Broughton, Richard K.; Parry, Wayne; Maziarz, Marta. 2020. **Wilding of a post-industrial site provides a habitat refuge for an endangered woodland songbird, the British willow tit *Poecile montanus kleinschmidti***. *Bird Study*, 67 (3). 269-278.

Wilding of a post-industrial site provides a habitat refuge for an endangered woodland songbird, the British Willow Tit *Poecile montanus kleinschmidti*

Running head: Willow Tits in a post-industrial habitat refuge

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Keywords: bird territories, coal mining, land cover maps, lidar, remote sensing, species conservation, woodland structure

Capsule Post-industrial sites that have become wilded by colonising vegetation can represent important habitat refuges for Willow Tits, which occupy large territories in early-successional wet woodland and scrub.

Aims Quantifying Willow Tit population density and territory characteristics on a habitat mosaic of wetland, grassland and woodland/scrub, which has developed on a 596 ha area of former coal mining activities in northwest England.

Methods Field surveys located all 35-37 nests per year during 2017-19. Territories were estimated using Thiessen polygons around nest sites. Remote sensing data (land cover mapping and lidar) characterised woody vegetation height and coverage across the site and within territories. Changes in coverage between 1990 and 2015 were assessed to estimate the age of woody vegetation. The relationship between territory size and woodland was tested to see if birds secure a similar area and volume of woody vegetation in each territory.

Results Mean breeding density was 7.3 pairs/km^2 (excluding 103 ha of ponds/lakes). Estimated territories averaged 13.7 ha, or 6.9 ha of wooded habitat only. The woodland and scrub was a maximum of 25-30 years old and had a mean height of 3.7 m. Larger territories contained a greater coverage and volume of wooded habitat. The site held 1.3% of the national and global population of the British subspecies of Willow Tit.

Conclusion Willow Tits occur at low density and require large areas of habitat. Wilded post-industrial sites appear to be important for Willow Tit conservation in Britain, but may require ongoing management to maintain the early-successional woodland and scrub associated with new wetlands in former mining areas. Such sites may have a broader conservation value for a range of species.

Habitat loss due to human activity is a major driver of the global biodiversity decline (Brooks et al. 2002, Mantyka-pringle et al. 2012). Industrialisation is a key mechanism of habitat destruction, transforming landscapes by urban expansion, agricultural intensification and exploitation of natural resources (Douglas & Lawson 2000). In many regions, industrialisation has created a legacy of impoverished biodiversity due to deforestation and destruction of wetlands and grasslands (Williams 1989, Samson & Knopf 1994, Hambler et al. 2011, Chen et al. 2016). These effects are particularly acute in Western Europe, including Britain.

The mining of rock, minerals and carbon-based fuels to power industrialisation is a significant cause of habitat loss from excavations and the associated dumping of waste (Ratcliffe 1974, Douglas & Lawson 2000). However, abandonment of mining activities can also create habitats of high conservation value once industrial activity ends and sympathetic management or natural succession begins (Ratcliffe 1974). Abandoned limestone quarries can be colonised by floristically rich grasslands that provide a refuge for butterflies (Davis 1979, Beneš et al. 2003), and new wetlands can form on flooded excavations or the subsidence of collapsing ground above underground mining, which may offset the loss of natural wetlands and provide refuges for waterbirds (Li et al. 2019), amphibians (Klimaszewski et al. 2016) and invertebrates (Dolný & Harabiš 2012, Lewin et al. 2015, Zhang et al. 2019).

Large parts of the British landscape have been transformed by coal mining since the 18th Century (Faull 2008), but this had mostly ended by the late 20th Century, leaving a legacy of post-industrial sites of waste heaps and flooded subsidence and excavations. Some of these sites were reclaimed for agriculture or development, but others were abandoned to natural colonisation by vegetation and/or reclaimed for recreation and nature conservation (Rotherham et al. 2003). The resulting habitat mosaics of wetlands, grassland and young woodland on these latter sites have developed in landscapes otherwise dominated by agriculture and urbanisation (Gemmell & Connell 1984, Rich et al. 2015, Champion 2019).

