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ORIGINAL ARTICLE

Quantification of the effects of hatchling number on nest weight as a proxy for nest size when measured post-fledging

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Abstract
The intraspecific variability of nest construction behavior in birds underlies environmental—as well as builder-dependent drivers. To draw correct conclusions about the bird's nest construction investment, an accurate assessment of the nest size or weight is crucial. The weight of a nest depends on the material collected by the builder but may still increase over time with the presence of chicks, for instance if fecal material accumulates. Here, we provide evidence from a nesting box population of European Pied Flycatchers (*Ficedula hypoleuca*) that nest weight was positively correlated to hatchling number when weighed post-fledging. We use a novel approach of sorting, washing, and sieving the nesting material to reduce the effects of the chick-rearing phase on nest weight. Finally, we compare nest height and nest bottom thickness as indirect measurements of nest size to nest weight. Both nest height and nest bottom thickness became significantly smaller throughout the course of breeding and chick-rearing, which is why these parameters should be measured right after nest completion. While neither pre-incubation nest height nor nest weight (post-sieving) was related to number of eggs or number of hatchlings, we found a significant positive correlation between nest weight before sieving and number of hatchlings, showing the impact of chick presence on nest weight. Based on our data, we want to highlight the importance of an accurate and well-timed assessment of nest size and weight to facilitate an accurate characterization of the investment of birds into nest construction.

Keywords Nest construction · Nest size · Nest building · Pied flycatcher · Breeding · Nest box

Zusammenfassung
Quantifizierung der Auswirkungen der Nestlingszahl auf das Nestgewicht, als Indikator für die Nestgröße, bei der Erfassung nach dem Ausfliegen der Jungvögel.
Die intraspezifische Variabilität des Nestbauverhaltens von Vögeln unterliegt Umwelteinflüssen sowie Einflüssen des nestbauenden Individuums. Um korrekte Schlussfolgerungen aus dem Nestbauinvestment zu ziehen, ist es von entscheidender Bedeutung, die Nestgröße oder das Nestgewicht präzise zu erfassen. Das Gewicht eines Nestes hängt von dem gesammelten Material ab, kann aber im Verlauf der Brutsaison zunehmen, beispielsweise durch die Anwesenheit von Jungvögeln und die Akkumulation von Fäkalien. In dieser Studie zeigen wir, dass das Nestgewicht einer Nistkastenpopulation von Trauerschnäppern (*Ficedula hypoleuca*) positiv mit der Anzahl der Jungvögel korreliert war, wenn es nach deren Ausflug

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gemessen wurde. Um diesen Effekt der Jungvogelzahl auf das Nestgewicht zu reduzieren, verwendeten wir eine neuartige Herangehensweise, bei der das Nistmaterial sortiert, gewaschen und gesiebt wurde. Abschließend vergleichen wir die Nesthöhe und die Nestbodendicke als indirekten Ausdruck der Nestgröße mit dem Nestgewicht. Sowohl Nestgröße als auch Nestbodendicke wurden signifikant kleiner während des Brutgeschehens, weswegen sie direkt nach Beendigung des Nestbaus gemessen werden sollten. Während weder die Nesthöhe vor Beginn des Brutgeschehens, noch das „bereinigte " Gewicht des Nistmaterials nach dem Sieben von der Gelegegröße oder der Anzahl an Nestlingen abhängig waren, zeigte sich ein signifikanter, positiver Zusammenhang zwischen dem „unbereinigten" Nestgewicht vor dem Sieben und der Anzahl an Nestlingen, was die Auswirkungen des Brutgeschehens auf das Nestgewicht belegt. Auf Basis dieser Daten möchten wir die Notwendigkeit einer akkuraten und präzise terminierten Erfassung des Nestgewichts und der Nestgröße betonen, um das individuelle Investment in den Nestbau möglichst exakt zu erfassen.

Introduction

Avian nests are primarily built to provide a suitable environment for the development of the offspring. As a time- and energy-consuming behavior, avian nest construction is considered to be a key life-history trait that attracted greater attention in recent years (Mainwaring and Hartley 2013; Deeming and Reynolds 2015; Lambrechts and Deeming 2024). Nest size is one of the best-studied aspects of nest architecture as it is easy to measure, specifically in cavity breeding songbirds that accept and occupy nesting boxes (e.g., as reviewed in Mainwaring 2017; Lambrechts and Deeming 2024). Intraspecific variation in nest size has been studied in relation to several builder-dependent and environmental factors (e.g., Wysocki et al. 2015; Mainwaring 2017; Guan et al. 2018; O'Neill et al. 2018; Briggs et al. 2019; Der Weduwen et al. 2021). Builder-dependent (endogenous) factors include the builder's state or condition (Tomás et al. 2006; Moreno et al. 2008; Mainwaring and Hartley 2009), first-egg date (Lambrechts et al. 2012), and clutch size (Slagsvold 1989a; Álvarez and Barba 2008; Mainwaring and Hartley 2013; Lambrechts and Deeming 2024). Environmental (exogenous) influences include size of the nest-chamber in cavity breeding birds (Lombardo 1994; Wesołowski 2002; Vergara 2007; Mazgajski and Rykowska 2008; Kaliński et al. 2014; Lambrechts et al. 2014; Mainwaring 2017), weather conditions (Britt and Deeming 2011; Deeming et al. 2012; Lambrechts et al. 2016), food availability (Smith et al. 2013), nest predation pressure (Kaliński et al. 2014), or latitude (Morton 1976). For instance, in cavity-nesting species that also accept nest-boxes for breeding, birds build larger or heavier nests in larger nest-chambers, in colder, drier, and/or darker environments, or when nest predation risks are lower (e.g., see review in Lambrechts and Deeming 2024).

Independently of the underlying hypotheses on potential causes and consequences of intraspecific variation in nest architecture, an accurate assessment of the nest's dimensions is crucial to draw precise conclusions about the factors contributing to its variability.

