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Seasonal adjustments in nest cup lining in Blue Tits *Cyanistes caeruleus*

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Nest building requires parental investment and we should expect to find trade-offs between building and other behaviours or demands. For example, species breeding in temperate zones face the seasonal shift from spring to summer and might alter their nest construction in relation to environmental conditions as the season progresses. We quantified seasonal variation in the length of the nest building period, nest mass, composition, Hen Flea *Ceratophyllus gallinae* abundance and egg production in nestbox breeding Blue Tits *Cyanistes caeruleus*. The nest building period decreased seasonally, possibly indicating individual adjustment of optimal time of reproduction. Despite this, there was no seasonal trend in overall nest mass, although nest composition did change. The mass of the nests' moss base and Hen Flea abundance showed no seasonal variation, but there was a seasonal decline in the mass of the cup lining material, suggesting that female Blue Tits selectively adjust the cup lining component of their nests to reflect increasing ambient temperatures in order to create an optimal microclimate for the developing embryos and nestlings.

Key words: reproduction, parental investment, life history, Paridae, ectoparasite, nest building

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Introduction

Nest construction is widespread amongst birds, where most species build a nest of some form in which to lay their eggs. The nest design will influence the conditions experienced by the developing embryos and nestlings, and may have important consequences for reproductive success (Collias & Collias 1984). Natural selection favours those individuals that breed at the optimal time, as the mistiming of reproduction commonly results in reduced reproductive success (Perrins 1991). Breeders may face a trade-off between timing their breeding to coincide with greatest food supply, and acquiring enough resources both to produce eggs and meet

the energy requirements of nest building. Therefore, if nest building carries costs that are traded-off against the demands of breeding within an optimal time frame, we should expect to find seasonal variation in nest characteristics, as the energetic demands of building are traded-off against subsequent egg production (Lens *et al.* 1994).

Although such variation has largely remained unstudied, McGowan *et al.* (2004) found a seasonal decline in the mass of feathers used to line the domed nests of Long-tailed Tits *Aegithalos caudatus*, which was associated with increasing ambient temperatures and a reduced need for nest

insulation. For hole-breeding passerines, available nest sites are likely to be limited and so in addition to abiotic influences such as temperature, other factors may influence nest characteristics. Hole-breeding species commonly re-use holes, and with that can come the increased risk of infection from parasites such as fleas. Hen Flea *Ceratophyllus gallinae* abundance in nestboxes has been shown to influence breeding behaviour of the hosts, with the least infected nestboxes being selected by the earliest breeding pairs (Oppliger *et al.* 1994). In this study, we investigated seasonal variation in the duration of the nest building period, nest mass and composition, Hen Flea abundance and egg production in Blue Tits *Cyanistes caeruleus*.

Methods

Blue Tits are small (11 g), single brooded, hole-nesting passerines that readily breed in man-made nestboxes (Perrins 1979). The female selects the nest site, and builds the nest which consists of a pad of moss mixed with plant material at the base of the nestbox, and a nest cup lined with fine dry grass, hair, wool and feathers (Perrins 1979). Females then produce a clutch of 8–12 eggs.

Data were collected between April and June 2006 from nestbox breeding Blue Tits in three separate, small (<30 ha) deciduous and mixed woods near Lancaster, UK (54°0'N, 02°47'W). A total of 66 uniform wooden nestboxes (width = 150 mm, depth = 150 mm, height = 200 mm, entrance hole diameter = 25 mm) were available for hole-breeding passerines to occupy, as was the case in previous breeding seasons although nests were routinely removed when breeding was completed. Nests were initiated in 53 nestboxes, and eggs were subsequently laid in 45; so only these nests were included in the study. Nestboxes were visited every fourth day from the beginning of April. Because nestboxes were not visited daily the precise initiation of nest building is unknown, but if it was not on the day of a visit it was estimated to be on the middle day between visits. The nest building period was defined as the number of days between the initiation of nest construction and the day when the first egg was laid, assuming a laying

rate of one egg per day (Perrins 1979). On the day following clutch completion, the mass (± 0.05 g), length (L; ± 0.05 mm) and width (W; ± 0.05 mm) of individual eggs was measured with an electronic balance and dial callipers, respectively. The volume of each egg was calculated using the formula $V = 0.507 \times L \times W^2$ (Hoyt 1979). Nests were collected on day 20 after hatching (± 2 days), after the nestlings had fledged, and were placed immediately into sealed plastic bags. Nests were later transferred to Tullgren funnels for 72 hours, where fleas were collected in 100% ethanol. Nests were then dried to a constant mass in a 60°C oven, and following the removal of dried faeces, nests were dissected and separated into component materials for the base and cup lining separately and each component was weighed (± 0.05 g). Data on fledging success were not considered as hatching patterns were manipulated as part of another experiment. Ambient temperature data were obtained from Lancaster University's Hazelrigg meteorological station located within 1 km of the study area. A five day running mean of the daily minimum and maximum temperatures were used in the analyses. As expected, there was a significant increase in the five-day mean temperature as spring progressed (quadratic regression: $F_{2,42} = 12.44$, $r^2 = 0.879$, $P = 0.001$). Analyses were conducted using S-PLUS v6.1 and SPSS v14.0. All tests were two-tailed and means ± 1 SD are presented. Linear and quadratic relationships were analysed using Generalised Linear Models with a normal error distribution, and linear models are presented where quadratic terms were non-significant. Models were simplified following the methods described by Crawley (1993), where step-wise procedure was used to remove non-significant terms from the full models.