As British coal mining declined from the 1960s, when industrial sites began to be abandoned or repurposed, parallel declines of many bird populations were occurring due to agricultural intensification and forestry practices in the wider landscape (Newton 2004, Fuller et al. 2007). Consequently, the semi-natural habitats on post-industrial sites became increasingly important refuges for once common and widespread species.

The fastest declining resident bird in Britain is the endemic subspecies of Willow Tit *Poecile montanus kleinschmidti*, a small (10 g) songbird. Willow Tits are non-migratory and territorial throughout the year, preferring early successional woodland and scrub in Britain but also mature forest and bog elsewhere in Europe, where they excavate a nest chamber in dead wood (Cramp & Perrins 1993, Lewis et al. 2009a). Willow Tit abundance fell by 93% in Britain between 1967 and 2017 (Massimino et al. 2019), and this unique taxon is globally threatened, with only 2750 pairs remaining (Woodward et al. 2020). Willow Tits are rapidly declining elsewhere in Europe (e.g. Boele et al. 2019), and in Scandinavia this has been attributed to climate change and logging of forests (Virkkala 2016, Lehikoinen & Virkkala 2018). Causes of the Willow Tit's decline in Britain may include habitat change, nest predation and competition from dominant species (Lewis et al. 2009a, Parry & Broughton 2018).

Siriwardena (2004) showed that British Willow Tits declined most strongly in farmland and dry woodland, with slower declines in wetlands and associated damp woodland. Lewis et al. (2009a) suggested that wet woodland developing around wetlands on post-industrial sites are potential refuges for this species. However, nothing is known of typical breeding densities in such habitats, and little is known of territory sizes or how much habitat is required by British Willow Tits. Limited information from Europe suggests that breeding territories are variable and relatively large, averaging 7-31 ha in Germany and Scandinavia (Cramp & Perrins 1993). Only two territories are described from Britain, which averaged 11 ha (Foster & Godfrey 1950).

This lack of basic information on the density and territory requirements of Willow Tits, particularly in Britain, limits the ability to implement conservation plans, as it is unknown how much habitat is needed to maintain pairs and populations. Understanding likely breeding densities and territory size also facilitates monitoring, enabling better design and interpretation of surveys to provide realistic estimates of population size. However, quantifying habitat for Willow Tits, and other woodland birds, has previously been limited to sampling due to issues of scale and complexity (Lewis et al. 2009b). The increasing availability of remote sensing and spatial analysis tools overcomes these limitations, and now enables comprehensive assessment of habitat characteristics at the whole territory and landscape scales (Hill et al. 2014).

We fill knowledge gaps for British Willow Tits by investigating the population density, territory size and composition in a post-industrial site habitat mosaic, combining remote sensing data and field surveys. We also test whether birds adjust territory area to encompass a similar amount of woodland habitat in each territory, regardless of its uneven distribution across the site (Smith 1976). Similar woodland coverage between territories may reflect minimum requirements for successful breeding or survival, and so may indicate benchmark values to assist with monitoring and management of habitat and populations.

The results are the first to quantify the breeding density, estimated territory size and composition of the endemic subspecies of British Willow Tit. This new information can be used by decision-makers to inform landscape-scale conservation strategies for this globally endangered population. The results also provide further evidence of the potential importance of post-industrial habitats for the conservation of threatened species, and is the first case study featuring a songbird.

METHODS

Study area

The study took place in northwest England during 2017-2019 on a 596 ha complex of mining subsidence (sunken ground) and reclaimed surface excavations on the southern edge of the Wigan conurbation, comprising a habitat mosaic of shallow lakes and wetlands, grassland, scrub and woodland. The site consisted of the 160 ha Amberswood Common (53° 31'N, 2° 35'W) and extended southeast and westwards to include contiguous areas of the 'Wigan Flashes' wetlands (see Parry & Broughton 2018).

