Nesting behaviour and breeding success of Willow Tits *Poecile montanus* in north-west England

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Summary

The British Willow Tit *Poecile montanus* has undergone a substantial decline in abundance and a severe contraction in range since the 1970s, for reasons that are poorly understood. Breeding failure, due to nest-site competition and predation, has been suggested as a potential factor in the decline, but limited data exist for the nesting ecology and breeding productivity of the species in Britain. We studied a sample of 128 Willow Tit nests in a habitat mosaic of early successional woodland, scrub and wetland in a post-industrial landscape in north-west England, which is increasingly becoming a key refuge for the species in Britain.

Results showed that nesting began in April, with standing deadwood of Silver Birch *Betula pendula*, Common Elder *Sambucus nigra* and Black Alder *Alnus glutinosa* being the most frequent nest-sites, and the characteristics of nest-sites are described. Daily survival rates and overall probability of nest survival are calculated, and details are given for the timing of breeding, clutch size, nestling survival and number of fledglings produced.

Overall, 55% of nesting attempts were successful, although many first breeding attempts failed due Willow Tits being evicted from their nest cavity by Blue Tits *Cyanistes caeruleus*, or nests being predated by Great Spotted Woodpeckers *Dendrocopos major* and, potentially, Grey Squirrels *Sciurus canadensis*. Repeat breeding attempts were relatively more successful, but produced fewer fledglings on average.

The results are discussed in the context of other studies of Willow Tits and some related species, and also the implications for the conservation of Willow Tits in Britain.

Introduction

The Willow Tit *Poecile montanus* is one of the fastest declining bird species in Britain, with its abundance falling by 92% between 1967 and 2017 (Woodward et al. 2018). Formerly widespread across England, Wales and southern Scotland, between 1968 and 2011 the Willow Tit had disappeared from most of southern and eastern England, most of its Scottish range, and large parts of Wales (Balmer et al. 2013). Remaining populations are concentrated in central and northern England and through mid Wales, with only small and isolated remnants elsewhere (Balmer et al. 2013). The exact causes of the decline of the Willow Tit population remain unknown, but may include increased nest-site competition or predation (Lewis et al. 2009a) and changes in habitat, such as maturation or fragmentation of preferred young woodland and scrub, possibly compounded by a requirement for extensive areas of well-connected habitat (Broughton et al. 2013).

Although the Willow Tit is a bird of extensive mixed forest in boreal and alpine regions across much of its Eurasian range (Cramp & Perrins 1993), in Britain the species inhabits varied marginal wooded habitats, with an apparent association with wet scrub and woodland, but also wooded valleys and drier habitats, such as thorn scrub, young woodland and deciduous strips bordering conifer plantations (Lewis et al. 2009a, 2009b). However, little is known of the main drivers of habitat preference in Britain, including the requirements of typical territory or home-range sizes. The limited information available from Britain (Foster & Godfrey 1950, Perrins 1979, Lewis et al. 2009a, Broughton et al. 2013) tallies with studies from Scandinavia (e.g. Orell & Ojanen 1983) indicating that pairs are sedentary in large territories (>10 ha) and natural breeding densities are correspondingly low.

Willow Tits excavate nest-sites in standing deadwood (occasionally in the end of a fallen log), typically in the dead stem of a deciduous sapling or shrub, and such sites can be vulnerable to predation (Cramp & Perrins 1993, Lewis et al. 2009a). Nest monitoring in several parts of Britain over the past 15 years has shown conflicting results for the extent of nest losses suffered by Willow Tits, ranging from 5% to 69% with an average of 32% in four studies (Lewis 2009a, Stewart 2010, Last & Burgess 2015, Rustell 2015). In these studies, which involved samples of up to 81 nests per site and 244 nests in total, losses were primarily due to Willow Tits being usurped from their nest excavations by other tits, especially Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major*, and predation of eggs and chicks by Great Spotted Woodpeckers *Dendrocopos major*. On a national level, however, Siriwardena (2004) found no associations between long-term national population trends of Willow Tits and their potential nest competitors or predators. As such, further data from additional locations are highly desirable to better understand the rate and causes of Willow Tit nest failure, the implications for breeding productivity, and its possible role in local and/or national declines.

In this study we focus on breeding behaviour and success, describing the fate and productivity of a relatively large sample of Willow Tit nests over six years in northwest England. In addition to the frequency, causes and timing of nest failure, we also document the nest-site choice and breeding parameters, including clutch size, number of fledglings produced and the timing of breeding behaviour. Such information is important in contributing to the wider body of knowledge of Willow Tit demographics and can aid the understanding of the causes of the species' decline in Britain.

Methods

Study area

The study took place in northwest England on scrub, woodland and wetland habitats on the southern outskirts of the town of Wigan, in Greater Manchester. The main study area was the 160 ha Amberswood Common (53° 31'N, 2° 35'W), with additional sites on adjacent parts of the Wigan Flashes: Scotsman's, Pearson's, Horrock's, Ochre, Turner's and Westwood Flashes, Bryn Marsh and Low Hall Local Nature Reserve (Fig. 1).

Most of the study sites are former open-cast mines that were abandoned between the 1960s and 1980s, and now comprise mosaics of open water, scrub, woodland, scattered reedbeds, meadows and rough grassland. Amberswood Common contains a total of approximately 85 ha of woodland and scrub, comprising plantations of approximately 30-year-old pines *Pinus* spp. and larch *Larix* spp. with some admixture and adjacent blocks of similarly-aged deciduous trees and shrubs, including 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., and extensive low undergrowth of Bramble *Rubus fruticosus*. There is one 6.6 ha body of water and numerous small ponds containing abundant Common Reed *Phragmites australis* and Great Reedmace *Typha latifolia*. The other study sites on the Wigan Flashes contain a similar mix of habitats, although conifers are few or absent.