Since the size of the cavity and/or distance from the entrance hole is known to impact nest size (Lombardo 1994; Wesołowski 2002; Vergara 2007; Mazgajski and Rykowska 2008; Kaliński et al. 2014; Lambrechts et al. 2014; Mainwaring 2017), a common approach to achieve a standardized setup in a free-living population is to provide cavity breeding songbirds with nesting boxes of standardized dimensions. Furthermore, the timing of measuring nest size or weight (pre-incubation vs. post-fledging) must be considered, since both parameters are affected by the process of incubation and chick-rearing. Nest height is expected to decrease throughout subsequent reproductive stages through the weight of eggs, chicks and breeding adult(s) in the nest (Slagsvold 1989b; Lambrechts et al. 2012, 2014). Part of this compression process is associated with the deterioration of nesting material when greenery, such as leaves, are incorporated in the nest (Lambrechts and Dos Santos 2000; Petit et al. 2002; Tomás et al. 2012). In most studies that used nesting box populations, nest size has been derived from measuring proxies such as nest height (as reviewed for Eurasian Blue Tits [*Cyanistes caeruleus*] and Great Tits [*Parus major*] by Mainwaring 2017) or from measuring parts of the nest such as the thickness of the nest's base layer (Briggs et al. 2019, in this study referred to as "nest bottom thickness"). Contrary to nest size, nest weight is expected to increase with the accumulation of various impurities within the nest, such as feces, arthropod exoskeletons, and dust from the feather growing process of the juveniles (McCarty 1999; Britt and Deeming 2011; Lambrechts et al. 2012; Dubiec and Mazgajski 2013; Cruz et al. 2016; Harnist et al. 2020; Glądalski et al. 2024; Lambrechts and Deeming 2024).

Due to these influences, nest size and weight would ideally be measured right after nest completion (Dubiec and Mazgajski 2013; Harnist et al. 2020). However, a temporal removal of the nest may disturb the incubating female or brood and harm the nest's structure. Even if some measurements can be carried out without a removal of the nest, disturbance of the incubating female or brood is unavoidable. To date studies on the quantitative effects of chick-rearing on nest size or weight are scarce (McCarty 1999; Dubiec and Mazgajski 2013; Cruz et al. 2016;

Harnist et al. 2020) but of great value, as they contribute to improve and refine methodological approaches when studying bird nests. With this study, we aim to quantify the effects of chick-rearing on nest size and weight in the European Pied Flycatcher (*Ficedula hypoleuca*) and thereby disentangle relations between nest dimensions and reproduction.

The European Pied Flycatcher is a long-distance migratory songbird frequently occupying nesting boxes (Lundberg and Alatalo 2010). Its breeding range covers great parts of Europe and extends across Morocco and Spain in the south-west to northernmost Norway and western Russia in the East. The nests of the European Pied Flycatcher are built mostly out of plant-derived materials, such as pieces of bark, leaves, or grass. The nest cup is built out of fibrous materials such as grass or animal fur or hair. To prevent the loss or destruction of nesting material, we measured nest size indirectly through the nest's height and bottom thickness right after construction had stopped (i.e., after the first egg was laid) as well as after fledging of the chicks. To minimize disturbance of the brood, nest weight was measured only after the chicks had fledged. We sorted, washed, and sieved the nesting material in the lab to remove impurities like dead juveniles, eggshells, dead insects, or feces before measuring its dry weight. We then assessed the effects of clutch size on nest size and nest weight. Additionally, we investigated potential relations between clutch size (egg and hatchling number), volumetric parameters (pre-incubation) and nest weight (post-sieving), using generalized linear models (GLMs). We expect, first, that nest weight (post-breeding) to be positively related to the number of hatchlings, as a higher number of offspring present in the nest should result in a stronger accumulation of impurities in the nest. Second, under the assumption that pre-incubation nest size as well as clutch size are positively related to female body condition, we expect that females laying larger clutches also build larger nests.

Methods

Study area

The study was carried out in southern Swedish Lapland, west of Ammarnäs (Västerbotten) at approximately 65° 58′ N, 16° 05′ E, at 500–650 m above sea level, in a subalpine birch forest. We used a local nesting box population that was established in the 1960s (Nyholm 2011). Nesting boxes of standardized dimensions (floor space 7 cm × 7 cm; distance to center of entrance hole 16 cm) allowed for comparability among nests. The boxes were hung at around 1.5 m height on birch trees and were grouped into different subplots as described in Nyholm (2011) (see electronic supplementary material Fig. S1 for a map of the study area and distribution of nest-boxes).

Field work

Nesting boxes in subplot E (empty boxes = 74) and V (empty boxes = 79) were visited every other day from the 15th of May 2023, and from the 2nd of June in subplot R (empty boxes = 71) and T (empty boxes = 44), until all nesting boxes occupied by *F. hypoleuca* contained the first egg (Fig. 1a), followed by irregular visits during the hatchling phase (Table 1). Throughout the regular visits on every other day between midday and early afternoon, we assessed first-egg date. When one egg was present in the nest, we considered