The region has a legacy of landscape modification from mining of the underlying Lancashire Coalfield, which was heavily exploited by shallow underground and surface mining that peaked during the early 20th century (Davies 2010). Mining and associated activities were abandoned on the study site between the 1960s and 1980s, and ceased in the wider region by 1993, leaving numerous abandoned excavations and flooded areas of subsidence (Forster et al. 1995). The study site, like many others, underwent reclamation, landscaping and natural succession of colonising vegetation since the 1980s to create a semi-natural habitat mosaic, which is now recognised for its recreational, scientific and wildlife conservation value (Champion 2019).

The study site contains subsidence lakes and ponds totalling 103 ha, fringed by Common Reed *Phragmites australis* and Great Reedmace *Typha latifolia*. Areas of woodland and scrub comprise Black Alder *Alnus glutinosa*, Common Elder *Sambucus nigra*, Silver Birch *Betula pendula*, Wild Cherry *Prunus avium*, Common Ash *Fraxinus excelsior*, willow *Salix* spp. and hawthorn *Crataegus* spp., with extensive low undergrowth of Bramble *Rubus fruticosus*. Approximately 14 ha of Scots Pine *Pinus sylvestris* and European Larch *Larix decidua* plantation are integrated with the deciduous trees and scrub. Excluding the open water, the area of woodland, scrub and rough grassland available to Willow Tits totals 493 ha. In the wider landscape, the site is largely surrounded by residential buildings, retail and light industry of the Wigan conurbation and its satellite settlements.

Willow Tit surveys

Intensive trapping of juvenile and adult Willow Tits, with mist nets with feeders or playback, took place throughout the year across the site. Birds were individually marked with a numbered metal leg ring and combinations of coloured rings. Between January and March each year, searches of all parts of the site took place every 1-7 days to locate Willow Tits on their territories.

From early March until April, each territory was monitored every 1-5 days as birds began trial excavations of nest holes in standing dead wood or in specially-designed nest-boxes, which were distributed across the site, although natural and artificial nest sites were not limiting (Parry & Broughton 2018). This excavation activity was monitored until each pair settled on a final nest-site within their territory during April, which was denoted by excavation of a complete nest chamber. These final nest locations were mapped using a handheld GPS unit. For a minority of territories where the final nest location was not found (2-3 per year), GPS coordinates were recorded at the location of most intensive activity during March and April, indicating the general location of the nest within an estimated radius of 15 m (pers. obs.). Repeat nesting attempts were common (see Parry & Broughton 2018) but are not included in analyses. With intensive survey effort across the site, it is assumed that all Willow Tit territories were identified each year.

Spatial habitat data

To characterise the woodland age and extent we used land cover data from the UK Centre for Ecology & Hydrology’s Land Cover Maps for 2015 (LCM2015) and 1990 (LCM1990), which are national 25 m resolution classified raster coverages derived from satellite multispectral imagery (Fuller et al. 1993, Rowland et al. 2017). For a valid comparison of land cover change between maps, the 21 land cover classes in LCM2015 and 25 in LCM1990 were combined into five aggregate classes to allow mapping of broad land cover types, based on the methodology of Rowland et al. (2020) that allows realistic change detection. The aggregate classes used were grasslands (including arable), woodland, urbanised, open water, and 'other' (e.g. bare ground). Comparing these land cover classes between 1990 and 2015 allows the development of broad habitat types on the site to be assessed using the change in extent over the 25 year period. The comparisons are primarily used to assess the age of woodland and scrub, where the area in 2015 that exceeds that of 1990 will represent immature woodland or scrub of a maximum 25-30 years growth (allowing several years for initial growth to develop sufficient cover to be classified in satellite imagery).

To characterise the woodland structure, we assess the vegetation heights for the entire site and in individual Willow Tit territories using the English Environment Agency's lidar data products (Environment Agency 2020). A 1 m resolution digital terrain model (DTM) and digital surface model (DSM) were available from airborne lidar data acquired during leaf-off conditions between 17 January and 14 February 2019, with a vertical accuracy of at least ±0.15 m and a horizontal error of ±0.40 m. These data provide elevation values for every 1 m^2 pixel of the ground (DTM) and the tallest feature in the pixel (DSM), such as trees or bushes. A canopy height model (CHM) was created by subtracting the DTM from the DSM, to create a coverage of relative vegetation heights representing trees, shrubs and scrub thickets, which we limited to values of 0.5 m and above to exclude ground vegetation (grasses etc.). Lidar data collected in 2019 were assumed to be representative of the entire 2017-2019 period of bird surveys. Some vegetation growth within the survey period was inevitable, but this is considered unlikely to be sufficient to invalidate results.

