

Male Blue Tits *Cyanistes caeruleus* choose early-leaving tree species during spring dawn chorus

TIMOTHY H. PARKER¹* and HEIDI TILLIN²

¹Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK and ²School of Biological Sciences, University of Wales – Bangor, Deiniol Road, Bangor, Gwynedd, LL57 2UW, UK, current address Dove Marine Laboratory, School of Marine Science and Technology, University of Newcastle-upon-Tyne, Cullercoats, North Shields, NE30 4PZ, UK

Capsule Blue Tits sang their dawn song in trees that provided greater concealment.

Aims To determine if dawn singing Blue Tits select trees that increase their concealment.

Methods We compared the timing of leaf growth initiation in Blue Tit song-post trees to the average timing of leaf growth initiation for other tree species within 25 m of the song-post.

Results Most Blue Tits (96%, $n = 23$) sang from tree species that begin leaf growth earlier than the average tree available within 25 m. If males singing in Hawthorns *Crataegus monogyna* were excluded, 92% ($n = 13$) sang from earlier leaving trees.

Conclusion Dawn singing Blue Tits select perches that offer greater concealment.

In many bird species, individuals sing in distinct bouts during which other activities are avoided. In cases where signalling is the primary activity, the spatial position chosen by an individual may not be the same as that used when foraging (Hunter 1980, Atienza & Illera 1997, Beck & George 2000). Instead, we expect the individual to choose a location that balances its need to broadcast a signal to intended recipients with the potential costs of eavesdroppers (e.g. predators) detecting and exploiting the signal.

Song-post location is typically considered in the context of sound propagation. Birds may choose elevated or exposed perches to broadcast their song with minimal vegetation- or ground-induced attenuation, or to facilitate hearing their neighbours' songs with minimal sound attenuation (Dabelsteen *et al.* 1993, Mathevon *et al.* 1996). In species whose behaviour conforms to these predictions, the risks of exposure to predators are presumably outweighed by the benefits of less impeded signal propagation. However, in some species, perch choice by singing males may be constrained by selection for greater concealment. For instance, male Great Tits *Parus major* often sing from Hawthorn (see Table 1 for plant

scientific names) trees, possibly because perching there renders them less conspicuous (Hunter 1980).

Most male Blue Tits *Cyanistes caeruleus* produce a song lasting approximately 20–60 minutes each dawn for the two to three weeks of their mate's fertile period (Poesel *et al.* 2001, T. Parker unpubl. data). During this dawn song, they vocalize as frequently as once every two or three seconds and they do not engage in other activities such as foraging (T. Parker unpubl. data). Because these distinct dawn song bouts occur after pair formation and are limited to the female's fertile period, this signal presumably plays a role in mate guarding or in attracting other fertile females for extra pair copulation (Mace 1989, Kempenaers *et al.* 1997), though a role in territorial defence has also been proposed (Slagsvold *et al.* 1994). A male's dawn song typically ends when his mate emerges from the nest cavity (or box) and copulates with him (T. Parker unpubl. data).

Unintended signal recipients might also see or hear a male Blue Tit during his dawn song. Although Blue Tit song consists primarily of pure-tone notes, males usually also incorporate multiple series of broad-frequency harmonic 'scold'-type calls in their dawn song (Bijnens & Dhondt 1984). Hawks can readily detect and locate these broad frequency vocalizations (Jones & Hill 2001), and Sparrowhawks *Accipiter nisus* are a documented predator of Blue Tits (Geer 1982,

*Correspondence author. Present address: Department of Biology, Whitman College, 345 Boyer Ave, Walla Walla, WA 99362, USA. Email: parkerth@whitman.edu

Dhondt *et al.* 1998). Several lines of evidence indicate that Blue Tits rely on dense vegetation as cover from Sparrowhawks and other predators when foraging (Morse 1973, Todd & Cowie 1990, Allen & Harper 2000, Telleria *et al.* 2001, Walther & Gosler 2001). Thus male Blue Tits may also choose song-post locations that lower predation risk through increased visual concealment.

