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Overlapping breeding attempts in the Bearded Tit (*Panurus biarmicus*)

Janusz Stępniewski¹ and Lucyna Halupka^{2*}

Abstract

Background: Overlapping of successive broods is a relatively rare breeding strategy that allows individuals to make effective use of the available reproductive window.

Methods: In this paper we analyse the occurrence of overlapping breeding attempts in the Bearded Tit (*Panurus biarmicus*), a non-migratory passerine species, whose peripheral populations vary enormously in numbers.

Results: The colour-ringed population of Bearded Tits was studied in western Poland in 1990, 2012–2013 and 2015–2017. Overlapping broods were found only during years with low population sizes and low densities (1.2–3.6 pairs per 10 ha), and pairs with such broods constituted 11.1–20%. In years with higher population densities (8.7–13.44 pairs per 10 ha) overlapping broods were not recorded. Pairs started building the next (overlapping) nests when their young were 3–10 days old. They divided their duties while rearing two broods simultaneously: females were occupied only with the new clutch, while males, in contrast to other species with brood overlap, not only fed the young from an earlier brood, but also helped the females with the building of a new nest and incubation of a new clutch.

Conclusions: Laying overlapping clutches enabled pairs to shorten their average breeding cycle by 15–21 days and produce more offspring. It is possible that overlapping breeding attempts is a density-dependant strategy, enabling the population to restore after severe declines, however, alternative explanations are also possible. Future studies are needed to better understand mechanisms underlying the occurrence of this phenomenon.

Keywords: Bearded Tit, Panurus biarmicus, Overlapping broods, Breeding biology

Background

To increase fitness, many species produce multiple broods (Cramp 1992; Podulka et al. 2004). The overlapping of successive broods is a strategy that allows individuals to make better use of the available reproductive window, and has been observed most often in food specialists breeding during periods of unfavourable weather or in seasonal environments where the period of favourable breeding conditions is limited. Overlapping broods have been found in a number of species, such as owls (Barn Owl *Tyto alba*, Boreal Owl *Aegolius funereus*), Eurasian Kingfisher (*Alcedo atthis*) or Tree Creepers (*Certhia* sp.) (Zöller 1980; Glutz von Blotzheim and

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Bauer 1993; Bäumler 2000; Kucharski 2009; Béziers and Roulin 2016). In most cases of overlapping broods a male continues to care for fledglings of the first brood, whereas the female incubates the second clutch (Haftorn 1978; Verhulst and Hut 1996). Previous research has suggested that it is possible for the Bearded Tit to lay overlapping broods (Kate 1928; Koenig 1951; Feindt and Jung 1968; Spitzer 1972; Wawrzyniak and Sohns 1986), and single cases of such broods have been described (Bibby 1983; Stępniewski 1995).

The Bearded Tit (*Panurus biarmicus*) is a non-migratory, passerine bird with bi-parental care: both sexes build the nest, incubate and feed the young (Cramp 1992; Glutz von Blotzheim and Bauer 1993). It breeds in reedbeds across middle latitudes of Palearctic (Bibby 1983; Cramp 1992). In the second half of the 20th century the species colonised new breeding sites in western and northern

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Europe, resulting in range expansion. Northern populations vary in abundance and have been reported to experience declines after severe winters (Spitzer 1972; Glutz von Blotzheim and Bauer 1993). However, they may also rapidly increase following these declines, which is associated with high productivity (Björkman and Tyrberg 1982; Bibby 1983). The Bearded Tit has an elongated breeding season lasting for 104-152 days (Feindt and Jung 1968; Wawrzyniak and Sohns 1986; Stępniewski 1995, 2012), and a breeding pair may successfully produce 2-3 broods annually (Wawrzyniak and Sohns 1986; Cramp 1992; Dittberner 1996; Stepniewski 2012), exceptionally 4-5 (Kate 1928; Spitzer 1972; Wawrzyniak and Sohns 1986), producing up to 20 fledged young (Bibby 1983). Bibby (1983) suggested that another adaptation allowing for maximising the annual number of fledged young may be brood overlapping. However, this phenomenon has never been the subject of a more detailed analysis. The goals of this study were to describe the occurrence of overlapping broods in a population of Bearded Tits in western Poland, and to establish the role of each parent in caring for the offspring from both broods.

Methods

The study was carried out on two water bodies in western Poland: Łoniewskie Lake near the town of Osieczna (51°54'N, 16°41'E) and a nearby fish-pond (51°56'N, 16°41′E). The main study plot, used in all study years (1990, 2012-2013 and 2015-2017), was Lake Łoniewskie, while in 2012–2013, when the population was very small, the research was conducted also within the area of the pond. Łoniewskie Lake is a shallow, post-glacial lake of the area of 134 ha. The study plot of 25 ha was situated in the eastern part of the lake, and was covered by emergent vegetation, primarily the Common Reed (Phragmites australis), Narrowleaf Cattail (Typha angustifolia), Common Cattail (Typha latifolia), and sedges (Carex sp.). The second study plot (23.5 ha), used only in some study years, was situated on a former fish pond of 28.2 ha, overgrown by an extensive reed-bed with some admixture of cattails and sedges (for details see Koenig 1951; Perrins and McCleery 1994).