Data analyses

For the three study years, we generated Thiessen polygons from each annual set of nest sites (point locations) to approximate individual Willow Tit territories, which were bounded by the study site. Thiessen polygons are tessellated polygons with boundaries equidistant between point (nest) locations, similar to the approach used for approximating territories of the related Great Tit *Parus major* in woodland (Wilkin et al. 2006). These polygons were used to calculate the density of occupied territories in the study area and the mean area of estimated territories.

The mean height and standard deviation of woodland vegetation in each Willow Tit territory were extracted from the CHM lidar data within each Thiessen polygon. These data were summarised for each survey year, generating the mean and range of the territory means and standard deviations. These height metrics allow comparison between years and with other lidar studies of woodland habitat of similar songbirds. For the entire study area, the frequency distribution of the lidar-derived height values was calculated in 1 m intervals to characterise the height profile of woody habitat that had developed on the site.

The area of woodland classified in LCM2015 was extracted from within the individual Willow Tit territory polygons to calculate the coverage of woodland per territory. As Willow Tits will use the three-dimensional structure of woodland, we also estimate the volume of space occupied by woody vegetation (including the foliage, stems and space beneath the canopy) in each territory, by multiplying the woodland area by the mean height derived from the lidar data. We use the non-parametric Spearman's rank-order correlation to test whether territory size is associated with the area or volume of woodland cover.

All territories are treated as independent between years. The average maximum overlap between individual territories in similar locations in consecutive years was 80% over all years. These shifts in territories, and annual mortality, meant that combinations of territory boundaries and pairs were unique each year, as also shown in a German population of Willow Tits (Ludescher 1973) and the related Marsh Tit in Britain *Poecile palustris* (Broughton et al. 2012a).

RESULTS

The number of Willow Tit nests on the study site showed very low annual variation during 2017-2019 (Table 1), giving a mean annual breeding density of 7.3 pairs/km^2 (excluding open water). Thiessen polygons around each annual set of nest locations give approximate territories with an overall mean area of 13.7 ha (SD = 9.0) (Table 1, Fig. 1). The minimum territory size in any year was 1.1 ha and maximum was 41.3 ha.

The area of the study site classified as woodland in 2015 totalled 250 ha, compared to 78 ha in 1990. The woodland extent in 2015 contains 40 ha of the coverage present in 1990, indicating that 84% of the woodland present in 2015 had developed (sufficient to be classified) only within the previous 25 years. The lidar data for the whole site gives an overall mean height of woody vegetation of 3.7 m (SD = 3.5 m) in 2019, indicating young woodland/scrub, which supports the comparison of woodland cover between 1990 and 2015. The frequency distribution of vegetation heights (Fig. 2) showed that most values (57%) are under 3 m tall, with only 8% being 10 m or taller. Relatively large standard deviations for the woodland heights in territories, compared to mean canopy height, indicates a wide variation in tree and shrub heights (Table 1).

Willow Tit nest locations fell mostly within the mapped woodland coverage of 2015, with 84.3% of all nest sites falling inside or within 25 m (i.e. in an adjacent mapped pixel, probably in tree stems at/outside the woodland edge) of this habitat class (Fig. 1). Thirteen percent of the nests were located in the 16% of woodland cover that had been present since at least 1990, indicating no disproportionate selection or avoidance of this older woodland by the birds.

The mean area of mapped woodland in each territory averages 6.9 ha (SD = 5.6) across all study years (Table 1), and woodland cover averages 53.1% (SD = 25.0) per territory, showing it to be the dominant habitat. In all years, the territory size strongly increased with woodland area (r_s = 0.78-0.82, P < 0.001). The territory size was also significantly and positively correlated with the volume of woody vegetation in territories across all years (r_s = 0.62-0.71, $P < 0.001$).

