat use.

Soil data

In order to assess earthworm biomass, soil samples were collected from fields representing four habitat types: 1) winter-drilled wheat, 2) winter-drilled oilseed rape, 3) stubbles (for spring-drilled crops), and 4) grazed permanent pasture. Three fields of each habitat type were sampled, with five soil samples collected from each of these. Soil samples were also collected from woodlands representing three habitat types: 1) wet woodland, 2) coniferous stands, and 3) oak mixed with hazel. Only one woodland block of each habitat type was sampled, with five soil samples collected from each of these. In all instances, soil samples measured

approximately 19 x 19 x 10 cm and were hand-sorted for earthworms. Worm length was measured (mm) and, where possible, worms were identified to genus. Total wet earthworm biomass per sample (g/m^2) was also calculated.

In addition to the collections of soil samples, soil penetrability (kg) was measured. This was achieved using a 0-20 kg spring-scale penetrometer, inserted to a depth of 10 cm. For each soil sample collected, three penetrometer readings were taken, and from these the mean was calculated.

Statistical Analyses

Soil data were analysed in GenStat version 14.0 (VSN International Ltd. 2011). Appropriate statistical tests were determined by assessing the distribution of the dependent variable. The Shapiro-Wilk test and visual inspection of histogram plots were used to achieve this (Figure A2.1). Where the dependent variable was found to be normally distributed, a parametric test was used, in cases of non-normality, the non-parametric equivalent was used.

Since soil data contained repeated measures, it was necessary to use Generalised Linear Mixed Models (GLMM). These enabled "site" and "sample number" to be incorporated into models as random factors, thereby controlling for repeated measures and avoiding problems associated with pseudo-replication. The appropriateness of specified error distributions and link functions for restricted maximum likelihood methods were determined from the normality of model residuals. The Shapiro-Wilk test and visual inspection of residual composite plots were used to achieve this. Where residuals were found to be normally distributed,

the Gaussian (normal) error distribution and identity link function were specified. In cases of non-normality, appropriate transformations were applied. A 5% level of significance was used in all statistical tests/models.

Earthworm biomass

Data on earthworm biomass were not normally distributed (Shapiro-Wilk: W = 0.8805, $P < 0.001$) but showed a right-skewed distribution. A square root transformation was applied, and, although this did not statistically normalise the data (Shapiro-Wilk: W = 0.9556, $P = 0.010$), it improved the shape of the distribution more so than any other transformation. This transformation enabled a GLMM with normal error distribution and identity link function to be specified. This was used to test for the effects of habitat type on the transformed data. In addition, an Analysis of Variance (ANOVA) test was performed on the transformed data to assess for significant differences between field types (there were insufficient data for an analysis of woodland types). To account for repeated measures of earthworm biomass taken from the same sampling sites (i.e. the same fields within field types), site was incorporated into models as a blocking factor.

Earthworm length

Only earthworms measured in field habitats were included in analyses, owing to a paucity of data obtained from woodland habitats. The restricted data were not normally distributed (Shapiro-Wilk: W = 0.9204, $P < 0.001$) but showed a right-skewed distribution. A square root transformation was applied, and, although

this did not statistically normalise the data (Shapiro-Wilk: W = 0.9823, $P < 0.001$), it provided the best model fit when running a GLMM with normal error distribution and identity link function. This was used to test for the effects of genus and field habitat type on the transformed data.

Soil penetrability

Data on soil penetrability were normally distributed (Shapiro-Wilk: W = 0.9827, $P = 0.395$), allowing a GLMM with normal error distribution and identity link function to be specified. This was used to test for the effects of habitat type on the raw data.

Results

Compositional analysis

Diurnal habitat use

Radio-tagged woodcock used diurnal habitats non-randomly, relative to the availability of woodland habitats ($\Lambda = 0.313$; d.f. = 6, 49; $P < 0.001$). A ranking matrix ranked diurnal habitat use in the order: wet woodland > strips > coniferous stands > oak mixed with hazel > mixed woodland > oak mixed with birch > young woodland, with woodcock showing significantly greater use of wet woodland, compared to all other habitat types (Figure 4.11, Tables 4.1 & 4.2).

Additional analyses revealed a significant effect of winter on diurnal habitat use (Λ = 0.407; d.f. = 12, 94; P < 0.001), as was its interaction with bird age (Λ = 0.265; d.f. = 18, 133; P < 0.001) and status (Λ = 0.211; d.f. = 18, 133; P < 0.001). There were no significant effects of bird age (Λ = 0.888; d.f. = 6, 48; P = 0.428), bird status (Λ = 0.797; d.f. = 6, 48; P = 0.079) or the age-status interaction (Λ = 0.906; d.f. = 6, 48; P = 0.551).

Nocturnal habitat use

Woodcock used nocturnal habitats non-randomly, relative to habitat availability (Λ = 0.333; d.f. = 6, 49; P < 0.001). A ranking matrix ranked nocturnal habitat use in the order: grazed permanent pasture > grazed and un-grazed leys > un-grazed permanent pasture > winter-drilled oilseed rape and beans > stubbles > woodland > winter-drilled wheat, barley, and rye. There were no detectable differences in the use of the three top-ranking habitats, but all were used significantly more than the remaining habitat types (Figure 4.12, Tables 4.3 & 4.4).

Additional analyses revealed a significant effect of bird age on nocturnal habitat use (Λ = 0.749; d.f. = 6, 48; P = 0.025), with adults showing significantly greater use of grazed permanent pasture, compared to juveniles (Figure 4.13). Notably, this was the top-ranking habitat type amongst adults (Table 4.5). However, there were no detectable differences in the use of the remaining habitat types (Table 4.6). There was no significant effect of bird status (Λ = 0.904; d.f. = 6, 48; P = 0.537) or the age-status interaction (Λ = 0.837; d.f. = 6, 48; P = 0.179) on nocturnal habitat preferences. However, there was a significant effect of winter

on nocturnal habitat use (Λ = 0.577; d.f. = 12, 94; P = 0.007), as were its interactions with bird age (Λ = 0.306; d.f. = 15, 132; P = 0.000), and status (Λ = 0.296; d.f. = 15, 132; $P < 0.001$).

Soil data

Earthworm biomass

Considering the entire dataset (woodland and field habitats, combined), earthworm biomass was found to vary significantly with habitat type (GLMM, $F_{6, 8}$ = 6.29, P = 0.010). Fields were shown to support much higher earthworm densities than woodland habitats (Figure 4.14). However, no significant differences in earthworm biomass were found between field types (ANOVA, $F_{3, 8}$ = 0.77, P = 0.544). Mean earthworm biomass (± standard error, SE) for each field type was as follows: winter-drilled wheat, mean = 2.8 g/m^2 (± 0.46 SE); winter-drilled oilseed rape, mean = 2.1 g/m^2 (± 0.51 SE); stubbles, mean = 3.5 g/m^2 (± 0.47 SE); and grazed permanent pasture, mean = 2.5 g/m^2 (± 0.57 SE).

Earthworm length

The lengths of earthworms did not vary significantly with field type (GLMM, $F_{3, 7.3}$ = 1.02, P = 0.439), although they did vary with genus (GLMM, $F_{3, 211.6}$ = 18.44, $P < 0.001$). The sample sizes and mean lengths (± SE) of earthworms for each identified genus were: *Allolobophora*, n = 225, mean = 34 mm (± 0.8 SE); *Aporrectodea*, n = 195, mean = 53 mm (± 1.4 SE); *Lumbricus*, n = 134, mean = 51 mm (± 2.2 SE); and *Octolasion*, n = 4, mean = 55 mm (± 12.0 SE). *Allolobophora*

comprised the largest proportion of earthworms in winter-drilled wheat (51.1%) and winter-drilled oilseed rape fields (58%), *Lumbricus* was the predominant genus in stubbles (42.2%), and *Aporrectodea* was the predominant genus in grazed permanent pasture (59%) (Table 4.7).

Soil penetrability

There was no-significant difference in soil penetrability between habitats (GLMM, $F_{6, 8} = 2.72$, $P = 0.096$). Although statistically non-significant, stubbles and grazed permanent pasture had the least penetrable soils (stubbles: mean = 7.5 kg ± 0.4 SE, grazed permanent pasture: mean = 7.5 kg ± 0.6 SE), whilst winter-drilled wheat fields had more penetrable soils (mean = 4.9 kg ± 0.4 SE). In woodland habitats, the lowest soil penetrability value was obtained in coniferous stands (mean = 8.2 kg ± 0.8 SE), whilst the softest soil was found in wet woodland (mean = 2.9 kg ± 0.8 SE).

Discussion

Compositional analysis revealed that, during the winter, woodcock use habitats in a non-random way, such that certain habitat types were selected over others. Although often used interchangeably, habitat selection and preference are not synonymous. Selection in this context is "the process by which an animal chooses a habitat", whilst preference is "the likelihood that a resource will be chosen if habitats are offered up equally" (Johnson 1980; Manly *et al.* 2002). In this study, habitat selections were ranked on the basis of actual habitat use, and these

rankings potentially reflect the habitat preferences of woodcock during the winter.

The analysis of diurnal habitat selection revealed that wet woodlands were the most commonly used habitat type, with birds showing no detectable differences in use of the remaining habitat types (i.e. coniferous stands, strips, young woodland, oak mixed with hazel, oak mixed with birch, and mixed woodland). Since earthworms comprise the primary prey for woodcock during the winter (Granval 1987), the selection of wet woodlands over other habitat types likely reflects the higher density of earthworms supported by this habitat type (at least, compared to coniferous stands and oak mixed with hazel). Indeed, Duriez *et al.* (2005b) found that the diurnal habitat selection of woodcock residing in Brittany, France, over the winter, was associated with the humus type of the soil, which itself was correlated with earthworm densities. In their study, woodcock showed a preference for mulls humus, which is typically rich in earthworms. Furthermore, the soil in wet woodlands was found to be more penetrable than those in alternative diurnal habitats, which would enable woodcock to better access food resources. Although this result was statistically non-significant, this was probably due to insufficient sampling.

Since woodcock are primarily considered nocturnal feeders in winter (Hirons & Bickford-Smith 1983; Duriez *et al.* 2005b), the accessibility and availability of earthworms at diurnal sites are unlikely to be the primary drivers of diurnal habitat selection. Although woodcock do undertake day-time feeding, this is considered to be supplementary and at a much reduced rate to that at night (Duriez *et al.* 2005c; Chapter 5). Diurnal habitat selection is therefore more likely

to represent the need for shelter from adverse weather conditions and protection from predators. The wet woodlands category used in this study represent habitats of sufficient structural complexity to afford the necessary protection from weather conditions and predators. Similarly, Duriez *et al.* (2005b) found that woodcock typically used diurnal habitats comprising dense shrub strata.

Another factor worth considering with regards diurnal habitat selection is proximity to night-time habitats. In this study, wet woodlands were typically located in close proximity to fields. It is therefore conceivable that birds select diurnal habitats with consideration for their night-time feeding habits. By selecting diurnal sites that are close to nocturnal habitats, birds are able to reduce both energy expenditure and exposure to aerial predators. Furthermore, wet woodlands were located away from the main forest blocks where hunting occurred. Thus, the selection of this habitat type over other woodland areas might represent an avoidance of disturbance. The impacts of hunting disturbance on waterbirds are well documented (Madsen 1995; Madsen & Fox 1995), with evidence suggesting that birds will actively avoid hunting areas (Meltofte 1982; Ebbinge 1991). For example, in western Jutland (Denmark), 90% of ducks were found concentrated on the small proportion (20%) of suitable habitat where shooting was not allowed (Meltofte 1982).

There were no effects of bird age or status on diurnal habitat use. This suggests that selected habitats were being used equally across birds, irrespective of their age and/or status, with no habitat segregation apparent. The lack of differential habitat use during the day also suggests that diurnal habitats were not limiting.

At night, woodcock most commonly used grazed permanent pasture, grazed and ungrazed leys, and un-grazed permanent pasture. These habitats all represent grass fields and were used in equal measure. All remaining habitat types (winter-drilled wheat, barley and rye; winter-drilled oilseed rape and beans; stubbles and woodland) were used to a lesser extent, with no detectable differences between them. Given the importance of earthworms in woodcock ecology (Granval 1987), it is likely that earthworm abundance drives nocturnal habitat selection. Therefore, the selection of grass fields over all remaining habitat types probably reflects their higher quality, with regards earthworm availability and accessibility. Indeed, Duriez *et al.* (2005b) found that woodcock selected meadows over other field types, and correlated habitat selection with earthworm biomass. Although, in this study, no significant differences were found in earthworm biomass between field types, this was probably due to insufficient sampling. Other studies of woodcock, during the winter, have found that birds select grass fields over other habitat types (Hirons & Bickford-Smith 1983; Wilson 1983; Hoodless 1994a). Furthermore, grass fields are considered an important winter habitat type for other wader species, such as northern lapwings *Vanellus vanellus* and European golden plover *Pluvialis apricaria* (Gillings & Fuller 1999; Mason & Macdonald 1999).

Adults showed significantly greater use of grazed permanent pastures, compared to juveniles, whilst there were no detectable differences in use of the remaining habitat-types. This finding appears unique to this study, as Duriez *et al.* (2005b) found no effect of age in their analysis of nocturnal habitat use ($P > 0.3$). Of all the habitats considered here, grazed permanent pastures probably represented the habitat type of highest quality. First, permanent pastures typically support

the highest densities of earthworms, with less in winter cereals and the least in row crops (Edwards & Lofty 1972; Pommeresche & Loes 2009). Indeed, earthworm biomass has been found to be four to five times higher in permanent pastures than in other cultivated fields (Duriez *et al.* 2005b). Permanent pastures also tend to attain a higher biomass of earthworms than do temporary grasslands, since earthworm biomass increases as a function of the time since last ploughing (Pommeresche & Loes 2009). Second, the short swards of grazed permanent pastures are likely to enhance foraging efficiency, through eased mobility, and enable better detection of prey and predators (Ferrand & Gossmann 1995; Whittingham & Evans 2004). Since woodcock predation most commonly occurs at night in fields (Duriez 2003), the latter is perhaps of particular prevalence. Indeed, Duriez *et al.* (2005b) found that woodcock avoided un-grazed meadows more than grazed meadows, and attributed this to the difference in vegetation structure.

The differential habitat use found between age classes might reflect differences in experience. Adults are likely to have acquired knowledge of optimal habitats over time, which can then be exploited to find and utilise such habitats, whilst juveniles lack such experience. Since woodcock obtain food by probing subterraneanlly, they are not able to assess prey visually. However, there may be proximal cues for habitat that birds are able to use. For instance, American woodcock *Scolopax minor* have been shown to use soil colour as an indicator of site quality, which typically correlates with soil conditions that directly influence earthworm abundance (Rabe *et al.* 1983). With age, birds are more likely to be accustomed to such proximal cues, thus placing adults at an advantage over juveniles. Notably, non-breeding habitat segregation is often driven by

dominance-mediated mechanisms (e.g. competitive exclusion) (Marra *et al.* 1998; Murphy *et al.* 2001; Norris *et al.* 2005). However, it was not possible to ascertain this for woodcock; there was no evidence to suggest that juveniles were being competitively excluded from optimal habitats. Whilst it has been suggested that individual woodcock might exhibit territorial defence of food-rich patches (Duriez *et al.* 2005b,d), evidence for such behaviour has yet to be documented.

Both diurnal and nocturnal habitat use were found to vary significantly across winters. Furthermore, conditions during the winter season appeared to influence the habitat selections of birds of different age and status classes, as indicated by their significant interactions. These findings contrast with those obtained by Duriez *et al.* (2005b). In their analyses, year effects on diurnal habitat selection could not be tested for, owing to too small sample sizes, whilst no effect of year was found on nocturnal habitat selection ($P > 0.3$). Here, the differential habitat use found across winters probably reflects temporal (inter-annual) changes in climate, as environmental conditions are known to influence woodcock behaviour (Boos *et al.* 2005; Duriez *et al.* 2005c; Brana *et al.* 2010). In accordance with changes in temperature, the availability and accessibility of earthworms changes (Edwards & Lofty 1972), which in turn is likely to influence woodcock habitat selection (Duriez *et al.* 2005b). Habitat segregation may become apparent at such times (i.e. when conditions are potentially limiting), as fitness advantages are conferred to those that are able to adapt to changing conditions and exploit optimal habitats. For example, Bearhop *et al.* (2004) found that migratory black-throated blue warblers *Dendroica caerulescens* occupying optimal habitats were in better migratory condition than were conspecifics. As a consequence, these birds were more likely to arrive earlier on the breeding grounds, gain access to

the highest-quality territories, and devote more resources to reproduction. Such patterns have also been described in American redstarts *Setophaga ruticilla*. Dominant birds occupying mesic (high-quality) non-breeding sites were found to have higher annual return rates (Marra & Holmes 2001), arrive earlier on breeding grounds (Marra *et al.* 1998), and were in better condition (Marra & Holberton 1998; Studds & Marra 2005). This resulted in improved reproductive success, with early-arriving birds fledging significantly more young than those from more xeric (low-quality) non-breeding habitats (Norris *et al.* 2004).

Implications

Finding suitable non-breeding habitat is clearly important for birds through associations with food availability and body condition (Holmes *et al.* 1989; Strong & Sherry 2000; Johnson & Sherry 2001; Brown & Sherry 2006). Unfortunately, for bird species associated with farming landscapes, suitable habitats are threatened by European-wide changes in agricultural policies and farming practices. These have led to widespread population declines across numerous bird species (Tucker & Heath 1994; Pain & Pienkowski 1997; Chamberlain *et al.* 2000; Donald *et al.* 2001), including little bustards *Tetrax tetrax* (De Juana *et al.* 1993; Goriup 1994) and skylarks *Alauda arvensis* (Chamberlain & Siriwardena 2000).

For woodcock, changes in woodland management and forestry policy are likely to impact the suitability of diurnal habitats. Dense shrub strata are considered to represent important features of diurnal habitats by providing protection from adverse weather conditions and predators (Duriez *et al.* 2005b). Therefore, reductions in the density and height of shrubs, and the removal of brambles, may

negatively impact woodcock, through increased exposure. Woodcock have also been shown to utilise hedges during the day (Duriez *et al.* 2005b), yet this habitat feature is threatened with destruction across much of Europe. For example, in France, there was a 60% loss of hedges between 1966 and 1996 (Schmutz *et al.* 1996). Similarly, in Britain, approximately 50% of hedges were removed between 1947 and 1990 (Barr & Parr 1994). Fortunately, agri-environmental schemes have since been implemented in Britain, which serve to plant and restore these important habitat features (Natural England 1994). Changes in the age and species composition of woodlands may also have a negative effect on bird species (Fuller *et al.* 2007). In Britain, between 1940 and 1990, there was a 199% increase in coniferous woodland, whilst managed coppice declined by 82% (Forestry Commission 2003). Such drastic changes to the woodland landscape may be detrimental to bird species, such as the woodcock, which have specific woodland habitat requirements, particularly during the breeding season (Hoodless & Hirons 2007).

Since woodcock are primarily considered nocturnal feeders (Hirons & Bickford-Smith 1983; Duriez *et al.* 2005a), perhaps the greatest threats to populations are those posed by large-scale agricultural changes that affect the suitability of nocturnal habitats, through associations with food availability. Across Europe, there has been a decrease in the surface area of permanent grazed meadows, which comprise an important nocturnal habitat for woodcock during the winter (see *Results*; Duriez *et al.* 2005b). Indeed, between 1975 and 1995, 12% of natural meadows and pastures disappeared from nine European countries (Poiret 1999). Ploughing, the loss of livestock, and the application of various chemicals have also led to reduced habitat quality, through the impoverishment of soil

macrofauna (Pain & Pienkowski 1997; Robinson & Sutherland 2002). Indeed, agricultural changes have reportedly affected the food availability of 25 declining bird species in Britain (reviewed by Newton 2004b), including the starling *Sturnus vulgaris* (Freeman *et al.* 2002), song thrush *Turdus philomelos* (Peach *et al.* 2004), and northern lapwing *Vanellus vanellus* (Shrubb 2007).

To ensure sustainable management of woodcock populations, it is necessary to protect and manage habitats that incorporate food and cover. Forestry practices should include the preservation of rich soil types that support high earthworm densities, alongside tree species that ameliorate the soil. Woodcock may also benefit from the development of set-asides, grass field margins and simplified farm practices (e.g. minimum tillage and direct sowing) (Duriez *et al.* 2005b).

Acknowledgements

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Tables & Figures

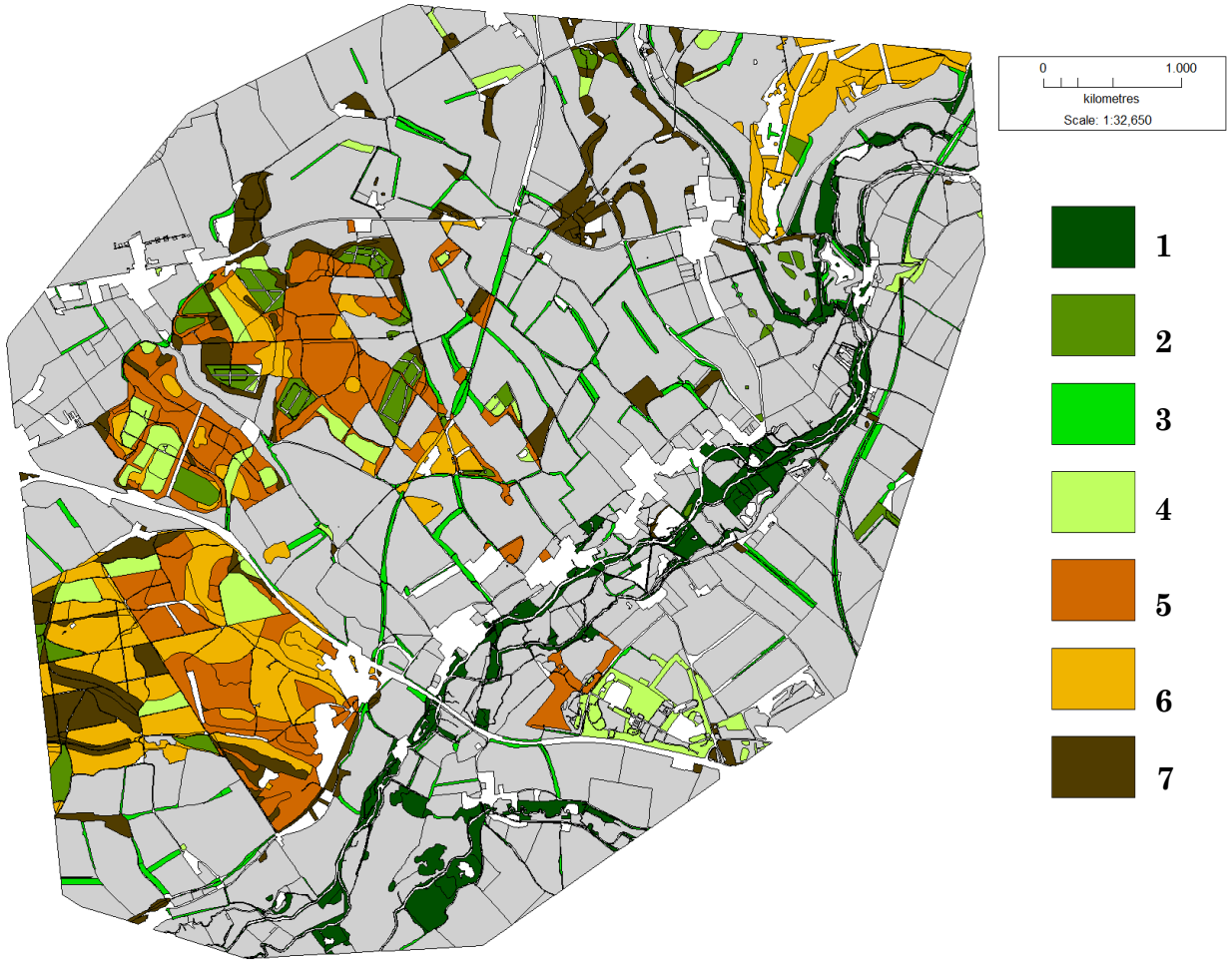


Figure 4.1 Map depicting the woodland categories present across the study area over three winters (2008/09, 2009/10, and 2010/11). Polygons shaded in colour 1 = wet woodland, 2 = coniferous stands, 3 = strips, 4 = young woodland, 5 = oak mixed with hazel, 6 = oak mixed with birch, and 7 = mixed woodland. Grey areas represent fields. White areas represent unsuitable/unavailable habitat e.g. roads, buildings, rivers. The study area was defined by a composite Minimum Convex Polygon (MCP) encompassing the combined diurnal and nocturnal fixes of 55 birds, collected over three winters (2008/09, 2009/10, and 2010/11) (total fixes = 4 011).

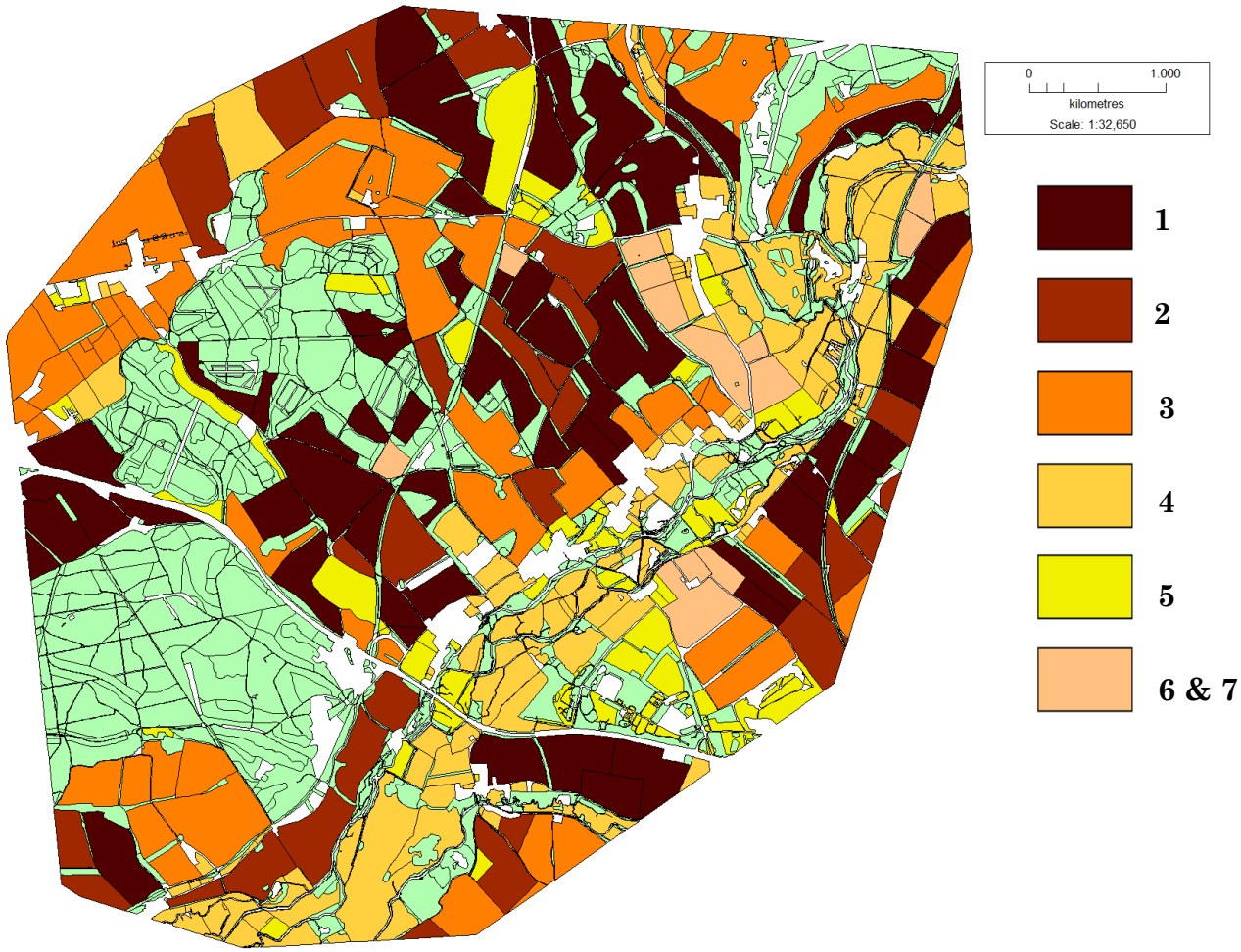


Figure 4.2 Map depicting the field categories present across the study area over the 2008/09 winter. Polygons shaded in colour 1 = winter-drilled wheat, barley and rye, 2 = winter-drilled oilseed rape and beans, 3 = stubbles (for spring-drilled crops), 4 = grazed permanent pasture, 5 = un-grazed permanent pasture, and 6 & 7 = grazed and un-grazed leys. Green areas represent woodlands. White areas represent unsuitable/unavailable habitat e.g. roads, buildings, rivers. The study area was defined by a composite Minimum Convex Polygon (MCP) encompassing the combined diurnal and nocturnal fixes of 55 birds, collected over three winters (2008/09, 2009/10, and 2010/11) (total fixes = 4 011).

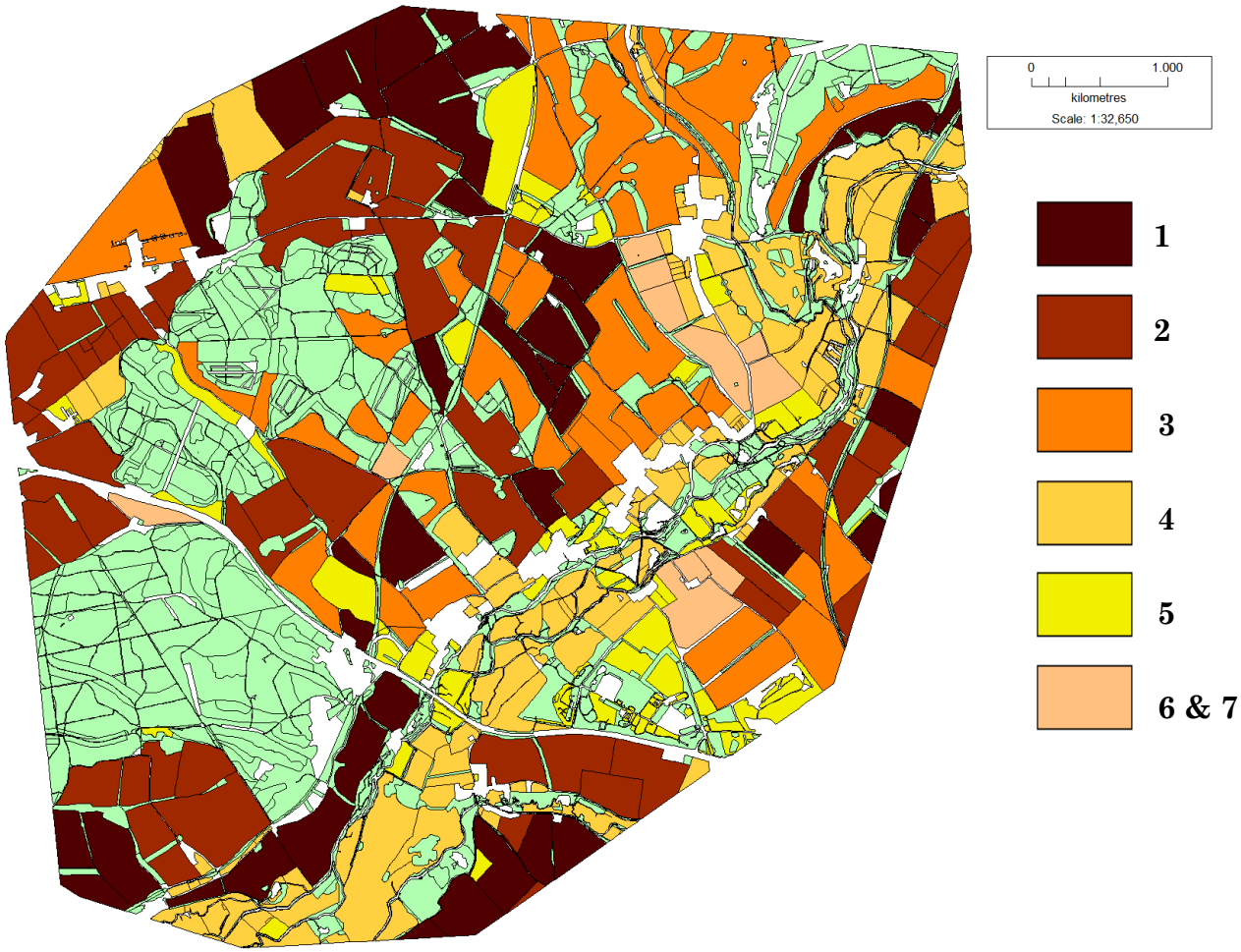


Figure 4.3 Map depicting the field categories present across the study area over the 2009/10 winter. Polygons shaded in colour 1 = winter-drilled wheat, barley and rye, 2 = winter-drilled oilseed rape and beans, 3 = stubbles (for spring-drilled crops), 4 = grazed permanent pasture, 5 = un-grazed permanent pasture, and 6 & 7 = grazed and un-grazed leys. Green areas represent woodlands. White areas represent unsuitable/unavailable habitat e.g. roads, buildings, rivers. The study area was defined by a composite Minimum Convex Polygon (MCP) encompassing the combined diurnal and nocturnal fixes of 55 birds, collected over three winters (2008/09, 2009/10, and 2010/11) (total fixes = 4 011).

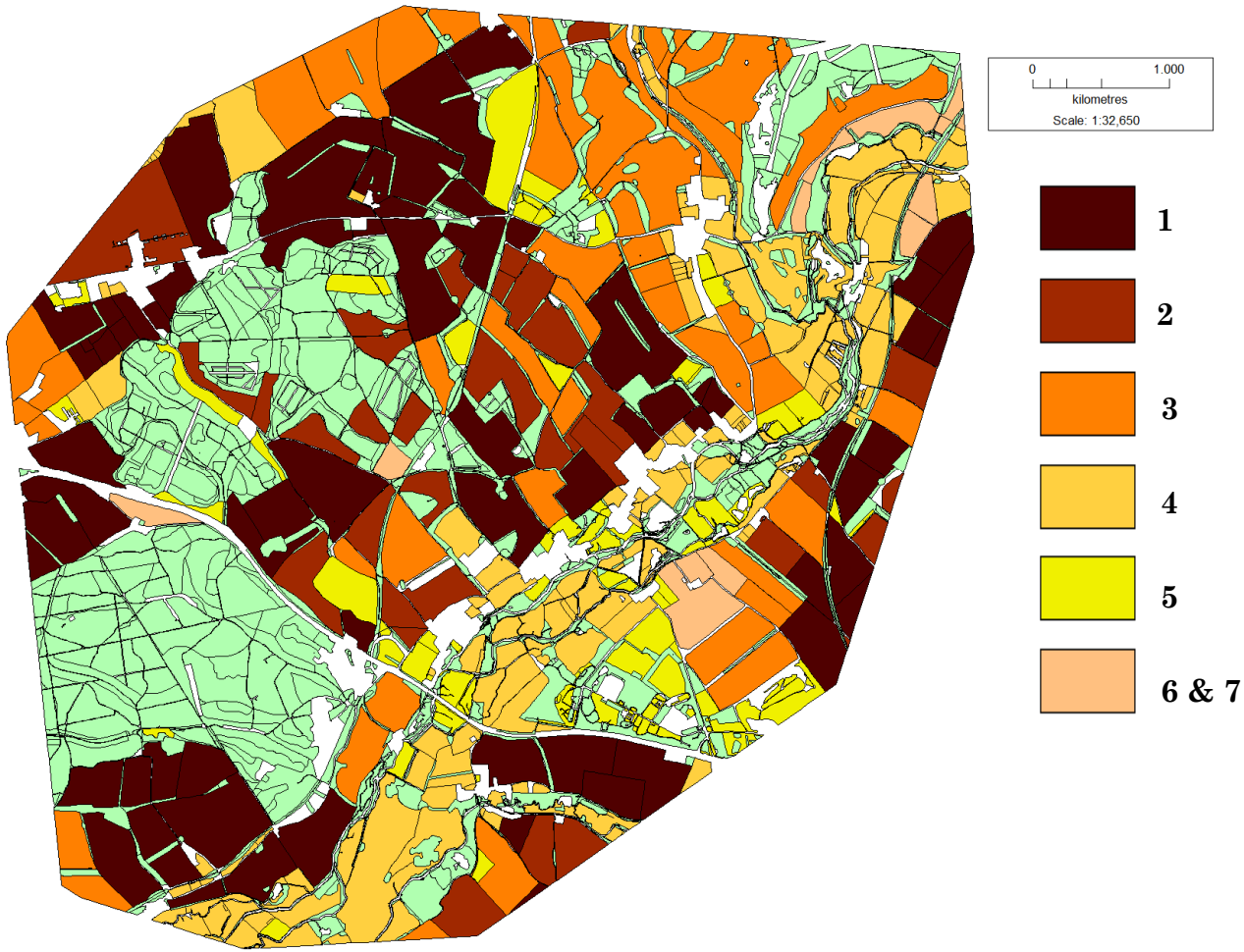


Figure 4.4 Map depicting the field categories present across the study area over the 2010/11 winter. Polygons shaded in colour 1 = winter-drilled wheat, barley and rye, 2 = winter-drilled oilseed rape and beans, 3 = stubbles (for spring-drilled crops), 4 = grazed permanent pasture, 5 = un-grazed permanent pasture, and 6 & 7 = grazed and un-grazed leys. Green areas represent woodlands. White areas represent unsuitable/unavailable habitat e.g. roads, buildings, rivers. The study area was defined by a composite Minimum Convex Polygon (MCP) encompassing the combined diurnal and nocturnal fixes of 55 birds, collected over three winters (2008/09, 2009/10, and 2010/11) (total fixes = 4 011).

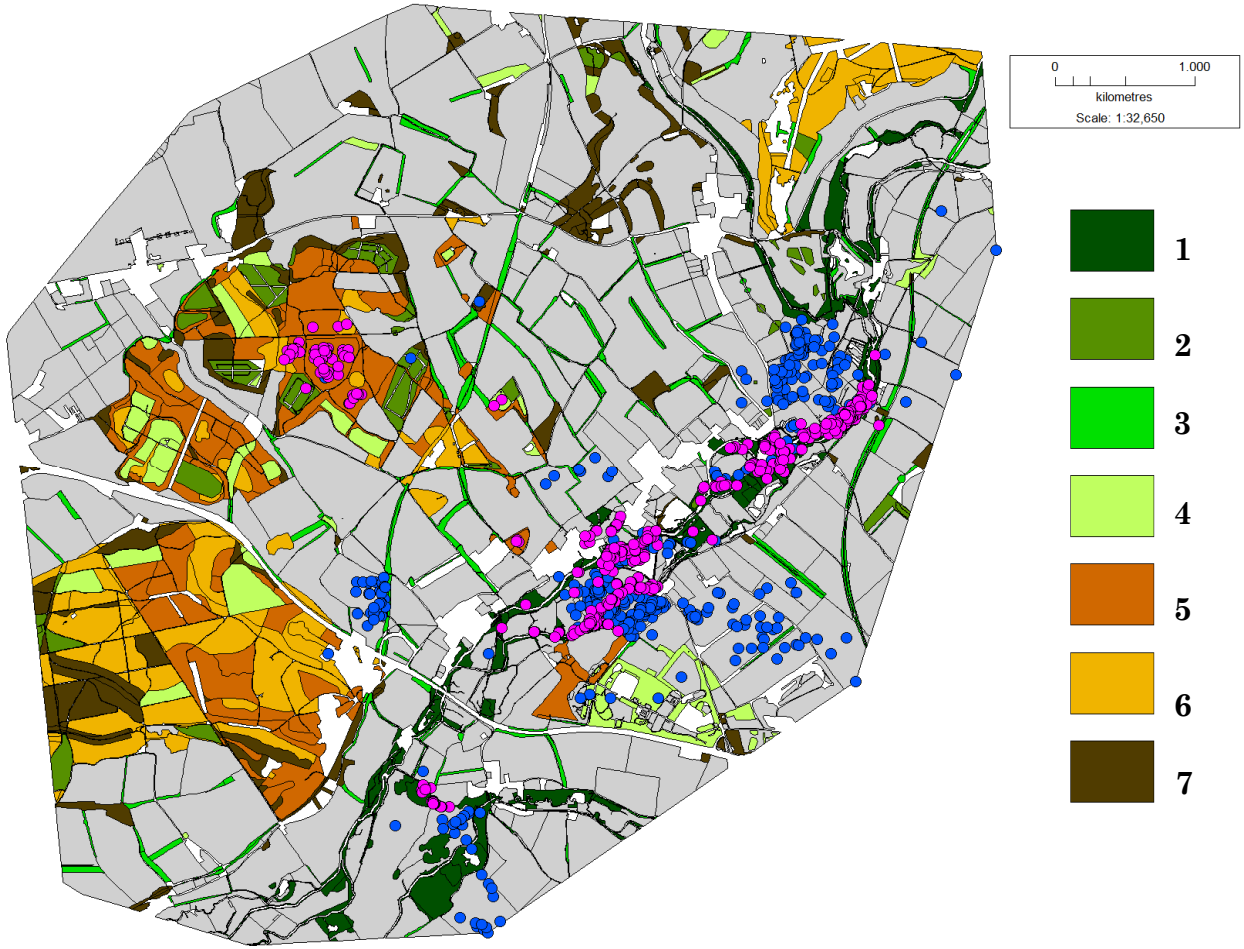


Figure 4.5 Map depicting woodland habitat use of Eurasian woodcock (n = 16) over the 2008/09 winter. Pink circles represent combined diurnal fixes (n = 561), blue circles represent combined nocturnal fixes (n = 499). Woodland categories are defined as follows: 1 = wet woodland, 2 = coniferous stands, 3 = strips, 4 = young woodland, 5 = oak mixed with hazel, 6 = oak mixed with birch, and 7 = mixed woodland. Grey areas represent fields. White areas represent unsuitable/unavailable habitat e.g. roads, buildings, rivers. The study area was defined by a composite Minimum Convex Polygon (MCP) encompassing the combined diurnal and nocturnal fixes of 55 birds, collected over three winters (2008/09, 2009/10, and 2010/11) (total fixes = 4 011).

