Significant effects of season and bird age on use of coppice woodland by songbirds

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Woodland birds have experienced widespread population declines across Europe, resulting partly from a decrease in management practices such as coppicing. Increasing fuel-wood demand may reverse the decline of coppicing, making it timely to attempt a fuller understanding of its effects. Here, the impact of coppicing on year-round habitat use by adults and juveniles of 16 songbird species was quantified from a quasi-experimental study over 32 years (1978–2009) in Treswell Wood, Nottinghamshire, UK. Habitat use was inferred using capture rates from more than 10 000 h of mist-netting (> 25 000 captures) and detailed information on coppicing. Capture rates varied with coppice age in different ways: (1) increases as coppice aged (e.g. Marsh Tit *Poecile palustris*, juvenile Eurasian Treecreepers *Certhia familiaris*); (2) declines as coppice aged (e.g. Eurasian Blue Tit *Cyanistes caeruleus*, Great Tit *Parus major*); (3) peaks in capture rates at intermediate coppice age (i.e. 5–15 years) (e.g. Garden Warbler *Sylvia borin*, Willow Warbler *Phylloscopus trochilus*, adult Treecreepers); and (4) a peak at intermediate ages, followed by a decline, before an increase in use again at the oldest coppice ages (i.e. > 20 years) (e.g. Common Blackbird *Turdus merula*, Eurasian Blackcap *Sylvia atricapilla*, Eurasian Bullfinch *Pyrrhula pyrrhula*). Responses to coppice age were similar in different seasons, although Willow Tits *Poecile montana* showed little preference during breeding but avoided older coppice at other times. Juveniles and adults often differed in their responses to coppice age. The analyses reveal patterns in habitat use that are relevant to woodland management and conservation policy. They suggest that a mosaic of age structures in woodland is beneficial to a wide range of woodland species, and that management should consider the requirements of all age-classes of birds at different times of year.

Keywords: bird of conservation concern, coppice management, habitat structure, habitat use, passerine, *Poecile montana*, ringing, succession, Willow Tit, woodland bird declines.

Habitat change over time results from the ageing of component organisms and species turnover (succession) (Walker & del Moral 2003). The accompanying changes in physical structure and food webs can alter habitat use and demography of populations of individual species (Fuller & Henderson 1992, Akçakaya *et al.* 2004, Hodgson *et al.* 2009). As a result, habitat change can have substantial effects on biodiversity, which often peaks early in the succession (Walker & del Moral 2003). Although

these patterns are well described in the ecological literature, their consequences for conservation seem less well explored and less widely appreciated than those resulting from, for example, habitat destruction (Akçakaya *et al.* 2004, Prach & Walker 2011). Management can alter temporal habitat change but its effects are not always well understood (Akçakaya *et al.* 2004), and this is a central concern of conservation science (Pullin & Stewart 2006).

Many woodland bird species have suffered severe declines across western Europe (Gregory *et al.* 2007, Hewson & Noble 2009). The causes of these are not well understood, but successional

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changes in woodland habitats are almost certainly involved for some species (Amar *et al.* 2006, 2010, Hewson *et al.* 2007, Hewson & Noble 2009). The 20th century saw dramatic alterations in the composition and management of European woodlands (Hopkins & Kirby 2007, Mason 2007, Bergmeier *et al.* 2010). In Britain, lowland woods, a high proportion of which were coppice and scrub after the Second World War, have aged into high forest, as weak markets for timber and other wood products have led to reduced management for production (Hopkins & Kirby 2007, Amar *et al.* 2010). The resulting habitat change has had contrasting impacts on different species (Amar *et al.* 2006, Quine *et al.* 2007, Hewson & Noble 2009). This has raised questions about the possible effects of management interventions on population trajectories (Quine *et al.* 2007). However, because many, although not all (Fuller *et al.* 2005), declining species tend to be associated with open or scrubby deciduous woods (Hinsley *et al.* 2007), the consensus is now that management to encourage such characteristics is likely to be beneficial (Quine *et al.* 2007, Plantlife 2011).

Coppicing is a traditional form of woodland management that maximizes the production of small-diameter wood for diverse markets (Rackham 2006). Management regimes and species vary greatly between woods, but generally coppicing repeatedly returns woodland to a more open, scrubby habitat structure, by cutting larger stems to ground level and encouraging re-growth from the stool. A revival of coppicing and other management techniques, both for conservation and due to increased fuelwood demand (Mason 2007, Forestry Commission England 2011), is likely to reverse the ageing of some woods and return them to younger structures in the coming decades. It is therefore timely to improve our understanding of the relationships between woodland management, age-structure and biodiversity so that managers can incorporate the best possible guidance into future practice. Coppicing has well-documented effects on a range of woodland biodiversity (Hill *et al.* 1990, Hodgson *et al.* 2009, Plantlife 2011). Its effect on breeding populations of passerines in southern England has been well researched (Fuller & Moreton 1987, Fuller & Henderson 1992, Fuller & Green 1998). These studies of different coppice systems produced broadly consistent results but were mainly short-term (although see Fuller & Green 1998) and confined to breeding adults. Similar analyses are lacking for juveniles (although see Holt *et al.* 2011) and for non-breeding adults. Indeed, the habitat use of non-breeding birds is poorly understood but is likely to be important for conservation, as population growth rates of passerines are often sensitive to juvenile survival rates (Saether & Bakke 2000, Siriwardena *et al.* 2000a).

Here we use a long-term, quasi-experimental approach to assess the effects of coppicing on year-round habitat use of both adult and juveniles of 16 woodland passerine species (Table 1), as a basis for future woodland management and conservation recommendations. Our study site has been repeatedly manipulated by coppicing over 32 years, and the impact on habitat use by birds recorded systematically by mist-netting. Capture rates of birds of all species have been recorded in different parts of the wood at a wide range of coppice ages, and in uncoppiced areas. The patterns we observe are therefore unlikely to be influenced by random spatial variation in habitat quality (e.g. soil type) over and above coppice age effects. We expected patterns of habitat use to vary between seasons and age classes because of different habitat requirements through the life cycle. In general we expected that birds preferring young coppice will be less common in uncoppiced areas, whereas those species selecting older coppice will show higher capture rates in uncoppiced woodland.

METHODS

Study area

Treswell Wood (53°18′N, 0°51′W) is a 47.8-ha ancient woodland (continuous record of woodland for > 1000 years) in Nottinghamshire in the English Midlands. Since 1976 it has been managed using a 'coppice with standards' system by the Nottinghamshire Wildlife Trust (NWT) and comprises predominantly coppiced Hazel *Corylus avellana*. 'Standards' are large trees that are left to grow uncoppiced, to overtop the coppiced understorey. In the late 1960s a wholesale extraction of Pedunculate Oak *Quercus robur* from the northern two-thirds of the wood resulted in the predominant standard tree there becoming Ash *Fraxinus excelsior*, while the southernmost parts have a higher proportion of mature Oak. For the purposes of analysis we divided the wood into two habitat types based on the predominance of standards: 'Ash' and 'mixed' (< 50% Ash, estimated

Table 1. Species included in the study, indicating number of captures of adults and juveniles in coppice up to 26 years old, and in the whole wood at Treswell, Nottinghamshire, UK. Other species caught in appreciable numbers (> 100) are listed at the bottom, along with the reason why they were not included in analyses.