DISCUSSION

The wilding of our post-industrial study site over several decades has resulted in a habitat mosaic of wetland, young woodland/scrub and grassland that supports a notable population of the endangered British Willow Tit. Based on the national estimate of 2750 breeding pairs in 2016 (Woodward et al. 2020), the 35-37 pairs on our single study site represent 1.3% of the British and global population of this endemic subspecies. To put this figure into some context, under the Ramsar Convention on Wetlands a site is considered as internationally important if it regularly supports 1% of the population of a waterbird species or subspecies (Grobicki et al. 2016). Willow Tits are not waterbirds, although the British subspecies is often associated with damp woodland and scrub integrated with wetlands, but if similar criteria to the Ramsar Convention were applied, hypothetically, then our site could be considered as internationally important for this taxon.

The breeding density of 7.3 pairs/km^2 in the post-industrial habitat mosaic is relatively high in the British context, although the only other published information are 4.9 pairs/km^2 in an English pine plantation (Gibb & Betts 1963) and an estimated 3-4 pairs/km^2 in wet woodland (derived from 7.7 individuals/km^2, Speck 2019). However, these other densities are extrapolated from few birds on small sites (26-72 ha). Our study is the first to quantify the density of British Willow Tits on a wider landscape scale of nearly 6 km^2, or 5 km^2 when excluding open water.

Elsewhere in Europe, Willow Tit densities in extensive study landscapes ranged from 3.6 to 12.8 pairs/km^2 in Scandinavian forest and bog (Brömsen & Jansson 1980, Orell & Ojanen 1983, Koivula et al. 1996) and 16 pairs/km^2 in German birch forest and bog (Ludescher 1973). As such, in the broader context, British Willow Tits in our study occur at low to moderate numbers compared to some Continental populations. This lower density may reflect the relatively low abundance of Willow Tits in Britain, which are on the westernmost margin of the global range.

The estimate of an average 13.7 ha for territory size on our site is close to the mean 11 ha for two territories at Wytham Woods, Oxford, which is the only other territory data for British Willow Tits (Foster & Godfrey 1950). Breeding territories of Willow Tits elsewhere have rarely been studied in detail (Cramp & Perrins 1993), although Ludescher (1973) found a much smaller average of 7.3 ha in Germany. Related species also tend to have smaller territories, mostly derived from observations of colour-marked birds in the field. Based on this method, Marsh Tit territories averaged 5.6 ha and Coal Tits *Periparus ater* 3.3 ha in mature British woodland (Broughton et al. 2012a, Broughton et al. 2019). Great Tits territories were a median 1.9 ha in Polish primeval forest (Maziarz and Broughton 2015), while estimates derived from Thiessen polygons in British woodland averaged 1.6 ha (Wilkin et al. 2006). In North America, Smith (1991) summarised Black-capped Chickadee *Poecile atricapillus* territories with means of 1.5-5.3 ha. The relatively large territories, or low densities, found for British Willow Tits on our site can have important conservation implications in ensuring that landscapes contain sufficient habitat and connectivity to support viable populations (Broughton et al. 2013).

The disparity in territory size between our study and others may reflect the coverage, maturity and volume of woodland in different sites. The relatively young and discontinuous woodland/scrub on our study site may have required Willow Tits to establish large territories to secure sufficient habitat for successful breeding and over-wintering. We found a strong positive correlation between territory size and woodland area, and also woodland volume, showing that larger territories contained more woody vegetation. This undermined the hypothesis that each pair of Willow Tits was simply securing a similar quantity of woodland. Instead, variation in territory size may reflect differing habitat quality or socially dominant pairs claiming relatively more habitat than subdominant neighbours (Smith 1976).