We asked if the locations chosen by Blue Tits for dawn singing during the peak spring singing period offered greater than average concealment. To address this question, we assessed the relative leafing phenology of trees in the vicinity of males' singing locations to determine whether they preferentially sang from earlier-leafing species that would provide greater concealment. We also explored the role of Hawthorns for singing male Blue Tits. This was the most frequently chosen song-post species, and so we wished to know whether its role as a preferred tree in which to seek cover in all seasons biased the results of our test of the spring leafing phenology hypothesis.

METHODS

We noted dawn song locations of male Blue Tits during spring 2004 in Wytham Woods near Oxford, UK (1°20'W, 51°47'N). Individual males were observed by one of five observers for one entire dawn song produced during their mate's fertile period. All songs considered here were observed between 14 April and 5 May, the period encompassing first-nest egg-laying for nearly all Blue Tits at Wytham in 2004. We include in our analyses only songs produced during a dawn period without rain. Many males ($n = 23$, whose precise dawn song locations were successfully noted) produced most or all of a given dawn song from one tree. In cases where we could unambiguously identify a single tree from which a male sang >50% of his song on the morning we observed him, we labelled that tree a primary song-post.

When the singing season was over, we returned to each labelled primary song-post tree and to the surrounding trees within a 25 m radius. For each tree we identified the species and measured the crown width at its widest point and perpendicular to its widest point. If a tree was part of a monospecific thicket, we took these measurements for the thicket as a whole. This allowed us to produce a rough estimate of the amount (in two dimensions) of potential singing substrate available to each Blue Tit male by tree species.

We ranked each tree species detected in our surveys based on date of first leafing, with rank 1 assigned to evergreen species, rank 2 to the earliest leafing deciduous species, rank 3 to the second deciduous species to leaf, and so on to the last species to leaf. Because some species have very similar leaf-out timing, we grouped similar species at the same rank. We decided that a ranking system with six classification levels, including one for dead trees with no leaves, captured most of the variation while accounting for the fact that many species were quite similar to each other (Table 1). Our estimates of leaf-out dates were based primarily on data available from the UK Phenology Network (UKPN), and were consistent with our casual observations at Wytham. The UKPN defines first leafing as the date that the first leaf on an adult tree (>30 years old) is completely open and recognizably in the shape of a fully developed leaf. Our initial ranking was based on the UKPN England-wide median first-leaf dates averaged across 1998–2003, though we also considered the earliest median date from these six years and the latest median date from these six years when choosing which species to place in the same rank bins. For species not included in this data set, we used relative rank data from the first half of the 20th century in

Table 1. Leafing phenology ranking of the tree species found in the vicinity of Blue Tit song-posts in Wytham Woods.

Rank	Tree species
1	White Cedar <i>Thuja occidentalis</i>
1	Spruces <i>Picea</i> spp.
1	Ivy <i>Hedera helix</i>
2	Hawthorns <i>Crataegus</i> spp.
2	Horse Chestnut <i>Aesculus hippocastanum</i>
2	Elder <i>Sambucus nigra</i>
3	Willows <i>Salix</i> spp.
3	Common Hazel <i>Corylus avellana</i>
3	Field Maple <i>Acer campestre</i>
3	Silver Birch <i>Betula pendula</i>
3	Orchard Apple <i>Malus domestica</i>
3	Sycamore <i>Acer pseudoplatanus</i>
4	Blackthorn <i>Prunus spinosa</i>
4	Common Alder <i>Alnus glutinosa</i>
4	European Beech <i>Fagus sylvatica</i>
5	Poplars <i>Populus</i> spp.
5	Common Oak <i>Quercus robur</i>
5	Common Ash <i>Fraxinus excelsior</i>
6	Dead

A rank of 1 indicates evergreens, 2 indicates those species first to leaf out, 5 indicates the last species to leaf out, and 6 indicates dead trees. Ivy occasionally covers large parts of trees. As three Blue Tits sang primarily from within Ivy, we consider it a distinct tree type for our analyses.