There are no 'standard' nest-boxes (small-hole type) for tits available on the study sites, although such nest-boxes (and birdfeeders) are likely to be available in residential gardens that border some of the sites (Fig. 1), and in the general area of south Wigan.

Ringing Willow Tits

Intensive trapping and ringing of Willow Tits took place throughout the year across the study area, from March 2012 to June 2018, with a particular focus on Amberswood Common. This resulted in 131 full-grown birds being marked with BTO alloy rings and individual combinations of colour rings. Birds were caught using mist-nets at locations across the sites, which were baited with temporary feeders (containing sunflower seeds) in winter, or with a sound lure of Willow Tit calls in the summer. Marked birds were aged as first-years or older, depending on the presence of unmoulted (juvenile) greater coverts and tail feathers (Svensson 1992). Additionally, a total of 469 nestlings were ringed 11-13 days after hatching in monitored nests (see below) between 2014 and 2018, including 161 with individual combinations of colour-rings.

Nest monitoring

From December to the end of February each year, regular (typically daily to weekly at different sites) intensive searches of study areas identified potential territories from the presence and activity of Willow Tits. At locations of regular activity, and/or close to known nests from previous years, the number of potential nest-sites in the vicinity was increased by clearing climbing vegetation and brambles from standing deadwood and tree stumps, to make them more accessible to Willow Tits. Additionally, logs of fallen deadwood (approximately 10-12 cm in diameter) were strapped to different saplings at approximately 0.5 to 1.5 m above the ground, to increase the standing deadwood available as potential nest-sites. Approximately three such logs were distributed in each of 20-25 territories per year, totalling around 70 logs per year.

From 2014, one or two nest-boxes were placed in approximately 20 territories, totalling 30 boxes per year, and these were attached to young trees at a height of 1 m above the ground. The nest-boxes were of a bespoke design, comprising a sawn timber exterior with a core of dry deadwood inserted for Willow Tits to excavate, which imitated natural nest-sites (see Parry 2017 for full details). Natural nest-sites may not have been uncommon within territories, due to frequent deadwood in the area, but the provision and maintenance of additional potential sites allowed for easier monitoring and access for ringing nestlings if they were used by the birds. Being filled with soft wood, the nest-boxes were not available to other species unless first excavated by Willow Tits.

Observations suggested that pairs frequently returned to breed within several metres of the previous year's nest, providing suitable dead stumps or standing deadwood were still available. To facilitate this, at the end of each breeding season sections of deadwood containing old nests were removed to increase the likelihood of pairs re-using the same stump in the following year, if the cut stump remained tall enough (about 0.6 m or taller). This removal was because old nest-sites (excavated holes) that were not removed and remained intact were generally occupied by Blue Tits in the following year (pers. obs.), which may have deterred Willow Tits from nesting close by due to aggression.

From early March, prospecting Willow Tits in each territory were monitored approximately every 1-5 days as they excavated small holes in various dead stumps, strapped deadwood or nest-boxes, perhaps testing the suitability of the substrate for sufficient softness and dryness to be chosen as a nest-site. This activity by both members of a pair was monitored throughout March until each pair finally settled on a nest-site by April. Nests were defined as excavations that progressed beyond initial prospecting to a substantial chamber that the birds could fully enter.

The characteristics of nest-sites that were recorded included the substrate (existing deadwood stump/stem, strapped deadwood, nest-box), species of tree/shrub (for holes in natural sites), and the nest entrance hole diameter (maximum value, i.e. the greater of the vertical or horizontal measurements), orientation and height above the ground. In 2014-2017 an annual sample of 10 nest chambers in deadwood that had been fully excavated (as shown by nest material being brought in by the birds) in standing deadwood were measured to record the diameter of the tree at the entrance hole, and also the chamber depth and volume.

Additionally, monitoring of excavating Willow Tits enabled the recording of the frequency of interference or eviction by other tits before nest-building was complete. Where nests were completed, the breeding parameters recorded included first egg date, clutch size, hatch date, brood size and number of fledglings (if ultimately successful), which was determined by inspection with an endoscope. Nest failures were recorded during the egg or chick stage, with the cause based on field signs, such as excavation or destruction of the nest chamber by a predator, or appearance of nest material (e.g. moss) indicating eviction by another tit species.

Due to intensive monitoring, repeated nesting attempts after an initial failure in a given year could generally be identified by noting the relocation of a pair to a nearby site within 50 m of the initial (failed) nest, which occurred within a few days of its loss. Relocating pairs could sometimes also be identified by colour-ring identification, although colour-rings were not routinely recorded at nests until 2018. Some nests could not be classified as a first or second attempt, due to the timing, location or birds remaining unidentified.

Statistical analysis

Descriptive statistics (mean, standard deviation, range) and the frequency of nest and breeding parameters were calculated for the following variables: nest-site characteristics (height, volume, hole diameter, tree type, orientation), clutch size of first and second breeding attempts, timing of egg-laying (first egg dates), hatching success, number of fledglings, and the timing and cause of breeding failure. Sample sizes of each variable differed due to nest failures or incomplete data collection at some nests.

Where precise dates of the first egg, hatching or fledging were not recorded directly, as was the case at most nests, then it was back-calculated from clutch size or chick age (based on experience of growth and feather development) by assuming one egg laid per day and an incubation period of 13 days, beginning from the date of the last egg to the day before hatching, and a nestling period of 18 days until fledging (Robinson 2018). Brood size was the number of chicks present at day 11-13 after hatching, which was used to infer hatching success relative to clutch size.

Comparative tests were used where applicable, and non-parametric tests were used where sample sizes were small and/or assumptions of normality were violated. All tests were conducted in Minitab 16 (Minitab Inc., Pennsylvania, USA).

The calculation of the nest failure rate can be biased by the duration of nest observation, as nest mortality is a function of time. As such, estimates of daily nest failure rate and total survival probability were calculated using the Mayfield (1975) method, which allowed for direct comparison between estimates from other regions and species.

