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The roles of temperature, nest predators and information parasites for geographical variation in egg covering behaviour of tits (Paridae)

Olli J. Loukola[1,2] | Peter Adamik[3] | Frank Adriaensen[4] | Emilio Barba[5] | Blandine Doligez[6] | Einar Flensted-Jensen[7] | Tapio Eeva[8] | Sami M. Kivelä[1] | Toni Laaksonen[8] | Chiara Morosinotto[9] | Raivo Mänd[10] | Petri T. Niemelä[11] | Vladimir Remeš[3,12] | Jelmer M. Samplonius[13,14] | Manrico Sebastiano[15,16] | Juan Carlos Senar[17] | Tore Slagsvold[18] | Alberto Sorace[19] | Barbara Tschirren[20] | János Török[21] | Jukka T. Forsman[1,22]

[1]Department of Ecology and Genetics, University of Oulu, Oulu, Finland

[2]Botanical Museum, Biodiversity Unit, University of Oulu, Oulu, Finland

[3]Laboratory of Ornithology, Department of Zoology, Palacky University, Olomouc, Czech Republic

[4]Department of Biology, Evolutionary Ecology Group, University of Antwerp, Antwerp, Belgium

[5]Terrestrial Vertebrates Research Unit "Cavanilles", Institute of Biodiversity and Evolutionary Biology, University of Valencia, Paterna, Spain

[6]CNRS, Department of Biometry & Evolutionary Biology, UMR 5558, University of Lyon 1, University of Lyon, Villeurbanne, France

[7]Cypresvej 1, Brønderslev, Denmark

[8]Department of Biology, University of Turku, Turku, Finland

[9]Bioeconomy Research Team, Novia University of Applied Sciences, Ekenäs, Finland

[10]Institute of Ecology & Earth Sciences, University of Tartu, Tartu, Estonia

[11]Department Biologie II, LMU-München, Munich, Germany

[12]Department of Ecology, Charles University, Praha, Czech Republic

[13]Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands

[14]Institute of Evolutionary Biology, The University of Edinburgh, The King's Buildings, Edinburgh, UK

[15]Behavioural Ecology and Ecophysiology Group, Department of Biology, University of Antwerp, Wilrijk, Belgium

[16]Centre d'Études Biologiques de Chizé (CEBC), UMR 7372 CNRS-Université de La Rochelle, Villiers-en-Bois, France

[17]Evolutionary and Behavioural Ecology Unit, Museu de Ciències Naturals de Barcelona, Barcelona, Spain

[18]Department of Biosciences, University of Oslo, Oslo, Norway

[19]ISPRA, Rome, Italy

[20]Centre for Ecology and Conservation, University of Exeter, Penryn, UK

[21]Department of Systematic Zoology and Ecology, Behavioural Ecology Group, Eötvös Loránd University, Budapest, Hungary

[22]Natural Resources Institute Finland (Luke, Oulu), University of Oulu, Oulu, Finland

Correspondence
Olli J. Loukola, Department of Ecology and Genetics, University of Oulu, Oulu, Finland.
Email: olli.loukola@oulu.fi

Abstract

Aim: Nest building is widespread among animals. Nests may provide receptacles for eggs, developing offspring and the parents, and protect them from adverse environmental conditions. Nests may also indicate the quality of the territory and its owner

and can be considered as an extended phenotype of its builder(s). Nests may, thus, function as a sexual and social signal. Here, we examined ecological and abiotic factors—temperature, nest predation and interspecific information utilization—shaping geographical variation in a specific nest structure—hair and feather cover of eggs—and its function as an extended phenotype before incubation in great (*Parus major*) and blue tits (*Cyanistes caeruleus*) across Europe. We also tested whether egg covering is associated with reproductive success of great tits.

Location: Fourteen different study sites and 28 populations across Europe.

Taxon: *Parus major, Cyanistes caeruleus.*

Methods: We recorded clutch coverage estimates and collected egg covering nest material from the tit nests. We also measured nest specific breeding parameters and phenotypic measurements on adults. We tested whether mean spring temperatures, nest predation rates and flycatcher (*Ficedula* spp) densities in the study areas explain the large-scale geographical variation of clutch coverage and reproductive success of tits.