Species		Captures in coppice		Total captures	
		Adults	Juveniles	Adults	Juveniles
Common Blackbird	*Turdus merula*	803	289	2080	750
Eurasian Blackcap	*Sylvia atricapilla*	866	173	1591	265
Eurasian Blue Tit	*Cyanistes caeruleus*	644	646	1692	1552
Eurasian Bullfinch	*Pyrrhula pyrrhula*	351	284	884	647
Common Chaffinch	*Fringilla coelebs*	303	74	665	174
Coal Tit	*Periparus ater*	128	186	356	383
Dunnock	*Prunella modularis*	694	326	1619	689
Garden Warbler	*Sylvia borin*	126	5	249	12
Great Tit	*Parus major*	643	339	1394	771
Marsh Tit	*Poecile palustris*	164	146	277	211
European Robin	*Erithacus rubecula*	762	794	1716	1653
Song Thrush	*Turdus philomelos*	235	30	780	96
Eurasian Treecreeper	*Certhia familiaris*	348	146	706	246
Willow Tit	*Poecile montanus*	211	142	657	265
Willow Warbler	*Phylloscopus trochilus*	148	22	431	34
Eurasian Wren	*Troglodytes troglodytes*	758	476	1602	1023

Also captured: Common Chiffchaff *Phylloscopus collybita* (only common in latter part of study), Goldcrest *Regulus regulus* (almost exclusively winter captures), Long-tailed Tit *Aegithalos caudatus* (excluded because of strong tendency to travel in flocks), Eurasian Tree Sparrow *Passer montanus* (only common in early years of study).

visually). Coppicing has taken place throughout both. The density of standards was typically 60–100/ha by the end of the study period, higher than the 30–80 standards per ha typical of most coppicing regimes (Fuller & Steel 1990). However, the trees generally have small crowns and canopy cover is approximately 30–50%. Deer (Muntjac *Muntiacus reevesi* and Roe *Capreolus capreolus*) are present in the wood, but were rare for most of the study period and had little effect on coppice structure.

Traditional coppicing in Treswell, which probably ceased in the early 20th century, was based on 10 approximately 5-ha compartments of woodland (Fig. 1) and would have led to a 10-year coppice rotation. Since NWT re-instituted coppicing in 1976, three compartments have remained uncoppiced as control areas. Two of these are in the south of the wood ('mixed') and one is in the north ('Ash'). In the seven coppiced compartments, coppicing in any 1 year generally covered less than a whole compartment (average approximately 0.7 ha), and has not followed a strict sequential rotation. Rotation length has varied from 12 to 30 years. The small areas of the oldest coppice, and the limited time for which they have been in the oldest age-classes, means that sample sizes for

this age group are small. We therefore restricted the analyses to captures of songbirds in coppice up to 26 years old.

Mist-netting study design

We used data from mist-netting carried out in the wood throughout the year from 1978 to 2009 (du Feu & McMeeking 1991). From the start of the ringing programme all captures of birds were recorded on a 63-m (1 acre) grid (Fig. 1). At any time, the age of the coppice in years could be assigned to each grid square. This took a value of zero in the first year after coppicing, one in the following year and so on (Fuller & Moreton 1987, Fuller & Steel 1990).

On a typical mist-netting visit, 10 nets of 18-m were set in one of seven 'normal sites' (Fig. 1). The position of these was consistent throughout the study, and they were each visited once every 10 weeks, in rotation. The habitat around these net positions was not substantially altered by management for setting the mist-nets. Rather, minimal 'slits' for the safe passage of nets were maintained through the vegetation by the trimming of overhanging twigs etc. Nets were usually erected within an hour of dawn. Normal (N) nets were in
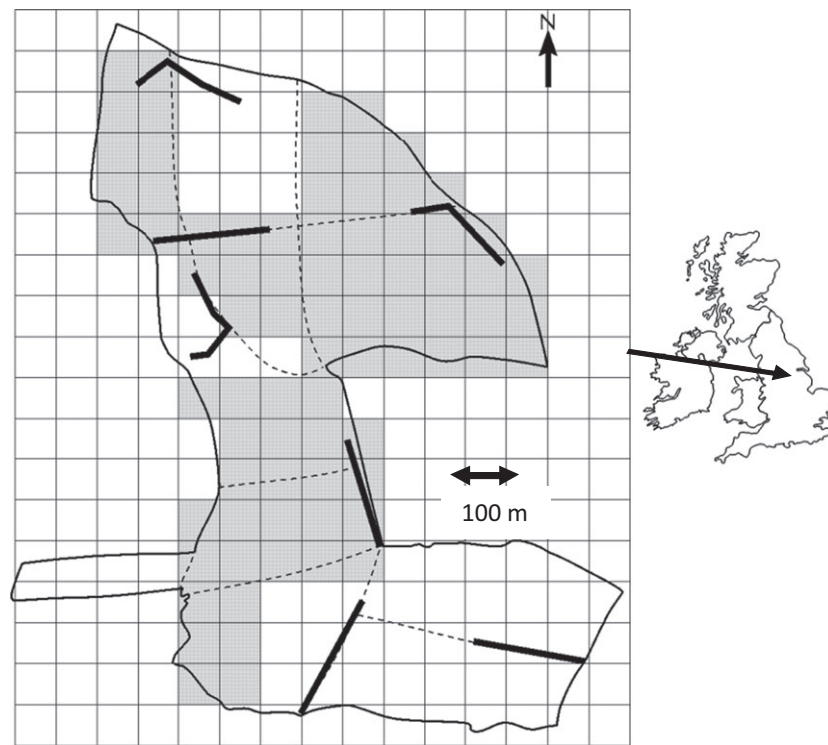
Figure 1. Map of Treswell Wood, Nottinghamshire, UK. The boundaries of the wood are shown as a continuous irregular line. Bold black lines indicate the positions of normal (N) runs of mist-nets. The square grid (spacing between lines = 63 m, or one square = 1 acre) is that used to locate the position of all bird captures. Shaded areas are those that have been coppiced since 1972. Dotted lines indicate the boundaries of traditional compartments.

place for about 5 h on each visit. Additional (A) nets were often erected according to the time and manpower available. These were generally shorter, older (with more net damage) nets, set later in the day, and for a shorter time than normal nets. Additional nets were set expeditiously in places where there was thought to be the best chance of catching birds (e.g. against a coppice panel as opposed to exposed in the middle of a cleared area), but not in 'hot-spots' (e.g. close to feeders or ponds). In all analyses, differences between normal and additional nets were controlled for with a factor 'net type' taking the value N or A. A little over half of all captures (54%) were made in normal nets. All captures were handled according to standard protocols (Redfern & Clark 2001 or predecessor editions). Ageing and sexing methods were according to Svensson (1992) or its predecessor editions. Birds were classified as juveniles if hatched in that calendar year (EURING age codes 3J and 3) or as adults if hatched in previous calendar years (EURING age codes 4, 5 or 6) (EURING 2010).

