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Seeing the wood for the trees: Understanding resource selection at multiple spatial scales to inform conservation of a critically endangered species

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Abstract

The blue-crowned laughingthrush (BCLT; *Pterorhinus courtoisi*) is a Critically Endangered bird restricted to southeast China. Breeding sites are situated within agricultural-forest mosaic habitats; it is unclear why the species is not more widely distributed across similar landscapes. Identifying factors that restrict the species' breeding range is essential for conservation planning. We quantified BCLT habitat preferences by combining fine-scale vegetation measures from 39 villages in Jiangxi and Anhui Provinces with topographic and satellite data across the species' breeding range, applying resource selection functions at both the breeding-site and the nest-site scale. We found that BCLT may be considered a broadly generalist species with little evidence of habitat differences between breeding sites and those with no known history of breeding BCLT at this spatial scale. However, nest-sites are more likely to contain larger broadleaf trees, bamboo stands, conifer or mixed forest, and to be on lower slope inclines. Our findings indicate that nest-site selection is important for BCLT and highlight the need to protect remaining large broadleaf trees across the landscape. These results also demonstrate the importance of integrating conservation-relevant data across multiple scales to provide new insights for threatened species management planning and landscape policy.

KEYWORDS

breeding site, China, *fengshui* forest, habitat selection, land cover, nest site, *Pterorhinus courtoisi*, resource selection function, songbird

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1 | INTRODUCTION

Reliable information on species' ecological requirements forms a core component of conservation planning (Hayward et al., 2006; Luck, 2002), and underpins the identification and mitigation of factors that drive declines or restrict recovery (Sutherland et al., 2004). One key ecological requirement is species' habitat preference. Information on this parameter can inform habitat management plans (Oppel et al., 2004a) and protected area design (Beatty et al., 2014; Roberts et al., 2010). Assessing which habitats are used disproportionately compared to those that are available also provides fundamental conservation-relevant information on the degree to which habitat availability restricts species' ranges (Behnke et al., 2016). This knowledge is necessary for understanding the importance of habitat loss, versus other potential threats, as determinants of the status of threatened species (Mellanby et al., 2008).

"Habitat preference" is defined as the likelihood of a habitat or resource being selected if offered on an equal basis to others (Johnson, 1980) and operates at multiple hierarchical biologically-relevant scales, which can be assessed separately (Manly et al., 2002). These scales encompass the species' geographic range (1st order), breeding-sites (2nd order), and parts of breeding-sites such as nest-sites (3rd order; Johnson, 1980). Many studies investigate habitat selection at multiple scales to inform conservation management (Donald et al., 2012; Oppel et al., 2004b), as habitat selection may be scale-dependent (Gustine et al., 2010; Johnson, 1980; Sawyer & Brashares, 2013). This in turn has implications for habitat restoration, land-use policy, and translocations (Colyn et al., 2020; Currie et al., 2003). Resource selection functions (RSFs), defined as probabilities of use for resource units of different types (Manly et al., 2002), are an important tool for elucidating habitat selection at different scales. RSFs have been applied to a range of ecological questions, including drivers of species' geographic ranges (Aldridge et al., 2008; Brambilla et al., 2009) and spatial predator–prey interactions (Courbin et al., 2013). However, few studies have investigated limiting factors across multiple scales for threatened species, in particular for species occurring in agriculturally converted landscapes where current landscape factors might be more likely to be limiting (Coulombe et al., 2011; Gastón et al., 2016).

The blue-crowned laughingthrush (BCLT; *Pterorhinus courtoisi*) is only known to breed in two counties (Wuyuan, Dexing) in Jiangxi Province, China, and is assessed as Critically Endangered by IUCN based on its restricted, fragmented breeding range and small population size (BirdLife International, 2018). Thus, understanding its breeding habitat requirements is crucial to identify potential limiting factors to its distribution and population size (Colyn et al., 2020; Segal et al., 2021). BCLTs breed in colonies, typically associated with large old trees and areas of human settlement, at low elevation and near rivers (Hong et al., 2003; M. Richardson, personal communication, May 2005). However, this generalization is complicated as not all breeding-sites occur near rivers; furthermore, most villages in this landscape are disproportionately close to rivers (Huang et al., 2018). BCLTs also breed in bamboo, fir, and fruit trees (M. Richardson, personal communication, May 2005; Zhang et al., 2017). Indeed, many villages in the surrounding regions have similar general physical characteristics as known breeding-sites but lack concrete BCLT breeding records (Gleave et al., 2024). Although there are several descriptive studies of BCLT habitat use (He et al., 2017; Hong et al., 2003; Liao et al., 2007), few systematic studies exist, and it remains unclear why BCLTs only breed within a restricted area. The species' breeding landscape is also changing rapidly due to tourism and development (Zhang et al., 2019), so understanding BCLT habitat preferences is important to ensure future change does not compromise the species' chance of persistence within this human-occupied landscape.

Previous work has compared forest breeding-sites with control patches of the same type and highlighted BCLT's breeding-sites preferences. Huang et al. (2018), however, used a small sample size and only compared specific forest patch characteristics rather than wider land use, potentially overlooking important breeding cues such as associated foraging habitat. Previous research on BCLT breeding preferences has offered contrasting results, with the species selecting for a variety of vegetation and land cover types (Huang et al., 2018; Liu et al., 2020; Zhang et al., 2017). No study has so far simultaneously considered both breeding site-specific features and features of the surrounding area while studying a larger sample of sites, including sites outside the known breeding range. Addressing these crucial points would allow more robust statistical inferences regarding habitat preferences to be made.

We establish a more comprehensive baseline on BCLT breeding requirements by comparing data from all known breeding-sites against control sites (sites with no known history of breeding BCLT) sampled across a greater geographic area than previous studies, across and outside the species' breeding range. We apply RSFs at the breeding-site and nest-site orders of habitat preference, and use ecological surveys and satellite imagery analysis to determine the environmental and land cover characteristics of the BCLT breeding landscape, breeding-sites, and nest-sites. Our findings have importance for BCLT conservation decision-making and wider implications for

