ORNITHOLOGISCHER ANZEIGER

Zeitschrift bayerischer und baden-württembergischer Ornithologen

Band 61 – Heft 1 April 2023

Ornithol. Anz., 61: 1–15

Picky Blue Tits – selective moss utilization for nest construction in *Cyanistes caeruleus*

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Abstract

Nests are an expression of the genotype of individuals as well as species (extended phenotype). Analyzing the materials used for nest construction provides insights into the ecological causes and consequences of different nest construction strategies. A frequently used nesting material in nests of tits (Paridae) are mosses, but its role within their breeding ecology is poorly understood. We studied the utilization of moss species within the nest bases of Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major*. We used standardized nesting boxes and compared the proportion of moss species in the nest bases with their abundance in the surrounding area to distinguish between an abundance-based and a selective collection of moss species. We found that the nest bases of Blue Tits are heavier than those of Great Tits, and we found no positive correlation between the moss species diversity of the nest and of the surroundings. However, only Blue Tits showed a selective behavior towards or against certain moss species, with *Hypnum cupressiforme* being the most abundant moss within their nest bases. Our results offer evidence for the hypothesis that the Blue Tit invests more in the construction of nests. We propose four drivers of a selective gathering of certain moss species that may be used as a guide for future studies: (1) chemical constituents – antimicrobial chemical compounds as potential insecticides; (2) moss characteristics – e.g. general size, rigidity, water-uptake capacity; (3) environmental pressures – e.g. predation pressure during gathering or ”pluckability” of certain moss species; (4) tit ecomorphology – differences in locomotion and use of space in their environment.

Keywords: Paridae, breeding ecology, nest base, nesting material, bryophytes, electivity

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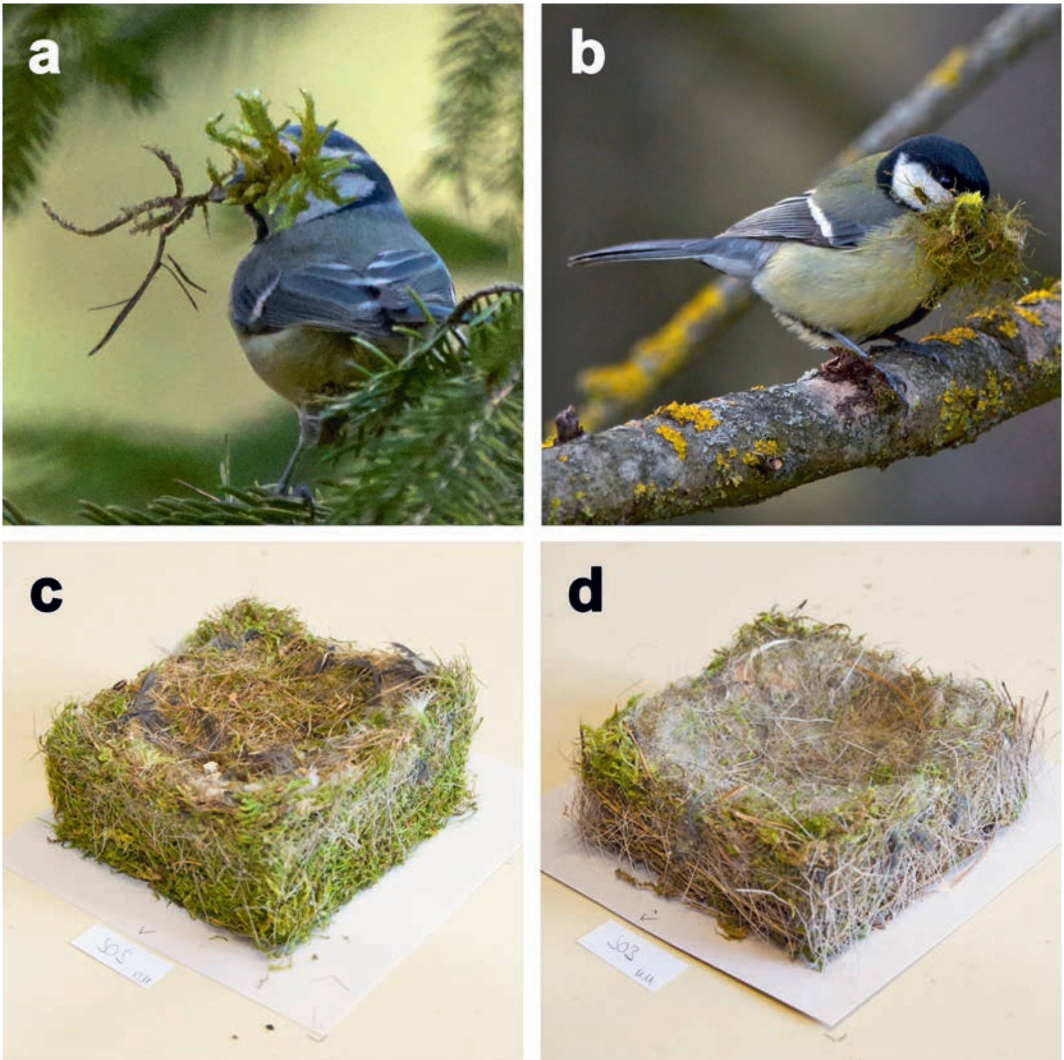
Introduction

The phenotype of an organism is the product of its genes. Moreover, individual organisms also modify their environment and these modifications outside the body are also the product of genes that are harbored by that body (extended phenotype, Dawkins 1982). Most bird species build nests to create a suitable environment for the development of their offspring (Deeming and Reynolds 2015, Hansell and Overhill 2000). Nest architecture is therefore also an expression of the bird's genotype, which evolved in response to environmental pressures. The extended pheno-