Results

Nest-site characteristics

Nest sites

A total of 128 active nest-sites were recorded between 2013 and 2018, numbering between four and 31 per year (annual mean = 21 nests; Table 1), including 78 first attempts, 30 repeated attempts and 20 unclassified. Overall, 81% of nests were in standing deadwood, 9% were in fallen deadwood that had been strapped upright to a living tree, and 10% were in nest-boxes.

Of 99 nest excavations in standing deadwood, the most frequently used tree/shrub species was Silver Birch (51%), followed by Common Elder (22%), Black Alder (14%), conifer (11%), and Wild Cherry and willow (1% each). The height above the ground of excavated holes was generally low (around 1 m) for nests in standing deadwood (Table 2), with those in nest-boxes and strapped deadwood being situated at heights of 0.5-2.1 m. The annual sample of 10 nests in standing deadwood that were examined in 2014-2017 showed that the nest trees chosen by Willow Tits were mostly slender young saplings and 'pole' stage trees (Table 2) that had probably died due to being outcompeted for light by their neighbours, or were decaying stems of shrubs, such as Common Elder.

Nest chamber excavation

Observations showed that, once a pair had settled on a nest-site, excavation of the complete nest chamber typically took 6-8 days during early April, although a late nest in June 2016 was wholly excavated within two days and was being lined with nesting material on the third day. Sites that were prospected during March were generally advanced to a depth of at least 7.5 cm deep by the first week of April, with completed chambers having a depth of at least 12.5 cm and typical volume of approximately half a decimetre (or half a litre), with an entrance hole of at least 20 mm diameter (Table 2).

General observations (not systematically recorded in detail) indicated that nest material was primarily composed of downy plant fibres from the seed-heads of Great Reedmace, with some fine animal hair and occasional small feathers and man-made fibres. Moss was not observed as a nest material in active Willow Tit nests, and its appearance indicated that the cavity had been taken over by another tit species (per. obs.).

Nest orientation

The orientation of 103 nest entrances in standing deadwood showed a bimodal distribution through the eight principal compass points, with the north-easterly and southerly directions being most frequent and 90% of nest orientations falling between these two directions, indicating a strong avoidance of a westerly or south-westerly aspect (Fig. 2).

Egg laying and clutch size

First egg dates

The first egg dates of an annual 5-18 first nesting attempts in 2014-2018 fell between 7 and 13 April, with the average first egg date for all first attempts each year falling within a remarkably narrow window of 13 to 17 April. For repeated nesting attempts (3-18 per year in 2013-2016), first egg dates were recorded as early as 15 April (after an early nest loss), and as late as 1 June, though in most (three out of four) years the latest first egg dates fell much earlier, from 28 April to 10 May.

In the five years for which reasonable data were available (2014-2018), the latest first egg date in the population averaged 30 days (range = 16-49 days) after the earliest laying of any pair that same year. The overall distribution of first egg dates for all 84 first or repeated nesting attempts was slightly bimodal, with the main peak occurring during the 5-day window of 11 to 15 April and the second, less prominent peak during 21 to 25 April, with 96% of all clutches in all years being initiated between 6 and 30 April (Fig. 3).

Clutch size

Completed clutch sizes of all breeding attempts ranged between four and 10 eggs, with eight or nine eggs being the most frequent by far (Fig. 4). Pooling data across years revealed that clutches in first breeding attempts were overall slightly larger than those in repeated attempts, but this was not statistically significant (Mann-Whitney test: $W = 2285.0$, $P = 0.220$; Table 3). There was insufficient data to test for differences between first and repeated clutches within years.

Hatching and fledging

Hatching success and brood survival

Of those nests that avoided predation or eviction, hatching success and chick survival was extremely high; first nesting attempts resulted in 100% of eggs hatching and all chicks surviving until 11-13 days (n = 46 nests), and 97.7% (75-100%) of chicks survived to a similar age in 26 repeated attempts, giving an overall minimum value of 98.8% hatching success and brood survival (n = 86 nests).

Fledging success

Surviving nests also had a very high rate of fledging success relative to clutch size, with an overall 97.8% of eggs surviving to successfully fledge as chicks (n = 68 nests). An average of approximately eight fledglings were produced from successful nests, although there was a significant difference (t-test: t = 3.39, P = 0.002) of more fledglings being produced from successful first attempts compared to repeated attempts (Table 3).

Of all 816 eggs laid (n = 98 nests), 68.5% survived to fledge, but this value was higher for repeated attempts (83.9% fledglings from 217 eggs, n = 28 nests) than for first attempts (65.8% of 476 eggs, n = 55 nests). Consequently, the reproductive rate, i.e. the average number of fledglings produced from each nest, derived from all nests where an egg had been laid and including subsequent failures, was 5.7 for 55 first attempts, 6.5 for 28 repeated attempts, and 5.7 for all 98 attempts.

Nest survival and causes of failure

Nest survival

Annual rates of nest survival for 2014-2018 ranged from 48.5% to 58.3% (n = 19-31 per year), with overall nest survival of 54.7% (n = 128 nests from 2013-2018). Of all 58 nest losses, the majority occurred during the egg stage (laying and incubation; 52%), but with a notable proportion occurring during the late stages of excavation (21%) and at the chick stage (28%).

Losses of first attempts (52% of 75 nests) were significantly greater than for repeated attempts (23% of 31; Fisher's exact test: $P = 0.009$). The daily survival rate calculated from 97 nests using the Mayfield (1975) method was 0.989, giving a daily failure rate of 0.011. Assuming a complete nesting cycle lasted 39 days (for a nest with the average of 8 eggs, 13 days incubation and 18 days for nestlings), raising the daily survival rate to the power of 39 gave an overall survival probability of 65.4% for a Willow Tit nest in this population. For 86 nests at the egg stage (laying and incubation), the daily survival rate was 0.989 and survival probability was 79.4%, and for 75 nests at the chick stage the respective daily survival rate and probability were 0.992 and 84.1%.

