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Calls of nestling and fledgling Marsh Tits *Poecile palustris*

Running title: Calls of nestling and fledgling Marsh Tits

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Abstract

Many knowledge gaps exist in the descriptions of the vocal repertoires of most bird species, and particularly for the calls of nestlings and fledglings. This short descriptive study presents the first sonograms and descriptions of the nestling calls of Marsh Tits in three nests, and also a previously unrecorded call of a female parent initiating begging by young chicks. A previously unrecorded defensive call by a nestling is also documented. Field observations of the calls of fledglings are also described, including the timing of the development of adult-type calls. The results show that short, simple 'peep' calls of 6-day-old nestlings developed into more complex 'begging trills' comprising clusters of several notes by day 13 after hatching. Several variant 'begging trills' appeared by day 19 (the day before fledging), and are distinctive from begging calls of closely-related species. Fledglings continued to use begging trills and also produced clear adult-type contact calls, 'pitchou' and 'chick-a-dee' calls by day 5 post-fledging. Young males were singing by 11 days post-fledging (one day after post-fledging dispersal). The results are discussed in the context of similar species, and how the increasing availability of sound recording equipment can encourage more knowledge gaps to be filled.

Introduction

The Marsh Tit *Poecile palustris* is a widespread hole-nesting passerine of mature woodland in Europe and East Asia, which is undergoing a severe population decline in Britain (Broughton & Hinsley 2015). Marsh Tits are sympatric with Willow Tits *P. montanus* across much of their ranges in Europe and Asia, and the two species have long been considered to be difficult to separate on visual appearance, even in the hand (Broughton 2009). This is especially true of the races inhabiting Britain (*P. p. dresseri* and *P. m. kleinschmidti*), which are the most alike in plumage. Some recently described plumage and morphological features have improved the identification criteria (Broughton 2009, Broughton et al. 2008, 2016, Broughton & Alker 2017), but much less attention has been given to the range of calls in both species.

57 The most common songs and calls of Marsh Tits and Willow Tits are moderately well
58 documented (Morley 1953, Ludescher 1973, Romanowski 1978, Hailman 1989, Haftorn
59 1993). Adult Marsh Tits and Willow Tits may be separated by certain species-specific
60 calls if these are heard or recorded, particularly the distinctive 'pitchoo' call commonly
61 given by Marsh Tits (Broughton 2009). Fledgling begging calls have also been
62 documented for both species, and were shown to be distinctly different (Broughton 2009).
63 The expansion of digital sound recording in recent decades, and the availability of
64 software to easily analyse and display it visually as sonograms (or spectrograms), has
65 enabled a massive increase in the number and variety of sound recordings of birds, as
66 can be found in online databases such as xeno-canto (www.xeno-canto.org). These
67 developments have expanded the documented repertoire of the Marsh Tit since Cramp &
68 Perrins (1993), to include fledgling begging calls (Broughton 2009) and the 'hissing'
69 defensive call of incubating or brooding females within the nest (Zub et al. 2017, Zhang
70 et al. 2020).
71 However, despite these advances, significant parts of the Marsh Tit's vocal repertoire
72 have still not been described, even though such gaps were highlighted several decades
73 ago by Cramp & Perrins (1993). In particular, there are still no descriptions of the begging
74 calls of Marsh Tit nestlings. As a consequence of the absence of any sonograms or
75 written descriptions, it also remains unknown how Marsh Tit nestling calls develop as the
76 chicks age, and whether they differ from the nestling calls of related species. This is
77 despite extensive studies of the nestling and post-fledging call development in the
78 closely-related Black-capped Chickadee *P. atricapillus* (Clemmons & Howitz 1990, Baker
79 *et al.* 2003), and also post-fledgling call development in Willow Tits (Haftorn 1993). These
80 studies showed that elements of adult-type calls develop gradually from a single, simple
81 call that is present from the day of hatching. Complex begging calls are present in Black-
82 capped Chickadees within around 10 days post-hatching, and persist for several weeks
83 post-fledging, but adult-type calls (e.g. alarm calls and contact calls) also begin to appear
84 within a few days of leaving the nest (Clemmons & Howitz 1990, Haftorn 1993, Baker et

al. 2003). It is likely that similar patterns occur in the development of Marsh Tit calls, but this requires confirmation.

The main aim of this paper is to provide the first detailed description and sonograms of the vocalisations of Marsh Tit nestlings, and to describe how they change over time as the chicks develop over the nestling period. I also describe a previously unreported call of a breeding female Marsh Tt in the nest, which was apparently used to stimulate begging and feeding of young (blind) nestlings, and a nestling defensive call. Finally, I also report some field observations of the calls of fledgling Marsh Tits and when they were first heard to give adult-type calls and song.