Blue Tit *Cyanistes caeruleus* carrying a piece of a long-stemmed moss species in the forest site (most probably *S. purum* or *P. schreberi*, a) and Great Tit *Parus major* carrying a bundle of smaller mosses in the Ecological Botanical Garden (b). Blue Tit nest from the forest site (c) and Great Tit nest from the forest site (d). All photographs by L. Fäth. – *Blaumeise* Cyanistes caeruleus *mit einer langstämmigen Moosart (wahrscheinlich* S. purum *oder* P. schreberi*, a) im Schnabel im Waldstandort und Kohlmeise* Parus major *mit einem Bündel kleinerer Moose im Ökologisch Botanischen Garten (b). Blaumeisennest (c) aus dem Waldstandort und Kohlmeisennest (d) aus dem Waldstandort.* Alle Aufn.: L. Fäth type provides a framework to understand the variation of the design and construction of nests within and across species.

Birds use a variety of materials within their nests (Hansell and Overhill 2000) including isolating materials (e.g. fur, feathers, wool) or structurally supportive materials (e.g. sticks), which vary across species and probably also within species. Especially the incorporation of fresh green plant materials like leaves, coniferous needles, or mosses into bird nests has received attention in recent years (Scott-Baumann and Morgan 2015). For example, mosses are frequently utilized by a variety of bird species (Glime 2017a). Particularly in the nests of tits (*Paridae*), mosses are an abundant material and moss collection for nest-building seems to be selective (Hamao et al. 2016, Wesołowski und Wierzcholska 2018, Glądalski et al. 2021). The role of mosses within bird nests, however, is poorly understood and studies which focus on this taxonomically diverse material are rather scarce (Álvarez et al. 2013, Balát 1976, Fontúrbel et al. 2020, Glądalski et al. 2021, Hamao et al. 2016, Hříbek 1985, Wesołowski und Wierzcholska 2018) and specific effects of moss species within nests have often been ignored (Hansell and Overhill 2000).

Tits use mosses mostly within the lower layers of their nests. In Blue and Great Tits even to the degree that their nests, which are built by the female, usually show a clear structuring into two parts – a nest base (mostly constructed of mosses) and a nest cup embedded in it. Few studies have analyzed which moss species were utilized within nests of Blue and Great Tits. Besides detailed observations from the Czech Republic (Balát 1976, Hříbek 1985), two recent studies from Poland (Glądalski et al. 2021, Wesołowski und Wierzcholska 2018) have investigated the utilization of mosses for nest construction by Blue and Great Tits. These studies point towards a selective behavior, as the abundance and diversity of moss species in the nest does not represent the abundance and diversity of moss species growing in the surroundings. Furthermore, these two bird species differ in their use of moss species (Wesołowski and Wierzcholska 2018). Recent studies also reported selective collection of aromatic plant material by Blue Tits (Lambrechts and Dos Santos 2000, Mennerat et al. 2009, Petit et al. 2002, Pires et al. 2012). Overall, these observations suggest that nests are an extended phenotype of species and perhaps even of individual genotypes.

Furthermore, the nest size of Blue Tits is an outlier in the generally positive relationship between nest size and bird size (Hansell and Overhill 2000, Slagsvold 1989). Nests of Blue Tits are heavier and larger in standardized nesting boxes than those of Great Tits (Alambiaga et al. 2020, Lambrechts et al. 2015, 2014, Smith et al. 2013). This is mainly due to the extensive nest base built by the Blue Tits. In part this is the result of a longer phase of nest construction in comparison to Great Tits (Smith et al. 2013). Based on the selection of nesting material and the species-specific nest construction behaviors reported in the literature, we studied the moss utilization of Blue and Great Tits within their nest bases and hypothesize: 1) that according to the concept of the extended phenotype, Blue and Great Tits selectively prefer certain moss species and the use of moss species is not a simple mirror of the abundance of mosses in the surrounding area; 2) Blue Tits show a more pronounced selective behavior than Great Tits in terms of moss utilization because the heavier nests of Blue Tits compared to Great Tits suggests that Blue Tits put more investment into individual broods (Mainwaring and Hartley 2013).

To test these hypotheses, we investigated the moss species composition of nests constructed by sympatrically breeding Blue and Great Tits in two different study sites and compared the moss species composition within the nest with the composition in the surroundings of the nest. In contrast to Wesołowski and Wierzcholska (2018) we used standardized nesting boxes to improve comparability between the nests of the two species as well as with other studies.

Material and Methods

Study sites. We analyzed nests from two nearby study sites, the Ecological Botanical Garden of the University of Bayreuth (hereafter "EBG", 49°55'25.3"N, 11°35'10.1"E) and the forest site "Studentenwald" (hereafter "SW", 49°55'18.9"N, 11°34'20.7"E). The two sites are located at the southern edge of Bayreuth, southern Germany, and represent two ecologically contrasting habitats. The EBG is a heterogeneous site with a high diversity of open and woody sites and hosts a remarkable moss diversity: 125 different moss species have been found in the EBG (Pickel and Streit 2019). The SW is a forest dominated by Scots pine *Pinus sylvestris* and Norway spruce *Picea abies* (Fig. 1) with interspersed smaller patches of Beech *Fagus sylvatica* and Pedunculate Oak *Quercus robur*.

Sampling method. Ten wooden nest boxes of a standardized size were hung at 2 m to 3 m height in each study site in 2020 and 2021. The internal dimensions of the nest boxes were 12 cm × 13 cm × 22.5 cm with an entrance diameter of 28 mm and a distance of ≈ 16 cm between the floor and the entrance.