However, the Thiessen polygons used to estimate Willow Tit territory size assume that birds are occupying the entire site (excluding water) as breeding territories, which may not be the case. Population studies of Marsh Tits, Great Tits and Coal Tits showed that 18-56% of the habitat area remained vacant between defended breeding territories (Broughton et al. 2006, Maziarz and Broughton 2015, Broughton et al. 2019). As such, it is possible that the mean 13.7 ha for the Thiessen polygons representing Willow Tit territories could be an overestimate, and some of the habitat could be unused, particularly the open grassland that covered almost half of a typical territory (e.g. Schlicht et al. 2014). If the average 47% grassland cover was considered as 'unused' habitat, this would be comparable to the 18-56% vacant area of the other tit studies mentioned above. However, the grassland likely contained some scattered shrubs, brambles and tall herbs that may well have been used by Willow Tits.

In Germany, Ludescher (1973) found that only the 68% of woodland cover in a typical Willow Tit territory was the 'usable' part, with open areas being unused, and so he revised the mean territory area from a gross 7.3 ha to 5.0 ha. Similarly, Smith (1976) found that the usable part of Black-capped Chickadee territories was the average 72% covered by woodland. If only the mapped woodland within the Willow Tit territories in our study is considered as being occupied, then this revises down the average size from 13.7 ha to 6.9 ha, which is more similar to the territories of Willow Tits and related species in other studies. Conservation plans for British Willow Tits on sites such as ours should therefore consider an average territory to be between approximately 7 and 14 ha, depending on the composition of different habitat elements (woodland, scrub, grassland/herbs). Further detailed studies would be valuable to examine vegetation and territory usage across a range of Willow Tit habitats, to better understand the species' requirements.

The woodland habitat on our study site had mostly developed within the previous 25-30 years, and so has a mean height of under 4 m and little vegetation over 10 m tall. These values closely match the preferred habitat of British Willow Tits identified by Lewis et al.

(2009b), which was specified as early-successional woodland of 20-25 years old, dominated by vegetation at 2-4 m tall, on moist soils. As such, the development stage of the woodland and scrub habitat on our post-industrial wetland site appears to be ideal for Willow Tits at present. Similar post-industrial sites are distributed across many parts of northern England, derived from the same processes of land subsidence and other mining activity, and many appear to have undergone some degree of wilding, with natural or planned colonisation by woodland and scrub (The Coal Authority 2014, Champion 2019). These sites therefore represent a network of potentially important habitat refuges for Willow Tits, and may partially explain the species' recent range contraction to include this region of northern England (Balmer et al. 2013).

The woodland metrics for our site are very different from lidar-derived canopy heights for some more mature woodland sites in Britain, where Willow Tits became locally extinct by the late 1990s. Hinsley et al. (2009) and Broughton et al. (2012b) describe mean canopy heights of 13-15 m for deciduous woodland after a century of regrowth since felling, and a mean height of 9 m for cropped ('coppiced') woodland after 20-50 years of regrowth. These taller woodlands were instead occupied by Marsh Tits, reflecting the habitat niche separation of the two closely-related species. Importantly, the structural differences of these older woodlands, which have lost their Willow Tits, highlight the likely consequence of habitat loss for this species if woodland maturation is unmanaged on the post-industrial sites that currently act as refuges. In several decades, if the woodland and scrub matures, these refuges may begin to favour species associated with older woodland, such as Marsh Tit, Great Spotted Woodpecker *Dendrocopos major* and Blue Tit *Cyanistes caeruleus*. These latter two species may hasten local extinctions of Willow Tits through nest competition and predation (Parry & Broughton 2018).

Creation and maintenance of early successional woodland and wet scrub on post-industrial sites to benefit Willow Tits may also provide refuges for other declining or range-restricted species associated with such habitats, such the Willow Warbler *Phylloscopus trochilus*

(Bellamy et al. 2009), Cetti's Warbler *Cettia cetti* (Robinson et al. 2007) and communities of amphibians, invertebrates and plants (Mortimer et al. 2000).