Causes of nest losses

All nest losses during excavation were caused by eviction by Blue Tits, which were also responsible for more than a third of losses during laying or incubation and 40% of all 58 nest failures (Fig. 5). During observations of interactions with Blue Tits at nests being excavated in 2018, including activity recorded on trail cameras positioned ad hoc near nests, Willow Tits were successful in defending only two of eight nest cavities (25%) that were attacked by Blue Tits, and were evicted from the remainder. Losses to Blue Tits accounted for 23% of all first attempts but only 3% of repeated attempts, whereas predation accounted for 26% and 17% respectively. Of 13 occupied nest-boxes, none were predated but 38% were lost to Blue Tits.

At the egg stage, most nest losses (62%) were due to predation, and predators were responsible for all losses at the chick stage (Fig. 5). At most depredated nests the nest chamber had been opened by the predator, and field signs suggested that the most frequent of these (at least 50%) was the Great Spotted Woodpecker, with other predation events possibly being due to Grey Squirrels, and one attributed to a Eurasian Jay *Garrulus glandarius*. However, the soft wood of the nest cavity was often heavily splintered and fragmented, meaning that positive identification from distinctive field signs was not possible in many cases (e.g. using grooved tooth-marks from a squirrel's incisors, or peck marks from a woodpecker).

Discussion

The very limited published information for the breeding ecology and nesting success of Willow Tits in Britain means that any new data on this topic is highly valuable, particularly with respect to understanding the causes of the species' severe national decline. The sample of 128 Willow Tit nests that were monitored in the current study forms a significant addition to the information available for nest-site choice, timing of breeding and productivity of the species in a region where it remains moderately widespread. Although data on the wider habitat in breeding territories was not considered (but is the focus of future study), the young woodland, scrub and wetland in the post-industrial, urban-fringe landscape of the Amberswood Common and Wigan Flashes complex in north-west England is similar to that of other parts of northern and central England, which is increasingly forming a core part of the Willow Tit's remaining British range (Lewis et al. 2009a). As such, the additional information from the current study is useful in building a picture of the requirements and viability of the remaining populations in such habitats.

Nest-site characteristics

The nest-site choice of Willow Tits in the study area was predominantly young Silver Birch, but also Black Alder, with these dead stems and stumps being common due to crowding and competition among dense stands of early successional scrub and young woodland. Common elder was also an important nest-site (22%), but this required mature shrubs where stems could develop to a suitable diameter before dying or decaying to allow excavation by the tits. The dead stumps and stems of plantation conifers were also used for 11% of nests, although a general preference for broadleaved species could not be confirmed due to a lack of information for overall availability of different tree species.

The types and sizes of trees and shrubs used for nesting were very similar to those documented in other areas. A review of European studies by Cramp & Perrins (1993) found that rotten trunks or stumps of birch spp. were favoured, but Black Alder, Common Elder and willow spp. and conifers were also used regularly, as in the current study. In more recent studies from Britain, mostly in Nottinghamshire (central England) but also southern Scotland and southern England, Lewis et al. (2009a) and Stewart (2010) found that willow spp., Silver Birch and Common Elder were the most frequent nest-sites. Rustell (2015) recorded 80% of nests in willow spp., mostly in Cheshire (north-west England), with most other nests in Common Elder and Black Alder.

Willow Tit nests were overwhelmingly within a few metres of the ground in the slender trunks or stumps of young dead trees, which were abundant in the area (pers. obs.). At Amberswood Common and the Wigan Flashes the typical diameter of a nesting tree was 11 cm, which was similar to the 12 cm diameter recorded by both Lewis et al. (2009a) and Stewart (2010), with the smallest stems in all studies measuring 5-7 cm. A maximum nest height of 4 m in the current study matched that of Rustell (2015), with most nests across Europe being situated less than 3 m high (Cramp & Perrins 1993), and the average of 1.2 m in the current study matched the typical 1-2 m high reported for most other British nests (Stewart 2010).

The clear consensus from our results, and those from the various other studies, is that standing deadwood of young Silver Birch, Black Alder, willow and mature Common Elder are all key species for nest-sites, and any habitat management to benefit Willow Tits should consider these species.

Very little previous information exists for the dimensions of the nest cavities excavated by Willow Tits, but this information is important for the design of artificial nest-sites, which may be useful for monitoring and accessing chicks for ringing (Last & Burgess 2015, Parry 2017). Foster & Godfrey (1950) recorded the depth of three empty nest chambers at 18, 27 and 30 cm, while Ludescher (1973) measured 60 chambers in Germany at 9-24 cm, with an average of 15 cm, which was similar to the range of 12-22 cm and average 17 cm found at

Amberswood Common and the Wigan Flashes. There appears to be no previous data in the literature for cavity volume, and so our findings of a typical nest chamber volume of approximately half a litre (or 500 decimetres), is apparently novel.

Additionally, very little data has previously been made available on the orientation of natural nest excavations. The apparent avoidance of westerly and south-westerly directions in the current study was remarkably similar to that recorded in Germany by Ludescher (1973). Such information may be useful for positioning nest-boxes to maximise uptake by Willow Tits, and the protocol used by Last & Burgess (2015) also recommends facing nest-boxes from east to south-east, avoiding the prevailing weather across Britain from the west and south-west. It is unknown whether the orientation of nests in deadwood reflects a directional preference by Willow Tits or an influence of weather on the development of suitable soft wood for excavation, but our data support the principle of facing nest-boxes from a north-easterly through to a southerly direction to mimic natural nests.

Nest-site competition

The nest trees used by Willow Tits were substantially smaller than those used by the closely related Marsh Tit *Poecile palustris* in Britain, which typically nests in pre-existing cavities in live wood of 10-30 cm diameter, at a higher average height of 3 m above the ground (Broughton et al. 2011). This demonstrates the Willow Tit's adaptation, as a nest excavator, to marginal wooded habitats, such as early successional woodland and scrub, where natural cavities for nesting are scarce but young standing deadwood can be common. The wooded vegetation at the Amberswood Common and Wigan Flashes complex was only 30-35 years old at most, similar to the preferred stands of 10-25 years old identified by Lewis et al. (2009b).