Fig. 1. Example of an investigated forest site with dense moss vegetation on the ground, dominated by *S. purum* (42 % of moss coverage), plus *P. formosum* (18 %), *P. schreberi* (16 %), *D. scoparium* (7 %), *H. cupressiforme* (7 %), *H. splendens* (6 %) and *T. tamariscinum* (4 %). The nesting box in the foreground was occupied by Blue Tits in 2021. – *Beispiel für einen untersuchten Waldstandort mit einer dichten Bodenmoosvegetation. Die häufigsten Arten (relativer Anteil an der Moosbedeckung) sind* S. Purum *(42 %),* P. formosum *(18 %),* P. schreberi *(16 %),* D. Scoparium *(7 %),* H. cupressiforme *(7 %),* H. splendens *(6 %) und* T. tamariscinum *(4 %). Der Nistkasten im Vordergrund wurde 2021 von einem Blaumeisenpaar belegt.*

During the breeding seasons nest boxes were checked at least once a week observing the activity of potential breeding pairs of tits around or at the nest boxes. After the offspring left the nests, nests were removed for further analyses and put into a freezer at -14 °C for at least seven days to kill arthropods occurring in them. Afterwards the nests were separated into two parts, the nest cup and the nest base (Fig. 2). Almost all Blue Tit nests allowed such clear differentiation between these two parts. Great Tit nests, however, rarely showed such a clear structure, which is related to their high hair or fur content (Alambiaga et al. 2020, Britt and Deeming 2011). In those cases, the mosses of the less felted and interwoven nest base were used for further analyses. Almost all mosses and moss fragments that were larger than 1.0 cm were identified to species level. Mosses belonging to the genera *Brachythecium*, *Eurhynchium*, *Plagiomnium*, *Lophocolea* or *Orthotrichum* were in some cases also identified to species level but were grouped into their respective genera for further analysis to reduce a potential bias due to misidentifications. To control for nest(-base) size, the proportion of the dry weight of each moss species was calculated from the total dry weight of all mosses analyzed from each nest. For this, the mosses were dried for 48 h at 45 °C and weighed (Mettler Toledo AE240, Precision 0.1 mg). Other studies estimated the volumetric proportion of moss species (Glądalski et al. 2021, Wesołowski und Wierzcholska 2018). However, such a metric might be biased by the packing of mosses within the nests.

To distinguish between a selective and an availability-based collection of mosses as nesting material by the tits, the abundance of moss species in the proximity to the nest boxes was estimated. This was done by 12 randomly placed quadrats of 1 m² within a radius of 10 m around each nesting box in early 2020 (Glądalski et al. 2021, Wesołowski und Wierzcholska 2018). The total moss cover (C) within each quadrat was visually estimated as was the cover of each moss species (C_i). If trees or tree stumps were present within a quadrat, only the mosses growing up to 30 cm height on those structures were scored. Subsequently, the proportion of each moss species in the nest surroundings (p_i) was calculated. This was done separately for each moss species (i) and nesting site.

$$p_i = \frac{C_i}{C}$$

Fig. 2. Separation of the nest cup and the nest base of a Blue Tit nest from the forest site. The nest cup consisted mainly of hair/fur, grass, feathers and smaller mosses. The nest base consisted of grass, feathers and mosses. The most abundant moss species (relative dry weight) in the nest base were *S. purum* (48 %), *H. cupressiforme* (46 %), *Eurhynchium sp.* (4 %). Less abundant mosses were *R. squarrosus*, *T. tamariscinum*, *Brachythecium sp.*, *C. piliferum* (< 1 %). In total the mosses weighed 9.7 g. – *Trennung von Nestnapf und Nestbasis bei einem Blaumeisennest aus dem Waldstandort. Der Nestnapf bestand hauptsächlich aus Haaren/Wolle, Gras, Federn und feineren Moosen. Die Nestbasis bestand aus Gras, Federn und Moosen. Die häufigsten Moose (relatives Trockengewicht) in der Nestbasis waren* S. purum *(48 %),* H. cupressiforme *(46 %),* Eurhynchium sp. *(4 %). Weniger häufig waren Moose wie* R. squarrosus, T. tamariscinum, Brachythecium sp., C. piliferum *(< 1 %). Insgesamt wogen die Moose 9,7 g.*

For statistical analyses, all moss species were furthermore split into two groups according to their size and growth form, following the hypothesis of Wesołowski and Wierzcholska (2018) that "pluckability" as well as the size (stem length) and rigidity (stem diameter) might explain a potential selective behavior. The two groups are long-stemmed, ground-growing mosses and smaller mosses growing on various substrates.

In total, the nest bases of 31 nests were analyzed, among them 14 nests in the EBG and 17 nests in the SW site (EBG: two Blue Tit and four Great Tit nests in 2020; three Blue Tit and five Great Tit nests in 2021; SW: seven Blue Tit and two Great Tit nests in 2020; five Blue Tit and three Great Tit nests in 2021).

Data analysis. Data analysis was conducted using R version 3.6.3 (R Core Team 2020). First, we compared the weight of the nest base between the two tit species and tested for differences between the two species and the two sites using a linear model with species and study site as factors and moss diversity and mean total moss cover (*C*) in the surroundings (see below) as independent variables. The latter two continuous variables were centered.

To compare the diversity of mosses within the nest and in the surroundings we used the Shannon-diversity (*H*) of the moss species in the tits' nest base.

$$H_i = -\sum p_i ln p_i$$

A linear model was used to evaluate which of five predictor variables explained the diversity of moss species in the nest base: tit species, study site, Shannon-diversity of moss species within the surroundings, mean total moss cover (*C*), and total dry weight of the nest base as a control for nest size. The number of moss species in the surroundings is closely correlated to the diversity ($r^2 = 0.56$). Thus, we only used the diversity of moss species in the surroundings as independent variable for both models presented in Table 2.