Results: The degree of egg coverage of great tits increased with lower mean spring temperature, higher nest predation rate and higher flycatcher density. We did not find egg covering of blue tits to be associated with any of the ecological or abiotic factors. Moreover, egg covering of great tits was not associated with reproductive success in our cross-sectional data, yet a rigorous assessment of fitness effects would require long-term data.

Main conclusions: Our findings suggest that, in great tits, egg covering may simultaneously provide thermal insulation against cold temperatures during egg-laying in spring and also represent a counter-adaptation to reduce information parasitism by flycatchers and nest predation. Hence, geographical variation in interspecific interactions, and consequently in co-evolutionary processes, may affect the evolution of nest characteristics besides environmental conditions.

KEYWORDS

bird nest, breeding success, *Cyanistes caeruleus*, extended phenotype, nest structure, *Parus major*

1 | INTRODUCTION

In the animal kingdom, nest building is a common behaviour. The basic functions of nest building are thought to be protection against elements of abiotic (e.g. low temperatures, humidity) and biotic (e.g. nest predators, parasites) risks for offspring until they hatch or become independent from parental care (Hansell, 2007). Nest structure shows large variation across species. Some species invest a considerable amount of time and resources in building complex and decorated nest structures while, in others, just a few pieces of rock or plant material are enough (Hansell, 2007). This implies that nests may also have functions other than offering security to offspring during development. In some species, such as the stickleback (*Gasterosteus aculeatus*) (Barber, Nairn, & Huntingford, 2001; Östlund-Nilsson & Holmlund, 2003), cichlid fishes (McKaye, Louda, & Stauffer, 1990; Schaedelin & Taborsky, 2006) and passerines

(Grubbauer & Hoi, 1996; Hoi, Schleicher, & Valera, 1994; Jelínek, Požgayová, Honza, & Procházka, 2016), the nest has become a signal in mate attraction and selection (Schaedelin & Taborsky, 2009). In black kites (*Milvus migrans*), the decoration of nests with pieces of white plastic is a reliable signal in dominance hierarchy among conspecifics (Sergio et al., 2011). Thus, a perceptible nest can be considered an extended phenotype of its builder(s) (Dawkins, 2016), because the placement, structure, materials and size of the nest affects the probability that the genes of the builder(s) are transmitted to the next generation by affecting mate selection and offspring survival probability.

Extended phenotypes, such as odour, chemical marks, nests and other constructions (webs, excavations, burrows, bowers, piles or pieces of various materials), are often important signals in intentional communication among conspecifics related to mate attraction and selection, dominance hierarchy, territory defence and

species recognition (Schaedelin & Taborsky, 2009). These signals may also be long-lasting and readily available to heterospecifics, actually providing a source of inadvertent information about the location, decisions, social structure and dominance, body condition, and cognitive capabilities of signal producers to those who can interpret the signals. For example, in bowerbirds (family Ptilonorhynchidae), the elaborateness of the display structure, the bower, reflects the species identity and also the age and experience of the focal male (Vellenga, 2016). Both con- and heterospecifics may thus use it to make inferences about the quality of the territory and its owner.

The use of inadvertent information is common among conspecifics (Danchin, Giraldeau, Valone, & Wagner, 2004) but also among heterospecifics (Seppänen, Forsman, Mönkkönen, & Thomson, 2007). Most valuable interspecific information is predicted to be provided by species with overlapping resource needs (Seppänen et al., 2007). Many traits defining extended phenotypes have been shown or suggested to be used by heterospecifics as sources of information: tit (Paridae) clutch size by flycatchers (*Ficedula* spp) for breeding habitat selection (Forsman & Seppänen, 2011; Loukola, Seppänen, Krams, Torvinen, & Forsman, 2013; Samplonius, Kappers, Brands, & Both, 2016; Seppänen & Forsman, 2007; Seppänen, Forsman, Mönkkönen, Krams, & Salmi, 2011), sibling vole's (*Microtus levis*) odour and chemical signals by field voles (*Microtus agrestis*) for predator avoidance (Hughes, Korpimäki, & Banks, 2010) and stingless bee's (*Melipona rufiventris*) odour and chemical signals by another stingless bee species (*Trigona spinipes*) for space use and foraging decisions (Nieh et al., 2004). However, in contrast to bodily phenotypes, we know very little about geographical variation of extended phenotypes (but see Deeming & Mainwaring, 2015; Hansell, 2000) and the potential processes behind the patterns.