The adaptation of Willow Tits to early successional or marginal woodland in Britain appears effective in avoiding competition with the similar Marsh Tit, which is largely excluded from such habitats by its inability to fully excavate a cavity. This inability restricts Marsh Tits to more mature woodland of at least 50 years old, where natural cavities have developed in larger trees (Broughton 2012, see also Ludescher 1973). However, despite Siriwardena (2004) finding no correlation in national population trends of Willow Tits and potential nest competitors, Willow Tits in the current study suffered high levels of nest-site competition from Blue Tits, which are present or common in most wooded habitats across Britain and have experienced a 24% increase in the UK from 1967-2016 (Woodward et al. 2018). Blue Tits also require pre-existing cavities for nesting (Cramp & Perrins 1993), but appear more adaptable than Marsh Tits, and took possession of almost a fifth of Willow Tit nests in our study area, with approximately half of the Willow Tits being evicted at the excavation stage and the remainder during the laying or incubation stages. In 75% of observed conflicts during excavation, Willow Tits were unable to prevent Blue Tits taking over their nest cavity. This forced the Willow Tits to delay breeding and begin excavating a new nest elsewhere. The frequency of eviction of Willow Tits by Blue Tits in our study area is much higher than previously reported in most other British studies. Rustell (2015) recorded only 7% of nests being taken over by Blue Tits or Great Tits, and a 45% success rate for Willow Tits in repelling any competitors and maintaining control of the cavity. Meanwhile, Lewis et al. (2009a) and Stewart (2010) recorded no instances of Willow Tits being evicted by other tits. However, Last & Burgess (2015) commented that Willow Tits in their Wiltshire nest-boxes had been usurped by Blue Tits, Coal Tits *Periparus ater*, Marsh Tits and occasionally Great Tits, all during the excavation, nest-building or laying stages, but gave no further details of its frequency. The highest rates of eviction were found in a now extinct population in western Scotland, where Maxwell (2002) reported 67% of Willow Tit nests being lost to eviction, mostly by Blue Tits.

The high rate of nest-cavity loss to Blue Tits and, to a lesser extent, Great Tits, seems to be largely a British phenomenon. As early as the 1930s, Johnston (1936) commented on the “menace” of Blue Tits and Great Tits that commonly evicted Willow Tits from nests in Cumbria. During a detailed study in Germany, however, Ludescher (1973) found that Marsh Tits evicted Willow Tits from 13% of 62 newly excavated nests, with none being taken over by Great Tits or Blue Tits, although the latter were known to take over nests occasionally.

Yet, in Finland, Orell & Ojanen (1983) recorded no instances of other tits evicting Willow Tits from a sample of 152 nests, although 3% of nests were taken over by Pied Flycatchers *Ficedula hypoleuca* or Eurasian Wrynecks *Jynx torquila*. It is likely that Blue Tits and Great Tits were much less abundant in the woods of Finland and Germany than in Britain, and this may underlie the much higher rate of nest-site competition in some areas.

Nest predation

The rate of nest loss due to predation (27%) was in line with the 20-35% reported in other studies of predominantly natural nest-sites in Britain (Lewis et al. 2009a, Stewart 2010, Rustell 2015). Predation accounted for 60% of all nests losses in the study area, and the major predator of Willow Tit eggs and chicks appeared to be the Great Spotted Woodpecker, which destroyed up to a quarter of all nests. Determining the precise number of nests attacked by Great Spotted Woodpeckers was hampered in many cases by the difficulty in distinguishing nests predated by this species from those attacked by Grey Squirrels. While field signs (gnaw marks) indicated that Grey Squirrels were almost certainly responsible for some predation, this species has not previously been recorded anywhere as a nest predator of Willow Tits, and generally appears a rare predator of hole-nesting tits (Broughton et al. 2011). As such, interpretation of these results required caution, so as not to under- or overestimate the relative impact of Grey Squirrels or Great Spotted Woodpeckers, and further work is planned in the study area to use nest cameras to confirm the identity of nest predators.

Nevertheless, even accounting for some predation by Grey Squirrels, the potential range of predation rates attributed to Great Spotted Woodpeckers in this study was similar to other areas of Britain, where predation by this species varied from 17% to 25% of natural nests (Lewis et al. 2009a, Stewart 2010, Rustell 2015). The stronger walls of wooden nest-boxes may offer more protection from woodpecker predation, compared to the thin bark and soft wood of many natural nests; Last & Burgess (2015) reported no losses to predators from 39 nest-boxes, and in the current study none of the 13 occupied nest-boxes were predated (although 38% were lost to Blue Tits). Elsewhere in Europe, Great Spotted Woodpeckers predated 61% of Willow Tit nests in Germany (Ludescher 1973) but only 3% of nests in Finland (Orell & Ojanen 1983).

Breeding success

The proportion of nest losses suffered by Willow Tits in the current study (45%), and in other recent studies in Britain (26%, Stewart 2010; 30%, Lewis et al. 2009a; 67%, Rustell 2015), are far greater than the 18% found for British Marsh Tits, which were also mostly in natural nest-sites (Broughton et al. 2011). Little data exists for the success of other tit species using natural holes in Britain, but East & Perrins (1988) found that only 25-36% of Blue Tits and Great Tits were successful when breeding in such sites in Wytham Woods (Oxfordshire), with many losses due to flooding/soaking by heavy rain. Willow Tit cavities may be relatively safe from such flooding, due to being in solid deadwood, often in short stumps, that are safe from stemflow running down trunks from the tree canopy after heavy rain.