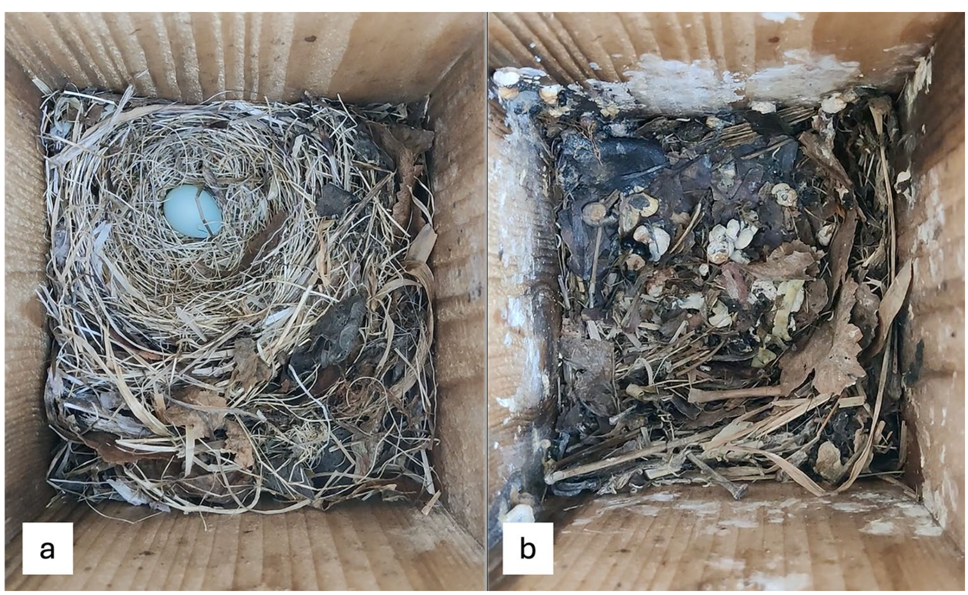

Fig. 1 Example of pre-breeding and post-fledging nest condition in box V9. **a** The photo was taken on the day of first-egg laying, i.e., right after nest completion (15th of June). **b** The photo was taken about 1 month later (19th of July) after the chicks fledged

Table 1 Overview of all parameters measured and their respective sample sizes, which were assessed during field- or lab-work of the occupied nesting boxes (containing incubating females of *F. hypoleuca*) in the respective subplots (E, V, R, and T)

Parameters	Subplot	E (**13**)	V (**11**)	R (**18**)	T (**7**)
Pre-breeding bottom thickness		13	11	0*	0*
Pre-breeding total height		13	11	0*	0*
Post-fledging bottom thickness		12	6	18	7
Post-fledging total height		11	6	18	7
Nest weight#		13	9	18	7
First egg-date		13	11	15	6
Clutch size		13	11	18	7

In sites R and T, we were unable to measure pre-breeding bottom thickness and total height of nests (marked with *). Total number of occupied nesting boxes are written in bold. #: nest weight was measured twice for each nest, once before washing and sieving and once afterward

this day as first-egg date, since females are laying one egg per day (Potti and Merino 1996; Lundberg and Alatalo 2010) mostly in the early hours of the day (Von Haartman 1990; Lundberg and Alatalo 2010). If there were two eggs in the nest, the previous day was regarded as first egg date.

We assessed the volumetric parameters when the first egg(s) were found in the nest. Volumetric parameters included the total nest height (mm) and bottom thickness (mm) (Briggs et al. 2019; Kang et al. 2022) and were measured without temporarily removing eggs or moving the nest out of the box. Total nest height was measured as distance between the upper edge of the nesting box and upper edge of the nest cup, which was then subtracted from the total box depth. Two measurements were taken from opposite sides of the nest cup and averaged. Nest bottom thickness was measured by pushing a pointy small wooden stick through the center of the nest cup and measuring the depth of the nesting material beneath the nest cup (electronic supplementary material Fig. S2).

Approximately one week after the first egg was laid, the nests were revisited to assess clutch size and to catch, ring, and measure the females. We assessed the number of hatchlings through irregular visits during the end of the breeding period, which is known to take approximately 14 or 15 days (Järvinen 1983; Laaksonen et al. 2006). The approximate age of the hatchlings was determined based on their appearance (size and molting stage) and data on hatching dates to be able to ring them between the age of 5 and 12 days (Nyholm 2011). After the breeding period, nests were checked for dead juveniles to adjust the number of actually fledged juveniles. When the nesting boxes were empty and all chicks had fledged (Fig. 1b), all nesting material was carefully removed from the nesting boxes, assuring that no material was left in the boxes or got lost during the packing of the nests. We stored the material in sealed and labeled plastic bags.

Determination of nest weight

We immediately brought the material to the lab, where it was frozen for at least four days at − 12 °C to kill any insects (Moreno et al. 2010; Loukola et al. 2014; Mainwaring et al. 2014; Briggs et al. 2019; Briggs and Mainwaring 2019). Later, we stored the material in paper bags, thawed, and dried it at 80 °C for 48 h in a drying cabinet to ease the following sorting process, as the dry nesting material did not stick together so much. We removed coarse impurities such as dead juveniles and/or larger dead insects. Afterward, each nest was soaked in a box in water to remove and solute feces which were stuck to nesting material and could not be removed from it in the previous process (Fig. 1b). After 30 min, we poured away the water, using a paper filter to prevent any loss of material. The soaked material was then put into paper bags and dried in a drying cabinet at 80 °C for at least 48 h. Afterward, the material was sieved for 10 min using a sieving tower (Retsch AS 200 basic, amplitude = 70) with five sieves of different mesh sizes (20, 10, 5, 2.5, and 1.25 mm) resulting in six fractions of different fragment sizes (Fig. 2). We found some nests to contain a lot of dust from feather growing of the chicks as well as their dissolved feces.

Data analysis

We used GLMs to test for effects of our explanatory variables (number of eggs, number of hatchlings, total nest height, and nest weight after sieving) on the dependent variables (pre-breeding total height, pre-breeding bottom thickness, reduction in nest height and bottom thickness after breeding, nest weight before sieving, and nest weight after sieving) and evaluated the models graphically via QQ and residual plots. If our dependent variables were normally distributed, we used Gaussian error distribution, and for right-skewed data, we used Poisson or quasi-Poisson for overdispersed data error-distributions. Data analysis was conducted using R version 4.1.2 (R Core Team 2020) using the package *readxl* (Wickham and Bryan 2015).

To assess whether the weight of the whole nest (hereafter "total nest weight") depended on the number of chicks reared in the nest (first hypothesis), we ran independent GLMs either with all sieving fractions included (and thus including dust and other particles) or stepwise exclusion of fractions beginning with those comprising the smallest particles removed by sieving. We assumed that impurities should be mostly present as dust and thus be contained in the smallest sieving fraction. After exclusion of the fraction

Fig. 2 Nesting material after sieving. Sorted by decreasing fragment size from bigger than 25 mm (**a**), 10 mm (**b**), 5 mm (**c**), 2.5 mm (**d**), 1.25 mm (**e**) to smaller than 1.25 mm (**f**)

containing particles smaller than 1.25 mm (mainly dust), nest weight was independent of hatchling number. The weight of the coarser material was then regarded as the weight of the nesting material that had been brought to the nesting box by the nest-building individual (hereafter "nest weight after sieving"). Nest weight after sieving was subsequently used in our analysis on potential relations to clutch size (first hypothesis) and nest size (total nest height and nest bottom thickness).