Methods

Data collection took place during the early years of a long-running study of Marsh Tits (Broughton & Hinsley 2015), and formed part of a sound recording trial that remained incomplete and unpublished. This work involved monitoring and recording calls at Marsh Tit nests in 2005 at the Monks Wood National Nature Reserve in Cambridgeshire, eastern England (52°24'N, 0°14'W). Monks Wood held 22 pairs of Marsh Tits in 2005, of which three nests were selected for vocalisation studies.

Marsh Tits breed nest in small tree cavities (occasionally nest boxes: Broughton & Hinsley 2014) and typically lay 6-8 eggs in Britain, which are incubated by the female for around 13 days. Chicks are in the nest for around 17-21 days after hatching, and are fed by both parents until fledgling. The family group of both parents and the fledglings remain together in or near the breeding territory for around 10-15 days, before the juveniles become independent and disperse. Dispersed juveniles then quickly establish their own home-ranges, and also form pairs, and defend these against other Marsh Tits (Broughton & Hinsley 2015).

These studied nests, one in a natural tree-hole and two in nestboxes, were chosen for ease of access and contained a total of 22 nestlings in broods of 8, 7 and 7. Nests were discovered and monitored from nest-building or incubation, and nestlings were fitted with

113 unique combinations of colour rings when they were 11 days old (Broughton et al. 2010,
114 2011).
115 Studies of the ontogeny of nestling calls in the Black-capped Chickadee (Clemmons &
116 Howitz 1990, Baker *et al.* 2003) detected successive phases in call development, with
117 simple begging calls in the first ten days of life developing into more complex calls over
118 the next seven days. Based on this, recordings of Marsh Tit nestlings in the current study
119 were made at days 6, 13 and 19 days after hatching, in order to detect the range of
120 begging calls from young nestlings, feathered nestlings, and those immediately prior to
121 fledging. Nestling calls were not recorded prior to day 6, as brooding females sat very
122 tightly on the chicks for long periods, and I was concerned to limit disturbance in the days
123 immediately after hatching.
124 Recordings were made with an Olympus Digital Voice Recorder DS-2200, with a
125 sampling frequency of 44.1 kHz and a wide-band frequency response of 0.3–8 kHz,
126 mounted next to the entrance hole of each nest. The recorder was left *in situ* during two
127 parental feeding visits at each nest on each day of recording, with begging calls of chicks
128 (and any calls of adults) being recorded at each feeding visit.
129 Sonograms of calls were produced using Spectrogram software, version 11.2 (Horne
130 2006). The individual nestling producing each call could not be identified, although
131 overlapping call traces in the sonograms indicated that multiple chicks called and were
132 recorded during the feeding episodes. Calls were isolated on sonograms from all nests,
133 from which the frequency range and temporal duration was observed. The calls were
134 described using functional names where a clear homolog existed in the literature for
135 other *Poecile* species, although descriptive English terms were also adopted where
136 necessary.
137 The calls of the Marsh Tit broods were not captured on sound-recording equipment after
138 fledging, so no sonograms are available. However, field notes of calls were taken and
139 could show at what age colour-ringed fledglings were first heard to produce adult-type
140 calls or song, based on my field experience of adult calls and descriptions in the literature

(Morley 1953, Ludescher 1973, Romanowski 1978, Broughton 2009). Some of these fledged juveniles were also subsequently sexed using wing length measurements or behaviour (Broughton et al. 2010, 2016).

The fledged broods were observed over periods of 1 hour between 09:00 and 14:00 hours (GMT), daily until independence and post-fledging dispersal. Two further fledged broods (of 10 and 7 birds) were also observed in 2007, again from fledging until independence. All five of the broods fledged at the same age (day 20), but the timing of dispersal varied at between 10 and 16 days post-fledging. The calls of any newly-independent juveniles found after dispersal were also noted and transcribed up to 40 days of age.

Results

Nestling calls at day 6

Sonograms of 52 begging calls of 6-day-old nestlings were isolated, comprising nine, 15 and 28 calls per nest. The spectrographs showed a single, repeated call of very short mean duration (Fig. 1, Table 1). The call consisted of a variable single-frequency band, single- or double-peaked chevron note on the spectrograph, with a frequency range of 6.5-8 kHz. The calls appeared to be delivered at approximately 0.5 s intervals (assumed to be per chick), and were audible up to a metre in range when I approached the nest. To the human ear, these calls resembled a rhythmic, variable squeak. This vocalisation appeared very similar to the ‘peep’ call described by Clemmons & Howitz (1990), and was labelled as such. On one occasion the ‘peep’ calls were elicited by a ‘squawk’ call (Clemmons 1995) given by the female parent on arrival (Fig. 2). On the other five occasions, begging calls appeared to have been elicited by the movement of a parent on arrival at the nest, as no call was given by the adult.

Nestling calls at day 13

Twenty-two calls were isolated on sonograms on day 13, comprising eight, five and nine calls per nest. There was considerable development in the acoustic structure of the begging call by day 13, which now consisted of a cluster of multiple notes that descended in frequency (Fig. 3). The notes displayed multiple-frequency bands combined with rapid frequency modulation, and were termed 'begging trill', analogous to the 'begging seep', 'begging dee' or 'tee-ship' calls of Black-capped Chickadee nestlings (Clemmons & Howitz 1990, Baker et al. 2003).