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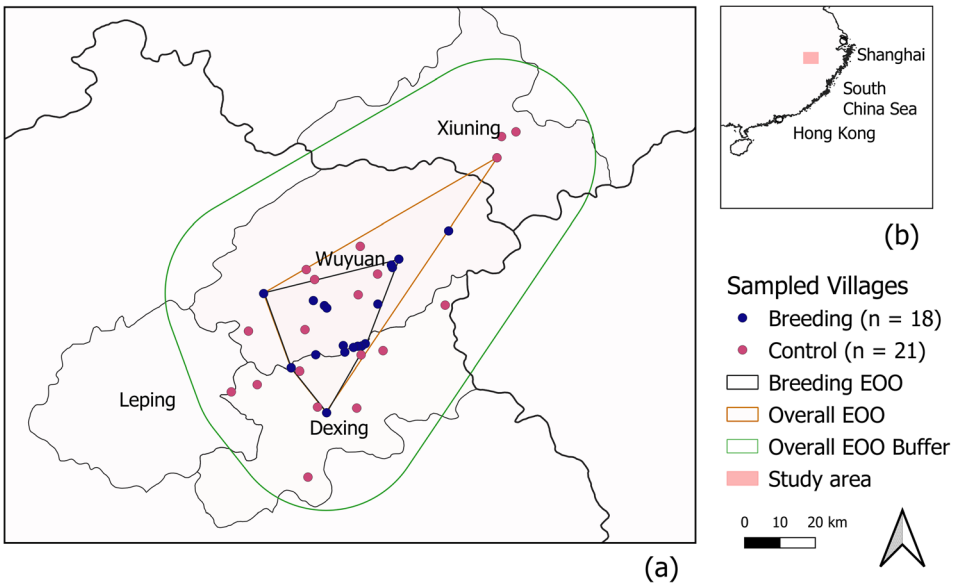


FIGURE 1 Distribution of sampled villages (colored circles). (a) Polygons show location of counties of interest in Jiangxi and Anhui provinces, China. Thick black lines indicate province boundaries. Black polygon indicates Extent of Occurrence around known Blue-crowned Laughingthrush breeding sites (Breeding EOO), the orange polygon represents a minimum convex polygon around all known Blue-crowned Laughingthrush sightings (Overall EOO), and the green polygon displays a 25 km buffer around the Overall EOO. (b) Inset map showing relative location of study area (pink rectangle) within China.

guiding management of other species and landscape policy.

2 | METHODS

2.1 | Study area

Habitat surveys were conducted between June 4 and July 31, 2019 in Wuyuan (29°14′53″N, 117°51′43″E), Dexing (28°55′50″N, 117°35′41″E) and Leping (28°58′41″N, 117°09′07″E) counties (Jiangxi Province) and Xiuning county (Anhui Province) (29°47′02″N, 118°11′38″E) (Figure 1). This region consists of a subtropical human-modified mosaic landscape characterized by villages within agricultural valleys interspersed with river networks and forested hills, similar to surrounding landscapes in southern China (Ellis, 2004). This landscape contains remnant evergreen broadleaf forests following heavy logging in the 1950s and 1960s (Coggins, 2003; Hong et al., 2006), including mature broadleaf trees and mixed forest stands (He et al., 2014). The landscape also has traditional village "*fengshui* forests" (stands or larger patches of mature broadleaf trees) with high cultural and spiritual importance. *Fengshui* forests have been locally protected for centuries (Coggins, 2003), and since 1993 many have formal protection by the Wuyuan County Government (Huang et al., 2018). Land surrounding villages also contains plantation stands of bamboo, fir, and pine (F. He, personal communication, May 1994; M. Richardson, personal communication, May 2005). Dominant crops are rice, tea, vegetables, and oilseed rape (M. Richardson, personal communication, May 2005; Hong et al., 2006; He et al., 2017), with recent declines in vegetable fields (He et al., 2017).

2.2 | Data collection

To select survey sites, human settlements were digitized using the Google Satellite plugin in QGIS v.3.16.5 (Hannover; QGIS Development Team, 2021). Analysis of BCLT breeding habitat selection was conducted at the settlement level, as all known breeding-sites have been either inside or directly adjacent to villages or towns (He et al., 2017). Over 900 settlements were digitized within two areas: a 1434.71 km^2 minimum convex polygon of all recorded BCLT sighting or breeding locations, hereafter referred to as the "overall EOO," and a surrounding 25 km buffer (Figure 1). A 725.93 km^2 minimum convex polygon around all recorded breeding locations from 2000 to 2019 (F. He, personal communication, 2019), representing the species' breeding extent of occurrence (EOO), was also created using QGIS.

All but one of the known active or former BCLT breeding villages ($n = 18$) were surveyed (with one additional site discovered following fieldwork completion; total breeding sites $n = 19$). A total of 21 control sites

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were selected, including nine non-breeding villages within 1 km of known BCLT localities on eBird ($n = 6$) and in unpublished field data ($n = 3$; He, personal communication, 1994), and 12 villages randomly chosen from across the overall EOO and buffer polygons where BCLTs had not nested within living memory. Local BCLT absence in these villages was confirmed during fieldwork through discussions with village inhabitants (Gleave et al., 2024). Mann–Whitney U tests showed that there were no significant differences between breeding and control villages across a set of characteristics potentially associated with BCLT presence or disturbance, determined from Google Earth imagery or measured within QGIS: approximate number of buildings ($W = 143$, $p = .14$), distance to main road ($W = 105$, $p = .91$), distance to river ($W = 124$, $p = .51$), and elevation ($W = 89$, $p = .43$), confirming minimal systematic sampling bias.

Characteristics of breeding-sites were investigated at the level of individual villages and their surroundings. Characteristics of nest-sites were investigated in the immediate vicinity of nests (Jones, 2001). Breeding-sites were defined as a past or present nest-site anywhere within the village boundary. Each survey area was established using QGIS, using a known past nest-site, or the village center if precise nest-sites were not known or if it was a control-site. A circular buffer was generated around each point (radius = 332 m, area = 0.346 km^2), representing the furthest distance estimation that BCLT will travel from nest-sites to forage (B. Mo, personal communication, 2018), and covering a greater area than the mean estimated BCLT home range (0.100 km^2; Shi, 2017; Liu et al., 2020). For each village, 20 points were randomly generated at least 10 m apart within the circular buffer, and all points located in water bodies removed to prevent potential sampling bias toward riparian trees (Figure 2). If >15 points were still available, only one of the pair of points that were closest was surveyed (point chosen at random or based upon accessibility in the field). Points located within inaccessible terrain (e.g., due to flooding) were also replaced with either the closest alternative point of the initial random sample of 20, or by getting as close as possible to the existing point ($n = 61$). In total, 15 points were surveyed at each village. At each point, the closest tree over 2 m in height was selected, with current or former nesting trees selected at known current or former BCLT nest-site points, and a 10 × 10 m (100 m^2) quadrat was measured with the tree at its center; 100 m^2 was chosen to capture the ground immediately around trees and to balance area surveyed with access issues around, for example, private property (too large quadrats could be unmeasurable for this reason). The following environmental variables were recorded as field data: central tree species, height, and diameter at breast height (DBH); number and species of trees over 2 m high; percentage of 13 land cover types within quadrat (broadleaf forest, conifer forest, bamboo forest, mixed forest, *fengshui* forest, bush/scrub, water, rice paddy, tea plantation, vegetable garden, oilseed rape, settlement/road and "other" land cover type); herb density and height; and disturbance level (collection method detailed in Section S1, and reasons for consideration given in Table S1). Data on elevation, slope and aspect for each point were generated post-fieldwork using QGIS (Section S1). Research was permitted by Jiangxi Wuyuan National Forest Bird Nature Reserve Management Office.