To assess whether clutch size (egg and hatchling number) is positively related to nest size and weight (second hypothesis), we ran separate GLMs with total nest height and nest weight after sieving as dependent variables and number of eggs and number of hatchlings as independent variables. Our dataset contained only nests in which at least one egg was laid to ensure that the studied nests were all completely built ($n=49$).

Results

From a total of 268 nesting boxes, 49 were occupied by European Pied Flycatchers and contained at least one egg. We excluded 18 cases of egg or juvenile predation from further reproduction related analysis. The nests contained a mean clutch size of 4.8 ± 1,0 eggs, mean number of 3.2 ± 2,6 hatchlings, and mean number of 3.1 ± 2.5 fledglings ($n=31$). The nest bottom was loosely packed and mainly composed of plant-based materials such as birch leaves and birch bark. The tightly woven nest cup was primarily composed of grass and reindeer hair (Fig. 1).

Nest weight

The total nest weight was significantly positively correlated to the number of hatchlings in the nest ($p=0.012$, SE = 0.017, $t=2.62$, Fig. 3a). After removal of the weight of the smallest fraction (< 1.25 mm, Fig. 4), the number of hatchlings had no significant effect on the rest of the nest weight anymore ($p=0.21$, SE = 0.020, $t=1.27$; Fig. 3b). The material in this smallest fraction was mainly composed of dust, likely derived from the feather growing process, arthropod exoskeletons, as well as feces from the hatchlings (Fig. 1b), but probably also heavily deteriorated nesting material. We subsequently regarded the cumulative weight of the coarser fragment sizes (> 1.25 mm; Fig. 2a–e) as the actual nest weight (i.e., weight after sieving). Mean dry nest weight after sieving was 15.1 g (standard deviation (SD) = 5.1 g) and showed a fourfold variation (min = 6.4 g, max = 26.3 g, Fig. 3b). The average proportion of the excluded material of the total nest weight before sieving was 26.9% (SD = 7.4%).

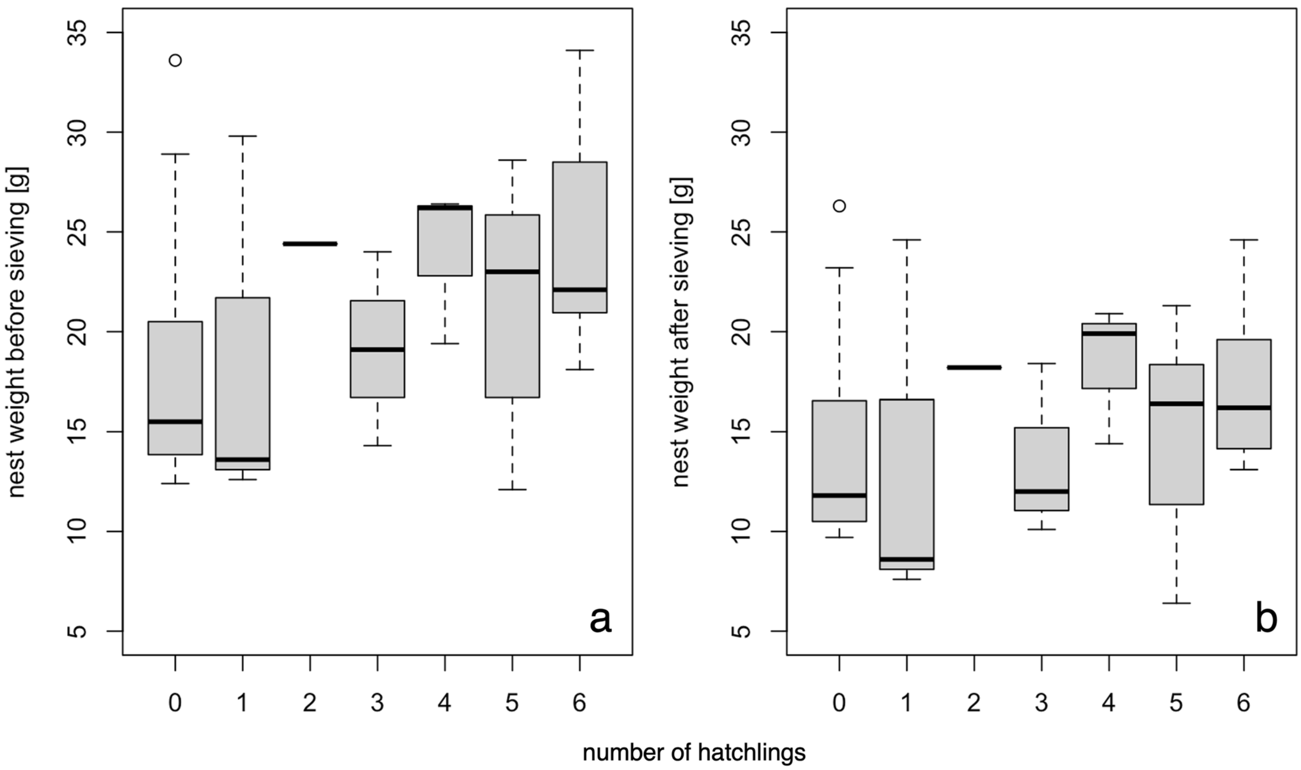

Fig. 3 Relation between the **a** nest weight [g] before sieving (total nest weight), and **b** after sieving to the number of hatchlings in the nest ($n = 47$). Boxplots show median (bold line), 25th and 75th quantiles (lower and upper hinges) and 1.5-fold interquartile range (whiskers) with outlier points for weights that exceed the 1.5-fold interquartile range

