

Article

Bryophyte Use in Bird Nests Varies with Nesting Location in a Tropical Montane Forest

Akekachoke Buranaanun ¹, Nantida Sutummawong ² and Ekaphan Kraichak ^{1,3,*}

¹ Department of Botany, Faculty of Science, Kasetsart University, Bangkok 10900, Thailand; akekachoke.b@ku.th

² Department of Forest Biology, Faculty of Forestry, Kasetsart University, Bangkok 10900, Thailand; nantida.su@ku.th

³ Special Research Incubation Unit on Cryptogam Biodiversity and Climate Responses, Kasetsart University, Bangkok 10900, Thailand

* Correspondence: ekaphan.k@ku.th

Abstract

Bryophytes serve as nest material for many temperate bird species, yet their role in tropical avian ecology remains poorly studied despite high bryophyte and passerine diversity. In this study, we quantified bryophyte use as nest material by passerine birds at Doi Inthanon National Park, Thailand, over one breeding season. We observed 47 nests from 22 species to contain bryophytes, of which 26 nests from 15 species were sufficiently complete for quantitative analysis. The mean proportion of bryophytes by dry weight was 0.513 ± 0.278 across all nests, with no significant overall preference for bryophytes over other materials. Of the three bryophyte groups identified, pleurocarpous mosses significantly dominated, comprising 0.851 ± 0.156 of the bryophyte proportion ($p < 0.001$). Beta regression model selection identified nest location as the strongest predictor of bryophyte use, the pseudo- R^2 value of 0.21 indicated a modest improvement from the null model. Tree-nesting species used a significantly higher proportion of bryophytes than ground-nesting species (0.60 ± 0.26 vs. 0.32 ± 0.23 ; $p = 0.011$). This study did not quantify ambient bryophyte availability surrounding nests, precluding differentiation between active avian selection and passive resource-driven material use. Our results highlight the importance of preserving intact forest canopies to maintain bryophyte–bird interactions in tropical montane ecosystems. Canopy loss may reduce epiphytic pleurocarpous moss resources and alters nest material composition for arboreal passerines, affecting breeding microhabitat conditions.

Keywords: mosses; liverworts; tropics; bird nest habitat; nest material

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1. Introduction

Most birds, except those that are brood-parasitized, build nests for reproduction [1,2]. This is especially well-documented for passerine birds, which construct nests mainly from available materials in their surroundings [2,3]. These nests provide an optimal microclimate that supports incubation by the parental birds. The nests maintain the humidity and temperature necessary for the development of the broods until they reach the juvenile stage and eventually leave the nests [2]. Plant material is often used as nest material, as it is the most abundant material in the landscape and can provide camouflage for the nest in the surrounding environment [4]. Some studies have also suggested that plant

material may have antimicrobial and insecticide properties, which can protect the broods [5,6]. Among many plant materials that birds use for nest construction, bryophytes may appear to be one of the less common options for the birds. Unlike other plant materials, bryophytes are able to absorb a large amount of water directly into their cells [6]. Therefore, they are hypothesized to play a crucial role in increasing water retention and thermal insulation in bird nests [6,7].

Many studies have recorded the use of bryophytes by passerine birds in Europe and North America [8–15], with a handful of studies from tropical ecosystems [5,16–18]. These studies have provided extensive quantitative records of bryophyte use in bird nests, indicating non-random selection of bryophytes as nest materials. For Southeast Asian countries, like Thailand, several studies have examined the plant materials in bird nests [19,20], but few have specifically identified the use of bryophytes as nest material [21]. In Thailand, at least 1300 bryophyte species [22,23] and 1092 bird species were reported [24]. Given such a high level of diversity of both birds and bryophytes, it is very likely that birds have utilized bryophytes as nest material in tropical systems in Thailand.

Doi Inthanon National Park is an ideal location for studying bird–bryophyte interactions. As the highest montane forest in Thailand, Doi Inthanon National Park is reported to host at least 210 bryophyte species [25,26], along with 525 bird species [27]. Here, bryophytes densely cover a wide variety of substrates from soil to tree bark. With such abundance in the landscape, a number of birders have recorded substantial photographic evidence for the use of bryophytes in bird nests. Despite the commonness of these occurrences and the high bird and bryophyte richness at this location, no detailed study has examined which bird species use bryophytes or whether they preferentially select them over other materials.

In this study, we aim to quantify the use of bryophytes as bird nest material, focusing on the passerine birds, the largest group of nest-constructing birds at Doi Inthanon National Park. Specifically, this study addresses the following research questions: (1) What proportion of nest material is composed of bryophytes in passerine bird nests at Doi Inthanon National Park, and how does this vary across species? (2) Which type of bryophytes is the most commonly found as nest material? (3) Which factors influence the proportion of bryophytes used as nest material? Our hypotheses are as follows:

H1. *Bryophytes are preferred as nest material in this habitat due to their high local abundance.*

H2. *Pleurocarpous mosses are preferred over other bryophyte groups due to their highly branched morphology, which facilitates collection and interwoven nest construction.*

H3. *Tree-nesting, canopy-foraging, small birds are more likely to have a higher proportion of bryophytes as nest material, due to their access to the materials and small nest size.*

To address these questions, we surveyed passerine bird nests during one breeding season and collected the abandoned nests to quantify the amount and type of bryophytes used in the nests. Because we did not quantify ambient bryophyte availability, we interpret these factors as correlates of bryophyte use rather than evidence of active selection by birds. In contrast to these earlier Thai surveys, which catalogued nest materials only qualitatively, the present study quantifies bryophyte use as dry-weight proportions, resolves bryophytes into three functional groups, and applies beta regression to identify the drivers of their use. The results will provide one of the few quantitative datasets on the use of bryophytes as nest material in tropical birds.

2. Materials and Methods

2.1. Study Area

Doi Inthanon National Park is located in the Northern region of Thailand, Chiang Mai province. The park covered the area of 482.4 km² with altitude of 400–2565 m above sea level (MASL), including the highest peak in Thailand. Mean annual temperature is approximately 20 °C, with the coldest period occurring in December and January, when minimum temperatures at the summit can fall to 0–5 °C. Mean annual precipitation ranges from 2000 to 2100 mm. During the breeding season (February to June) of 2023, the average maximum and minimum temperature were 18.0 °C and 9.8 °C, respectively. The average daily precipitation was 5.1 mm/day [28]. Generally described as Tropical Montane Rainforest, Doi Inthanon National Park has at least three vegetation types according to their elevations. First, the low-elevation vegetation type (Altitude 400–1000 MASL) consists of Deciduous dipterocarp forest, Dry evergreen forest, Mixed deciduous forest, and Pine-deciduous dipterocarp forest. Second, the mid-elevation vegetation type (Altitude 1000–2000 MASL) consists of Lower montane forest, Lower montane oak forest, Lower montane pine-oak forest, and Lower montane coniferous forest. Third, the high-elevation vegetation type (Altitude 2000–2565 MASL) consists of Upper montane forest and Montane peat bog [25,29]. Our study sites focused on only the montane forest area, where bryophytes were found in abundance. To cover different vegetation types within montane forest area, we chose four nature trails for the survey of bird nests. These were Angka Nature Trail (2535–2568 MASL), Kew Mae Pan Nature Trail (2189–2291 MASL), Jeep Track Nature Trail (1658–1686 MASL), and Pha Tang Nature Trail (1605–1653 MASL; Figure 1; Table S1).