Satellite image-derived land cover types for breeding-site RSFs included broadleaf forest, vegetable plots, other forests, tea plantations, rice paddy, bush/scrub, settlement/road, and water. These types were chosen to be broadly comparable to those collected in field surveys, but with some categories merged (further details in Data Analysis section below). Land cover percentages were calculated using atmospherically-corrected Sentinel-2 Level-2A Surface Reflectance imagery (10 × 10 m resolution), overlapping with all village locations (representing the least cloudy images available between February 1, 2019 and August 31, 2019), within Google Earth Engine (Gorelick et al., 2017). Cloud masks were applied using a function that detected the probabilities of pixels being cloud, cloud shadow or snow, and supervised imagery classification (Wegmann et al., 2016) was conducted using the random forest algorithm (Breiman, 2001). Masked-out cloudy areas were assigned the value of "-9999" prior to export, to prevent confusion with classified pixels. Training and validation points for accuracy assessment were taken from both very high-resolution (5–0.5 m; Hunt et al., 2019) Google Earth Pro imagery (Google Earth, 2019) and ground-truthed GPS data collected in April–May 2019, as well as points taken from Google Earth imagery of villages and other areas visited during fieldwork. Points from very high-resolution and ground-truthing were split and re-merged in a 3:1 ratio in Google Earth Engine, so both types were used for training and validation. A confusion matrix was generated with overall accuracy, producer's accuracy and user's accuracy calculated for each land cover type.

2.3 | Data analysis

We wanted to understand probabilities of use for different habitat types across scales, so resource selection models were developed for five spatial analyses, at the breeding-site and nest-site scales: comparing habitat characteristics from field surveys between (a) breeding versus control-sites, (b) sites within breeding EOO versus

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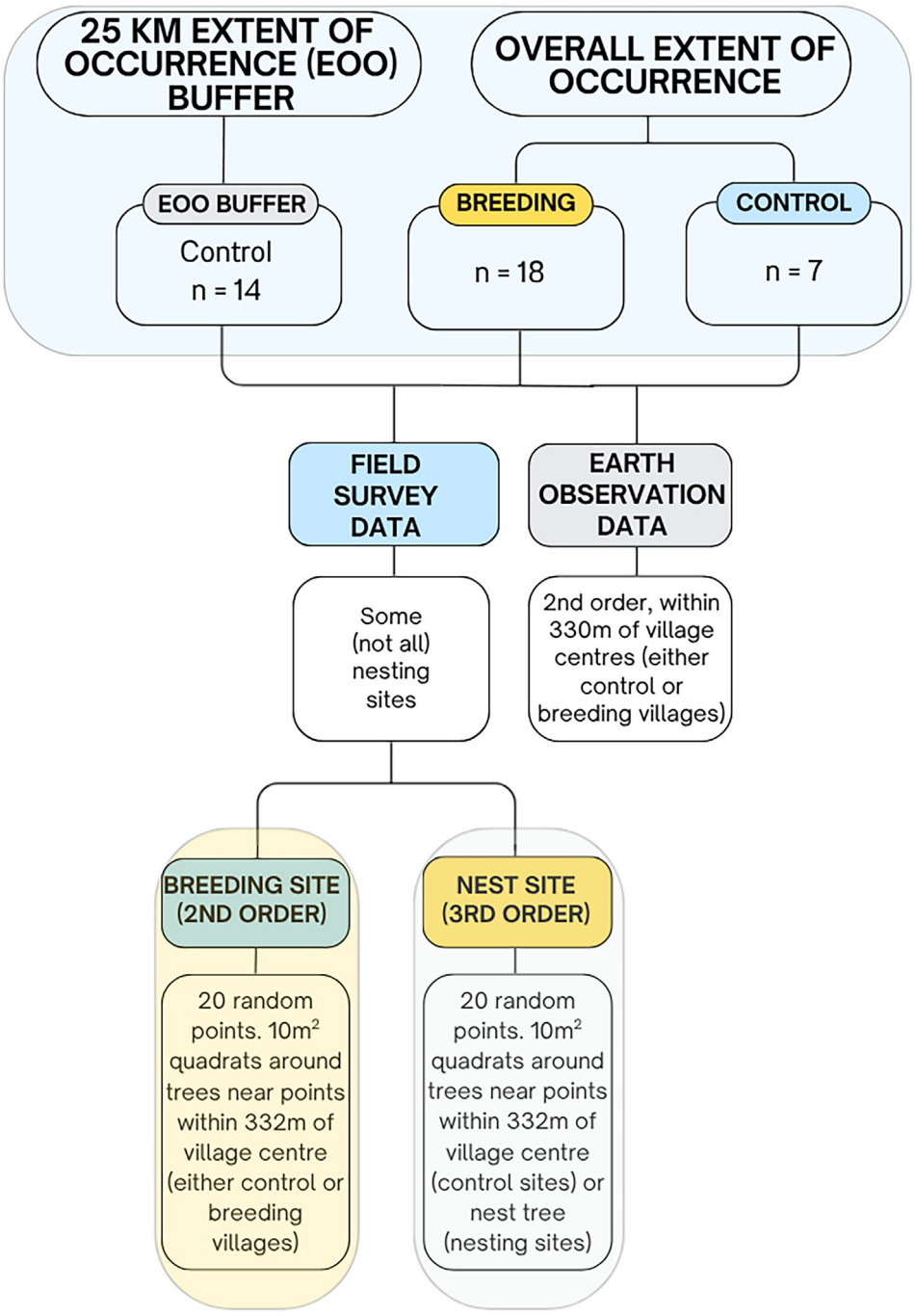


FIGURE 2 Schematic showing sampling comparisons between breeding, control, EOO and buffer data; field survey and earth observation data; and breeding and nest-site models. The blue transparent box shows the topmost layer in the spatial hierarchy, capturing analysis performed at the landscape (1st order) scale. The yellow transparent box shows the middle layer in the spatial hierarchy, capturing analysis performed at the breeding-site (2nd order) scale; the gray transparent box shows the lowest layer in the spatial hierarchy, capturing analysis performed at the nest-site (3rd order) scale.

the overall EOO buffer (outside the EOO; hereafter referred to as the "buffer"), and (c) nest versus control-sites; and comparing proportions of land cover types from earth observation imagery between (d) breeding versus control-sites, and (e) sites within breeding EOO versus buffer (Figure 2).