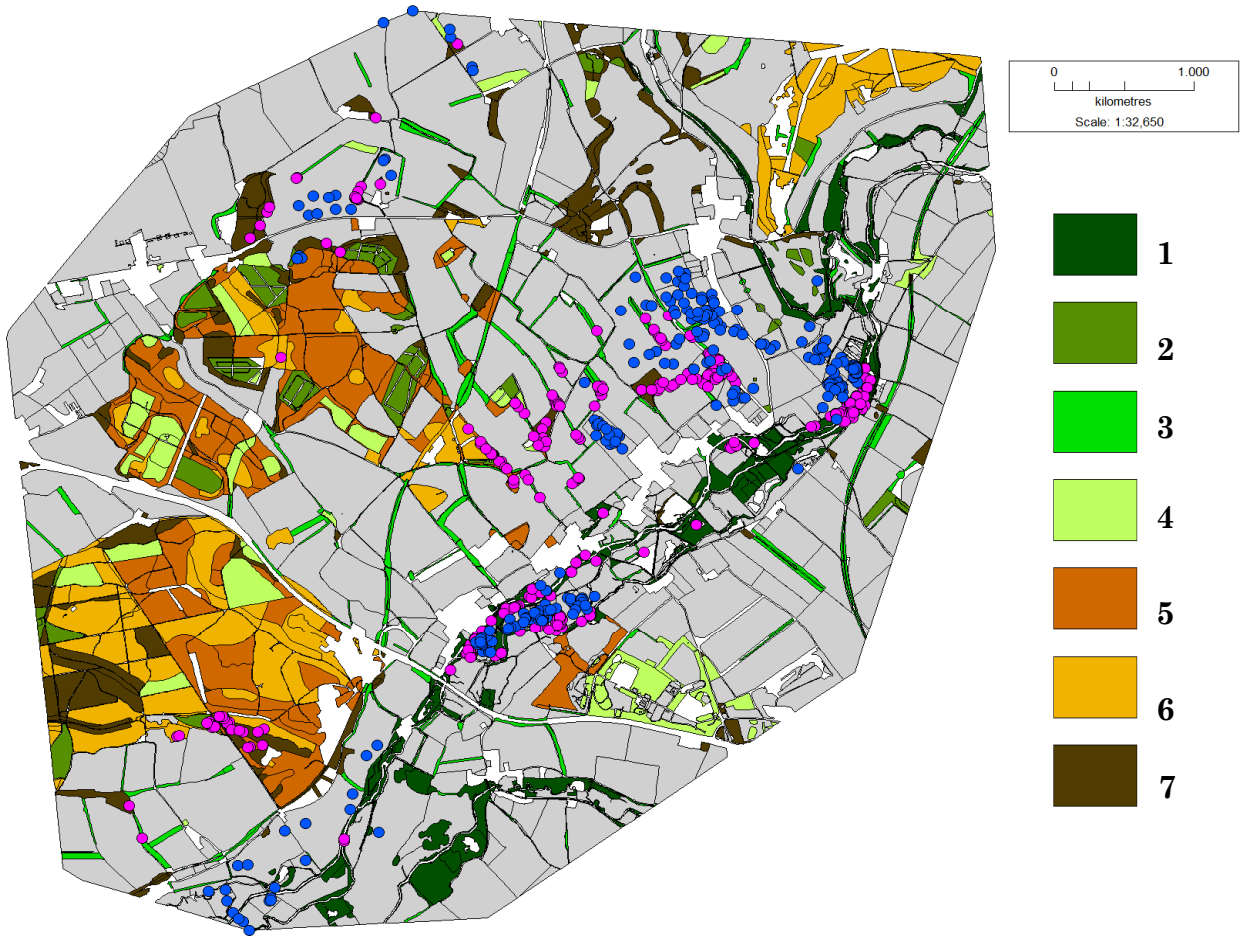


Figure 4.6 Map depicting woodland habitat use of Eurasian woodcock (n = 12) over the 2009/10 winter. Pink circles represent combined diurnal fixes (n = 348), blue circles represent combined nocturnal fixes (n = 293). Woodland categories are defined as follows: 1 = wet woodland, 2 = coniferous stands, 3 = strips, 4 = young woodland, 5 = oak mixed with hazel, 6 = oak mixed with birch, and 7 = mixed woodland. Grey areas represent fields. White areas represent unsuitable/unavailable habitat e.g. roads, buildings, rivers. The study area was defined by a composite Minimum Convex Polygon (MCP) encompassing the combined diurnal and nocturnal fixes of 55 birds, collected over three winters (2008/09, 2009/10, and 2010/11) (total fixes = 4 011).

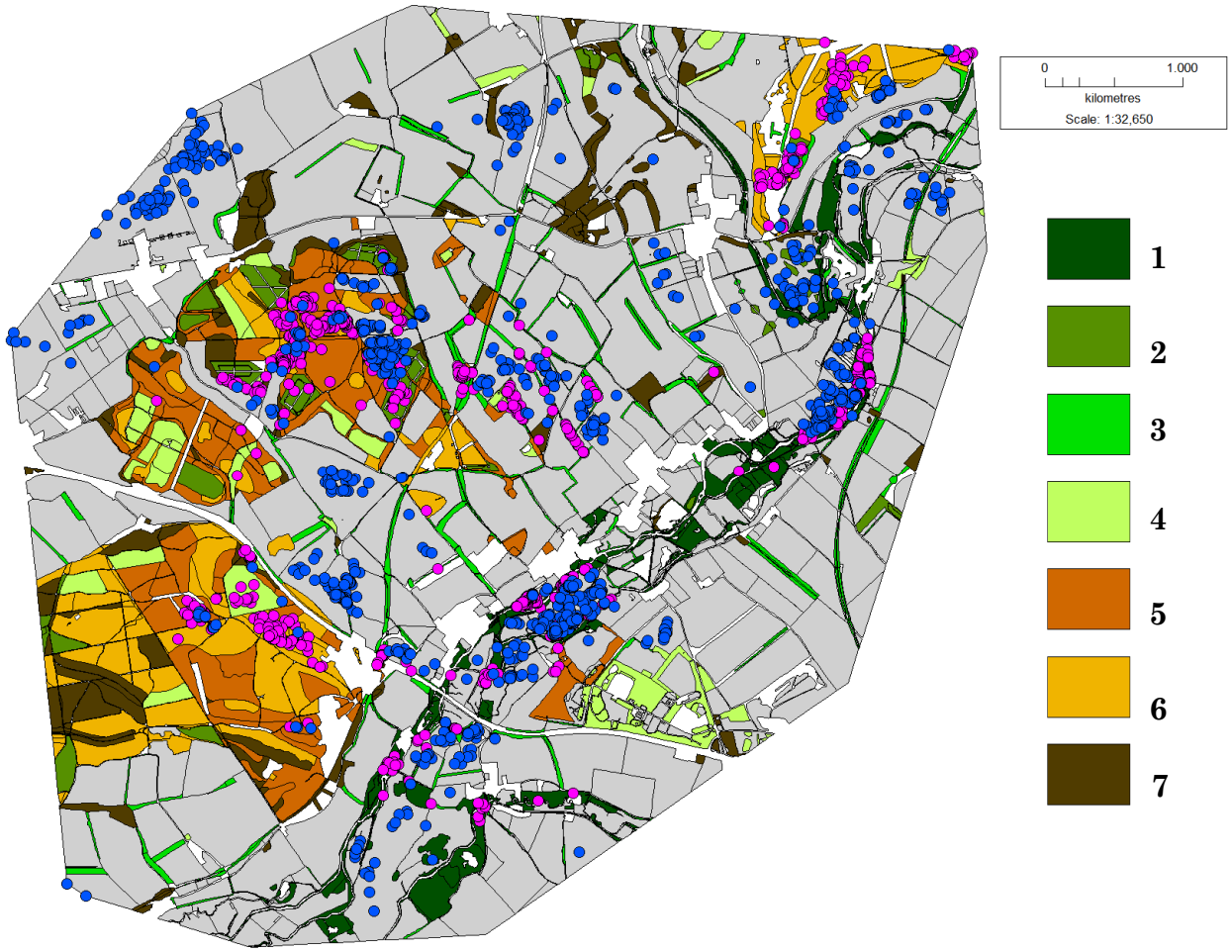


Figure 4.7 Map depicting woodland habitat use of Eurasian woodcock (n = 27) over the 2010/11 winter. Pink circles represent combined diurnal fixes (n = 1 189), blue circles represent combined nocturnal fixes (n = 1 121). Woodland categories are defined as follows: 1 = wet woodland, 2 = coniferous stands, 3 = strips, 4 = young woodland, 5 = oak mixed with hazel, 6 = oak mixed with birch, and 7 = mixed woodland. Grey areas represent fields. White areas represent unsuitable/unavailable habitat e.g. roads, buildings, rivers. The study area was defined by a composite Minimum Convex Polygon (MCP) encompassing the combined diurnal and nocturnal fixes of 55 birds, collected over three winters (2008/09, 2009/10, and 2010/11) (total fixes = 4 011 fixes).

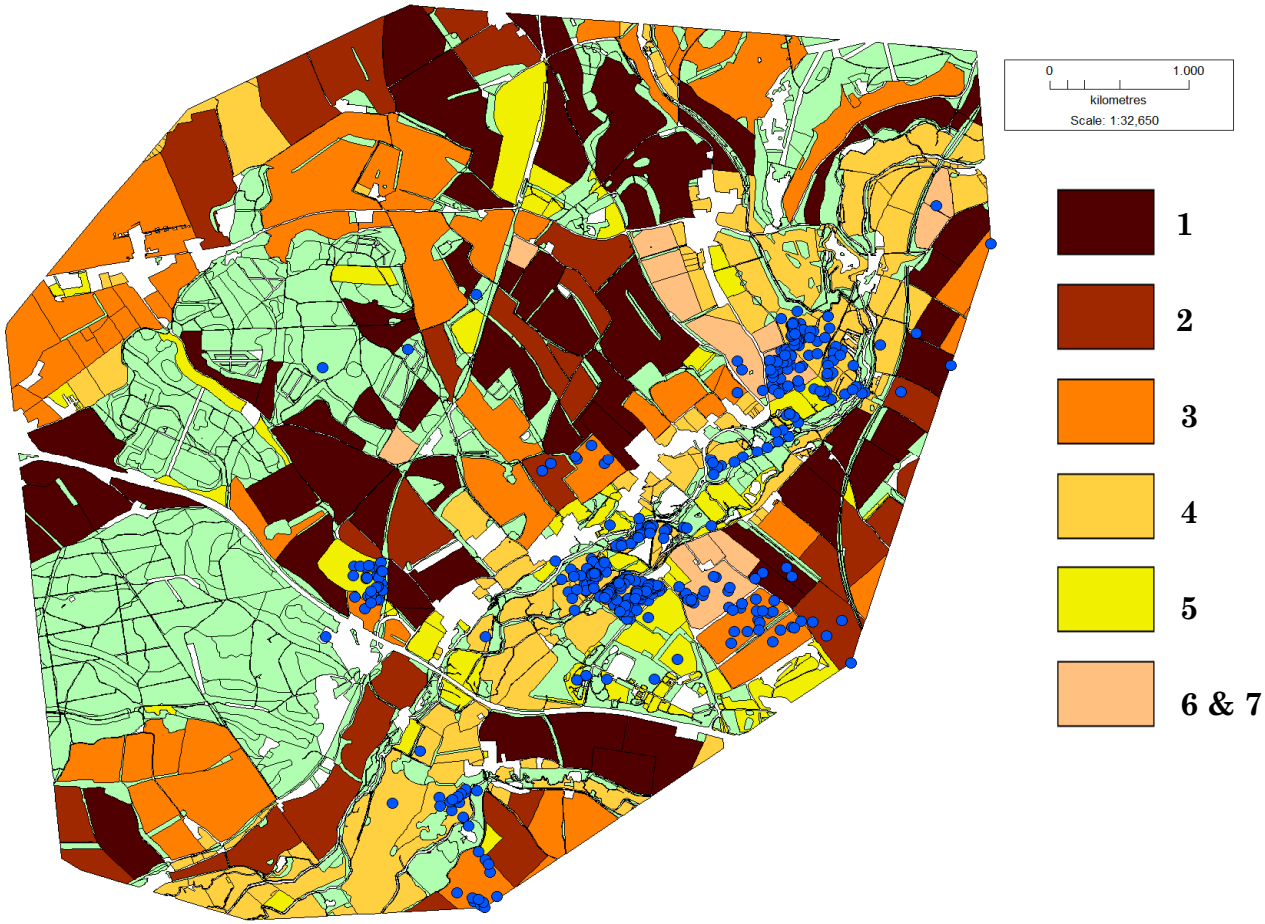


Figure 4.8 Map depicting field habitat use of Eurasian woodcock (n = 16) over the 2008/09 winter. Blue circles represent combined nocturnal fixes (n = 499). Field categories are defined as follows: 1 = winter-drilled wheat, barley, and rye, 2 = winter-drilled oilseed rape and beans, 3 = stubbles (for spring-drilled crops), 4 = grazed permanent pasture, 5 = un-grazed permanent pasture, and 6 & 7 = grazed and un-grazed leys. Green areas represent woodlands. White areas represent unsuitable/unavailable habitat e.g. roads, buildings, rivers. The study area was defined by a composite Minimum Convex Polygon (MCP) encompassing the combined diurnal and nocturnal fixes of 55 birds, collected over three winters (2008/09, 2009/10, and 2010/11) (total fixes = 4 011 fixes).

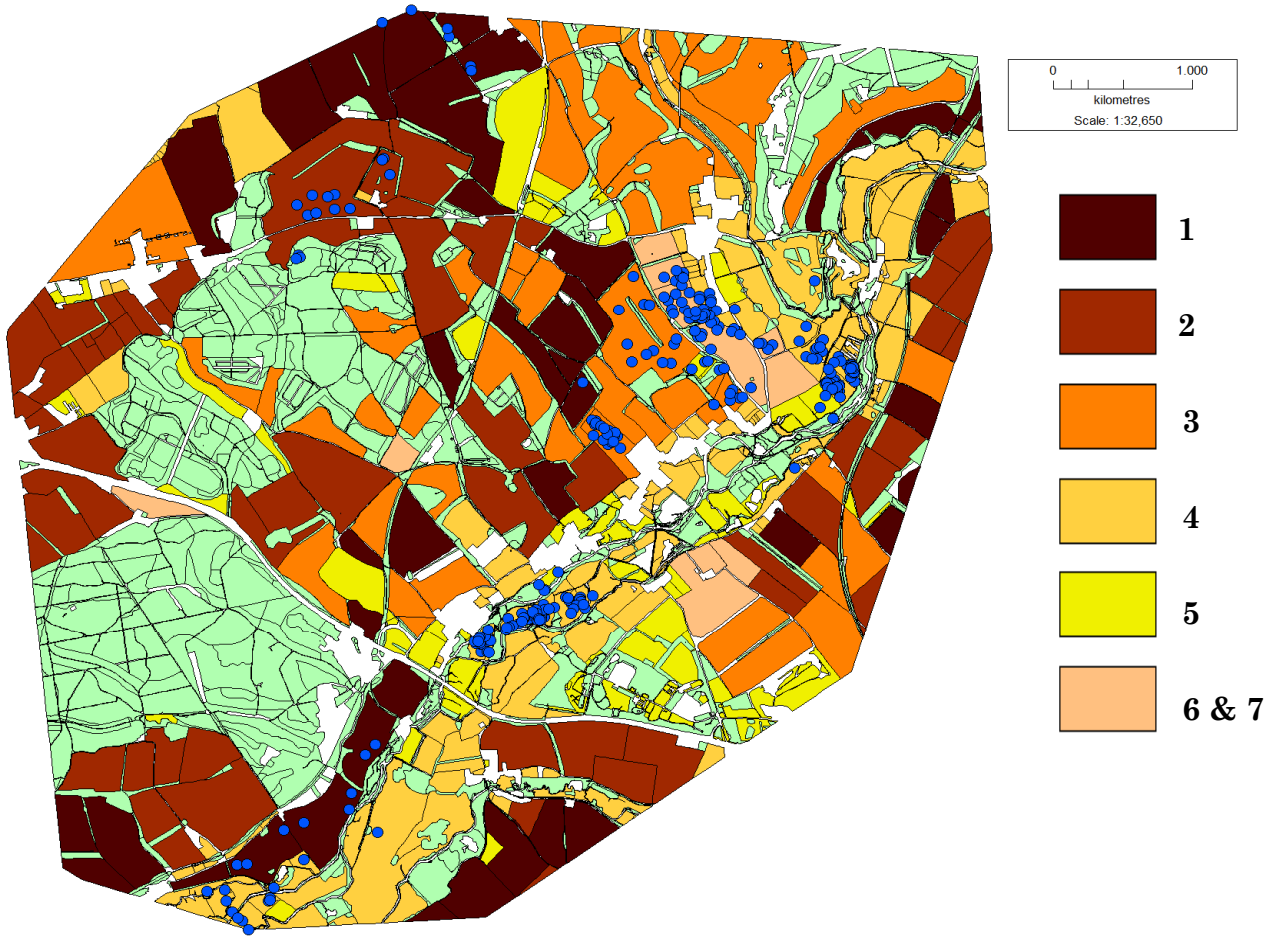


Figure 4.9 Map depicting field habitat use of Eurasian woodcock (n = 12) over the 2009/10 winter. Blue circles represent combined nocturnal fixes (n = 293). Field categories are defined as follows: 1 = winter-drilled wheat, barley, and rye, 2 = winter-drilled oilseed rape and beans, 3 = stubbles (for spring-drilled crops), 4 = grazed permanent pasture, 5 = un-grazed permanent pasture, and 6 & 7 = grazed and un-grazed leys. Green areas represent woodlands. White areas represent unsuitable/unavailable habitat e.g. roads, buildings, rivers. The study area was defined by a composite Minimum Convex Polygon (MCP) encompassing the combined diurnal and nocturnal fixes of 55 birds, collected over three winters (2008/09, 2009/10, and 2010/11) (total fixes = 4 011 fixes).

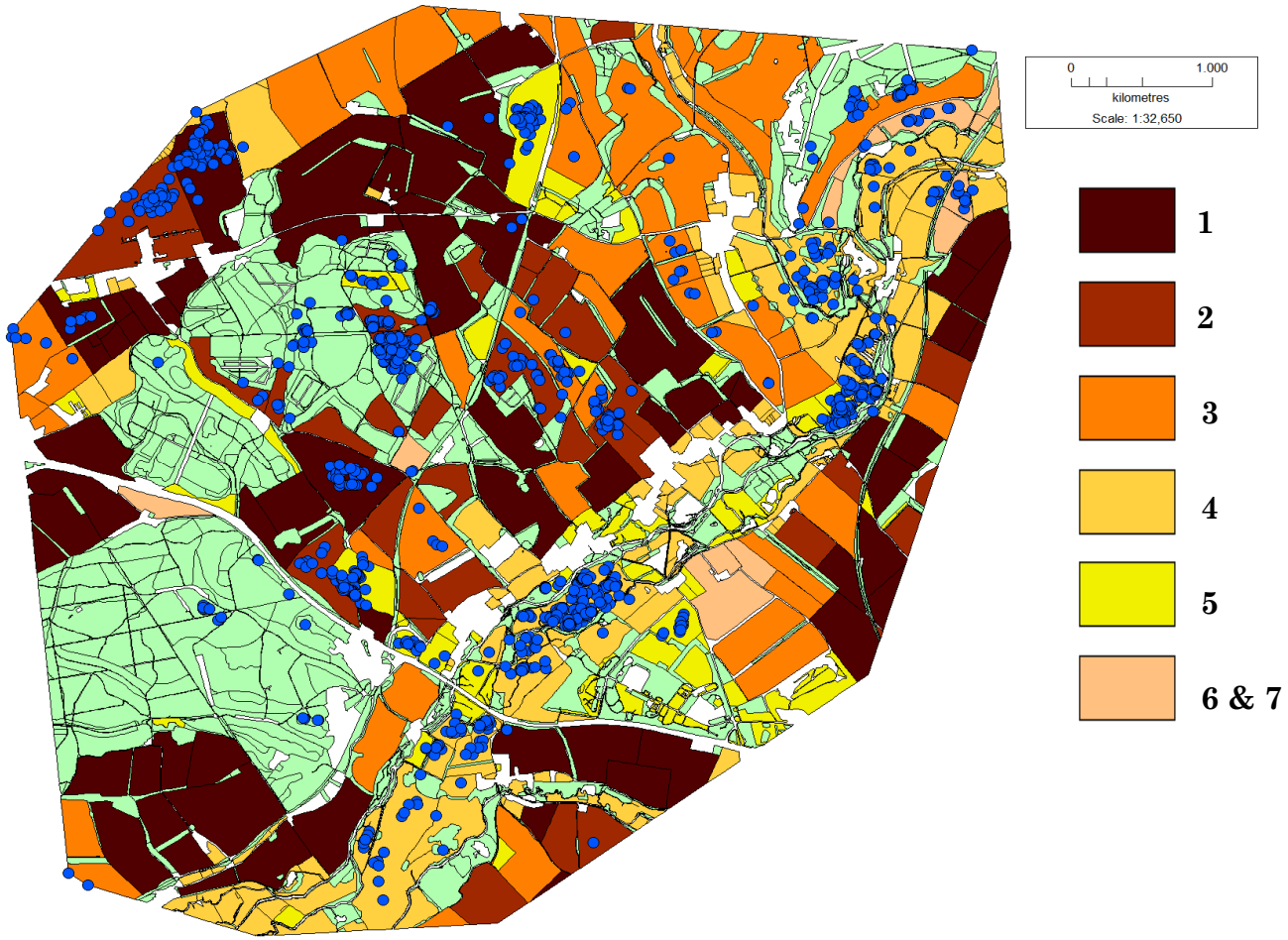


Figure 4.10 Map depicting field habitat use of Eurasian woodcock (n = 27) over the 2010/11 winter. Blue circles represent combined nocturnal fixes (n = 1 121). Field categories are defined as follows: 1 = winter-drilled wheat, barley, and rye, 2 = winter-drilled oilseed rape and beans, 3 = stubbles (for spring-drilled crops), 4 = grazed permanent pasture, 5 = un-grazed permanent pasture, and 6 & 7 = grazed and un-grazed leys. Green areas represent woodlands. White areas represent unsuitable/unavailable habitat e.g. roads, buildings, rivers. The study area was defined by a composite Minimum Convex Polygon (MCP) encompassing the combined diurnal and nocturnal fixes of 55 birds, collected over three winters (2008/09, 2009/10, and 2010/11) (total fixes = 4 011 fixes).

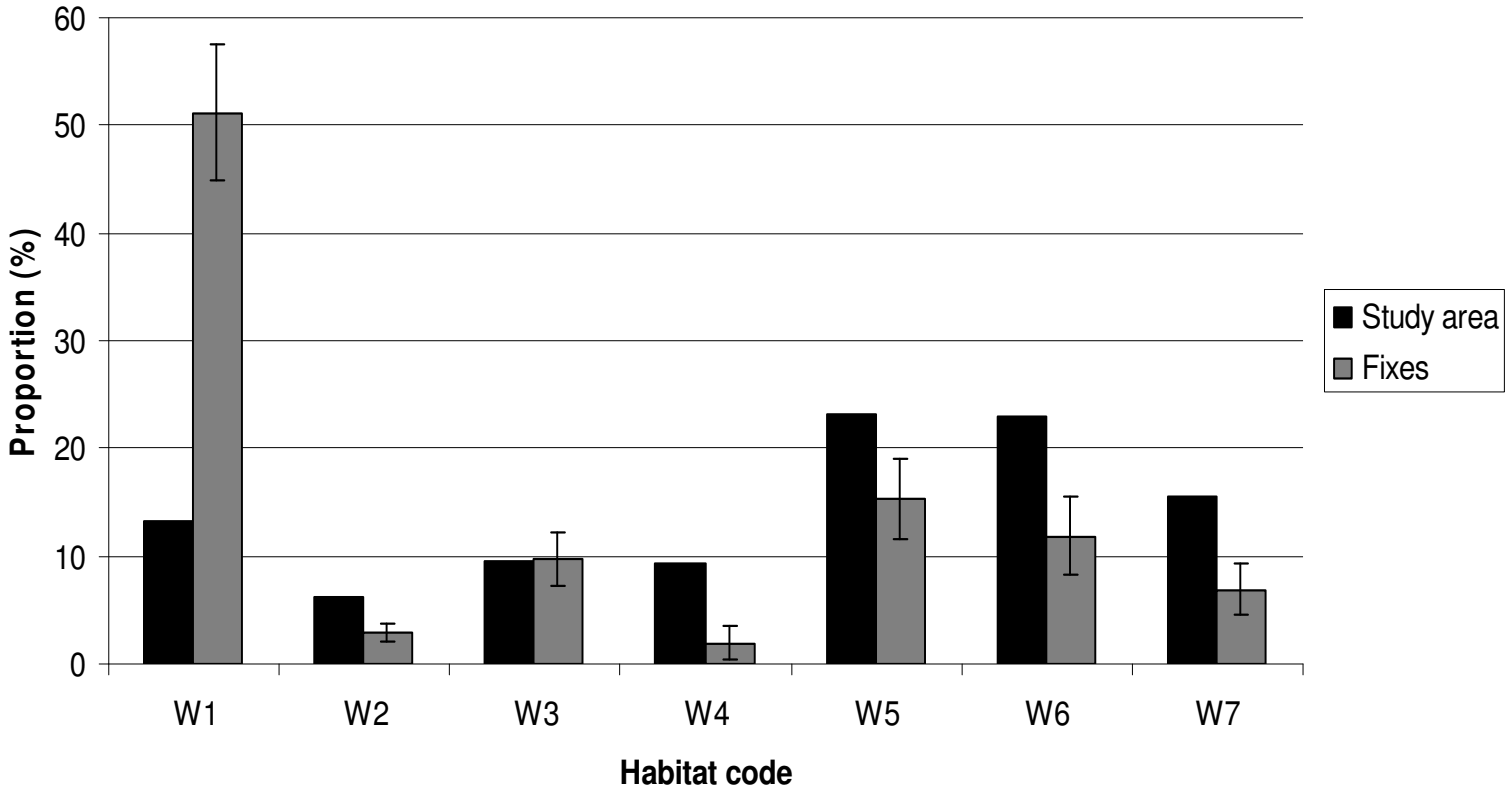


Figure 4.11 Mean proportional use of diurnal habitats (± standard errors) (grey bars) by Eurasian woodcock, compared with the availability of diurnal habitats (black bars). Habitat code W1 = wet woodland, W2 = coniferous stands, W3 = strips, W4 = young woodland, W5 = oak mixed with hazel, W6 = oak mixed with birch, and W7 = mixed woodland. Results represent the combined diurnal fixes (n = 2 098) of 55 birds, collected over three winters (2008/09, 2009/10, and 2010/11).

Table 4.1 Simplified ranking matrix reflecting diurnal habitat use of Eurasian woodcock (n = 55), over three combined winters (2008/09, 2009/10, and 2010/11). Diurnal habitat W1 = wet woodland, W2 = coniferous stands, W3 = strips, W4 = young woodland, W5 = oak mixed with hazel, W6 = oak mixed with birch, and W7 = mixed woodland. Rankings represent the results of one-sample t.tests, where mean log-ratio differences were compared against zero. Each element in the matrix represents the sign of the mean (positive or negative), and its significance. A triple sign represents significant departure of the mean log-ratio difference from zero at $P < 0.05$.

Used habitat	**Available habitat**							**Rank**
	W1	**W2**	**W3**	**W4**	**W5**	**W6**	**W7**	
W1		+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	6th
W2	− − −		−	+ + +	+	+ + +	+ + +	4th
W3	− − −	+		+ + +	+	+ + +	+ + +	5th
W4	− − −	− − −	− − −		−	−	−	0
W5	− − −	−	−	+		+	+	3rd
W6	− − −	− − −	− − −	+	−		−	1st
W7	− − −	− − −	− − −	+	−	+		2nd

Table 4.2 Differences in diurnal habitat rankings of Eurasian woodcock (n = 55), based on t.tests comparing mean log-ratio differences with zero (Table 4.1). Markers (*) represent habitats that do not have significantly different rankings.

		Marker		
Rank	**Habitat code**	**i**	**ii**	**iii**
6	**W1**			
5	**W3**	*		*
4	**W2**	*		*
3	**W5**	*	*	*
2	**W7**		*	*
1	**W6**		*	*
0	**W4**		*	*

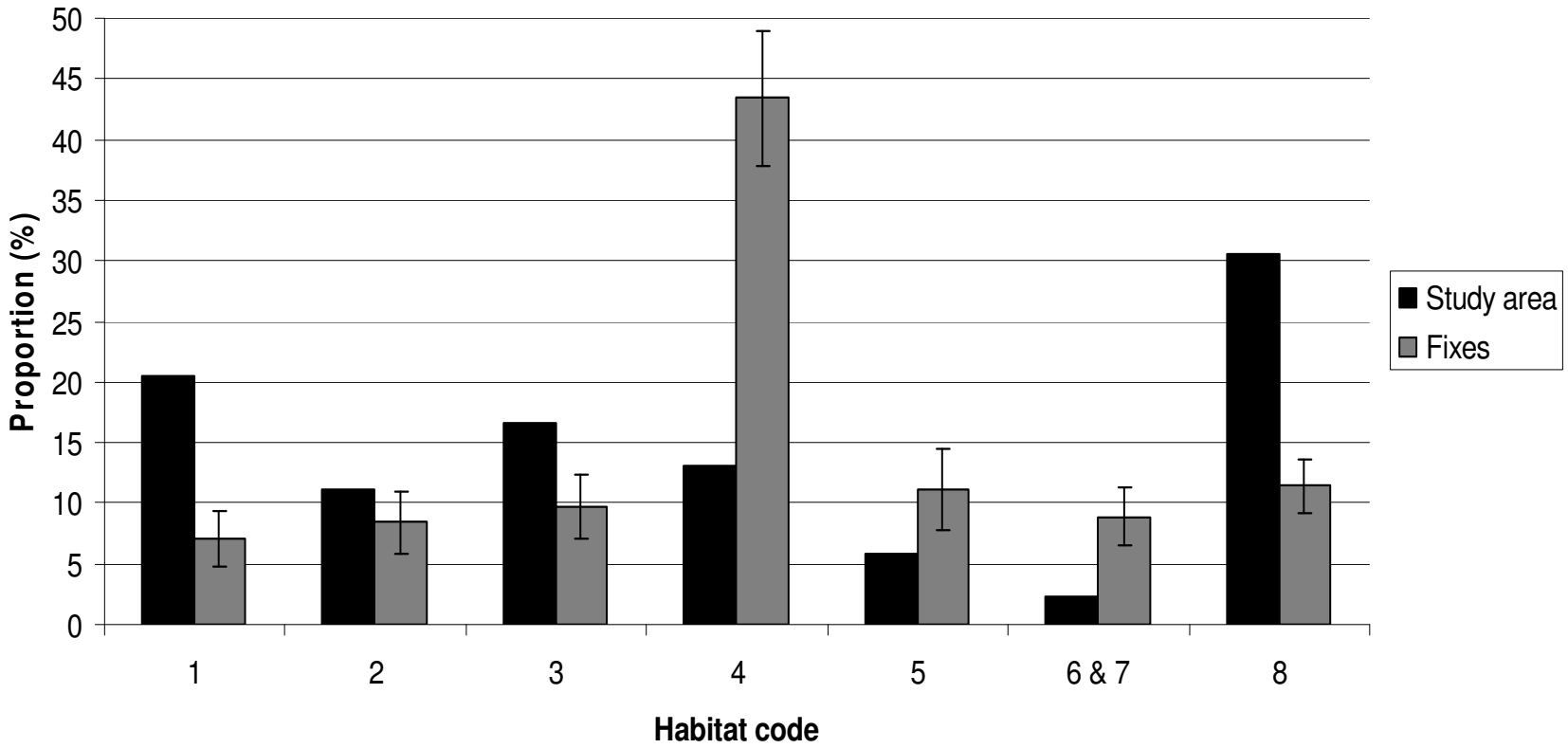


Figure 4.12 Mean proportional use of nocturnal habitats (± standard errors) (grey bars) by Eurasian woodcock, compared with the availability of nocturnal habitats (black bars). Habitat code 1 = winter-drilled wheat, barley, and rye, 2 = winter-drilled oilseed rape and beans, 3 = stubbles (for spring-drilled crops), 4 = grazed permanent pasture, 5 = un-grazed permanent pasture, 6 & 7 = grazed and un-grazed leys, and 8 = woodland. Results represent the combined nocturnal fixes (n = 1 913) of 55 birds, collected over three winters (2008/09, 2009/10, and 2010/11).

Table 4.3 Simplified ranking matrix reflecting nocturnal habitat use of Eurasian woodcock (n = 55), over three combined winters (2008/09, 2009/10, and 2010/11). Nocturnal habitat 1 = winter-drilled wheat, barley, and rye, 2 = winter-drilled oilseed rape and beans, 3 = stubbles (for spring-drilled crops), 4 = grazed permanent pasture, 5 = un-grazed permanent pasture, 6 & 7 = grazed and un-grazed leys, and 8 = woodland. Rankings represent the results of one-sample t.tests, where mean log-ratio differences were compared against zero. Each element in the matrix represents the sign of the mean (positive or negative), and its significance. A triple sign represents significant departure of the mean log-ratio difference from zero at $P < 0.05$.

Used habitat	**Available habitat**							**Rank**
	1	**2**	**3**	**4**	**5**	**6 & 7**	**8**	
1		− − −	−	− − −	− − −	− − −	−	0
2	+ + +		+	− − −	− − −	− − −	+	3rd
3	+	−		− − −	− − −	− − −	+	2nd
4	+ + +	+ + +	+ + +		+	+	+ + +	6th
5	+ + +	+ + +	+ + +	−		−	+ + +	4th
6 & 7	+ + +	+ + +	+ + +	−	+		+ + +	5th
8	+	−	−	− − −	− − −	− − −		1st

Table 4.4 Differences in nocturnal habitat rankings of Eurasian woodcock (n = 55), based on t.tests comparing mean log-ratio differences with zero (Table 4.3). Markers (*) represent habitats that do not have significantly different rankings.

		Marker			
Rank	**Habitat code**	**i**	**ii**	**iii**	**iv**
6	**4**				*
5	**6 &7**				*
4	**5**				*
3	**2**		*	*	
2	**3**	*	*	*	
1	**8**	*	*	*	
0	**1**	*		*	

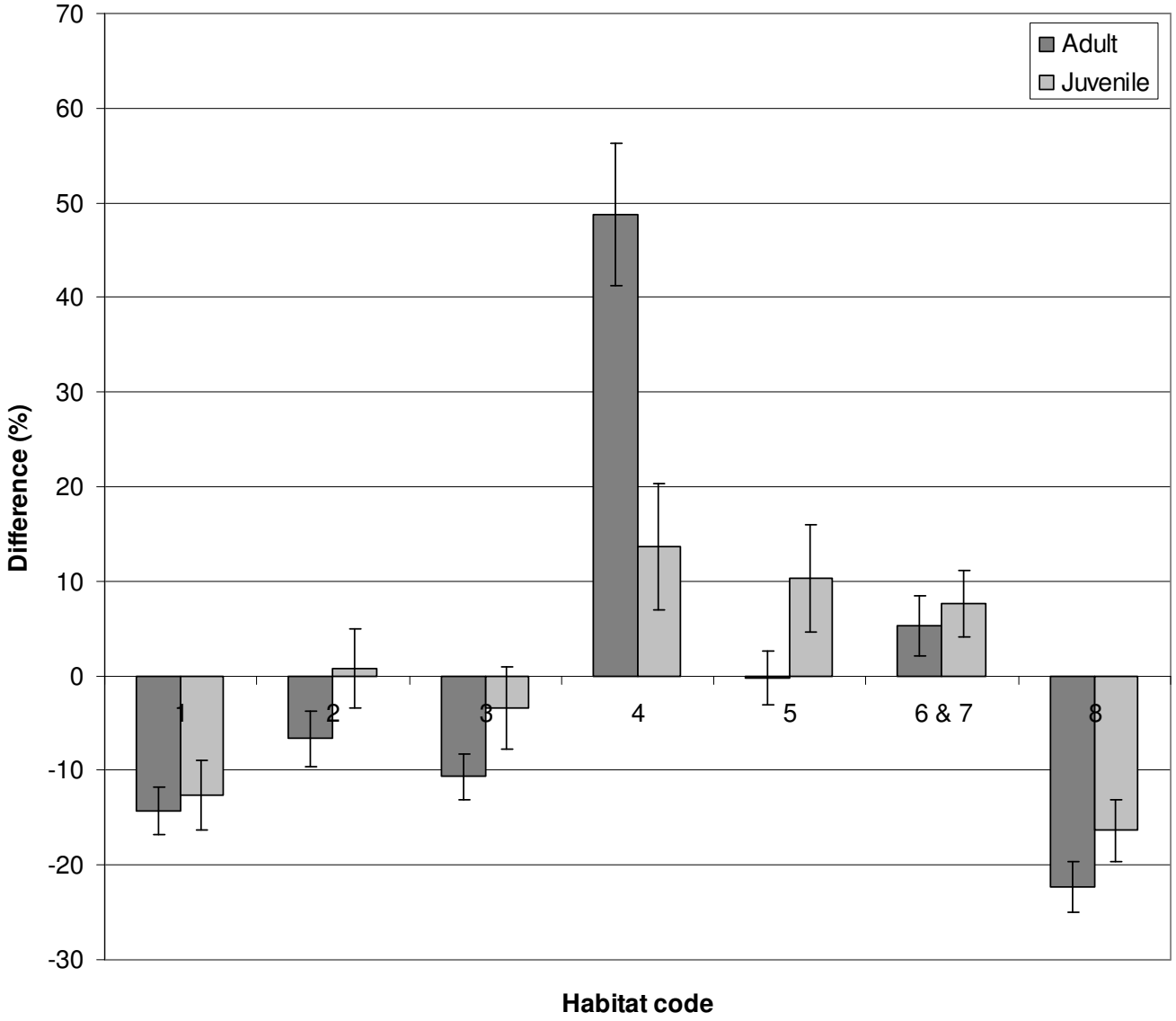


Figure 4.13 Mean differences (± standard error) between nocturnal habitat use and availability, for adult (n = 26) and juvenile (n = 29) Eurasian woodcock, across three combined winters (2008/09, 2009/10, and 2010/11). Habitat code 1 = winter-drilled wheat, barley, and rye, 2 = winter-drilled oilseed rape and beans, 3 = stubbles (for spring-drilled crops), 4 = grazed permanent pasture, 5 = un-grazed permanent pasture, 6 & 7 = grazed and un-grazed leys, and 8 = woodland.

Table 4.5 Simplified ranking matrix reflecting differences in nocturnal habitat use between adult (n = 26) and juvenile (n = 29) Eurasian woodcock, over three combined winters (2008/09, 2009/10, and 2010/11). Nocturnal habitat 1 = winter-drilled wheat, barley, and rye, 2 = winter-drilled oilseed rape and beans, 3 = stubbles (for spring-drilled crops), 4 = grazed permanent pasture, 5 = un-grazed permanent pasture, 6 & 7 = grazed and un-grazed leys, and 8 = woodland. Rankings represent the results of one-sample t.tests, where mean log-ratio differences were compared between adults and juveniles. Each element in the matrix represents the sign of the mean (positive or negative), and its significance. A triple sign represents significant departure of the mean log-ratio difference from zero at $P < 0.05$.

Adult	**Juvenile**							**Rank**
	1	**2**	**3**	**4**	**5**	**6 & 7**	**8**	
1		+	+	− − −	+	+	+	5th
2	−		−	− − −	+	−	+	2nd
3	−	+		− − −	+	−	+	3rd
4	+ + +	+ + +	+ + +		+ + +	+ + +	+ + +	6th
5	−	−	−	− − −		−	+	1st
6 & 7	−	+	+	− − −	+		+	4th
8	−	−	−	− − −	−	−		0

Table 4.6 Differences in nocturnal habitat rankings of adult (n = 26) and juvenile (n = 29) Eurasian woodcock, based on t.tests comparing mean log-ratio differences with zero (Table 4.5). Markers (*) represent habitats that do not have significantly different rankings.

		Marker
Rank	**Habitat code**	**i**
6	**4**	
5	**1**	*
4	**6 & 7**	*
3	**3**	*
2	**2**	*
1	**5**	*
0	**8**	*

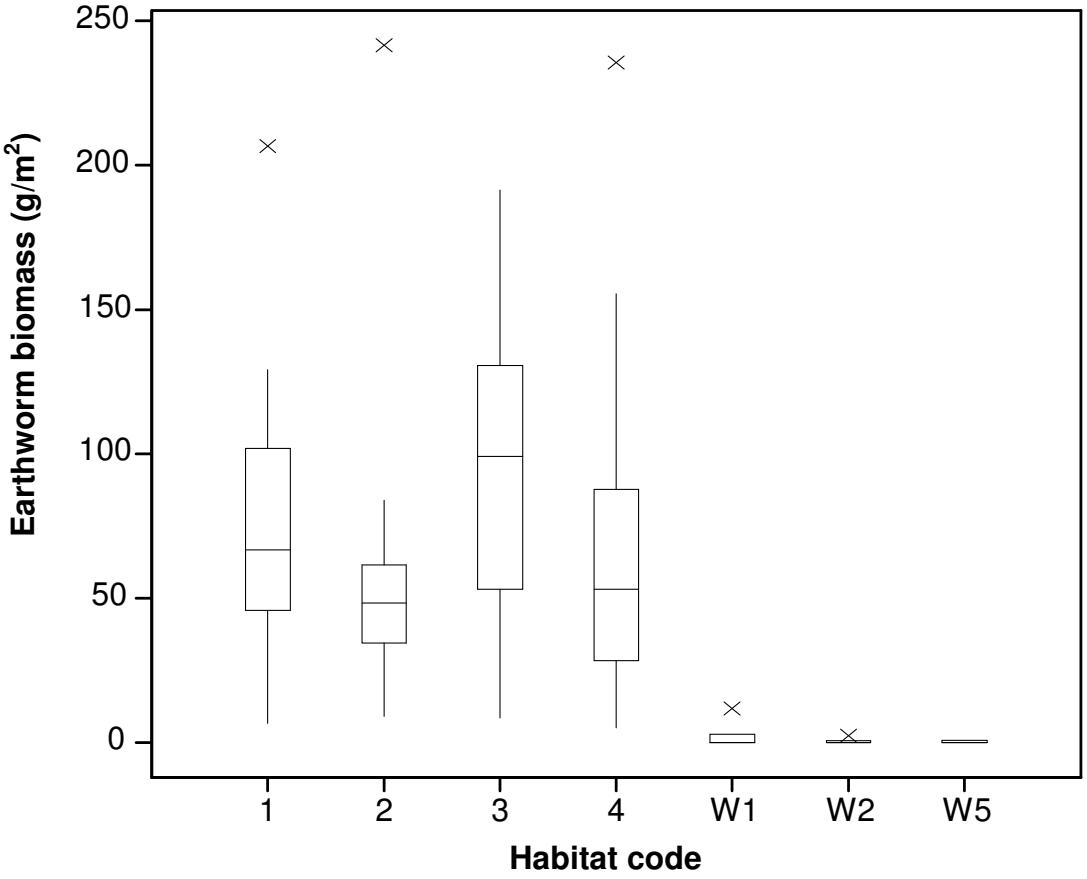


Figure 4.14 Differences in earthworm biomass between sampled habitat types, where 1 = winter-drilled wheat, 2 = winter-drilled oilseed rape, 3 = stubbles (for spring-drilled crops), 4 = grazed permanent pasture, W1 = wet woodland, W2 = coniferous stands, and W5 = oak mixed with hazel. Each box spans the interquartile range of values. The middle 50% of the data lie within the box, with the intersecting line representing the median. Whiskers extend as far as the minimum and maximum values. Crosses represent outliers.

Table 4.7 Proportions of earthworms found within each genus, for the field habitat types sampled, where 1 = winter-drilled cereal, 2 = winter-drilled oilseed rape and beans, 3 = stubbles (for spring-drilled crops), and 4 = grazed permanent pasture. n = the total number of earthworms sampled within each habitat type.