Statistical analysis of capture patterns

The response variable in all analyses was the number of captures of adults or juveniles of a particular species in one net on 1 day. Capture rates are expressed per net, rather than per set of nets, because sets of nets ran through habitat of different ages. Throughout our results and their discussion, we consider that capture rates are a proxy for habitat use. Analyses were confined to 16 species that occurred regularly and in sufficient numbers (> 100 captures) throughout the 32 years of ringing to make analysis meaningful (Table 1).

We accounted for seasonal differences in bird behaviour by including a factor 'season'. This took three levels: breeding ('spring'), from 1 April to 30 June (approximately 12 netting sessions per year); post-breeding ('summer'), from 1 July to 30 October (~15 sessions per year); and 'winter', from 1 November to 31 March (~18 sessions per year). Migrant species were not present in the winter, and we excluded records of juveniles for the

breeding season because of probable non-independence from their parents. We also controlled for year-to-year variation in the breeding density in Treswell Wood (see below), using an independent estimate for the whole wood obtained from breeding territory mapping (Peach *et al.* 1995).

We included repeated captures of the same birds (except same-day recaptures) in spite of the small risk of non-independence. Inclusion of re-traps would be a statistical problem if re-trapping had taken place on the same small area week after week. However, our seven normal sites were sufficiently far apart that birds rarely moved between them, so recapture events are rarely closer in time than the 10-week length of our mist-netting cycle.

We carried out two sets of analyses. First, we examined the relationship between capture rates and age of coppice for areas of the wood that have been coppiced since the winter of 1975/76. Secondly, we analysed differences in overall capture rates between areas of the wood that have been coppiced since 1975, and those uncoppiced areas that have not. For both sets of analyses, number of captures of adults and juveniles of each species were modelled separately in GENSTAT (12th edition), using a generalized linear mixed model (GLMM) framework with negative binomial error structure and log link. We used a hypothesis testing approach to select the best-fitting fixed effects models. Significance testing was only carried out in nested comparisons of models, and therefore there was no need for an information-theoretic approach to model validation. Despite philosophical differences between opposing model selection techniques, balanced analyses of the relative merits of differing statistical methodologies do not reveal any important differences between them (Bolker *et al.* 2009, Murtaugh 2009). We confined our analysis to a fully parametric technique (rather than, for example, generalized additive mixed models) because we intend to use the results in subsequent simulation models of the effect of different management strategies, which will employ the parameters estimated here. A parametric approach also leads to easier characterization of different responses to coppice age across species, which should facilitate the application of our results.

In all models we fitted the following fixed effects: breeding density (territory mapping estimate), net type (N or A), season (breeding, post-breeding and winter) and habitat (Ash or mixed).

In the first set of analyses we also included coppice age (in years) as a covariate and its quadratic and cubic terms. A quadratic term is useful for modelling the previously observed optimal coppice age for some species (e.g. Fuller & Henderson 1992), which probably comes about due to corresponding changes in habitat structure. However, some elements of structure such as ground cover (Fuller & Henderson 1992) show a more complex relationship to coppice age, especially as coppice matures into more open woodland. This suggested the possibility that some birds might also have habitat preferences that were more complex than could be modelled with a quadratic term and we therefore also included a cubic term. In the second set of analyses we included instead a fixed factor with two levels, 'coppiced' and 'uncoppiced'. We also included first-order interactions that we considered to be important (see Supporting Information Table S1). Non-significant terms were removed from the model one at a time and the model refitted, with the constraint that main effects that were marginal to higher order terms (quadratic or cubic) or to significant interactions had to be retained. Previously removed terms were tested again for re-inclusion after others had been eliminated. In this way each fitting process proceeded to a minimum adequate model (MAM). We report the significance of fitting terms last in the MAM, subject to marginality constraints.

The 63-m grid square (Fig. 1) in which a capture was made was fitted as a random term ('grid') in all models. The intention of including this term was to control for unmeasured spatial variation within the wood, beyond that accounted for by the fixed effects of coppice age and habitat. Intuitively, this seemed the most appropriate spatial scale at which to control for such unknown differences, given that it is the same as the spatial scale used to record coppice information, and most grid squares were of a single coppice age. It also seemed possible that capture rates in neighbouring squares could be related to each other because of habitat similarities. Thus, as an alternative to fitting grid as a random term, we also tried fitting easting and northing in the grid with a first-order autoregressive covariance structure, but the estimate of the variance component was small in relation to its standard error, and it made no qualitative difference to the outcome of trial models for a number of species, suggesting that capture rates in any one square are not generally related to

those in adjoining squares. Thus we report only results using 'grid' as the random term.

RESULTS

Habitat use in coppiced parts of the wood

All analyses of resident species are based on captures in 21 683 net settings (approximately 100 000 net-hours) up to the end of 2009, including 10 383 net settings in coppiced areas (Fig. 2). Data for migratory species are from 15 378 nets (7412 in coppiced areas) set in the breeding and post-breeding seasons. Each normal net position was visited 151 ($\pm$ 0.3 se) times on average during the course of the study.

Among adults, the habitat use of 14 of the 16 species analysed (Table 1, Table S1) was related to the age of coppice (Fig. 3). For 10 species there was an overall effect of coppice age (or its quadratic or cubic terms) on habitat use, whereas in four others the response depended on season or habitat type. Adults of only two species (Common Chaffinch *Fringilla coelebs* and European Robin *Erithacus rubecula*) were catholic in relation to their use of different coppice ages.