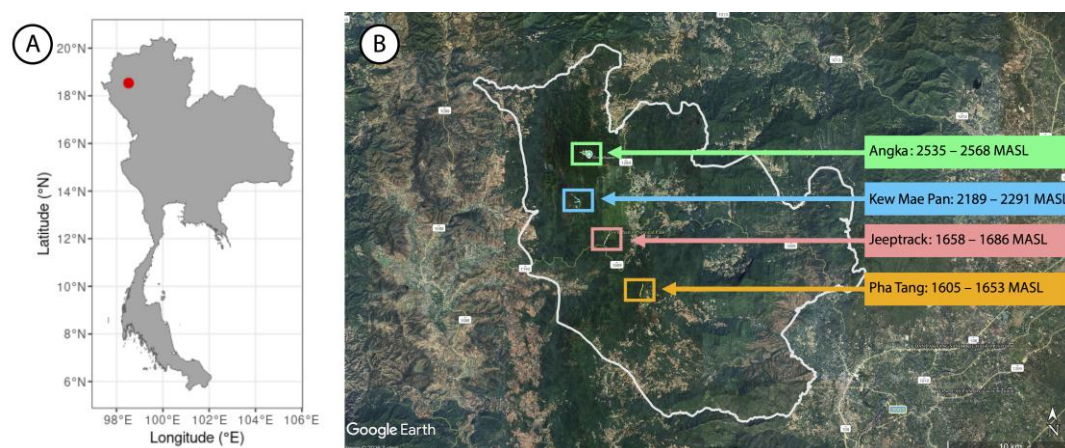


Figure 1. Sampling locations of the current study: (A) the location of Doi Inthanon National Park (red dot); (B) sampling locations in four nature trails within Doi Inthanon National Park, including Pha Tang and Jeep Track in the mid-elevation vegetation type at 1606–1686 MASL (meters above sea level); and Kew Mae Pan and Angka in the high-elevation vegetation type at 2188–2535 MASL.

2.2. Collection and Handling of Bird Nests

Bird nest surveys were carried out from January 2023 to September 2023, at least one trip per month. During the breeding period (February 2023 to June 2023), the visits were doubled to twice per month to observe and collect passerine bird nests after they leave a nest [30,31]. The observation and collection of bird nests were approved by the Department of National Parks, Wildlife and Plant Conservation (Permit Number MNR 0907.4/26790). Additional field metadata are provided in Table S2.

We used KOWA SVII 8 × 32 binoculars to observe nesting behavior and foraging locations, a Canon EOS R7 camera (Kunisaki, Japan) with a Canon RF 100–400 mm f/5.6–

8 IS USM lens to record photographic evidence, and a GARMIN eTrex 10 GPS unit (New Taipei City, Taiwan) to record nest coordinates. A nest was considered abandoned when no bird was seen visiting or using it for at least one week. We then collected the nest and recorded the following information: owner species, collection date, nest height above the ground, nest size, nest habitat (tree or ground), nest type, and nest weight. Following the field measurements, each nest was placed in a sealed plastic bag for subsequent examination in the laboratory.

For the laboratory study, only complete nests were examined. The chosen nests were dried for 24 h in an oven at 60 °C. Then, the dried nests were carefully dismantled under a microscope, following the previous protocols [1,3,13]. The dismantled materials were grouped into bryophytes and non-bryophytes. The weight of each material type was measured and calculated into percentages of total dry nest weight [16].

2.3. Identification of Bryophytes in the Nests

In our pilot study conducted in 2022, we observed only mosses and liverworts in the nests, with no hornworts being identified. Hornworts are typically found on the moist soil and often found in low abundance in tropical montane ecosystems [32]. Consequently, we decided to focus on the identification of bryophyte materials categorized into three broad groups: pleurocarpous mosses, acrocarpous mosses, and liverworts. These categories were defined by morphological characteristics and growth forms rather than by taxonomic groups, because our focus was on the functional differences among these groups. Pleurocarpous mosses (Superorder Hypnanae W. R. Buck, C. J. Cox, A. J. Shaw & Goffinet) are distinguished by a creeping main stem that branches laterally, whereas acrocarpous mosses have an upright main stem with minimal or no branching. Acrocarpous morphology spans many lineages within Phylum Bryophyta Schimp., likely as a result of convergent evolution. Liverworts (Phylum Marchantiophyta Stotler & Crand.-Stotl.) found in the bird nests predominantly belong to the leafy liverwort group (Class Jungermanniopsida Stotler & Crand.-Stotl.), which differs from mosses in possessing two-ranked lateral leaves and oil bodies [32].

2.4. Analysis of Data

All statistical analyses were conducted in R (version 4.6) [33]. Bryophyte content was expressed as a proportion of total nest dry weight. The data from incomplete or broken nests, defined as losing more than 20% of their supposed volume, were excluded. Prior to analysis, all proportions were adjusted using the transformation of Smithson & Verkuilen [34] to avoid boundary values of 0 and 1, which are undefined under logit transformation and beta regression:

$$\text{prop}_{\text{adj}} = \frac{\text{prop} \times (n-1) + 0.5}{n}$$

where prop_{adj} is the adjusted proportion, and n is the total number of nests. In this case, $n = 26$ for the complete nests was used.

To test whether birds used bryophytes as a greater proportion of nest material than expected by chance, we applied a one-sample t -test on logit-transformed total bryophyte proportions against a null value of $\text{logit}(0.5) = 0$. We used a one-tailed alternative (greater than). The Shapiro–Wilk test of the logit-transformed values did not significantly deviate from the normal distribution ($p = 0.54$), allowing the application of the one-tailed t -test.

To test whether pleurocarpous mosses dominated the bryophyte component of nests, we applied a one-sample t -test on logit-transformed pleurocarpous proportions against $\text{logit}(1/3) = -0.693$, representing the null expectation of equal representation among the three bryophyte groups. A one-tailed alternative (greater than) was used to test the H1 (bryophytes are preferred nest material). The Shapiro–Wilk test of the logit-transformed

values did not significantly deviate from the normal distribution ($p = 0.24$), allowing the application of the one-tailed t -test.

To identify factors associated with variation in total bryophyte proportion as nest material, we used beta regression via the R package “betareg” [35], which is designed for continuous response variables bounded between 0 and 1. The candidate predictors included nest location (tree vs. ground), foraging stratum of the bird species (canopy, mid-story, understory), and bird body size, derived from the first principal component (PC1) of body size and mass. Nest location and foraging stratum for each species were determined from field observations, while bird size and mass were obtained from the Birds of the World database [36]. The reported ranges of bird size and mass were averaged and used as a trait value for each species.