Tits' distribution ranges are large, and thus, their nesting behaviours provide a good model system to examine large-scale geographical patterns of extended phenotypes. All tit species are cavity nesting, and the basic structure of the nest consists of moss and a layer of animal hair or feathers on top, on which eggs are laid. During egg-laying, eggs are usually covered with a loose tuft of hair, feathers, moss, hay or other light material. This characteristic, the covering of eggs, is our trait of interest because it occurs widely in genus *Parus* and *Cyanistes* (Haftorn & Slagsvold, 1995), yet the propensity to cover the eggs varies both among individuals within populations and among geographically distinct populations (Loukola, Laaksonen, Seppänen, & Forsman, 2014). In great tits, usually all eggs are totally covered with hair, but sometimes the cover is partial or does not exist at all (Loukola et al., 2013).

Three mutually non-exclusive hypotheses have been put forward to explain great and blue tit nest structure and egg covering behaviour (Haftorn & Slagsvold, 1995). First, *the insulation hypothesis* predicts that the cover provides thermal insulation against cold temperatures during egg-laying in spring. Indeed, recent studies show that the mass and insulation capacity of great and blue tit nests are lower at high ambient temperature (Deeming, Mainwaring, Hartley, & Reynolds, 2012; Mainwaring, Hartley, Lambrechts, & Deeming, 2014).

Second, *the nest predation hypothesis* postulates that egg covering is a protection against nest predators (Haftorn & Slagsvold, 1995; Saavedra & Amo, 2019) or interspecific competitors that may damage the nest. For example, recent experiment by Saavedra and Amo (2019) showed that blue tits covered their eggs more frequently when they detected an increase in the perceived risk of predation. Kreisinger and Albrecht (2008) showed experimentally that mallard (*Anas platyrhynchos*) nests that were covered with nest material, suffered significantly lower rates of nest predation than nests which were left uncovered. An example of the interspecific competition is found in house wrens (*Troglodytes aedon*) in North America that may destroy the nests of black-capped chickadees (*Poecile atricapillus*) and tufted titmice (*Baeolophus bicolor*; White & Kennedy, 1997). In general, nest predation is a major factor affecting the behaviour and life history traits in birds (Martin & Briskie, 2009).

Finally, the most recent hypothesis, *the information parasitism hypothesis*, suggests that great tits cover eggs to protect against information acquisition by flycatchers (Loukola et al., 2014). Upon arrival, migratory flycatchers are attracted to the proximity of resident tits during their nest-site selection that results in fitness benefits (Forsman, Seppänen, & Mönkkönen, 2002) and the visible clutch size of tits seems to be an important source of information for flycatchers. In general, the tits are still in egg-laying stage when the Flycatchers prospect tits' nests in spring (Forsman et al., 2018; Forsman & Thomson, 2008; Samplonius & Both, 2019) and may use tit clutch size to adjust their own investment in the offspring (clutch size and egg mass) (Forsman, Seppänen, & Nykänen, 2011), and in deciding whether they would copy or reject nest-site preferences of the focal tits (Forsman & Seppänen, 2011; Loukola et al., 2013; Seppänen et al., 2011). Flycatchers' interest in the clutch size of tits makes sense as environmental variation explains a large amount of variance in clutch size in blue tits (e.g. Tremblay, Thomas, Lambrechts, Blondel, & Perret, 2003) and great tits (e.g. Beldal et al., 1998), implying that tit clutch size reliably reflects the quality of the environment and/or parents and can readily be used as a cue on territory quality. Thus, tit nests can be considered to include two components of an extended phenotype that are used by information parasites: clutch size (reflecting parental/territorial quality) and nest structure that covers the clutch totally, partially or not at all.