Among juveniles (Supporting Information Table S2), there were insufficient (< 100) captures for four species (Table 1). The cut-off of 100 was subjectively defined, but models with fewer than this number of captures performed poorly. Among the remaining 12 species, only juvenile Coal Tits *Periparus ater* and Eurasian Wrens *Troglodytes troglodytes* did not adjust their habitat use in relation to coppice age. The data suggested that juvenile
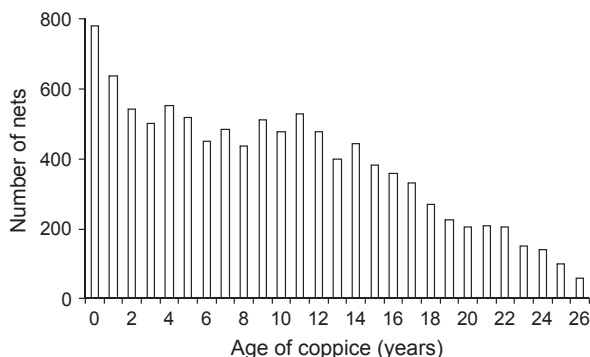
Wrens used older coppice less than young coppice, especially during the summer (Fig. 4). However, the modelling did not support this inference (Table S2). Instead it appears that this pattern is driven by a decline in capture rates of juvenile Wrens in both habitats in summer over the course of the study (as older coppice became more common). A similar explanation accounts for the apparent discrepancy between raw data and model fit for adult Song Thrushes *Turdus philomelos* (Fig. 3).

Four common patterns of habitat use in relation to coppice age were identified (Fig. 3): (1) an increase in habitat use with age of coppice (e.g. juvenile Eurasian Treecreeper *Certhia familiaris* and breeding Marsh Tit *Poecile palustris*); (2) a decline in habitat use with age of coppice (e.g. adult Blue Tit *Cyanistes caeruleus* and breeding Great Tit *Parus major*); (3) a clear peak in habitat use (quadratic relationship with coppice age) at intermediate coppice age (i.e. 5–15 years) (e.g. Garden Warbler *Sylvia borin*, Willow Warbler *Phylloscopus trochilus* and adult Treecreeper); and (4) a peak in use at intermediate ages, followed by a decline, before some suggestion of an increase in use again at the oldest coppice ages (cubic relationship between usage and coppice age, e.g. Common Blackbird *Turdus merula*, Eurasian Blackcap *Sylvia atricapilla*, Eurasian Bullfinch *Pyrrhula pyrrhula*). Habitat use of Dunnock *Prunella modularis* and Willow Tit *Poecile montana* was intermediate to (2) and (3).

Pattern (4) relies on the robustness of fitting models with cubic effects of coppice age. We were cautious in our analysis of those species for which the modelling suggested that the fitting of such a term was valid. Sample sizes (number of nets set) necessarily declined for the oldest coppice, and we were aware that a small number of netting sessions with high capture rates by chance could produce cubic terms of spurious significance. However, careful inspection of the data for those species where the coppice age cubic term was significant satisfied us that the fit did not rely on very small numbers of points of high leverage.

Use of habitat by adult birds in other seasons was qualitatively similar to that in the breeding season, with some important differences, especially among the tits (Coal, Great, Marsh and Willow, Table S1, Fig. 3). From a conservation and management perspective, the most important difference may be for Willow Tit, given its severe

Figure 2. Numbers of nets set in coppice of different ages, during the whole course of the study.
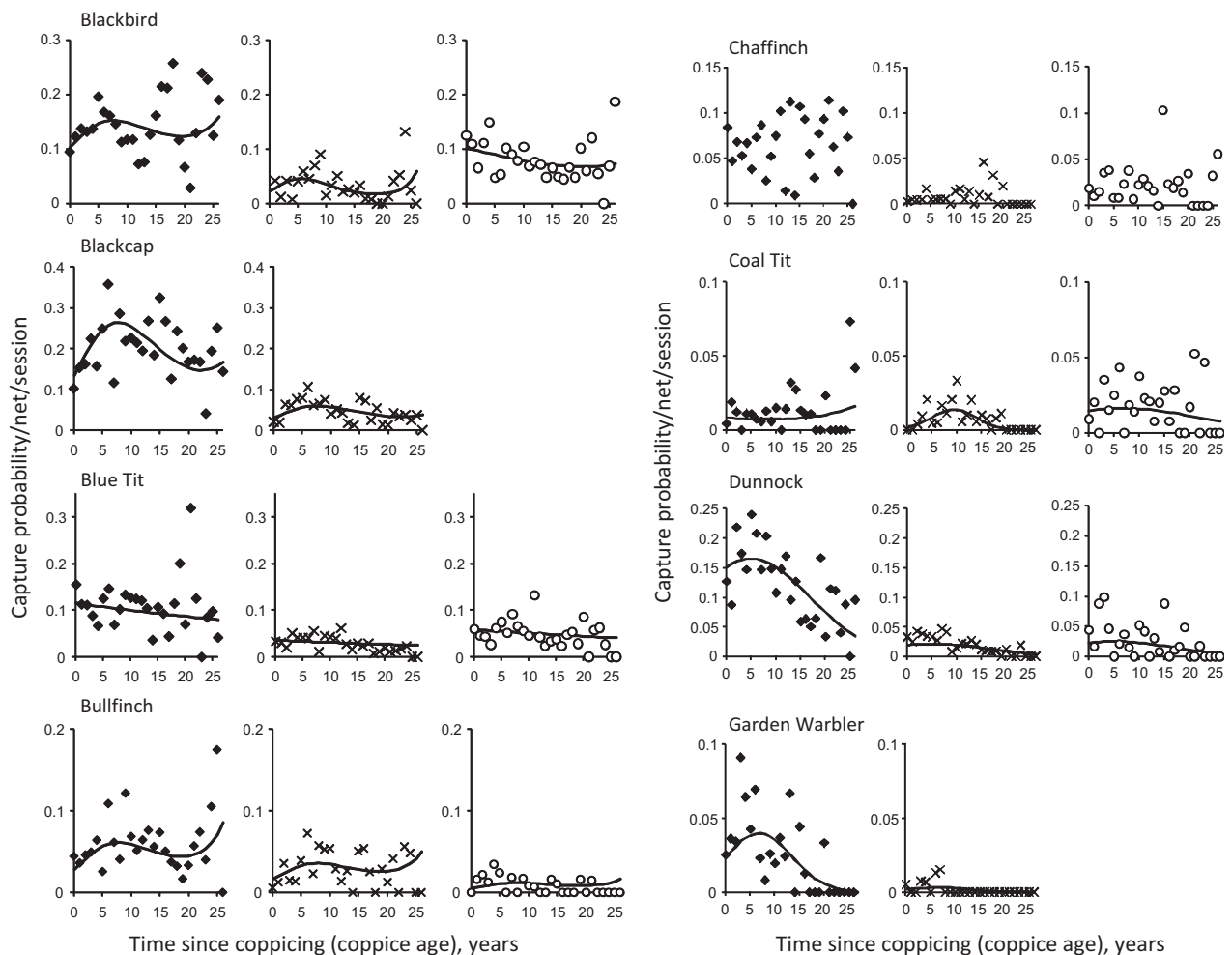
Figure 3. Capture rates (birds per net per trapping session) of adult songbirds of 16 species in relation to coppice age in Treswell Wood, 1978–2009. For each species, capture rates in breeding (spring), post-breeding (summer) and winter are shown, from left to right. Plotted points show average capture rates (across years) in each age of coppice, from 0 to 26 years. Lines show the best fit from GLMMs (Table S1). If there is no fitted line, capture rates were independent of coppice age. All plotted points are for normal nets in Ash habitat.

population decline (Balmer *et al.* 2013). The species showed little preference for different ages of coppice during the breeding season (spring), but use of coppice declined with its age during the summer and winter, and birds were absent from coppice more than 21 years old. Habitat use by Coal Tit and Great Tit also differed greatly between the breeding season, summer and winter. Marsh Tits preferred older coppice during the breeding season, but coppice of an intermediate age at other times.