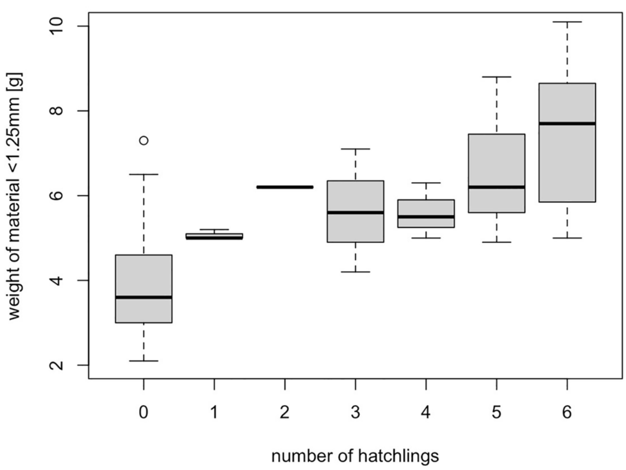

Fig. 4 Weight [g] of the excluded material (fragments < 1.25 mm) in relation to the number of hatchlings per nest ($n = 47$). Boxplots show median (bold line), 25th and 75th quantiles (lower and upper hinges), and 1.5-fold interquartile range (whiskers) with outlier points for weights that exceed the 1.5-fold interquartile range

Nest size

The mean thickness of the nest bottom (beneath the nest cup) was 3.2 cm (SD = 1.3 cm; min = 0.9 cm, max = 5.3 cm) and the mean total nest height was 9.4 cm (SD = 1.2 cm; min = 7.4 cm, max = 12.2 cm) right after completion of nest-building. During incubation and chick-rearing, total nest height decreased on average by 4.0 cm, which is an average reduction of 42%. In contrast, the reduction of nest bottom thickness was only 0.4 cm, corresponding to an average reduction of 7%. While the reduction of nest height was significantly correlated with the number of hatchlings that were reared in the nest ($p < 0.001$, SE = 0.17, $t = -4.09$), the reduction of the nest bottom thickness showed no significant correlation ($p = 0.47$, SE = 0.095, $t = -0.74$).

Both volumetric parameters were highly correlated with each other ($p < 0.0001$, SE = 0.10, $t = 8.62$) and showed a significantly positive correlation with nest weight after sieving (Table 2) showing that nest weight after sieving is a reliable indicator of overall nest size and vice versa (Mainwaring et al. 2008). However, the total nest height showed a stronger correlation with the nest weight after sieving than nest bottom thickness.

Table 2 Output table from the GLM examining the relation between nest bottom thickness as well as total nest height to nest weight after sieving ($n = 22$)

Response variable	Predictor	Coefficient	SE	t	p
Nest bottom thickness	(Intercept)	− 0.112	0.622	− 0.18	0.859
	nest weight after sieving	0.215	0.0392	5.49	**2.24e−05**
Total nest height	(Intercept)	5.94	0.437	13.6	**1.48e−11**
	nest weight after sieving	0.227	0.028	8.25	**7.19e−08**

Does nest size or weight correlate with clutch size?

We neither found nest height (pre-incubation) nor nest weight after sieving to be related to number of eggs or number of hatchlings (Table 3, Fig. 5).

Discussion

Effects of chick-rearing on nest weight and nest size

Here, we showed that the total weight of the unprocessed nest was positively correlated to the number of the chicks. In contrast, after removal of mostly juvenile derived impurities, such as feces and dust from feather growth through sorting and sieving, the weight of the nesting material was independent of the number of chicks present in the nest. The most important contaminant was dust that was present in the < 1.25 mm fraction after sieving. We assume that this dust mostly stems from the feather growing process of the juveniles (Britt and Deeming 2011; Dubiec and Mazgajski 2013) and dried feces that stuck onto the nesting material prior to washing (Fig. 1). However, we cannot exclude that the smallest sieving fraction also contains heavily deteriorated nesting material, making this fraction also dependent on the degree of deterioration. Both, contaminations as well as heavily deteriorated nest material are evidently dependent on the number of reared hatchlings.

Nest height and nest bottom thickness decreased during the breeding season (Slagsvold 1989b; Lambrechts et al. 2012). This effect was more pronounced for the total nest height than for nest bottom thickness. We suppose that the nest cup loses its depth and the whole nest becomes flatter through trampling and flattening of the nest cup rim by the brood when growing larger and heavier, with a stronger effect on the total nest height that includes the nest cup rim.

Methodological implications

We suggest measuring nest height rather than nest weight (pre-incubation) directly after completion of nest-building, as a reliable proxy for overall nest size, since it is less invasive and easy to measure. However, this parameter might raise some methodological difficulties as the nests' upper edge (i.e., the nest cup rim) usually shows no clear and well-defined edge (Fig. 2a). Usually, there are always some pieces of nesting material sticking out, which then make it difficult to judge whether they should be included when measuring nest height. Additionally, nest height might not be uniform around the nest cup. In some corners of the nesting box, more material might have accumulated, resulting in a higher nest height when measuring or including this part of the nest. Therefore, multiple measurements of nest height of one nest should be averaged to obtain more precise data. We tried to address this heterogeneity of nest height by averaging the height of two sides (electronic supplementary material Fig. S2). Finally, measuring nest weight post-fledging might be the least invasive method of assessing nest weight but requires elaborate processing of nesting material to minimize the effects of chick-rearing, as described in this study.

Coherent with the previous literature (e.g., Lambrechts et al. 2010; Lambrechts and Deeming 2024), we want to emphasize the need to use nesting boxes of standardized dimensions to increase comparability between studies. Particularly, as more research is needed to understand and quantify the effects of nest-box dimensions (i.e., floor space, internal height, and location of the entrance hole) on nest architecture.