At around 0.3 s, the average duration of the full begging trill call was three times longer than the peep call given at day 6 (Table 1). The begging trill was transcribed as a rapid, squeaking *sur-didud*, with audible emphasis on the initial note/syllable.

Later in the day, when one of the broods was removed from the nest for ringing (banding) with leg-rings, for later identification, one chick gave a harsh '*cherrrh!*' call when it was handled.

Nestling calls at day 19

Thirty-one individual calls were identified at day 19, comprising nine, 10 and 12 per nest. The trisyllabic begging trill call was still the primary vocalisation among nestlings at day 19 (Table 2), although the mean duration was slightly longer than at day 13 (Table 1). Greater variation in the begging trills could also now be detected in all nests. A more excited trisyllabic call, emitted when an adult bird first arrived with food, had equal emphasis and peak frequency across all three notes, and showed increased complexity in the frequency modulation (Fig. 4). This variant of the begging trill call lacked a sequential drop in pitch, and was transcribed as a strident evenly-pitched *sur-didit*. Some calls lacked the terminal note of the standard trisyllabic begging call, being transcribed as *sur-did*.

A third variant contained four notes, again with equal peak frequency across all components, and showing short-duration multiple-frequency bands with irregular modulations, fused with sharp chevron-shaped elements that covered a wide frequency

196 range (Fig. 4). This call had a highly sibilant quality, being noted as a trilling *sissisissud*,
197 and was somewhat reminiscent of the contact calls of the Eurasian Treecreeper *Certhia*
198 *familiaris*. Begging trill calls at day 13 and 19 were audible up to 6 m from the nest cavity.
199
200 Calls of Marsh Tit fledglings
201 All nestling begging calls recorded at day 19 (the day before fledging) were audibly
202 detectable from all broods throughout the post-fledging period until independence and
203 dispersal at day 30-36 (10-16 days after fledging). Begging trill calls were accompanied
204 by rapid wing fluttering and gaping when an adult approached.
205 Begging trills were the only calls heard from fledglings for the first 3-4 days after leaving
206 the nest, the one exception being a 2007 brood that scolded the observer with
207 rudimentary 'chick-a-dee' alarm calls (Hailman 1989) at day 21 (the day after fledging).
208 This call consisted of imperfect and somewhat squeaky 'pitchou' and 'dee' notes, which
209 is the Marsh Tit analog of the generic chick-a-dee call in *Poecile* species ('pitchou-dee'
210 and variants in adults, Broughton 2009).
211 From day 5 post-fledging, the vocal repertoire of all fledged broods was extensive, with a
212 variety of adult-type calls given in recognisable contexts. The first contact calls ('sip'), and
213 clear 'pitchou' calls were detected at this stage and were audibly similar to those of adults
214 (Morley 1953, Ludescher 1973, Romanowski 1978). 'Chick-a-dee' calls were common,
215 along with churring alarm or mobbing calls (a variable number of 'dee' notes strung
216 together), although calls tended to be a little slurred or disjointed compared to adults.
217 Self-feeding with insects was first observed on day 7 post-fledging, and the 'freeze'
218 response to an aerial threat (Morley 1953) was first observed on day 4.
219 Subsong (Morley 1953, Haftorn 1993), a quiet and often extensive sequence of warbling
220 song-type notes, was first heard from three newly-independent male juveniles at 31 days
221 of age (day 11 post-fledging and day 1 post-dispersal). 'Gargle' calls (a 'bubbling' jumble
222 of notes) were heard from several fledglings in a brood at day 35, the day prior to
223 dispersal (day 15 post-fledging), amid high levels of aggression between siblings that

included threat postures and combat (Cramp & Perrins 1993). The ‘gargle’ call, variously termed the ‘fighting call/song’, ‘attack call’ or ‘aggressive call’ throughout the *Poecile* genus (Hailman 1989), is strongly associated with antagonistic encounters.

True song was first heard from two newly-independent male juveniles at day 31 (day 11 post-fledging and day 1 post-dispersal). Another juvenile male was producing full song at day 33 (day 13 post-fledging and day 2 post-dispersal). Singing was common among virtually all independent juvenile males (where sex was known) by 38 days of age, in all instances being accompanied by antagonistic behaviour towards other adults or juveniles, including displacement, chasing, posturing and combat (Cramp & Perrins 1993, Broughton et al. 2010). Known juvenile females were not observed singing or giving gargle calls.