Genus	**Earthworms (%)**			
	1	**2**	**3**	**4**
Allolobophora	51.1	58.0	28.6	28.6
Aporrectodea	33.3	26.9	28.1	59.0
Lumbricus	15.6	13.4	42.2	12.4
Octolasion	-	1.7	1.0	-
n	135	119	199	105

Chapter 5

Behaviour of Eurasian woodcock on the wintering grounds in Britain, in relation to bird age and predicted migratory status

Behaviour of Eurasian woodcock on the wintering grounds in Britain, in relation to bird age and predicted migratory status

Abstract

Knowledge pertaining to the non-breeding ecology of the Eurasian woodcock *Scolopax rusticola* (hereon woodcock) is somewhat lacking, owing to its cryptic plumage and elusive nature. Such information, however, is of importance, given uncertainties surrounding this bird's conservation status. Only by obtaining adequate knowledge on the natural history of the woodcock can the necessary conservation plans be put in place to ensure its sustainability.

In a unique attempt to understand the non-breeding movements and behaviour of woodcock in relation to age (adult vs. juvenile) and predicted migratory status (resident vs. migrant), a radio-tracking programme was undertaken in Hampshire, Britain, over the course of three winters (2008/09, 2009/10 & 2010/11). The resulting data were used to investigate six aspects of woodcock non-breeding ecology: 1) commuting flights, 2) area use, 3) core sites, 4) foraging activity, 5) night-time habitat occupancy, and 6) departure events.

For commuting flights, adult residents were found to travel greater distances than migrants during the winter of 2008/09, whilst the converse was true in 2009/10 and 2010/11. Similar results were obtained in the home range analysis. This variation between years was attributed to temporal (inter-annual) changes in climate, as environmental conditions are considered a key determinant of woodcock behaviour. The number of sites used did not vary with bird age and/or

predicted migratory status. Rather, all birds had a distinct primary core that represented the area of most frequent use and all appeared to apply the same site-use strategy to both day and night ranges. Activity patterns showed intra- and inter-individual variation. However, birds exhibiting high levels of activity during the day typically showed lower levels of activity at night, with the converse also true. Migrants were found to be more active during the day than residents and, since activity was synonymous with feeding, this suggests that migrants are undertaking higher levels of supplementary day-time feeding than their resident counterparts. On occasion, woodcock were found to remain in woodland-type habitats at night, with no effects of age and/or predicted migratory status apparent. This decision probably reflected the complex relationship between weather conditions, foraging success during the day and the starvation-predation risk trade-off. Two types of departure events were also found to occur over the study period. The departures of migrant birds in March/April were attributed to spring-migration, whilst departures preceding these were deemed cold-weather movements.

Introduction

Although the international conservation status of Eurasian woodcock *Scolopax rusticola* (hereon woodcock) remains uncertain (Wetlands International 2002; BirdLife International 2004a,b), concerns have been raised regarding the British-breeding woodcock population. There has been an apparent long-term decline in breeding numbers (-76%, 1974-1999) and range (-31%, 1968/72-1988/91) (Gregory *et al.* 2002), which has resulted in the British-breeding woodcock population being amber-listed as a population of conservation concern (Eaton *et al.* 2009).

Understanding the cause(s) of these declines will help guide the conservation plans necessary to ensure the sustainability of the national population. However, this requires information pertaining to woodcock ecology, which is currently lacking.

The most current woodcock studies in Britain have primarily focused on the breeding season (Hirons 1983, 1988; Hirons & Johnson 1987; Hoodless & Coulson 1998; Hoodless & Hirons 2007; Hoodless *et al.* 2009), despite evidence that the non-breeding season plays an important role in the population dynamics of bird species (Marra *et al.* 1998; Studds & Marra 2005; Norris & Marra 2007). This bias is likely due to the common assumption that animals maximise their lifetime reproductive success (i.e. their fitness) by investing optimally in reproduction (Hedenstrom 2006). As a consequence, studies tend to be directed toward breeding biology and habitat needs. This issue, however, needs to be re-addressed, given that there appears to be an equivalent "non-breeding fitness currency" (Hedenstrom 2006). In Britain and Ireland, only three small-scale studies have focused on woodcock during the non-breeding season; these were based on just three (Wilson 1983), five (Hirons & Bickford-Smith 1983) and 13 (Hoodless 1994a) radio-tagged individuals. Given the limits of these studies, a more intensive radio-tracking programme is needed to better understand the non-breeding ecology of woodcock in Britain.

Non-breeding season

Birds do not mate or breed during the non-breeding season; rather, bird movements and behaviour during this time are primarily driven by the need to

access resources necessary for self-maintenance and survival (Sherry & Holmes 1996; Studds & Marra 2005; Brown & Sherry 2006). If birds are unable to sustain their basic needs during the non-breeding season, they may have reduced survival, as either a direct result of starvation, or indirectly through increased sensitivity to predation and/or hunting pressure (Tavecchia *et al.* 2002). The survival of individuals may then go on to impact the mortality rates of the population by, for example, density-dependent mechanisms ("buffer effects") (Newton 2004a). Alternatively, birds may incur carry-over effects, whereby ecological factors, such a poor habitat quality, limit individual condition in one part of the annual cycle, and thereby alter the timing or capacity of an individual to migrate, reproduce, or survive at a subsequent stage (Gill *et al.* 2001; Norris 2005; Studds & Marra 2005). For example, the quality of non-breeding habitats occupied by American redstarts *Setophaga ruticilla* have been shown to determine the body condition and spring departure dates of migrants, which then carry over to influence arrival schedules and body condition in the breeding season (Marra *et al.* 1998). As such, it is important to understand the movements and behaviours of birds during the non-breeding season, as these likely impact success at the individual level, and may contribute to wider reaching effects at the population level.

The non-breeding movements and behaviour of woodcock typically reflect the need to access optimal habitats and food resources. By day, woodcock appear to select habitats characterised by a dense shrub strata (Duriez *et al.* 2005; Chapter 4), which provides protection from both adverse weather conditions and predators. By night, birds preferentially seek out grass fields (Duriez *et al.* 2005b; Chapter 4), which allow for optimal feeding opportunities. However, despite these

preferences, survival and self-maintenance requirements often come into conflict during the course of the non-breeding season. For instance, as temperatures decrease, woodcock thermoregulatory demands increase, but earthworms, which comprise the primary prey for woodcock during the non-breeding season (Granval 1987), become less accessible to woodcock. This is because, with declining temperatures, ground soil becomes difficult to penetrate and/or earthworms burrow deeper into the soil (Edwards & Lofty 1972). There also exists a dichotomy between feeding success and risk of predation, with habitats offering optimal feeding opportunities often posing higher predation risk (Duriez 2003). Consequently, non-breeding movements and behaviour are likely to reflect a compromise between these tradeoffs, and will change in accordance with individual needs. By considering the non-breeding movements and behaviours of woodcock in relation to age and predicted migratory status (hereon status), important insights might be gained into ecological differences between groups.

Across much of Britain, woodcock populations during the winter comprise British breeding and non-British breeding birds. Discerning ecological differences between these two groups, however, has proved difficult, since they are morphologically indistinguishable (Clausager 1973; Rochford & Wilson 1982; Ferrand & Gossmann 2009). Whilst early work suggested that variation in plumage coloration was an indicator of origin, with the "reds" believed to represent resident birds and the "greys" migrants (Seigne 1930; Bartholomew 1931), it is now accepted that such colour aberrations are merely a product of individual variation (Stronach *et al.* 1974; Kalchreuter 1983). Other morphological characteristics (Clausager 1973; Rochford & Wilson 1982; Ferrand & Gossmann 2009) have also, so far, failed to distinguish birds from different

breeding populations. Fortunately, the development of genetic and biogeochemical techniques now offers a means of obtaining this information (Clegg *et al.* 2003; Kelly *et al.* 2005; Smith *et al.* 2005; Boulet *et al.* 2006).

In this study, woodcock considered to be Hampshire breeders (hereon residents) were distinguished from those breeding outside of Hampshire (hereon migrants), using the discriminatory ability provided by stable isotopes (General Method II). Used in this way, the stable isotope approach enabled differential winter behaviours across individuals to be assessed in terms of status.

Since comparisons between woodcock of different migratory status have never been made before, this work provides a unique insight into the behaviours of these two groups, and might have important conservation consequences for both (McGregor & Peake 1998; Kenward 2001). If resident-defined birds are indeed considered to be local to the study area (General Method II), then they might be expected to have fitness advantages and increased survival, relative to migrants. This is because local birds are more likely to be familiar with the area, and therefore able to use their experience and spatial knowledge to optimise movements and behaviours. As a consequence, residents may be able to optimise their exploitation of food-rich patches and satisfy their daily energy requirements more efficiently than their migratory counterparts, which lack familiarity with the site. For similar reasoning, differences in the non-breeding ecology of adults and juveniles were also explored, as knowledge pertaining to optimal behaviours may improve with age and experience.

Aims

Radio-telemetry and stable isotope methods were combined here in an attempt to discern the non-breeding movements and behaviour of woodcock in relation to bird age (adult vs. juvenile) and status (resident vs. migrant). Six aspects of woodcock non-breeding ecology were investigated: 1) commuting flights, 2) area use, 3) core sites, 4) foraging activity, 5) night-time habitat occupancy, and 6) departure events.

Methods

Study site details, and information pertaining to capture methods, radio-tracking, and the assignment of status can be found in General Methods II.

Movement patterns

Commuting flights

At twilight, woodcock undertake flights between woodland and field habitats; these movements are hereon referred to as commuting flights (Duriez *et al.* 2005d). The distances travelled during commuting flights were calculated using the inter-location measures tool in Ranges 8 (version 2.5) (Kenward *et al.* 2008). Individuals yielding one (or no) distance(s) were excluded from the final dataset. Distances obtained in October (n = 14) were merged with those in November (n = 131), so as to balance the data across month categories. Similarly, distances obtained in April (n = 6) were merged with those in March (n = 913).

Area use

Home range estimates represent the "area traversed" (Burt 1943) by an animal and require a minimum number of radio-locations (hereon fixes) to be reliable (Kenward 2001). In this analysis, three home range estimators were applied to the data-set: (1) ellipses (95%), requiring a minimum of 10 fixes, (2) kernel contours (95% cores), requiring a minimum of 15 fixes, and (3) Minimum Convex Polygons (MCP) (100%), requiring a minimum of 30 fixes (Figure A5.1). Home range estimates were calculated for combined day and night fixes, using Ranges 8 (version 2.5) (Kenward *et al.* 2008). For inclusion in analysis, the combined total of fixes had to meet the minimum requirement (as stipulated above), but also comprise a minimum of 10 day fixes and 10 night fixes, to ensure a balance between the two time periods. All home range estimates were measured in hectares (ha).

In addition to the calculation of traditional home range estimates, MapInfo Professional version 11.0.3 (Pitney Bowes Software Inc. 2009) was used to generate an area measurement reflective of woodcock land use (as opposed to land coverage), derived from buffers cropped to polygons. This measure was considered a better representation of woodcock ecology. It was calculated by first adding buffers to each fix, to allow for potential movements. A radius value of 100 m was assigned to day fixes, and 150 m for night fixes, with a smoothness value of 50 segments per circle (Figure A5.2). These buffer sizes were determined from an analysis of 24-hour radio-tracking data (see *Preliminary analysis: 24-hour radio-tracking*), and from the findings of previous works (Duriez 2003). Second, all unavailable habitats enclosed by buffers (e.g. rivers, roads, housing)

were excluded (Figure A5.3). Third, buffers were cropped to the map-polygon containing each fix (Figure A5.4). In MapInfo Professional version 11.0.3 (Pitney Bowes Software Inc. 2009), each polygon is a closed object, marking a region of land that has been separated from its neighbour, based on differential land attributes and/or features (Figure A5.5). Since birds appear faithful to their chosen day/night site and are unlikely to cross any form of land boundary (unless disturbed/flushed), cropping areas to map-polygons made ecological sense for the woodcock, and enabled more accurate measures of area to be calculated. Area estimates derived from buffers cropped to polygons were analysed for birds with a minimum of 10 day fixes and 10 night fixes. All area estimates were measured in hectares (ha).

Core sites

The number of polygons and number of fixes within each polygon were determined for each bird's diurnal and nocturnal distributions, separately. This enabled polygons to be ranked in order of use, with polygon one representing the area containing the greatest number of fixes. From this, the number of polygon "cores" was determined. These were defined as polygons containing fixes equal to or greater than the mean number of fixes across all polygons (Figure A5.6). Only individuals with a minimum of 10 day fixes and 10 night fixes were included in this analysis.

Behaviour

Temperature data

Average daily temperatures were downloaded for each day of the field-season. Averages were derived from temperature recordings taken at five-minute intervals, throughout a 24-hour period (midnight to midnight). These data were collected from a weather-station located ~8.5 km north-west of the centre of the study area, in Charlton village, near Andover (latitude: 51.224; longitude: -1.503). It comprised WeatherDisplay: 10.37 software and WMR100 hardware. On occasion, equipment failure resulted in the absence of data. However, the problem of missing data was overcome using data from a second weather station, which allowed reduced major axis (RMA) regression to derive a predictive equation for missing values. This is the most suitable method when both variables measured on the same scale are characterised by similar levels of uncertainty/error (Sokal & Rholf 1994). The second weather station was located ~5.0 km south-east of the centre of the study area, in Sutton Scotney (latitude: 51.169; longitude: -1.331). It comprised Wunderground v.1.15 software and Davis Vantage Pro hardware.

The least squares estimator of the RMA regression slope (m) was calculated as follows:

m = sd(Andover)/sd(SuttonScotney)

where sd(Andover) was the standard deviation for Andover daily temperatures, and sd(SuttonScotney) was the standard deviation for Sutton Scotney daily temperatures.

The RMA regression slope (*m*) was then used to calculate the intercept (*c*):

c = Andover _Mean – [sd(Andover)/sd(SuttonScotney)]* SuttonScotney_Mean

where Andover _Mean was the mean for Andover daily temperatures, and SuttonScotney_Mean was the mean for Sutton Scotney daily temperatures.

The complete RMA regression/conversion equation was derived as follows:

AndoverCALIB = {Andover_Mean – [sd(Andover)/sd(SuttonScotney)]* SuttonScotney_Mean} + [sd(Andover)/sd(SuttonScotney)]* SuttonScotney

where AndoverCALIB was the Andover-equivalent daily temperatures, and SuttonScotney was the Sutton Scotney daily temperatures.

This yielded the following equation:

AndoverCALIB = (0.91456) + 0.96615*SuttonScotney

Where necessary (i.e. where there was missing data from the Andover weather-station), this equation was used to convert environmental data from the Sutton Scotney weather-station into Andover weather-station equivalents.

Foraging activity

Across the three winters, 24 woodcock were fitted with 12 gram radio-tags containing activity tilt-switches (Biotrack TW3, Wareham, UK), (2008/09: n = 2, 2009/10: n= 7, 2010/11: n = 15) (General Methods II). Insufficient data were collected during the winters of 2008/09 and 2009/10, therefore foraging activity was only analysed for the winter of 2010/11. During this winter, activity data were recorded on 71 occasions, across 12 individuals, between 09/12/2010 and

14/04/2011. Of these, 30 recording occasions related to adult migrants (n = 5), 25 to juvenile migrants (n = 5), and 16 to juvenile residents (n = 2). Notably, no data were collected from adult residents.

An automatic data logger (Televilt/TVP Positioning AB, RX-900, Lindesberg, Sweden), powered by a 12 volt car battery, was used to record changes in signal strength and pulse period i.e. the parameters indicative of changes in activity. In addition, date and time (to the nearest second) were recorded. The logger was connected to a three-element directional Yagi antenna, and positioned in a location that enabled signal detection throughout a 24-hour period. Unfortunately, due to the distances between birds tagged with activity tilt-switches, continual signal detection was only possible for one individual at a time.

Activity data were imported into Microsoft Office Excel 2003 (Microsoft Corporation 2003), where data files were split into 24-hour periods (start time: 08:00:00, finish time: 07:59:59). Notably, the logger was not always active for the entire duration, and so the timings of data collection varied between 24-hour periods. Files were then imported into GenStat version 14.0 (VSN International Ltd. 2011) for coding. Variations in pulse rates were used as indicators of activity, whilst continuous pulse rates (whether slow or fast) were taken as indicators of relative inactivity (Duriez 2003). For all individuals, periods of inactivity were defined as pulse rates greater than or equal to 1 200 ms, or less than or equal to 950 ms. All values in between were categorised as periods of activity. To be conservative, cut-off values were set 50 ms lower/higher than the average slow/fast pulse rates calculated across tags, respectively. Using these

cut-offs, it was possible to code data at the minute-level, with "0" representing a minute of inactivity and "1" representing an active minute i.e. a minute containing period(s) of activity. Active minutes were then summed over 1-hour periods to derive hourly counts of activity. These were used to derive 24-hour foraging profiles for individual birds. Furthermore, total activity counts i.e. the sum of hourly activity counts, for day (08:00-18:00) and night (19:00-07:00) time periods, were used to discern differential diurnal and nocturnal foraging patterns across birds.

Night-time habitat occupancy

The frequency with which woodcock remained in woodland at night was examined by coding night locations as 0 (fields) or 1 (woods). Individuals with only one (or no) night locations were excluded from analyses. Locations obtained in October (n = 11) were merged with those in November (n = 108), so as to balance the data across month categories. Similarly, locations obtained in April (n = 3) were merged with those in March (n = 556). Average daily temperatures (see *Temperature data*) matching the dates of each night fix were also added to the dataset, to explore the relationship between temperature and night-time habitat occupancy.

Departure events

Loss of tag-signal was used as an indicator of departure events when birds went undetected for two or more consecutive tracking dates. However, it was important to distinguish likely departure events from tag-failure. Tag-life varied

with battery size (12g = ~6 months, 5g = ~4.5 months) and so, considering this, birds with tags approaching the end of their battery life were excluded from this analysis (n = 2).

Departure events relating to spring-migration were inferred from a loss of tag-signal coinciding with likely spring-migration dates (mid-Feb through to early April). In this analysis, only birds with confirmed migratory status, as determined by stable isotope analysis (General Methods II), were considered. A separate investigation was conducted for departure events preceding those pertaining to spring-migration. This analysis included both resident and migrant birds, with signal-loss considered in relation to average daily temperatures.

Statistical Analyses

Appropriate statistical tests were determined by assessing the distribution of the dependent variable. The Shapiro-Wilk test and visual inspection of histogram plots were used to achieve this (Figure A2.1). Where the dependent variable was found to be normally distributed, a parametric test was used. In cases of non-normality, the non-parametric equivalent was used.

For regression analysis and restricted maximum likelihood methods, the appropriateness of specified error distributions and link functions were determined from the normality of model residuals. Again, the Shapiro-Wilk test and visual inspection of residual composite plots were used. Where binomial and poisson error distributions were specified, the effects of dispersion were assessed by comparing the residual deviance of each model to its corresponding Chi-square

critical value, at the 0.05 level. In cases of over-dispersion, the dispersion parameter was estimated. Otherwise, the dispersion parameter was fixed at one.

Retraps (n = 2) were excluded from all analyses to ensure independence across birds. This enabled datasets containing one measure per bird to be analysed using Generalised Linear Models (GLM). Datasets containing repeated measures per bird, however, necessitated the use of Generalised Linear Mixed Models (GLMM). These enabled "bird" to be incorporated into models as a random factor, thereby controlling for repeated measures and avoiding problems associated with pseudo-replication. All statistical analyses were conducted using GenStat version 14.0 (VSN International Ltd. 2011). A 5% level of significance was used in all statistical tests/models.

Movement patterns

Commuting flights

Distance data were not normally distributed (Shapiro-Wilk: W = 0.8140, $P < 0.001$) but showed a right-skewed distribution. A square root transformation was applied, and, although this did not normalise the data (Shapiro-Wilk: W = 0.9583, $P < 0.001$), it improved the shape of the distribution more so than any other transformation. A GLMM with normal error distribution and identity link function was used to test for the effects of age, status and winter (and their interactions) on the transformed data. Month was also added to the model as a structural (categorical) variable. Winter and month were retained in the model, to control for temporal variation.

Area calculations

Home range estimates were not normally distributed (Ellipses (95%): W = 0.8065, $P < 0.001$; Kernel contours (95%): W = 0.7927, $P < 0.001$; MCP: W = 0.7985, $P < 0.001$) but showed a right-skewed distribution. A log transformation was therefore applied, to normalise the data (Ellipses (95%): W = 0.9624, $P = 0.083$; Kernel contours (95%): W = 0.9659, $P = 0.120$; MCP: W = 0.9699, $P = 0.210$). Paired samples t-tests were used to assess for significant differences between pairs of home range estimators. Generalised Linear Models (GLM), with normal error distribution and identity link function, were used to analyse the transformed home-range data. These GLMs tested for the effects of age, status and winter (and their interactions), with the total number of fixes added to the model as a covariate. Winter was retained in each model, to control for temporal variation, whilst total number of fixes was retained, to account for differential accuracy of home range estimates.

Similarly, areas derived from buffers cropped to polygons, for day and night ranges, were not normally distributed (day: W = 0.8839, $P < 0.001$; night: W = 0.9140, $P < 0.001$) but showed a right-skewed distribution. A log transformation was therefore applied, to normalise the data (day: W = 0.9761, $P = 0.316$; night: W = 0.9805, $P = 0.510$). A Generalised Linear Model (GLM) with normal error distribution and identity link function was used to test for the effects of age, status and winter (and their interactions) on day and night areas. The total number of day/night fixes was also included, as a covariate, to the respective day/night model. Winter was retained in each model, to control for temporal

variation, whilst total number of fixes was retained, to account for differential accuracy.

Core sites

Using the raw data, non-parametric Wilcoxon matched-pairs sign rank tests were used to test for differences between the total number of day and night polygons used, the total number of day and night cores used, and the proportion of fixes found in day polygon-one and night polygon-one (i.e. the day and night primary cores). Following this analysis, the total number of polygons, total number of cores, and total number of fixes in polygon-one were analysed separately, for day and night distributions. Data were analysed using a GLM with Poisson error distribution and log link function applied to the raw data. Each model tested for the effects of age, status and winter (and their interactions) on the data. The total number of day/night fixes was included, as a covariate, in each day/night model. Winter was retained in each model, to control for temporal variation, whilst total number of fixes was retained, to account for differential accuracy. The proportions of day/night fixes between pairs of ranked cores were compared using Wilcoxon matched-pairs sign rank tests.

Behaviour

Foraging activity

Hourly counts of activity were not normally distributed but showed right-skewed distributions. Transformations (square root, log) did not help to normalise the

data, therefore Wilcoxon matched-pairs sign rank tests were applied to the raw data, to assess for significant changes in activity between successive 1-hour intervals. Total day and night activity counts were analysed, separately, using a GLMM with Poisson error distribution and log link function applied to the raw data. Both models tested for the effects of age, status and temperature on the data. Month was incorporated (and retained) in the model, as a structural (categorical) variable, thereby controlling for temporal variation.

Total night activity counts were also analysed in relation to habitat occupancy. Data from birds with unconfirmed locations were excluded from this analysis. A Mann-Whitney U test was performed to assess for significant differences between those occasions when birds (tagged with activity-tilt switches) remained in woodland habitats during the night (seven occasions, across three birds) and those when birds flew out to fields (35 occasions, across nine birds). This habitat occupancy factor was also incorporated into a GLMM, with Poisson error distribution and log link function, to assess for the effects of habitat occupancy and temperature on the data. Month was incorporated (and retained) in the model, as a structural (categorical) variable, thereby controlling for temporal variation.

Night-time habitat occupancy

Total numbers of night-time woodland fixes were not normally distributed (Shapiro-Wilk: W = 0.6362, $P < 0.001$) but showed a right-skewed distribution. A square root transformation was applied, and, although this did not statistically normalise the data (Shapiro-Wilk: W = 0.8458, $P < 0.001$), it improved the shape

of the distribution more so than any other transformation. This transformation allowed a GLM with normal error distribution and identity link function to be specified, which was used to test for the effects of age, status and winter (and their interactions) on the transformed data. Winter was retained in the model, to control for temporal variation.

A separate model was run to test for the effects of average daily temperature, alongside the interaction between month and winter, on the occupancy of woodland habitats at night. A GLMM with binomial error distribution and logit link function was used, with bird as a random factor, and winter and month retained to control for temporal variation.

Results

In total, 77 unique individuals were radio-tagged over three winters (2008/09: n = 22, 2009/10: n = 19, 2010/11: n = 36). Of these, two birds in 2009/10 and four birds in 2010/11 were never found after their initial capture. There were annual fluctuations in the structural composition of each population, yet the ratio of resident to migrant birds was relatively consistent between years (resident-migrant: 2008/09 = 1:3, 2009/10 = 1:2, 2010/11 = 1:2), as was the ratio of adult to juvenile birds (adult-juvenile: 2008/09 = 1:1, 2009/10 = 2:1, 2010/11 = 1:1). Over the three winters combined, 69% of birds were determined to be migrants and 31% residents. Of these, 51% of migrants and 50% of residents were aged as adults (for annual break down see Figure 5.1).

As with most radio-tracking studies, data collection was not equal across all individuals, owing to tag loss or tag retrieval. The former were typically attributed to departure events, whilst tag retrieval occurred under a number of different circumstances. Of all tags, 4% were retrieved from shooting events (on and off the study site), whilst 10% were retrieved following predation events (mammalian: n = 4, avian: n = 3), as indicated by the presence of feathers and/or bones. However, the majority of retrieved tags (21% of all tags) were shed by the birds owing to wear and tear, likely resulting from the occupancy of dense shrubbery/undergrowth. The absence of feathers and/or bones indicative of predation events, and the fact that tags were often found in close proximity to fresh droppings, suggested that birds were alive around the time of tag detachment.

Movement patterns

Preliminary analysis: 24-hour radio-tracking

During the winter of 2008/09, 14 birds were monitored at two-hour intervals for a period of up to 24-hours (24-hours: n = 9, day only: n = 1, night only: n = 4). Detection distances were 10 m in woodland and 20-40 m in open fields, with care being taken not to flush birds. All birds tracked throughout the day (n = 10) were faithful to their woodland sites, with 90% of birds not making any detectable movements. Only one bird was recorded as moving, travelling a distance of approximately 20 m. Since this bird had returned to its original location during the succeeding two-hour interval, this small movement may have been caused by some form of disturbance (not induced by the radio-tracker). Of the birds tracked

throughout the night (n = 13), 92% remained in the field chosen at the beginning of the night, with one bird (8%) moving to an adjacent field. Given the general lack of movement across day and night habitats, it was decided that collecting just one diurnal and one nocturnal fix was sufficient for each day of radio-tracking.

On average, the maximum distance travelled by birds at night was 130 m, whilst during the day movements were negligible. Similar results were found by Duriez *et al.* (2005c); they found that, at night, birds tended to remain in the same field for the duration of the night (80%) and/or within a radius of 150 m (89%), whilst woodcock did not generally leave their diurnal sites, or only moved by walking (usually less than 100 m). These results were used to determine appropriate buffer sizes in the area analysis (see *Methods, Area use*).

Preliminary analysis: breeding relocation events

There is no clear distinction between the end of the non-breeding season and the onset of the breeding season; rather, there exists a transitional period whereby these stages of the annual cycle overlap. During this transitional period, the movements and behaviour of resident birds may change in accordance with nesting and egg-laying events. This is because breeding woodcock have specific habitat requirements (Hoodless & Hirons 2007) that may necessitate birds relocating from non-breeding sites to more suitable breeding areas. As such, commuting flights, home ranges, area estimates and core site use may vary in accordance with breeding relocation events. For purposes of this study, it was necessary to ensure that the movements and behaviours of all birds represented

equal conditions and that those of residents were not being driven by breeding behaviours exclusive to them. Although migrant birds have been known to undertake reproductive display flights ("roding") on the non-breeding grounds, none have been reported as staying to breed (Hoodless & Coulson 1994).

In an attempt to detect the presence of breeding relocation events, the area ranges of birds before mid-February ("before") were compared with those throughout the entire field-season, until the first week of April ("total"). A mid-February (15th) cut-off was used, as this marks the earliest (and is therefore the most conservative) roding date recorded for woodcock in Britain (Raynsford 1959), and roding is an early indicator of breeding behaviour. Any significant shifts found in the area range of residents may be indicative of breeding relocation events, and may have important consequences for subsequent analyses.

Centroid locations were determined for "before" and "total" area ranges, using elliptical (99%) home range estimates calculated in Ranges 8 (version 2.5) (Kenward *et al.* 2008), for day and night fixes, separately (Figure A5.7). Only birds with a minimum of 10 day or 10 night fixes were used to establish "before" ranges (Kenward 2001), whilst a minimum of 10 additional fixes were required for the corresponding "total" day/night ranges. Distances between centroid locations (centroid distance) were then calculated, using the difference between the eastings and northings co-ordinates of the "before" and "total" centroids.

Centroid distances for separated day and night ranges were not normally distributed (Shapiro-Wilk: day, $W = 0.7391$, $P < 0.001$; night, $W = 0.8746$, $P =$

0.004), so a log transformation was applied to normalise the data (Shapiro-Wilk: day, W = 0.9456, P = 0.118; night, W = 0.9328, P = 0.091). This enabled one-sample parametric t.tests to be used. For separated day (n = 31) and night (n = 26) ranges, centroid distances differed significantly from the test mean of 0 (day: two-sided, t = 14.71, d.f. = 30, $P < 0.001$; night: two-sided, t = 19.64, d.f. = 25, $P < 0.001$). Since these results were indicative of significant range shifts between the two time periods, Generalised Linear Models (GLM) were conducted to determine whether differences between the transformed distances were attributable to age and/or status factors. In addition, winter was included (and retained) in the model, as a structural (categorical) variable, to control for temporal variation, whilst the difference in fixes (between before and total time periods) was included (and retained), to account for differential effort/accuracy. For separated day and night ranges, the age-status interaction did not have a significant effect on logged distances (day: GLM, $F_{1, 24} = 1.99$, $P = 0.171$; night: GLM, $F_{1, 19} = 0.93$, $P = 0.347$), nor did age (day: GLM, $F_{1, 25} = 0.27$, $P = 0.605$; night: GLM, $F_{1, 20} = 0.60$, $P = 0.447$), or status (day: GLM, $F_{1, 26} = 0.78$, $P = 0.385$; night: GLM, $F_{1, 21} = 1.96$, $P = 0.176$). Winter (day: GLM, $F_{2, 27} = 0.89$, $P = 0.423$; night: GLM, $F_{2, 22} = 1.37$, $P = 0.274$) and the difference in fixes (day: GLM, $F_{1, 27} = 0.11$, $P = 0.740$; night: GLM, $F_{1, 22} < 0.001$, $P = 0.973$) did not have a significant effect either.

Given there were no significant effects of age and/or status on range shifts, variation in distances cannot be attributed to breeding relocation events. Rather, the significant shifts in range detected by the one-sample parametric t.tests are likely just an artefact of the increased number of fixes over time, resulting in increased range size. As such, the movements and behaviour of all birds can be considered to represent non-breeding events, exclusively, and datasets

encompassing fixes from the entire field-season can be reliably used in subsequent analyses.

Commuting flights

The distance dataset comprised 3 133 distances, collected over three combined winters (2008/09: n = 632, 2009/10: n = 507, 2010/11: n = 1 994) (Figure 5.2). Across all birds (n = 68), the maximum and minimum distances travelled were 4 417 m and 0 m, respectively, with a mean distance (± standard error, SE) of 661 m (± 12 SE). Individual mean distances varied from 126 m (± 40 SE) to 3 169 m (± 13 SE), representing a mean difference of 3 043 m.

A three-way interaction between age, status and winter had a significant effect on distance travelled (GLMM, $F_{2, 58.8} = 3.94$, $P = 0.025$) (Table 5.1). Month also had a significant effect (GLMM, $F_{4, 3103} = 19.14$, $P < 0.001$). Given this, separate analyses were conducted for each winter, to enable age, status and month effects to be better assessed.

For the 2008/09 winter, there was a significant three-way interaction between age, status and month on distance travelled (GLMM, $F_{1, 602.3} = 14.14$, $P < 0.001$). Overall, adult residents travelled greater distances than juvenile residents and both age-classes of migrant. However, in December, adult residents travelled shorter distances than adult migrants (Table 5.2).

For the 2009/10 winter, there was insufficient data to run a three-way interaction, but two-way interactions between age and status (GLMM, $F_{1, 11.5} =$

9.22, $P = 0.011$), and status and month (GLMM, $F_{4, 486.4} = 7.61$, $P < 0.001$) were significant. Generally, adult residents travelled shorter distances than conspecifics, and adult migrants travelled greater distances than juveniles (Table 5.3).

For the 2010/11 winter, a three-way interaction between age, status and month had a significant effect on distance travelled (GLMM, $F_{2, 1954.1} = 10.31$, $P < 0.001$). Overall, adult residents travelled shorter distances than juvenile residents and both age-classes of migrant. Notably, this trend with migrant birds was apparent in January and February, but in March/April, the converse was found to be true i.e. in March/April adult residents travelled greater distances than migrant birds. Adult migrants were found to travel greater distances than juvenile migrants, although the extent of this difference lessened as the winter progressed. Adult migrants were also found to travel shorter distances than juvenile residents. Juvenile residents travelled greater distances than juvenile migrants (Table 5.4).

Area use

A significant difference was found between pairs of home range estimators: Ellipse-Kernel, n = 55, t = 16.66, $P < 0.001$; Ellipse-MCP, n = 52, t = 9.30, $P < 0.001$; Kernel-MCP, n = 52, t = -5.19, $P < 0.001$. Given this, subsequent analyses were run for each home range estimator, independently.

Areas derived from the ellipse (95%) home range estimator ranged from 8.8 ha to 776.7 ha, across all birds, with a mean of 189.4 ha (± 25.71 SE). The variation in area estimates were found to be significantly affected by a three-way interaction

between age, status and winter (GLM, $F_{1, 43} = 4.54$, $P = 0.039$), whilst controlling for number of fixes (GLM, $F_{1, 43} = 0.32$, $P = 0.573$). The mean areas for this three-way interaction (i.e. across age, status and winter) are shown in Table 5.5. Following this result, the dataset was split according to winter and further analyses conducted. For the 2008/09 winter, a two-way interaction between age and status could not be run, as data were lacking for juvenile resident birds. Therefore, in a model comprising individual terms only, status (GLM, $F_{1, 12} = 11.92$, $P = 0.018$) was found to significantly affect the area derived from the ellipse (95%) home range estimator, whilst age (GLM, $F_{1, 12} = 4.74$, $P = 0.050$) and total number of fixes (GLM, $F_{1, 12} = 0.77$, $P = 0.245$) had non-significant effects. On average, ellipse (95%) home range estimates were larger for residents than for migrants (resident: 408.0 ha ± 99.31 SE, migrant: 127.3 ha ± 42.75 SE). For the 2009/10 winter, a two-way interaction between age and status (GLM, $F_{1, 7} = 7.28$, $P = 0.031$) was found to have a significant effect, whilst controlling for total number of fixes (GLM, $F_{1, 7} = 4.58$, $P = 0.070$). On average, adult migrants had larger ellipse (95%) home range areas than juvenile migrants (mean difference = 72.6 ha), but used a smaller area than juvenile residents (mean difference = 51.3 ha). Adult residents had home ranges smaller than those of juvenile residents (mean difference = 233.4 ha) and both age-classes of migrant (adult migrant: mean difference = 182.1 ha, juvenile migrant: mean difference = 109.5 ha). Juvenile residents typically had larger home range areas than their migrant counterparts (mean difference = 123.9 ha) (means and standard errors are reported in Table 5.5). No significant effects were found for the winter of 2010/11 (GLM, age: $F_{1, 23} = 0.01$, $P = 0.927$; status: $F_{1, 24} = 0.64$, $P = 0.432$; number of fixes: $F_{1, 25} = 0.69$, $P = 0.413$), however, this was likely attributable to the large standard errors associated with adult residents.

Similarly, areas derived from the kernel contour (95% cores) home range estimator ranged from 5.5 ha to 471.2 ha, across all birds, with a mean of 101.5 ha (± 14.84 SE). The variation in area estimates were found to be significantly affected by a three-way interaction between age, status and winter (GLM, $F_{1, 43}$ = 5.30, P = 0.026), whilst controlling for total number of fixes (GLM, $F_{1, 43}$ = 0.06, P = 0.807). The mean areas for this three-way interaction (i.e. across age, status and winter) are shown in Table 5.6. Following this result, the dataset was split according to winter and further analyses conducted. For the 2008/09 winter, status (GLM, $F_{1, 13}$ = 7.97, P = 0.014) was found to significantly affect the area derived from the kernel contour (95% cores) home range estimate, whilst age (GLM, $F_{1, 12}$ = 3.19, P = 0.099) and total number of fixes (GLM, $F_{1, 13}$ = 0.97, P = 0.342) had non-significant effects. On average, kernel contour (95% cores) home range estimates were larger for residents than for migrants (resident: 205.3 ha ± 13.44 SE, migrants: 55.2 ha ± 18.64 SE). For the 2009/10 winter, a two-way interaction between age and status (GLM, $F_{1, 7}$ = 9.20, P = 0.019) was found to have a significant affect, as was the number of fixes (GLM, $F_{1, 7}$ = 7.77, P = 0.027, estimate = 0.03 (± 0.01 SE), t(7) = 2.79). On average, adult migrants had larger kernel contour (95% cores) home range areas than juvenile migrants (mean difference = 10.0 ha), but smaller areas than juvenile residents (mean difference = 41.1 ha). Adult residents had home ranges smaller than those of juvenile residents (mean difference = 128.2 ha) and both age-classes of migrant (adult migrant: mean difference = 87.1 ha, juvenile migrant: mean difference = 77.1 ha). Juvenile residents typically had larger home range areas than their migrant counterparts (mean difference = 51.1 ha) (means and standard errors are reported in Table 5.6). No significant effects were found for the winter of 2010/11 (GLM, age: $F_{1, 23}$ = 0.00, P = 0.987; status: $F_{1, 24}$ = 1.07, P = 0.311; number of fixes:

$F_{1, 25}$ = 0.44, P = 0.514), however, this was likely attributable to the large standard errors associated with adult residents.

Areas derived from the MCP home range estimator ranged from 7.1 ha to 603.4 ha, across all birds, with a mean of 135.1 ha (± 19.76 SE). The variation in area estimates were not significantly affected by age (GLM, $F_{1, 44}$ = 1.46, P = 0.234), status (GLM, $F_{1, 47}$ = 2.72, P = 0.106), winter (GLM, $F_{2, 48}$ = 0.07, P = 0.935), or number of fixes (GLM, $F_{1, 48}$ = 0.01, P = 0.942) (Table 5.7).

Area estimates derived from buffers cropped to polygons were analysed across individuals for day (n = 57) and night (n = 55) ranges, separately. For the former, area estimates were significantly affected by status (GLM, $F_{1, 52}$ = 4.83, P = 0.032), but not by age (GLM, $F_{1, 51}$ = 2.22, P = 0.142), or winter (GLM, $F_{2, 52}$ = 0.37, P = 0.690). The total number of day fixes did not have a significant effect either (GLM, $F_{1, 52}$ = 0.11, P = 0.744). On average, resident birds utilised a greater day-time area than migrants (mean: resident, 10.1 ha (± 1.38 SE); migrant, 6.7 ha (± 0.76 SE)). For the night range, area estimates were not significantly affected by age (GLM, $F_{1, 49}$ = 0.20, P = 0.655), status (GLM, $F_{1, 50}$ = 0.35, P = 0.555), or winter (GLM, $F_{2, 51}$ = 0.04, P = 0.965). The total number of night fixes, however, did have a significant effect (GLM, $F_{1, 51}$ = 4.65, P = 0.036, estimate = 0.005 (± 0.002 SE), t(51) = 2.16).

Core sites

Across the three winters (combined), the maximum number of polygons used ranged from 2-14 for day distributions (n = 57) and 1-20 for night distributions (n

= 55), with both yielding an average of seven. At the individual level, the total number of day polygons used did not differ significantly from the total number of night polygons (n = 49, t = 490.0, $P = 0.212$). Similarly, the total number of day cores used did not differ significantly from the total number of night cores (n = 45, t = 402.5, $P = 0.107$).

Considering day and night ranges separately, the total number of day polygons used did not vary significantly with age (GLM, $F_{1, 51} = 0.23$, $P = 0.632$), or status (GLM, $F_{1, 52} = 3.14$, $P = 0.082$). There was, however, a significant effect of winter (GLM, $F_{2, 53} = 3.95$, $P = 0.025$). On average, nine polygons were used during the winter of 2008/09 (mean = 8.5 ± 0.84 SE), eight during the winter of 2009/10 (mean = 8.1 ± 1.00 SE) and six during the winter of 2010/11 (mean = 6.0 ± 0.54 SE). There was no significant effect attributable to the total number of fixes (GLM, $F_{1, 53} = 0.64$, $P = 0.428$). Similarly, the total number of night polygons used did not vary significantly with age (GLM, $F_{1, 49} = 1.58$, $P = 0.215$), or status (GLM, $F_{1, 50} = 2.65$, $P = 0.110$). There was also a non-significant effect of winter (GLM, $F_{2, 51} = 0.51$, $P = 0.605$), whilst there was a significant effect attributable to the total number of fixes (GLM, $F_{1, 51} = 6.49$, $P = 0.014$, estimate = 0.01 (± 0.004 SE), t(51) = 2.55, antilog of estimate = 1.01). The mean proportions of fixes found within polygons were plotted for day (Figure 5.3) and night (Figure 5.4) locations.

Across the three winters (combined), the number of day cores ranged from 1-6, yielding an average of three. The proportion of day-polygons representing cores was 36% (± 3 SE) in 2008/09 (n =17), 41% (± 6 SE) in 2009/10 (n = 13), and 36% (± 3 SE) in 2010/11 (n = 27). The total number of day cores used did not vary significantly with age (GLM, Wald $X^2 = 1.540$, d.f. = 1, 52, $P = 0.215$), status

(GLM, Wald X^2 = 0.083, d.f. = 1, 51, P = 0.744), or winter (GLM, Wald X^2 = 5.209, d.f. = 2, 53, P = 0.074). There was also no significant effect attributable to the total number of day fixes (GLM, Wald X^2 = 0.087, d.f. = 1, 55, P = 0.768).

For night distributions, the number of core areas used ranged from 1-7 across the three winters (combined), yielding an average of two. The proportion of night-polygons representing cores was 36% (± 5 SE) in 2008/09 (n = 16), 43% (± 5 SE) in 2009/10 (n = 12), and 34% (± 3 SE) in 2010/11 (n = 27). The total number of night cores used did not vary significantly with age (GLM, Wald X^2 = 1.272, d.f. = 1, 52, P = 0.259), status (GLM, Wald X^2 = 0.227, d.f. = 1, 49, P = 0.633), or winter (GLM, Wald X^2 = 1.129, d.f. = 2, 50, P = 0.569). There was also no significant effect attributable to the total number of night fixes (GLM, Wald X^2 = 2.711, d.f. = 1, 53, P = 0.100).