Data exploration was conducted on all variables using Principal Component Analysis (PCA) to reduce the number of explanatory variables necessary in models while limiting collinearity-related issues (Figures S1 and S2). An initial PCA of all field survey-derived land cover percentages captured c.10% of data variance per axis, so some types were combined to allow stronger associations among the environmental variables: *fengshui* forest was combined with other broadleaf forest into a "broadleaf forest" category; conifer forest, mixed forest and bamboo forest were combined as an "other forest" category, and oilseed rape was included within rice paddy, as these crops occupied the same fields (rice following the spring oilseed rape harvest). These were also chosen for the satellite image-derived land cover types for breeding-site RSFs. The subsequent PCA captured slightly higher variance in axis 1 (c.16%), and assessment of contribution to PCA axes and quality of representation for variables

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TABLE 1 Response variables (*) and covariates used in resource selection models for blue-crowned laughingthrush (BCLT).

Variable	Description	Justification
Breeding site*	Village verified as former or current BCLT breeding site between 2000 and 2017	
Nesting site*	Tree verified as former or current tree used by breeding BCLT (can include single or multiple nests) between 2000 and 2017	
Elevation	Elevation (meters) at recorded waypoint	BCLT breeding sites thought to be at <100 m elevation (Huang et al., 2018)
Slope	Percentage slope	Observation that breeding sites were often in flat areas (R.Gleave, personal communication, 2019) and importance of slope in avian habitat Sutherland (2006)
Total broadleaf diameter at breast height (DBH)	Combined DBH of broadleaf trees (>20 cm DBH) within quadrat	BCLT thought to prefer nesting in large broadleaf trees (Zhang et al., 2017)
Village/Town percent	Percentage of "village or town" land type within quadrat. "Village or town" defined as a building, or area of concrete or gravel	Nesting trees often close to human habitation (Hong et al., 2003)
Other forest percent	Percentage of "Other forest" land type within quadrat. "Other forest" defined as conifer forest, bamboo forest or mixed forest/trees	Nesting trees sometimes bamboo or fir trees (Hong et al., 2006; Zhang et al., 2017)
Broadleaf forest percent	Percentage of "Broadleaf forest" land type within quadrat. "Broadleaf forest" defined as broadleaf forest or *fengshui* forest/trees	Nesting trees sometimes broadleaf or *fengshui* trees (Huang et al., 2018, Zhang et al., 2017)
Total *Cinnamomum*	Total number of *Cinnamomum* sp. trees (>2 m tall) within quadrat	BCLT showed preference for nesting in *Cinnamomum* trees (Zhang et al., 2017)
Village	Random effect term (identity of each breeding or control site village)	

revealed that only "other forest" and "village/town" were strongly represented on the first two PCA axes, so these alone were used. Final variables included in the models were: elevation, slope, "other forest" percent, broadleaf forest percent, village/town percent, total broadleaf DBH (by summing DBH of all broadleaf trees over 20 cm DBH within each quadrat, including the central tree; Table S1) and total number of *Cinnamomum* trees (Tables 1 and 2; reasons for variable inclusion explained below). Correlation among continuous variables was tested using the "corrplot" package in R (Wei & Simko, 2021); all variables had correlation coefficients <0.7, so were retained within models (Green, 1979). All analyses were performed in R v.4.0.2 (R Core Team, 2021).

2.4 | Understanding breeding-site determinants from field data

Binomial regression models defining the probability of observing a breeding EOO site ($n = 25$) versus a buffer site ($n = 14$), or a breeding-site ($n = 18$) versus a control-site ($n = 21$) were generated and expressed as linear functions of the selected environmental covariates (using a logit-link function) to investigate breeding-site differences in habitat selection. For all models, response variables were converted to "1" for "breeding," "inside breeding EOO," or "0" for "control" and "buffer." Models were analyzed using a "case–control" sampling design (Keating & Cherry, 2004), with outputs expressed as odds ratios rather than probabilities. Two surveyed villages had possible but unverified past breeding activity, so were alternately modeled as either "breeding" or "control" villages to contrast and test the robustness of the results. Landscape changes may have occurred over the period that breeding locations have been recorded (2000 onward), so models were also fitted with just the villages where breeding was recorded only in 2019 ($n = 9$), with all other villages classed as control-sites. All models were fitted with a Bayesian multilevel framework, using the "brms" package (Bürkner, 2017). We used a Bernoulli distribution and a logit link-function, and included a varying intercept for village to account for between-site variation and to control for pseudo-replication from using 15 sampling points per village. All

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TABLE 2 Full model and candidate sub-model resource selection functions for blue-crowned laughingthrush.

Model name	Breeding site and EOO selection	Nesting site selection
Full model (random intercept and slope)	NA	Nesting ~ Elevation + Slope + Total *Cinnamomum* + Other Forest % + Broadleaf Forest % + Village/Town % + Total broadleaf DBH + (1 + Total broadleaf DBH|village)
Full model (random intercept)	Breeding/EOO ~ Elevation + Slope + Other Forest % + Broadleaf Forest % + Village/Town % + Total broadleaf DBH + (1|village)	Nesting ~ Elevation + Slope + Total *Cinnamomum* + Other Forest % + Broadleaf Forest % + Village/Town % + Total broadleaf DBH + (1|village)
Sub-model 1	Breeding/EOO ~ Slope + Total broadleaf DBH + (1|village)	Nesting ~ Elevation + Slope * Total broadleaf DBH + Total *Cinnamomum* + (1|village)
Sub-model 2	Breeding/EOO ~ Elevation + Total broadleaf DBH + (1|village)	Nesting ~ Elevation + Slope + Total broadleaf DBH * Total *Cinnamomum* + (1|village)
Sub-model 3	Breeding/EOO ~ Elevation + Slope + Other Forest % + Village/Town % + (1|village)	Nesting ~ Elevation + Slope + Total broadleaf DBH + (1|village)
Sub-model 4	Breeding/EOO ~ Elevation + Slope + Total broadleaf DBH + (1|village)	Nesting ~ Elevation + Slope + Total *Cinnamomum* + (1|village)

Note: Model specification uses R notation.
Abbreviations: EOO, extent of occurrence; DBH, diameter at breast height.

predictors (Table 1) were standardized prior to analysis to ease the attribution of plausible weakly informative priors and to facilitate model convergence (Harrison et al., 2018; McElreath, 2020).