Discussion

The sonograms recorded during this trial at the Monks Wood nests are the first recorded examples of the nestling calls of Marsh Tits. The general developmental sequence of the nestling vocalisations was similar to the ontogeny of calls in the Black-capped Chickadee (Clemmons & Howitz 1990, Baker *et al.* 2003), Willow Tit (Haftorn 1993) and Long-tailed Tit (Sharp & Hatchwell 2006), with a simple ‘peep’ call of young nestlings developing into a complex begging call in older nestlings and fledglings, and adult-type calls developing soon after fledging.

The high-frequency ‘peep’ call of 6-day-old Marsh Tits appears very similar to descriptions and sonograms for small nestlings of other tits (Clemmons & Howitz 1990, Cramp & Perrins 1993, Baker *et al.* 2003). Calls were not recorded for younger nestlings, but in Black-capped Chickadees the ‘peep’ calls appear from the day of hatching (Clemmons & Howitz 1990, Baker *et al.* 2003), and this may be similar in Marsh Tits. In Black-capped Chickadees these calls consisted of ‘simple peeps’ for first 4-6 days after hatching, which are individual notes with a single peak in the frequency. Simple peeps are gradually replaced by ‘modulated peeps’ from around day 4-6 post-hatching, which

become dominant until around day 9-10. Modulated peeps have multiple peak frequencies in a single note, and an increasingly multi-band frequency. As such, the 'peep' calls recorded in 6-day-old Marsh Tits may have been at the transition between simple and modulated peeps, with some calls appearing to have be simple, with a single peak frequency (Fig. 2), and others showing more complexity with a double peak (Fig. 1). The 'squawk' call of the female parent on entering the nest appears to have been directed at the nestlings, to alert them to her arrival and elicit them to beg. This call has not previously been recorded in Marsh Tits, and perhaps only in Black-capped Chickadees among the parids (Clemmons 1995). The squawk call is similar to a very short version of the defensive 'hissing call', used by Marsh Tits and other tits to repel predators, consisting of a broad frequency 'white noise' sound (Zub et al. 2017, Zhang et al. 2020). A hiss-type call has also previously been reported from 15-day-old Marsh Tit nestlings in response to a perceived threat (Broughton 2005). In the current study we additionally recorded a second defensive call, the '*cherrrh!*' distress call given by a 13-day-old nestling when it was handled for ringing/banding. This second call has been termed the 'squeal', and has been documented for 12-day-old Black-capped Chickadees and Boreal Chickadees *P. hudsonicus* in the same context as for Marsh Tits, i.e. when nestlings were removed from the nest and handled during ringing/banding (McLaren 1976, Clemmons & Howitz 1990). This is the first record of the squeal call in Marsh Tits, and it sounded similar to the descriptions and sonograms for the chickadee species: a harsh, wide-frequency call lasting several milliseconds. As such, this confirms that Marsh Tit nestlings give both of the defensive calls recorded for Black-capped Chickadees (hisses and squeals; Clemmons & Howitz 1990), which may be common to the wider *Poecile* genus.

However, a striking feature of this study was how very different the begging calls of older Marsh Tit nestlings (and fledglings, see also Broughton 2009) are from those reported for other parids, both in sonograms and descriptions (Ficken *et al.* 1978, Gaddis 1985, Clemmons & Howitz 1990, Cramp & Perrins 1993, Haftorn 1993, Dahlstein *et al.* 2002,

Baker *et al.* 2003, Sharp & Hatchwell 2006). As such, the begging calls of older nestlings and fledglings of Marsh Tits appear diagnostic for species identification.

In particular, compared to the begging calls of young Willow Tits, and also Black-capped and Boreal Chickadees *P. hudsonicus*, the Marsh Tit begging trills lacked the long, wide-band 'dee' type notes present in these other species, and sounded much more rapid, trilling and sibilant.

Adult-type calls appeared to develop rapidly among the fledgling Marsh Tits at just 3-4 days after leaving the nest (23-24 days of age), and an extensive vocal repertoire seems to have been in place by independence and dispersal at around day 31-36 after hatching. This is broadly similar to vocal development and dispersal in the Willow Tit (Haftorn 1993) and Black-capped Chickadee (Clemmons & Howitz 1990, Baker *et al.* 2003) at around day 40. Fledgling Great Tits (*Parus major*) also produce some adult-type calls almost immediately after leaving the nest at day 16-22, attaining independence 8-15 days post-fledging (Hinde 1952, Gompertz 1961, Cramp and Perrins 1993). Long-tailed Tits similarly produce adult calls only a few days after fledging (Sharp & Hatchwell 2006), although there is little information for other tits.

Haftorn (1993) showed that family break-up and dispersal in Willow Tits coincided with the development of song and 'gargle' vocalisations, and aggression between siblings, and my observations were broadly similar for Marsh Tits. Black-capped Chickadees, in contrast, develop their 'fee-bee' song shortly after fledging and well before dispersal (Baker *et al.* 2003), although the 'gargle' call was not well developed until just before dispersal. It seems likely that these vocalisations, used in territorial aggression and disputes, is a pre-requisite for dispersal, as independent Marsh Tits can be defending a new home-range the very next day (Broughton et al. 2010).