The information utilization by flycatchers is not neutral to tits. The selective copying of nest-site characteristics by flycatchers may lead to niche convergence (Loukola et al., 2013) and results in fitness losses in great tits in terms of the number and condition of fledglings (Forsman, Thomson, & Seppänen, 2007). Once flycatchers (i.e. the information parasite) have evolved a strategy for taking advantage of a tit (i.e. the host), tits are expected to evolve counter-adaptations, which may lead to an evolutionary arms race (Dawkins & Krebs, 1979) between the tits and the flycatchers on acquiring and hiding information (Seppänen et al., 2007). Indeed, a recent study by Loukola et al. (2014) experimentally demonstrated that the simulated presence of pied flycatchers increased

the amount of hair great tits brought on the eggs and covered them more carefully when exposed to flycatcher playback song compared to the control treatment with a playback song of a non-information-parasitic species. Thus, great tits' nest structure and covering eggs with hair may also be a counter-adaptation to reduce information parasitism.

Phenotypes (bodily and extended) often show geographical variation suggesting spatial variation in selection regimes (Mayr, 1956; Slatkin, 1973). The nests of birds make no exception (Deeming & Mainwaring, 2015; Hansell, 2000). Comparing egg covering behaviour of great and blue tits among different populations at a large geographical scale facilitates testing the insulation, nest predation and information parasitism hypotheses. This is because each of temperature during egg-laying period, the abundance of nest predators and potential information parasites (flycatchers) of tits vary geographically. As we do not know whether the hypothesized mechanisms have additive or interactive effects on egg covering behaviour, we test our hypotheses based on these perspectives; if the insulation, nest predation and information parasitism have additive effects on egg covering behaviour, the extent of egg covering should increase with lower mean spring temperature and higher nest predation rate. Based on results of Loukola et al. (2014), we also predict an increased extent of egg covering in the presence and density of potential information parasites. If there is an interactive component in how the hypothesized mechanisms affect egg covering behaviour, interactions among mean spring temperature, nest predation rate and density of information parasites should be found in statistical analysis.

In addition to main hypotheses, other variables, such as nest floor area and habitat type, may affect tits egg covering behaviour. Tits establish the fully lined nest cup only at the start of incubation (Deeming, Morton, & Laverack, 2019). If the eggs are spread out over a wider area in nest boxes with larger floor area, we expect that more material is needed to cover the eggs. If the density and the species composition of local bird and mammal communities, which are linked to various characteristics of the habitat, including tree species, affect the availability of feathers and hairs (egg covering material), we expect to find differences in the extent of egg covering in study sites with different habitat types. Finally, we explore whether reproductive success of the tits (number of hatched eggs and fledglings) is positively associated with extent of egg covering, as would be expected if egg covering behaviour is under positive natural selection.

2 | MATERIALS AND METHODS

2.1 | Study areas

The great tit data for this study were collected in spring 2013 from 10 different countries, 14 study areas (Figure 1, Table S1) and 28 populations in Europe. The blue tit data were collected in the same year from 6 of the 10 countries, 8 of the 14 study areas and 22
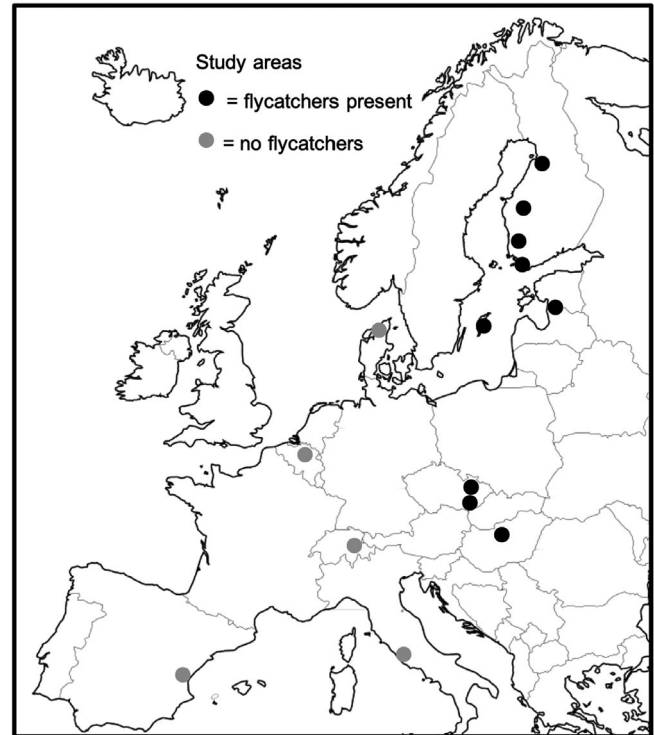
FIGURE 1 A map of Europe showing the locations of the study areas. See Table S1 for more details concerning the study populations