Behaviour

Foraging activity

Profiles depicting individual foraging activity, over a 24-hour period, revealed intra-individual variation between dates (Figure 5.5). Boxplots for day and night activity counts, across all individuals, revealed inter-individual variation within each 1-hour interval (Figure 5.6). Means for day activity counts ranged from one to 45 minutes per hour, with an overall average of 16 minutes per hour. At night, means ranged from one to 50 minutes per hour, with an overall average of 21 minutes per hour. Activity counts between successive hours (e.g. 08:00-09:00, 09.00-10:00 etc.) across recording periods (n) did not differ significantly, except

between 15:00 and 16:00 (t = 142, n = 38, P = 0.001), 22:00 and 23:00 (t = 333, n = 45, P = 0.046), 02:00 and 03:00 (t = 240.5, n = 40, P = 0.028), and 04:00 and 05:00 (t = 339.5, n = 49, P = 0.006).

Assessing the variation for total day-time activity counts, a GLMM revealed no significant effects of age (GLMM, $F_{1, 30} = 0.31$, $P = 0.582$), or average daily temperature (GLMM, $F_{1, 31} = 3.51$, $P = 0.070$). There was, however, a significant effect of status (GLMM, $F_{1, 32} = 9.76$, $P = 0.004$) and month (GLMM, $F_{4, 32} = 16.6$, $P < 0.001$). On average, migrants were found to be more active during the day than residents (migrant: n = 28, back-transformed mean = 155.4 minutes, raw-data mean = 189.0 minutes ± 24.85 SE; resident: n = 10, back-transformed mean = 81.4 minutes, raw-data mean = 121.6 minutes ± 25.64 SE) (Figure 5.7). The magnitude of the effect, calculated against migrant birds, was -0.65 (± 0.21 SE). Across all birds, activity was found to be lowest in January and highest in February (Table 5.8). A GLMM for total night activity counts revealed no significant effects of age (GLMM, $F_{1, 7.1} = 0.00$, $P = 0.960$), status (GLMM, $F_{1, 11.6} = 2.69$, $P = 0.128$), average daily temperature (GLMM, $F_{1, 45.6} = 0.02$, $P = 0.877$), or month (GLMM, $F_{4, 38.8} = 0.70$, $P = 0.597$).

Total activity counts for birds that remained in woodland habitats throughout the recording period were isolated from those showing the typical behaviour of flying out to fields at night. Activity profiles for these birds appear to show higher levels of activity at dawn and dusk (Figure 5.8). Averages for total night activity counts were found to differ significantly between those occasions when woodland habitats were occupied at night, compared to those when fields were occupied (Mann-Whitney U: U = 29.0, $P = 0.001$). On average, night activity was lower for

the former (woodland: mean = 71.57 minutes (± 24.73 SE), median = 59 minutes; fields: mean = 327.1 minutes (± 34.22 SE), median = 281 minutes). A GLMM revealed the same trend, with a significant effect of habitat-occupancy on total night activity counts (GLMM, $F_{1, 31.5} = 10.11$, $P = 0.003$). Back-transformed means were 54.6 minutes for birds occupying woodland habitats at night, compared to 239.1 minutes for birds occupying fields at night. The magnitude of the effect, calculated against field occupancy, was -1.48 (± 0.46 SE). Average daily temperature (GLMM, $F_{1, 34.2} = 0.09$, $P = 0.771$) and month (GLMM, $F_{4, 28.1} = 1.36$, $P = 0.274$) were not significant.

Night-time habitat occupancy

Nocturnal locations were assessed across the three winters, with results based on data from 21 individuals in 2008/09, 16 individuals in 2009/10, and 32 individuals in 2010/11. The percentage of birds occupying woodland habitats at night, on one or more occasion, was calculated as 43% in 2008/09, 31% in 2009/10 and 81% in 2010/11, with an overall value of 58%, for the three winters combined. Of these, the mean proportion of night fixes spent in woodland habitats was 21% (± 5 SE) for birds in 2008/09, 35% (± 13 SE) in 2009/10, and 18% (± 3 SE) in 2010/11, with an overall average of 21% (± 3 SE), for the three winters combined. The age-status composition of birds occupying woodland habitats at night, as proportions of the entire study population (n = 69), were as follows: adult resident = 9%, juvenile resident = 13%, adult migrant = 13%, and juvenile migrant = 23%.

A GLM found no significant effects of age (GLM, $F_{1, 64} = 2.19$, $P = 0.144$), or status (GLM, $F_{1, 63} = 1.00$, $P = 0.322$), on total numbers of night-time woodland fixes. Notably, winter was found to have a significant effect (GLM, $F_{2, 65} = 3.72$, $P = 0.030$), with total numbers of night-time woodland fixes significantly greater in the 2010/11 winter (estimate = 0.72 (± 0.33 SE), t(65) = 2.17, $P = 0.034$). Total number of fixes was also found to have a significant effect (GLM, $F_{1, 65} = 7.41$, $P = 0.008$, estimate = 0.02 (± 0.01 SE), t(65) = 2.72).

Considering habitat occupancy each night to be independent, a GLMM revealed no significant effects of average daily temperature (GLMM, Wald $X^2 = 2.30$, d.f. = 1, 2.30, $P = 0.129$) on night-time habitat occupancy. However, a two-way interaction between month and winter was found to be significant (GLMM, Wald $X^2 = 22.22$, d.f. = 8, 2.78, $P = 0.005$). Results revealed that woodland occupancy at night was highest in January for the 2008/09 (12%) and 2009/10 (21%) winters, whilst, in 2010/11, night-time woodland occupancy was greatest in December (34%). The lowest proportions occurred in February during the 2008/09 (3%) and 2010/11 (8%) winters, whilst, in 2009/10, no woodland habitats were occupied at night during October/November. The proportions of nights that birds spent in woodland habitats for each winter, stratified by month, are reported in Table 5.9.

Departure events

In total, there were 28 instances of tag-signal loss that could be attributed to spring-migration departures (2008/09: n = 9, 2009/10: n = 6. 2010/11: n = 13). Departure dates ranged from 14 February to 07 April (Table 5.10), but the majority of departing birds (75%) left in late March/early April. Notably, there

were only two departures in February (7%) and five departures between 1 and 15 March (18%).

Departure events preceding those associated with spring-migration were also considered. Such events occurred during cold spells in the winters of 2008/09 and 2009/10. Considering the total number of tags that were active between the first and last departures (i.e. the number of birds actively being tracking during the departure period), the proportion of birds leaving the study area was determined to be 75% in 2008/09 (n = 9) and 80% in 2009/10 (n = 8). In addition, the age and status composition of departed birds were calculated as proportions of the active population. In 2008/09, 100% of adult residents departed (n = 3), 67% of adult migrants (n = 2), and 67% of juvenile migrants (n = 4). In 2009/10, 75% of adult residents departed (n = 3), 100% of adult migrants (n = 3), and 67% of juvenile migrants (n = 2). Notably, there were no juvenile residents actively being tracked during the 2008/09 or 2009/10 departure periods. Of departing birds, migrants generally departed before residents. In 2008/09, 86% of departing migrants left before departing residents. In 2009/10, 80% of departing migrants left before departing residents. Of all departed birds, 100% reappeared in 2008/09 and 50% in 2009/10. Departure events were also considered in relation to average daily temperatures (2008/09: Figure 5.9, 2009/10: Figure 5.10). From the figures, it appears that departures generally succeed or coincide with decreasing temperatures. Furthermore, the majority of departures seem to occur when temperatures drop to 1°C or below.

Discussion

Over the course of the three winters (2008/09, 2009/10, and 2010/11), 10% of tags were retrieved following predation events. Although stoats *Mustela erminea* are known to occasionally predate upon woodcock (Hoodless 1994a), red foxes *Vulpes vulpes* were considered the most likely mammalian predator to be encountered across the study site (despite control efforts). Close inspection of one tag (and the surrounding retrieval site), however, was suggestive of a domestic cat attack. In addition to mammalian predation, there was evidence for avian attacks, most likely from tawny owl *Strix aluco*. Indeed, the killing of woodcock by avian predators, such as sparrowhawk *Accipiter nisus*, goshawk *Accipiter gentilis*, and tawny owl, have all been previously documented (Zomerdijk 1983; Newton 1986; Hoodless 1994a; Hoodless & Coulson 1998; Toyne 1998).

The ratio of resident to migrant birds caught over the study period was 1:2, which was not as extreme as might be expected, given current population estimates. The British resident population is believed to comprise approximately 157 000 individuals (Hoodless *et al.* 2009), whilst the migratory population is estimated to be between 800 000 (Hirons & Linsley 1989) and 1.4 million birds (The RSPB 2012). This would yield a resident to migrant ratio between 1:5 and 1:9, respectively. However, it is important to note that the structural composition of woodcock sampled on the study site might be biased by capture time, date and location. The study site used here was known to host a reasonable breeding and non-breeding population (Andrew Hoodless, pers. comm), yet other areas of Britain have an absence of breeding birds and/or attract a larger number of migrants (e.g. Cornwall, see Chapter 3).

Movement patterns

Commuting flights

In this study, the average (661 m) and maximum (4 417 m) distances travelled by woodcock during commuting flights were greater than those previously reported for woodcock in Britain over winter. For eight radio-tagged woodcock tracked in Cornwall in 1992, the mean distance of flights (± standard deviation, SD) to fields was 289 m (± 195 SD), with a maximum of 780 m (Hoodless 1994a). For five woodcock tracked in Cornwall over the winters of 1977/78 and 1978/79, the mean distance was 444 m (± 388 SD), with a maximum of 1 370 m (Hirons & Bickford-Smith 1983). The average distance calculated in this study was therefore 1.5 to 2.3 times greater than these previous reports, with a maximum distance 3.2 to 5.7 times greater.

The distances travelled by Eurasian woodcock during commuting flights reflected a large degree of intra and inter-individual variation. Some birds were consistent in the approximate distance travelled, as reflected by their small average ranges. This likely represented movements to/from the same locations, which is indicative of site faithfulness. Indeed, such behaviour is commonly reported for woodcock during the non-breeding season (Wilson 1983; Hoodless 1994a,b). Conversely, other birds showed great variability in the distances travelled, reflective of alternative site use. Following from this, the variation in distances travelled during commuting flights was assessed in relation to temporal effects (winter, month) and bird characteristics (age, status). The results suggested that

temporal effects may have a large impact on woodcock behaviour, at both the intra- and inter-annual level.

Any number of conditions may vary over time, and these will often interact in complex ways to affect higher organisms. For instance, changes in habitat, food abundance and climate are all likely to impact woodcock behaviour during the non-breeding season, yet these may not be mutually exclusive. Across the study period, the only appreciable change, within and between years, was in climate. During the winter of 2008/09, conditions on the study site were typical for the time of year (i.e. they complied with climatic averages, Met Office 2012a), although average daily temperatures (see *Temperature data*) were mild for December (mean 5°C). During the winter of 2009/10, average daily temperatures were also mild in December (mean 5°C), but heavy snowfalls were experienced in February. During 2010/11, severe winter weather conditions were experienced in December, whilst temperatures in February were mild (mean 7°C). These monthly and annual climate patterns potentially explain the temporal trends found in the distance analysis. During 2008/09 and 2009/10, the furthest distances were travelled in December, whilst, during 2010/11, the furthest distances were travelled in February. Furthermore, during 2009/10, the shortest distances were travelled in February, whilst, during 2010/11, the shortest distances were travelled in December. Considering these results in relation to the aforementioned temporal climate changes, it appears that birds travel greater distances when conditions are milder, whilst during colder periods, the converse is true. This makes ecological sense; birds are more likely to be able to afford the metabolic costs associated with increased travelling distance when conditions are

milder, compared to colder periods when thermoregulatory costs are higher (Boos *et al.* 2005).

Temporal effects were found to interact with bird characteristics (age, status). Overall, adult residents were found to travel greater distances than conspecifics during the winter of 2008/09. In contrast, during the winters of 2009/10 and 2010/11, adult residents were found to travel shorter distances than conspecifics. Again, considering these results in relation to the aforementioned temporal climate changes, it appears that adult residents travel greater distances when conditions are milder, whilst during colder periods, the converse is true. Since adult residents are likely to have experience and prior knowledge of the surrounding area, this group is more likely to invest in longer commuting flights when conditions are mild, in order to seek out the best feeding grounds (comprising a rich supply of earthworms, at relatively low predation risk). However, during colder periods, adult residents are probably in a better position to reduce travelling distance and conserve metabolic costs, compared to conspecifics.

Area use

Significant differences were found between home range estimators based on the same data and, as a consequence, different trends were apparent depending on the home range estimator under analysis. For studies that are concerned with home range size for conservation purposes, this highlights the need for caution when basing results on a single home-range estimator. Furthermore, the

variability between home range estimators is problematic for making comparisons between studies using different estimators.

Irrespective of the home-range estimator used here, maximum areas greatly exceeded those calculated in similar studies. For example, in this study, the maximum MCP area calculated for combined day and night fixes, across all birds, was 603.4 ha (2008/09: 453.0 ha, 2009/10: 190.6 ha, 2010/11: 603.4 ha), whilst the equivalent value for woodcock tracked in Cornwall in 1992 was 57.5 ha (Hoodless 1994a), and 22 ha for woodcock tracked in Cornwall across the winters of 1977/78 and 1978/79 (Hirons & Bickford-Smith 1983). Thus, the maximum MCP area calculated here is 10 to 27 times greater than these previous reports. Whilst these results appear to reflect range expansion over time, this is not necessarily the case. First, the sample sizes of the two previous studies were small, based on 13 (Hoodless 1994a) and five (Hirons & Bickford-Smith 1983) woodcock, and so the home ranges calculated in these studies might not be an accurate representation of the area covered by a larger population. Second, both previous studies were based in Cornwall, where non-breeding habitat typically comprised grass fields (Hirons & Bickford-Smith 1983; Hoodless 1994a). This habitat type is believed to offer optimal nocturnal feeding opportunities for woodcock, supporting high densities of earthworms (Duriez *et al.* 2005b), and is typically selected over other habitat types (Duriez *et al.* 2005b; Chapter 4). The high proportion of grass fields available to woodcock in Cornwall would mean that birds would not have to fly very far to find optimal feeding habitats, thus potentially explaining their small home ranges. In contrast, home range estimates in this study were calculated for birds residing in a mixed farming landscape in Hampshire. Therefore, birds may need to travel further to locate suitable feeding grounds,

resulting in increased home ranges. Indeed, changes in home range size in relation to food availability have been documented in other bird species, such as raptors (Kenward 1982; Village 1982), ducks (Legagneux *et al.* 2009) and grouse (Whitaker *et al.* 2007). Third, woodcock residing in Cornwall during the non-breeding season are predominantly migratory and/or juvenile birds, whilst birds in Hampshire comprise a mixed population of residents and migrants. Since differences in bird characteristics may account for the observed variation in home range areas, this was further investigated.

Intuitively, trends for home range estimates reflected those of commuting flights. A significant interaction between age, status and winter was found for ellipse (95%) and kernel contour (95% cores) home range estimators, although no significant effects were found for the MCP estimator. During the winter of 2008/09, residents tended to use larger ellipse (95%) and kernel contour (95% cores) home range areas, compared to migrants. Conversely, during the 2009/10 winter, adult residents tended to use smaller ellipse (95%) and kernel contour (95% cores) home range areas, compared to conspecifics. Thus, as found in the analysis of distances travelled during commuting flights, the trends in home range area during the winter of 2008/09 show the converse of those in 2009/10. As previously discussed, this individual variation exhibited between years likely reflects temporal (inter-annual) changes in climate, as environmental conditions are known to influence woodcock behaviour, through associations with thermoregulation and/or the starvation-predation risk trade-off (Boos *et al.* 2005; Duriez *et al.* 2005c; Brana *et al.* 2010). Notably, there was an absence of any trends for the winter of 2010/11, probably due to the large standard errors found amongst adult residents.

Woodcock home ranges gave estimates of complete area coverage (for day and night fixes, combined). Since this included the area traversed by birds (Burt 1943), the large distances travelled by birds during commuting flights will have resulted in increased home range areas. Areas derived from buffers cropped to polygons, however, were thought to better reflect actual area use by woodcock. For day ranges only, residents were found to use a larger area than migrants, whilst at night, no such trends were apparent. This result may reflect the ability of resident birds to use their spatial knowledge to exploit optimal diurnal feeding sites, at relatively low predation risk (Duriez *et al.* 2005b). Although day-time feeding is typically considered supplementary to the preceding night's feeding activity, if birds are able to meet their energy requirements from day-time feeding alone, they may not need to feed in fields that night. This would enable them to avoid the higher thermoregulatory costs associated with lower night-time temperatures and the higher levels of predation apparent in fields (Duriez *et al.* 2005b). Given that earthworm densities are typically lower in diurnal sites (Duriez *et al.* 2005b; Chapter 4) and that, over the course of the non-breeding season, the accessibility and/or availability of earthworms changes (Edwards & Lofty 1972), the larger diurnal areas used by residents may reflect an ability to adapt to these spatio-temporal changes in earthworms. For migrants, however, finding such high quality diurnal sites would involve trial and error, and this would be more energetically costly, owing to a lack of experience and familiarity with the study site. Alternatively, movement within and between diurnal patches might reflect the exploitation of different prey items (e.g. beetles and/or other high protein prey) to those taken at night. Whilst this has yet to be shown for woodcock, other wader species are known to consume different prey items by day (Hulscher 1976; Dugan 1981). Residents may therefore be able to use their

experience and familiarity with key sites to find alternative dietary items, whilst migrants lack such knowledge.

Core sites

The number of polygons utilised by birds, both during the day and night, varied between individuals, yet there were no temporal (winter), age, or status effects to account for this variation. Furthermore, at the individual level, the total number of polygons used during the day did not differ significantly from the total number of polygons used at night. Given that woodcock typically forage at night, it might be expected that birds utilise a greater number of sites/polygons during this time. However, the lack of difference between the numbers of day and night sites/polygons used suggests that birds may apply the same site-use strategy to both day and night ranges i.e. birds that are site-faithful during the day are site-faithful at night, whilst birds that utilise a large variety of sites during the day also utilise a large number of night-time sites. This finding is in contrast to the work of Duriez *et al.* (2005d) who found differences in diurnal and nocturnal site-use strategies.

Polygons categorised as cores were a distinct subset, representing areas of regular activity. The number of cores utilised by birds both during the day and night varied between individuals, yet there were no temporal (winter), age, or status effects to account for this variation. At the individual level, the total number of cores used during the day did not differ significantly from the total number of cores used at night. Variation in the proportions of fixes between cores was statistically assessed, in an attempt to discern the areas (cores) of highest

activity. For both day and night fixes, results revealed significant differences between pairs of successive cores, up to polygon number four. Since the differences between core pairings, listed in ascending order, represented declines in activity, this enabled cores to be ranked as primary, secondary, tertiary and quaternary cores. No significant differences were found between additional core pairings (where analyses were possible); this suggests that activity across remaining cores was similar.

Despite the suggestion that woodcock may adopt differential site-use strategies over the course of the non-breeding season (Duriez *et al.* 2005d), all birds in this study had a distinct primary core that represented the area/polygon of highest activity. Whilst the frequency of primary core use did vary between individuals, there were no apparent trends attributable to age or status characteristics. There was, however, an effect of winter on primary core use during the day. In 2010/11, the proportions of diurnal fixes in primary cores (polygon one) were greater than in other years, suggestive that birds were more site-faithful to diurnal sites during the winter of 2010/11. This effect is likely to be attributable to the severe weather conditions experienced during the winter of 2010/11 (Met Office 2010b, 2012a). Although severe winter weather conditions are believed to induce cold-weather movements, whereby birds leave their existing sites in search of milder climes and more suitable feeding grounds, such departure events were not apparent during the 2010/11 winter (see *Departure events*). Rather, it appears that birds chose to remain on the study site and occupy familiar sites (typified by the primary core), as opposed to risking the high energetic costs associated with searching for alternative sites.

Behaviour

Foraging activity

Although a qualitative analysis of individual activity profiles revealed intra- and inter- individual variation, general trends were also apparent. First, commuting flight times were easily identifiable, and these seemed to coincide within an hour of sun-rise/set times, in accordance with other studies (Brana *et al.* 2010). Notably though, commuting flights may also be influenced by prevailing cloud conditions (Hirons & Bickford-Smith 1983; Brana *et al.* 2010), and/or air temperatures (Brana *et al.* 2010). Second, all birds showed a degree of day time activity. Since activity is synonymous here with feeding, this suggests that feeding during the day is an important component of woodcock non-breeding season ecology. Indeed, day-time feeding has been reported for woodcock in Cornwall (Hoodless 1994a) and France (Duriez *et al.* 2005c). Third, birds that showed high levels of activity during the day, typically showed lower levels of activity at the night, whilst the converse was also true. This finding is intuitive, as activity during the night will be dependent on feeding success earlier that day, whilst feeding during the day will be dependent on feeding success the preceding night.

Analysis of total counts for day activity revealed that migrants are typically more active during the day than residents, which suggests that migrants are undertaking more daytime feeding than their resident counterparts. Although daytime feeding is common across both groups, the heightened activity levels of migrants suggest these birds might be continually failing to meet their energy

demands at night, and/or have a tendency to occupy low quality (food-poor) daytime sites. Since earthworm densities are typically higher in fields than woodlands (Duriez *et al.* 2005b), the former is unlikely to be the constraining factor. Rather, it is more likely that the latter influences daytime activity. Although not investigated here, the depletion of resources might also be an important consideration in habitats, such as woods, where earthworm densities tend to be lower. Most studies have found bird predation to have only a minor effect on earthworm populations, with depletion ranging between 3-11% (Judas 1989). However, Bengtson *et al.* (1976) reported a depletion of 50%, following 22 days of predation by European golden plovers *Pluvialis apricaria*.

There were no age or status effects on total counts of night activity, although this is not surprising. Woodcock are generally considered nocturnal feeders in the non-breeding season (Hirons & Bickford-Smith 1983; Duriez 2003), and given that densities of earthworms are typically high in night locations (e.g. grass fields) (Duriez *et al.* 2005b; Chapter 4), the depletion effect is probably negligible. This would enable all birds to feed, at night, without constraint. Some birds, however, will remain in daytime (woodland) habitats during the night (see *Night-time habitat occupancy*). Here, such birds were found to have significantly lower activity (feeding) levels than birds occupying fields. Since there were no temporal effects, or effects of average daily temperature, this result supports the suggestion that birds remain in woodland habitats at night when they have sufficient food reserves (Duriez *et al.* 2005c). In doing so, birds do not incur the risks and energetic costs associated with flying out to fields at night (Lima & Dill 1990).

Night-time habitat occupancy

Since earthworms comprise the primary prey for woodcock during the non-breeding season (Granval 1987), the main benefit of flying to grass fields at night is the higher density of earthworms, compared to woodlands (Granval & Bouche 1993; Duriez *et al.* 2005b). However, in accordance with studies in France (Duriez *et al.* 2005c), it is apparent that birds will, on occasion, remain in woodlands during the night. The decision to do so has been correlated with mean air temperatures at night, with birds remaining in diurnal sites on colder nights (Duriez *et al.* 2005c). Whilst, in this study, there was no direct influence of temperature on night-time habitat occupancy, the temporal effects found (month and winter) appear to coincide with colder periods. For instance, the highest proportions of fixes in woodland habitats were found to occur in January during the winters of 2008/09 and 2009/10, and in December during the 2010/11 winter. These were months when weather conditions were poor (Met Office 2010b, 2012a). Alternatively (or perhaps in addition to), the decision to remain in woodland habitats at night might be linked to foraging success during the day and/or the starvation-predation risk trade-off.

In accordance with the starvation-predation risk trade-off, it is favourable for woodcock to feed in areas of high earthworm biomass, whilst simultaneously reducing the risk of predation (Duriez *et al.* 2005b,c). Fields offer optimal nocturnal feeding opportunities for woodcock, supporting high densities of earthworms (Duriez *et al.* 2005b), yet predation tends to be higher in fields than in woods. Indeed, Duriez (2003) found that at least 75% of woodcock deaths occurred in fields. The decision to remain in woodland at night may therefore be

reflective of the trade-off between foraging success and predation risk (Lima & Dill 1990). Depending on foraging success during the day, it may be more beneficial for birds to remain in woodland during the night, thus avoiding the higher predation risk associated with feeding in fields. Indeed, it was found in France that young forest stands with rich soil (mull humus) and dense shrub strata appear to offer the best balance between food supply and protection from predators (Duriez *et al.* 2005b). Furthermore, it has been suggested that woodcock may remain in optimal diurnal habitats at night to protect such sites from conspecifics (Duriez *et al.* 2005c). However, work is needed to determine whether territoriality exists in non-breeding woodcock, and what impacts this may have on non-breeding season behaviour.

Occupancy of optimal diurnal sites may thus provide a sufficient compromise between feeding success and predation risk, enabling birds to remain in woodland habitats at night. However, if birds are found to occupy sub-optimal diurnal sites, it may be necessary for them to undertake nocturnal feeding in fields. Furthermore, hunting activities may cause disturbance to birds, which inhibits daytime feeding opportunities. As a consequence, birds may be forced to commute at night, to supplement poor foraging success during the day.

Departure events

The majority of continental migrants are believed to depart during late February and early March, with only 4% of foreign ring recoveries found in Britain throughout March, and up to 15 April (Hoodless & Coulson 1994). In this study, however, only 25% of birds departed before mid-March, with the majority

departing in late March/early April. By this time, resident birds may be on nests (Hoodless & Coulson 1998).

Departure events preceding those associated with spring-migration were also apparent during the winter periods. These seemed to coincide with sudden decreases in temperature. Whilst the data here are not suitable to infer cause and effect, they lend support to the occurrence of cold-weather movements (Alexander 1939; Spencer 1982), whereby the onset of severe weather conditions triggers an adaptive response in woodcock to abandon their existing feeding grounds (Hirons & Bickford-Smith 1983; Wilson 1983). These departures were often on a temporary basis, until conditions improved, although a number of birds remained missing for the duration of the field-season.

Clearly there is some plasticity with regards to this behaviour. As evidenced by departure dates, migrants appear to leave first, whilst adult residents seem to linger a day or two before moving. In some instances, as in the winter of 2010/11, birds may not depart at all. The decision to delay departure, or not depart at all, suggests that there are benefits in doing so. As highlighted by Spencer (1982), prompt departures might prove unnecessary, if the cold spell is short-lived. Furthermore, if known feeding sites are abandoned, these may be exploited by new birds moving in. However, if birds hesitate too long before departing, they may deplete fat reserves and set off in poor body condition (Spencer 1982). This could threaten survival, if birds then fail to find better feeding conditions elsewhere. Indeed, this was believed to be the case for song thrushes making south-westerly movements to Cornwall and Devon in January 1963 (Spencer 1964).

The cold-weather movements of birds seem to favour a south/south-westerly direction (Spencer 1982), and there are potentially two reasons for this. First, movements in a south/south-westerly direction are more economical in terms of energy demands, compared to movements in other directions. This is because, in Britain, cold spells are usually associated with the build-up of high pressure, which typically brings a period of calm, or winds from north/north-easterly regions (Met Office 2012b). Second, environmental conditions are generally milder in south/south-westerly regions (Met Office 2010a), therefore these areas are more likely to provide improved feeding opportunities. In this study, support for the suggestion of such south/south-westerly movements comes from a departed woodcock tag that was recovered in Dorset, located approximately 70 miles south west of the study site.

Whilst departure events can be readily linked to severe weather conditions, it is less easy to explain return movements. Upon finding milder feeding grounds, one would presume it is more beneficial to remain there, rather than undertake the energetically-costly flight back to a site that, potentially, may still be unsuitable. Whilst birds appear to minimise the risk of the latter, by returning during mild spells, this return behaviour is still intriguing. It has been suggested that over-crowding at milder sites, resulting in intense competition, may be the impetus for return movements (Lack 1968).

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Tables & Figures

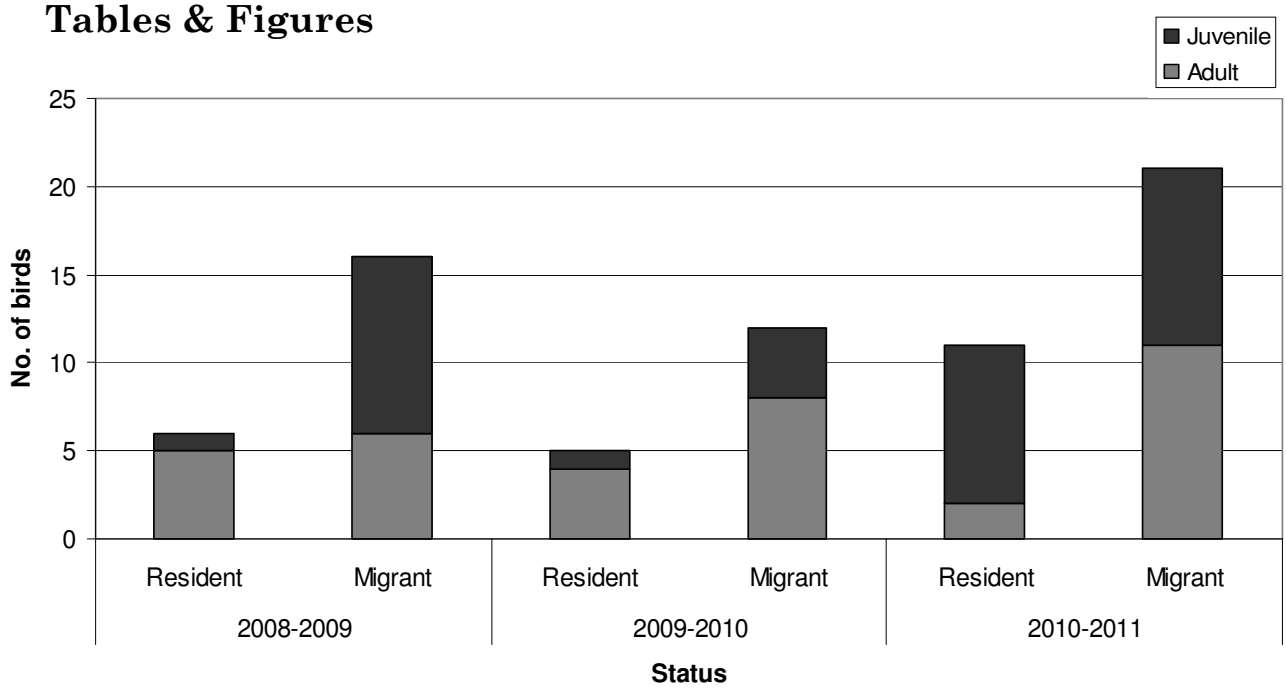


Figure 5.1 Numbers of Eurasian woodcock radio-tracked across three winters (2008/09: n = 22, 2009/10: n = 17, 2010/11: n = 32), according to age (adult, juvenile), and predicted migratory status (residents = Hampshire breeders, migrants = non-Hampshire breeders). Re-trap birds have been excluded.

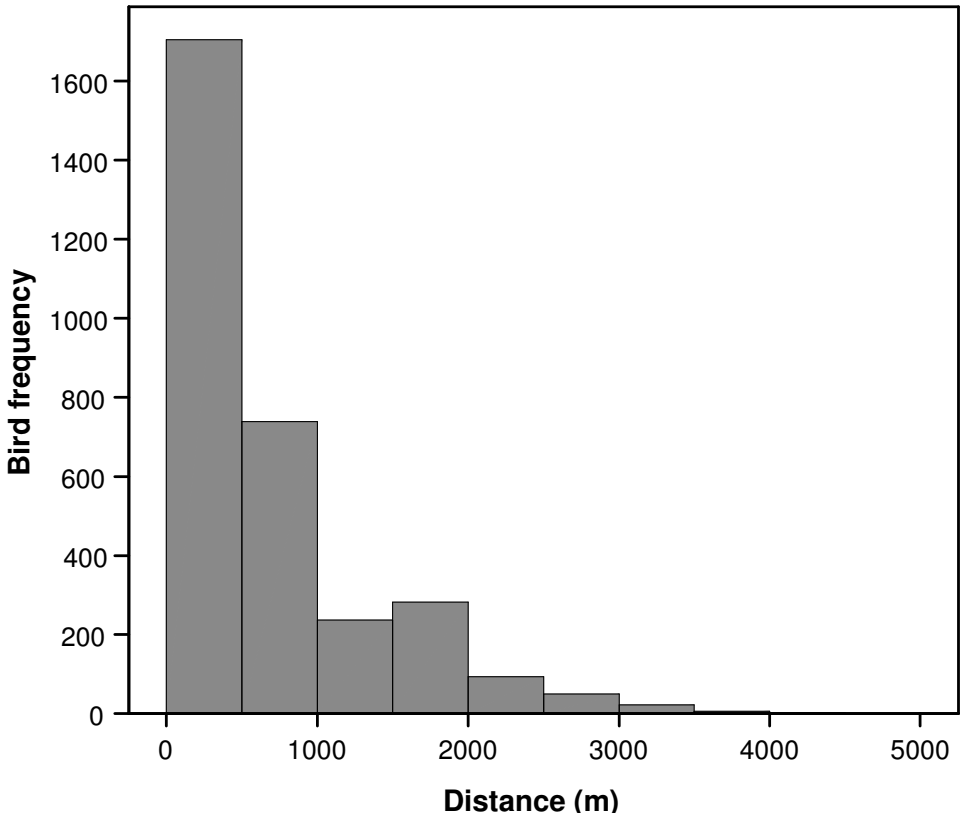


Figure 5.2 Frequencies of distances flown by Eurasian woodcock (n = 68), between day and night locations. Results are based on data collected over three combined winters (2008/09, 2009/10, and 2010/11).

Table 5.1 Mean commuting flight distances, and standard errors (SE), travelled by Eurasian woodcock (n = 68). Results are based on 3 133 measurements. Distances are stratified according to winter (1 = 2008/09, 2 = 2009/10, 3 = 2010/11), bird age (adult, juvenile), and predicted migratory status (residents = Hampshire breeders, migrants = non-Hampshire breeders).

			Distance (m)			
Winter	**Number of birds**		**Adult**		**Juvenile**	
			Resident	**Migrant**	**Resident**	**Migrant**
1	**20**	Mean	1061	356	614	677
		SE	82	17	188	39
2	**16**	Mean	274	752	1661	726
		SE	13	33	70	86
3	**32**	Mean	510	608	886	550
		SE	62	20	35	24

Table 5.2 Mean commuting flight distances, and standard errors (SE), travelled by Eurasian woodcock (n = 20) during the winter of 2008/09. Results are based on 632 measurements. Distances are stratified according to winter month, bird age (adult, juvenile), and predicted migratory status (residents = Hampshire breeders, migrants = non-Hampshire breeders). * indicates an absence of data.

		Distance (m)			
2008/09		**Adult**		**Juvenile**	
		Resident	**Migrant**	**Resident**	**Migrant**
Oct/Nov	Mean	552.20	241.30	*	*
	SE	149.30	29.80	*	*
Dec	Mean	466.20	1015.60	*	410.60
	SE	162.90	607.70	*	230.30
Jan	Mean	1165.00	401.50	889.60	691.30
	SE	180.80	79.20	108.10	102.00
Feb	Mean	926.20	340.90	62.20	733.80
	SE	109.50	22.70	62.20	58.40
Mar/Apr	Mean	1295.30	348.30	*	617.50
	SE	162.90	20.70	*	64.40

Table 5.3 Mean commuting flight distances, and standard errors (SE), travelled by Eurasian woodcock (n = 16) during the winter of 2009/10. Results are based on 507 measurements. Distances are stratified according to winter month, bird age (adult, juvenile), and predicted migratory status (residents = Hampshire breeders, migrants = non-Hampshire breeders). * indicates an absence of data.

		Distance (m)			
2009/10		**Adult**		**Juvenile**	
		Resident	**Migrant**	**Resident**	**Migrant**
Oct/Nov	Mean	225.10	*	*	886.30
	SE	20.09	*	*	179.97
Dec	Mean	315.50	800.00	*	958.40
	SE	31.57	451.51	*	134.02
Jan	Mean	381.50	667.90	*	200.10
	SE	66.69	91.46	*	32.74
Feb	Mean	294.10	638.90	1564.00	289.80
	SE	24.33	45.89	159.12	38.50
Mar/Apr	Mean	221.70	879.40	1729.40	*
	SE	21.12	49.30	42.13	*

Table 5.4 Mean commuting flight distances, and standard errors (SE), travelled by Eurasian woodcock (n = 32) during the winter of 2010/11. Results are based on 1 994 measurements. Distances are stratified according to winter month, bird age (adult, juvenile), and predicted migratory status (residents = Hampshire breeders, migrants = non-Hampshire breeders). * indicates an absence of data.

		Distance (m)			
2010/11		**Adult**		**Juvenile**	
		Resident	**Migrant**	**Resident**	**Migrant**
Oct/Nov	Mean	*	390.30	1251.70	77.70
	SE	*	120.68	235.68	25.44
Dec	Mean	*	455.10	681.80	122.90
	SE	*	61.38	94.28	14.36
Jan	Mean	96.60	612.70	895.30	542.10
	SE	7.40	35.74	58.12	56.82
Feb	Mean	432.00	691.60	917.70	628.80
	SE	96.98	34.26	62.11	40.87
Mar/Apr	Mean	711.00	625.90	888.40	582.00
	SE	101.55	40.89	67.61	27.34

Table 5.5 Mean elliptical (95%) home range estimates, and standard errors (SE), for Eurasian woodcock (n = 55). Area estimates are stratified according to winter (1 = 2008/09, 2 = 2009/10, 3 = 2010/11), bird age (adult, juvenile), and predicted migratory status (residents = Hampshire breeders, migrants = non-Hampshire breeders). Area estimates encompass both day and night locations. * indicates an absence of data.

			Ellipse (95%) (ha)			
Winter	**Number of birds**		**Adult**		**Juvenile**	
			Resident	**Migrant**	**Resident**	**Migrant**
1	**16**	Mean	408.00	42.80	*	180.00
		SE	99.31	10.17	*	63.40
2	**12**	Mean	33.20	215.30	266.60	142.70
		SE	10.51	74.65	*	62.85
3	**27**	Mean	479.20	133.60	205.00	217.80
		SE	297.52	32.30	89.3.0	75.21

Table 5.6 Mean kernel contour (95%) home range estimates, and standard errors (SE), for Eurasian woodcock (n = 55). Area estimates are stratified according to winter (1 = 2008/09, 2 = 2009/10, 3 = 2010/11), bird age (adult, juvenile), and predicted migratory status (residents = Hampshire breeders, migrants = non-Hampshire breeders). Area estimates encompass both day and night locations. * indicates an absence of data.

			Kernel contour (95%) (ha)			
Winter	**Number of birds**		**Adult**		**Juvenile**	
			Resident	**Migrant**	**Resident**	**Migrant**
1	**16**	Mean	205.30	23.90	*	74.70
		SE	13.44	7.50	*	28.39
2	**12**	Mean	22.10	109.20	150.30	99.20
		SE	14.26	36.21	*	60.48
3	**27**	Mean	285.10	61.70	124.70	123.40
		SE	89.35	18.01	61.17	48.10

Table 5.7 Mean Minimum Convex Polygon (MCP) home range estimates, and standard errors (SE), for Eurasian woodcock (n = 52). Area estimates are stratified according to winter (1 = 2008/09, 2 = 2009/10, 3 = 2010/11), bird age (adult, juvenile), and predicted migratory status (residents = Hampshire breeders, migrants = non-Hampshire breeders). Estimates encompass both day and night locations. * indicates an absence of data.

			MCP (ha)			
Winter	**Number of birds**		**Adult**		**Juvenile**	
			Resident	**Migrant**	**Resident**	**Migrant**
1	**16**	Mean	325.70	31.30	*	127.80
		SE	70.20	9.95	*	49.77
2	**10**	Mean	25.40	116.10	132.30	151.00
		SE	6.97	37.07	*	21.67
3	**26**	Mean	390.00	96.20	153.50	131.20
		SE	213.39	36.18	70.19	42.69

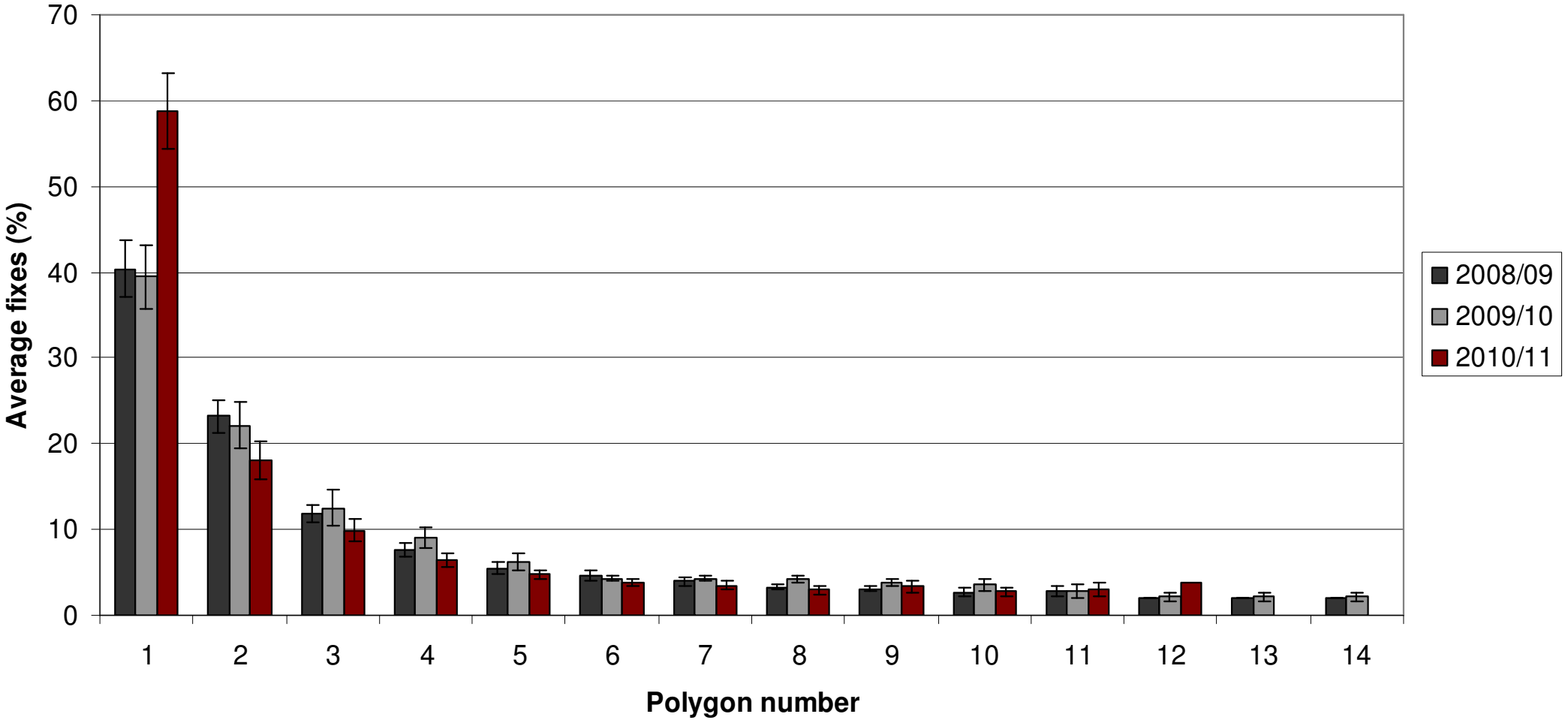


Figure 5.3 Mean proportions (± standard errors) of diurnal fixes found across ranked polygons for Eurasian woodcock radio-tracked across three winters (2008/09, 2009/10, and 2010/11). Results are based on data collected from 17 birds in 2008/09, 13 birds in 2009/10, and 27 birds in 2010/11. Polygon numbers reflect the relative ranking positions of polygons, according to their utilisation by birds. For instance, polygon number one represents those polygons most frequently used by birds, whilst polygon number 14 represents the fourteenth most commonly used polygons.