To distinguish between a selective and an availability-based collection of moss species, the Electivity Index (*E*) of Ivlev (Lechowicz 1982) was calculated, using each moss species proportion within a 10-m radius (p_i) and their proportion within the tits' nest bases. This was done separately for each moss species (i) and nest.

$$E_i = \frac{r_i - p_i}{r_i + p_i}$$

This index varies between -1 for moss species not used for nest site construction (negative selection) and +1 (positive selection) with i indicating moss species, r_i the proportion of the moss species i in the nest base and p_i the proportion within the surroundings. If a moss species was found neither in the examined nest nor in the surroundings E_i is not defined and the number of indices varied across moss species. For moss species where it was possible to calculate at least five indices, linear models incorporating only the intercept for each tit and moss species were used to analyze whether the mean of each index differed significantly from 0 (random use of moss species). The error probability was adjusted for multiple tests using a sequential Bonferroni correction (see Holm 1979) using the function p.adjust (method – "holm") in R.

Results

A total of 20 moss species was found in the surroundings of the nesting boxes; 13 species occurred at the SW site and 15 species in the EBG (Tab. 1 and Fig. 3 for examples of species).

Tab. 1. List of moss species and genera, grouped into long-stemmed, ground-growing mosses, and smaller mosses which grow on different substrates. Study site were the Ecological Botanical Garden in Bayreuth (EBG) and a forest site "Studentenwald" (SW). Moss species belonging to the genera *Brachythecium, Eurhynchium, Plagiomnium, Lophocolea* or *Orthotrichum* were grouped into their respective genera. – *Liste der Moosarten und Gattungen, aufgeteilt in langstämmige, bodenbewachsende Moose und kleinere Moose, die auf unterschiedlichen Substraten wachsen. Untersuchungsgebiete waren der Ökologisch Botanische Garten Bayreuth (EBG) und der Waldstandort „Studentenwald" (SW). Moosarten der Gattungen* Brachythecium, Eurhynchium, Plagiomnium, Lophocolea *oder* Orthotrichum *wurden auf Gattungsniveau zusammengefasst.*

Long-stemmed, ground-growing mosses	**Site**	**Smaller mosses growing on different substrates**	**Site**
Rhytidiadelphus squarrosus ((Hedw.) Warnst., Fig 3 b)	EBG, SW	*Hypnum cupressiforme* (Hedw., Fig. 3 a)	EBG, SW
Scleropodium purum ((Hedw.) Limpr., Fig. 3 c)	EBG, SW	*Eurhynchium sp.* (Fig. 3 f)	EBG, SW
Pleurozium schreberi ((Brid.) Mitt., Fig. 3 d)	EBG, SW	*Brachythecium sp.* (Fig. 3 e)	EBG, SW
Thuidium tamariscinum ((Hedw.) Schimp.)	SW	*Orthotrichum sp.*	EBG
Hylocomium splendens ((Hedw.) Schimp.)	SW	*Didymodon vinealis* ((Brid.) R. H. Zander)	EBG
Plagiomnium sp.	EBG, SW	*Homalothecium lutescens* ((Hedw.) Robins)	EBG
Polytrichum formosum (Hedw.)	EBG, SW	*Lophocolea sp.*	EBG, SW
Dicranum scoparium (Hedw.)	EBG, SW		
Cirriphyllum piliferum ((Hedw.) Grout)	EBG		
Calliergonella cuspidata ((Hedw.) Loeske)	EBG		
Sphagnum palustre (L.)	SW		
Atrichum undulatum ((Hedw.) P. Beauv)	EBG, SW		

Fig. 3. The six most abundant mosses in the nest bases of Blue Tits and Great Tits. *Hypnum cupressiforme* (a), *Rhytidiadelphus squarrosus* (b), *Scleropodium purum* (c), *Pleurozium schreberi* (d), *Brachythecium sp.* (e), *Eurhynchium sp.* (f). – *Die sechs häufigsten Moose innerhalb der Moosbasen von Blau- und Kohlmeisennestern.* Hypnum cupressiforme *(a),* Rhytidiadelphus squarrosus *(b),* Scleropodium purum *(c),* Pleurozium schreberi *(d),* Brachythecium sp. *(e),* Eurhynchium sp. *(f).*

The weight of the nest base of Blue Tits (raw mean = 8.5 g, SD = 2.9 g) was higher than that of Great Tits (3.2 g, 2.5 g), even after correcting for tit species and study site as well as two continuous variables (Tab. 2).

Furthermore, we found a marginally positive relationship between the weight of the nest base and the moss cover. Nests with more mosses in their surroundings tend to be heavier (Tab. 2). Shannon-diversity of the mosses within the nest was negatively correlated with the Shannon-diversity of the surroundings (Fig. 4). None of the other independent variables (tit species, site, diversity of moss in the surroundings and weight of the nest) had a significant influence on the diversity of moss species used in a nest in the linear model.

The most frequently used moss in the Blue Tits nest base was *Hypnum cupressiforme* (Fig. 5, mean proportion = 69%). Blue Tits showed a positive selective behavior towards four moss species (Fig. 6). *H. cupressiforme* (number of defined indices n = 17, mean of Electivity = 0.75, p < 0.001), *Eurhynchium sp.* (n = 13, mean of Electivity = 0.95, p < 0.001), *Cirriphyllum piliferum* (n = 6, mean of Electivity = 1, p < 0.001). By contrast, *Hylocomium splendens* (n = 7, mean of Electivity = -0.99, p < 0.001) was negatively selected. Furthermore, Blue Tits discriminated against large-stemmed, ground-growing mosses (n = 17, mean of Electivity = -0.57, p < 0.001) and preferred smaller, epiphytic mosses (n = 17, mean of Electivity = 0.68, p = < 0.001). A similar pattern was found in an analysis concentrating only on the nest boxes in the SW.