Table 3 Output table from the GLM examining the relation between total nest height and number of eggs ($n = 24$), respectively, number of hatchlings ($n = 16$), as well as nest weight after sieving and number of eggs ($n = 49$), respectively, number of hatchlings ($n = 31$)

Response variable	Predictor	Coefficient	SE	t	p
Total nest height	(Intercept)	8.18	1.984	4.12	**4.50e−04**
	number of eggs	0.233	0.378	0.62	0.54
	(Intercept)	8.96	0.893	10.0	**8.95e−08**
	number of hatchlings	0.08	0.177	0.45	0.66
Nest weight after sieving	(Intercept)	18.6	3.38	5.51	**1.66e−06**
	number of eggs	− 0.755	0.704	− 1.07	0.289
	(Intercept)	14.6	1.51	9.6	**2.16e−10**
	number of hatchlings	0.325	0.373	0.87	0.391

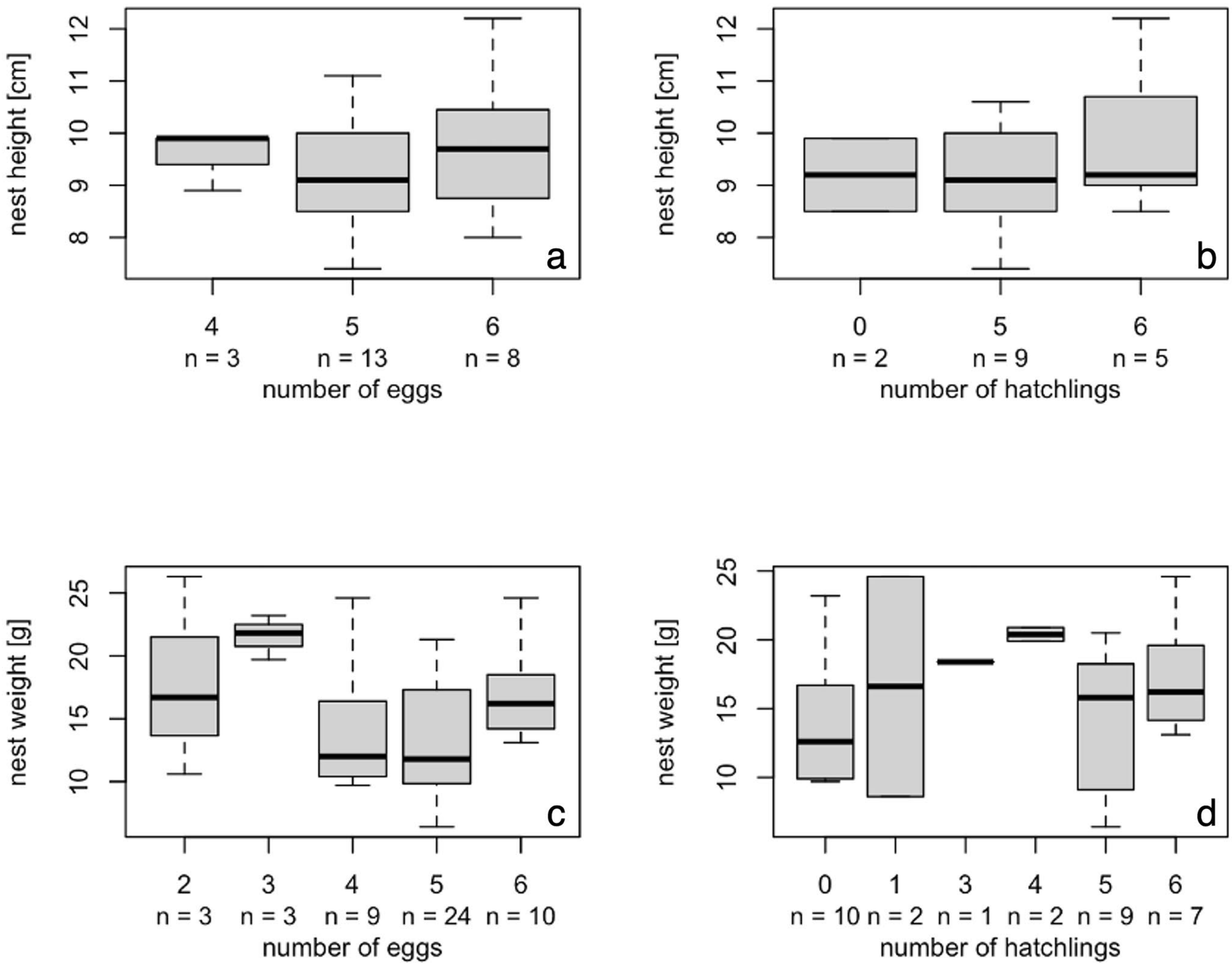

Fig. 5 Nest height (measured pre-incubation) in relation to **a** number of eggs and **b** number of hatchlings, as well as nest weight after sieving in relation to **c** number of eggs and **d** number of hatchlings. Boxplots show median (bold line), 25th and 75th quantiles (lower and upper hinges), and 1.5-fold interquartile range (whiskers)

No correlation of nest weight or nest size with reproduction

Neither number of eggs nor number of hatchlings was related to pre-incubation nest height or nest weight after sieving. In relation to nest construction, these two reproductive parameters can be interpreted differently. While the number of eggs may be related to nest construction investment through the bird's physical condition and energetic capabilities pre-incubation (Tomás et al. 2006; Mainwaring and Hartley 2009, 2013), the number of hatched or fledged chicks might at least partly be affected by the nest's architecture (Lambrechts and Deeming 2024). In this study, particularly the absence of both positive and negative correlations between pre-incubation reproductive investment (i.e., number of eggs, Fig. 5a,c) and nest construction investment is remarkable, considering the fourfold variation in nest weight after sieving, and the variations in nest height and nest bottom thickness. In contrast, Moreno et al. (2010) provide experimental evidence that the investment in nest construction is traded off against the investment in incubation and/or chick-rearing. Furthermore, clutch mass was positively correlated with nest construction rate (Moreno et al. 2008) as well as male-participation during nest construction (Martínez-de La Puente et al. 2009). The absence of reproductive consequences (i.e., effects on hatchling number, Fig. 5b, d) in relation to intraspecific variation in nest construction behavior in this study might be due to the high predation rates observed in this breeding population and the associated reduction in sample size, with 18 of 49 nests being predated.