Species identity was not modelled as a random effect because most species were represented by only one or two nests (range 1–5 nests per species). Because of the opportunistic nature of the sampling, the dataset was insufficient to reliably estimate between-species variance or to test species-specific preferences directly. Instead, bird body size was used as a proxy for species identity, under the hypothesis that larger birds are more likely to use sturdier nesting material than bryophytes. The size and mass data were then scaled and subjected to principal component analysis (PCA) using the function “prcomp” to reduce the dimensionality of potentially correlated data. The resulting first principal component (PC1) accounted for 90.6% of the variation and was subsequently used as the variable for bird size.

Given the small sample size ($n = 26$) relative to the number of predictors, models were restricted to a maximum of two predictors, with one main variable (nest location or foraging stratum) and bird size as a controlled variable. No interaction term was modeled to reduce the number of estimated parameters. A null intercept-only model was also included as a reference. Model selection was performed using the corrected Akaike Information Criterion (AICc), which applies a stronger penalty for model complexity in small samples (R package “MuMIn” [37]). Delta AICc (ΔAICc) was calculated by subtracting the AICc of the model with the smallest AICc (the best model). Models within $\Delta\text{AICc} < 2$ of the best model were considered competitive. Among the competitive models, the model with the smallest number of estimated parameters was chosen as the best (most parsimonious) model [37]. A pseudo- R^2 for the final model was calculated from the likelihood ratio between the fitted model and the null model. This metric reflects how much more likely the data are under the fitted model relative to the null, rather than the proportion of variance explained in the ordinary least squares (OLS) sense. It is best interpreted as a measure of relative support for the fitted model over the null, rather than as an index of explanatory power, and OLS-based benchmarks for “good” or “poor” fit do not directly apply [36].

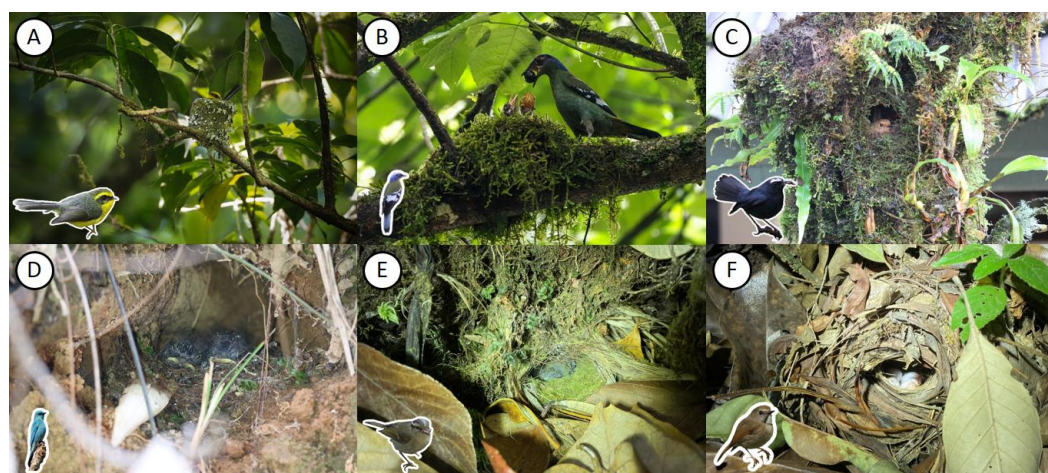
3. Results

3.1. Bird Preference of Bryophytes as Nest Material

From surveys conducted between February and September 2023, a total of 47 nests from 22 passerine bird species were observed to contain bryophytes as nest material (Figure 2). Of these, 26 nests from 15 species were sufficiently complete for further examination (Table 1), with one to five nests collected per species. By nest location, five species had ground nests and ten had tree nests. By foraging stratum, two species foraged in the canopy, seven in the midstory, and six in the understory. Seven nest shapes were recorded—dome, globular, cavity adopter, adherent cup, pendulous cup, pensile cup, and statant cup—with nest shape consistent within species.

Table 1. List of passerine bird species with bryophytes as nest material from Doi Inthanon National Park for the current study.

Species	Common Names	Nest Location	Foraging Stratum	Nest Shape	Number of Nests
<i>Aethopyga nipalensis</i>	Green-tailed Sunbird	tree	midstory	pendulous cup	2
<i>Alcippe fratercula</i>	Yunnan Fulvetta	tree	understory	pensile cup	1
<i>Anthipes monileger</i>	White-gorgeted Flycatcher	ground	understory	domed nest	1
<i>Brachypteryx cruralis</i>	Himalayan Shortwing	tree	understory	globular nest	1
<i>Chelidorhynch hypoxanthus</i>	Yellow-bellied Fantail	tree	canopy	statant cup	3
<i>Cochoa viridis</i>	Green Cochoa	tree	midstory	statant cup	5
<i>Dicrurus remifer</i>	Lesser Racket-tailed Drongo	tree	midstory	pensile cup	1
<i>Enicurus leschenaulti</i>	White-crowned Forktail	ground	understory	adherent cup	1
<i>Eumyias thalassinus</i>	Verditer Flycatcher	ground	canopy	cavity adopters	2
<i>Ficedula hyperythra</i>	Snowy-browed Flycatcher	tree	understory	globular nest	2
<i>Niltava grandis</i>	Large Niltava	tree	midstory	cavity adopters	1
<i>Phylloscopus intensior</i>	Davison's Leaf Warbler	ground	midstory	domed nest	2
<i>Phylloscopus reguloides</i>	Blyth's Leaf Warbler	ground	midstory	domed nest	2
<i>Schoeniparus castaneiceps</i>	Chestnut-crowned Warbler	tree	midstory	globular nest	1
<i>Tesia olivea</i>	Slaty-bellied Tesia	tree	understory	pendulous cup	1

**Figure 2.** Types of bird nests with bryophytes as nest material. (A) pendulous cup nest of *Chelidorhynch hypoxanthus*, (B) statant cup nest of *Cochoa viridis* (photo by Akkarachai Rojbandit), (C) domed nest of *Brachypteryx cruralis*, (D) cavity adopter nest of *Eumyias thalassinus*, (E) adherent cup nest of *Phylloscopus reguloides*, and (F) domed nest of *Anthipes monileger*. Each panel contains the picture of the adult bird on the lower left.

The mean bryophyte proportion by dry weight across all nests was 0.513 ± 0.278 (mean $\pm$ 1 SD). Values ranged from 0.037 in the single nest of *Alcippe fratercula* to 0.885 ± 0.07 in the three nests of *Chelidorhynch hypoxanthus* (Figure 3). The bryophyte proportion did not differ significantly from the null expectation of 0.5 (one-tailed one-sample *t*-test, $p = 0.54$), as the large variation in bryophyte proportion was observed across the nests and bird species (coefficient of variation = 54%).