Our results using the Mayfield (1975) method to account for bias of observation time showed that, once it had reached the egg stage, a typical Willow Tit nest in the study population then had a 65% probability of fledging at least one chick. This probability of nest survival is lower than the 73% calculated for British Marsh Tits (derived from Broughton et al. 2011), which have suffered an 80% population decline compared to the 92% decline of the Willow Tit (Woodward et al. 2018), hinting that a lower probability of nest survival may be related to a more severe decline in population abundance.

The daily mortality rate (0.011) of Willow Tit nests was virtually identical to the 0.011-0.012 reported for 72 nests in Nottinghamshire, southern Scotland and southern England during 2005-2008, but these were lower than the averages of approximately 0.014-0.019 derived from British Trust for Ornithology Nest Record Scheme (NRS) data, collected from Willow Tit nests across Britain from 1948 until 2003 (Stewart 2010). This NRS data translated into a probability of success of only 50% for a typical Willow Tit nest containing eight eggs, similar to that in our study; this suggested that nest predation rates were historically higher when

Willow Tits were more widespread, but are now lower in the remaining habitat and regions where populations have survived to date.

Where nests were successful, Willow Tits appeared highly productive, hatching almost all of their eggs and rearing almost all of their chicks to produce a relatively large number of fledglings (approximately eight young per nest). This absence of significant brood reduction indicated that chick starvation or sufficient food provisioning by the adults was not a problem in the study area, in contrast to Finland (Orell & Ojanen 1983) where the major causes of nest losses were chick starvation and desertion, which was probably weather-related.

Successful first nesting attempts produced one more fledgling, on average, than repeat attempts. This reduction was associated with slightly smaller clutches and lower hatching success or survival of nestlings in repeat attempts. Ludescher (1973) and Orell & Ojanen (1983) also reported a decline in clutch size and the number of fledglings produced from nests as the breeding season progressed, and this may be related to the birds adjusting their clutches to a decline in available insect food with the advancement of spring (Perrins 1979).

When considering this reduction in the number of fledglings produced from later nests, the high proportion of first breeding attempts that were lost to eviction by Blue Tits and destruction by predators may have important implications for Willow Tit productivity, by reducing the number of potential fledglings that the population might produce if more pairs were able to breed at their first attempt. However, the higher rate of predation and eviction among first attempts meant that repeat attempts were actually more successful on average, and produced a greater number of fledglings per breeding attempt. Repeat nesting attempts after an initial failure were therefore important in contributing at least a third of the fledglings produced during the study period. Nevertheless, these pairs would likely have produced significantly more young if their first attempt had not failed due to Blue Tits, Great Spotted Woodpeckers or other predators.

Conclusions

The results from the study of a large sample of nests on the Amberswood Common and Wigan Flashes complex are an important contribution to the understanding of Willow Tit breeding ecology, and can help to inform efforts to conserve the species in Britain. The study highlights the high productivity of successful nests in the early successional woodland, scrub and wetland habitat mosaic on former industrial land in northern England, which is increasingly representing a core habitat refuge for Willow Tits.

However, the results also highlight that the Willow Tits' potential productivity was reduced due to a high number of failed nesting attempts, which were caused by interference from Blue Tits and predation by Great Spotted Woodpeckers and, potentially, Grey Squirrels. These three species of competitor and predator have all increased in national or local abundance in Britain as the Willow Tit has declined over recent decades (Massimino et al. 2018, Woodward et al. 2018), which may have had some effect on Willow Tit breeding success.

Further work to monitor the breeding success, and confirm the identity of nest predators, would be valuable throughout the remaining British range of the Willow Tit. Conservation of the species' existing habitat in north-west England and beyond is also essential, and management objectives should aim to maintain and expand the current habitat mosaic while attempting to find solutions to minimising the high levels of nest competition and predation.

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TABLES

Table 1. Sample sizes and location of Willow Tit nests by year at study sub-sites on the Amberswood Common and Wigan Flashes complex. See Fig. 1 for a map of locations.

Site	2013	2014	2015	2016	2017	2018
Amberswood Common	4	11	15	7	13	19
Scotsman's Flash		1	6	4	10	2
Pearson's Flash		2	1		4	1
Low Hall LNR				5	2	4
Westwood Flash						2
Horrock's Flash		4	1			
Turner's Flash			1	2		1
Other		1		3		2
Total	4	19	24	21	29	31

Table 2. Characteristics of Willow Tit nest cavities in natural sites on the Amberswood Common and Wigan Flashes complex. Entrance height is the height above the ground of the bottom rim of the entrance hole. The entrance hole diameter is the maximum value (the greater of the vertical or horizontal measurements).

Characteristic	Mean	s.d.	Minimum	Maximum	*n*
Entrance height (m)	1.2	0.5	0.5	4.0	103
Entrance diameter (mm)	29.1	4.8	20.0	38.0	51
Chamber depth (cm)	17.1	2.4	12.5	22.0	50
Chamber volume (cm^3)	567	87	425	765	50
Tree diameter at hole (cm)	10.9	4.4	6.5	26.0	40

Table 3. Clutch size (number of eggs) and number of fledglings in Willow Tit nests in first and repeated (after initial failure) breeding attempts, and for all nests including those where the attempt status was unknown. Fledgling values are derived from successful nests only.