Use of habitat by juveniles was sometimes strikingly different from that of adults (Fig. 4). Adult Bullfinches avoided only the youngest coppice,

whereas juveniles were captured most frequently in this habitat. Adult Dunnocks had a clear preference for young coppice (approximately 2–7 years), whereas juveniles showed no strong pattern of habitat use in relation to coppice age. Adult Treecreepers clearly preferred coppice approximately 10–15 years old, whereas juvenile capture rates were higher in older coppice.

Use of coppiced vs. uncoppiced parts of the wood

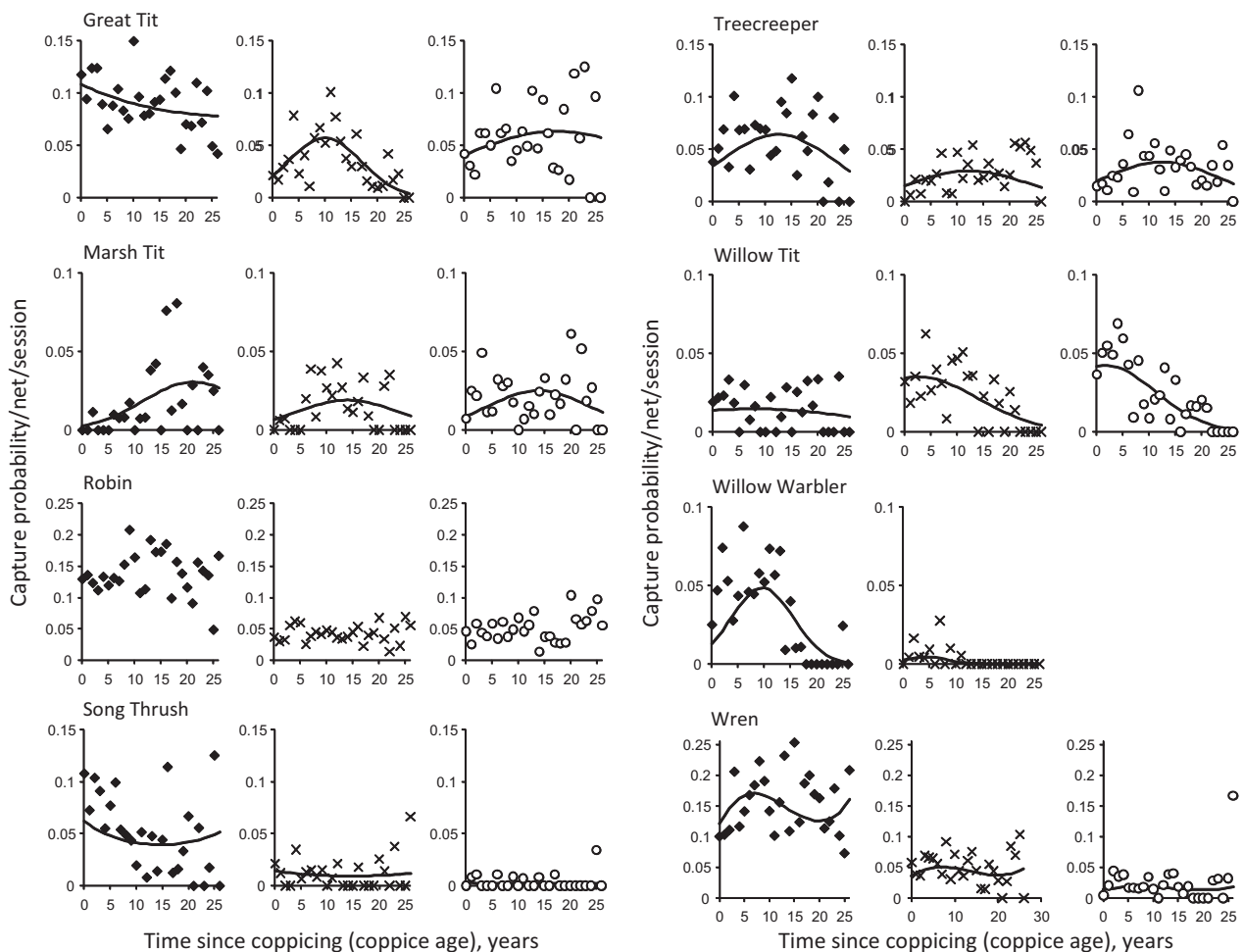The patterns of use with respect to coppice age in coppiced woodland were generally consistent with

Figure 3. Continued

the differences in capture rates between coppiced and uncoppiced woodland in Treswell Wood (Tables 2 and 3). For example, if birds preferred young or intermediate coppice to old coppice, they also tended to be captured at lower rates in uncoppiced (i.e. structurally older) woodland. Among adults there were exceptions to this among the tits: Blue Tits, Great Tits and Marsh Tits did not show overall differences in capture rates between coppiced and uncoppiced areas, despite showing preferences for younger areas within the coppiced woodland. Willow Tits actually had higher overall capture rates in uncoppiced woodland, despite a general preference for younger coppiced areas. Treecreepers had higher mean capture rates in uncoppiced areas, despite preferring coppice of intermediate age. Juvenile Blue Tits, Willow Tits and Blackbirds showed no overall differences in

capture rates between coppiced and uncoppiced areas, despite preferring younger coppice.