Worcestershire, also provided by UKPN. For species included in both data sets, relative ranks were similar and so use of the older data was justified. We lumped species at the same rank when species had reversed ranks in different data sets or showed similar leafing dates within data sets. Based on UKPN data from recent years, average leaf-out dates for species grouped at rank 2 were before or near 1 April, those species at rank 3 began leafing in mid-April, species at rank 4 first leafed in mid- to late April, and those at rank 5 began leafing towards the end of April or even early May. Because leaf growth rate may vary, the first-leaf date may not predict differences in leaf density between species later in leaf development. Although precise rank order of tree species by leaf-out dates varies somewhat depending on the data used, and might vary with different methods of determining leaf phenology rank, by lumping species of similar rank into the same rank bin, the influence of such differences on analysis outcomes is minimized.

In 2004, the peak Blue Tit dawn song period lasted from mid-April to early May. During this period, our casual observations indicated that differences in leafing among tree species were dramatic and led to differences in concealment for singing Blue Tits depending on the tree species from which they sang. Through the duration of the study, Blue Tits in early-leafing species such as hawthorns (leaves well developed prior to the beginning of the study) were much more difficult to see than those in a late-leafing species such as Common Oak (leaves still only partially developed at end of study). Thus if Blue Tit males seek concealment when singing, we expected them to sing from trees species that began leafing earlier in the season.

To test our hypothesis, we asked if the chosen song-post tree species had a higher or lower leafing phenology rank than the mean rank of trees available in the vicinity. For each 25-m-radius circle, we multiplied the width by the length for each canopy measurement and summed these values among all the tree species within a leafing phenology rank to produce a value approximating the area of cover for each rank. We then generated a mean leafing phenology rank for each 25-m-radius circle by multiplying the rank by the cover sum for that rank, adding these values together for all ranks, and dividing this value by the sum of all cover values:

$$\begin{aligned} &\text{Mean phenology rank per circle} \\ &= \{\sum [\text{rank (area covered)}]\} / \{\sum (\text{area covered})\} \end{aligned}$$

For each circle, we then asked whether the singing location was in a tree of higher or lower phenology rank than the mean rank for that circle. Finally, we conducted a sign test to determine if the trend in choosing trees with earlier or later leaf-out than the per-circle mean was significant ($P = 0.05$) across our sample of Blue Tit males.

Amount of leaf cover may not be the only factor influencing selection of song-post trees. The tree most frequently sung from in our study was Hawthorn, a tree preferred by Wytham tits as cover even in winter when leaves are absent (Walther & Gosler 2001), presumably because of the protection offered by its spines and densely grouped, stiff branches. Thus, we asked an additional question. Among those Blue Tit males that did not sing from Hawthorn, was there a tendency to sing from earlier-leafing species? We asked this question to determine if a relationship between tree leafing and song-post selection was independent of the already-observed relationship between Blue Tits seeking cover and Hawthorns. We employed the same statistical methods as those described above, but we excluded the ten Hawthorn song-post territories.

RESULTS

For 23 male Blue Tits, we identified a single tree from which they sang >50% of their dawn song. We observed that Blue Tits produce dawn song from many of the tree species found in Wytham. However, certain canopy cover types, particularly Hawthorn and Ivy, were used very often despite being only a small proportion of overall canopy coverage (Table 2).

We found that Blue Tit males tended to sing in tree species that were further along in their leafing phenology than the average available in the vicinity (22 of 23 song-posts had lower phenology ranks than the mean available: sign test, $P < 0.00001$). When Blue Tits singing from Hawthorns were excluded, there was still a strong trend to sing from tree species further along in their leaf growth (12 of 13 song-posts had lower phenology ranks than the mean available: sign test, $P = 0.003$). These patterns are also evident when comparing the mean phenology rank of song-post trees to the weighted mean phenology ranks of the trees within 25 m of the song-post.

DISCUSSION

Male Blue Tits appear to choose locations of higher than average concealment for their dawn song.

Table 2. Tree species available for use as primary song-posts by Blue Tits, the approximate percentage canopy coverage by these species in the sampled areas surrounding song-posts, the number of birds expected to use a given tree species if song-posts were selected proportional to availability, and the observed number of birds using a given tree species.