Holleback (1974) documented increasing parental aggression towards fledgling Black-capped Chickadees that peaked just prior to dispersal, and concluded that parental aggression was responsible for initiating family break-up. This hypothesis was not supported by observations during Haftorn's (1993) Willow Tit study, nor in my

observations of Marsh Tits. The idea of parental aggression instigating juvenile dispersal is also rejected by Nilsson & Smith's (1985) and Nilsson's (1989) work on Marsh Tits, which showed very low levels of aggression between family members. Indeed, Haftorn (1993) proposed that the late development of aggressive song and 'gargle' calls was adaptive in maintaining family coherence during the fledglings' post-fledging dependence on their parents.

Instead, Haftorn (1993) noted that it was contact, alarm and scolding calls that developed quickly after fledging, as supported by my observations of Marsh Tits here. These calls would be most beneficial to recent fledglings by maintaining family cohesion and warning of predators.

Clemmons & Howitz (1990) and Baker *et al.* (2003) found that the adult 'chick-a-dee' call of the Black-capped Chickadee develops from the begging calls of nestlings, while Sharp & Hatchwell (2006) found similar origins for some adult calls of the Long-tailed Tit. Sonograms of adult Marsh Tit calls (Ludescher 1973, Romanowski 1978, Cramp & Perrins 1993, Broughton 2009) also revealed some similarities with features of the nestling begging calls recorded in this study.

In particular, the narrow chevrons featuring rapid frequency modulation and covering a wide frequency range, present in the begging trill calls of older nestlings, appear structurally similar (on visual inspection) to notes in adult 'chick-a-dee' and 'pitchou' calls used in territorial and antagonistic situations. It seems likely, therefore, that the 'chick-a-dee', 'pitchou' and allied calls of adult Marsh Tits may also be derived from the begging calls, as shown for the Black-capped Chickadee.

Further study is necessary to understand the detailed development of vocalisations in the Marsh Tit, and so far there has been no comprehensive documentation of its full vocal repertoire. The chick-a-dee call system of *Poecile* species, which is shared by Marsh Tits, has been shown in Black-capped Chickadees and Carolina Chickadees *P. carolinensis*, to be a sophisticated recombinant system of communication, with different combinations of notes conveying different detailed information, similar to language (Hailman & Ficken

1986, Soard & Ritchison 2009, Freeberg & Lucas 2012). This sophisticated communication appears to be related to complex social structures among the birds (Freeberg 2006), although British Marsh Tits seem to have a smaller social network of close relationships (Broughton et al. 2015), similar to British Coal Tits *Periparus ater* (Broughton et al. 2019).

Nevertheless, there is still much to discover about Marsh Tit communication, and documenting unrecorded parts of the vocal repertoire, such as in this study, is an important step. The greater availability of better (and cheaper) sound-recording equipment and software since this small trial was conducted means that producing sonograms has become relatively straightforward for those willing to conduct the fieldwork. As with nest recording (e.g. Parry & Broughton 2018), sound recording is therefore an area of study where those with enough time and dedication can make significant contributions to ornithology and fill many long-standing knowledge gaps.

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References

Baker, M.C., Baker, M.S.A. & Gammon D.E. (2003) Vocal ontogeny of nestling and fledgling black-capped chickadees (*Poecile atricapilla*) in natural populations. Bioacoustics **13**, 265-296.

Broughton, R.K. (2005) Hissing display of incubating Marsh Tit and anti-predator response of young. British Birds **98**, 267.

Broughton, R.K. (2009) Separation of Willow Tit and Marsh Tit in Britain: a review. British Birds **102**, 604-616.

Broughton, R.K., Hinsley, S.A. & Bellamy, P.E. (2008) Separation of Marsh Tit *Poecile palustris* from Willow Tit *Poecile montana* using a bill criterion. Ringing & Migration **24**, 101-103.

Broughton, R.K. & Hinsley, S.A. (2014) A nestbox trial for British Marsh Tits *Poecile palustris*. Ringing & Migration **29**, 77-80.

Broughton, R.K. & Hinsley, S.A. (2015) The ecology and conservation of the marsh tit in Britain. British Birds **108**, 12-28.

Broughton, R.K., Hill, R.A., Bellamy, P.E. & Hinsley, S.A. (2010) Dispersal, ranging and settling behaviour of Marsh Tits *Poecile palustris* in a fragmented landscape in lowland England. Bird Study **57**, 458-472.

Broughton, R.K., Hill, R.A., Bellamy, P.E. & Hinsley, S.A. (2011) Nest-sites, breeding failure and causes of non-breeding in a population of British Marsh Tits *Poecile palustris*. Bird Study **58,** 229-237.

Broughton, R.K., Bellamy, P.E., Hill, R.A. & Hinsley, S.A. (2015) Winter social organisation of marsh tits Poecile palustris in Britain. Acta Ornithologica **50,** 11-21.