DISCUSSION

Our study is the first to examine the impact of coppice management on habitat use of both adult and juvenile woodland birds throughout the year, and the results reveal important differences in habitat use between age-classes of birds and between the seasons. In particular, we have shown that there are important differences between the habitat preferences of adults and juveniles, especially for Blue Tit, Treecreeper, Bullfinch and Dunnock. The latter two are of special interest because they are of conservation concern in the UK (Eaton *et al.* 2009). Capture rates of young Bullfinches declined monotonically with coppice age, in contrast to the
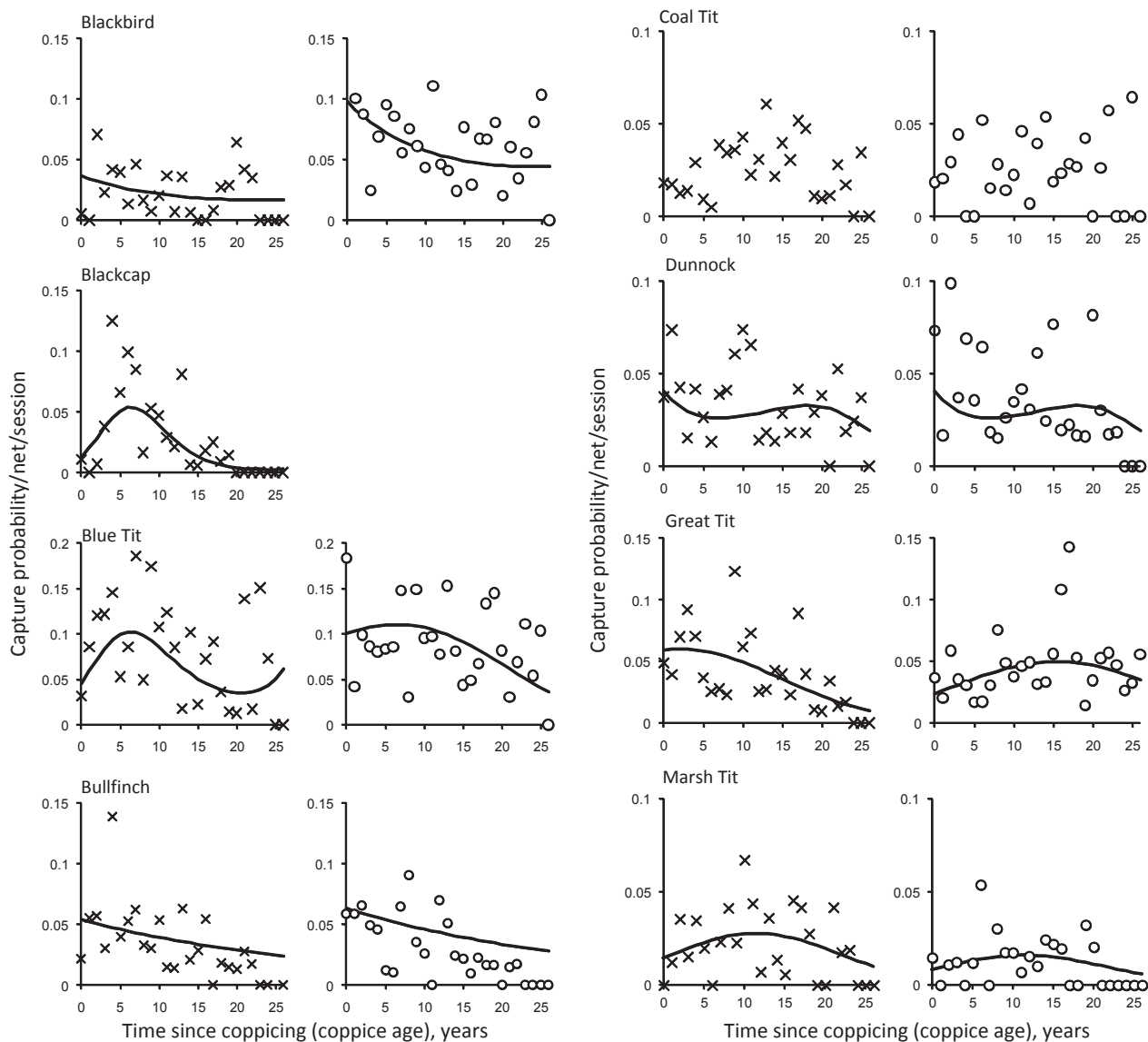
Figure 4. Capture rates (birds per net per trapping session) of juvenile songbirds of 12 species in relation to coppice age in Treswell Wood, 1978–2009. For each species capture rates in post-breeding (summer) and winter are shown, from left to right. See Figure 3 legend for details.

more complex preferences of their parents. The preferences of juvenile Dunnocks were not strongly expressed, in sharp contrast to the strong preference of adults for young coppice. It may be that these differences result from intraspecific competition, with juveniles being obliged to use suboptimal habitat (Holt *et al.* 2011). Alternatively, the habitat use of young birds such as Bullfinches may be more determined by the threat of predation than is their parents' (Marquiss 2007). Whatever the mechanism, our results suggest that managers should ensure

availability of young coppice for Bullfinch, and a diversity of ages for Dunnock, which is a different conclusion from that which would have been reached by considering breeding adults in isolation. We also found seasonal differences in the habitat use for some species (Blackbird and tits).

Differences in habitat use between age-classes and seasons strongly suggest that management recommendations for most species should take account of the likely demographic cause of population declines or fluctuations (Saether & Bakke 2000,
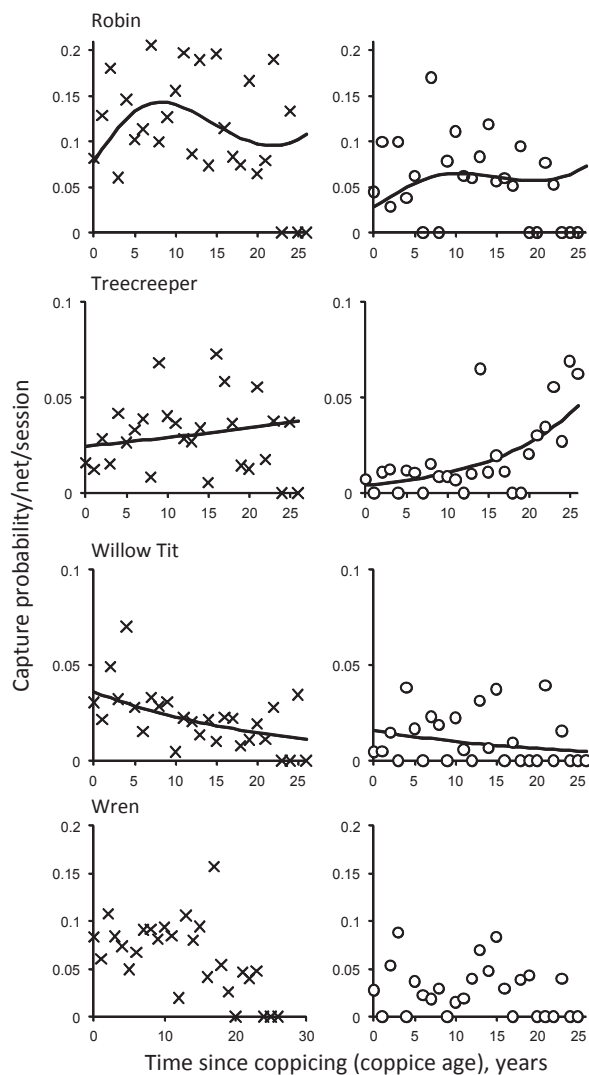
Figure 4. Continued.