The multilevel binomial models were defined as illustrated here for the response variable Y "being a nesting site":

$$Y_{i,s} \text{Bernoulli}\left(p_{i,s}\right)$$

$$\text{logit}\left(p_{i,s}\right) = \beta_{00} + \beta_{0_s} + \sum_{j=1}^{7} \beta_j \times x_{j_s}$$

$$\beta_{00} \text{Normal}(0, 1)$$

$$\beta_{0_s} \text{Normal}\left(0, \sigma_{\text{village}}\right)$$

$$\beta_{1-7} \text{Normal}(0, 0.5)$$

$$\sigma_{\text{village}} \text{Half} - \text{Normal}(0, 1)$$

where β_{00} is the overall intercept, β_{0s} is the random intercept for village s, where x_1 to x_7 are the explanatory environmental variables for the full model including all selected environmental variables (see below for explanatory variables and justifications), using weakly informative priors on parameters β_{00}, β_{1-7}, and σ_{village}, and adaptive regularizing priors on the varying intercepts β_{0s}. To balance risks of model overfitting and multicollinearity while avoiding stepwise variable selection issues (McElreath, 2020; Mundry & Nunn, 2009), the above full model was compared to a set of four sub-models (Table 2). For the models of EOO/breeding-site selection, sub-models contrasted the effects of variables previously hypothesized to be most influential on site selection: elevation, slope, and total broadleaf DBH (Huang et al., 2018; Sutherland, 2006; Zhang et al., 2017). Model comparison was performed using leave-one-out cross-validation (LOOCV) (McElreath, 2020; Vehtari et al., 2017).

Posterior predictive checks were performed for all models to assess how well they retrodicted real observations, with response variable predictions generated from the fitted joint posterior distribution of each model, and compared to real observations (McElreath, 2020). We only report covariates for which the 90% credible interval (CI) of the slope posterior distribution excluded zero (i.e., the effect was either clearly positive or clearly negative). Bayesian updating of model parameters was performed through the No-U-Turn Sampler (NUTS) in Stan, with models fitted using 2000 iterations on four chains with 1000 warmups per chain. Model convergence was checked using Rhat values, with posterior distributions assessed using the R package "tidybayes" (Kay, 2022). All models converged well, as indicated by Rhats within 0.01 of 1 and through visual inspection of chain mixing, and had parameters with sufficiently high effective sample sizes to trust the estimates ($N_{\text{eff}} > 2502$; McElreath, 2020).

We present models with the best accuracy, as well as outputs from alternative candidate models with the next-best accuracy (especially those with expected log pointwise predictive density [ELPD] and Standard Error

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difference of <1.0; Table S2). We assessed the explanatory power of our different models using a pseudo-R2 developed for Bayesian models (Gelman et al., 2019) using the performance package (Lüdecke et al., 2021; Table S3).

2.5 | Understanding nest-site determinants from field data

We also modeled the probability of having a known nest-site ($n = 23$) versus a control-site ($n = 562$) in a similar way to investigate nest-site differences in habitat selection.

For nest-site models, the procedure and equation were identical to the prior section, except the response variable was converted to "1" for "nesting" and "0" for "control."

Nest-site models, as indicated in the example with equations above, also contained an extra variable—the total number of *Cinnamomum* trees—which are suggested to be the most selected nest-site tree type (Zhang et al., 2017) and an interaction term was included to understand if the effect of having more large broadleaf trees differed among villages (Table 2).

2.6 | Understanding breeding-site determinants from earth observation data

To understand whether the proportions of land cover types differed between breeding and control villages, four Bernoulli regression analyses with a log-link function were conducted, alternately defining unverified potential breeding-sites as either "breeding" or "control," using 2019 breeding site-data only, and using EOO versus buffer villages. To collect data, circular shapefiles (332 m radius) were generated from the classified Sentinel-2 imagery, centered around known nest-sites or village center-points in QGIS. Pixel values (0–7) were extracted from each shapefile using the "terra" package in R, and raw values of each land cover type were converted to percentages within the shapefile area, generating a dataset of one datapoint per village ($n = 40$), each with eight variables containing land cover percentages.

All response variables were again converted to "1" or "0," and with "breeding" and "control" response models fitted to variations on these data. Predictors for these models were selected a priori, based on past observations of BCLT breeding habitat use: percentages of broadleaf forest, vegetable plot, and bush/scrub around villages (He et al., 2017; Huang et al., 2018; Liu et al., 2020). Models were fitted the same way as previous models, except without any random intercept term.

3 | RESULTS

In total, 585 habitat quadrats across 39 villages were surveyed, including 5414 trees of 223 species (Table S4; mean = 1.95 species per quadrat, range = 1–7 species). Bamboo (*Phyllostachys heterocycla*) and Chinese fir (*Cunninghamia lanceolata*) were the most abundant species, occurring in >30% of quadrats, and quadrats also contained 179 fruit trees belonging to 17 species. The highest tree densities were seen when quadrats contained bamboo stands.

3.1 | Breeding-site determinants from field data

For breeding-site selection, no predictors (elevation, slope, total broadleaf DBH, or percentage of quadrat comprised of village/town, broadleaf forest or other forest) influenced the odds of a potential site being a breeding-site (Figure 3b, Table S5). There were minimal differences between LOOCV scores of all candidate models, and patterns were consistent for all model variations (when two "unsure" villages were assigned as either breeding or control, or when only breeding locations from 2019 were included) (Figures S3 and S4). Village-level parameters of deviation from the average intercept did not encompass zero, indicating important between-village variation, and that models contain some residual variation structured at the village level that cannot be explained by fixed effects (Figure 3a,b). R^2 estimate was 0.995 (Table S3). The conditional and marginal R^2 values support the residual variation captured by the random effect of village, with conditional (fixed and random effects) models having much higher R^2 values.

Based on the quadrat-level data (breeding-site analyses), elevation was lower within the EOO versus the buffer (odds ratio = 1.54; [−1.77, −0.06] 90% CI, second most optimal model; EOO mean = 76.86 m, buffer mean = 115.75 m) (Figure 3a), but slope and total broadleaf tree DBH did not differ between EOO and buffer (Figure 3a, Table S5). There was little difference in measures of fit between optimal (best accuracy) and comparative models (maximum ELPD difference: −0.3, SE difference: 0.1). R^2 estimate of the optimal model was 0.995 (Table S3).