Nesting attempt	Mean	s.d.	Minimum	Maximum	*n*
Clutch size					
First	8.7	1.0	7	10	55
Repeated	8.3	1.0	6	9	23
All	8.4	1.1	4	10	97
Fledglings					
First	8.7	1.0	6	10	36
Repeated	7.6	1.4	5	9	24
All	8.2	1.2	5	10	68

FIGURE LEGENDS

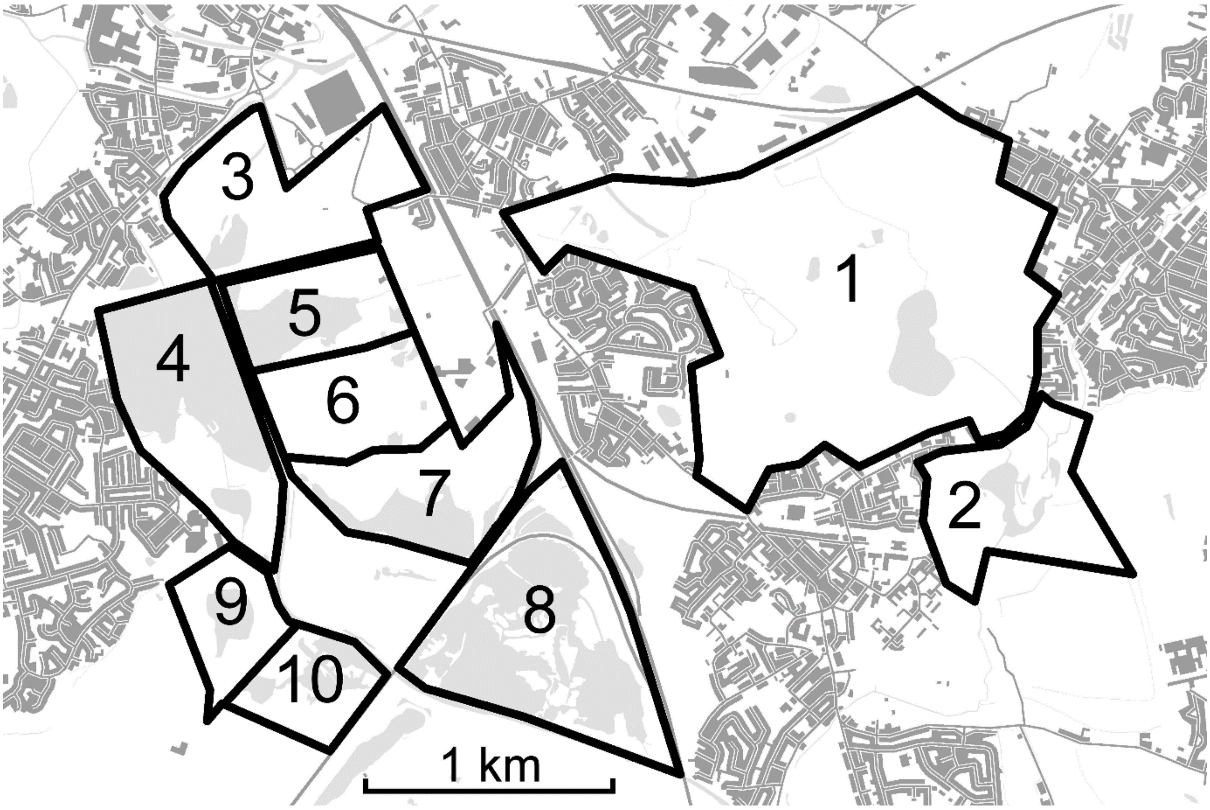

Figure 1. Study area at the Amberswood Common and Wigan Flashed Complex, on the southern outskirts of Wigan in north-west England. Mid-grey features are residential and industrial buildings, roads and railway lines, light grey areas are open water, and heavy dark lines delineate the study sub-sites: 1 Amberswood Common; 2 Low Hall Local Nature Reserve; 3 Westwood Flash; 4 Scotsman's Flash; 5 Pearson's Flash; 6 'the old tip'; 7 Turner's Flash; 8 Horrock's Flash; 9 Ochre Flash; 10 Bryn Marsh. Contains Ordnance Survey data © Crown copyright and database right 2018.

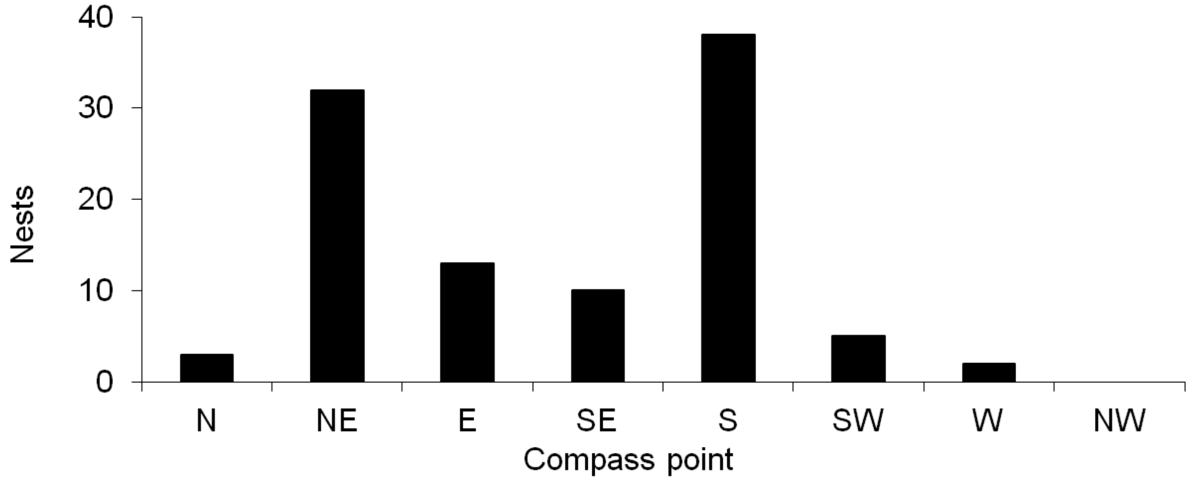

Figure 2. Orientation on the principal compass points of 103 Willow Tit nest cavities in natural deadwood.