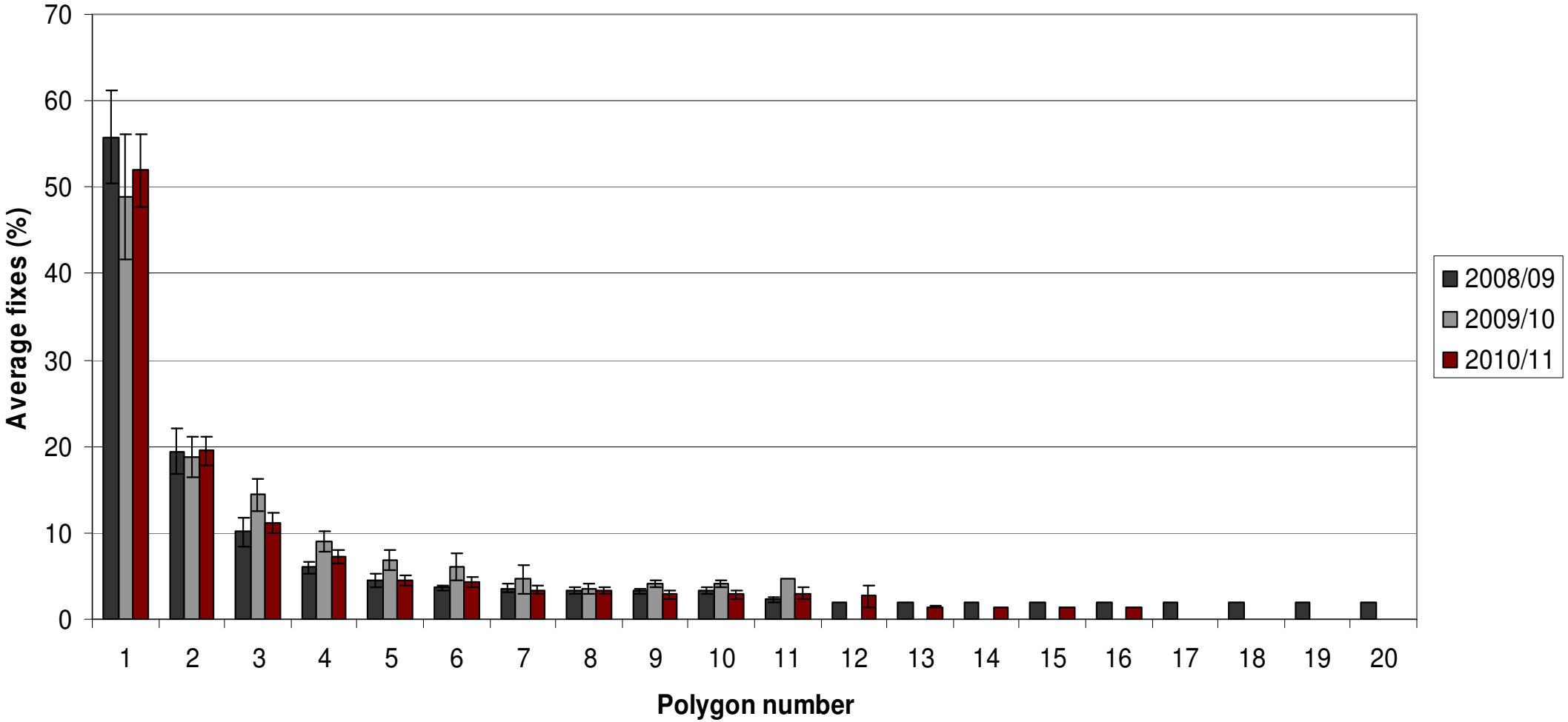
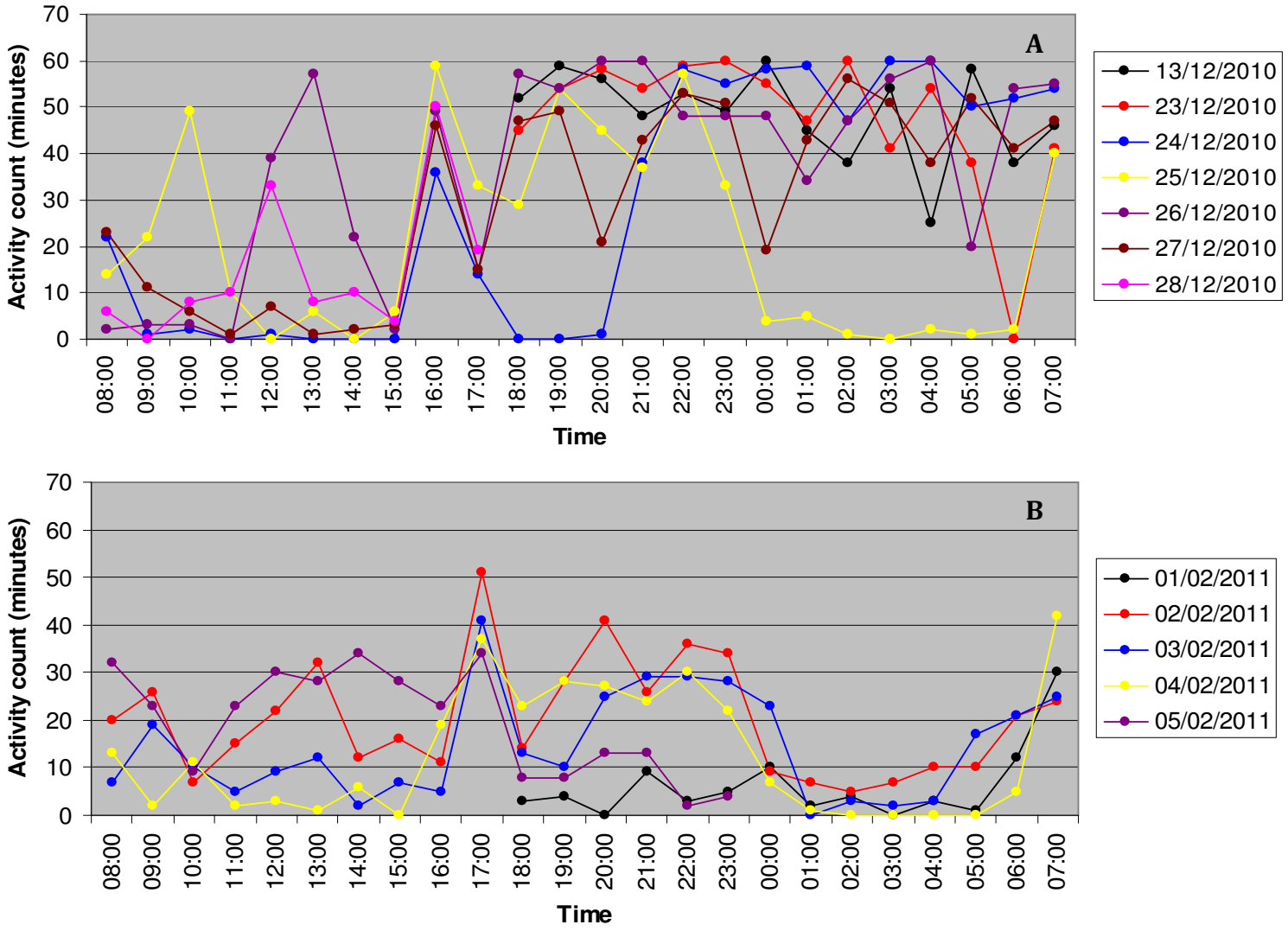


Figure 5.4 Mean proportions (± standard errors) of nocturnal fixes found across ranked polygons for Eurasian woodcock radio-tracked across three winters (2008/09, 2009/10, and 2010/11). Results are based on data collected from 16 birds in 2008/09, 12 birds in 2009/10, and 27 birds in 2010/11. Polygon numbers reflect the relative ranking positions of polygons, according to their utilisation by birds. For instance, polygon number one represents those polygons most frequently used by birds, whilst polygon number 14 represents the fourteenth most commonly used polygons.


A
Activity count (minutes)
70
60
50
40
30
20
10
0
08:00
09:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
20:00
21:00
22:00
23:00
00:00
01:00
02:00
03:00
04:00
05:00
06:00
07:00
Time
13/12/2010
23/12/2010
24/12/2010
25/12/2010
26/12/2010
27/12/2010
28/12/2010
B
Activity count (minutes)
70
60
50
40
30
20
10
0
08:00
09:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
20:00
21:00
22:00
23:00
00:00
01:00
02:00
03:00
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05:00
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Time
01/02/2011
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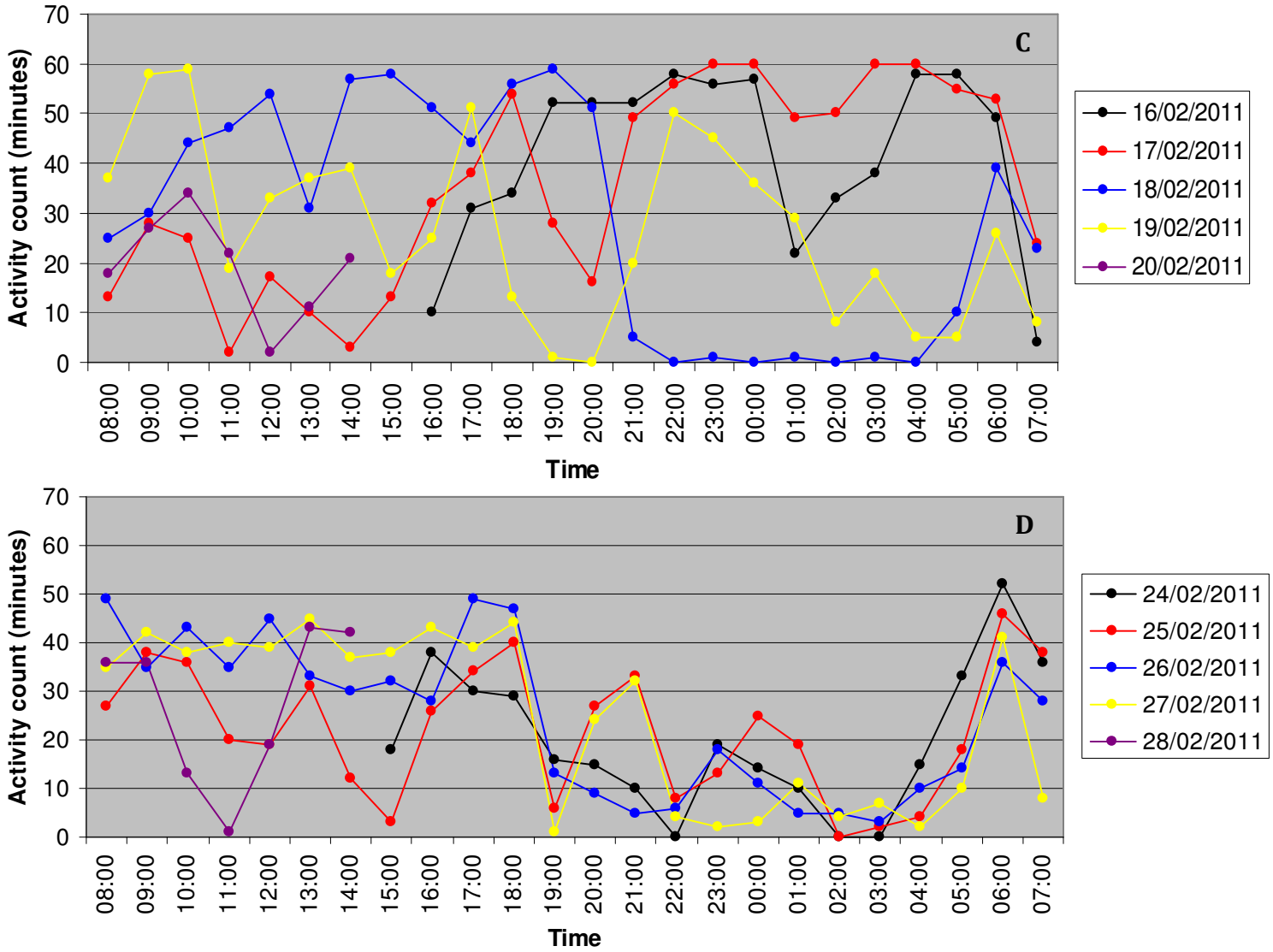


Figure 5.5 Activity profiles for individual Eurasian woodcock recorded over distinct 24-hour periods. Plot A = tag ID 476 (juvenile migrant), B = tag ID 478 (juvenile resident), C = tag ID 958 (adult migrant), and D = tag ID 634 (juvenile migrant). Activity counts represent the number of minutes that contained activity.

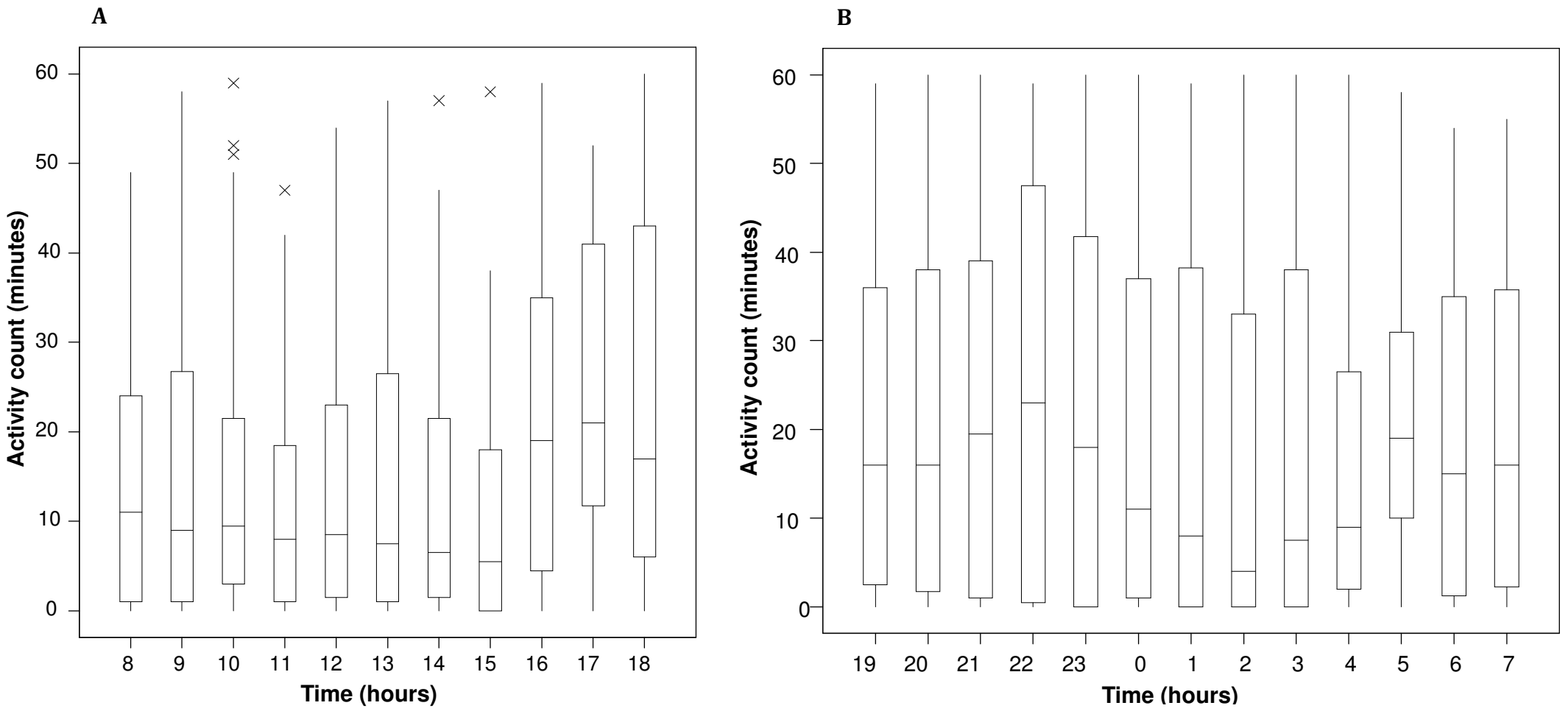


Figure 5.6 Activity counts at 1-hour time intervals for Eurasian woodcock recorded during the winter of 2010/11. Plot A represents diurnal activity, with data collected from 11 birds, over 38 recording periods. Plot B represents nocturnal activity, with data collected from 12 birds, over 54 recording periods. Activity counts represent the number of minutes that contained activity. Each box spans the interquartile range of values. The middle 50% of the data lie within the box, with the intersecting line representing the median. Whiskers extend as far as the minimum and maximum values. Crosses represent outliers.

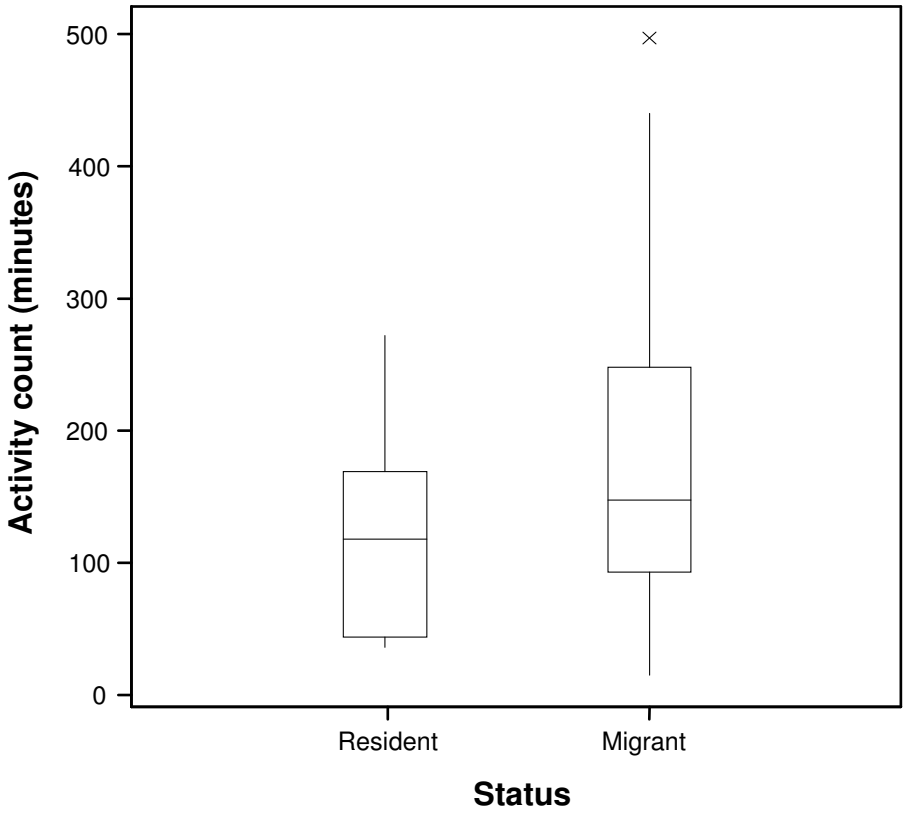


Figure 5.7 Total day-time activity count data for Eurasian woodcock, stratified according to predicted migratory status (residents = Hampshire breeders, migrants = non-Hampshire breeders). Results are based on data collected from 11 birds, over 38 recording periods, during the winter of 2010/11. Activity counts represent the number of minutes that contained activity. Each box spans the interquartile range of values. The middle 50% of the data lie within the box, with the intersecting line representing the median. Whiskers extend as far as the minimum and maximum values. The cross represents an outlier.

Table 5.8 Means, and standard errors (SE), for total day-time activity counts of Eurasian woodcock, recorded during the winter of 2010/11. Results are stratified according to winter month.

Month	Mean activity count		Magnitude of effect (± SE)	Number of recording events
	Back-transformed	Raw data (± SE)		
Dec	129.4	178.8 (± 38.94)	0.8 (± 0.30)	4
Jan	59.0	81.5 (± 13.88)	0.0	6
Feb	250.2	295.1 (± 32.24)	1.4 (± 0.30)	13
Mar	78.4	103.2 (± 18.83)	0.3 (± 0.30)	10
Apr	120.2	87.0 (± 24.76)	0.7 (± 0.30)	5

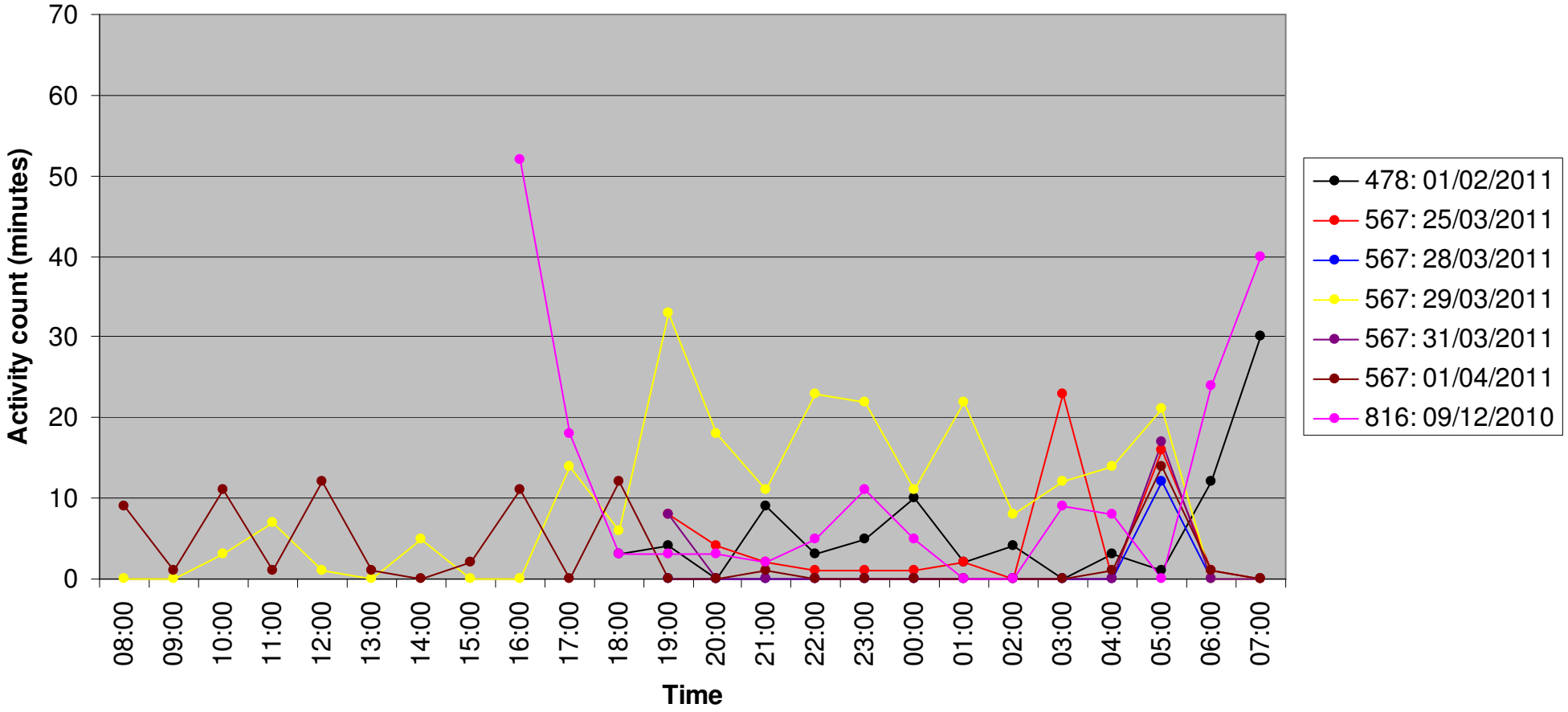


Figure 5.8 Activity profiles for individual Eurasian woodcock occupying woodland habitats during the recording period(s). Activity counts represent the number of minutes that contained activity.

Table 5.9 Mean proportions, and standard errors (SE), of night-time fixes found in woodland habitats for Eurasian woodcock (n = 40). Proportions are stratified according to winter year (1 = 2008/09, 2 = 2009/10, 3 = 2010/11), and winter month.

Winter	Number of birds		Fixes in woodland (%)				
			Oct/Nov	Dec	Jan	Feb	Mar/Apr
1	**9**	Mean	10	6	12	3	7
		SE	5	6	3	1	2
2	**5**	Mean	0	6	21	2	3
		SE	0	3	7	1	2
3	**26**	Mean	27	34	11	8	11
		SE	7	4	2	1	2

Table 5.10 Loss of signal dates for Eurasian woodcock with predicted migratory status (i.e. non-Hampshire breeders). Dates refer to the first date the tag was undetected.

Winter	Tag ID	Age	Loss of signal
2008/09	336	Juvenile	09/03/2009
	255	Adult	16/03/2009
	701	Juvenile	16/03/2009
	797	Adult	24/03/2009
	285	Juvenile	07/04/2009
	538	Adult	07/04/2009
	635	Adult	07/04/2009
	907	Juvenile	07/04/2009
	949	Juvenile	07/04/2009
2009/10	967	Adult	01/03/2010
	217	Adult	15/03/2010
	74	Adult	19/03/2010
	686	Adult	22/03/2010
	278	Adult	26/03/2010
	206	Adult	07/04/2010
2010/11	909	Juvenile	14/02/2011*
	938.7	Adult	22/02/2011
	216	Adult	01/03/2011
	634	Juvenile	14/03/2011
	69	Juvenile	18/03/2011
	479	Juvenile	21/03/2011
	848.1	Juvenile	21/03/2011
	141	Adult	25/03/2011
	196	Juvenile	28/03/2011
	824.4	Adult	25/03/2011
	537	Juvenile	29/03/2011
	586	Adult	30/03/2011
	958	Adult	31/03/2011

*Early departure

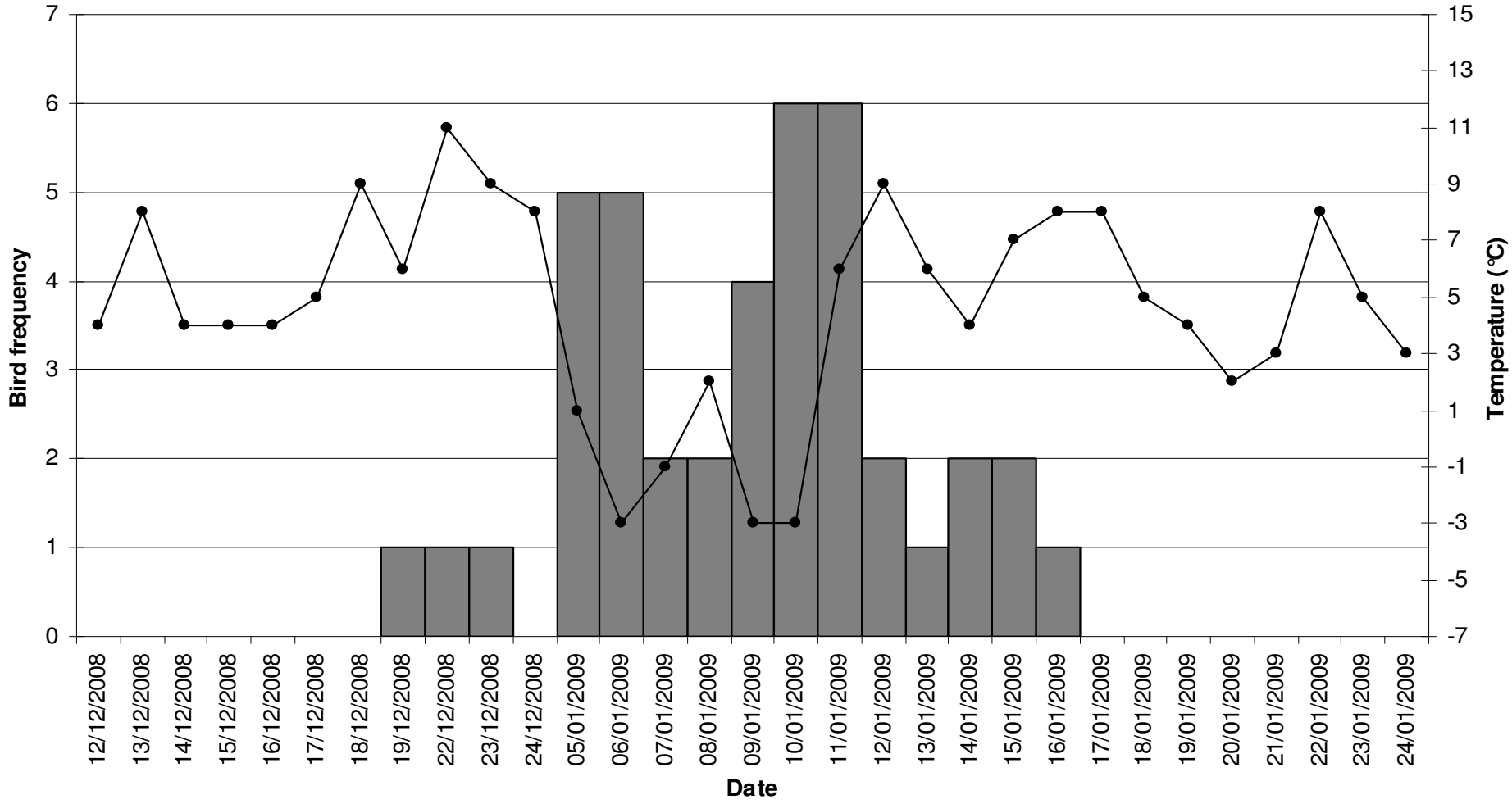
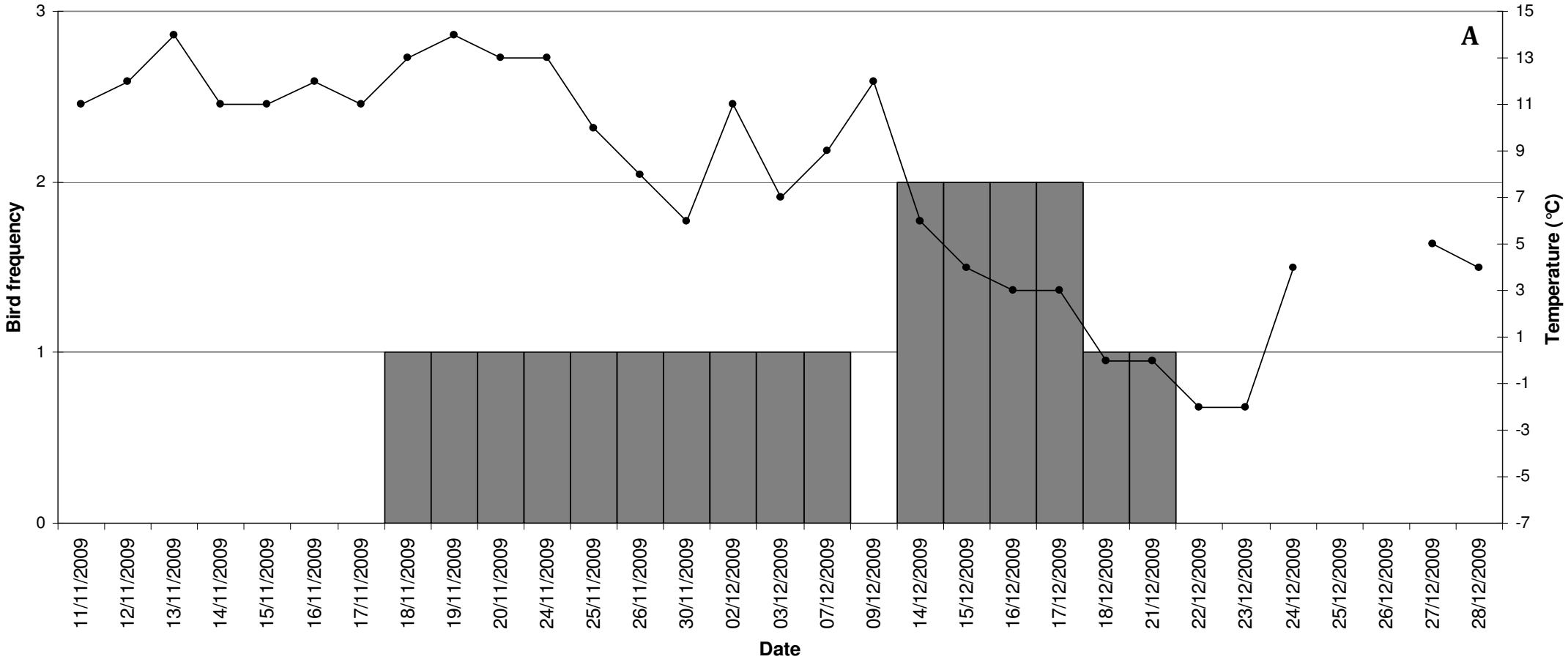


Figure 5.9 Numbers of Eurasian woodcock that undertook departure events, prior to spring-migration, during the winter of 2008/09. Numbers of departures are plotted alongside average daily temperature. Dates represent the first occasions tags went undetected. Bars represent the number of birds. Points represent average daily temperature.


A
Bird frequency
Temperature (°C)
Date
3
2
1
0
15
13
11
9
7
5
3
1
-1
-3
-5
-7
11/11/2009
12/11/2009
13/11/2009
14/11/2009
15/11/2009
16/11/2009
17/11/2009
18/11/2009
19/11/2009
20/11/2009
24/11/2009
25/11/2009
26/11/2009
30/11/2009
02/12/2009
03/12/2009
07/12/2009
09/12/2009
14/12/2009
15/12/2009
16/12/2009
17/12/2009
18/12/2009
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25/12/2009
26/12/2009
27/12/2009
28/12/2009

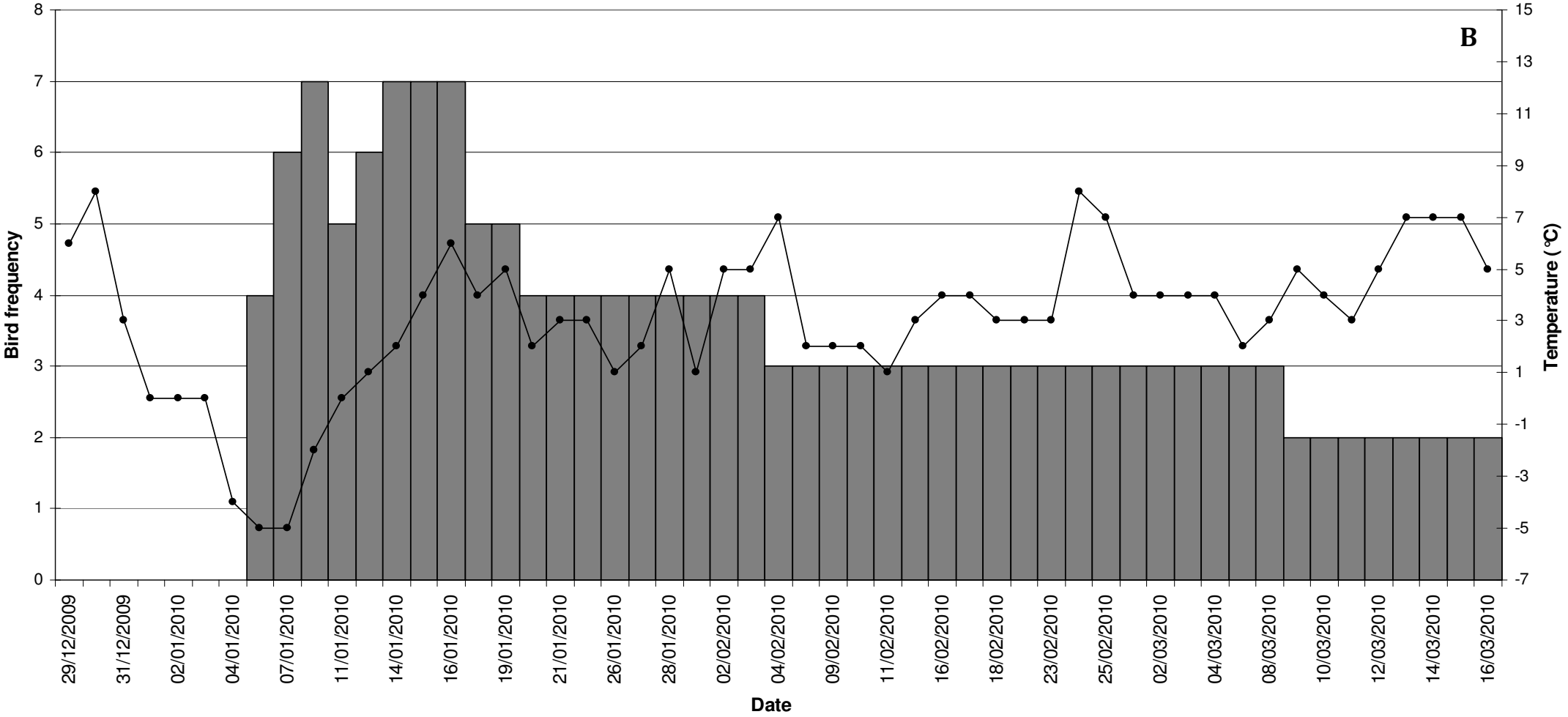


Figure 5.10 Numbers of Eurasian woodcock that undertook departure events, prior to spring-migration, during the winter of 2009/10. Numbers of departures are plotted alongside average daily temperature. Dates represent the first occasions tags went undetected. Bars represent the number of birds. Points represent average daily temperature. Plot B is a continuation of plot A.

Chapter 6

Discussion

Discussion

Aims and motivation

The conservation status of the Eurasian woodcock *Scolopax rusticola* (hereon woodcock) remains uncertain, at both the national and international level (Wetlands International 2002; BirdLife International 2004a,b). This quarry species is susceptible to changes in hunting pressure, habitat, and climate, yet the impact of these effects on populations has been difficult to assess, owing to limited information regarding woodcock ecology. Whilst the cryptic plumage and elusive nature of the woodcock makes it a challenging bird to study, the development of new technologies is now advancing woodcock research.

The aims of this thesis were to develop an understanding of the origins and ecology of woodcock residing in Britain during the non-breeding season. Given the non-breeding woodcock population in Britain comprises both resident and migrant birds, there was a unique opportunity to discern ecological differences between these groups.

Application of stable isotope analysis to the study of migration

Feather stable hydrogen isotopes (δ^2H_f) were found to be a suitable broad-scale geographic marker for woodcock, which allowed for more detailed investigations into their migratory behaviour. However, in a broader context, this finding suggests that bird species eating a similar diet to woodcock and undertaking

broadly similar migration routes (from northern and eastern Europe to Britain), e.g. common snipe *Gallinago gallinago*, common blackbird *Turdus merula*, redwing *Turdus iliacus* and fieldfare *Turdus pilaris*, may show similar stable hydrogen isotope (δ^2H) trends in their feathers. As such, δ^2H_f may serve as a suitable geographic marker for these bird species also.

Isotopic variation was found to be minimal and hence unlikely to have any major influence on the assignment of woodcock to likely origins. Variation between individuals from the same breeding location, variation between samples from different feather tracts, and variation within and between laboratories (reproducibility) were all of small magnitude. The only significant effect found was that between woodcock of different age classes, with adults yielding consistently more positive isotope values than those of juveniles (mean difference: -35.2‰). This was attributed to temporal (seasonal) isotopic variation coinciding with moult phenology. Woodcock feather samples taken from museum specimens were also judged to be suitable as an additional source of known origin sampling material, despite the fact that isotopic values for a given location were more variable than contemporary samples. To date, migration studies in the USA have employed stable isotope analysis far more routinely than in Europe. However, the results of this study suggest that stable isotope analysis could be more widely applied to migration studies in Europe and, for species which are difficult to sample on the breeding grounds, museum-derived samples could provide a valid source of known origin material.

Whilst a number of studies have found that δ^2H fails to discriminate between different breeding origins (Farmer *et al.* 2008; Fraser *et al.* 2010), the use of prior

probabilities to generate migration direction models, within the Bayesian framework, clearly facilitates geographic assignments of origin. Advocators of the European δ^2H isoscape (Hobson *et al.* 2004; Bowen *et al.* 2005) typically use amount-weighted growing season average (GSD) as the predictor for allocating assignments. However, woodcock δ^2H_f was found to better reflect amount-weighted mean annual δ^2H_p (MAD). Given their diet typically comprises earthworms (Granval 1987; Hoodless & Hirons 2007) and is therefore dissociated from the growing season, this finding is somewhat intuitive. For other works, this finding highlights the need to carefully consider the foraging ecology of the study species when choosing an appropriate predictor to make assignments. It may be that MAD is the best predictor of δ^2H_f for soil-probing species. The first calibration equations for woodcock were also derived in this study: one for adults and one for juveniles. The use of such species-specific calibration equations is advised over the use of the generic equation for European birds (Hobson *et al.* 2004), so as to reduce error and enhance the accuracy of assignments.

Woodcock origins and spatial distribution

This study has provided a far more detailed insight into the likely origins of woodcock wintering in Britain and Ireland, compared to those of previous works, which were solely reliant on ring recoveries. Here, stable isotope data and prior information from ring recovery data were used to determine the breeding origins and spatial distribution of the non-breeding woodcock population in Britain and Ireland. Although the use of prior probabilities based on ring recoveries does make the results prone to some of the biases applicable to ring recoveries, the spatially explicit assignment approach employed here permitted origin estimates

from a much larger sample of individuals, and a contemporary comparison of breeding origins between different wintering areas. It also has power in enabling repeat sampling at intervals in the future, which will allow changes in the composition of wintering populations to be assessed e.g. in response to factors such as climate change, or habitat destruction, on the breeding grounds.

Russia and Fennoscandia were found to comprise the most likely origins for migratory woodcock residing in Britain during the non-breeding season, but regional differences in the distributions of birds were also apparent. These were probably attributable to differences in the migratory flyways of birds from different breeding origins (Bauthian *et al.* 2007). The spatial distributions of woodcock during the non-breeding season did not appear to be influenced by age, refuting any suggestion for differential age-related migration (Lack 1943; Clausager 1974). Notably, a proportion of resident birds appeared to relocate to alternate non-breeding sites (within Britain), along a southwards and/or westwards trajectory. These movements probably reflected seasonal movements associated with changing weather conditions (Spencer 1982).

There was a large degree of mixing of birds from different breeding locations across sampling regions and this was indicative of weak connectivity. It was important to establish this, due to the relationship between connectivity and population dynamics. Populations exhibiting weak connectivity are believed to be less vulnerable to changing selective pressures than those exhibiting strong connectivity (Webster *et al.* 2002; Webster & Marra 2005). This is because populations showing weak connectivity typically have high genetic variation,

which may enhance their ability to evolve adaptive responses (Webster *et al.* 2002; Webster & Marra 2005).

Habitat selection

During the non-breeding season, the relationship between weather conditions, the accessibility and availability of food resources, and levels of predation, all represent key drivers of habitat selection. Whilst these may have independent effects on birds, they're not always mutually exclusive. Rather, their interaction represents the classic starvation-predation trade-off (Lima 1986), which may effect bird behaviour (Nolan & Ketterson 1983; Rogers 1987; Gentle & Gosler 2001) and act as key form of population limitation (Newton 1998; Rogers 2005).