Broughton, R.K., Alker, P.J., Bellamy, P.E., Britton, S., Dadam, D., Day, J.C., Miles, M. & Hinsley, S.A. (2016) Comparative biometrics of British Marsh Tits *Poecile palustris* and Willow Tits *P. montana*. Ringing & Migration **31**, 30-40.

Broughton, R.K. & Alker, P.J. (2017) Separating British Marsh Tits *Poecile palustris* and Willow Tits *P. montana* using a new feature trialled in an online survey. Ringing & Migration **32**, 43-49.

Broughton, R.K., Maziarz, M., Hinsley, S.A. (2019) Social structure of Coal Tits *Periparus ater* in temperate deciduous forest. Journal of Ornithology **160,** 117-126.

Clemmons, J. & Howitz, J.L. (1990) Development of early vocalizations in the chick-a-dee call in the Black-capped Chickadee, *Parus atricapillus*. Ethology **86**, 203-223.

Clemmons, J.R. (1995) Vocalizations and other stimuli that elicit gaping in nestling Black-capped Chickadees (*Parus atricapillus*). The Auk **112**, 603-612.

Cramp, S. & Perrins, C.M. (eds) (1993) The Birds of the Western Palearctic Vol. VII. Oxford, UK.

Dahlstein, D.L., Brennan, L.A., McCallum, D.A. & Gaunt S.L.L. (2002) Chestnut-backed Chickadee (*Poecile rufescens*). In: The Birds of North America (ed. Poole, A. & Gill, F.): No. 689. The Birds of North America, Inc., Philadelphia, PA.

Ficken, M.S., Ficken, R.W. & Witkin, S.R. (1978) Vocal repertoire of the Black-capped Chickadee. The Auk **95**, 34--48.

Freeberg, T.M. (2006) Social Complexity Can Drive Vocal Complexity: Group Size Influences Vocal Information in Carolina Chickadees. Psychological Science **17,** 557-561.

Freeberg, T.M. & Lucas, J.R. (2012) Information theoretical approaches to chick-a-dee calls of Carolina chickadees (*Poecile carolinensis*). Journal of Comparative Psychology 126, 68–81.

Gaddis, P.K. (1985) Structure and variability in the vocal repertoire of the Mountain Chickadee. Wilson Bulletin **97,** 30--46.

Gompertz, T. (1961) The vocabulary of the Great Tit. British Birds **54**, 369-417.

Haftorn, S. (1993) Ontogeny of the vocal repertoire in the Willow Tit *Parus montanus*. Ornis Scandinavica **24**, 267-289.

Hailman, J.P. (1989) The organization of major vocalisations in the Paridae. Wilson Bulletin **101**, 305-343.

Hailman, J.P. & Ficken, M.S. (1986) Combinatorial animal communication with computable syntax: Chick-a-dee calling qualifies as "language" by structural linguistics. Animal Behaviour **34,** 1899–1901.

Hinde, R.A. (1952) The behaviour of the Great Tit (*Parus major*) and some other related species. Behaviour **Supplement 2**, 1-201.

Holleback, M. (1984) Behavioral interactions and the dispersal of the family in Black-capped Chickadees. Wilson Bulletin **86**, 466--468.

Horne, R. (2006) Audio spectrum analysis. http://www.visualizationsoftware.com/gram.html

Ludescher, F.B. (1973) Sumpfmeise (*Parus palustris* L.) und Weidenmeise (*P. montanus salicarius* Br.) als sympatrische zwillingsarten. Journal für Ornithologie **114**, 3-56. (In German)

McLaren, M.A. (1976) Vocalizations of the Boreal Chickadee. The Auk **93**, 451-463.

Nilsson, J.-A. & Smith, H.G. (1985) Early fledging mortality and the timing of juvenile dispersal in the marsh tit *Parus palustris*. Ornis Scandinavica **16**, 292-298.

Nilsson, J.-A. (1989) Causes and consequences of natal dispersal in the marsh tit *Parus palustris*. Journal of Animal Ecology **58**, 619-636.

Parry, W. & Broughton, R.K. (2018) Nesting behaviour and breeding success of Willow Tits *Poecile montana* in north-west England. Ringing & Migration **33**, 75-85.

Romanowski, E. (1978) Der gesang von Sumpf- und Weidenmeise (*Parus palustris* und *Parus montanus*) – variation und function. Vogelwarte **29**, 235-253. (In German)

Sharp, S.P. & Hatchwell, B.J. (2006) Development of family specific contact calls in the Long-tailed Tit *Aegithalos caudatus*. Ibis 148, 649-656.

Soard, C.M. & Ritchison, G. (2009) 'Chick-a-dee' calls of Carolina chickadees convey information about degree of threat posed by avian predators. Animal Behaviour **78,** 1447-1453.