3.2 | Nest-site determinants from field data

Based on the nest-site analyses, using quadrat data, we found that in the optimal model, the probability of a quadrat representing a nest-site increased with broadleaf tree DBH (odds ratio = 1.16; [0.15, 0.53] 90% CI, full

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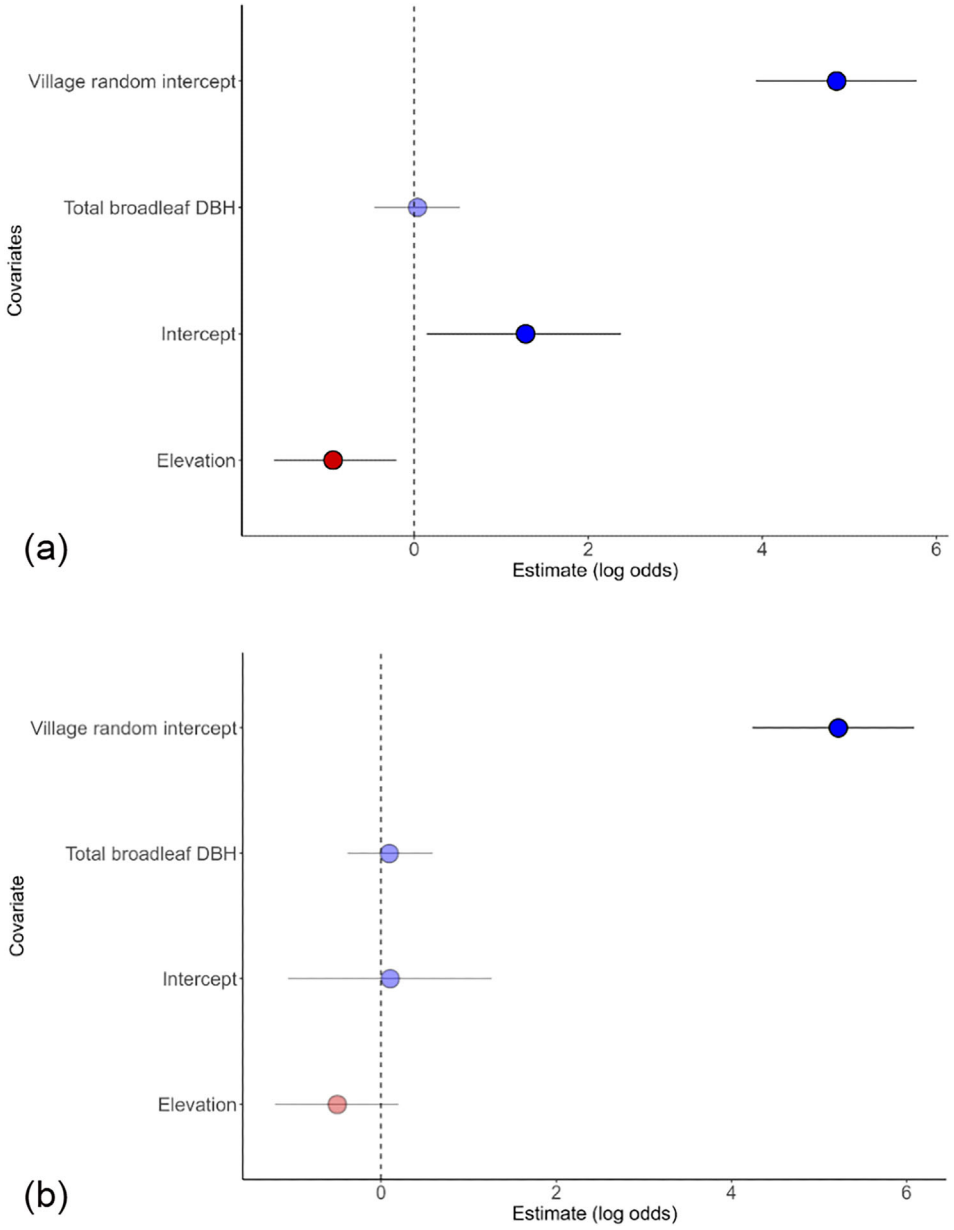


FIGURE 3 Interval plot showing the median (colored circles) and 90% credible intervals (CI, black lines) for the posterior distributions of predictors, in relation to whether a village was (a) within the EOO or (b) a breeding site. Predictor levels are considered to have a clear effect if CI does not encompass zero on x axis (colored circle in bold). Blue circles denote a positive effect and red circles a negative effect. Plot displays (a) the second most optimal candidate model and (b) the optimal candidate model.

random intercept model in Table S2) and percentage of other forest (odds ratio = 1.26; [0.17, 0.93] 90% CI, full random intercept model in Table S2), and decreased with slope (odds ratio = 1.33; [−1.00, −0.05] 90% CI, full random intercept model in Table S2) (Figure 4). No strong relationship was detected between nest-sites and elevation, number of *Cinnamomum* trees, or percentage of broadleaf forest or village/town in the quadrats. R^2 estimate was 0.195 (Table S3).

3.3 | Breeding-site determinants from earth observation data

Using the earth observation data for breeding-site analyses, the mean percentages of land cover types within 332 m-diameter areas around sampled villages were: broadleaf forest, 9.9%; other forest, 15.3%; vegetable plot, 13.5%; tea plantation, 8.5%; rice paddy, 17.1%; bush/scrub, 9.5%; settlement/road, 18.7%; water, 7.5%. Classification distinguished land cover across satellite images with good overall accuracy (overall mean: 72.74%; range across land cover types: 66.77–94.37%; Table S6). There was no evidence of variation in proportions of different land cover types between breeding versus control villages, or between EOO versus buffer villages, with wide 90% credible intervals showing high levels of uncertainty in models (Figure S5).