3.2. Preference for a Bryophyte Group

Three groups of bryophytes were found as bird nest material (Figure 4). First, pleurocarpous mosses accounted for 0.851 ± 0.156 of the bryophyte material. This group consisted of moss genera with long, creeping stem, such as *Meteorium* and *Neckera*. Second, acrocarpous mosses accounted for 0.127 ± 0.146 of the bryophyte material, including genera with short, erect stems, such as *Dicranodontium* and *Fissidens*. Finally, liverwort was found at 0.022 ± 0.028 of the bryophyte materials. Most of the liverworts were leafy liverworts with robust stems, such as *Plagiochila* and *Bazzania*. Smaller and more delicate leafy

and thalloid liverwort, such as *Lejuenea* and *Metzgeria*, were also found as epiphytes on other bryophytes or non-bryophyte materials.

The proportion of pleurocarpous mosses was significantly different from the null expectation of 0.33 (one-tailed one-sample *t*-test, $p < 0.001$), indicating that pleurocarpous mosses were the most common form of bryophytes as nest material (Figure 5). In contrast, some tree-nesting species, including *Brachypteryx cruralis*, *Niltava grandis*, and *Ficedula hyperythra*, had a relatively higher proportion of liverwort, ranging from 0.264 to 0.604.

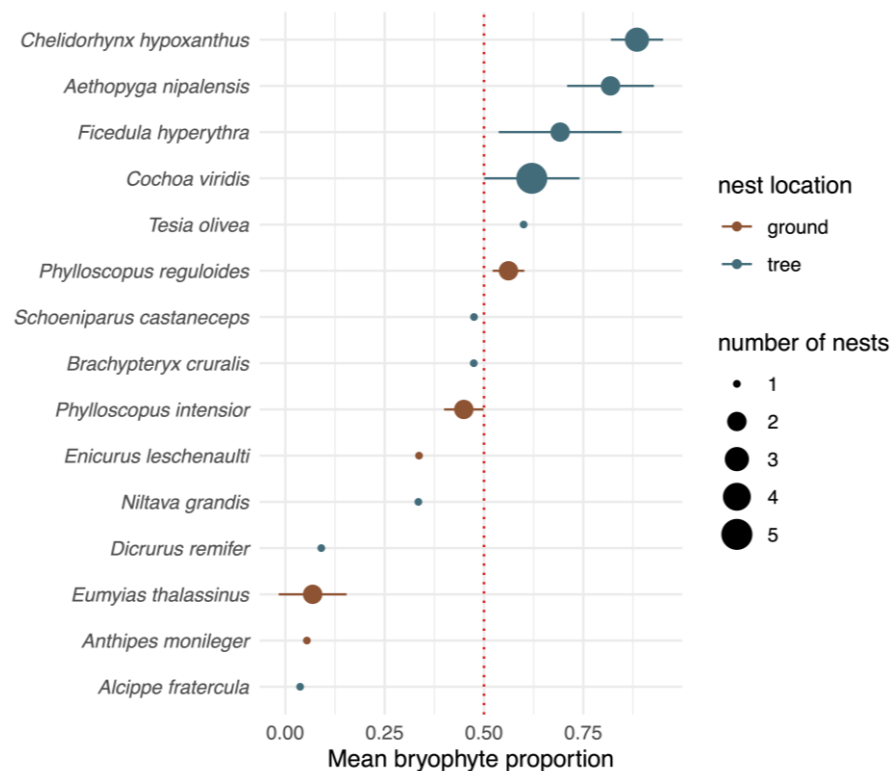


Figure 3. Mean proportion of bryophytes (dry weight) used as nest material in 15 passerine bird species. Dot size corresponds to the number of nests sampled per species, and dot color indicates nest location. Line segments represent the mean $\pm$ 1 standard deviation. The red dashed line marks a proportion of 0.5, indicating equal use of bryophytes and non-bryophytes as nest material.

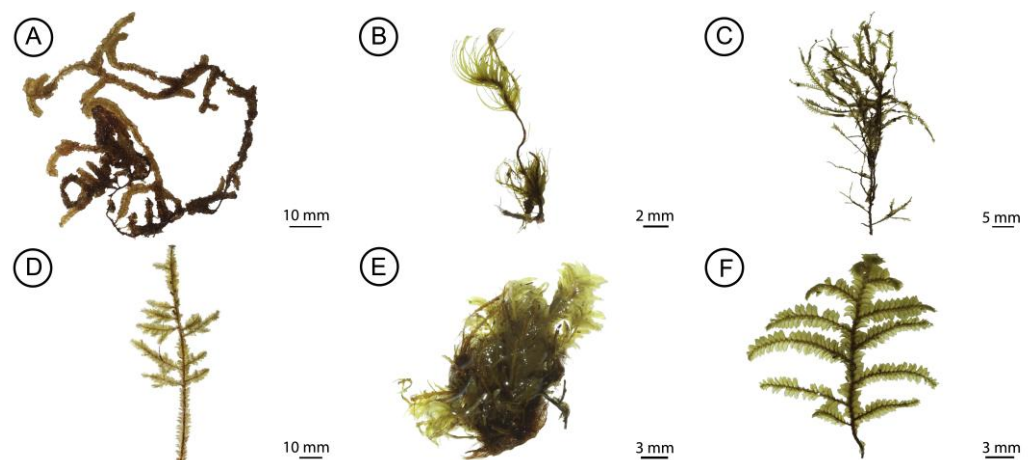


Figure 4. Examples of bryophyte genera found in the bird nests. Pleurocarpous mosses, (A) *Metesorium*, (D) *Neckera*; Acrocarpous mosses, (B) *Dicranodontium*, (E) *Fissidens*; Liverworts, including (C) *Plagiochila*, (F) *Bazzania*. The primary habitat for these taxa is epiphyte, with exception of *Fissidens* (E) that are found mostly on ground or at the base of the tree.

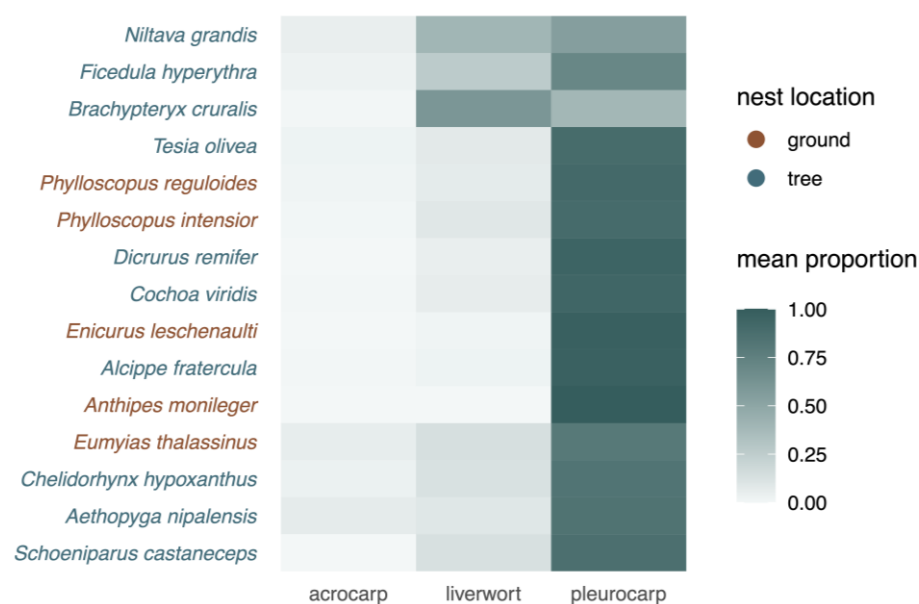


Figure 5. Heatmap of mean bryophyte proportions in nests across bird species and bryophyte groups: acrocarp = acrocarpous mosses, liverwort = leafy liverworts, pleurocarp = pleurocarpous mosses. Bird species (rows) are clustered by similarity in bryophyte composition. Colors of bird species names indicate nest location.