Zhang, L., Liu, J., Gao, Z., Zhang, L., Wan, D., Liang, W. & Møller, A.P. (2020) Comparative analysis of hissing calls in five tit species. Behavioural Processes **171**, 104029.

Zub, K., Czeszczewik, D., Ruczyński, I., Kapusta, A. & Walankiewicz, W. (2017) Silence is not golden: the hissing calls of tits affect the behaviour of a nest predator. Behavoral Ecology and Sociobiology 71, 79.

Table 1. Duration and frequency range of the ‘peep’ and trisyllabic begging calls of nestling Marsh Tits. Note: the contribution of individual nestlings to the sample is unknown.

Begging call	Age in days	Mean duration ± SD (s)	Frequency range (kHz)	Number of calls
‘Peep’	6	0.09 ± 0.05	6.5-8.0	52
Begging trill	13	0.27 ± 0.03	2.0-7.5	22
Begging trill	19	0.32 ± 0.04	2.0-8.0	31

Figure legends

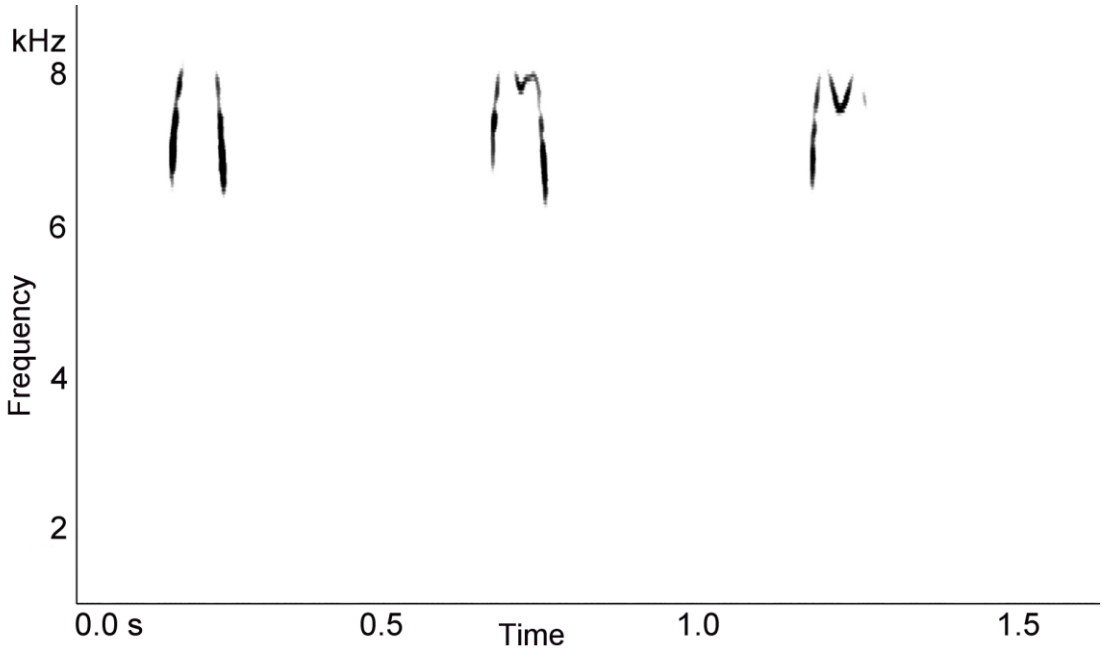
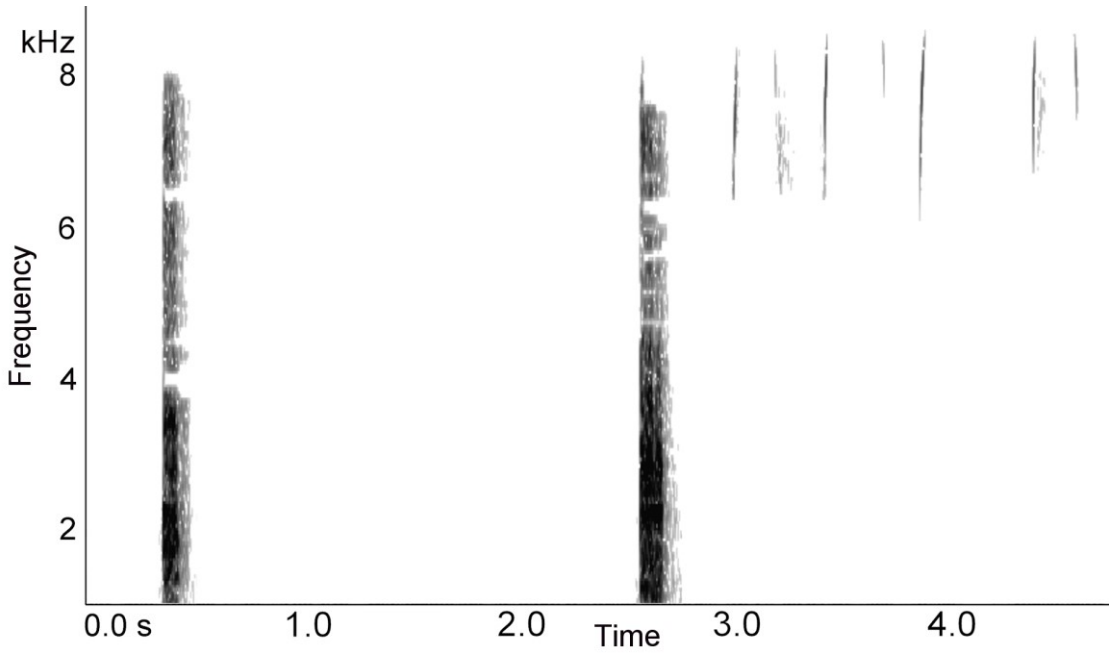