4 | DISCUSSION

Our study shows that habitat selection studies of threatened species persisting within modified agricultural

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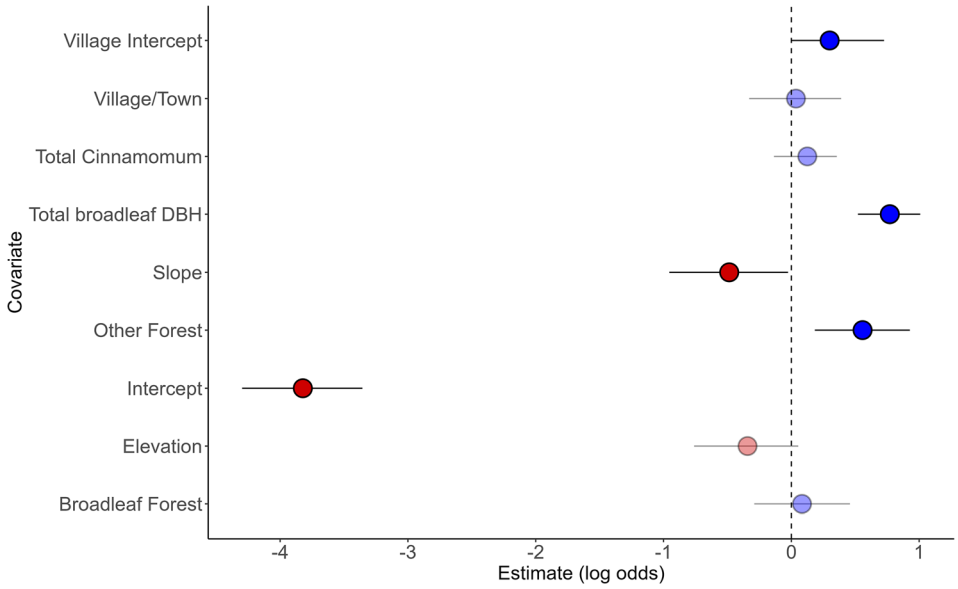


FIGURE 4 Interval plot showing the median (colored circles) and 90% credible intervals (CI, black lines) for the posterior distributions of predictors, in relation to whether a survey quadrat was ever a nesting site. Predictor levels are considered to have a clear effect if CI does not encompass zero on x axis (colored circles in bold). Blue circles denote a positive effect and red circles a negative effect. Plot displays optimal candidate model.

landscapes, conducted across multiple spatial scales, can provide new ecological insights for conservation planning and landscape policy. Here, we assessed data across the largest geographic area and number of breeding-sites for our study species to date. To do so, we developed breeding-site and nest-site RSFs to identify habitat-related factors that influence BCLT distribution at both breeding-sites and nesting-sites. Our findings establish a new baseline for identifying factors that potentially restrict recovery of the last surviving population of BCLT, one of the world's rarest birds.

No habitat selection based on topography, tree characteristics or land cover proportions was clearly detected in our models at the breeding-site level across a total of 39 breeding and control sites. However, differences were detected between sites inside and outside the BCLT's breeding EOO, with EOO villages situated at a lower elevation. This result is consistent with previous smaller-scale studies of BCLT breeding habitat (Hong et al., 2006; Huang et al., 2018), where breeding-sites were also found at lower elevation than control sites. However, the overall difference in elevation detected in our study was small, with only ca. 40 m difference between mean elevations inside and outside the EOO. Indeed, elevation may not necessarily be a direct causal factor determining BCLT range. Elevation typically affects species distributions by influencing factors such as temperature and precipitation and generating habitat gradients (Franklin, 2009; Jankowski et al., 2013), which may not be present across the limited elevational variation observed across sampling points (35–217 m, mean = 90 m) and the study landscape (15–1567 m, mean = 262 m). These findings, therefore, potentially indicate that while lower-elevation sites might represent more suitable habitat at the breeding-site scale, the BCLT is otherwise unlikely to have its breeding range strongly limited by habitat within the study landscape. Additionally, breeding-site models had high residual village level variation, suggesting that much of the models' explanatory power is explained by unmeasured factors specific to each village. These could be human factors such as disturbance for instance, removal of bamboo stands containing BCLT nests, presence of aggressive dogs, building developments, and loud markets with firecrackers (F. He, personal communication, 2019; L. Gardner, personal communication, 2020). These factors however would be infeasible for including as quantitative model variables in this particular analysis due to a lack of suitably structured data.

Our study also found no differences in land cover proportions at the breeding-site scale between breeding and control villages, or between villages inside or outside the EOO. Conversely, previous studies have identified vegetable gardens, scrub and broadleaf forests as potentially important BCLT foraging habitats (He et al., 2017; Liu et al., 2020). Our results do not contradict past suggestions that such habitats are important to BCLT; they may simply reflect that these land cover types are common across the study landscape (mean of 9.9% broadleaf forest and 13.5% vegetable gardens around sampled villages), and are not limiting BCLT distribution within our study area. Sites with larger amounts of these habitats may, therefore, not influence breeding-site selection at the breeding-site scale. In contrast, other bird species' home ranges can be more selective and contain higher proportions of certain habitats than expected by chance (Lee et al., 2005; Van Schmidt et al., 2014). These findings, therefore, also suggest that BCLT habitat selection may be weaker at the breeding-site scale.

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In contrast to the lack of signal in breeding-site analyses, analysis of nest-site selection showed that nesting-sites contained significantly higher broadleaf tree DBH compared to control-sites. This result is also consistent with past findings that BCLTs prefer nesting in broadleaf trees with higher DBH, or in taller trees, which typically have higher DBH (Huang et al., 2018; Zhang et al., 2017). This preference has not been reported in other Chinese laughingthrush species (Li et al., 2017; Liu et al., 2021; Wang et al., 2011). This may supply indirect evidence for why BCLT are rare compared to other laughingthrush species. Nesting-sites also contained significantly higher proportions of bamboo, fir, or mixed forest, which are typically dense and thus provide good cover for nesting birds. The selection of large broadleaf trees or dense forest stands as nest-sites may, thus, be related to nest protection (Martin & Roper, 1988; Oppel et al., 2004c).

Although nest-sites were also less steep than control-sites, nest-site selection was otherwise not associated with any other investigated habitat characteristics, contrasting with past suggestions that BCLTs prefer to nest in specific tree species or forest types such as Camphor (*Cinnamomum*) (Zhang et al., 2017) or Chinese sweetgum (*Liquidambar*), Hackberry (*Celtis*), and Chinese Ash (*Pterocarya*) (Huang et al., 2018). This departure from previous studies could be due to our dataset containing greater numbers of sampled sites (Huang et al., 2018 had $n = 9$ breeding sites). Other threatened species such as the Tuamoto Kingfisher (*Todiramphus gambieri gertrudae*) have shown an equal or greater preference for non-native forests and utilization of cultivated land through RSF studies, demonstrating how some species may persist in modified landscapes better than expected (Coulombe et al., 2011).