The most abundant mosses in Great Tit nest bases (Fig. 5) were *Rhytidiadelphus squarrosus* (mean proportion = 41%), *Scleropodium purum* (mean proportion = 24%), *Pleurozium schreberi* (mean proportion = 27%). Great Tits however showed selective tendencies neither towards any moss species nor towards one of the two growth forms (large-stemmed and ground-growing vs. small and epiphytic).

Tab. 2. Results of linear models with nest-base weight and diversity of mosses in nest base as dependent variables. The continuous independent variables were centered and thus the intercept represents the nest-base weight or the diversity of mosses in the nest base for the reference category of the factors Species and Site (in our case Blue Tit and Ecological Botanical Garden) and using the averages of the continuous independent variables. The estimates of the factors give the difference to the reference categories. For example, the nest-base weight in nests of the Blue Tit in the Ecological Botanical Garden is 6.7 g and in nests of the Great Tit 3.4 g less (note the negative sign of the estimate for the factor Species). The table shows the estimates, the standard error (SE) of the estimates, as well as the t (= estimate divided by SE) and associated error probability. Number of nests in both models is 31. – *Ergebnisse der linearen Modelle mit Nestbasisgewicht respektive Diversität der Moose in der Nestbasis als abhängige Variable. Die kontinuierlichen unabhängigen Variablen wurden zentriert, sodass der Achsenabschnitt den Wert der abhängigen Variable für die Referenzkategorie der Faktoren (im vorliegend Fall Blaumeise und Ökologisch Botanischer Garten) angibt. Zum Beispiel beläuft sich dann das Gewicht der Nestbasis für die Blaumeise im Ökologisch Botanischen Garten auf 6,7 g. Das Nestgewicht der Kohlmeise ist dabei um 3,4 g leichter (beachte das negative Vorzeichen des Schätzers). Die Tabelle zeigt den Schätzer mit Standardfehler (SE) sowie den t-Wert (= Schätzer dividiert durch SE) und die zugehörige Irrtumswahrscheinlichkeit. Anzahl der Nester in beiden Modellen 31.*

	nest-base weight				diversity of mosses in nest base			
	estimate	SE	|t|	P	estimate	SE	|t|	P
Intercept	6.66	0.867	7.8	< 0.001	0.771	0.170	4.5	< 0.001
Factors:								
Species – Great Tit	-3.42	1.02	3.4	0.002	0.0234	0.237	0.099	> 0.5
Site –Forest site	1.65	1.20	1.4	0.2	0.0526	0.241	0.22	> 0,5
Continuous variables – centered:								
Diversity mosses	-0.0700	0.998	0.070	> 0.5	-0.484	0.194	2.5	0.02
Moss cover	4.68	2.83	1.7	0.1	0.664	0.578	1.1	0.3
Weight nest base					-0.0708	0.0381	1.9	0.07

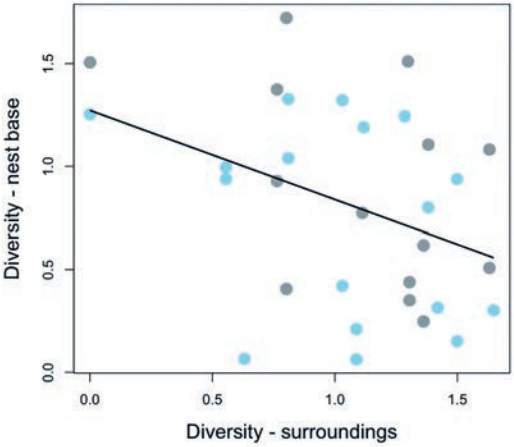


Fig. 4. Shannon-diversity of mosses in the nest base and the surrounding area were negatively correlated (simple correlation coefficient across all nests 0.12, p = 0.03, df = 29). The regression line is for illustrative reasons only. Blue dots: Blue Tit, grey dots: Great Tit. For a more elaborated test see Tab. 2. – *Die Shannon-Diversität der Moose innerhalb der Nestbasis und der Umgebung waren negativ korreliert (einfacher Korrelationskoeffizient über alle Nester 0,12, p = 0,03, df = 29). Die Regressionsgerade wurde zur Illustration eingezeichnet. Blaue Punkte: Blaumeise, graue Punkte: Kohlmeise. Siehe auch Tab. 2 für ein Modell mit mehr unabhängigen Variablen.*