Figure 1. Simple ‘peep’ begging calls of a Marsh Tit nestling at day 6 after hatching.



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457 Figure 2. Two ‘squawk’ calls of a female Marsh Tit on entering the nest, apparently used

458 to elicit begging calls in 6-day-old nestlings.

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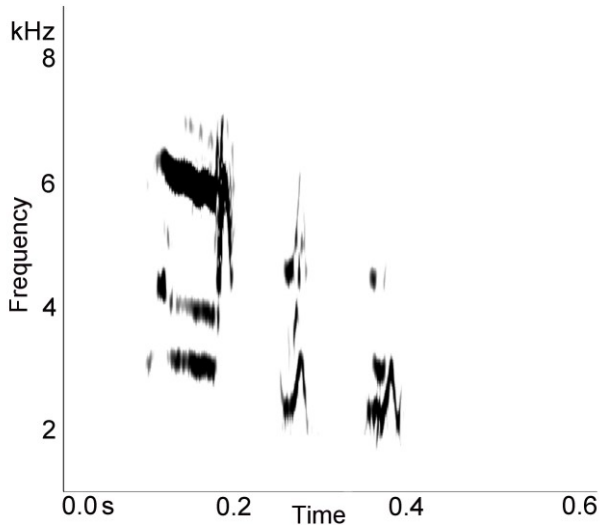

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461 Figure 3. A typical ‘begging trill’ call of a Marsh Tit nestling at day 13 after hatching,

462 phonetically-rendered as *sur-didud*. The call consists of a cluster of three notes that

463 descend in frequency.

464

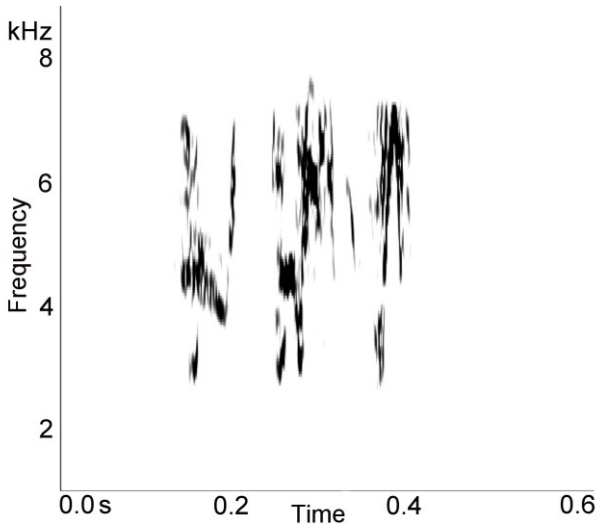

Figure 4. A variant ‘begging trill’ call of a Marsh Tit nestling at day 19, phonetically-rendered as *sur-didit*. The composite notes have a similar frequency, rather than a descending pitch (see Fig. 3).

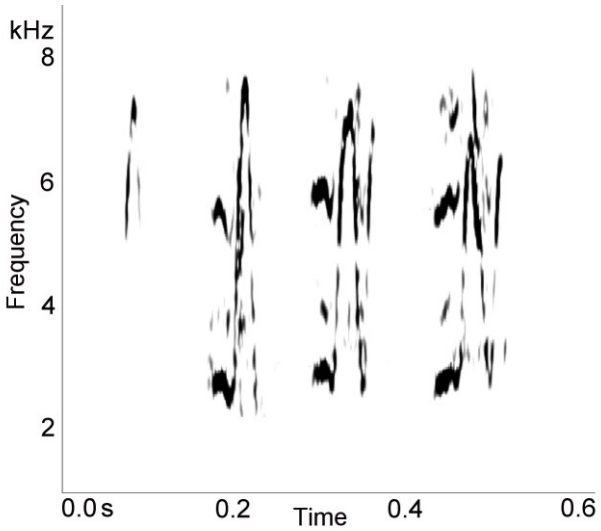

Figure 5. A variant ‘begging trill’ call of a Marsh Tit nestling at day 19 after hatching, phonetically rendered as *sisssissisud*, and having a sibilant, trilling quality.