Results

There was no significant correlation between the dates of initiation of nest building and dates of laying the first egg (linear regression: $F_{1,42} = 0.33$, $r^2 = 0.008$, $P = 0.568$). In this study, there was a range of 25 days between the dates when the first and last pairs commenced nest building, but

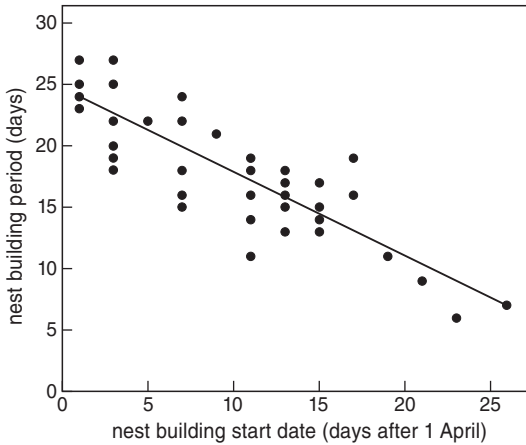


Figure 1. Relationship between the date of initiation of nest building and the duration of nest construction.

because the length of time taken to build a nest declined seasonally (Fig. 1; linear regression: $F_{1,42} = 18.42$, 42 , $r^2 = 0.715$, $P < 0.001$), the comparable range in dates of laying the first eggs was only 15 days. Whilst the period of nest construction declined with season, there was no independent effect of increasing ambient temperatures on the period of nest construction (linear regression: $F_{1,42} = 52.71$, $r^2 = 0.715$, $P = 0.802$). There was no seasonal trend in the whole nest mass (linear regression: $F_{1,42} = 0.11$, $r^2 = 0.032$, $P = 0.742$), although the composition of nests varied seasonally. The mass of the nest base showed no significant variation in relation to date (Fig. 2A; linear regression: $F_{1,42} = 0.36$, $r^2 = 0.009$, $P = 0.550$), but the mass of the cup lining declined significantly as the season progressed (Fig. 2B; linear regression: $F_{1,42} = 1.34$, $r^2 = 0.277$, $P = 0.025$). There was no significant relationship between the numbers of fleas found in nests and the date of construction (linear regression: $F_{1,42} = 1.20$, $r^2 = 0.030$, $P = 0.280$). Clutch size (quadratic regression: $F_{2,40} = 5.40$, $r^2 = 0.297$, $P = 0.025$), total clutch mass (quadratic regression: $F_{2,40} = 6.39$, $r^2 = 0.303$, $P = 0.016$) and total clutch volume (quadratic regression: $F_{2,40} = 5.81$, $r^2 = 0.306$, $P = 0.021$) all declined in relation to the initiation

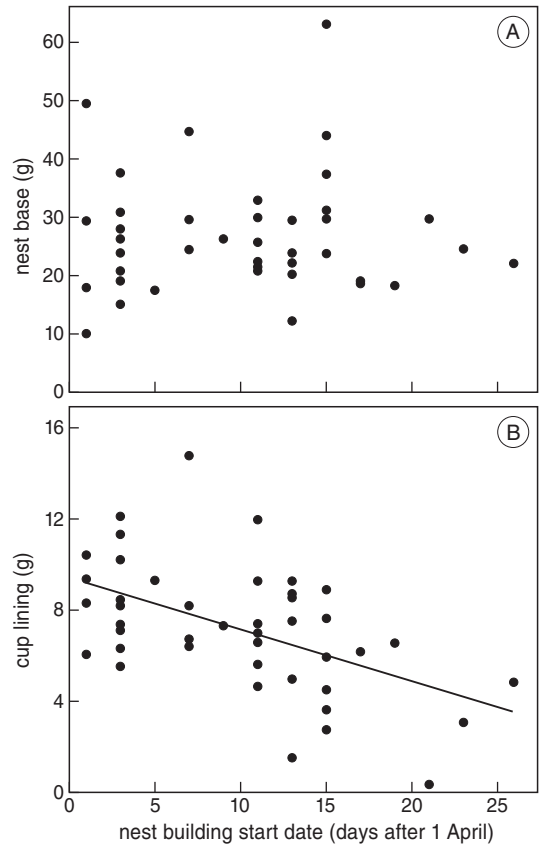


Figure 2. Seasonal variation in the mass of (A) nest base and (B) nest cup lining.

of nest building. There were no significant correlations between any other nest structure characteristics and clutch variables described above (all tests; $P > 0.05$).