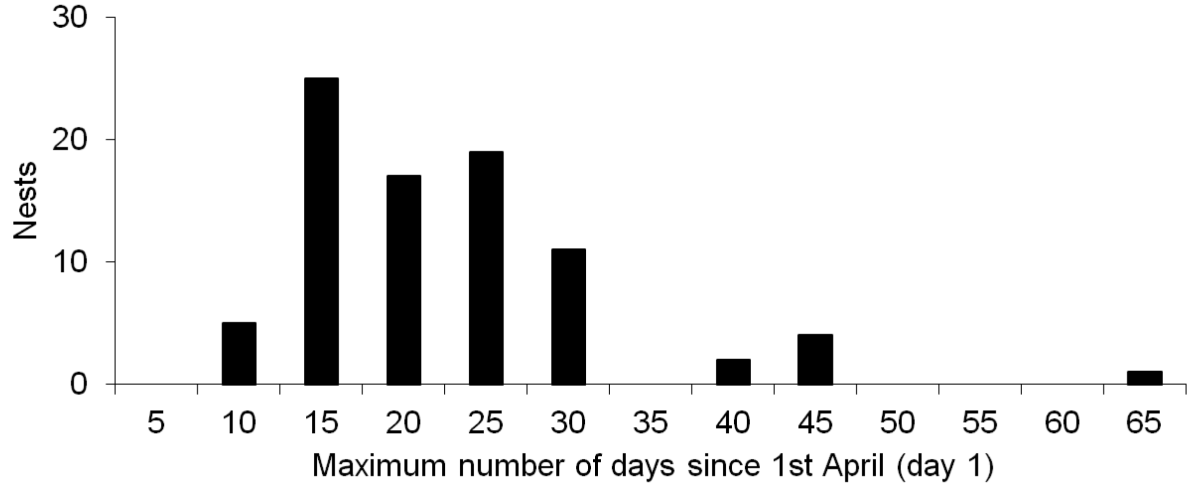

Figure 3. Timing of laying (first egg date) for 84 Willow Tit nests (first and repeated breeding attempts) in 2013-2018, grouped into periods of five days from the beginning of April (where April 1st = 1).

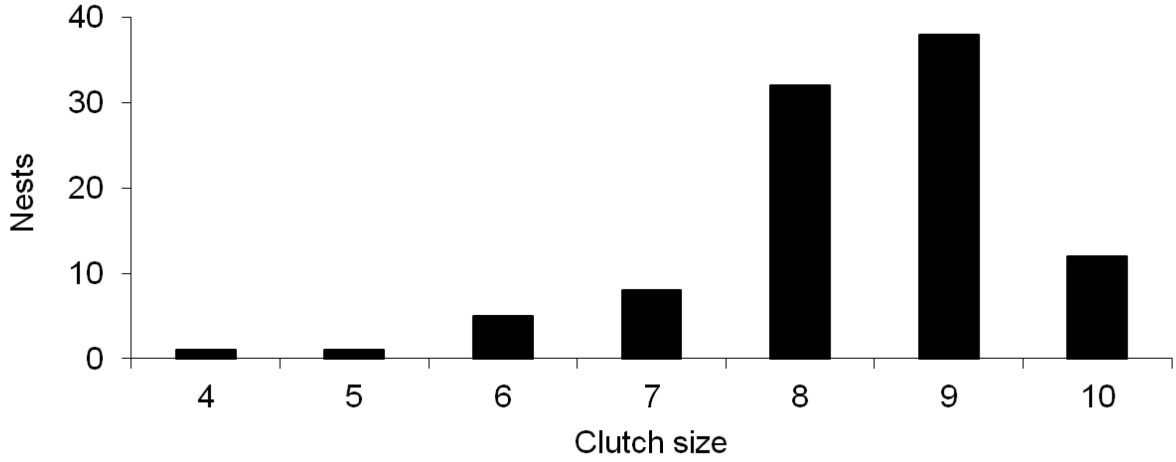

Figure 4. Frequency distribution of clutch sizes among 97 Willow Tit nests, derived from 55 first breeding attempts, 23 repeated (second) attempts and 19 unclassified attempts during 2013-2018.

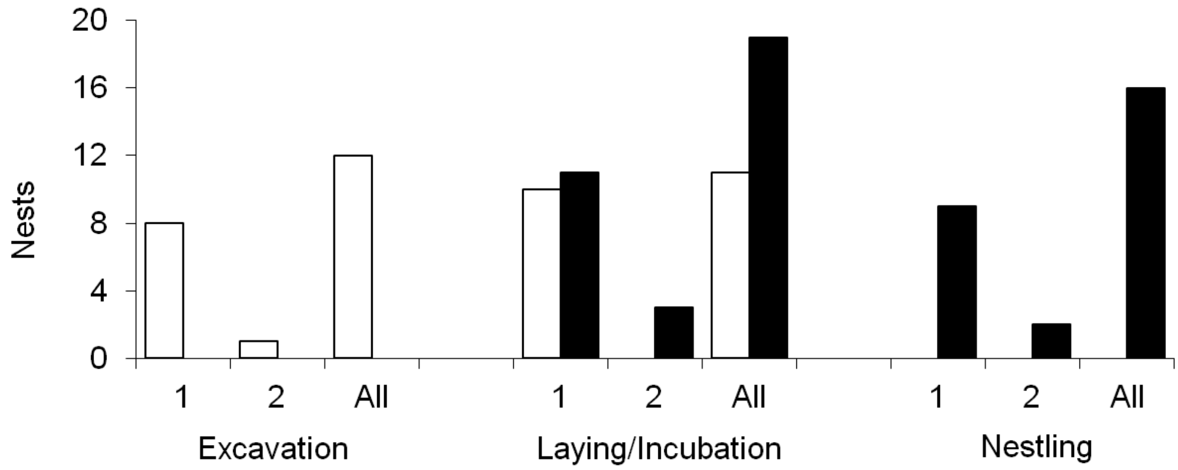

Figure 5. Known losses of Willow Tit nests due to eviction by Blue Tits (open bars) or attack by a predator (black bars) at the nest excavation, egg (laying/incubation), and nestling stages of the breeding cycle, with values shown for 1: first breeding attempts (*n* = 39 losses from 75 nests), 2: repeated breeding attempts (*n* = 6 losses from 30 nests), and all breeding attempts (*n* = 58 losses from 128 nests).