3.3. Factors Associated with Variation in Bryophyte Proportion

Among the seven candidate beta regression models with bryophyte proportion as the response variable, the model with nest location alone had the lowest AICc (−0.06). A second competitive model—nest location combined with PC1 of bird body size—fell within $\Delta\text{AICc} < 2$ ($\text{AICc} = 1.23$, $\Delta\text{AICc} = 1.29$). Because both models included nest location and the simpler model had fewer parameters, the nest-location-only model was selected as the best model (Table 2).

Table 2. Candidate models and associated AICc for factors attributable to bryophyte proportion in the bird nests from beta regression ($n = 26$). ΔAICc is calculated by subtracting each model's AICc from the smallest AICc value. The bold models are competitive as best models.

Model ¹	Number of Parameter ²	AICc	ΔAICc	Bird Group with More Bryophytes in Their Nest ³
~location	3	−0.06	0.00	tree-nesting *
~location + size	4	1.23	1.29	small, tree-nesting *
~1 (null model)	2	3.46	3.52	none
~location + stratum + size	6	4.40	4.46	small, tree-nesting *, canopy-foraging
~size	3	5.72	5.78	none
~stratum	4	7.50	7.56	canopy-foraging
~stratum + size	5	9.85	9.91	small, canopy-foraging

¹ variable names are location = nest location, size = PC1 of bird size, stratum = foraging stratum. ² The number of parameters in beta regression includes one parameter from the intercept, one from the precision parameter ($\varphi - \phi$), and one per additional level in each explanatory variable. ³ Interpretation based on the β coefficients from beta regression and summary statistics. Asterisks (*) denote significant coefficients in that model.

Nest location significantly predicted bryophyte proportion in nest construction (beta regression, pseudo- $R^2 = 0.21$). Tree-nesting species incorporated a significantly higher proportion of bryophytes than ground-nesting species (0.60 ± 0.26 vs. 0.32 ± 0.23 ; $\beta = 1.07$, $p = 0.011$). The precision parameter was significantly greater than zero ($\varphi = 3.28$, $p < 0.001$),

indicating relatively low dispersion in the response variable. The relatively modest pseudo- R^2 (0.21) indicated that the fitted model offers only a limited improvement in likelihood over the null model.

When considering bird body size, larger birds tended to use a lower proportion of bryophytes in their nests than smaller birds. However, the trend is not significant ($\beta = -0.18$, $p = 0.21$; Figure 6), and therefore the effect of bird size cannot be ascertained with the current dataset.

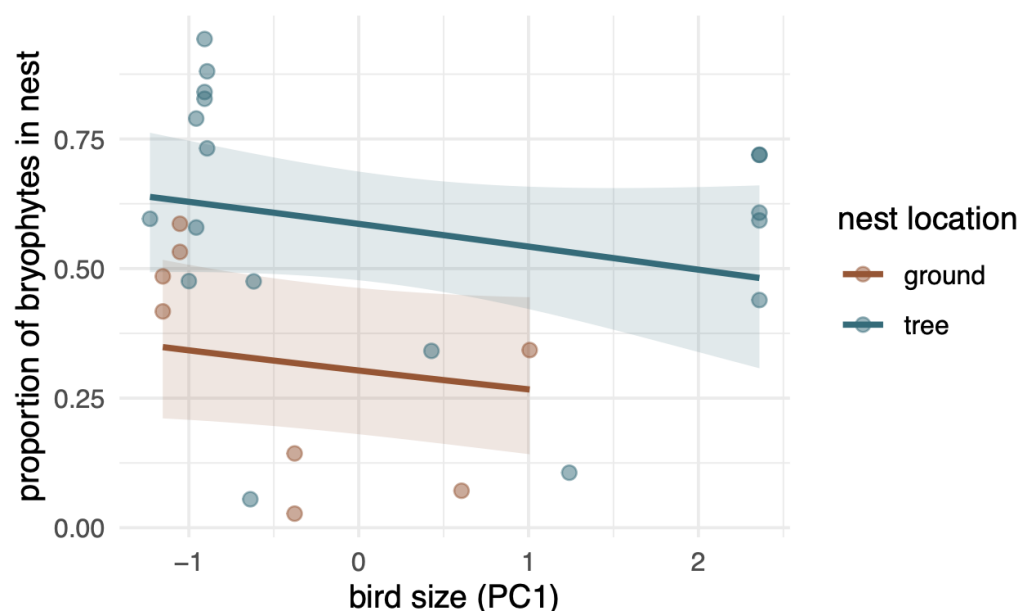


Figure 6. Scatter plot showing the relationship between the proportion of bryophytes (dry weight) used as nest material and bird size, derived from PC1 of size parameters, for 26 nests. Colors indicate nest location as either ground (brick red) or tree (teal). Solid lines represent model predictions from the beta regressions between bird size and bryophyte proportion in nests. The ribbons around the solid lines represent 95% confidence interval of the predicted values.

4. Discussion

4.1. Preference of Bryophytes as Nest Material

Among the 26 nests from 15 passerine bird species, the mean proportion of bryophytes was 0.513, with no significant preference for bryophytes as a dominant material. Of the three major bryophyte groups, pleurocarpous mosses were the most frequently used nest material. Tree nests contained significantly more bryophytes than ground nests, indicating that nest location is an important determinant of bryophyte use.

The increased bryophyte proportion in some nests could arise from two non-mutually exclusive mechanisms: passive incorporation of locally abundant resource and active preference for bryophytes. Bryophytes are abundant in montane forests such as our study site at Doi Inthanon National Park, and their high local density increases the probability that birds incorporate them into nests. To test this, a survey at a drier site with fewer bryophytes would likely yield a lower proportion of bryophytes used as nest material than observed in the present study. Using locally common materials may also improve nest camouflage, as nest materials that match the surrounding landscape reduce visibility to predators.