The starvation-predation trade-off is believed to influence the diurnal and nocturnal habitat selections of woodcock (Duriez *et al.* 2005b,c). Wet woodlands were found to be the most commonly selected diurnal habitat type, and were probably selected based on their high earthworm densities and easily penetrable soils. Grass fields (grazed permanent pasture, grazed and ungrazed leys, and ungrazed permanent pasture) were the most commonly selected nocturnal habitats, and probably reflected the field types of highest quality, with regards earthworm availability and accessibility (Hoodless 1994a; Duriez *et al.* 2005b). Notably, at night, adults showed significantly greater use of grazed permanent pastures than juveniles. However, this non-breeding habitat segregation could not be attributed to dominance-mediated mechanisms (Marra *et al.* 1998; Murphy *et al.* 2001; Norris *et al.* 2005), as there was no evidence to suggest that juvenile woodcock were being competitively excluded from optimal habitats. Both diurnal and

nocturnal habitat selections were also found to vary significantly with the interactions between winter and age, and winter and predicted migratory status (hereon status). This variation between years was attributed to temporal (inter-annual) changes in climate, as environmental conditions are known to influence woodcock behaviour (Duriez *et al.* 2005c). These findings are all unique to this study, as previous works have failed to investigate or establish differential patterns of habitat use according to time factors and/or bird characteristics (Duriez *et al.* 2005b).

Winter movements and behaviours

Woodcock commuting flights were much longer than those previously reported (Hirons & Bickford-Smith 1983; Hoodless 1994a), with a significant interaction between winter, age and status found. During the mild winter of 2008/09, adult residents tended to fly greater distances than migrants, whilst during the harsher winters of 2009/10 and 2010/11, the converse was true. Similar results were obtained in the analyses of home-ranges. These differences were attributed to temporal (inter-annual) changes in climate that probably influenced bird behaviour through associations with thermoregulation and/or the starvation-predation risk trade-off (Boos *et al.* 2005; Duriez *et al.* 2005c; Brana *et al.* 2010). Since adult residents are likely to have experience and prior knowledge of the surrounding area, their behaviour probably reflects the optimal strategy, resulting in increased fitness, compared to conspecifics.

The number of sites used varied between individuals, but there were no apparent trends between birds of different age or status classes. Individuals appeared to

apply the same site-use strategy to both day and night ranges, and all birds had a distinct primary core that represented the area of most frequent use. The mean proportion of fixes (± standard error, SE) found in diurnal primary cores was 49% (± 3 SE) and for nocturnal primary cores was 52% (± 3 SE). This tendency for birds to use a primary core makes ecological sense for the woodcock because, in doing so, they reduce the time and energy spent searching for alternative sites, which also reduces their chances of detection by predators. Indeed, the threat of predation is clearly a prominent one for woodcock, hence its morphological adaptations; the woodcock has cryptic plumage, to aid concealment, and the position of its eyes allows panoramic vision in a horizontal plane, which is an adaptation believed to have developed primarily for detection of predators (Martin 1994; Schwab 2001). Woodcock are able to repeatedly use the same site because, unlike other bird species that forage in flocks e.g. European golden plovers *Pluvialis apricaria* (Bengtson *et al.* 1976), woodcock feed largely solitarily and occur at lower densities (Hoodless 1995), which means food depletion is unlikely to occur.

Activity profiles revealed that birds exhibiting high levels of activity during the day typically showed lower levels of activity at the night, whilst the converse was also true. Since activity during the night is likely to be dependent on feeding success earlier that day, and additional feeding during the day is probably dependent on feeding success the preceding night, these findings were somewhat intuitive. Notably, migrants were found to be more active during the day than residents. Given activity is synonymous with feeding, this finding suggests that migrant birds may be continually failing to meet their energy demands at night and/or have a tendency to occupy low quality (food-poor) daytime sites, therefore

necessitating the need to undertake higher levels of supplementary feeding during the day.

In accordance with previous works, woodcock were found to remain in woodland habitats on some nights, as opposed to flying out to fields (Duriez *et al.* 2005c). It was postulated that the decision to commute probably reflects the complex relationship between weather conditions, foraging success during the day, and the starvation-predation risk trade-off (Duriez *et al.* 2005c). Over the entire study-period, 58% of birds remained in woodland habitats on one or more occasion. Although there were no effects of age or status, night-time woodland occupancy is probably preferential to flying out to fields. In doing so, birds avoid the risk and costs associated with commuting flights, and the lowered temperatures in exposed fields. Furthermore, birds in woodland reduce the risk of predation, which is reported to be higher in fields at night (Duriez 2003). In this study, only 10% of tag retrievals were attributed to predation events (n = 7) but, of these, 57% occurred in fields.

Two types of departure events were found to occur over the study period. The departures of migrant birds in March/April were attributed to spring-migration, whilst departures preceding these were deemed cold-weather movements. Notably, the latter often occurred on a temporary basis, with birds returning to the study site in accordance with improved environmental conditions. This is an important finding with implications for woodcock conservation. It is apparent from ring recoveries (and more recently from geolocators, Andrew Hoodless pers. comm) that a proportion of woodcock show winter site fidelity, returning to the same wintering area year on year (Wilson 1983; Hoodless 1994a; Hirons,

unpublished data). The fact that both residents and migrants were found to return to the study site following hard weather probably reflects the strength of this site faithfulness. Importantly, this may have implications for shooting; if too many birds are shot one year in a given location, then there are likely to be fewer the following year.

Constraints and limitations

The traditional home-range estimates used in this study were helpful in providing information regarding the area covered by woodcock, even if these do not best reflect the actual area use of birds. Whilst such information may be of benefit in the development of conservation plans, significant differences in results were found between different home-range estimators applied to the same dataset. This highlights the need for caution, as conclusions based on a single home range estimator may not be accurate. For conservation purposes it might be more useful to apply a mechanistic framework, enabling predictive home range models to be developed (Moorcroft & Barnett 2008).

A detailed analysis of foraging activity was not possible within this study, due to a paucity of activity data. It would be informative to collect activity data from multiple individuals over the same recording period, to enable inter-individual comparisons to be made. Furthermore, insights into behaviour during periods of cold-weather might be better understood, if sufficient activity data could be collected at such times.

The soil samples collected in this study provided only a crude representation of earthworm biomass between different habitat types. Whilst it was recognised that intensive sampling would need to be carried out for a more robust analysis, this was deemed both impractical and unnecessary. Both time and labour constraints prevented more intensive sampling during the study period, but it was felt that the findings of previous works (Duriez *et al.* 2005b) were sufficient to allow relationships to be inferred.

General perspectives

Future work

Whilst this body of work has served to improve our knowledge of woodcock migration and non-breeding ecology, it does not provide a full understanding of these vast topics. Rather, it provides a framework and point of reference for further development. Where possible, analyses accounted for differences between age groups (adult vs. juvenile) and birds of different migratory status (resident vs. migrant). The latter represented a unique feature of this thesis, as previous works have not attempted to distinguish between resident and migrant woodcock. It was not possible, however, to reliably distinguish between male and female birds, and so differential behaviours relating to sex could not be ascertained. Given that sex-mediated differences are apparent amongst other bird species (Marra *et al.* 1998; Murphy *et al.* 2001; Norris *et al.* 2005), this may be worth investigating for the woodcock. Whilst bill length has been used to sex woodcock (Rochford & Wilson 1982; Ferrand & Gossmann 2009), there exists a lot of overlap in measurements (Rochford & Wilson 1982; Ferrand & Gossmann

2009), making this method of sexing unreliable. Rather, molecular techniques provide the most reliable means of determining sex, and such methods have been successfully applied to woodcock, using blood samples (Vali & Elts 2002). In this study, however, feathers were the only available source of sampling material. A molecular analysis was attempted using the same protocols applied to blood (Hogan *et al.* 2008), but this failed to produce any positive results. This was not due to the quality of the samples, as DNA was successfully extracted from all feathers; rather, it appeared to be a failure of the steps succeeding DNA extraction i.e. Polymerase Chain Reaction (PCR) methods. Unfortunately, time and financial constraints prevented further molecular investigations and so questions pertaining to sex-related differences could not be pursued. For future studies, however, this may be an area worth further investigating, since the prevalence of sex biases could have importance consequences for conservation (Marchant *et al.* 1990).

In this study, differential behaviours were apparent across age groups and/or birds of different migratory status. Whilst causal relationships were often inferred, future work should expand on the findings here to better establish the causes of differential behaviours. For instance, earthworm activity and ground visibility (i.e. vegetation structure) could be sampled at feeding sites used by adult residents and compared against those used by other age and/or status categories. This would provide the evidence necessary to determine whether adult residents are more likely to exploit optimal (high-quality) feeding sites than conspecifics. Given that non-breeding movements and behaviours were found to vary between winters, future work should also examine changes in the relationship between environmental conditions, woodcock energetics and

earthworm availability. Furthermore, changes in foraging efficiencies between age and/or status groups over the course of the winter would be worth investigating.

The rapid invent of new technologies will continue to enhance our understanding of woodcock. In this study, the stable hydrogen isotopes of feathers were used to determine the likely origins of birds. Whilst the reliability of this technique has been criticised, owing to problems associated with isotopic variation (Smith *et al.* 2009a,b), analytical methods are continually being refined and developed to account and correct for spatial and analytical error (Wunder & Norris 2008a). Furthermore, the resolution of the technique may be increased by using a multi-facet approach. Isotopes such as strontium (Sr) are influenced by geological patterns and may serve to supplement data obtained from hydrogen isotopes (Chamberlain *et al.* 1997; Font *et al.* 2007; Hobson 2011). Furthermore, the resolution of assignments may be enhanced by using isotopes in conjunction with molecular markers. Indeed, a combination of these techniques was recently used to describe the population structure and infer the origins of woodcock residing in Italy, during the non-breeding season (Trucchi *et al.* 2011).

In addition, data from devices such as geolocators and satellite tags will provide important information on the migratory flyways used by woodcock, including details of stop-over sites. Since events at one stage of the annual cycle are known to interact and influence events at subsequent stages (Gill *et al.* 2001; Norris 2005; Studds & Marra 2005), it is necessary to consider all stages of the avian annual cycle to obtain a complete understanding, at both the individual and population level (Webster *et al.* 2002). Knowledge pertaining to the spring and

autumn migrations of woodcock, however, is lacking. To rectify this, the Game and Wildlife Conservation Trust (GWCT), and other organisation outside the UK (e.g. *Office National de la Chasse et de la Faune Sauvage* (ONCFS), France; *Club de Cazadores de Becada* (CCB), Spain), have been using geolocators and satellite tags in an attempt to better understand the migratory ecology of woodcock.

Conservation

Hunting

Although woodcock are heavily hunted across Europe, a better understanding of woodcock populations and conservation measures to protect them are in the direct interests of hunters, if shooting is to remain viable and sustainable in the future. In Britain, there is no maximum bag limit and no legal requirement to submit bag records, yet some hunters appear to have developed self-monitoring activities for the conservation of the species. For example, personal experience of local declines in breeding woodcock numbers has resulted in some hunters taking smaller bags than in the past. Some are also willing to assist research by contributing to the National Gamebag Census (NGC), a voluntary system established by the GWCT, in 1961. Inevitably though, this is a self-selected sample, which probably reflects the best practice end of the spectrum, with regards attitudes towards hunting and bag size. In Britain, hunters are often people in positions to influence land management and, with better scientific data translated into practical habitat management or harvesting policies, they are well placed to ensure sustainability of woodcock populations.

Weather

Woodcock are sensitive to changes in weather conditions, due to associations with thermoregulation, food availability and accessibility, and/or the starvation-predation risk trade-off (Baillie *et al.* 1986; Lima 1986). For example, in accordance with declining temperatures, woodcock thermoregulatory demands increase, yet earthworms become less accessible, as ground soil becomes difficult to penetrate and/or earthworms burrow deeper into the soil (Edwards & Lofty 1972). If birds are unable to meet their food requirements, starvation may ensue, which may then increase their vulnerability to predation and hunting. In Britain, "cold weather bans" may be instigated, in an attempt to alleviate the impact of the latter. Under contract to the *Joint Nature Conservation Committee* (JNCC), the UK Meteorological Office monitors daily ground conditions at 23 meteorological stations across Britain. If more than half of these stations record frozen conditions for a period of seven consecutive days, the *British Association for Shooting and Conservation* (BASC) calls for voluntary restraint in water-bird shooting in affected regions. After 15 days, if conditions have not improved, then a statutory suspension comes into force, which prohibits the shooting of any species on Schedule 2 Part 1 of the Wildlife and Countryside Act 1981 (Stroud *et al.* 2006). Similar procedures should be implemented in other countries where woodcock are hunted over the winter, so as to minimise the effects of hunting mortality.

Habitat change

Given the importance of earthworms to woodcock ecology, changes to associated habitats are likely to affect local populations. Although not examined in this study, dense shrub strata appear to represent important features of diurnal habitats by providing protection from adverse weather conditions and predators (Duriez *et al.* 2005b). Therefore, reductions in the density and height of shrubs, and the removal of brambles, may negatively impact woodcock, through increased exposure. Woodcock have also been shown to utilise hedges during the day (Duriez *et al.* 2005b), yet this habitat feature is threatened with destruction across much of Europe. For example, in France, there was a 60% loss of hedges between 1966 and 1996 (Schmutz *et al.* 1996). Similarly, in Britain, approximately 50% of hedges were removed between 1947 and 1990 (Barr & Parr 1994). Changes in the age and species composition of woodlands may also have a negative effect on bird species (Fuller *et al.* 2007). In Britain, between 1940 and 1990, there was a 199% increase in coniferous woodland, whilst managed coppice declined by 82% (Forestry Commission 2003). Such drastic changes to the woodland landscape may be detrimental to bird species such as the woodcock, which have specific woodland habitat requirements, particularly during the breeding season (Hoodless & Hirons 2007).

Since woodcock are primarily considered nocturnal feeders in winter (Hirons & Bickford-Smith 1983; Duriez 2003), perhaps the greatest threats to populations are those posed by large-scale agricultural changes that affect the suitability of nocturnal habitats. Across Europe, there has been a decrease in the surface area of permanent grazed meadows, which comprise an important nocturnal habitat

for woodcock during the winter. Indeed, between 1975 and 1995, 12% of natural meadows and pastures disappeared from nine European countries (Poiret 2003). In addition, ploughing, loss of livestock, and chemical applications have all led to reduced habitat quality, through the impoverishment of soil macrofauna (Pain & Pienkowski 1997; Robinson & Sutherland 2002).

To ensure sustainable management of woodcock populations, it is necessary to protect and manage habitats that incorporate both food and cover. Forestry practices should include the preservation of rich soil types that support high earthworm densities, alongside tree species that ameliorate the soil. In doing so, this might allow more woodcock to stay in woods at night, decreasing their energy expenditure and risk of predation (Duriez *et al.* 2005b,c). With regards agricultural practices, the development of set-asides, grass field margins and simplified farm practices (e.g. minimum tillage and direct sowing) may benefit woodcock (Duriez *et al.* 2005b). The details of management practices suited to woodcock conservation are provided by Duriez (2003).

An integrated approach

Migratory woodcock that cross international boundaries represent a shared resource. Therefore, the development of management strategies, to ensure their sustainability, requires collaboration at the international level. A clear priority for international collaboration is the co-ordination of flyway-wide approaches to refuge management, so that birds are offered the same level of protection across all the geographical areas where they may be expected to occur, throughout the annual cycle.

References

References

Adriaensen, F. & Dhondt, A.A. (1990) Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. *Journal of Animal Ecology*, **59**, 1077-1090.

Aebischer, N.J, Robertson, P.A. & Kenward, R.E. (1993) Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, **74**, 1313-1325.

Aitchison, J. (1986) *The statistical analysis of compositional data*. Chapman & Hall, London, UK.

Alerstam, T., Hedenstrom, A. & Akesson, S. (2003) Long-distance migration: evolution and determinants. *Oikos*, **103**, 247-260.

Alexander, W.B. (1939) *Woodcock in the British Isles*. British Trust for Ornithology (BTO), London, UK.

Asbirk, S., Berg, L., Hardeng, G., Koskimies, P. & Petersen, A. (1997) *Population sizes and trends of birds in the Nordic countries 1978-1994*. Nordic Council of Ministers, Copenhagen, Denmark.

Atkinson, P.W., Baker, A.J., Bevan, R.M., Clark, N.A., Cole, K.B., Gonzalez, P.M., Newton, J., Niles, L.J. & Robinson, R.A. (2005) Unravelling the migration and moult strategies of a long-distance migrant using stable isotopes: red knot *Calidris canutus* in the Americas. *Ibis*, **147**, 738-749.

Bailey, R.S. (1967) An index of bird population changes on farmland. *Bird Study*, **14**, 195-209.

Baillie, S.R., Clark, N.A. & Ogilvie, M.A. (1986) *Cold weather movements of waterfowl and waders: an analysis of ringing recoveries*. Wildfowl Trust, Peterborough, UK.

Baker, R.R. (1978) *The evolutionary ecology of animal migration*. Holmes & Meier, New York, USA.

Barr, C.J. & Parr, T.W. (1994) Hedgerows: linking ecological research and countryside policy. *Hedgerow management and nature conservation* (eds T.A. Watt & G.P. Buckley), pp. 119-136. Wye College Press, Wye, UK.

Bartholomew, J. (1931) Woodcock. *The Glasgow naturalist. Volume X* (eds Glasgow and Andersonian Natural History and Microscopical Society), pp. 24-32. Andersonian Naturalists of Glasgow, Glasgow, UK.

Bauthian, I., Gossmann, F., Ferrand, Y. & Julliard, R. (2007) Quantifying the origin of woodcock wintering in France. *Journal of Wildlife Management*, **71**, 701-705.

Bearhop, S., Fiedler, W., Furness, R.W., Votier, S.C., Waldron, S., Newton, J., Bowen, G.J., Berthold, P. & Farnsworth, K. (2005) Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science*, **310**, 502-504.

Bearhop, S., Hilton, G.M., Votier, S.C. & Waldron, S. (2004) Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, 215-218.

Belthoff, J.R. & Gauthreaux, S.A., Jr. (1991) Partial migration and differential winter distribution of house finches in the eastern United States. *The Condor*, **93**, 374-382.

Bengtson, S.A., Nilsson, A., Nordstrom, S. & Rundgreen, S. (1976) Effect of bird predation on lumbricid populations. *Oikos*, **27**, 9-12.

Berthold, P. (1984) The endogenous control of bird migration: a survey of experimental evidence. *Bird Study*, **31**, 19-27.

Berthold, P. (1990) Wegzugbeginn und Einsetzen der Zugunruhe bei 19 Vogelpopularionen - eine vergleichende Untersuchung. *Current topics in avian biology: proceedings of the international centennial meeting of the Deutsche Ornithologen-Gesellschaft* (eds R. van den Elzen, K.L. Schuchmann & K. Schmidt-Koenig), pp. 217-222. Deutsche Ornithologen-Gesellschaft, Bonn, Germany.

Berthold, P. (2001) *Bird migration: a general survey*. Oxford University Press, Oxford, UK.

Bety, J., Gauthier, G. & Jean-François, G. (2003) Body condition, migration, and timing of reproduction in snow geese: a test of the condition-dependent model of optimal clutch size. *The American Naturalist*, **162**, 110-121.

Biebach, H. (1983) Genetic determination of partial migration in the European robin (*Erithacus rubecula*). *The Auk*, **100**, 601-606.

Bingham, R.L. & Brennan, L.A. (2004) Comparison of type I error rates for statistical analyses of resource selection. *Journal of Wildlife Management*, **68**, 206-212.

Bingham, R.L., Brennan, L.A. & Ballard, B.M. (2007) Misclassified resource selection: compositional analysis and unused habitat. *Journal of Wildlife Management*, **71**, 1369-1374.

BirdLife International (2004a) *Birds in the European Union: a status assessment*. BirdLife International, Wageningen, Netherlands.

BirdLife International (2004b) *Birds in Europe: population estimates, trends and conservation status*. BirdLife International, Cambridge, UK.

BirdLife International (2008) The BirdLife Checklist of the birds of the world with conservation status and taxonomic sources. Version 1. *http://ww.birdlife.org/datazone/species/downloads/BirdLife_Checklist_Version_1.xls*

BirdLife International (2010) Stable isotope analysis reveals the wintering grounds of the aquatic warbler. *http://www.birdlife.org/datazone/sowb/casestudy/24*

BirdLife International (2011) Birds on the IUCN Red List. *http://www.birdlife.org/action/science/species/global_species_programme/red_list*

BirdLife International (2012) Species factsheet: *Scolopax rusticola.* *http://www.birdlife.org*

BirdLife International & Natureserve (2011) Bird species distribution maps of the world. 2009. *Scolopax rusticola. IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2.*

Boidot, J.-P. & Aurousseau, G. (2011) Evaluation of the 2010/11 woodcock hunting season in France. *Woodcock and snipe specialist group newsletter. Number 37* (ed Y. Ferrand), pp. 21-22. Office national de la chasse et de la faune sauvage, Le Perray-en-Yvelines, France.

Boos, M., Boidot, J.-P. & Robin, J.-P. (2005) Body condition in the Eurasian woodcock wintering in the west of France: practical study for wildlife management during cold spells. *Wildlife Biology in Practice*, **1**, 15-23.

Boulet, M., Gibbs, H.L. & Hobson, K.A. (2006) Integrated analysis of genetic, stable isotope, and banding data reveal migratory connectivity and flyways in the northern yellow warbler (*Dendroica petechia*; *aestiva* group). *Ornithological Monographs*, **61**, 29-78.

Bowen, G.J. (2008) Spatial analysis of the intra-annual variation of precipitation isotope ratios and its climatological corollaries. *Journal of Geophysical Research*, **113**, 1-10.

Bowen, G.J. (2010) Isoscapes: spatial pattern in isotopic biogeochemistry. *Annual Review of Earth and Planetary Sciences*, **38**, 161-187.

Bowen, G.J., Wassenaar, L.I. & Hobson, K.A. (2005) Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia*, **143**, 337-348.

Bowen, G.J. & West, J.B. (2008) Isotope landscapes for terrestrial migration research. *Tracking animal migration with stable isotopes* (eds K.A. Hobson & L.I. Wassenaar), pp. 79-105. Academic Press, London, UK.

Boyle, W.A. (2008) Can variation in risk of nest predation explain altitudinal migration in tropical birds? *Oecologia*, **155**, 397-403.

Brana, F., Prieto, L. & Gonzalez-Quiros, P. (2010) Habitat change and timing of dusk flight in the Eurasian woodcock: a trade-off between feeding and predator avoidance? *Annales Zoologici Fennici*, **47**, 206-214.

Brattström, O., Bensch, S., Wassenaar, L.I., Hobson, K.A. & Åkesson, S. (2010) Understanding the migration ecology of European red admirals *Vanessa atalanta* using stable hydrogen isotopes. *Ecography*, **33**, 720-729.

Brattström, O., Wassenaar, L.I, Hobson, K.A. & Åkesson, S. (2008) Placing butterflies on the map - testing regional geographical resolution of three stable isotopes in Sweden using the monophagus peacock *Inachis io*. *Ecography*, **31**, 490-498.

Brochard, C., Spaans, B., Prop, J. & Piersma, T. (2002) Use of individual colour-ringing to estimate annual survival in male and female red knot *Calidris canutus islandica*: a progress report for 1998 – 2001. *Wader Study Group Bulletin*, **99**, 54-56.

Broekhuizen, S., Van'T Hoff, C.A., Jansen, M.B. & Niewold, F.J.J. (1980) Application of radio-tracking in wildlife research in the Netherlands. *A handbook on biotelemetry and radio-tracking* (eds C.J. Amlaner & D.W. Macdonald), pp. 65-84. Pergamon Press Ltd, Oxford, UK.

Brown, D.R. & Sherry, T.W. (2006) Food supply controls the body condition of a migrant bird wintering in the tropics. *Oecologia*, **149**, 22-32.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multi-model inference: a practical information-theoretic approach*. Springer Verlag, Berlin, Germany.

Burt, W.H. (1943) Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, **24**, 346-352.

Casas, F., Mougeot, F., Viñuela, J. & Bretagnolle, V. (2009) Effects of hunting on the behaviour and spatial distribution of farmland birds: importance of hunting-free refuges in agricultural areas. *Animal Conservation*, **12**, 346-354.

Catry, P., Campos, A., Almada, V. & Cresswell, W. (2004) Winter segregation of migrant European robins *Erithacus rubecula* in relation to sex, age and size. *Journal of Avian Biology*, **35**, 204-209.

Chamberlain, C.P., Blum, J.D., Holmes, R.T., Feng, X., Sherry, T.W. & Graves, G.R. (1997) The use of isotope tracers for identifying populations of migratory birds. *Oecologia*, **109**, 132-141.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubb, M. (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology*, **37**, 771-788.

Chamberlain, D.E. & Siriwardena, G.M. (2000) The effects of agricultural intensification on skylarks (*Alauda arvensis*): evidence from monitoring studies in Great Britain. *Environmental Reviews*, **8**, 95-113.

Clark, J.A. (2004) Ringing recoveries confirm higher wader mortality in severe winters. *Ringing & Migration*, **22**, 43-50.

Clark, J.A., Robinson, R.A., du Feu, C., Wright, L.J., Conway, G.J., Blackburn, J.R., Leech, D.I., Barber, L.J., de Palacio, D., Griffin, B.M., Moss, D. & Schäfer, S. (2010) Bird ringing in Britain and Ireland in 2009. *Ringing & Migration*, **25**, 88-127.

Clark, N.A. (1982) The effects of the severe weather in December 1981 and January 1982 on waders in Britain. *Wader Study Group Bulletin*, **34**, 5-7.

Clark, R.G., Hobson, K.A. & Wassenaar, L.I. (2006) Geographic variation in the isotopic (δD, $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) composition of feathers and claws from lesser scaup and northern pintail - implications for studies of migratory connectivity. *Canadian Journal of Zoology*, **84**, 1395-1401.

Clausager, I. (1973) Age and sex determination of the woodcock (*Scolopax rusticola*). *Danish Review of Game Biology*, **8**, 3-18.

Clausager, I. (1974) Migration of Scandinavian woodcock (*Scolopax rusticola*) with special reference to Denmark. *Danish Review of Game Biology*, **8**, 1-38.

Clegg, S.M., Kelly, J.F., Kimura, M. & Smith, T.B. (2003) Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's warbler (*Wilsonia pusilla*). *Molecular Ecology*, **12**, 819-830.

Copete, J.L., Marine, R., Bigas, D. & Martinez-Vilalta, A. (1999) Differences in wing shape between sedentary and migratory reed buntings *Emberiza schoeniclus*. *Bird Study*, **46**, 100-103.

Cormie, A.B., Schwarcz, H.P. & Gray, J. (1994) Determination of the hydrogen isotopic composition of bone collagen and correction for hydrogen exchange. *Geochimica et Cosmochimica Acta*, **58**, 365-375.

Cox, G.W. (1985) The evolution of avian migration systems between temperate and tropical regions of the New World. *The American Naturalist*, **126**, 451-474.

Cramp, S. & Simmons, K.E.L. (1983) *Handbook of the birds of Europe, the Middle East and north Africa: the birds of the western Palearctic. Volume 3*. Oxford University Press, Oxford, UK.

Cresswell, B. (2000) *Practical radiotracking*. Biotrack Ltd., Dorset, UK.

Davidson, N.C. (1982) The effects of severe weather in 1978/79 and 1981/82 on shorebirds at Teesmouth: a preliminary view. *Wader Study Group Bulletin*, **34**, 8-10.

Davidson, N.C. & Evans, P.R. (1982) Mortality of redshanks and oystercatchers from starvation during severe weather. *Bird Study*, **29**, 183-188.

Davis, P. (1966) The movements of pied wagtails as shown by ringing. *Bird Study*, **13**, 147-162.

de Grammont, P.C. & Cuaron, A.D. (2006) An evaluation of threatened species categorization systems used on the American continent. *Conservation Biology*, **20**, 14-27.

del Hoyo, J., Elliott, A. & Sargatal, J. (1996) *Handbook of the birds of the world. Volume 3*. Lynx Edicions, Barcelona, Spain.

de Juana, E., Martín-Novella, C., Naveso, M.A., Pain, D. & Sears, J. (1993) Farming and birds in Spain: threats and opportunities for conservation. *RSPB Conservation Review*, **7**, 67-73.

Dingle, H. (1996) *Migration: the biology of life on the move*. Oxford University Press, New York, USA.

Dobinson, H.M. & Richards, A.J. (1964) The effects of the severe winter of 1962-63 on birds in Britain. *British Birds*, **57**, 373-434.

Dobrynina, I.N. & Kharitonov, S.P. (2006) The Russian waterbird migration atlas: temporal variation in migration routes. *Waterbirds around the world* (eds G.C. Boere, C.A. Galbraith & D.A. Stroud), pp. 582-589. The Stationery Office, Edinburgh, UK.

Dolman, P.M. & Sutherland, W.J. (1995) The response of bird populations to habitat loss. *Ibis*, **137**, 38-46.

Donald, P.F., Green, R.E. & Heath, M.F. (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**, 25-29.

Dugan, P.J. (1981) The importance of nocturnal feeding in foraging shorebirds: a consequence of increased invertebrate prey activity. *Feeding and survival strategies of estuarine organisms* (eds N.V. Jones & W.J. Wolff), pp. 251-260. Plenum Press, New York, USA.

Duriez, O. (2003) *Stratégies individuelles d'hivernage chez la Bécasse des bois (Scolopax rusticola): compromis énergétiques pour la sélection de l'habitat*. PhD thesis, University of Paris VI.

Duriez, O., Eraud, C., Barbraud, C. & Ferrand, Y. (2005a) Factors affecting population dynamics of Eurasian woodcocks wintering in France: assessing the efficiency of a hunting-free reserve. *Biological Conservation*, **122**, 89-97.

Duriez, O., Ferrand, Y., Binet, F., Corda, E., Gossmann, F. & Fritz, H. (2005b) Habitat selection of the Eurasian woodcock in winter in relation to earthworms availability. *Biological conservation*, **122**, 479-490.

Duriez, O., Fritz, H., Binet, F., Tremblay, Y. & Ferrand, Y. (2005c) Individual activity rates in wintering Eurasian woodcocks: starvation versus predation risk trade-off? *Animal Behaviour*, **69**, 39-49.

Duriez, O., Fritz, H., Said, S. & Ferrand, Y. (2005d) Wintering behaviour and spatial ecology of Eurasian woodcock *Scolopax rusticola* in western France. *Ibis*, **147**, 519-532.

Duxbury, J.M., Holroyd, G.L. & Muehlenbachs, K. (2003) Changes in hydrogen isotope ratios in sequential plumage stages: an implication for the creation of isotope-base maps for tracking migratory birds. *Isotopes in Environmental and Health Studies*, **39**, 179-189.

Eaton, M.A., Brown, A.F., Noble, D.G., Musgrove, A.J., Hearn, R., Aebischer, N.J., Gibbons, D.W., Evans, A. & Gregory, R.D. (2009) Birds of Conservation Concern 3: the population status of birds in the United Kingdom, Channel Islands and the Isle of Man. *British Birds*, **102**, 296-341.

Ebbinge, B.S. (1991) The impact of hunting on mortality rates and spatial distribution of geese wintering in the western Palearctic. *Ardea*, **79**, 197-210.

Edwards, C.A. & Lofty, J.R. (1972) *Biology of earthworms*. Chapman and Hall, London, UK.

ESRI (2005) ArcGIS version 9.1. Redlands, CA, USA.

Estoppey, F. (2001) Demographics of a breeding population of Eurasian woodcock *Scolopax rusticola* in western Switzerland from 1989 to 2000. *Nos Oiseaux*, **48**, 105-112.

Fadat, C. (1994) Propositions pour la gestion cynégétiques des populations de bécasses en Europe. *Fourth European woodcock and snipe workshop* (ed H. Kalchreuter), pp. 71-80. International Waterfowl Research Bureau (IWRB), Saarbrucken, Germany.

Farmer, A., Cade, B.S. & Torres-Dowdall, J. (2008) Fundamental limits to the accuracy of deuterium isotopes for identifying the spatial origin of migratory animals. *Oecologia*, **158**, 183-192.

Ferrand, Y. & Gossmann, F. (1986) Repartition spatiale des becasses des bois sur leurs habitats nocturnes en Bretagne. *Third European woodcock and snipe workshop* (eds P. Havet & G. Hirons), pp. 48-52. International Waterfowl Research Bureau (IWRB), Slimbridge, UK.

Ferrand, Y. & Gossmann, F. (1995) *La becasse de bois*. Hatier, Paris, France.

Ferrand, Y. & Gossmann, F. (2000) Trend of the breeding woodcock population in France from 1992 to 1997. *Fifth European woodcock and snipe workshop* (ed H. Kalchreuter), pp. 34-36. International Waterfowl Research Bureau (IWRB), Czempin, Poland.

Ferrand, Y. & Gossmann, F. (2001) Elements for a woodcock (*Scolopax rusticola*) management plan. *Game and Wildlife Science*, **18**, 115-139.

Ferrand, Y. & Gossmann, F. (2009) Ageing and sexing the Eurasian woodcock *Scolopax rusticola*. *Wader Study Group Bulletin*, **116**, 75-79.

Ferrand, Y., Gossmann, F., Bastat, C. & Guenezan, M. (2008) Monitoring of the wintering and breeding woodcock populations in France. *Revista Catalana d'Ornitologia*, **24**, 44-52.

Fokin, S., Blokhin, Y., Zverev, P., Kozlova, M. & Romanov, Y. (2004) Spring migration of the woodcock *Scolopax rusticola*, and roding in Russia in 2004. *Wetlands International Woodcock and Snipe Specialist Group*, **30**, 4-8.

Font, L., Nowell, G.M., Pearson, D.G., Ottley, C.J. & Willis, S.G. (2007) Sr isotope analysis of bird feathers by TIMS: a tool to trace bird migration paths and breeding sites. *Journal of Analytical Atomic Spectrometry*, **22**, 513-522.

Forestry Commission (2003) *National inventory of woodland and trees: Great Britain*. Forestry Commission, Edinburgh, UK.

Fox, T.A.D., Christensen, T.J., Bearhop, S. & Newton, J. (2007) Using stable isotope analysis of multiple feather tracts to identify moulting provenance of vagrant birds: a case study of Baikal teal *Anas formosa* in Denmark. *Ibis*, **149**, 622-625.

Fraser, K.C., McKinnon, E.A. & Diamond, A.W. (2010) Migration, diet, or molt? Interpreting stable-hydrogen isotope values in neotropical bats. *Biotropica*, **42**, 512-517.

Freeman, S.N., Robinson, R.A., Clark, J.A., Griffin, B.M. & Adams, S.Y. (2002) Population dynamics of starlings *Sturnus vulgaris* breeding in Britain: an integrated analysis. *Investigation into the causes of the decline of starlings and house sparrows in Great Britain. BTO Research Report no. 290* (eds H.Q.P. Crick, R.A. Robinson, G.F. Appleton, N.A. Clark & A.D. Rickard), pp. 121-138. Department for Environment, Food and Rural Affairs (DEFRA), Bristol, U.K.

Fretwell, S.D. (1972) *Populations in a seasonal environment*. Princeton University Press, New Jersey, USA.

Fretwell, S.D. (1980) Evolution of migration in relation to factors regulating bird numbers. *Migrant birds in the Neotropics: ecology, behaviour, distribution and conservation* (eds A. Keast & E.S. Morton), pp. 517-527. Smithsonian Institute Press, Washington D.C., USA.

Fry, D.M. (1995) Reproductive effects in birds exposed to pesticides and industrial chemicals. *Environmental Health Perspectives*, **103**, 165-171.

Fuller, R.J., Smith, K.W., Grice, P.V., Currie, F.A. & Quine, C.P. (2007) Habitat change and woodland birds in Britain: implications for management and future research. *Ibis*, **149**, 261-268.

Gat, J.R. (1996) Oxygen and hydrogen isotopes in the hydrologic cycle. *Annual Review of Earth and Planetary Sciences*, **24**, 225-262.

Gauthreaux, S.A., Jr. (1982) The ecology and evolution of avian migration systems. *Avian biology. Volume 6* (eds D.S. Farner & J.R. King), pp. 93-167. Academic Press, New York, USA.

Gentle, L.K. & Gosler, A.G. (2001) Fat reserves and perceived predation risk in the great tit, *Parus major*. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**, 487-491.

Gibbons, D.W., Amar, A., Anderson, G.Q.A., Bolton, M., Bradbury, R.B., Eaton, M.A., Evans, A.D., Grant, M.C., Gregory, R.D., Hilton, G.M., Hirons, G.J.M., Hughes, J., Johnstone, I., Newbery, P., Peach, W.J., Ratcliffe, N., Smith, K.W., Summers, R.W., Walton, P. & Wilson, J.D. (2007) *The predation of wild birds in the UK: a review of its conservation impact and management. RSPB Research Report no. 23*. Royal Society for the Protection of Birds (RSPB), Sandy, UK.

Gill, F.B. (1990) *Ornithology*. W.H. Freeman & Company, New York, USA.

Gill, J.A., Norris, K., Potts, P.M., Gunnarsson, T.G., Atkinson, P.W. & Sutherland, W.J. (2001) The buffer effect and large-scale population regulation in migratory birds. *Nature*, **412**, 436-438.

Gillings, S. & Fuller, R.J. (1999) *Winter ecology of golden plovers and lapwings: a review and consideration of extensive survey methods*. British Trust for Ornithology (BTO), Thetford, UK.

Goriup, P. (1994) Little bustard *Tetrax tetrax*. *Birds in Europe: their conservation status* (eds G.M. Tucker & M.F. Heath), pp. 236-237. Birdlife International, Cambridge, UK.

Gosler, A.G. (1987) Pattern and process in the bill morphology of the great tit *Parus major*. *Ibis*, **129**, 451-476.

Gossmann, F., Bastat, C., Coreau, D. & Ferrand, Y. (2011) 2010-2011 French woodcock report. *Woodcock and snipe specialist group newsletter. Number 37*, pp. 17-21. Office national de la chasse et de la faune sauvage, Le Perray-en-Yvelines, France.

Gossmann, F. & Ferrand, Y. (2004) 2003-2004 French Woodcock report. *Woodcock and snipe specialist group newsletter. Number 30*, pp. 36-39. Office national de la chasse et de la faune sauvage, Le Perray-en-Yvelines, France.

Gossmann, F., Ferrand, Y., Loidon, Y. & Sardet, G. (1986) Methodes et resultats de baguages des becasses des bois (*Scolopax rusticola*) en Bretagne. *Third European woodcock and snipe workshop* (eds P. Havet & G. Hirons), pp. 34-41. International Waterfowl Research Bureau (IWRB), Slimbridge, UK.

Granval, P. (1987) Regime alimentaire diurne de la Becasse des bois (*Scolopax rusticola*) en hivernage: approche quantitative. *Gibier Faune Sauvage*, **4**, 125-147.

Granval, P. & Bouche, M.B. (1993) Importance of meadows for wintering Eurasian woodcock in the west of France. *Proceedings of the eighth American woodcock symposium* (eds J.R. Longcore & G.F. Sepik), p. 135. U.S. Fish and Wildlife Service, Washington D.C., USA.

Graves, G.R., Romanek, C.S. & Navarro, A.R. (2002) Stable isotope signature of philopatry and dispersal in a migratory songbird. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 8096-8100.

Greenberg, R., Marra, P.P. & Wooller, M.J. (2007) Stable isotope (C, N, H) analyses help locate the winter range of the coastal plain swamp sparrow (*Melospiza georgiana nigrescens*). *The Auk*, **124**, 1137-1148.

Gregory, R.D., Wilkinson, N.I, Noble, D.G., Robinson, J.A., Brown, A.F., Hughes, J., Procter, D.A., Gibbons, D.W. & Galbraith, C.A. (2002) The population status of birds in the United Kingdom, Channel Islands and Isle of Man: an analysis of conservation concern 2002-2007. *British Birds*, **95**, 410-450.

Gustafsson, L., Nordling, D., Andersson, M.S., Sheldon, B.C. & Qvarnstrom, A. (1994) Infectious diseases, reproductive effort and the cost of reproduction in birds. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **346**, 323-331.

Guzman, J.L., Ferrand, Y. & Beatriz, A. (2011) Origin and migration of woodcock *Scolopax rusticola* wintering in Spain. *European Journal of Wildlife Research*, **57**, 647-655.

Hagemeijer, W.J.M. & Blair, M.J. (1997) *The EBCC atlas of European breeding birds: their distribution and abundance*. T. & A.D. Poyser, London, UK.

Harrison, C. (1982) *An atlas of the birds of the western palearctic*. Collins, London, UK.

Hayes, F.E. (1995) Definitions for migrant birds: what is a Neotropical migrant ? *The Auk*, **112**, 521-523.

Heath, M., Borggreve, C. & Peet, N. (2000) *European bird populations: estimates and trends*. BirdLife International, Cambridge, UK.

Hebert, C.E. & Wassenaar, L.I. (2001) Stable nitrogen isotopes in waterfowl feathers reflect agricultural land use in western Canada. *Environmental science & technology*, **35**, 3482-3487.

Hedenstrom, A. (2006) Scaling of migration and the annual cycle of birds. *Ardea*, **94**, 399-408.

Hepp, G.R., Blohm, R.J., Reynolds, R.E., Hines, J.E. & Nichols, J.D. (1986) Physiological condition of autumn-banded mallards and its relationship to hunting vulnerability. *Journal of Wildlife Management*, **50**, 177-183.

Heppleston, P.B. (1971) The feeding ecology of oystercatchers (*Haematopus ostralegus L.*) in winter in northern Scotland. *Journal of Animal Ecology*, **40**, 651-672.

Hirons, G. (1983) A five-year study of the breeding behaviour and biology of the woodcock in England - a first report. *Second European woodcock and snipe workshop* (ed H. Kalchreuter), pp. 51-67. International Waterfowl Research Bureau (IWRB), Slimbridge, UK.

Hirons, G. (1988) Habitat use by woodcock (*Scolopax rusticola*) during the breeding season. *Third European woodcock and snipe workshop* (eds P. Havet & G. Hirons), pp. 42-47. International Waterfowl Research Bureau (IWRB), Slimbridge, UK.

Hirons, G. & Bickford-Smith, P. (1983) The diet and behaviour of Eurasian woodcock wintering in Cornwall. *Second European woodcock and snipe workshop* (ed H. Kalchreuter), pp. 11-17. International Waterfowl Research Bureau (IWRB), Slimbridge, UK.

Hirons, G. & Johnson, T.H. (1987) A quantitative analysis of habitat preferences of woodcock *Scolopax rusticola* in the breeding season. *Ibis*, **129**, 371-381.

Hirons, G. & Linsley, M. (1989) Counting woodcock. *Game Conservancy Annual Review*, **20**, 47-48.

Hirons, G. & Owen, R.B. (1982) Radio tagging as an aid to the study of woodcock. *Symposium of the Zoological Society of London*, **49**, 139-152.

Hobson, K.A. (1999) Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia*, **120**, 314-326.

Hobson, K.A. (2003) Making migratory connections with stable isotopes. *Avian migration* (eds P. Berthold, E. Gwinner & E. Sonnenschein), pp. 379-391. Springer-Verlag, Berlin, Germany.