of the 28 populations. All study populations breed in nest boxes. Research was carried out in accordance with legislation of each country.

2.2 | Field procedure

Nest building state and the beginning of the egg-laying (laydate) were checked during regular field observations. Use of egg cover tends to increase during the first day of the laying stage (Haftorn & Slagsvold, 1995). During the egg-laying stage, when tits had laid their fourth to eighth egg, (a) the nest was photographed to get a measurement of the extent of the clutch coverage, that is, the proportion of the visible clutch surface (%) and (b) all the hair and other material that covered tit eggs and nest cup was removed to expose the eggs and placed in a zip lock bag for later measurement of hair mass and the nest was photographed again. After photographing the nest, the removed material was replaced by same quantity of sheep hair. The onset of incubation was determined by observing the presence of female on the nest and touching eggs to determine whether the eggs were cold or warm. Nest specific breeding parameters (number of hatched eggs and fledglings) and phenotypic measurements on adults (Table 1) were also collected. We recorded clutch coverage estimates and mean spring temperatures (from the nearest available meteorological stations to each of the study area) from 476 great tit nests and 123 blue

TABLE 1 List of variables. Model sets refer to the different sets of models that were used in assessing the study hypotheses (see Statistical methods section for details)

Name of the variable	Model set	Type of the variable	Definition of the variable
Clutch coverage	1–5, 10, 6–9	Response explanatory	First principal component of clutch covering rate and the mass of the covering material
Number of hatched eggs	6, 7	Response	
Number of fledglings	8, 9	Response	
Dominant tree genus in the study area	1–5, 10	Explanatory	Defines the habitat type. Affects egg covering material availability
Age of the tit parent(s)	6–9	Explanatory	Binary variable; 1-year-old or older
Flycatcher density	1–9	Explanatory	Proportion of nest boxes occupied by flycatchers in the study area. Standardized in model sets 6–9
Flycatcher presence	10	Explanatory	Binary variable; flycatcher present or not
Mean spring temperature	1–9, 10	Explanatory	Mean daily temperatures (°C) between the beginning of the nest building and fledging, from the nearest available meteorological stations to each of the study area. Standardized in model sets 6–9
Clutch size	6–9	Explanatory	Final number of eggs in the nest
Nest predation rate	1–10	Explanatory	The proportion of predated nests within a study site. Standardized in model sets 6–9. Nests where devices had been added to prevent nest predation (e.g. wire netting) were removed from the analysis
Study population	1–5, 10	Random factor	
Nest floor surface	1–5, 10	Explanatory	Surface area of the nest box floor in cm^2. Standardized in model sets 4 and 5
Geographical location	1–5, 10	Explanatory	First principal component of altitude, latitude and longitude

tit nests and nest predation rates from 345 great tit nests and 74 blue tit nests. Flycatcher (either *Ficedula hypoleuca* or *Ficedula albicollis*) density was measured in the end of breeding season as the proportion of nest boxes occupied by flycatchers in the study population.

2.3 | Measurement of nest characteristics

The clutch coverage rate was measured by comparing the proportions of the visible clutch surfaces from the digital photographs taken from the nest before and after cover removals using ImageJ software (US National Institutes of Health, http://imagej.nih.gov/ij). The clutch surface was measured using freehand tracing and area calculator tools. Clutch surfaces were measured twice from each picture to minimize measurement error and average values were used in the analyses. Masses of the collected hair samples were weighed to the nearest 0.0001 g by using an Ohaus AS120S analytical balance. Phenotypic measurements on adult tits were obtained when they were captured during food provisioning. Age was classified in the field as 1-year-old (second calendar year) or older (at least third calendar year) (Jenni & Winkler, 1994). Adult and young birds were handled under the ringing licenses of the authors. Hence, our study complied with the national legislation of Belgium, Czech Republic, Denmark, Estonia, Finland, Hungary, Italy, Spain, Sweden and Switzerland concerning handling wild animals. Variables used in statistical analyses are listed in Table 1.