Camouflage may be one benefit favoring active selection, particularly for the tree nests. Epiphytic bryophytes lend a tree nest an outer surface whose color and texture match the bryophyte-covered branches on which it sits, and such background matching is widely regarded as a means of reducing detection by visually hunting nest predators

[4,38–40]. The outer padding of nests with epiphytic material, including mosses and lichens, has long been interpreted as crypsis through branch-matching [39]. Experimental work shows that closer visual matching between a ground nest or clutch and its background improves survival against predators [41]. Because exposed tree nests are generally more visible to predators than concealed ground nests, selection for color-matching bryophyte cladding could reinforce the higher bryophyte proportions we observed in tree nests, complementing the availability-based explanation.

The moderate overall contribution of bryophytes in the current study is consistent with other warm-climate studies and stands in contrast to colder systems. In Brazil, bryophytes were a frequent but generally non-dominant nest component [16], and Neotropical surveys in the Andes [42] and in the Ecuadorian tropics [18] likewise report bryophytes as one of several materials rather than the structural bulk of the nest. In cold temperate and boreal systems, bryophytes may additionally enhance nest thermal properties, since thicker, denser walls improve insulation, a pattern documented in cooler regions [43,44]. However, this thermal benefit is likely marginal in the milder breeding-season conditions (mean temperature between 9 to 18 °C) at Doi Inthanon and other places in the tropics. That bryophytes were not dominant in all surveyed nests suggests their proportion varies with bird species or other ecological factors.

With the current dataset, we cannot yet fully distinguish passive incorporation vs. active selection of bryophytes, because we did not quantify ambient bryophyte coverage in the microhabitat immediately surrounding each nest. Resolving this ambiguity is the most important next step. We recommend that future work pair each nest sample with a quantitative vegetation survey of substrate and surrounding bryophyte cover along with bryophyte identification to assess selectivity.

4.2. *Pleurocarpous Mosses as a Preferred Material*

The preference for pleurocarpous mosses could be the results of their three characteristics: ease of collection, higher biomass per foraging bout, and interlocking branched morphology ideal for nest wall construction. Pleurocarpous mosses are distinguished by their creeping stems and highly branched structure [32,45]. They are easy to collect and yield a larger quantity per gathering event compared with acrocarpous mosses [8,17]. Furthermore, this branching architecture facilitates the interlocking of material during nest construction. Acrocarpous mosses, in contrast, have mostly erect stems and grow only a few centimeters above the substrate [32]. They are therefore less likely to be picked up by birds, and less material is collected per picking event. Their short, loosely arranged, erect shoots also offer few points of attachment, making acrocarpous mosses less suitable as nest material.

Interestingly, leafy liverworts saw an increased proportion in nest of some species, including *Brachypteryx cruralis*, *Niltava grandis*, and *Ficedula hyperythra*. These tree nests were located below 1–2 m, typically on tree trunks supporting an abundance of *Plagiochila* and *Neckeraceae* [46], suggesting that birds collect liverworts in proportion to the local availability of these plants. In the study area, pleurocarpous mosses and leafy liverworts are more abundant as epiphytes, whereas acrocarpous and pleurocarpous mosses are equally abundant on the ground [25,26]. Thus, the increased liverwort proportion in these low arboreal nests could be better explained by the local microhabitat resource pool than by a species-specific preference for liverworts alone. Additional sampling of nests from target bird species from multiple seasons will be needed to determine active selection for liverworts.

4.3. *Effects of Nest Location and Bird Size*

Bryophytes are abundant in montane forests, yet different species prefer distinct microhabitats, including ground, rock, rotten wood, leaf surfaces, tree trunks, and the canopy [32]. They also occupy a range of vertical strata within the forest. The primary explanation for why tree-nesting birds use a higher proportion of bryophytes than ground-nesting birds is moss growth habit: pleurocarpous mosses predominantly occupy tree substrates [46,47]. As a result, tree-nesting birds encounter pleurocarpous mosses more frequently than ground-nesting birds do. The higher bryophyte proportion in tree nests is therefore best interpreted as a consequence of this vertical stratification of bryophyte resources [46] with pleurocarpous mosses dominating epiphytic tree substrates, rather than an active preference of tree-nesting birds for bryophyte material per se.

Recent work examining the relationships among beak morphology, species diet, and access to materials has demonstrated that foraging location predicts nest material composition [48]. When foraging location was considered among tree-nesting species, canopy-foraging species used the highest proportion of bryophytes as nest material. Understory species used the lowest proportion, a finding consistent with a study of bryophytes and nest material conducted in Poland [11]. In contrast, among ground-nesting species the canopy-foraging group showed the lowest proportion of bryophytes. Only one ground-nesting, canopy-foraging species was recorded in our study, *Eumyias thalassinus* (Verditer Flycatcher), which typically forages in open areas [49] and therefore has fewer opportunities to encounter and collect bryophytes. The pattern of canopy-foraging species using higher bryophyte proportion than understory foragers is consistent with the vertical stratification of epiphytic bryophytes in montane forests [46]. The results reinforce that access to bryophyte resources, rather than active preference, structures their use.

Bird size may also play a role. Larger birds tend to have larger beaks and build larger nests. They are more likely to select bigger, sturdier materials such as twigs and other vascular plant parts to support these nests [48]. Our data show only a weak, non-significant negative association between body size and bryophyte use, which we caution against over-interpreting. Because large passerines are uncommon in tropical montane forests [31], the sampled community spanned a narrow body-size gradient that, together with low within-species replication, likely leaves insufficient power to test this hypothesis reliably.

The use of bryophytes may also be species-specific. In studies from the temperate zone, several tit species (family Paridae) preferentially select particular groups of bryophytes [11]. A study in Ecuador, however, found no difference in the species composition of bryophytes among nest materials, suggesting that any species-specific preference may be weak [17]. We hypothesize that the apparently weaker interspecific selectivity in this tropical montane system reflects relaxed selection pressure: where many species of bryophytes and vascular plants are abundant and encountered year-round, birds gain little by specializing on particular taxa, whereas the highly specialized moss choice documented in temperate Paridae [11,14] may be favored under the lower and more seasonal availability of bryophytes and other plant materials in those systems. Testing this hypothesis will require detailed, species-level data on bryophyte use. To date, most studies report the occurrence of bryophytes in the nests of various bird species without testing for species-specific preference [8,15–17].

4.4. Limitations and Future Directions

Several limitations should be considered when interpreting these results, and each points to a direction for future research. First, we did not quantitatively survey ambient bryophyte coverage in the microhabitat surrounding each nest. Therefore, we cannot separate the passive use of locally abundant material from active selection by birds. Future studies should pair nest sampling with quantitative surveys of substrate bryophyte cover to disentangle availability from preference.

Second, our sampling was confined to a single breeding season and therefore lacks the interannual replication needed to capture seasonal pattern in bryophyte availability and use. Repeated sampling across multiple years and climatic conditions would clarify the temporal stability of these patterns.

Third, the small sample size, low within-species replication, and narrow range of body sizes limited statistical power and precluded the inclusion of potential confounding covariates, such as nest morphology, elevation, and host-tree identity. A future dataset with more nests from a few bird species with different sizes and nest morphologies will allow us to better evaluate these covariates.