Conclusion

With this study, we provide quantitative evidence for the effect of hatchling number on nest height, nest bottom thickness, and nest weight in a cavity breeding songbird. Additionally, we showed that both nest height and nest weight serve as reliable indicators of overall nest size. While the former should be measured right after nest completion, the latter can be assessed post-fledging followed by sufficient processing of the nest, as described in this study. The advantage of measuring nest weight is that breeding birds or their offspring are not disturbed during the breeding period. Contrary to our expectations, clutch size (number of eggs and hatchlings) was neither related to nest size nor weight. With this study, we want to highlight the importance of processing (i.e., sort, wash, and sieve) the nesting material post-fledging to accurately assess its weight, allowing to draw more precise conclusions when studying drivers of intraspecific variation in nest-building of songbirds.

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Data availability All data generated or analyzed during this study are included in this published article and the electronic supplementary material S3.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical statement The handling and ringing of adults and nestling European Pied Flycatchers in Vindelfjällens Nature Reserve was carried out under permit 10311-2023 to the LUVRE project from the Västerbotten regional county board and ringing permit no. 180 (LUVRE project) from the Bird Ringing Centre at the Swedish Museum of Natural History. Bird handling and ringing was done by personnel with a ringer's license with the highest possible care. The experiments that were carried out comply with the current laws of Sweden.

References

Álvarez E, Barba E (2008) Nest quality in relation to adult bird condition and its impact on reproduction in Great Tits *Parus major*. Acta Ornithol 43:3–9. https://doi.org/10.3161/000164508X345275

Briggs KB, Biddle LE, Deeming DC (2019) Geographical location affects size and materials used in the construction of European Pied Flycatcher (*Ficedula hypoleuca*) nests. Avian Res 10:1–15

Briggs KB, Mainwaring MC (2019) Experimental evidence of non-random nest material selection in Pied Flycatchers. Behav Processes 164:59–64. https://doi.org/10.1016/j.beproc.2019.04.008

Britt J, Deeming DC (2011) First-egg date and air temperature affect nest construction in Blue Tits *Cyanistes caeruleus*, but not in Great Tits *Parus major*. Bird Study 58:78–89. https://doi.org/10.1080/00063657.2010.524916

Cruz Á, Álvarez E, Barba E (2016) Nest insulating capacity during incubation and after fledging are related. Avian Biol Res 9:22–27. https://doi.org/10.3184/175815516X14453606332392

Deeming DC, Mainwaring MC, Hartley IR, Reynolds SJ (2012) Local temperature and not latitude determines the design of Blue Tit and Great Tit nests. Avian Biol Res 5:203–208. https://doi.org/10.3184/175815512X13528874959581

Deeming DC, Reynolds SJ (2015) Nests, eggs, and incubation: new ideas about avian reproduction. Oxford University Press, Oxford

Der Weduwen D, Keogan K, Samplonius JM et al (2021) The correlates of intraspecific variation in nest height and nest building duration in the Eurasian Blue Tit *Cyanistes caeruleus*. J Avian Biol 52:02528. https://doi.org/10.1111/jav.02528

Dubiec A, Mazgajski TD (2013) Nest mass variation over the nesting cycle in the Pied Flycatcher (*Ficedula hypoleuca*). Avian Biol Res 6:127–132. https://doi.org/10.3184/175815513X13612847142708

Glądalski M, Bańbura M, Kaliński A et al (2024) Nest structure and breeding success in two tit species: a long-term study. J Ornithol 166:67–74. https://doi.org/10.1007/s10336-024-02193-w

Guan H, Wen Y, Wang P et al (2018) Seasonal increase of nest height of the Silver-throated Tit (*Aegithalos glaucogularis*): can it reduce predation risk? Avian Res 9:42. https://doi.org/10.1186/s40657-018-0135-4

Harnist I, Dubiec A, Mazgajski TD (2020) Changes of nest mass in relation to nesting stages in the Great Tit *Parus major*. Bird Study 67:292–299. https://doi.org/10.1080/00063657.2020.1864283

Järvinen A (1983) Breeding strategies of hole-nesting passerines in northern Lapland. Ann Zool Fenn 20:129–149

Kaliński A, Wawrzyniak J, Bańbura M et al (2014) Does the threat of European Pine Marten (*Martes martes*) predation influence the height of nests built by Blue Tits (*Cyanistes caeruleus*) and Great Tits (*Parus major*)? Avian Biol Res 7:83–90. https://doi.org/10.3184/175815514X13983550506873

Kang K-H, Nam K-B, Kim J-S, Yoo J-C (2022) Nest characteristics and composition of the colonial nesting Azure-winged Magpie *Cyanopica cyanus* in South Korea. PeerJ 10:e13637. https://doi.org/10.7717/peerj.13637

Laaksonen T, Ahola M, Eeva T et al (2006) Climate change, migratory connectivity and changes in laying date and clutch size of the Pied Flycatcher. Oikos 114:277–290. https://doi.org/10.1111/j.2006.0030-1299.14652.x

Lambrechts MM, Adriaensen F, Ardia DR et al (2010) The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases. Acta Ornithol 45:1–26. https://doi.org/10.3161/000164510X516047

Lambrechts MM, Aimé C, Midamegbe A et al (2012) Nest size and breeding success in first and replacement clutches: an experimental study in Blue Tits *Cyanistes caeruleus*. J Ornithol 153:173–179. https://doi.org/10.1007/s10336-011-0722-1

Lambrechts MM, Blondel J, Bernard C et al (2016) Exploring biotic and abiotic determinants of nest size in mediterranean Great Tits (*Parus major*) and Blue Tits (*Cyanistes caeruleus*). Ethology 122:492–501. https://doi.org/10.1111/eth.12494

Lambrechts MM, Deeming DC (2024) Nest design and breeding success: replicability of methodologies and research findings in secondary hole-nesting passerines. Birds 5:278–307. https://doi.org/10.3390/birds5020019

Lambrechts MM, Demeyrier V, Fargevieille A et al (2014) Great Tits build shallower nests than Blue Tits. Avian Biol Res 7:251–254. https://doi.org/10.3184/175815514X14162394225987