Tree species	Canopy cover (%)	Number of birds using this species	
		Expected	Observed
Hawthorns	7.3	2	10
Ivy	0.6	0	3
Field Maple	2.6	1	2
Willows	3.0	1	2
Orchard Apple	0.4	0	1
Common Ash	23.7	5	1
Beech	0.1	0	1
White Cedar	0.3	0	1
Common Hazel	31.6	7	1
Spruces	0.5	0	1
Common Oak	14.0	3	0
Sycamore	6.4	1	0
Silver Birch	4.3	1	0
Blackthorn	2.8	1	0
Elder	1.8	0	0
Dead	0.4	0	0
Horse Chestnut	0.2	0	0
Poplars	< 0.1	0	0

Hawthorn, a particularly early-leafing species, was the most frequent song-post species. Even after excluding Blue Tits that sang from Hawthorns, we still found a strong trend towards singing in earlier-leafing trees, further supporting our hypothesis that leafing phenology influences Blue Tit song-post choice. Of course this does not rule out the likely possibility that the protection afforded by the dense branching and spines of the Hawthorn is an important factor promoting its use by dawn-singing Blue Tits.

Is it possible that Blue Tits' song-post choice is influenced by foraging opportunities rather than concealment? Several lines of evidence suggest this is unlikely. First, Blue Tits do not forage during their dawn song (T. Parker, pers. obs.). Second, Blue Tits frequently move among trees when foraging (T. Parker, pers. obs.). The cost of flying from their song-post tree to forage after the chorus presumably is similar to the costs of moving among trees at other times. Third, Blue Tits have a well-documented preference, across many habitats, for foraging in Oaks, especially in spring (Gibb 1954, Clamens 1990, Atienza & Illera 1997). However, none of the Blue Tits we observed chose Oak as a primary song-post, despite the fact that

Oak was the third most common tree, with approximately 15% of the canopy coverage on our survey plots.

Singing in dense vegetation or closer to the ground impedes signal propagation, and thus should be selected against, all else being equal (Dabelsteen *et al.* 1993, Mathevon *et al.* 1996). A study in Spain found that Blue Tits tended to forage in Oaks, but that they often chose tall Umbrella or Stone Pines *Pinus pinea* as song-posts (Atienza & Illera 1997). This was interpreted as evidence that the birds were choosing the highest available perches to maximize the propagation of their vocal signal. However, it might also be that Blue Tits were choosing the densest cover from which to sing. Although in the Spanish study tits avoided a short tree providing dense cover, the Prickly Juniper *Juniperus oxycedrus*, it may be that if provided with two trees of dense cover, the taller will be chosen. Although we did not note the height from which Blue Tits sang in our study, they certainly did not always choose the highest perch. We frequently observed Blue Tits singing most of their song well below the canopy. In fact, the Hawthorns used so frequently by Blue Tits in this study were mostly sub-canopy trees. It may be that at our study location, selection to sing from a high location is countered by selection to maximize concealment, while at the Spanish site both selection pressures favour the same song-post choice.

Blue Tits' choice of greater concealment is likely to be influenced by predation risk. Sparrowhawks are a common predator of tits in Wytham Woods (Geer 1982, Gosler *et al.* 1995) and they may be less likely to detect and capture a Blue Tit well hidden by foliage. Also, dense cover can act to reduce heat loss from birds in inclement weather (Grubb & Greenwald 1982), and we cannot rule out the possibility that trees with more advanced leafing were sought by dawn singing Blue Tits for such protection.

ACKNOWLEDGEMENTS

N. Aspey, J. McMahon and R. Whitfield helped observe dawn songs. We are grateful to Oxford University for providing access to the study site. T.H.P. thanks B. Sheldon and S. Griffith for the invitation to join their Blue Tit studies. T. Sparks at the UK Phenology Network kindly provided further data beyond those available on the web. K. Kosciuch, D. Harper and an anonymous reviewer provided helpful suggestions regarding the manuscript. T.H.P. was supported by a US National Science Foundation International Research Fellowship (INT-0202704).