The population of Bearded Tits nesting in the area has been the subject of earlier research, and its size ranged widely between years from 1 to 34 pairs (Stępniewski 1995, 2011, 2012; Surmacki et al. 2003). However, individual marking of birds, necessary to detect the overlapping broods (Bibby 1983), was performed only during some breeding seasons. The data were gathered during six breeding seasons (1990, 2012–2013 and 2015–2017), when most breeding pairs (70–100%) were individually marked, and study effort was high and consistent throughout the breeding season. Adult birds were colourringed using a combination of one metal ring and 1-3colour rings.

The study plots were visited every 1-2 days during the breeding season. Nests were searched for from portable ladders by observing behaviour of parental birds. Breeding pairs carrying nest material were followed, as well as those feeding the nestlings or during an incubation switch. Nests were visited every 1-4 days to determine the date of laying of the first egg and to follow the nest fate. If a nest was found at the stage of incubation the first-egg date was established by backdating, assuming the incubation starts on the day of laying of penultimate egg and lasts 12 days (Feindt and Jung 1968; Glutz von Blotzheim and Bauer 1993; Stepniewski 2012). If a nest with nestlings was found, the age of the offspring was determined based on comparisons with known ageassociated features (size, degree of eye opening, feather development etc.). A brood that survived to 10 days after hatching was classified as successful (following Honza et al. 1998; Halupka et al. 2014), as the young of this age are able to leave the nest when threatened (Glutz von Blotzheim and Bauer 1993; Stępniewski 2012).

Results

Overlapping broods and population density

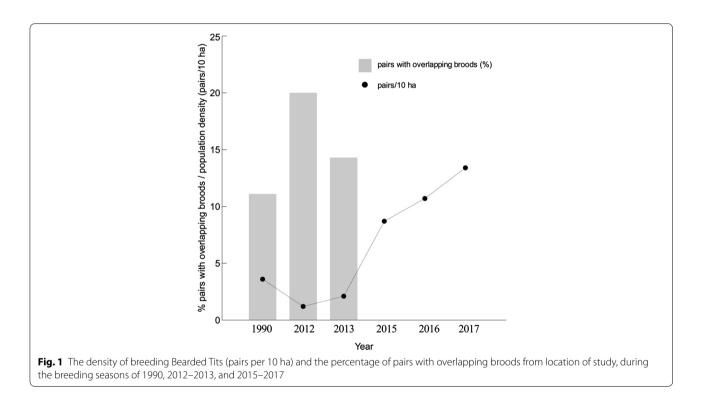
Overlapping broods were observed during three of the 6 years of our study (1990, 2012 and 2013), and they constituted 4.8–15.4% of all broods (median 10%) (Table 1). Pairs with overlapping broods made up 11.1-20% of all colour-ringed pairs (median 14.3%) in the 3 years where overlapping broods were observed (Fig. 1; Table 1). In addition, the years that overlapping broods were observed were characterised by low population sizes and hence low densities of the breeding population (1.2-3.6 pairs per 10 ha). During the remaining three study years, when population was larger and densities of breeding pairs higher (8.7-13.44 pairs per 10 ha) overlapping broods were not observed. The proportion of pairs with and without overlapping broods varied significantly between years with high and low population density (Fisher exact test, p = 0.014, $n_1 = 68$, $n_2 = 21$) (Fig. 1).

Estimation of the overlapping period

Pairs with overlapping breeding attempts started building their next nest when the young of the first nest were 3-9 days old (med=6). The first egg in the overlapping breeding attempt was laid when the young from the first nest were 8-14 days (med=10 days) of age. Assuming that nestlings spend on average 13 days in the nest, fledglings are fed for 10 days, and it takes 5 days to build a

Year	Number of ringed pairs	% of pairs with overlapping broods	Number of nests	% of overlapping broods	Breeding density (pairs per 10 ha)
1990	9	11.1	21	4.76	3.56
2012	5	20	10	10	1.23
2013	7	14.03	13	15.38	2.05
2015	17	0	23	0	8.7
2016	22	0	47	0	10.67
2017	29	0	58	0	13.44

Table 1 Breeding statistics of the studied population of Bearded Tits in six study years: number of colour-ringed pairs, percentage of pairs with overlapping broods, total number of nests of colour ringed pairs, percentage of overlapping broods, and population density



new nest (Cramp 1992), we estimate that the overlapping period was 15-21 days (med = 17.5 days).