Fourth, we quantified bryophyte use only as a dry-weight proportion and did not collect functional data linking bryophyte nest content to outcomes such as microclimate buffering, parasite load, or fledging success. Integrating such measurements would help establish the adaptive significance of bryophyte use.

Fifth, the relatively modest pseudo- R^2 (0.21) indicates that the fitted model offers only a limited improvement in likelihood over the null model, suggesting that factors beyond nest location, such as bryophyte availability and bird species, likely contribute to variation in bryophyte proportion and merit investigation in future work.

5. Conclusions

This study provides one of the few quantitative assessments of bryophyte use as nest material by passerine birds in a tropical montane forest. Across 26 nests from 15 species at Doi Inthanon National Park, bryophytes made up roughly half of the nest material on average, with no overall preference over other materials. Pleurocarpous mosses dominated the bryophyte fraction. Nest location was the strongest predictor of bryophyte use, with tree-nesting species using a higher proportion of bryophytes than ground-nesting species. The overall pattern could be the result of the local abundance and growth form of pleurocarpous mosses on tree substrates.

These findings indicate that bryophyte use by tropical birds is closely associated with local availability and the vertical distribution of bryophytes within the forest. Maintaining intact forest canopies is therefore essential to sustaining bryophyte–bird interactions in tropical montane ecosystems. Future studies that directly quantify bryophyte availability and resolve species-level preferences will further clarify the ecological roles that bryophytes play in these systems.

Our results also carry conservation implications for tropical montane forests, which are increasingly threatened by fragmentation and canopy disturbance. Because epiphytic pleurocarpous mosses are concentrated under the forest canopy, disturbance of canopy layer directly depletes bryophyte biomass and subsequently a key nest material for tree-nesting passerines. We therefore recommend that the retention of continuous, intact forest canopy as a core management target for protected montane areas, both to safeguard epiphytic bryophyte communities and to preserve the bird–bryophyte interactions that depend on them.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d18080463/s1>, Table S1: Coordinates of trails for the surveys

<https://doi.org/10.3390/d18080463>

of bird nests with bryophytes in Doi Inthanon National Park, Chiang Mai, Thailand; Table S2: Field sampling metadata for the surveys of bird nests with bryophytes in Doi Inthanon National Park, Chiang Mai, Thailand in 2003.

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Abbreviations

The following abbreviations are used in this manuscript:

AIC	Akaike Information Criterion
AICc	Corrected Akaike Information Criterion
$\Delta AICc$	Delta AICc
GPS	Global Positioning System
MASL	Meters above sea level
PCA	Principal Component Analysis
PC1	First principal component
SD	Standard Deviation

References

1. Biddle, L.E.; Broughton, R.E.; Goodman, A.M.; Deeming, D.C. Composition of bird nests is a species-specific characteristic. *Avian Biol. Res.* **2018**, *11*, 132–153.
2. Deeming, D.C. A Review of the Roles Materials Play in Determining Functional Properties of Bird Nests. *Acta Ornithol.* **2023**, *58*, 1–28. <https://doi.org/10.3161/00016454ao2023.58.1.001>.
3. Briggs, K.B.; Biddle, L.E.; Deeming, D.C. Geographical location affects size and materials used in the construction of European Pied Flycatcher (*Ficedula hypoleuca*) nests. *Avian Res.* **2019**, *10*, 17.
4. Bailey, I.E.; Muth, F.; Morgan, K.; Meddle, S.L.; Healy, S.D. Birds build camouflaged nests. *Auk* **2015**, *132*, 11–15. <https://doi.org/10.1642/auk-14-77.1>.
5. Fontúrbel, F.E.; Osorio, F.; Rizzo, V.; Nuñez, M.; Bastias, R.; Carvallo, G.O. Mamma knows best: Why a generalist hummingbird selects the less abundant moss for nest building. *Ecology* **2020**, *101*, e03045.