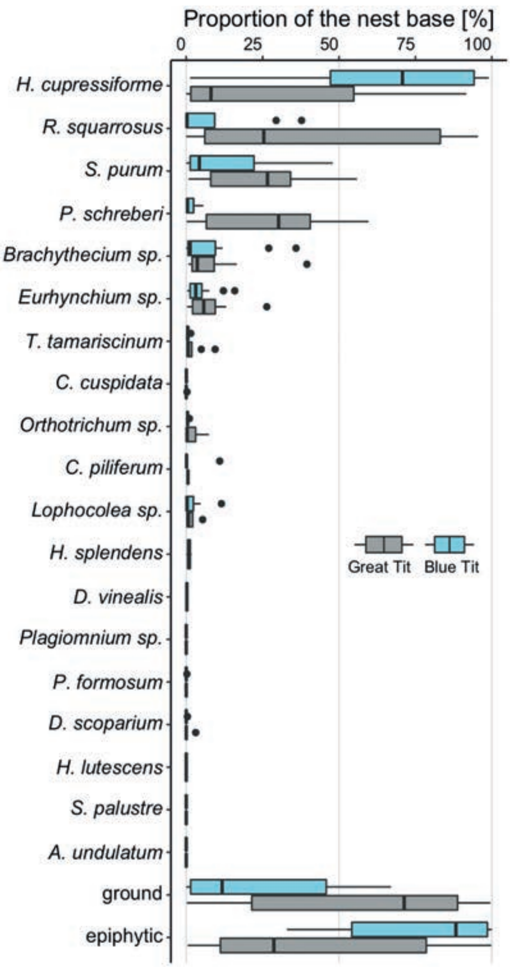


Fig. 5. Proportion of dry weight of moss species in the nest bases of Blue Tits and Great Tits. Boxplots include the median, interquartile range, and whiskers with 1.5-fold interquartile range. Filled symbols indicate values beyond the whiskers. Moss species were ordered by descending total mean of their proportion in both tit nest bases; epiphytic = small, epiphytic mosses; ground = long-stemmed, ground-growing mosses. – *Mittleres relatives Trockengewicht der Moosarten an den Nestbasen von Blaumeisen und Kohlmeisen. Boxplots enthalten den Median (fette Linie), Grenzen der ersten und dritten Quartile (Rechteck) und die Antennen („Fehlerbalken“) zeigen das 1,5-Fache des Interquartilabstands. Ausreißer jenseits der Antennen sind durch einzelne gefüllte Symbole vermerkt. Die Moosarten wurden nach ihrem mittleren Anteil in allen Nestbasen in absteigender Reihenfolge aufgeführt, epiphytic = kleine, epiphytische Moose, ground = langstämmige, bodenbewachsende Moose.*

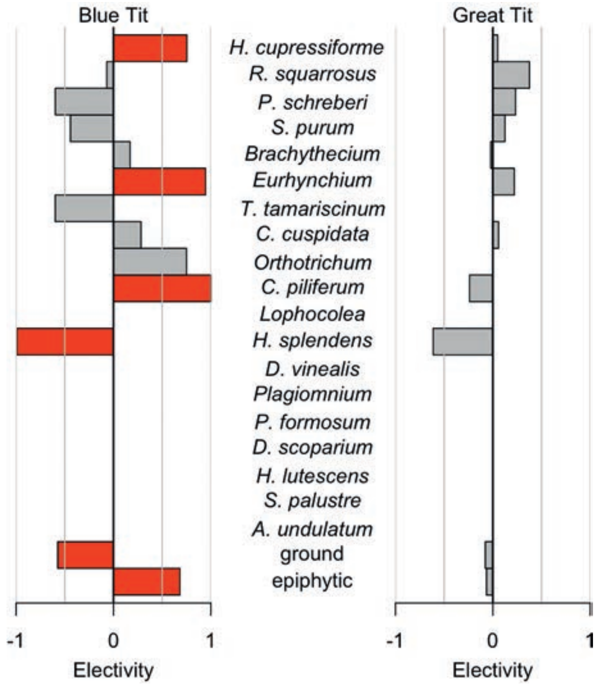


Fig. 6. Electivity index of the moss species across all nests where at least 5 indices were available. Positive indices indicate a positive selection (preferential use) and negative indices a negative selection (discrimination against) of the respective moss species. Red-colored bars represent significant deviation from 0 using a sequential Bonferroni correction. Moss species ordered by descending total mean of their proportion in the tit nest bases; epiphytic = small, epiphytic mosses; ground = large-stemmed, ground-growing mosses. – *Elektivitäts-Index der Moosarten für Arten, bei denen mindestens 5 Indices über alle verfügbaren Nester einer Meisenart berechnet werden konnten. Positive Indices deuten auf eine positive Selektion (Präferenz) und negative Indices auf eine negative Selektion (Diskriminierung) der jeweiligen Moosart. Rote Balken repräsentieren eine signifikante Abweichung von 0 unter Anwendung einer sequentiellen Bonferroni-Korrektur. Die Moosarten wurden nach ihrem mittleren Anteil in den Nestbasen in absteigender Reihenfolge aufgeführt, epiphytic = kleine, epiphytische Moose, ground = langstämmige, bodenbewachsende Moose.*

Discussion

Similar to other studies, we found that the weight of Blue Tit nest (-bases) is higher in comparison to Great Tit nests, although the Blue Tit (7.5–14.7 g) only weighs about ~60% of a Great Tit (11.9–22.1 g, del Hoyo et al. 2007). In both species the diversity of mosses in the surroundings is negatively correlated to the diversity of mosses in the nest base, a first indication of selective behavior in both tit species when collecting nesting material. More important are the results of the evaluation of the Electivity index for individual moss species: Blue Tits are particularly selective, as their nest bases consist mainly of one moss species – *H. cupressiforme* (Fig. 5). Alongside the positive selection of *H. cupressiforme,* Blue Tits also showed selective behavior against and towards the two growth forms (Fig. 6). The results are in line with the findings of other studies from other countries (Glądalski et al. 2021, Hříbek 1985, Wesołowski und Wierzcholska 2018). Furthermore, some moss species seem to be completely ignored or seem to be only accidentally brought to the nest. *H. splendens* as well as *Thuidium tamariscinum*, two large, long stemmed and rather weft-forming (tightly woven) woodland mosses, were both slightly (*T. tamariscinum*) or significantly (*H. splendens*) discriminated against by Blue Tits. *C. piliferum* was significantly preferred as a nesting material, however the sample size of this moss species is rather low.