Parental behaviour during the period of brood overlap

Observations at the overlapping breeding attempts revealed that during the overlapping period (the time when a pair was caring for two nests simultaneously) a female was occupied only with the new clutch, while a male took care for an earlier brood, but also helped the female with the incubation of a new one. Both parents were busy building a new (overlapping) nest, but males were observed building more often. Nestlings and fledglings from the first (earlier) nest were provisioned mostly by a male, while a female after laying eggs in a new nest devoted her parental effort to the incubation of a new clutch.

Discussion

Bearded Tit populations are characterised by huge changes in their numbers (Glutz von Blotzheim and Bauer 1993). Among the most important factors that may contribute to this phenomenon are adverse weather conditions, both during winter and breeding season, deficiency of food during the winter, and (locally) high water levels (Spitzer 1972; Glutz von Blotzheim and Bauer 1993; Wilson and Peach 2006; Surmacki and Stępniewski 2007). Bearded Tits compensate for this mortality through (1) laying multiple clutches throughout a long breeding season (Bibby 1983; Cramp 1992; Dittberner 1996), (2) laying two successive clutches in the same nest (Stępniewski 2003; Wilson pers. comm.), and (3) producing overlapping broods (Bibby 1983). The overlapping broods reported in this study were found in years with low population sizes, hence low population densities. Conversely, despite similar research efforts, overlapping broods were not observed during years with high densities. During the three seasons where overlapping broods were observed, the population was recovering after dramatic population declines linked to severe winter weather, characterized by low temperatures and increased, long-lasting snow cover (Kuźniak 2001; Stępniewski 2011; Stępniewski unpubl. data).

Brood overlap allows to increase the number of breeding attempts and annual number of offspring by reducing the time interval between the broods (Grüebler and Naef-Daenzer 2010). In some species overlapping broods are associated with brood desertion and mate switching (Hunt et al. 2015; Béziers and Roulin 2016). For example, in the Barn Owl double-brooded females desert their first nests and re-mate with a new individual to start a second brood, while their first male cares for the offspring from the first nest. In this way, they save time and are able to become double-brooded (Béziers and Roulin 2016). In other species females remain mated to a previous partner, and brood overlap is possible due to division of labour between mates: males usually care for the fledglings from the first nest while females lay eggs and incubate the second clutch (Haftorn 1978; Verhulst and Hut 1996). In the Bearded Tit, the females always remained with the same partners that shared parental duties between the two nests. Males not only cared for the young from first brood, which is common in species with overlapping breeding attempts (Haftorn 1978; Verhulst and Hut 1996; Grüebler and Naef-Daenzer 2010; Béziers and Roulin 2016), but also helped in nest-building which occurs very rarely in other species (Haftorn 1978), and incubated. Combining building of a new nest with other activities is often observed in the Bearded Tits, also at non-overlapping attempts: birds regularly bring nest material to nests at the incubation stage (Stępniewski unpubl. data), and build a new nest while feeding the grown-up fledglings (Bibby 1983; Stępniewski unpubl. data). We are not aware of any study reporting male incubation during the period of brood overlap. Furthermore, we have been able to find only one study documenting a relationship between population density and the occurrence of the second (and overlapping) broods, similar to this found in our population of Bearded Tits. Piping Plovers (Charadrius melodus) are usually monogamous but second broods with a new mate were found in years with male-biased sex ratio and low nesting density (Hunt et al. 2015).

Conclusions

This study revealed that Bearded Tits can shorten their average breeding cycle by 15-21 days with overlapping broods. This constitutes an important proportion of the whole nesting cycle which lasts on average 39 days (from the beginning of nest building to the end of feeding of fledglings). Therefore, it seems that overlapping breeding attempts are an effective strategy to increase the number of clutches each year and produce more young. At the same time, caring for two broods simultaneously is assumed to be costly, and some studies suggest that brood overlap may be performed only by high-quality individuals (Grüebler and Naef-Daenzer 2010). This may explain why this behaviour was observed relatively rarely in our study population. The occurrence of overlapping breeding attempts only during years with low population sizes might indicate that it constitutes a density-dependent adaptive mechanism allowing to restore populations after severe declines (Orell and Ojanen 1983; Dhondt et al. 1992; Perrins and McCleery 1994). However, it is also possible that other, density-related factors may be involved, e.g. suitable nest sites allowing for locating a new nest close to the old one may be limited if a population is large. Future studies, involving colour-ringing, are needed to better understand mechanisms underlying the occurrence of overlapping broods in the Bearded Tit.

Authors' contributions

JS designed the study, performed all the fieldwork, while LH performed statistical analyses. Both authors contributed to writing. Both authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The datasets used in the present study are available from the corresponding author on request.

Consent for publication

Not applicable.

Ethics approval and consent to participate

All the study procedures have complied with the current laws of Poland. Ringing licences have been issued by the General Directorate of Nature Protection in Poland (2012–2013) and General Director of Nature Protection and the Ministry of Environment of Poland (2015–2017).

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