The positive relationship observed between the BCLT's EOO and relative lower elevations might suggest some restriction across the study landscape, with the observed nest-site preference for gentler slopes potentially influencing wider-scale distribution patterns resulting in preferences for valleys and river sides. Lower-elevation or lowland landscapes in China have historically supported higher human population densities and experienced greater habitat modification, which has artificially shaped the observed distribution of numerous species (Li et al., 2002; Turvey et al., 2015; Zhu et al., 2013). Alternatively, BCLT distribution may not naturally be restricted to low elevations; instead, its present-day range might be shaped by current or past anthropogenic activities. Moreover, the species' distribution may not be restricted by its breeding habitat, with its population dynamics potentially affected by habitat or anthropogenic factors associated with its non-breeding distribution, which remains poorly understood (Martinez & Lewthwaite, 2013). For example, southern China experienced intensified deforestation from 1700 CE onwards (Marks, 1998), and earlier conversion to plantation forest (Miller, 2020), with pronounced loss of *fengshui* forest during the early-mid 20th century (Coggins, 2003). Presence of *fengshui* forests is positively correlated with distance from urban centers, so they occur more frequently in remote regions such as Wuyuan (Tang et al., 2012), which may explain its persistence in this region. Other factors beyond those investigated in this study might, therefore, also play a role in determining the breeding distribution of the BCLT.

Altogether, our findings help to suggest why BCLTs are not more widely distributed across similar landscapes. The combination of selecting flatter ground, broadleaf trees with a high DBH, and more mixed forest at nesting-sites indicates a preference for landscapes with more forest and larger trees. Moreover, these sites occur in areas that are more likely to also support human settlements, all of which may be more prevalent within their range. However, both extrinsic and intrinsic factors may be involved with BCLT nest-site choice. Human disturbance is a recognized threat to BCLT breeding success (He et al., 2017), with nests or entire breeding-sites reported as being abandoned due to disturbance (He et al., 2017). This behavior is consistent with studies showing that colonially breeding birds can be more vulnerable to disturbance (Buckley & Buckley, 1976), with cooperative-breeding birds showing more flighty behavior in response to human approach than non-cooperative breeders (Blumstein, 2006). Other direct human impacts (e.g., persecution for the bird trade) might also influence the BCLT's restricted current distribution within a wider landscape containing potentially suitable habitat (Yang et al., 2018). Additionally, tourism in Wuyuan is and has been expanding rapidly in the past couple of decades (Yu, Y., personal communication, 2003), with many new resorts under construction as of 2019, and a newly built hotel at one former BCLT breeding-site (R. Gleave, personal communication, 2019). This may contribute to loss of breeding or foraging habitat, or disturbance of potential breeding colonies. In terms of intrinsic factors, several BCLT breeding-sites ($n = 8$) have been used for multiple continuous years (He et al., 2017); BCLTs also sometimes nest in the same tree for multiple years (F. He, personal communication, 2019). This behavioral pattern suggests some site fidelity, a well-documented phenomenon in birds that might contribute to the species' observed distribution (Greenwood et al., 1979).

Future work should address landscape-scale habitat selection by BCLT, as habitat conditions may change beyond the surveyed landscape, potentially revealing clearer insights about BCLT range limits. This knowledge

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gap can be overcome by performing landscape-scale analyses such as species distribution modeling. Other future studies could also look into BCLT forage availability, which is likely to determine breeding habitat preferences (Bruun & Smith, 2003). Our sampling approach had many strengths, including the most comprehensive and spatially broad assessment of BCLT habitat use to date. We also acknowledge that the placement of sampling points might have affected ecological patterns detected in our study. Known nest-sites could either be at the edge of, adjacent to, or in the center of villages, whereas the centers of control-sites were always placed centrally in villages, which could result in the inclusion of more built-up land for these sites. Future analyses could, thus, randomize placement of control-sites within a set boundary. However, village sizes varied considerably, with some extremely small control villages, and central point placement thus making little difference to the area surveyed; and no between-village bias was detected in models or in statistical comparisons of village characteristics. Furthermore, nesting-sites included within our analysis represent a subset of all known nesting-site trees, with their selection based on expert knowledge across multiple seasons rather than a survey of nest-sites within a single year. While this approach may bias the selection of more memorable nest-sites, we consider our nest-site selection to be generally representative due to their aforementioned site fidelity. We sampled nesting-sites representing different species and habitats, countering previous assumptions about BCLT nesting restrictions (e.g., Huang et al., 2018; Zhang et al., 2017). Another potential study limitation is around the choice of 100 m^2 quadrats, which may not capture much variation in variables such as land cover. While control sites were verified using both in-person visits in 2019 and social surveys with residents to establish past BCLT presence and absence, and many of these control sites may have been annually surveyed in the past for breeding BCLT, we cannot be sure which have and have not been surveyed, nor in which years, as information on absences was never recorded (F. He, personal communication, 2019).

These findings highlight both the importance of protecting remaining broadleaf trees and other forest stands associated with villages across the study landscape (Liu et al., 2020) and of integrating conservation-relevant data across multiple spatial scales. Maintaining forest stands within agricultural landscapes in Jiangxi Province and surrounding regions will also support other bird populations, as although many bird species persist within human-occupied agricultural mosaic landscapes in China (Wang & Young, 2003), bird diversity is positively influenced by non-crop vegetation quantities and habitat heterogeneity in these mixed habitats (Li et al., 2020). In particular, scaling up legal protection of *fengshui* forests across southern China would help to ensure that suitable habitat remains available for future BCLT population expansion, and will maintain important habitat refugia for many other species (Coggins, 2003; Liao et al., 2007). In contrast to some other threatened species (Sawyer & Brashares, 2013), we only found evidence for BCLT habitat selection existing mainly at the nest-site scale. This pattern may be linked to BCLT life history traits (Jedlikowski et al., 2016); as the species is known to engage in nest defense, nest-site selection may be more important than foraging opportunities in surrounding areas. More fundamentally, these results highlight that had we only investigated the breeding-site scale, the important relationship of BCLT nest-sites with large broadleaf and plantation trees would have gone undetected. Our approach can therefore constitute a useful, rapid tool for elucidating potential determinants of range restriction for rare species found within agriculturally modified landscapes.

AUTHOR CONTRIBUTIONS

RAG, STT, SKP, SJP, and WZ developed study design. RAG and YY collected data. RAG and DB analyzed data. RAG, STT, SKP, and SJP contributed to interpretation of data and writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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DATA AVAILABILITY STATEMENT

Spatial data for this study has been made available on Figshare but anonymised and at a 50 km resolution, as sharing breeding locations of the Critically Endangered study species may increase its risk of trapping for the caged bird trade. https://figshare.com/articles/dataset/Habitat_data_of_breeding_and_control_sites_for_the_Blue-crowned_Laughingthrush_Pterorhinus_courtoisi_in_southeast_China/25723911.

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