H. cupressiforme is the most common moss in the nests of Blue Tits in a variety of studies from different countries in different habitats (Glądalski et al. 2021, Hříbek 1985, Wesołowski und Wierzcholska 2018). *H. cupressiforme* is a cosmopolitan species, growing on different substrates with a wide range of tolerance to environmental conditions (Frahm and Frey 2004, van der Wijk et al. 1964). In our study, it seems that mainly epiphytic growing shoots of *H. cupressiforme* were brought to the nests. This could explain the large difference between the low abundance of *H. cupressiforme* found growing on the ground and its high proportion in the Blue Tit's nest bases, as epiphytic growing mosses were excluded in the fieldwork if they grew on tree trunks or deadwood higher than 30 cm. From their study, conducted in a deciduous forest, Wesołowski and Wierzcholska (2018) report that mostly epiphytic mosses were found in the nests of Blue Tits as well as in those of Great and Marsh Tits *Poecile palustris*. Other studies also assessed only some of the epiphytic mosses, as it is practically impossible to identify them to species level in the field at a distance of several meters. Furthermore, it is difficult to estimate the abundance of these mosses within the surroundings as they can grow up to several meters along a tree trunk. Glądalski et al. (2021) recorded mosses up to 2 m above the ground while Wesołowski and Wierzcholska (2018) assessed mosses up to 4 m. Not being able to accurately assess the availability of all epiphytic mosses is a methodological flaw of the available studies, including ours.

Great Tits showed no selective behavior in relation to any moss species. According to Balát (1976), *Polytrichum formosum* was rarely found, while *P. schreberi* and *S. purum* were found in high abundances in the nests of Great Tits. A similar pattern can be found in our study, where *P. schreberi* and *S. purum*, rather common ground-growing (coniferous) forest mosses, were often used according to their abundances in the nest bases of Great Tits. In addition, *R. squarrosus*, a ground-growing moss, was also found at higher abundances in their nest base (Fig. 5), which was also reported by Hříbek (1985). Contrary to the findings of Wesołowski and Wierzcholska (2018) from a deciduous forest, Great Tits used ground-growing mosses in this study and did not selectively utilize epiphytic mosses. However, the abundance and diversity of ground-growing mosses varies between deciduous and coniferous forests, due to the annual leaf litter affecting the growth of ground-growing moss species (Cleve et al. 1983, Légaré et al. 2005, Natalia et al. 2008). This suggests that breeding habitat does have a large influence on the use of different moss species as it restricts potential selective behavior to the set of moss species present or available in the breeding habitat (Glądalski et al. 2021).

One hypothesis regarding those interspecific differences is that the mostly single-brooded Blue Tits may invest more in nest construction than Great Tits, which are known to occasionally have second broods (Perrins 1979). This argument is based on a trade-off between construction of high quality nests, which need a certain investment, and the number of broods per year. Blue Tit nests are also larger (higher in standardized nest boxes) and heavier than Great Tit nests, whereby especially the nest base contributes to this difference (Alambiaga et al. 2020, Lambrechts et al. 2015, 2014, Smith et al. 2013). This is remarkable as it contradicts the generally positive correlation between nest weight and bird weight (Hansell and Overhill 2000, Slagsvold 1989). However, evidence for this correlation is mostly derived from studies on open-nesting birds. This reversed pattern among cavity-breeding songbirds (e.g. Paridae-members, Alambiaga et al. 2020) indicates different pressures shaping the nesting ecology of cavity breeders compared to open-nesting species. Blue Tits also need more time to build the nest base than Great Tits (Smith et al. 2013). Furthermore, Blue Tits make use of aromatic plants and their parasite-repelling compounds by incorporating them into their nests (Lambrechts and Dos Santos 2000, Petit et al. 2002).

In summary, Blue Tits seem to be rather picky during nest construction and their selective utilization of mosses is a consistent phenomenon across regions and habitats. The interspecific differences compared with Great Tits indicate that the ecological drivers behind the selective utilization of mosses for nest construction might differ between these two species. To elucidate this ecologically complex topic, we propose four perspectives under which the (selective) utilization of mosses should be looked at:

1. Some moss species have antimicrobial compounds (Bukvicki et al. 2012, Klavina et al. 2015, Lunić et al. 2020) and the utilization of certain species might depend on these compounds that function inside nests as insecticides (Glądalski et al. 2021, Wesołowski und Wierzcholska 2018). Additionally, the selection of moss species might depend on the nesting site. A comparative study, analyzing the different bioactive compounds between used vs.

unused moss species in tit nests compared to the parasitic load of nest sites, might contribute to a better understanding of the utilization of mosses as nesting materials.

2. That the utilization of certain mosses is related to conservation of temperature is rather unlikely, as the moss base contributes very little to the insulation of the nest compared to the nest cup (Mainwaring 2017, Schöll and Hille 2014). In relation to structurally supportive characteristics of certain moss species, Wesołowski and Wierzcholska (2018) argue that the interspecific selective differences between Great Tits and Blue Tits are related to the differences in the weight of their broods. Following this hypothesis, Great Tits need structurally more supportive, larger, long-stemmed mosses for their brood which can be up to 70 g heavier before fledging, including one adult (Wesołowski and Wierzcholska 2018). In comparison to Blue Tits, Great Tits therefore need to utilize rather long-stemmed, more rigid mosses. Furthermore, mosses can take up large quantities of water and can therefore contribute to a suitable nesting environment as they protect the brood from moisture. However, Wesołowski and Wierzcholska (2018) state that the water uptake ratio did not differ between the used and non-used mosses, indicating that the water-absorbing aspect of the moss base might not influence the tits moss utilization.