Siriwardena *et al.* 2000a). For example, if population declines are driven by variation in juvenile or adult survival, and post-breeding or winter habitat use differs from breeding habitat use, management for optimal breeding habitat may not be the highest priority. Numerous analyses of avian demography have shown that songbird population growth rates are generally more sensitive to variation in survival than in fecundity (Saether & Bakke 2000, Siriwardena *et al.* 2000b), and that first-year survival may be especially important (Sim *et al.* 2011). Such a demographic perspective suggests that managers should often concentrate on providing high-quality habitat for post-breeding and wintering birds.

Table 2. Capture probabilities (per net per day) of adult songbirds (se, two values are given because they are back-transformed from the logit scale and are therefore not symmetrical) in uncoppiced and coppiced parts of Treswell Wood, for seven species for which capture probabilities differed significantly with respect to coppicing. For species for which there was an overall difference between coppiced and uncoppiced woodland, we give only the overall means. For other species for which the effect of coppicing was significant only in interaction with habitat or season, we give appropriate mean values for the different habitats or seasons.

	Uncoppiced						Coppiced					
	Overall	Ash	Mixed	Breeding	Post-breeding	Winter	Overall	Ash	Mixed	Breeding	Post-breeding	Winter
Eurasian Blackcap	0.059 (0.055, 0.064)						0.098 (0.090, 0.106)					
Common Chaffinch				0.070 (0.063, 0.079)	0.004 (0.003, 0.005)	0.011 (0.009, 0.013)				0.058 (0.051, 0.065)	0.008 (0.007, 0.010)	0.016 (0.014, 0.019)
Coal Tit	0.016 (0.014, 0.018)						0.009 (0.008, 0.011)					
Dunnock		0.046 (0.042, 0.050)	0.038 (0.035, 0.043)					0.046 (0.042, 0.050)	0.088 (0.078, 0.100)			
Garden Warbler		0.00003 (0.00001, 0.00010)	0.00003 (0.00001, 0.00009)					0.00004 (0.00001, 0.00013)	0.00007 (0.00002, 0.00022)			
Eurasian Treecreeper		0.023 (0.020, 0.026)	0.032 (0.028, 0.037)					0.030 (0.027, 0.033)	0.021 (0.017, 0.026)			
Willow Tit	0.019 (0.018, 0.021)						0.015 (0.014, 0.017)					

Table 3. Capture probabilities (per net per day) of juvenile songbirds (se, two values are given because they are back-transformed from the logit scale and are therefore not symmetrical) in uncoppiced and coppiced parts of Treswell Wood, for eight species for which capture probabilities differed significantly with respect to coppicing. See Table 2 legend for details.

	Uncoppiced					Coppiced				
	Overall	Ash	Mixed	Post-breeding	Winter	Overall	Ash	Mixed	Post-breeding	Winter
Eurasian Blackcap	0.009 (0.007, 0.011)					0.036 (0.031, 0.042)				
Eurasian Bullfinch	0.021 (0.019, 0.024)					0.039 (0.036, 0.044)				
Common Chaffinch		0.001 (0.000, 0.014)	0.001 (0.000, 0.009)				0.000 (0.000, 0.005)	0.002 (0.000, 0.022)		
Dunnock	0.024 (0.021, 0.027)					0.037 (0.033, 0.042)				
Marsh Tit	0.00001 (0.00000, 0.00004)					0.00003 (0.00001, 0.00008)				
European Robin				0.119 (0.111, 0.127)	0.052 (0.048, 0.057)				0.131 (0.122, 0.140)	0.082 (0.076, 0.090)
Song Thrush				0.002 (0.001, 0.006)	0.001 (0.000, 0.003)				0.001 (0.000, 0.003)	0.002 (0.001, 0.004)
Eurasian Treecreeper		0.002 (0.000, 0.009)	0.003 (0.001, 0.014)				0.003 (0.001, 0.013)	0.001 (0.000, 0.006)		

The differences in habitat use between adults and juveniles and among seasons may be especially significant for Willow Tits, the numbers of which have declined by 90% in Britain in the past 40 years (Eaton *et al.* 2009, Balmer *et al.* 2013). They showed little preference for specific coppice ages during the breeding season, but a strong preference for younger coppice at other times. Lewis *et al.* (2009) found that adult Willow Tits in the same area as our study preferred young woodlands, although a study over a wider area of England failed to find any correlation between woodland abandonment by Willow Tits and any structural component of the wood (Lewis *et al.* 2007). A more detailed follow-up study that examined habitat associations of the Willow Tit during the breeding season across a large part of the UK range found no associations with woodland age (Stewart 2010). It may be that the preference of Willow Tits for younger coppice is only expressed outside the breeding season.

Employing a demographic perspective could be especially useful for Willow Tit conservation because they are relatively long-lived and have low fecundity for a parid (Saether & Bakke 2000). Consequently, their population growth rates may be relatively sensitive to variation in adult survival. However, an analysis of the demographic causes of decline in the Willow Tit has not yet been carried out, suggesting that management recommendations should be made and acted on with caution, given the possibility of maladaptive habitat choice (Robertson & Hutto 2006, Gilroy *et al.* 2011). On balance it is prudent to recommend that Willow Tits should have access to young woodland habitats including scrub throughout the year, as remaining healthy populations in the English Midlands generally live in such areas (Stewart 2010). Ensuring such access may require habitat managers to refrain from common management practices such as clearance of scrub from reed beds or woodland margins. Mitigating the effects that deer might have on winter habitat may also be important, as an increase in deer numbers has also been implicated in Willow Tit declines (Newson *et al.* 2012).

Our results using long-term mist-netting data and a quasi-experimental approach are in general agreement with previous studies that relied on surveys of breeding birds (Fuller & Moreton 1987, Fuller & Steel 1990, Fuller & Henderson 1992, Fuller & Green 1998). Use of habitat in relation to

coppice age in the breeding season is similar to that recorded from other woods using different survey techniques. In particular, warblers and Dunnocks were commonest in young coppice, 5–10 years old, and Blackbirds and Wrens showed no strong pattern except some avoidance of the youngest coppice. In contrast to our study, these previous survey-based studies found that Great Tits showed little change or tended to increase slowly in numbers as coppice aged, whereas there was a shallow but definite decline with age in Treswell Wood. Robins in Treswell Wood showed no significant pattern of change with coppice age, but in Fuller's studies they avoided young coppice (Fuller 1992).