REFERENCES

- Allen, A.J. & Harper, D.G.C.** 2000. Foraging Blue Tits *Parus caeruleus* may trade-off calorific value of food items and distance from cover. *Bird Study* **47**: 232–234.
- Atienza, J.-C. & Illera, J.-C.** 1997. Tree species selection to perform singing and foraging behaviour of Great and Blue Tits: A trade-off between food gathering and territorial behaviour? *Bird Study* **44**: 117–119.
- Beck, M.J. & George, T.L.** 2000. Song post and foraging site characteristics of breeding Varied Thrushes in northwestern California. *Condor* **102**: 93–103.
- Bijnens, L. & Dhondt, A.A.** 1984. Vocalizations in a Belgian Blue Tit, *Parus c. caeruleus*, population. *Le Gerfaut* **74**: 243–269.
- Clamens, A.** 1990. Influence of oak (*Quercus*) leafing on Blue Tits (*Parus caeruleus*) laying date in Mediterranean habitats. *Acta Oecol., Int. J. Ecol.* **11**: 539–544.
- Dabelsteen, T., Larsen, O.N. & Pedersen, S.B.** 1993. Habitat-induced degradation of sound signals – quantifying the effects of communication sounds and bird location on blur ratio, excess attenuation, and signal-to-noise ratio in Blackbird song. *J. Acoust. Soc. Am.* **93**: 2206–2220.
- Dhondt, A.A., Kempenaers, B. & Clobert, J.** 1998. Sparrowhawk *Accipiter nisus* predation and Blue Tit *Parus caeruleus* adult annual survival rate. *Ibis* **140**: 580–584.
- Geer, T.A.** 1982. The selection of tits *Parus spp* by Sparrowhawks *Accipiter nisus*. *Ibis* **124**: 159–167.
- Gibb, J.A.** 1954. Feeding ecology of tits, with notes on Treecreepers and Goldcrest. *Ibis* **96**: 513–543.
- Gosler, A.G., Greenwood, J.J.D. & Perrins, C.** 1995. Predation risk and the cost of being fat. *Nature* **377**: 621–623.
- Grubb, T.C. & Greenwald, L.** 1982. Sparrows and a brush pile: foraging responses to different combinations of predation risk and energy cost. *Anim. Behav.* **30**: 637–640.
- Hunter, M.L.J.** 1980. Micro habitat selection for singing and other behaviour in Great Tits, *Parus major*: Some visual and acoustical considerations. *Anim. Behav.* **28**: 468–475.
- Jones, K.J. & Hill, W.L.** 2001. Auditory perception of hawks and owls for passerine alarm calls. *Ethology* **107**: 717–726.
- Kempenaers, B., Verheyen, G.R. & Dhondt, A.A.** 1997. Extrapair paternity in the Blue Tit (*Parus caeruleus*): female choice, male characteristics, and offspring quality. *Behav. Ecol.* **8**: 481–492.
- Mace, R.** 1989. The dawn chorus in the Great Tit *Parus major* is directly related to female fertility. *Nature* **330**: 745–746.
- Mathevon, N., Aubin, T. & Dabelsteen, T.** 1996. Song degradation during propagation: Importance of song post for the Wren *Troglodytes troglodytes*. *Ethology* **102**: 397–412.
- Morse, D.H.** 1973. Interactions between tit flocks and Sparrowhawks *Accipiter nisus*. *Ibis* **115**: 591–593.
- Poesel, A., Foerster, K. & Kempenaers, B.** 2001. The dawn song of the Blue Tit *Parus caeruleus* and its role in sexual selection. *Ethology* **107**: 521–531.
- Slagsvold, T., Dale, S. & Saetre, G.P.** 1994. Dawn singing in the Great Tit (*Parus Major*) – mate attraction, mate guarding, or territorial defence. *Behaviour* **131**: 115–138.
- Telleria, J.-L., Virgos, E., Carbonell, R., Perez-Tris, J. & Santos, T.** 2001. Behavioural responses to changing landscapes: Flock structure and anti-predator strategies of tits wintering in fragmented forests. *Oikos* **95**: 253–264.
- Todd, I.A. & Cowie, R.J.** 1990. Measuring the risk of predation in an energy currency field experiments with foraging Blue Tits *Parus caeruleus*. *Anim. Behav.* **40**: 112–117.
- Walther, B.A. & Gosler, A.G.** 2001. The effects of food availability and distance to protective cover on the winter foraging behaviour of tits (*Aves: Parus*). *Oecologia* **129**: 312–320.

(MS received 7 March 2005; revised MS accepted 7 July 2005)