3. In addition to certain attributes of the selected moss species, environmental pressures or restrictions might also influence the behavior of tits during the collection of nesting materials. Wesołowski and Wierzcholska (2018) argue that the selected moss species were more profitable to pluck. Depending on the environment, tits can choose between various growth forms of mosses on different substrates like wefts of pleurocarpous mosses, dense mats of pleurocarpous mosses, or tall turf mosses (Glime 2017b). Wefts of pleurocarpous mosses like *H. splendens* often have very long shoots and are strongly connected with the substrate. Dense mats of pleurocarpous mosses seem to be more profitable to pluck (Wesołowski and Wierzcholska 2018) as they yield larger bundles when plucked and are often rather loosely connected with the substrate (like the epiphytic growth form of *H. cupressiforme*). In contrast, tall turf mosses (e.g. *Dicranum scoparium* and *Polytrichum formosum*) often show an acrocarpous growth form with long shoots and a strong connection to the substrate. As Wesołowski and Wierzcholska (2018) state, the 'pluckability' undoubtedly restricts or influences the tits' choice and (at least partly) shapes the observed selective tendencies. Furthermore, the preference of epiphytic moss species may be related to a potentially lower predation pressure during moss-gathering on tree trunks or branches compared to gathering on the ground (Wesołowski and Wierzcholska 2018) and might therefore be a strong *in situ* environmental pressure, potentially shaping the tits' nest construction behavior. Furthermore, the distance from their nests largely determines the tits' nest construction costs. Therefore it could be expected that the birds prefer to gather their nesting material in close proximity to their breeding cavity and therefore might prefer epiphytic mosses perhaps growing at a similar height on the surrounding trees. Tits also gather mosses from up to 60 or even 80 meters away (personal observations, Wesołowski and Wierzcholska 2018), suggesting that they are willing to fly relatively long distances to gather suitable nesting materials. However, if environmental pressures were the only cause of this selective behavior, they must be very strong and consistent across regions since the selective gathering of certain moss species seems to be a general pattern among Blue Tits.

4. The tits' perception of their environment offers a fourth perspective on their selective moss gathering. The observed interspecific differences in their moss-gathering behavior in particular may relate to the ecomorphological differences between Blue Tits and Great Tits. Among their various morphological attributes, Blue Tits and Great Tits show differences in locomotion (Carrascal et al. 1990, Leisler and Winkler 1991). In relation to how and where the two Paridae species feed, these ecomorphological differences become obvious. Blue Tits feed more often at greater heights on twigs and buds, whereas Great Tits prefer to feed on the ground or on thicker branches and trunks (Lack 1971, Suhonen et al. 1994). This differentiation in feeding behavior may also apply to the gathering of certain nesting materials, whereby Great Tits would gather their nesting materials mainly from the ground and Blue Tits would rather use nesting materials from trees.

Our study presents evidence for a complex ecology of nest construction within cavity breeders like the

Paridae. The prominent interspecific differences in terms of selective collection of nesting materials and nesting investment between Blue Tits and Great Tits shed new light on the breeding ecology of these two tit species. Further research is needed to unravel the drivers of such different nest construction strategies in two closely related bird species. For example, we found even a negative correlation of the diversity of mosses between nests and surroundings also for Great Tits, which might be interpreted as an indication of some selective behavior. But the more detailed analysis of moss species failed to find a selective behavior. This might also be an effect of sample size and estimating availability of moss species for nest construction. Therefore in further studies we suggest an increased sample size across more habitat types with a more comprehensive sampling of the moss availability within the surroundings. Detailed observation of the collection of moss species by individual birds, as well as choice experiments in aviaries, are options to better understand the selection of moss species. Furthermore, there is also a need to expand the taxonomic coverage of tits: very few studies have been carried out on other members of this interesting bird family.

Zusammenfassung

Nester sind der Ausdruck des Genotyps von Individuen und Arten (erweiterter Phänotyp). Eine Analyse der zum Nestbau verwendeten Materialien kann Einblicke in die brutökologischen Ursachen und Folgen verschiedener Nestbaustrategien liefern. Eines der häufigsten Nistmaterialien in Nestern von Meisen sind Moose, jedoch ist deren Rolle in deren Nestökologie wenig erforscht. Wir analysierten die Moosarten in den Nestbasen von Blaumeisen *Cyanistes caeruleus* und Kohlmeisen *Parus major*. Dafür verwendeten wir standardisierte Nistkästen und verglichen die Anteile an Moosarten in den Nestbasen mit deren Abundanz in der Nestumgebung, um zwischen einem selektiven oder abundanzbestimmten Verhalten unterscheiden zu können. Wir konnten zeigen, dass bei beiden Meisenarten keine positive Korrelation zwischen der Moosarten-Diversität in den Nestbasen und der Nestumgebung besteht. Allerdings fanden wir nur für Blaumeisen einen selektiven Eintrag von gewissen Moosarten, wobei *Hypnum cupressiforme* die häufigste Moosart in deren Nestbasen war. Außerdem waren die Nestbasen von Blaumeisen schwerer als die von Kohlmeisen. Dieses Ergebnis erlaubt die Hypothese, dass Blaumeisen mehr in die Konstruktion des Nestes investieren als Kohlmeisen. Abschließend schlagen wir für künftige Untersuchungen vier Perspektiven vor, die die Verwendung von Moosen beeinflussen könnten: (1) chemische Inhaltsstoffe – als potenzielle Insektizide, (2) Mooseigenschaften – z. B. Größe, Festigkeit, Wasseraufnahmekapazität, (3) Umwelteinflüsse – z. B. Prädationsdruck während des Sammelns von Moosen oder Pflückbarkeit verschiedener Moosarten, (4) Ökomorphologie der Meisen – Unterschiede in der Fortbewegung und Raumnutzung.

Acknowledgements. We thank Roland Brandl (Philipps University of Marburg) for his support on the statistical analysis as well as his constructive suggestions and comments on the manuscript and Eduard Hertel † (University of Bayreuth) for contributing to this study through his bryological expertise. We thank Martin Hertel (BaySF, Bavarian Forestry Authority – forest management unit Fichtelberg) as well as Dirk Muschik (Forestry Department of Bayreuth) for their consent to conduct research in the areas under their administration, the former also for the manufacture of the nesting boxes in the workshops of the forest management unit Fichtelberg.

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Received: 12. September 2022
Accepted after revision: 4. October 2022



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