Discussion

The seasonal decline in the nest building period is likely to reflect one of three non-mutually exclusive hypotheses. First, nest construction material may be limited in supply, either because earlier nesting pairs reduce its availability to later builders or it is seasonally limited, possibly resulting in smaller nests. Second, decreasing construction periods may reflect the need to synchronise the period of maximal offspring demand with

maximal prey availability. Third, the increasing ambient temperature leads to a reduction in the need for insulating material. As there was no seasonal change in overall nest mass, this suggests that the availability of nest building material was not limited through the breeding season; a finding that supports a similar conclusion by Hansell & Ruxton (2002) who experimentally demonstrated that nesting material was not in limited supply to woodland breeding birds. This suggests that the need to optimise the timing of reproduction determined the nest building period, which may indicate a mechanism by which seasonally breeding birds optimise their timing of reproduction.

Total nest mass showed no significant seasonal variation, despite the seasonal decline in the nest building period, which suggests that females might face different energetic trade-offs as the season progressed. No data currently exist concerning the energetic demands of nest building amongst hole-breeding passerines. However, in a Spanish population of Blue Tits, nest weights correlated with the health of the breeding female, as indicated by the prevalence of the parasite *Trypanosoma avium* and immunoglobulin levels (Tomás *et al.* 2006). Therefore, it might be expected that nest weight declines seasonally, given that more experienced and competent second-year Blue Tits lay earlier than first-year birds (Dhondt 1989). However, the absence of such a relationship may not be surprising, given that it has previously been shown that female Blue Tits that were handicapped, by clipping their wing feathers, did not build smaller nests than control females (Slagsvold & Lifjeld 1990). Seasonal variations in composition of nests were detected, with the mass of moss bases showing no variation with season, whilst the mass of the cup lining declined seasonally. This is similar to the pattern found in the domed nests of Long-tailed Tits (McGowan *et al.* 2004), where there was no associated reduction in the temperature within nests, which was probably attributable to increasing ambient temperatures counteracting the effect of declining feather mass. This may suggest that Blue Tits selectively adjust the cup lining material to create a microclimate that reduces the

key threats to embryo viability: chilling and water loss (Hansell 2000).

There was no seasonal trend in Hen Flea abundance within nests, which is seemingly paradoxical as earlier breeding females are expected to select those nestboxes that contain fewer adult Hen Fleas (Oppliger *et al.* 1994). However, the absence of a relationship may reflect the greater period of time in which the fleas can breed in earlier nests (Oppliger *et al.* 1994). Moreover, Hen Flea abundance may have been influenced by the number of fleas in the previous breeding season's nest, despite old nests being routinely removed at the end of each breeding season. Nest boxes have cracks and gaps for fleas to hide and we did not use any killing agents, so fleas were able to survive in unoccupied nestboxes during the non-breeding season. They have been shown to relocate from unoccupied to occupied nests early in the season, thereby eliminating any correlation between nestbox occupation and Hen Flea abundance (e.g. Oppliger *et al.* 1994). Seasonal declines in clutch and egg parameters are widely reported trends (e.g. Perrins 1979), although the absence of any significant correlations between any nest structure characteristics and clutch variables suggests that female Blue Tits were not trading off the energetic demands of nest building and egg production. In conclusion, female Blue Tits appear able to gauge environmental conditions and adjust their nest building behaviour accordingly, thereby producing an optimal microclimate for their offspring.

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SAMENVATTING

Het bouwen van een nest is een van de inspanningen die een vogel moet leveren in het broedseizoen om jongen te krijgen. Vogels zullen waarschijnlijk kosten en baten van het aandraagen van nestmateriaal tegen elkaar afwegen, en die balans zou anders kunnen uitvallen naarmate het seizoen vordert, bijvoorbeeld omdat het warmer wordt in de loop van het voorjaar. In dit artikel worden seizoensveranderingen in de nestbouw van Pimpelmezen *Cyanistes caeruleus* beschreven. De auteurs kwantificeerden de duur van de nestbouwperiode, het nestgewicht, de nestsamenstelling, de aantallen Kippenvlooiën *Cerato-phyllus gallinae* en het aantal eieren. De duur van de nestbouw nam in de loop van het seizoen af, maar dat ging niet ten koste van het totale gewicht van het nest. Wel veranderde de nestsamenstelling in de loop van het seizoen omdat minder materiaal waarmee de nestkom werd bekleed werd gebruikt. Tegelijkertijd bleven het gewicht van de mossige basis van het nest en de hoeveelheid vlooiën stabiel. Dit is een aanwijzing dat het Pimpelmeesvrouwtje selectief de bekleding van het nest aanpast wanneer de omgevingstemperatuur toeneemt. Daarmee creëert ze een optimaal microklimaat voor het uitbroeden van de eieren en het opgroeien van de jongen. (IV)

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