Lambrechts MM, Dos Santos A (2000) Aromatic herbs in Corsican Blue Tit nests: the 'Potpourri' hypothesis. Acta Oecologica 21:175–178. https://doi.org/10.1016/S1146-609X(00)00122-3

Lombardo MP (1994) Nest architecture and reproductive performance in Tree Swallows (*Tachycineta bicolor*). Auk 111:814–824. https://doi.org/10.2307/4088813

Loukola OJ, Seppänen J-T, Forsman JT (2014) Pied Flycatchers nest over other nests, but would prefer not to. Ornis Fenn 91:201–208. https://doi.org/10.51812/of.133857

Lundberg A, Alatalo RV (2010) The Pied Flycatcher. A & C Black, London

Mainwaring MC (2017) Causes and consequences of intraspecific variation in nesting behaviors: insights from Blue Tits and Great Tits. Front Ecol Evol 5:39. https://doi.org/10.3389/fevo.2017.00039

Mainwaring MC, Benskin CMcWH, Hartley IR, (2008) The weight of female-built nests correlates with female but not male quality in the Blue Tit *Cyanistes caeruleus*. Acta Ornithol 43:43–48. https://doi.org/10.3161/000164508X345310

Mainwaring MC, Deeming DC, Jones CI, Hartley IR (2014) Adaptive latitudinal variation in Common Blackbird *Turdus merula* nest characteristics. Ecol Evol 4:851–861. https://doi.org/10.1002/ece3.952

Mainwaring MC, Hartley IR (2009) Experimental evidence for state-dependent nest weight in the Blue Tit, *Cyanistes caeruleus*. Behav Process 81:144–146

Mainwaring MC, Hartley IR (2013) The energetic costs of nest building in birds. Avian Biol Res 6:12–17. https://doi.org/10.3184/175815512X13528994072997

Martínez-de La Puente J, Merino S, Lobato E et al (2009) Male nest-building activity influences clutch mass in Pied Flycatchers *Ficedula hypoleuca*. Bird Study 56:264–267. https://doi.org/10.1080/00063650902792015

Mazgajski TD, Rykowska Z (2008) Dependence of nest mass on nest hole depth in the Great Tit *Parus major*. Acta Ornithol 43:49–55. https://doi.org/10.3161/000164508X345329

McCarty JP (1999) Nest-building behavior in PCB-contaminated Tree Swallows. Auk 116:55–63. https://doi.org/10.2307/4089453

Moreno J, Lobato E, González-Braojos S, Castañeda RR-D (2010) Nest construction costs affect nestling growth: a field experiment in a cavity-nesting passerine. Acta Ornithol 45:139–145. https://doi.org/10.3161/000164510X551291

Moreno J, Martínez J, Corral C et al (2008) Nest construction rate and stress in female Pied Flycatchers *Ficedula hypoleuca*. Acta Ornithol 43:57–64. https://doi.org/10.3161/000164508X345338

Morton ML (1976) Adaptive strategies of *Zonotrichia* breeding at high latitude or high altitude. Proc 16th Int Ornithol Congr 322–336

Nyholm NEI (2011) Dynamics and reproduction of a nest-box breeding population of Pied Flycatcher *Ficedula hypoleuca* in a subalpine birch forest in Swedish Lapland during a period of 46 years. Ornis Svec 21:133–156. https://doi.org/10.34080/os.v21.20232

O'Neill LG, Parker TH, Griffith SC (2018) Nest size is predicted by female identity and the local environment in the Blue Tit (*Cyanistes caeruleus*), but is not related to the nest size of the genetic or foster mother. R Soc Open Sci 5:172036. https://doi.org/10.1098/rsos.172036

Petit C, Hossaert-McKey M, Perret P et al (2002) Blue Tits use selected plants and olfaction to maintain an aromatic environment for nestlings. Ecol Lett 5:585–589. https://doi.org/10.1046/j.1461-0248.2002.00361.x

Potti J, Merino S (1996) Causes of hatching failure in the Pied Flycatcher. Condor 98:328–336. https://doi.org/10.2307/1369151

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Slagsvold T (1989a) On the evolution of clutch size and nest size in passerine birds. Oecologia 79:300–305. https://doi.org/10.1007/BF00384308

Slagsvold T (1989b) Experiments on clutch size and nest size in passerine birds. Oecologia 80:297–302. https://doi.org/10.1007/BF00379030

Smith JA, Harrison TJE, Martin GR, Reynolds SJ (2013) Feathering the nest: food supplementation influences nest construction by Blue (*Cyanistes caeruleus*) and Great Tits (*Parus major*). Avian Biol Res 6:18–25. https://doi.org/10.3184/175815512X13530764553094

Tomás G, Merino S, Martínez-de La Puente J et al (2012) Interacting effects of aromatic plants and female age on nest-dwelling ectoparasites and blood-sucking flies in avian nests. Behav Processes 90:246–253. https://doi.org/10.1016/j.beproc.2012.02.003

Tomás G, Merino S, Moreno J et al (2006) Nest weight and female health in the Blue Tit (*Cyanistes caeruleus*). Auk 123:1013–1021. https://doi.org/10.2307/25150216

Vergara PM (2007) Effects of nest-box size on the nesting and renesting pattern of *Aphrastura spinicauda* and *Troglodytes aedon*. Ecol Austral 17:133–141

von Haartman L (1990) Breeding time of the Pied Flycatcher *Ficedula hypoleuca*. In: Blondel J, Gosler A, Lebreton J-D, McCleery R (eds) Population biology of passerine birds. Springer, Berlin Heidelberg, Berlin, Heidelberg, pp 1–16

Wesołowski T (2002) Anti-predator adaptations in nesting Marsh Tits *Parus palustris*: the role of nest-site security. Ibis 144:593–601. https://doi.org/10.1046/j.1474-919X.2002.00087.x

Wickham H, Bryan J (2015) readxl: Read Excel files. 1.4.3

Wysocki D, Jankowiak Ł, Greño JL et al (2015) Factors affecting nest size in a population of Blackbirds *Turdus merula*. Bird Study 62:208–216. https://doi.org/10.1080/00063657.2015.1030722