In summary, our results provide valuable information to inform practical conservation of Willow Tits in Britain, and potentially more widely in Europe (e.g. Boele.et al. 2019). As suggested by Lewis et al. (2009a), post-industrial sites that have become 'wilded' through the establishment of wetland, woodland and scrub appear to represent important habitat refuges. However, in order to maintain and enhance the value of existing or newly-generating habitats, the woodland and scrub cover must not become over-mature. Waterlogged soils on wetlands may delay or prevent succession to mature closed-canopy woodland, but active management to maintain woodland/scrub of the required 20 to 30-years age structure, broadly averaging 2-4 m tall, would require long-term planning and investment. Woodland cover could also be expanded on or between post-industrial sites, by planting or natural succession on open areas. The territory and density estimates provided by our results can be used in management plans to estimate likely population densities and ensure that sufficient habitat is created and maintained to support viable populations.

The study provides further evidence for the conservation value of habitats on former industrial sites. Although such benefits have previously been shown for aquatic species, such as wildfowl, amphibians and dragonflies (Dolný and Harabiš 2012, Klimaszewski et al. 2016, Li et al. 2019), our study is the first to demonstrate the value of post-industrial sites as a habitat refuge for a songbird. Developing and maintaining such sites for conservation, rather than the competing land uses of agriculture, urbanisation or waste disposal (Ratcliffe 1974), could play an important role in preventing biodiversity loss on a regional and global scale.

ACKNOWLEDGEMENTS

The authors thank landowners for access to the study site. All fieldwork complied with current local and national laws.

FUNDING

The study was self-funded.

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TABLES

Table 1. Density, territory and habitat characteristics of Willow Tits on a 596 ha study site in northwest England. The area used to calculate breeding density was 493 ha, which excluded 103 ha of open water.

	2017	2018	2019
No. of nests (territories)	36	35	37
Breeding density (territories/km^2)	7.3	7.1	7.5
Mean (SD) territory area (ha)	13.7 (9.3)	14.1 (10.0)	13.1 (8.1)
Mean woodland area per territory (ha)	6.9 (6.0)	7.1 (6.2)	6.7 (4.8)
Mean (range) values of territory canopy height means (m)	3.0 (1.7-6.6)	3.1 (1.3-6.6)	3.1 (1.8-6.9)
Mean (range) of territory canopy height SD (m)	2.9 (1.9-4.3)	3.0 (1.4-4.3)	3.0 (1.9-4.2)