Hobson, K.A. (2011) Isotopic ornithology: a perspective. *Journal of Ornithology*, **152**, 49-66.

Hobson, K.A., Atwell, L. & Wassenaar, L.I. (1999a) Influence of drinking water and diet on the stable-hydrogen isotope ratios of animal tissues. *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 8003-8006.

Hobson, K.A., Barnett-Johnson, R. & Cerling, T. (2010a) Using isoscapes to track animal migration. *Isoscapes: understanding movement, pattern, and process on Earth through isotope mapping* (eds J. B. West, G. J. Bowen, T. E. Dawson & K. P. Tu), pp. 273-298. Springer, Dordrecht, Netherlands.

Hobson, K.A., Bowen, G.J., Wassenaar, L.I., Ferrand, Y. & Lormée, H. (2004) Using stable hydrogen and oxygen isotope measurements of feathers to infer geographical origins of migrating European birds. *Oecologia*, **141**, 477-488.

Hobson, K.A. & Clark, R.G. (1992) Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. *The Condor*, **94**, 181-188.

Hobson, K.A., Greenberg, R., Van Wilgenburg, S.L. & Mettke-Hofmann, C. (2010b) Migratory connectivity in the rusty blackbird: isotopic evidence from feathers of historical and contemporary specimens. *The Condor*, **112**, 778-788.

Hobson, K.A., Lormée, H., Van Wilgenburg, S.L., Wassenaar, L.I. & Boutin, J.M. (2009a) Stable isotopes delineate the origins and migratory connectivity of harvested animals: the case of European woodpigeons. *Journal of Applied Ecology*, **46**, 572-581.

Hobson, K.A., McFarland, K.P., Wassenaar, L.I., Rimmer, C.C. & Goetze, J.E. (2001) Linking breeding and wintering grounds of Bicknell's thrushes using stable isotope analyses of feathers. *The Auk*, **118**, 16-23.

Hobson, K.A. & Norris, D.R. (2008) Animal migration: a context for using new techniques and approaches. *Tracking animal migration with stable isotopes* (eds K.A. Hobson & L.I. Wassenaar), pp. 1-19. Academic Press, London, UK.

Hobson, K.A., Van Wilgenburg, S.L., Wassenaar, L.I., Hands, H., Johnson, W.P., O'Meilia, M. & Taylor, P. (2006) Using stable hydrogen isotope analysis of feathers to delineate origins of harvested sandhill cranes in the central flyway of north America. *Waterbirds*, **29**, 137-147.

Hobson, K.A. & Wassenaar, L.I. (1997) Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia*, **109**, 142-148.

Hobson, K.A. & Wassenaar, L.I. (2008) *Tracking animal migration with stable isotopes*. Academic Press, London, UK.

Hobson, K.A., Wassenaar, L.I., Milá, B., Lovette, I., Dingle, C. & Smith, T.B. (2003) Stable isotopes as indicators of altitudinal distributions and movements in an Ecuadorean hummingbird community. *Oecologia*, **136**, 302-308.

Hobson, K.A., Wassenaar, L.I. & Taylor, O.R. (1999b) Stable isotopes (δD and $\delta^{13}C$) are geographic indicators of natal origins of monarch butterflies in eastern north America. *Oecologia*, **120**, 397-404.

Hobson, K.A., Wunder, M.B., Van Wilgenburg, S.L., Clark, R.G. & Wassenaar, L.I. (2009b) A method for investigating population declines of migratory birds using stable isotopes: origins of harvested lesser scaup in north America. *PloS ONE*, **4**, e7915.

Hogan, F.E., Cooke, R., Burridge, C.P. & Norman, J.A. (2008) Optimizing the use of shed feathers for genetic analysis. *Molecular Ecology Resources*, **8**, 561-567.

Holmes, R.T., Sherry, T.W. & Reitsma, L. (1989) Population structure, territoriality and overwinter survival of two migrant warbler species in Jamaica. *The Condor*, **91**, 545-561.

Hoodless, A.N. (1994a) *Aspects of the ecology of the European woodcock Scolopax rusticola L.* PhD thesis, University of Durham.

Hoodless, A.N. (1994b) The density and distribution of woodcock wintering in Cornwall, England. *Fourth European woodcock and snipe workshop* (ed H. Kalchreuter), pp. 27-34. International Waterfowl and Wetlands Research Bureau (IWRB), Slimbridge, UK.

Hoodless, A.N. (1995) Studies of west Palearctic birds no.195. Eurasian woodcock *Scolopax rusticola*. *British Birds*, **88**, 578-592.

Hoodless, A.N. & Coulson, J.C. (1994) Survival rates and movements of British and Continental woodcock *Scolopax rusticola* in the British Isles. *Bird Study*, **41**, 48-60.

Hoodless, A.N. & Coulson, J.C. (1998) Breeding biology of the woodcock *Scolopax rusticola* in Britain. *Bird Study*, **45**, 195-204.

Hoodless, A.N. & Hirons, G.J.M. (2007) Habitat selection and foraging behaviour of breeding Eurasian woodcock *Scolopax rusticola*: a comparison between contrasting landscapes. *Ibis*, **149**, 234-249.

Hoodless, A.N., Lang, D., Aebischer, N.J., Fuller, R.J. & Ewald, J.A. (2009) Densities and population estimates of breeding Eurasian woodcock *Scolopax rusticola* in Britain in 2003. *Bird Study*, **56**, 15-25.

Hoodless, A. & Saari, L. (1997) Woodcock *Scolopax rusticola. The EBCC atlas of European breeding birds: their distribution and abundance* (eds W.J.M. Hagemeijer & M.J. Blair), pp. 292-293. T. & A.D. Poyser, London, UK.

Hudson, P.J., Dobson, A.P. & Newborn, D. (1998) Prevention of population cycles by parasite removal. *Science*, **282**, 2256-2258.

Hulscher, J.B. (1976) Localisation of cockles (*Cardium edule L.*) by the oystercatcher (*Haematopus ostralegus L.*) in darkness and daylight. *Ardea*, **64**, 292-310.

Imbert, G. (1988) Distribution spatio-temporelle des becasses (*Scolopax rusticola*) dans leur habitat diurne en foret domaniale de Boulogne-sur-Mer (Pas-de-Calais) France. *Third European woodcock and snipe workshop* (eds P. Havet & G. Hirons), pp. 53-59. International Waterfowl and Wetlands Research Bureau (IWRB), Slimbridge, UK.

IUCN (2001) *IUCN Red List categories and criteria: version 3.1.* International Union for Conservation of Nature (IUCN), Gland, Switzerland & Cambridge, UK.

IUCN (2005) Guidelines for using the IUCN Red List categories and criteria. *http://www.iucn.org/webfiles/doc/SSC/RedList/RedListGuidelines.pdf*

IUCN (2012) The IUCN Red List of Threatened Species. Version 2011.2. *http://www.iucnredlist.org*

Jardine, T.D. & Cunjak, R.A. (2005) Analytical error in stable isotope ecology. *Oecologia*, **144**, 528-533.

Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65-71.

Johnson, M.D. & Sherry, T.W. (2001) Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. *Journal of Animal Ecology*, **70**, 546-560.

Judas, M. (1989) Predator-pressure on earthworms: field experiment in a beechwood. *Pedobiologia*, **33**, 339-354.

Kaitala, A., Kaitala, V. & Lundberg, P. (1993) A theory of partial migration. *The American Naturalist*, **142**, 59-81.

Kalchreuter, H. (2000) Activities and preliminary results of research on woodcock (*Scolopax rusticola*) in Europe. *Proceedings of the ninth American woodcock symposium* (eds D.G. McAuley, J.G. Bruggink & G.F. Sepik), pp. 36-41. Patuxent Wildlife Research Centre, Maryland, USA.

Kalchreuter, H. (1983) *The woodcock*. Verlag Dieter Hoffman, Mainz, Germany.

Keller, G.S. & Yahner, R.H. (2006) Declines of migratory songbirds: evidence for wintering-ground causes. *Northeastern Naturalist*, **13**, 83-92.

Kelly, J.F., Atudorei, V., Sharp, Z.D. & Finch, D.M. (2002) Insights into Wilson's warbler migration from analyses of hydrogen stable isotope ratios. *Oecologia*, **130**, 216-221.

Kelly, J.F., Johnson, M.J., Langridge, S. & Whitfield, M. (2008) Efficacy of stable isotope ratios in assigning endangered migrants to breeding and wintering sites. *Ecological Applications*, **18**, 568-576.

Kelly, J.F., Ruegg, K.C. & Smith, T.B. (2005) Combining isotopic and genetic markers to identify breeding origins of migrant birds. *Ecological Applications*, **15**, 1487-1494.

Kennedy, R.S., Fisher, T.H., Harrap, S.C.B., Diesmos, A.C. & Manamtam, A.S. (2001) A new species of woodcock (Aves: Scolopacidae) from the Philippines and a re-evaluation of other Asian/Papuasian woodcock. *Forktail*, **17**, 1-12.

Kenward, R.E. (1982) Goshawk hunting behaviour, and range size as a function of food and habitat availability. *Journal of Animal Ecology*, **51**, 69-80.

Kenward, R.E. (2001) *A manual for wildlife radio-tagging*. Academic Press, London, UK.

Kenward, R.E., Walls, S.S., South, A.B. & Casey, N.M. (2008) *Ranges 8: for the analysis of tracking and location data. Online manual*. Anatrack Ltd, Wareham, UK.

Ketterson, E.D. & Nolan, V., Jr. (1982) The role of migration and winter mortality in the life history of a temperate-zone migrant, the dark-eyed junco, as determined from demographic analyses of winter populations. *The Auk*, **99**, 243-259.

Ketterson, E.D. & Nolan, V., Jr. (1983) The evolution of differential bird migration. *Current ornithology* (ed R. Johnston), pp. 357-402. Plenum Press, New York, USA.

Kirby, J.S., Stattersfield, A.J., Butchart, S.H.M., Evans, M.I., Grimmett, R.F.A., Jones, V.R., O'Sullivan, J., Tucker, G.M. & Newton, I. (2008) Key conservation issues for migratory land- and waterbird species on the world's major flyways. *Bird Conservation International*, **18**, 49-73.

Kozlova, E.V. (1962) *Charadriiformes. Suborder Limicolae. Fauna of the USSR. Birds 2 (1), Part 3*. Publishing House of the USSR Academy of Sciences, Moscow-Leningrad, USSR.

Kristiansen, J.N. & Jarrett, N.S. (2002) Inter-specific competition between Greenland white-fronted geese *Anser albifrons flavirostris* and Canada geese *Branta canadensis* interior moulting in west Greenland: mechanisms and consequences. *Ardea*, **90**, 1-13.

Lack, D. (1943) The age of some more British birds. *British Birds*, **36**, 193-197, 214-221.

Lack, D. (1954) *The natural regulation of animal numbers*. Clarendon Press, Oxford, UK.

Lack, D. (1968) Bird migration and natural selection. *Oikos*, **19**, 1-9.

Langin, K.M., Reudink, M.W., Marra, P.P., Norris, D.R., Kyser, T.K. & Ratcliffe, L.M. (2007) Hydrogen isotopic variation in migratory bird tissues of known origin: implications for geographic assignment. *Oecologia*, **152**, 449-457.

Larson, K.W. & Hobson, K.A. (2009) Assignment to breeding and wintering grounds using stable isotopes: a comment on lessons learned by Rocque *et al.* *Journal of Ornithology*, **150**, 709-712.

Legagneux, P., Blaize, C., Latraube, F., Gautier, J. & Bretagnolle, V. (2009) Variation in home-range size and movements of wintering dabbling ducks. *Journal of Ornithology*, **150**, 183-193.

Lima, S.L. (1986) Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology*, **67**, 377-385.

Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619-640.

Loiselle, B.A. & Blake, J.G. (1991) Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology*, **72**, 180-193.

Lott, C.A. & Smith, J.P. (2006) A geographic-information-system approach to estimating the origin of migratory raptors in north America using stable hydrogen isotope ratios in feathers. *The Auk*, **123**, 822-835.

Lund, U. & Agostinelli, C. (2011) circular: circular statistics. *http://cran.r-project.org/package=circular*

Lundberg, P. (1988) The evolution of partial migration in birds. *Trends in Ecology & Evolution*, **3**, 172-175.

Lundberg, P. & Eriksson, L.-O. (1984) Postjuvenile moult in two northern Scandinavian starling *Sturnus vulgaris* populations: evidence for difference in the circannual time-program. *Ornis Scandinavica*, **15**, 105-109.

Lutz, M. & Jensen, F.P. (2006) *European management plan for woodcock Scolopax rusticola 2006-2009*. European Commission, unpublished report.

Madsen, J. (1985) Habitat selection of farmland feeding geese in west Jutland, Denmark: an example of a niche shift. *Ornis Scandinavica*, **16**, 140-144.

Madsen, J. (1995) Impacts of disturbance on migratory waterfowl. *Ibis*, **137**, 67-74.

Madsen, J. & Fox, A.D. (1995) Impacts of hunting disturbance on waterbirds - a review. *Wildlife Biology*, **1**, 193-207.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002) *Resource selection by animals: statistical design and analysis for field studies*. Kluwer Academic Publishers, Dordrecht, Netherlands.

Marchant, J.H., Hudson, R., Carter, S.P. & Whittington, P.A. (1990) *Population trends in British breeding birds*. British Trust for Ornithology (BTO), Tring, UK.

Marquiss, M., Hobson, K.A. & Newton, I. (2008) Stable isotope evidence for different regional source areas of common crossbill *Loxia curvirostra* irruptions into Britain. *Journal of Avian Biology*, **39**, 30-34.

Marra, P.P., Hobson, K.A. & Holmes, R.T. (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science*, **282**, 1884-1886.

Marra, P.P. & Holberton, R.L. (1998) Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. *Oecologia*, **116**, 284-292.

Marra, P.P. & Holmes, R.T. (2001) Consequences of dominance-mediated habitat segregation in American redstarts during the nonbreeding season. *The Auk*, **118**, 92-104.

Marshall, J.D., Brooks, J.R. & Lajtha, K. (2007) Sources of variation in the stable isotopic composition of plants. *Stable isotopes in ecology and environmental science* (eds R.H. Michener & K. Lajtha), pp. 22-60. Blackwell Scientific Publications, London, UK.

Martin, G.R. (1994) Visual fields in woodcocks *Scolopax rusticola* (Scolopacidae; Charadriiformes). *Journal of Comparative Physiology A*, **174**, 787-793.

Martin, T.G., Chadès, I., Arcese, P., Marra, P.P., Possingham, H.P. & Norris, D.R. (2007) Optimal conservation of migratory species. *PloS ONE*, **2**, e751.

Mason, C.F. & Macdonald, S.M. (1999) Habitat use by lapwings and golden plovers in a largely arable landscape. *Bird Study*, **46**, 89-99.

Maynard Smith, J. (1982) *Evolution and the theory of games*. Cambridge University Press, Cambridge, UK.

Mazerolle, D.F., Hobson, K.A. & Wassenaar, L.I. (2005) Stable isotope and band-encounter analyses delineate migratory patterns and catchment areas of white-throated sparrows at a migration monitoring station. *Oecologia*, **144**, 541-549.

McCutchan, J.H., Jr., Lewis, W.M., Jr., Kendall, C. & Mcgrath, C. (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos*, **102**, 378-390.

McGregor, P. & Peake, T. (1998) The role of individual identification in conservation biology. *Behavioural ecology and conservation biology* (ed T. Caro), pp. 261-284. Oxford University Press, Oxford, UK.

McKechnie, A.E., Wolf, B.O. & Martínez del Rio, C. (2004) Deuterium stable isotope ratios as tracers of water resource use: an experimental test with rock doves. *Oecologia*, **140**, 191-200.

Meehan, T.D., Rosenfield, R.N., Atudore, V.N., Bielefeldt, J., Rosenfield, L.J., Stewart, A.C., Stout, W.E. & Bozek, M.A. (2003) Variation in hydrogen stable isotope ratios between adult and nestling Cooper's hawks. *The Condor*, **105**, 567-572.

Mehl, K.R., Alisauskas, R.T., Hobson, K.A. & Merkel, F.R. (2005) Linking breeding and wintering areas of king eiders: making use of polar isotopic gradients. *Journal of Wildlife Management*, **69**, 1297-1304.

Meltofte, H. (1982) Shooting disturbance of waterfowl. *Dansk ornithologisk Forenings Tidsskrift*, **76**, 21-35.

Met Office (2010a) UK mapped climate averages. *http://www.metoffice.gov.uk/climate/uk/averages/ukmapavge*

Met Office (2010b) December 2010 likely to be coldest in UK series. *http://metofficenews.wordpress.com/2010/12*

Met Office (2012a) UK climate summaries.
http://www.metoffice.gov.uk/climate/uk

Met Office (2012b) Understanding weather.
http://www.metoffice.gov.uk/education/teachers/in-depth/understanding

Microsoft Corporation (2003) Microsoft Office Excel 2003.

Miller, D.A., Hurst, G.A. & Leopold, B.D. (1999) Habitat use of eastern wild turkeys in central Mississippi. *Journal of Wildlife Management*, **63**, 210-222.

Mineau, P. (2005) Direct losses of birds to pesticides - beginnings of a quantification. *Proceedings of the third international partners in flight conference* (eds C.J. Ralph & T.D. Rich), pp. 1065-1070. USDA Forest Service PSW-GTR-191, California, USA.

Mitchell, P.I., Scott, I. & Evans, P.R. (2000) Vulnerability to severe weather and regulation of body mass of Icelandic and British redshank *Tringa totanus*. *Journal of Avian Biology*, **31**, 511-521.

Moorcroft, P.R. & Barnett, A. (2008) Mechanistic home range models and resource selection analysis: a reconciliation and unification. *Ecology*, **89**, 1112-1119.

Murphy, M.T., Pierce, A., Shoen, J., Murphy, K.L., Campbell, J.A. & Hamilton, D.A. (2001) Population structure and habitat use by overwintering neotropical migrants on a remote oceanic island. *Biological Conservation*, **102**, 333-345.

Myers, J.P. (1981) A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. *Canadian Journal of Zoology*, **59**, 1527-1534.

Natural England (1994) Hedgerow Biodiversity Action Plan.

Neto, J.M., Newton, J., Gosler, A.G. & Perrins, C.M. (2006) Using stable isotope analysis to determine the winter moult extent in migratory birds: the complex moult of Savi's warblers *Locustella luscinioides*. *Journal of Avian Biology*, **37**, 117-124.

Newton, I. (1986) *The sparrowhawk*. T. & A.D. Poyser Ltd, London, UK.

Newton, I. (1993) Predation and limitation of bird numbers. *Current Ornithology*, **11**, 143-198.

Newton, I. (1998) *Population limitation in birds*. Academic Press, California, USA & London, UK.

Newton, I. (2004a) Population limitation in migrants. *Ibis*, **146**, 197-226.

Newton, I. (2004b) The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis*, **146**, 579-600.

Newton, I. (2008) *The migration ecology of birds*. Academic Press, London, UK.

Newton, I. (2012) Obligate and facultative migration in birds: ecological aspects. *Journal of Ornithology*, **153**, 171-180.

Newton, I., Hobson, K.A., Fox, A.D. & Marquiss, M. (2006) An investigation into the provenance of northern bullfinches *Pyrrhula p. pyrrhula* found in winter in Scotland and Denmark. *Journal of Avian Biology*, **37**, 431-435.

Nolan, V., Jr. & Ketterson, E.D. (1983) An analysis of body mass, wing length and visible fat deposits of dark-eyed juncos wintering at different latitudes. *The Wilson Bulletin*, **95**, 603-620.

Norris, D.R. (2005) Carry-over effects and habitat quality in migratory populations. *Oikos*, **109**, 178-186.

Norris, D.R. & Marra, P.P. (2007) Seasonal interactions, habitat quality and population dynamics in migratory birds. *The Condor*, **109**, 535-547.

Norris, D.R., Marra, P.P., Bowen, G.J., Ratcliffe, L.M., Royle, J.A. & Kyser, T.K. (2006) Migratory connectivity of a widely distributed songbird, the American redstart (*Setophaga ruticilla*). *Ornithological Monographs*, **61**, 14-28.

Norris, D.R., Marra, P.P., Kyser, T.K. & Ratcliffe, L.M. (2005) Tracking habitat use of a long-distance migratory bird, the American redstart *Setophaga ruticilla*, using stable-carbon isotopes in cellular blood. *Journal of Avian Biology*, **36**, 164-170.

Norris, D.R., Marra, P.P., Kyser, T.K., Sherry, T.W. & Ratcliffe, L.M. (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, 59-64.

Owen, R.B., Jr. & Krohn, W.B. (1973) Molt pattern and weight changes of the American woodcock. *The Wilson Bulletin*, **85**, 31-41.

Pain, D.J., Green, R.E., Giebing, B., Kozulin, A., Poluda, A., Ottosson, U., Flade, M. & Hilton, G.M. (2004) Using stable isotopes to investigate migratory connectivity of the globally threatened aquatic warbler *Acrocephalus paludicola*. *Oecologia*, **138**, 168-174.

Pain, D.J. & Pienkowski, M.W. (1997) *Farming and birds in Europe*. Academic Press, London, UK.

Paritte, J.M. & Kelly, J.F. (2009) Effect of cleaning regime on stable isotope ratios of feathers in Japanese quail (*Coturnix japonica*). *The Auk*, **126**, 165-174.

Peach, W.J., Robinson, R.A. & Murray, K.A. (2004) Demographic and environmental causes of the decline of rural song thrushes *Turdus philomelos* in lowland Britain. *Ibis*, **146**, 50-59.

Perdeck, A.C. (1977) The analysis of ringing data: pitfalls and prospects. *Vogelwarte*, **29**, 33-44.

Pérez, G.E. & Hobson, K.A. (2007) Feather deuterium measurements reveal origins of migratory western loggerhead shrikes (*Lanius ludovicianus excubitorides*) wintering in Mexico. *Diversity and Distributions*, **13**, 166-171.

Pérez-Tris, J., Carbonell, R. & Telleria, J.L. (1999) A method for differentiating between sedentary and migratory blackcaps *Sylvia atricapilla* in wintering areas of southern Iberia. *Bird Study*, **46**, 299-304.

Phillips, D.L. & Eldridge, P.M. (2006) Estimating the timing of diet shifts using stable isotopes. *Oecologia*, **147**, 195-203.

Piersma, T., van Gils, J. & Wiersma, P. (1996) Family Scolopacidae (sandpipers, snipes and phalaropes). *Handbook of the birds of the world. Volume 3. Hoatzin to auks* (eds J. del Hoyo, A. Elliott & J. Sargatal), pp. 444-533. Lynx Edicions, Barcelona, Spain.

Pineiro, G., Perelman, S., Guerschman, J.P. & Paruelo, J.M. (2008) How to evaluate models: observed vs. predicted or predicted vs. observed? *Ecological Modelling*, **216**, 316-322.

Pitney Bowes Software Inc. (2009) MapInfo Professional version 11.0.3.

Poiret, M. (1999) Crop trends and environmental impacts. *Agriculture, environment, rural development: facts and figures - a challenge for agriculture* (eds Statistical Office of the European Communities, European Commission; Directorate-General for Agriculture, European Commission; & Directorate-General for Environment, Nuclear Safety, and Civil Protection), pp. 54-77. Office for Official Publications of the European Communities, Luxembourg, Luxembourg.

Pommeresche, R. & Loes, A.-K. (2009) Relations between agronomic practice and earthworms in Norwegian arable soils. *Dynamic soil, Dynamic Plant*, **3**, 129-142.

Powell, L.A. & Hobson, K.A. (2006) Enriched feather hydrogen isotope values for wood thrushes sampled in Georgia, USA, during the breeding season: implications for quantifying dispersal. *Canadian Journal of Zoology*, **84**, 1331-1338.

R Development Core Team (2011) R: a language and environment for statistical computing. Vienna, Austria.
http://www.r-project.org

Rabe, D.L., Prince, H.H. & Beaver, D.L. (1983) Feeding-site selection and foraging strategies of American woodcock. *The Auk*, **100**, 711-716.

Rappole, J.H., King, D.I. & Diez, J. (2003) Winter vs. breeding-habitat limitation for an endangered avian migrant. *Ecological Applications*, **13**, 735-742.

Rappole, J.H. & McDonald, M.V. (1994) Cause and effect in population declines of migratory birds. *The Auk*, **111**, 652-660.

Raynsford, L.J. (1959) Early roding of woodcock. *British Birds*, **52**, 268.

Regan, T.J., Burgman, M.A., McCarthy, M.A., Master, L.L., Keith, D.A., Mace, G.M. & Andelman, S.J. (2005) The consistency of extinction risk classification protocols. *Conservation Biology*, **19**, 1969-1977.

Reichlin, T.S., Hobson, K.A., Wassenaar, L.I., Schaub, M., Tolkmitt, D., Becker, D., Jenni, L. & Arlettaz, R. (2010) Migratory connectivity in a declining bird species: using feather isotopes to inform demographic modelling. *Diversity and Distributions*, **16**, 643-654.

Reichlin, T.S., Schaub, M., Menz, M.H.M., Mermod, M., & Portner, P., Arlettaz, R. & Jenni, L. (2009) Migration patterns of hoopoe *Upupa epops* and wryneck *Jynx torquilla*: an analysis of European ring recoveries. *Journal of Ornithology*, **150**, 393-400.

Robinson, R.A. & Sutherland, W.J. (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, **39**, 157-176.

Rochford, J.M. & Wilson, H.J. (1982) Value of biometric data in the determination of age and sex in the woodcock (*Scolopax rusticola*). *Proceedings of the seventh American woodcock conference* (eds T.J. Dwyer & G.L. Storm), pp. 158-167. United States Fish and Wildlife Service, Pennsylvania, USA.

Rocque, D.A., Ben-David, M., Barry, R.P. & Winker, K. (2006) Assigning birds to wintering and breeding grounds using stable isotopes: lessons from two feather generations among three intercontinental migrants. *Journal of Ornithology*, **147**, 395-404.

Rodrigues, A.S.L., Pilgrim, J.D., Lamoreux, J.F., Hoffmann, M. & Brooks, T.M. (2006) The value of the IUCN Red List for conservation. *Trends in Ecology & Evolution*, **21**, 71-76.

Rogers, C.M. (1987) Predation risk and fasting capacity: do wintering birds maintain optimal body mass? *Ecology*, **68**, 1051-1061.

Rogers, C.M. (2005) Food limitation among wintering birds: a view from adaptive mass models. *Birds of two worlds: the ecology and evolution of migration* (eds R. Greenberg & P.P. Marra), pp. 106-113. The John Hopkins University Press, London, UK.

Roodbergen, M. (2010) *Population dynamics of black-tailed godwits in the light of heavy metal pollution*. PhD thesis, Wageningen University.

Royle, J.A. & Rubenstein, D.R. (2004) The role of species abundance in determining breeding origins of migratory birds with stable isotopes. *Ecological Applications*, **14**, 1780-1788.

Rubenstein, D.R., Chamberlain, C.P., Holmes, R.T., Ayres, M.P., Waldbauer, J.R., Graves, G.R. & Tuross, N.C. (2002) Linking breeding and wintering ranges of a migratory songbird using stable isotopes. *Science*, **295**, 1062-1065.

Rubenstein, D.R. & Hobson, K.A. (2004) From birds to butterflies: animal movement patterns and stable isotopes. *Trends in Ecology & Evolution*, **19**, 256-263.

Sandercock, B.K., Nilsen, E.B., Brøseth, H. & Pedersen, H.C. (2011) Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. *Journal of Animal Ecology*, **80**, 244-258.

Schenk, J. (1925) The migration of woodcock in Europe. *British Birds*, **19**, 34-44.

Schimmelmann, A. (1991) Determination of the concentration and stable isotopic composition of non-exchangeable hydrogen in organic matter. *Analytical Chemistry*, **63**, 2456-2459.

Schmutz, T., Bazin, P. & Garapon, D. (1996) *L'arbre dans le paysage rural*. Institut pour le De´veloppement Forestier, Paris, France.

Schwab, I.R. (2001) Eyes in the back of your head. *British Journal of Ophthalmology*, **85**, 904.

Seigne, J.W. (1930) *A bird watcher's notebook*. Phillip Allan, London, UK.

Sherry, T.W. & Holmes, R.T. (1996) Winter habitat quality, population limitation, and conservation of neotropical nearctic migrant birds. *Ecology*, **77**, 36-48.

Shorten, M. (1974) *The European woodcock (Scolopax rusticola): a search of the literature since 1940*. The Game Conservancy, Hampshire, UK.

Shrubb, M. (2007) *The lapwing*. T. & A.D. Poyser, London, UK.

Smith, A.D., Donohue, K. & Dufty, A.M., Jr. (2008) Intrafeather and intraindividual variation in the stable-hydrogen isotope content of raptor feathers. *The Condor*, **110**, 500-506.

Smith, A.D. & Dufty, A.M., Jr. (2005) Variation in the stable-hydrogen isotope composition of northern goshawk feathers: relevance to the study of migratory origins. *The Condor*, **107**, 547-558.

Smith, A.D., Lott, C.A., Smith, J.P., Donohue, K.C., Wittenberg, S., Smith, K.G. & Goodrich, L. (2009a) Deuterium measurements of raptor feathers: does a lack of reproducibility compromise geographic assignment? *The Auk*, **126**, 41-46.

Smith, A.D., Lott, C.A., Smith, J.P., Donohue, K.C., Wittenberg, S., Smith, K.G. & Goodrich, L. (2009b) Poor reproducibility and inference in hydrogen-stable isotope studies of avian movement: a reply to Wunder *et al.* (2009). *The Auk*, **126**, 926-931.

Smith, H.G. & Nilsson, J.-A. (1987) Intraspecific variation in migratory pattern of a partial migrant, the blue tit (*Parus caeruleus*): an evaluation of different hypotheses. *The Auk*, **104**, 109-115.

Smith, T.B., Clegg, S.M., Kimura, M., Ruegg, K.C., Milá, B. & Lovette, I.J. (2005) Molecular genetic approaches to linking breeding and overwintering areas in five Neotropical migrant passerines. *Birds of two worlds: the ecology and evolution of migration* (eds R. Greenberg & P.P. Marra), pp. 222-234. Johns Hopkins University Press, Maryland, USA.

Snow, D.W. (1966) Movements of British robins as shown by ringing. *British Birds*, **59**, 67-74.

Snow, D.W. (1968) Movements and mortality of British kestrels *Falco tinnunculus*. *Bird Study*, **15**, 65-83.

Sokal, R.R. & Rholf, F.J. (1994) *Biometry: the principles and practices of statistics in biological research*. W.H. Freeman, New York, USA.

Solorzano, S., Castillo, S., Valverde, T. & Avila, L. (2000) Quetzal abundance in relation to fruit availability in a cloud forest in southeastern Mexico. *Biotropica*, **32**, 523-532.

Spencer, R. (1964) Report on bird ringing for 1963. *British Birds*, **57**, 525-582.

Spencer, R. (1982) Birds in winter - an outline. *Bird Study*, **29**, 169-182.

Stronach, B., Harrington, D. & Wilkens, N. (1974) An analysis of Irish woodcock data. *Proceedings of the fifth American woodcock workshop*. Unpublished manuscript.

Strong, A.M. & Sherry, T.W. (2000) Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. *Journal of Animal Ecology*, **69**, 883-895.

Stroud, D.A., Harradine, J.H., Shedden, C., Hughes, J., Williams, G., Clark, J.A. & Clark, N.A. (2006) Reducing waterbird mortality in severe cold weather: 25 years of statutory shooting suspensions in Britain. *Waterbirds around the world* (eds G.C. Boere, C.A. Galbraith & D.A. Stroud), pp. 784-790. The Stationery Office, Edinburgh, UK.

Studds, C.E. & Marra, P.P. (2005) Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. *Ecology*, **86**, 2380-2385.

Summers, R. & Buckland, S. (1996) Numbers of wintering woodcock *Scolopax rusticola* in woodlands in the Highlands of Scotland. *Wader Study Group Bulletin*, **80**, 50-52.

Svensson, L. (1992) *Identification guide to European passerines*. British Trust for Ornithology (BTO), Thetford, UK.

Swingland, I.R. & Greenwood, P.J. (1983) *The ecology of animal movement*. Oxford University Press, Oxford, UK.

SYSTAT Software Inc. (2011) SYSTAT version 13.1. California, USA.

Tavecchia, G., Pradel, R., Gossmann, F., Bastat, C., Ferrand, Y. & Lebreton, J.-D. (2002) Temporal variation in annual survival probability of the Eurasian woodcock *Scolopax rusticola* wintering in France. *Wildlife Biology*, **8**, 21-30.

Telleria, J.L. & Carbonell, R. (1999) Morphometric variation of five Iberian blackcap *Sylvia atricapilla* populations. *Journal of Avian Biology*, **30**, 63-71.

The European Parliament and the Council of the European Union. (2010) Directive 2009/147/EC of the European Parliament and of the Council of 30 November 2009 on the conservation of wild birds. *Official Journal of the European Union L20,* **53**, 7-25.

The RSPB (2012) Woodcock.
http://www.rspb.org.uk/wildlife/birdguide/name/w/woodcock

Thiollay, J.M. (2005) Effects of hunting on guianan forest game birds. *Biodiversity and Conservation*, **14**, 1121-1135.

Toyne, E.P. (1998) Breeding season diet of the goshawk *Accipiter gentilis* in Wales. *Ibis*, **140**, 569-579.

Trucchi, E., Allegrucci, G., Riccarducci, G., Aradis, A., Spina, F. & Sbordoni, V. (2011) A genetic characterization of European woodcock (*Scolopax rusticola*, Charadriidae, Charadriiformes) overwintering in Italy. *Italian Journal of Zoology*, **78**, 146-156.

Tucker, G.M. & Heath, M.F. (1994) *Birds in Europe: their conservation status*. Birdlife International, Cambridge, UK.

Vali, U. & Elts, J. (2002) Molecular sexing of Eurasian woodcock *Scolopax rusticola. Wader Study Group Bulletin*, **98**, 48.

Van Wilgenburg, S.L. & Hobson, K.A. (2011) Combining stable isotope (δD) and band recovery data to improve probabilistic assignment of migratory birds to origin. *Ecological Applications*, **21**, 1340-1351.

Vickery, P.D. & Herkert, J.R. (1999) *Ecology and conservation of grassland birds of the western hemisphere*. Cooper Ornithological Society, California, USA.

Village, A. (1982) The home range and density of kestrels in relation to vole abundance. *Journal of Animal Ecology*, **51**, 413-428.

VSN International Ltd. (2011) GenStat version 14.

Wada, E., Mizutani, H. & Minagawa, M. (1991) The use of stable isotopes for food web analysis. *Critical Reviews in Food Science and Nutrition*, **30**, 3361-371.

Walther, B.A., Schäffer, N., Van Niekerk, A., Thuiller, W., Rahbek, C. & Chown, S.L. (2007) Modelling the winter distribution of a rare and endangered migrant, the aquatic warbler *Acrocephalus paludicola*. *Ibis*, **149**, 701-714.

Wassenaar, L.I. (2008) An introduction to light stable isotopes for use in terrestrial animal migration studies. *Tracking animal migration with stable isotopes* (eds K.A. Hobson & L.I Wassenaar), pp. 21-44. Academic Press, London, UK.

Wassenaar, L.I. & Hobson, K.A. (2000a) Improved method for determining the stable-hydrogen isotopic composition (δD) of complex organic materials of environmental interest. *Environmental Science & Technology*, **34**, 2354-2360.

Wassenaar, L.I. & Hobson, K.A. (2000b) Stable-carbon and hydrogen isotope ratios reveal breeding origins of red-winged blackbirds. *Ecological Applications*, **10**, 911-916.

Wassenaar, L.I. & Hobson, K.A. (2003) Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. *Isotopes in Environmental and Health Studies*, **39**, 211-217.

Wassenaar, L.I. & Hobson, K.A. (2006) Stable-hydrogen isotope heterogeneity in keratinous materials: mass spectrometry and migratory wildlife tissue subsampling strategies. *Rapid Communications in Mass Spectrometry*, **20**, 2505-2510.

Watson, A. (1985) Social class, socially induced loss, recruitment and breeding of red grouse. *Oecologia*, **67**, 493-498.

Watson, A. & Jenkins, D. (1968) Experiments on population control by territorial behaviour in red grouse. *Journal of Animal Ecology*, **37**, 595-614.

Weaver, P. (1981) *The birdwatcher's dictionary*. T. & A.D. Poyser, London, UK.

Webster, M.S. & Marra, P.P. (2005) The importance of understanding migratory connectivity and seasonal interactions. *Birds of two worlds: the ecology and evolution of migration* (eds R. Greenberg & P.P. Marra), pp. 199-221. The John Hopkins University Press, Baltimore, USA & London, UK.

Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S. & Holmes, R.T. (2002) Links between worlds: unravelling migratory connectivity. *Trends in Ecology & Evolution*, **17**, 76-83.

Wernham, C.V., Toms M.P., Marchant, J.H., Clark, J.A., Siriwardena, G.M. & Baillie, S.R. (eds). (2002) *The migration atlas: movements of the birds of Britain and Ireland*. T. & A.D. Poyser, London, UK.

West, J.B., Bowen, G.J., Dawson, T.E. & Tu, K.P. (2010) *Isoscapes: understanding movement, pattern, and process on earth through isotope mapping*. Springer, New York, USA.

Wetlands International (2002) *Waterbird population estimates. Wetlands International Global Series No. 12*. BirdLife International, Wageningen, Netherlands.

Wetlands International (2006) *Waterbird population estimates. Fourth edition.* Wetlands International, Wageningen, Netherlands.

Wheeler, B.K. (2003) *Raptors of western north America*. Princeton University Press, New Jersey, USA.

Whitaker, D.M., Stauffer, D.F., Norman, G.W., Devers, P.K., Edwards, J., Giuliano, W.M., Harper, C., Igo, W., Sole, J., Spiker, H. & Tefft, B. (2007) Factors associated with variation in home-range size of Appalachian ruffed grouse (*Bonasa umbellus*). *The Auk*, **124**, 1407-1424.

White, G.C. & Garrott, R.A. (1990) *Analysis of wildlife radio-tracking data.* Academic Press, California, USA.

Whittingham, M.J. & Evans, K.L. (2004) The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis*, **146**, 210-220.

Williamson, K. (1958) Reports from bird observatories, autumn migration. *Bird Migration*, **1**, 2-27; **1**, 97-147; **1**, 249-272; **2**, 121.

Wilson, H.J. (1982) Movements home-ranges and habitat use of wintering woodcock in Ireland. *Woodcock ecology and management* (eds T.J. Dwyer & G.L. Storm), pp. 167-178. United States Fish and Wildlife Service, Washington D.C., USA.

Wilson, H.J. (1983) Wintering site fidelity of woodcock in Ireland. *Second European woodcock and snipe workshop* (ed H. Kalchreuter), pp. 18-27. International Waterfowl Research Bureau (IWRB), Slimbridge, UK.

Wingfield, J.C. (2008) Organization of vertebrate annual cycles: implications for control mechanisms. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **363**, 425-441.

Witherby, H.F., Jourdain, F.C.R., Ticehurst, N.F. & Tucker, B.W. (1940) *The handbook of British birds*. H.F. & Witherby Ltd, London, UK.

Wunder, M.B. (2010) Using isoscapes to model probability surfaces for determining geographic origins. *Isoscapes: understanding movement, pattern, and process on Earth through isotope mapping* (eds J.B. West, G.J. Bowen, T.E. Dawson & K.P. Tu), pp. 251-270. Springer, New York, USA.

Wunder, M.B., Hobson, K.A., Kelly, J.F., Marra, P.P., Wassenaar, L.I., Stricker, C.A. & Doucett, R.R. (2009) Does a lack of design and repeatability compromise scientific criticism? A response to Smith *et al.* (2009). *The Auk*, **126**, 922-926.

Wunder, M.B., Kester, C.L., Knopf, F.L. & Rye, R.O. (2005) A test of geographic assignment using isotope tracers in feathers of known origin. *Oecologia*, **144**, 607-617.

Wunder, M.B. & Norris, D.R. (2008a) Improved estimates of certainty in stable isotope-based methods for tracking migratory animals. *Ecological Applications*, **18**, 549-559.

Wunder, M.B. & Norris, D.R. (2008b) Analysis and design for isotope-based studies of migratory animals. *Tracking animal migration with stable isotopes* (eds K.A. Hobson & L.I. Wassenaar), pp. 107-128. Academic Press, London, UK.

Zockler, C., Syroechkovskiy, E.E., Jr., Lappo, E.G. & Bunting, G. (2006) Stable isotope analysis and threats in the wintering areas of the declining spoon-billed sandpiper *Eurynorhynchus pygmeus* in the east Asia-Pacific flyway. *Waterbirds around the world* (eds G.C. Boere, C.A. Galbraith & D.A. Stroud), pp. 147-153. The Stationery Office, Edinburgh, UK.

Zomerdijk, P. (1983) De houtsnip (*Scolopax rusticola*). *De Graspieper,* deel I. (eds R. Brouwer, R. van der Hut, W. Ruitenbeek, T. Tuinman & H. Verhoeven), pp. 107-121. Samenwerkende Vogelwerkgroepen Noord-Holland (SVN), Noord-Holland, Netherlands.

Appendices

Appendix A1

Table A1.1 The international conservation status of Eurasian woodcock, as evaluated by different authorities.

Global	European		
IUCN Red List[1]	**BirdLife International[2,3]**		**Wetlands International[4,5]**
	2004 Pan European Status	**2004 EU25 Conservation Status**	
Least concern	**Unfavourable**	**Unfavourable** **Depleted**	**Stable (although some populations have unknown trends)**

1. IUCN (2012) The IUCN Red List of Threatened Species. Version 2011.2. *http://www.iucnredlist.org*
2. BirdLife International (2004) *Birds in the European Union: a status assessment*. BirdLife International, Wageningen, Netherlands.
3. BirdLife International (2004) *Birds in Europe: population estimates, trends and conservation status*. BirdLife International, Cambridge, UK.
4. Wetlands International (2002) *Waterbird population estimates. Wetlands International Global Series No. 12*. BirdLife International, Wageningen, Netherlands.
5. Wetlands International (2006) *Waterbird population estimates. Fourth edition*. Wetlands International, Wageningen, Netherlands.

Table A1.2 Migratory bird species in which temporal changes in breeding density have been linked with changes in previous winter conditions. + indicates the presence of an upward or downward long-term trend and/or annual fluctuations (adapted from Newton 2004a).

Species	**Location**	**Long-term trend**	**Annual fluctuations**
Twite *Carduelis flavirostris*	Germany-Netherlands	+	
Snow bunting *Plectrophenax nivalis*	Germany-Netherlands	+	
Shore lark *Eremophila alpestris*	Germany-Netherlands	+	
Sedge warbler *Acrocephalus schoenobaenus*	England		+
	Netherlands		+
Blackcap *Sylvia atricapilla*	Britain		+
Whitethroat *Sylvia communis*	Britain	+	+
	Sweden		+
Willow warbler *Phylloscopus trochilus*	Britain	+	+
Loggerhead shrike *Lanius ludovicianus*	Minnesota	+	
Barn swallow *Hirundo rustica*	Denmark		+
	Britain		+
Sand martin *Riparia riparia*	Britain		+
	Hungary		+
Avocet *Recurvirostra avosetta*	England		+
European golden plover *Pluvialis apricaria*	Scotland	+	
Puffin *Fratercula arctica*	Scotland	+	+
Night heron *Nycticorax nycticorax*	France		+
Purple heron *Ardea purpurea*	Netherlands		+
Barnacle goose *Branta leucopsis*	Svalbard	+	
Dark-bellied brent goose *Branta bernicla*	Netherlands	+	
Lesser snow goose *Chen caerulescens*	Canada	+	

Table A1.3 The hunting status of Eurasian woodcock in the Member States of the European Union (EU), where H = huntable, P = protected. * indicates no information available (adapted from Lutz & Pagh Jensen 2005).