Our study has also documented patterns of change with coppice age for Bullfinch, Coal Tit, Marsh Tit and Treecreeper, species for which there were insufficient data in previous studies of coppice age. These relationships are generally consistent with previous studies of these species (Hinsley *et al.* 2007, Smart *et al.* 2007, Carpenter *et al.* 2009). However, our finding that Treecreepers prefer coppice of intermediate age appears to contradict findings from Fennoscandia, where they are seldom found outside mature forest (Suorsa *et al.* 2005). This may highlight a consistent difference in habitat preferences between the British (*Certhia familiaris britannica*) and Scandinavian (*Certhia familiaris familiaris*) subspecies of Eurasian Treecreeper, as Holt *et al.* (2011) found a similar pattern to ours. Across much of continental Europe where Short-toed Treecreepers *Certhia brachydactyla* are present, they occupy broadleaved woodland, whereas the Eurasian Treecreeper tends to be found in conifers (du Feu 2002).

Most studies of habitat use by birds are similar to those mentioned above, in which the relationships between some quantitative or qualitative measure of bird abundance and measures of the physical structure of habitat are analysed. The measures of bird abundance are usually based on quantifying behaviours that demonstrate actual use of the habitat, such as feeding or breeding. This raises two challenges to our study. First, we have used capture rates as a proxy for habitat use, although it is possible that birds caught in mist-nets are only passing through habitat, rather than using it. It is impossible to avoid such effects in a mosaic of habitats. However, while they might increase the variances of our estimates of use, they should not affect the means. Given the

very large sample sizes in our study, it seems likely that capture rates do estimate genuine selection by birds of habitat of different ages. Secondly, we did not measure structure directly but have used coppice age as a surrogate for a complex of habitat attributes that change as the coppice grows, especially understorey structures providing nesting and feeding sites. These issues make it difficult to understand the mechanistic basis for change in use that we have seen. In future research, we hope to measure the relationships between capture rates and direct measures of structure.

Any method of assessing bird abundance is susceptible to biases. Our method records where birds are but may be biased by seasonal, habitat-specific or interspecific differences in susceptibility to capture (Feare *et al.* 1980, Pagen *et al.* 2002). Interspecific differences are not of concern here, but it is possible that within-species capture efficiency is affected by habitat, particularly in the first years after coppicing. That lack of natural cover to camouflage nets will have an adverse effect on capture rates is so well recognized that it is literally proverbial ('How useless to spread a net where every bird can see it!' Proverbs 1, 17). However, the aim of the long-term study at Treswell has always been to sample the species in the understorey rather than the canopy, and by the time the understorey is growing higher than mistnets, it has generally reached coppicing age again. In fact, because capture rates in uncoppiced woodland are, if anything, higher than expected from the trend in coppiced woodland, over-topping of nets by the understorey does not seem to be a major problem. For these reasons, and because our results are generally consistent with those obtained by other methods (Fuller & Moreton 1987, Fuller & Henderson 1992, Fuller & Green 1998), we do not believe that change in capture rates with age is seriously confounded by variation in capture susceptibility.

The relative preference of songbirds for coppiced over uncoppiced woodland has been less well explored than patterns of use within coppice (Fuller 1992). In this study, patterns of change in use with age of coppiced areas were generally consistent with differences between coppiced and uncoppiced parts of the wood. However, this was not true for all species; Willow Tits generally preferred younger areas in the coppice, but their capture rates were higher in uncoppiced woodland. This

suggests that habitat preference is not a simple function of habitat age for some species. This could come about if these species are responding to some parameter of habitat that does not change linearly with age, or are choosing habitat of different ages for different reasons (e.g. Willow Tits choosing dead wood in which to nest). Differences in the habitat age preferences of songbirds may be caused by changes in structure *per se* (Hinsley *et al.* 2009, Lewis *et al.* 2009), by changes in food availability (Hill *et al.* 1990, Hodgson *et al.* 2009), which may depend on plants (Van Calster *et al.* 2008), or by avoidance of predation (Capizzi 2000). In Treswell, the oldest coppice is generally similar in structure to uncoppiced areas. Although Hazel at 26 years will not have developed into the aged, derelict specimens that can be seen on uncoppiced areas, trees are full height, cropping well and mature in every sense except that instead of one trunk, they have multiple stems. This similarity in structure suggests that preference differences may be driven by biotic attributes of different habitats. Alternatively, it remains possible that differences in capture rates between coppiced and uncoppiced woodland could be accounted for by differences in capture susceptibility, although we consider this unlikely as previously discussed.

Overall, our study emphasizes the great influence of coppice management, and young successional stages more generally, on adults and juveniles of several species of woodland songbirds, especially declining species in the UK such as Bullfinch, Dunnock, Marsh Tit, Song Thrush, Willow Tit and Willow Warbler. Each species has different preferences for coppice age structure, but overall it is the young to middle ages (5–15 years) of coppice that are most preferred across species of songbirds. This agrees with previous breeding season studies and suggests that the current coppicing regime at Treswell, with rotations up to 30 years, is better for songbirds than the historical 10-year rotation. Other coppiced sites in the UK commonly have rotations of between 20 and 30 years (Fuller & Henderson 1992, Fuller & Warren 1993), although in exceptional cases these may be as long as 40 years (Fuller *et al.* 1989).

Despite the coppice management at Treswell, and the apparent preference of many species for the coppice, trends of breeding numbers at Treswell are generally consistent with national trends (Amar *et al.* 2006). Where trends at Treswell differ substantially, it is not obvious that coppice-

loving species have done well there. For example, Garden Warbler, the only species to decline at Treswell in the face of a positive national trend, has a strong affinity for young coppice. Great Tit, the only species which did conspicuously better at Treswell than the national trend, has a preference for 5- to 15-year-old coppice in summer, but has also benefited from the provision of nestboxes. It may be that small islands of coppice management are insufficient to counter other changes at larger scales, especially for migratory species such as the Garden Warbler.

In future work we intend to use our data to investigate the demographic parameters of songbird species with respect to coppice age, in order to make stronger recommendations about optimal age structure (Fuller 1992). Our results notwithstanding, it is also important to acknowledge other aspects of coppiced woodlands that require management. In particular, the density of standards (i.e. the effect of shading) and the effect of deer browsing are important factors that need to be considered (Holt *et al.* 2011). Finally, our study suggests that the best way to manage short rotation woody crops to maximize their conservation value will be to increase rotation length or, where this is not economically possible, to ensure that some older coppice is available, as few species show year-round preference for the very earliest years in the rotation (Fry & Slater 2011, Riffell *et al.* 2011).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Results of GLMMs (with negative binomial errors and logarithm link functions) of capture probabilities of adult songbirds in Treswell Wood, Nottinghamshire, UK.

Table S2. Results of GLMMs (with negative binomial errors and logarithm link functions) of capture probabilities of juvenile songbirds in Treswell Wood, Nottinghamshire, UK.

Table S3. Results of models to compare differences in capture rates of adults between uncoppiced and coppiced woodland.

Table S4. Results of models to compare differences in capture rates of juveniles between uncoppiced and coppiced woodland.