FIGURES

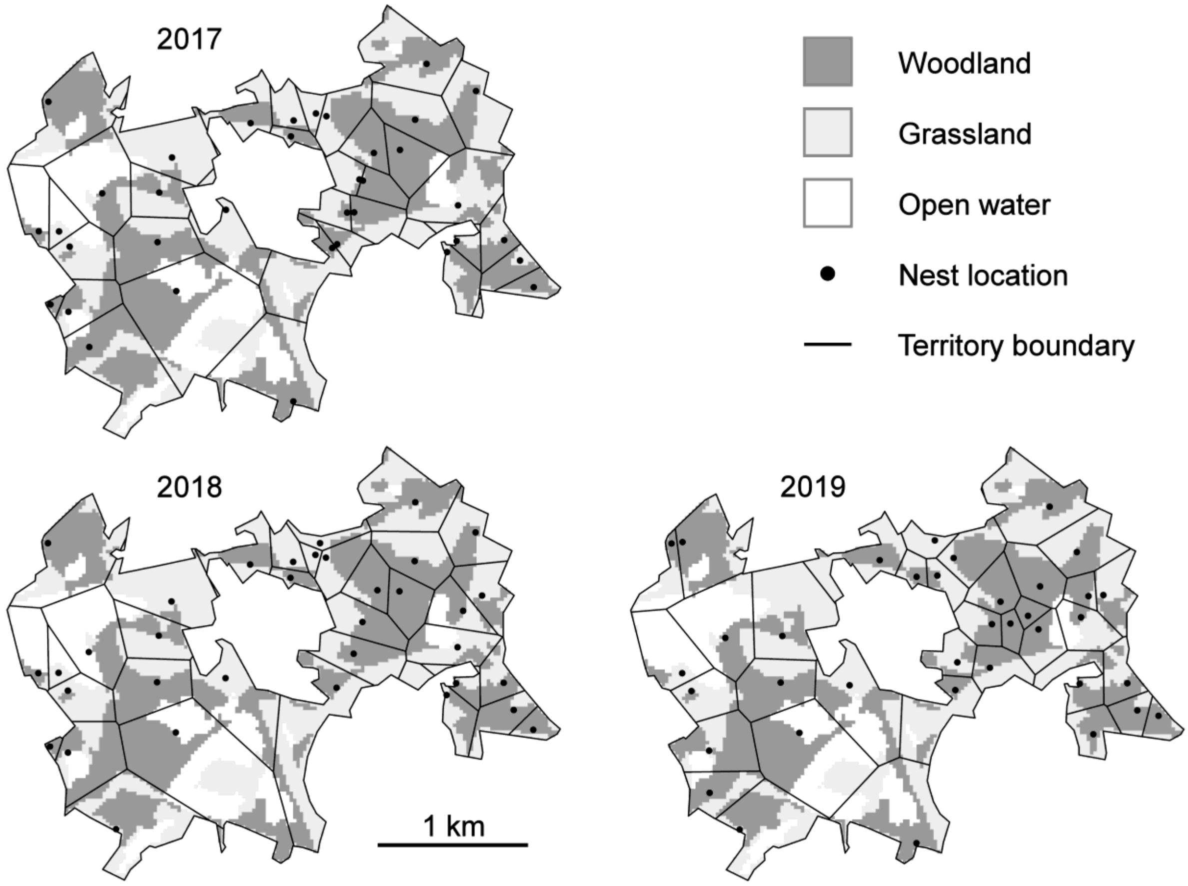

Figure 1. Location of Willow Tit annual nest locations and estimated territory boundaries (Thiessen polygons) in relation to habitat class on a 596 ha study site (incorporating 103 ha of open water) in northwest England. The large excluded area in the centre is occupied by urban residential housing and gardens.

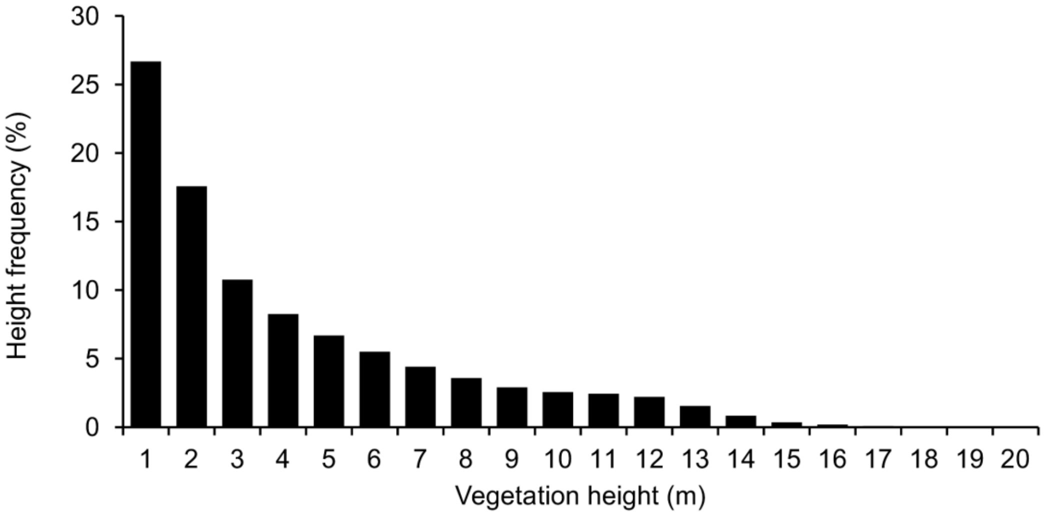

Figure 2. Frequency distribution of height values of tree and shrub vegetation on the study site in northwest England. Height values are extracted from a 1 m resolution lidar canopy height model. Values below 0.5 m are excluded, corresponding to field layer vegetation.