Member State	Hunting status	Hunting period	Annual harvest estimate	Source†
Austria	H	01.09 – 30.04 (regional variations)	2 700 – 6 000	1
Belgium	Flanders: P	N/A	N/A	1
	Wallonia: H	15.10 – 31.11	*	
Bulgaria	H	20.10 – 28.02	*	2
Cyprus	H	01.01 – 28.02 (Wednesdays & Sundays, only)	*	3
Czech Rep	P	N/A	N/A	4
Denmark	H	01.10 – 31.12	25 000	1, 5
Estonia	H	20.08 – 31.10	*	5
Finland	H	20.08 – 31.12	5 200	5
France	H	01.10 – 20.02	1 168 290 (+/- 2.3%) for season 1998/99	1
Germany	H	16.10 – 15.01	6 000	1
Greece	H	15.09 – 28.02	450 000 – 550 000	1
Hungary	H	01.03 – 10.04	9 500 in 2001	5, 6
Ireland	H	01.11 – 31.01	*	1, 5
Italy	H	30.09 – 31.01 North: 31.12	500 000 – 1 500 000	1
Latvia	H	from arrival to 1 May	*	5
		01.08 – 15.11		
Lithuania	H	15.08 – 01.12	*	7
Luxembourg	H	01.10 – 31.01	*	1
Malta	H	01.09 – 31.01	*	5
Netherlands	P	N/A	N/A	1
Poland	H	01.09 – 21.12	*	8

Portugal	H	05.10 – 28.02	*	1
		Madeira: 05.10 – 06.12		
		Azores: annual & regional variations		
Romania	H	15.09 – 15.04	4 500 – 5 500	1, 9
Slovakia	H	16.03 – 30.04	*	1
Slovenia	P	N/A	N/A	1
Spain	H	12.10 – 31.01	*	1
	Canaries: P	N/A	N/A	
Sweden	H	North: 21.08 – 31.10	1 300	5
		South: 21.08 – 30.11		
UK	H	01.09 – 31.01 (regional variations)	150 000	1

† Source:

1. Ferrand, Y. & Gossmann, F. (2001) Elements for a woodcock (*Scolopax rusticola*) management plan. *Game and Wildlife Science*, **18**, 115-139.
2. *http://www.woodcock-hunting.com*
3. *http://www.cypruswildlife.gov.cy*
4. *http://www.yeswehunt.eu*
5. *http://www.face-europe.org*
6. Farago, S. (2003) Trend of the woodcock hunting bag in Hungary and its effect on the population. *WSSG newsletter*, **29**, 6-8.
7. *http://www.tourslithuania.com*
8. *http://www.contactpologne.com*
9. *http://www.artemis.ro*

Table A1.4 The hunting status of the Eurasian woodcock in European countries outside the European Union (EU), where H = huntable, P = protected. * indicates no information available (adapted from Lutz & Pagh Jensen 2005).

Country	Hunting status	Hunting period	Annual harvest estimate	Source†
Azerbaidjan	H	Nov to Feb	*	1
Norway	H	10.09 – 23.12	5 000 – 10 000	1
Russia	H	01.04 – 20.05 (10 days per region)	150 000	1
		end of Aug to Oct	*	
Switzerland	H (excl. Bern & Geneva cantons)	15.09 – 15.12 (regional variations)	1 000 – 2 500	1
Ukraine	H	Mid-Aug to mid-Oct (regional variations)	*	1

† Source:
1. Ferrand, Y. & Gossmann, F. (2001) Elements for a woodcock (*Scolopax rusticola*) management plan. *Game and Wildlife Science*, **18**, 115-139.

Appendix A2

Table A2.1 Stratification of feather samples collected from Eurasian woodcock sampled on the breeding grounds, prior to migration (April-September). Samples were collected from adult and juvenile birds, over six years and across 10 countries in Europe.

	Number of feather samples													
	Adult							Juvenile						Grand Total
Country	**2002**	**2005**	**2007**	**2008**	**2009**	**2010**	**Total**	**2002**	**2007**	**2008**	**2009**	**2010**	**Total**	
Belarus	20			6		2	28	5		3	1	2	11	39
Britain	1		3	5	2	2	13			1		1	2	15
Estonia											1		1	1
Finland												3	3	3
Germany											1		1	1
Latvia												1	1	1
Norway												1	1	1
Russia		1	6	10	16		33		5	12	18		35	68
Spain		4					4							4
Sweden					2		2					1	1	3
Grand Total	21	5	9	21	20	4	80	5	5	16	21	9	56	**136**

Table A2.2 Stratification of feather samples collected from museum Eurasian woodcock specimens. Samples were taken from a) adult and b) juvenile specimens that were collected on the breeding grounds, prior to migration (April-September), between 1885 and 2002. Samples represent 10 European countries.

A	Azores	Finland	Norway	Poland	Sweden	Switzerland	UK	W.Siberia	Total
1885		5							5
1887			1						1
1906							1	1	2
1907					1		2		3
1908							3		3
1913					1				1
1915		1						1	2
1916		1							1
1917								1	1
1920					2				2
1926		1							1
1931	1								1
1934		1					1		2
1935				3					3
1936		1							1
1944		1							1
1945		1							1
1952					1				1
1957					1				1
1960						1	1		2
1961							1		1
1966		1							1
1972		2							2
1973		1							1
1974		1							1
1977			1						1
1986			5						5
1987			6						6
1989			4						4
1998		2							2
2001		1							1
2002		1							1
Total	1	21	17	3	6	1	9	3	**61**

B	Austria	Azores	Germany	Norway	Sweden	UK	Total
1905				1			1
1908						1	1
1916						4	4
1930		3					3
1931		3				1	4
1932		3					3
1964			1				1
1974					1		1
1976					1		1
1987				5			5
1988				4			4
1989						1	1
1991				1			1
1992	1						1
1993				1			1
1998			1				1
Total	1	9	2	12	2	7	**33**

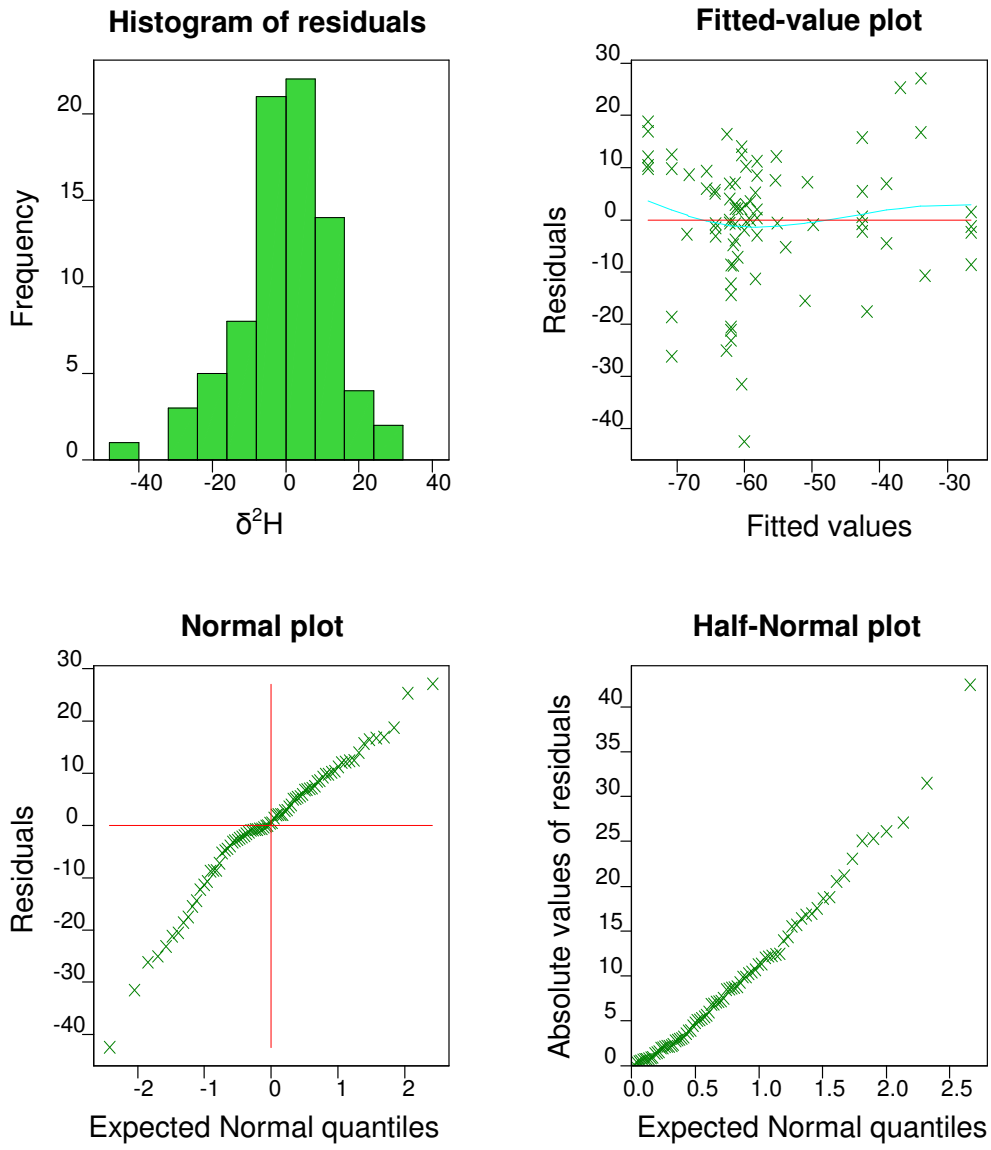


Figure A2.1 Example of a Generalised Linear Mixed Model (GLMM) residual composite plot output from GenStat version 14.0 (VSN International Ltd., 2011). This example was derived from a model assessing variation in δ^2H of adult Eurasian woodcock (n = 80) sampled on the breeding grounds against latitude and longitude. Year of feather growth was included in the model as a random factor. A normal error distribution and identity link function were specified.

Appendix A3

Table A3.1 Stratification of feather samples collected from adult and juvenile Eurasian woodcock of unknown breeding origins. Samples were collected across six geographic regions within Britain and Ireland, over four winters. Sample collection was restricted to December and January.

	Number of feather samples										
	Adult					Juvenile					Grand Total
Region	**2004/05**	**2008/09**	**2009/10**	**2010/11**	**Total**	**2004/05**	**2008/09**	**2009/10**	**2010/11**	**Total**	
Scotland	18	29	27	35	109	33	23	23	15	94	203
Norfolk	22	25	28	27	102	29	26	22	23	100	202
Cornwall	20	26	26	26	98	32	36	24	24	116	214
Wales	25	19	31	34	109	27	20	19	16	82	191
Hants	9	16	20	14	59	14	15	9	19	57	116
Ireland	23	24	26	31	104	28	28	24	19	99	203
Grand Total	117	139	158	167	581	163	148	121	116	548	**1 129**

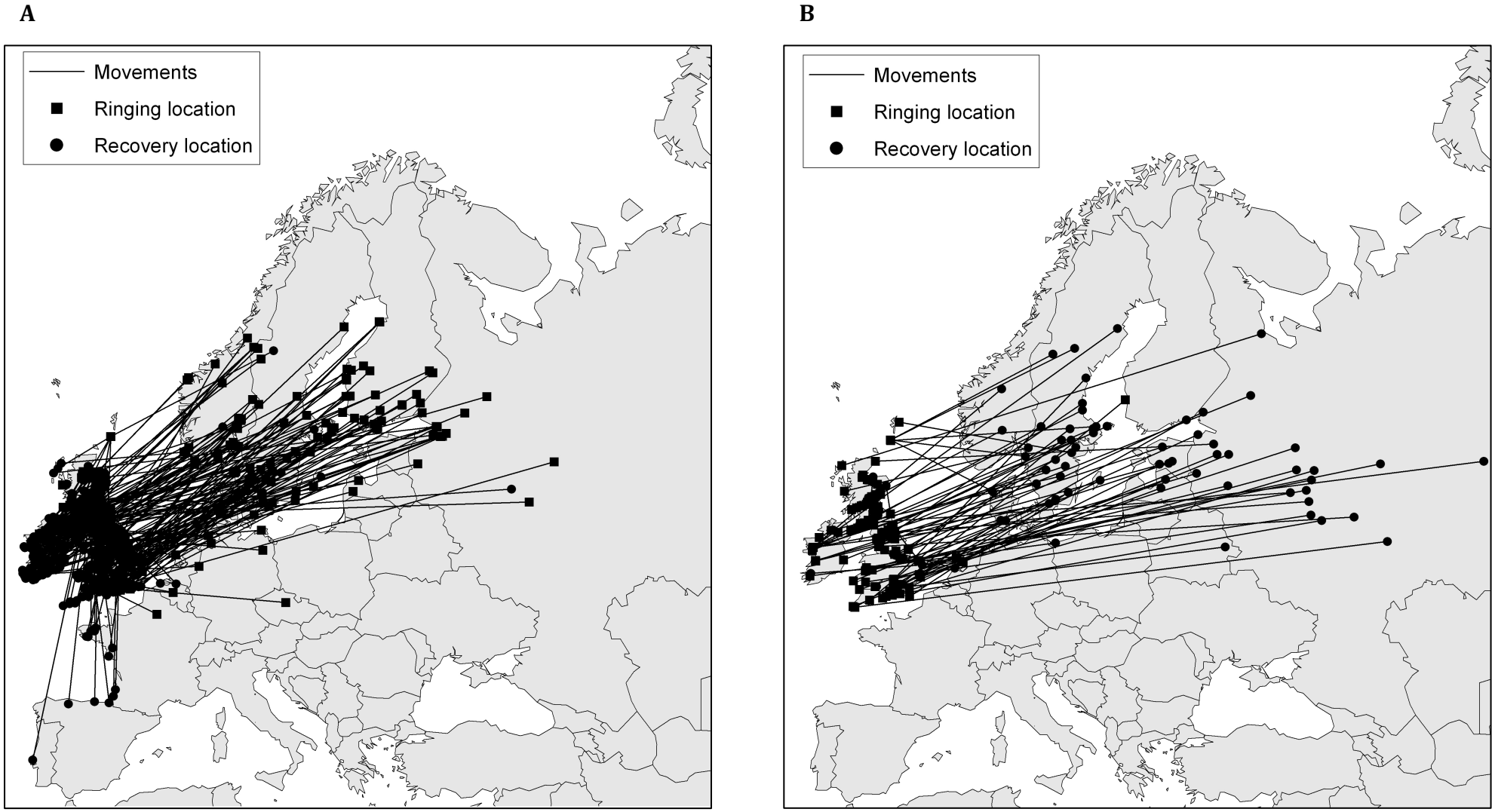


Figure A3.1 Movements of Eurasian woodcock based on British ring-recovery data for a) birds ringed during the breeding season and recovered in the non-breeding season (n = 549), and b) birds ringed during the non-breeding season and recovered in the breeding season (n = 130). Ring-recovery records were supplied by the British Trust for Ornithology (BTO) (February 2011).

Table A3.2 Total numbers of Eurasian woodcock ringed and/or recovered during the breeding season (April-Sept), across five regions in Britain and one region in Ireland. Ring-recovery records were dated from 1909-2010, and were supplied by the British Trust for Ornithology (BTO) (February 2011).

	Number of ring-recovery records						**Total**
	Scotland	**Cornwall**	**Norfolk**	**Wales**	**Hampshire**	**Ireland**	
Ringed	165	26	102	79	69	69	549
Recovered	27	7	38	16	26	26	130
Total	192	33	140	95	95	124	679

Appendix A5

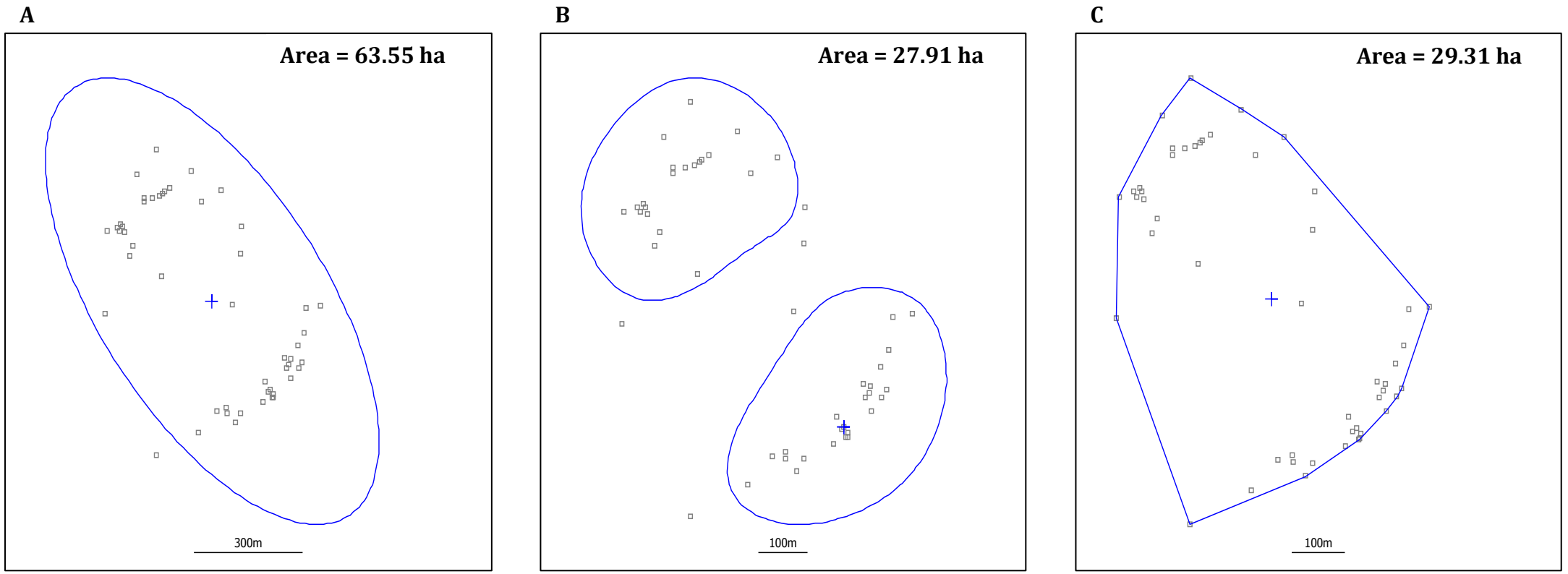


Figure A5.1 Examples of home range estimates applied to the combined diurnal and nocturnal fixes of an individual Eurasian woodcock (tag ID 255), tagged during the winter of 2008/09. Plots represent the following home range estimators: A = ellipses (95%), B = kernel contours (95%) and C = Minimum Convex Polygons (MCP) (100%). Total areas are reported in hectares (ha).

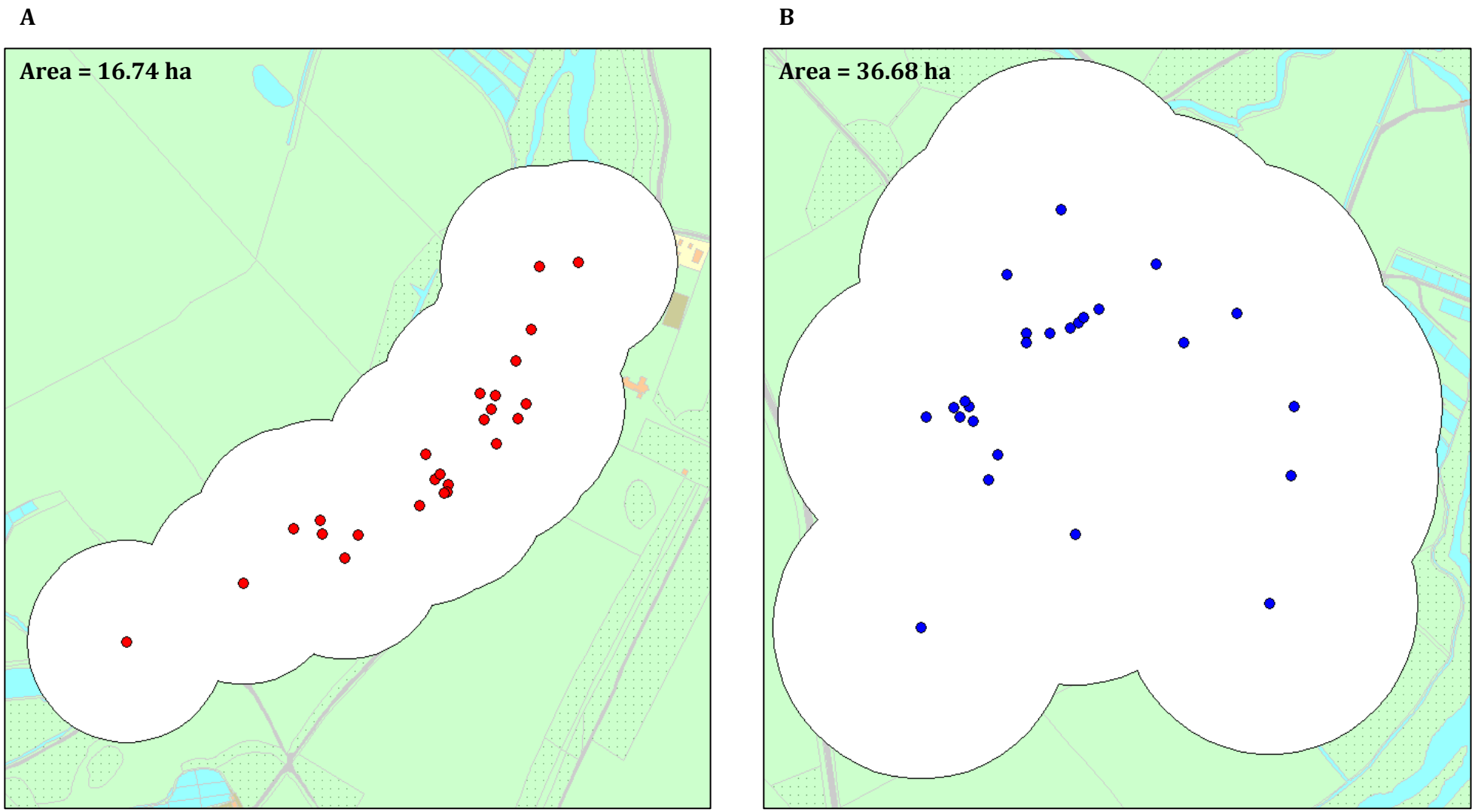


Figure A5.2 Examples of area estimates based on habitats enclosed within buffers. Plots depict buffers centred round a) day fixes (buffer radius = 100m) and b) night fixes (buffer radius = 150m), for an individual Eurasian woodcock (tag ID 255), tagged during the winter of 2008/09. Total buffer areas are reported in hectares (ha).

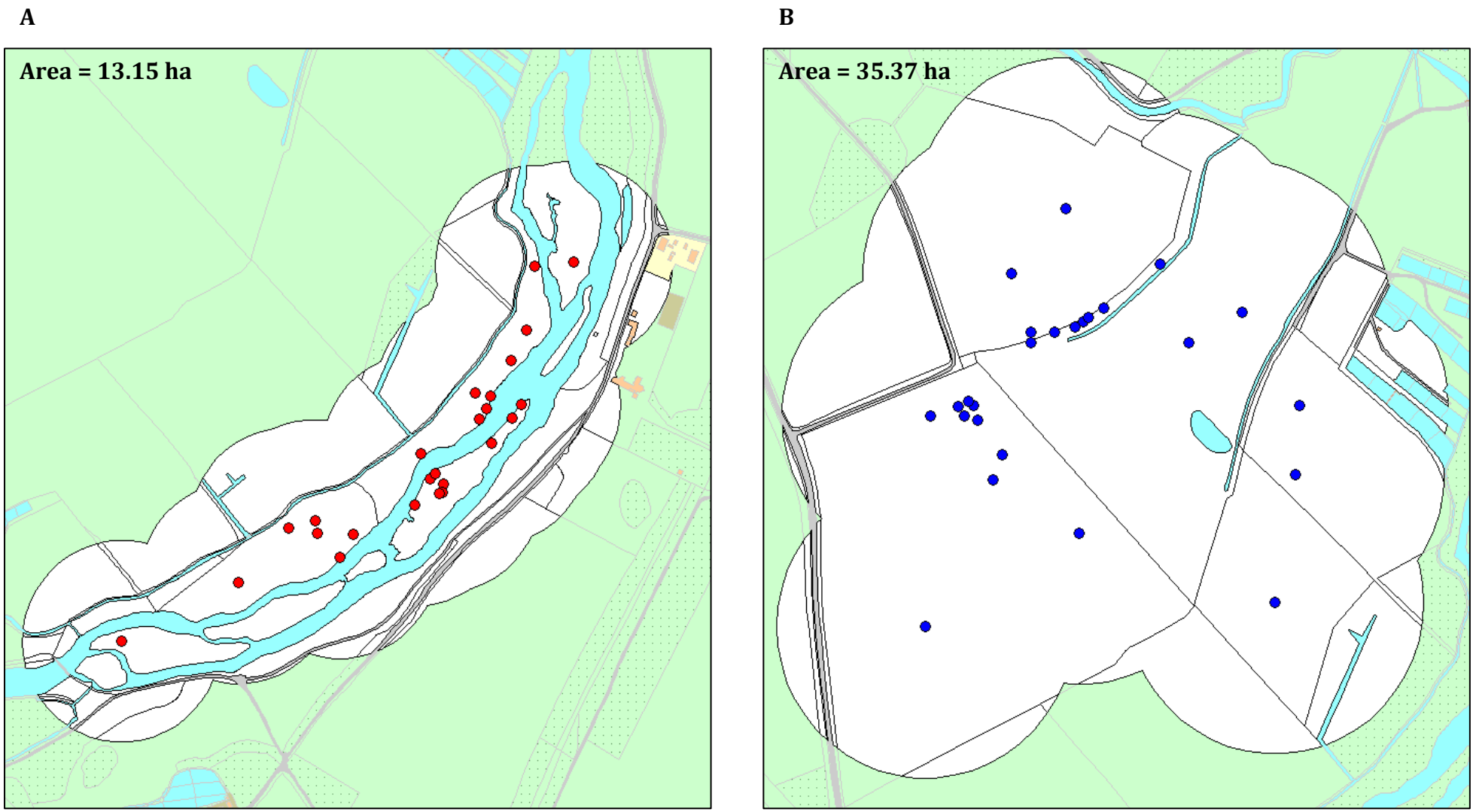


Figure A5.3 Examples of area estimates based on available habitats (excluding roads, paths, rivers, buildings etc.) enclosed within buffers. Plots depict buffers centred round a) day fixes (buffer radius = 100m) and b) night fixes (buffer radius = 150m), for an individual Eurasian woodcock (tag ID 255), tagged during the winter of 2008/09. Total area summations are reported in hectares (ha).

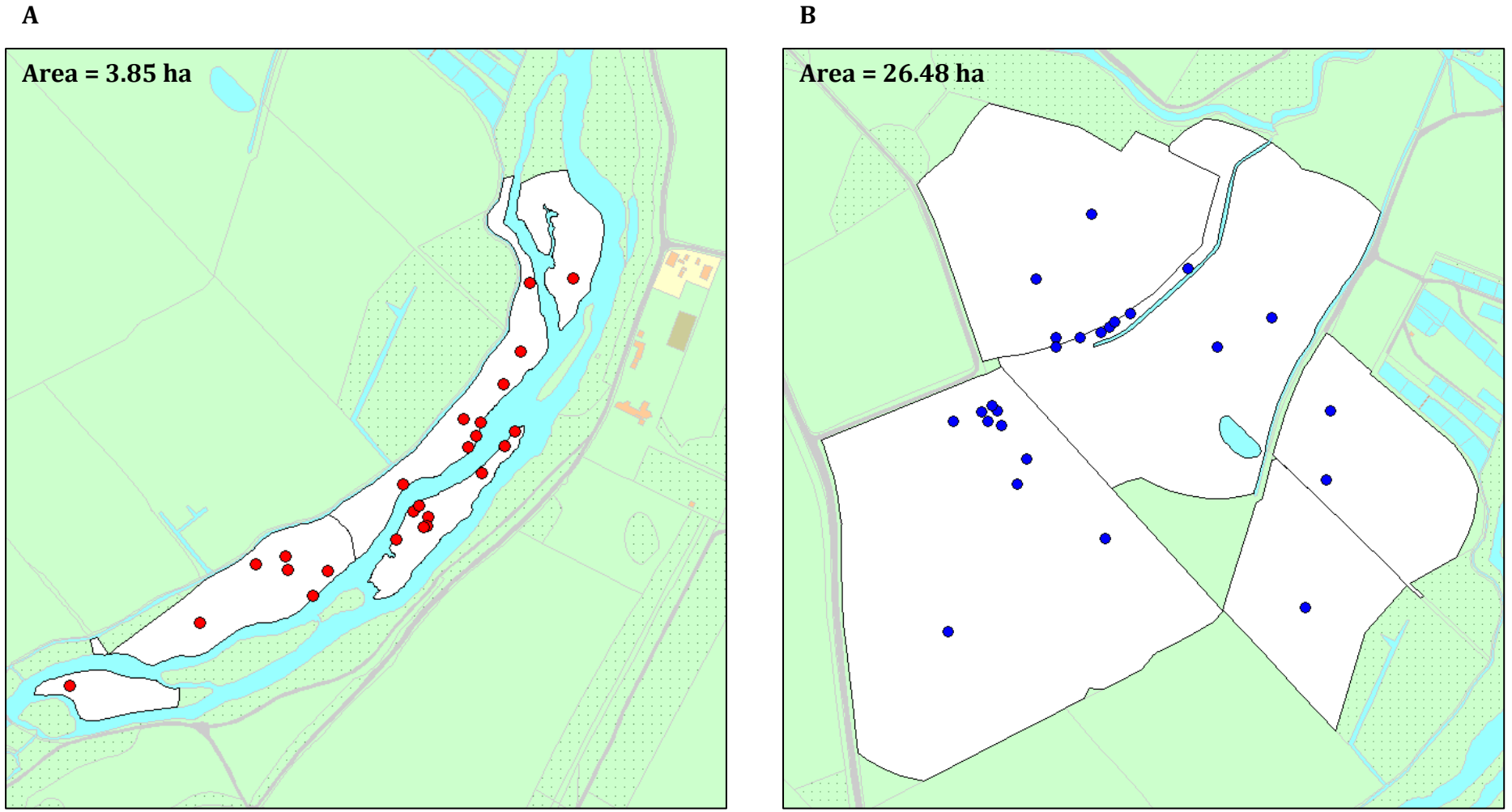


Figure A5.4 Examples of area estimates based on available habitats enclosed within buffers that have been cropped to polygons. Plots depicts cropped buffers centred round a) day fixes (buffer radius = 100m) and b) night fixes (buffer radius = 150m), for an individual Eurasian woodcock (tag ID 255), tagged during the winter of 2008/09. Total area summations are reported in hectares (ha).

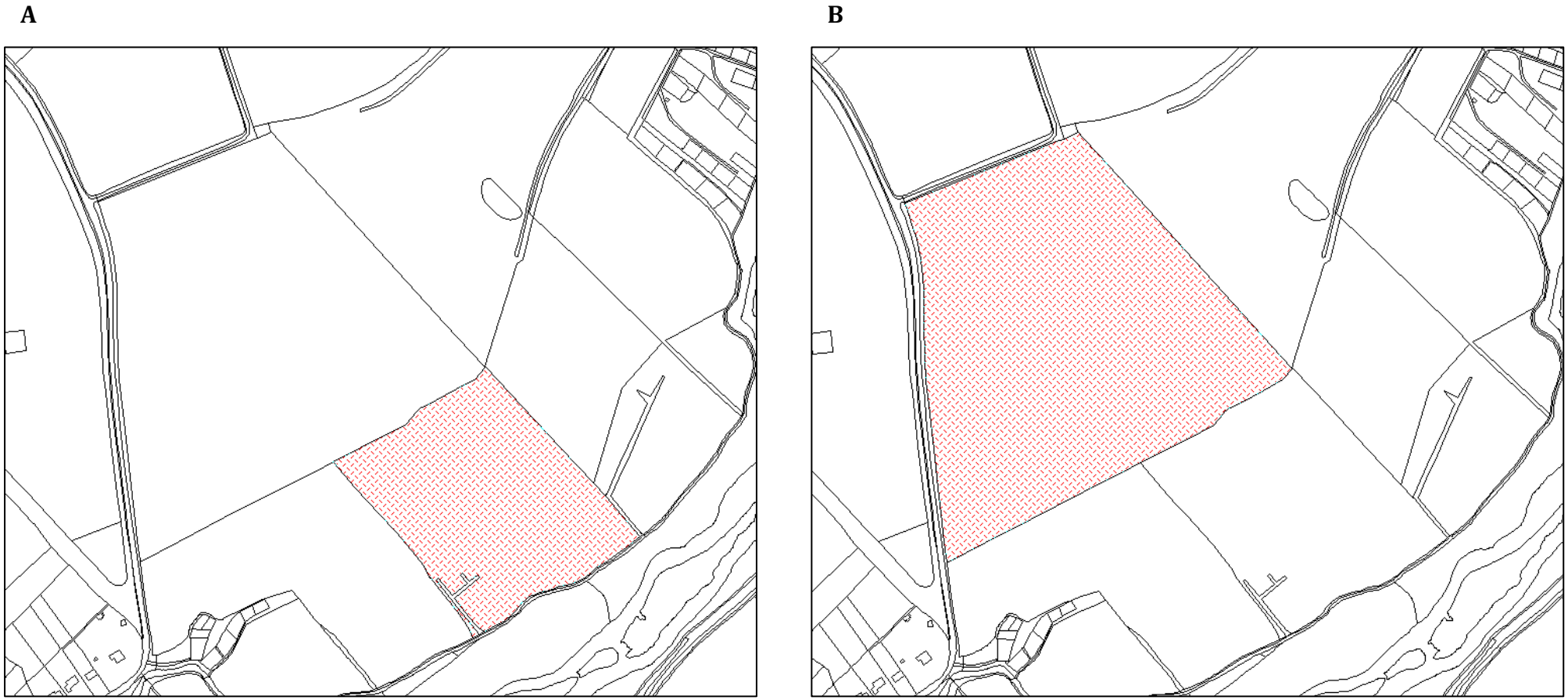


Figure A5.5 Examples of polygons, as defined by MapInfo Professional version 11.0.3 (Pitney Bowes Software Inc., 2009). Plot A shows a small field polygon, plot B shows a large field polygon. Each polygon is a closed object, marking a region of land that has been separated from its neighbour(s) based on differential land attributes and/or features.

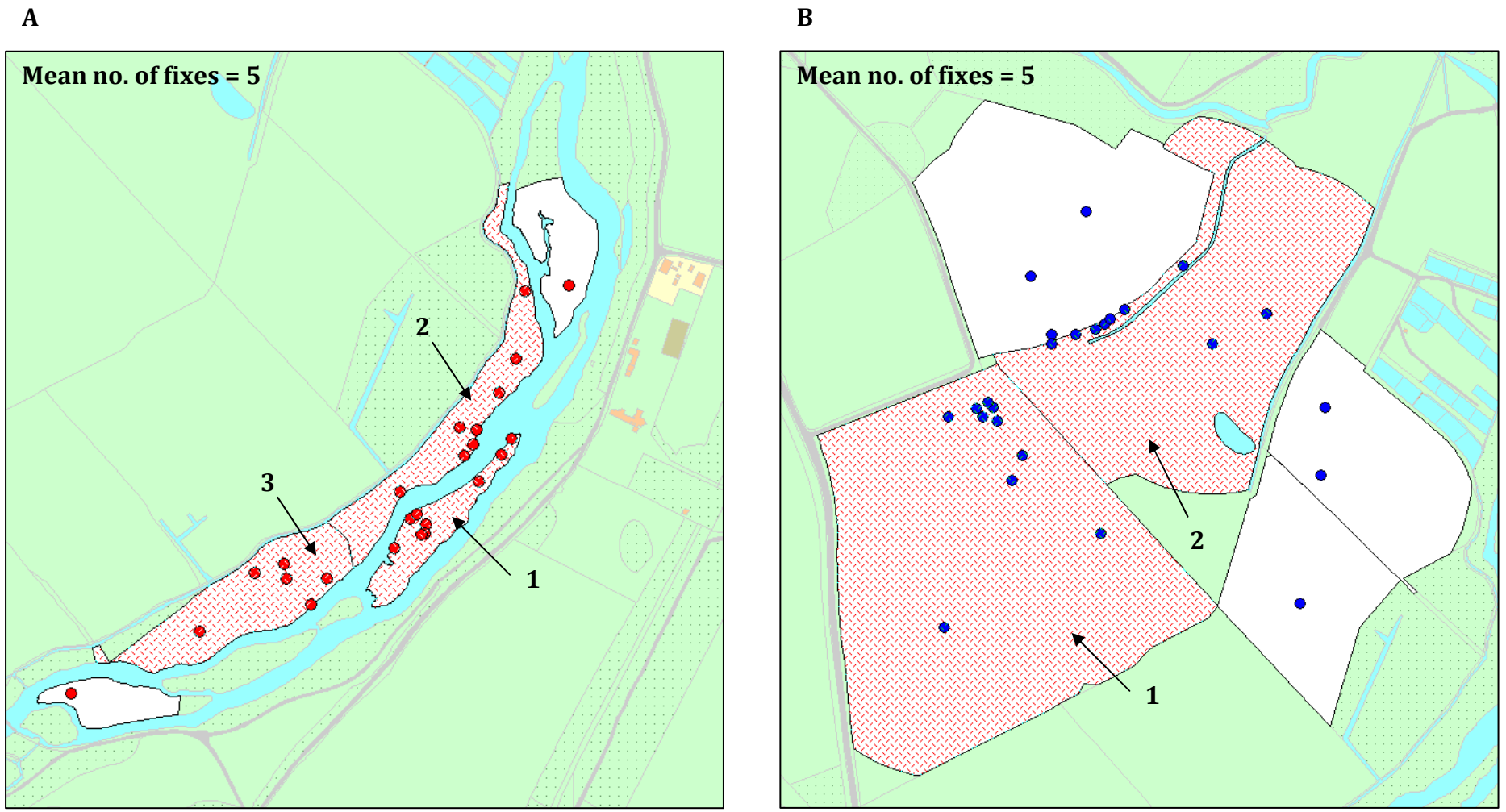


Figure A5.6 Core polygons for a) day fixes and b) night fixes, of an individual Eurasian woodcock (tag ID 255), tagged during the winter of 2008/09. Cores are defined as polygons containing fixes equal to or greater than the mean and are ranked in accordance with descending number of fixes, such that polygon 1 represents the core with the greatest number of fixes.

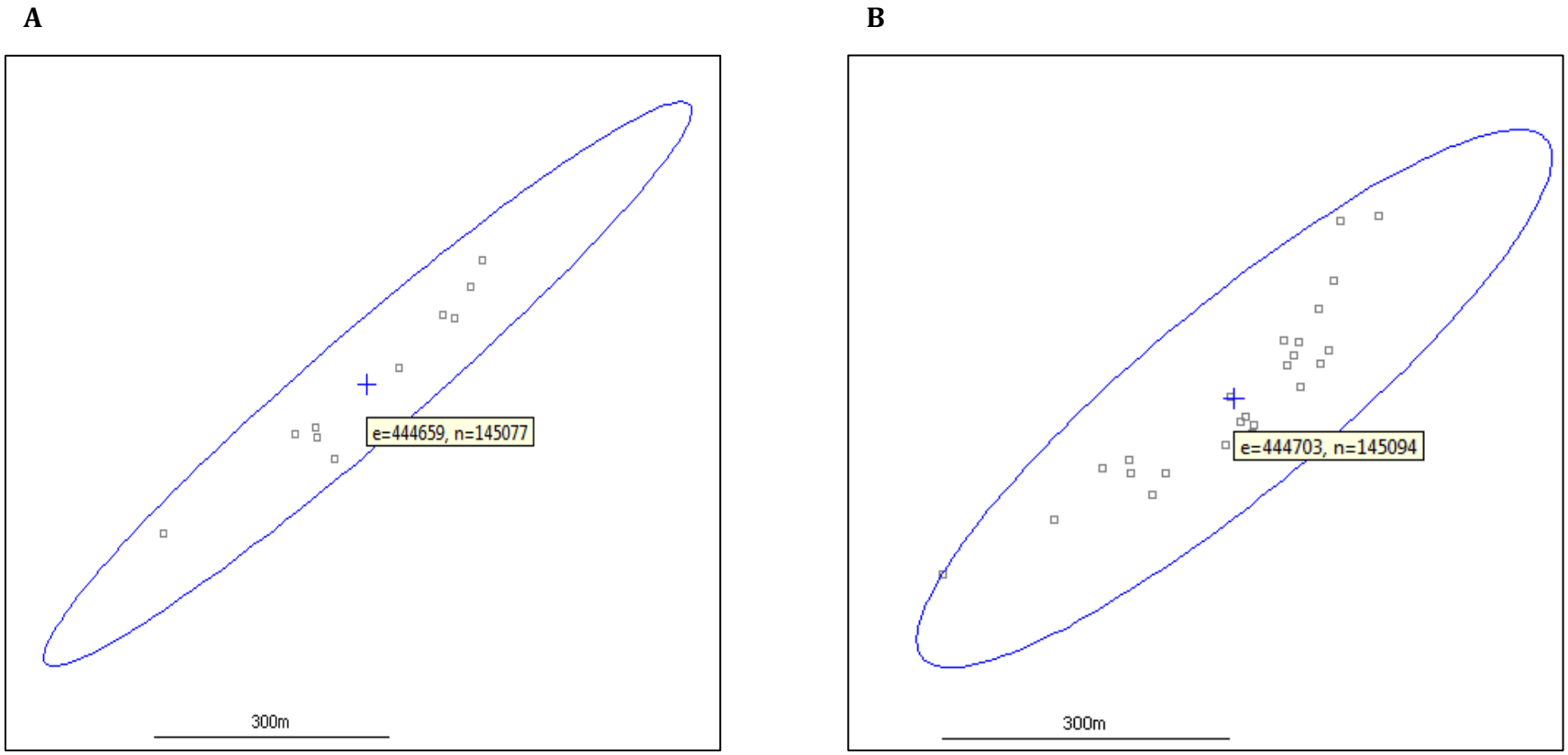


Figure A5.7 Elliptical (99%) home ranges for an individual Eurasian woodcock (tag ID 255), tagged during the winter of 2008/09. The home range in plot A encompasses day fixes obtained before 15th Feb. The home range in plot B encompasses day fixes obtained throughout the entire field-season. Blue crosses indicate the centroid (central location) for the fixes within the given range. Labels display co-ordinates for the centroid, where e = eastings, n = northings.