6. Glime, J.M. *Bryophyte Ecology*; Michigan Technological University: Houghton, MI, USA, 2021.
7. Biddle, L.E.; Dickinson, A.M.; Broughton, R.E.; Gray, L.A.; Bennett, S.L.; Goodman, A.M.; Deeming, D.C. Construction materials affect the hydrological properties of bird nests. *J. Zool.* **2019**, *309*, 161–171. <https://doi.org/10.1111/jzo.12713>.
8. Breil, D.A.; Moyle, S.M. Bryophytes used in construction of bird nests. *Bryologist* **1976**, *79*, 95–98.
9. Wolf, A.L. *Bird Use of Epiphyte Resources in an Old-Growth Coniferous Forest in the Pacific Northwest*; Evergreen State College: Olympia, WA, USA, 2009.
10. Álvarez, E.; Belda, E.J.; Verdejo, J.; Barba, E. Variation in Great Tit Nest Mass and Composition and Its Breeding Consequences: A Comparative Study in four Mediterranean Habitats. *Avian Biol. Res.* **2013**, *6*, 39–46. <https://doi.org/10.3184/175815513X13609517587237>.
11. Wesołowski, T.; Wierzcholska, S. Tits as bryologists: Patterns of bryophyte use in nests of three species cohabiting a primeval forest. *J. Ornithol.* **2018**, *159*, 733–745. <https://doi.org/10.1007/s10336-018-1535-2>.
12. Gładalski, M.; Wolski, G.J.; Bańbura, M.; Kaliński, A.; Markowski, M.; Skwarska, J.; Wawrzyniak, J.; Bańbura, J. Differences in use of bryophyte species in tit nests between two contrasting habitats: An urban park and a forest. *Eur. Zool. J.* **2021**, *88*, 807–815. <https://doi.org/10.1080/24750263.2021.1947397>.
13. Dickinson, A.M.; Locke, E.; Gray, L.A.; Bennett, S.L.; Biddle, L.E.; Goodman, A.M.; Deeming, D.C. Composition of nests constructed by species in the Motacillidae, Sylviidae and Prunellidae. *Avian Biol. Res.* **2022**, *15*, 21–33.
14. Rydgren, K.; Indreeide, B.; Slagsvold, T.; Lampe, H.M. Nest building in titmice Paridae: Selectivity in bryophyte use. *Ecol. Evol.* **2023**, *13*, e9852.
15. Andreas, B.K. Use of Bryophytes by Carolina Chickadees (*Poecile carolinensis*) in Nest Construction. *Evansia* **2010**, *27*, 23–29. <https://doi.org/10.1639/0747-9859-27.1.23>.
16. De Almeida Amélio, L.; Do Carmo, D.M.; Soares de Lima, J.; Fernandes Peralta, D. Bryophytes as a material to build birds' nests in Brazil. *Bol. Soc. Argent. Botán.* **2017**, *52*, 199–208. <https://doi.org/10.31055/1851.2372.v52.n2.17434>.
17. Benítez, Á.; Jaramillo, E.; Yangua-Solano, E.; Greeney, H.F. Bryophytes Present in the Nests of Birds in Yanayacu Biological Station, Ecuador. *Diversity* **2023**, *15*, 1123.
18. Torres-Dowdall, J.; Osorio Zúñiga, F.; Suarez, G. Materiales utilizados por el Picaflor Rubí (*Sephanoides sephanoides*) para la construccion de nidos en la selva Valdiviana, Chile. *Ornithol. Neotrop.* **2007**, *18*, 433–437.
19. Sripen, S.; Khobkhet, O.; Masuthon, S.; Supanuchai, S. Growth Period of Aquatic Plants for Birds Nesting at Bung Borapet, Nakhon Sawan. *Agric. Nat. Resour.* **2000**, *34*, 17–24.
20. Liengpornpan, S. Benefits of Fresh Plants in Bird Nests. *Thai Sci. Technol. J.* **2020**, *29*, 508–515. <https://doi.org/10.14456/tstj.2021.43>.
21. Khamcha, D.; Gale, G.A. Nest-site selection, nesting success, and the value of older pine plantations for the globally Endangered Giant Nuthatch *Sitta magna* in northern Thailand. *Bird Conserv. Int.* **2026**, *36*, e17. <https://doi.org/10.1017/s0959270926100458>.
22. Sukkharak, P.; Chantanaorrapint, S. Bryophyte Studies in Thailand: Past, Present, and Future. *Cryptogam. Bryol.* **2014**, *35*, 5–17.
23. He, S. An Annotated Checklist and Atlas of the Mosses of Thailand. Available online: <https://www.mobot.org/mobot/moss/thailand/thailand.htm> (accessed on 1 December 2022).
24. Bird Conservation Society of Thailand. *Checklist_ThaiBirds_2022 (Ver. July 2022)*; Bird Conservation Society of Thailand: Bangkok, Thailand, 2022.
25. Nathi, Y. Mosses Diversity in Kew Mae Pan and Ang Ka Areas, Doi Inthanon National Park, Chaing Mai Province. Master's Thesis, Chulalongkorn University, Bangkok, Thailand, 2009.
26. Akiyama, H.; Furuki, T.; Sri-ngernyuang, K.; Kanzaki, M. Alphabetical list of bryophytes occurring in a 15ha long-term monitoring plot at Doi Inthanon, Northern Thailand. *Bryol. Res.* **2011**, *10*, 153–164. https://doi.org/10.24474/bryologicalresearch.10.6_153.
27. eBird. 2022. eBird: An online database of bird distribution and abundance [web application]. eBird, Cornell Lab of Ornithology, Ithaca, New York. Available: <http://www.ebird.org>. (accessed on 1 Feb 2022).
28. Academic Sector, Doi Inthanon National Park. *Doi Inthanon National Park Climate Report: 2017–2023*; Doi Inthanon National Park: Chiang Mai, Thailand, 2024.
29. Department of National Parks Wildlife and Plant Conservation. Doi Inthanon National Park. Available online: <http://portal.dnp.go.th/Content/nationalpark?contentId=915> (accessed on 1 December 2023).
30. Round, P.D. Notes on breeding birds in north-west Thailand. *Nat. Hist. Bull. Siam Soc.* **1982**, *30*, 1–14.
31. Round, P.D. Some recent bird records from northern Thailand. *Nat. Hist. Bull. Siam Soc.* **1983**, *31*, 123–138.
32. Gradstein, S.R.; Churchill, S.P.; Salazar-Allen, N. *Guide to the Bryophytes of Tropical America*; New York Botanical Garden Press: Bronx, NY, USA, 2001.

33. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2026.
34. Smithson, M.; Verkuilen, J. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychol. Methods* **2006**, *11*, 54–71. <https://doi.org/10.1037/1082-989X.11.1.54>.
35. Cribari-Neto, F.; Zeileis, A. Beta Regression in R. *J. Stat. Softw.* **2010**, *34*, 1–24.
36. Birds of the World (2026). Edited by S. M. Billerman, B. K. Keeney, G. M. Kirwan, F. Medrano, N. D. Sly, and M. G. Smith. Cornell Laboratory of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow>.
37. Bartoń, K. *MuMIn: Multi-Model Inference. R Package*, version 1.48.19; R Foundation for Statistical Computing: Vienna, Austria, 2026.
38. Martin, T.E. Nest Predation and Nest Sites. *BioScience* **1993**, *43*, 523–532. <https://doi.org/10.2307/1311947>.
39. Hansell, M.H. The function of lichen flakes and white spider cocoons on the outer surface of birds' nests. *J. Nat. Hist.* **1996**, *30*, 303–311. <https://doi.org/10.1080/00222939600771181>.
40. Akresh, M.E.; Mandell, D.; Grima, P.P.; King, D.I.; Lauer, K. Differential use of nest materials and niche space among avian species within a single ecological community. *Ecol. Evol.* **2024**, *14*, e70142. <https://doi.org/10.1002/ece3.70142>.
41. Troscianko, J.; Wilson-Aggarwal, J.; Stevens, M.; Spottiswoode, C.N. Camouflage predicts survival in ground-nesting birds. *Sci. Rep.* **2016**, *6*, 19966. <https://doi.org/10.1038/srep19966>.
42. Calvelo, S.; Trejo, A.; Ojeda, V. Botanical composition and structure of hummingbird nests in different habitats from northwestern Patagonia (Argentina). *J. Nat. Hist.* **2006**, *40*, 589–603. <https://doi.org/10.1080/00222930500371000>.
43. Heenan, C.B.; Goodman, B.A.; White, C.R. The influence of climate on avian nest construction across large geographical gradients. *Glob. Ecol. Biogeogr.* **2015**, *24*, 1203–1211. <https://doi.org/10.1111/geb.12378>.
44. Perez, D.M.; Gardner, J.L.; Medina, I. Climate as an Evolutionary Driver of Nest Morphology in Birds: A Review. *Front. Ecol. Evol.* **2020**, *8*, 566018. <https://doi.org/10.3389/fevo.2020.566018>.
45. Bates, J.W. Is 'Life-Form' a Useful Concept in Bryophyte Ecology? *Oikos* **1998**, *82*, 223–237. <https://doi.org/10.2307/3546962>.
46. Sporn, S.G.; Bos, M.M.; Kessler, M.; Gradstein, S.R. Vertical distribution of epiphytic bryophytes in an Indonesian rainforest. *Biodivers. Conserv.* **2010**, *19*, 745–760.
47. Huttunen, S.; Bell, N.; Hedenäs, L. The evolutionary diversity of mosses—taxonomic heterogeneity and its ecological drivers. *Crit. Rev. Plant Sci.* **2018**, *37*, 128–174.
48. Sheard, C.; Street, S.E.; Evans, C.; Lala, K.N.; Healy, S.D.; Sugawara, S. Beak shape and nest material use in birds. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **2023**, *378*, 20220147. <https://doi.org/10.1098/rstb.2022.0147>.
49. eBird. 2026. Verditer Flycatcher (*Eumyias thalassinus*). eBird, Cornell Lab of Ornithology, Ithaca, New York. Available: <https://ebird.org/species/verfly4>. (Accessed on 1 Jun 2020).

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