2.4 | Statistical methods

The distribution of clutch covering rate (proportion of covered eggs) was slightly U-shaped with a high peak at one (all eggs covered), which is problematic for analysis. Therefore, we measured clutch coverage by combining clutch covering rate and the mass of material used to cover the eggs, because these variables together measure the investment of the tit parents in covering their clutch. For this purpose, we ran principal component analysis for the data on egg coverage and the mass of the covering material and used the first principal component ('clutch coverage' hereafter, explains 72.3% of the variance, eigenvalue = 1.0) as a response variable when analysing variation in clutch covering behaviour. Clutch coverage variable was symmetrically (approximately normally) distributed, and positively correlated with both clutch covering rate and mass of the covering material, higher values, thus, indicating higher investment in clutch covering (Figure S1).

All statistical analyses were conducted with R version 3.4.3 (R Core Team, 2017). Linear mixed-effects models (LMMs; function *lme* in package 'nlme' (Pinheiro et al., 2017)) were used to analyse variation in the clutch covering of great (Model sets 1–4) and blue tits (Model set 5). Generalized linear mixed-effects models (function *glmer* in package 'lme4'; Bates, Mächler, Bolker, & Walker, 2014) with Poisson distribution and a logarithmic link function were used to analyse variation in the number of hatched eggs and fledglings of the great tits (Model sets 6–9). In model sets 6–9, we standardized all continuous explanatory variables of the model. Standardization

makes the quantitative interpretation of model parameters less intuitive, which is the reason why standardization was used only when it was really needed for aiding/facilitating model convergence. We used multi-model inference; effects of analysed variables were summarized by model averaging (Burnham & Anderson, 2002) (function *model.avg* in package 'MuMIn'; Barton, 2009).

We derived 10 model sets. *Model set 1* (Table 2a) tested if the alternative hypotheses (i.e. insulation, nest predation, information parasitism), nest floor surface area or forest type (dominant tree genus) in the study site explain variation in clutch coverage in great tits. This model set was fitted to data ($N_{observations}$ = 341) including observations from all the study sites, also including sites where the flycatcher density was zero. Mean spring temperature, nest predation rate, flycatcher density, nest floor surface area, first principal

component of geographical variables (altitude, latitude and longitude) and dominant tree genus in the study site were set as fixed effects, and population as a random effect in the global model. Time of the year (Laydate) was not included in the analysis because it is strongly negatively correlated with the first principal component of geographical variables (Pearson's correlation, $r = -.61$, $t = -3.41$, $df = 343$, $p < .001$) (see Laydate in Table S3). Nest predation rate positively correlates with mean spring temperature ($r = .67$) but both of these variables were retained in all models because of their importance for assessing the study hypotheses. No interactions were included in any model. The set of all meaningful models simpler than the global model was derived with the function 'dredge' (package 'MuMIn'; Bartón & Barton, 2017) for model averaging, the global model being included in model averaging (see Table S2a for the set

TABLE 2 Model-averaged (full average) fixed effects in model sets 1 and 2 explaining clutch coverage in the great tit. Model set 1 is based on the assumption that temperature, nest predation and information parasitism act additively on clutch coverage, whereas interactive effects of these variables were assumed in model set 2

Model set	Variables	Estimate	Adjusted SE	z value	Pr(>|z|)
(a) Model set 1	(Intercept)	1.078	0.556	1.939	0.053
	Nest floor surface	0.009	0.003	3.527	**<0.001**
	Predation rate	0.045	0.015	3.075	**0.002**
	Temperature	−0.238	0.046	5.145	**<0.001**
	DTG (Citrus)	1.750	0.608	2.876	**0.004**
	DTG (Fagus)	−0.754	0.679	1.110	0.267
	DTG (Mixed)	0.037	0.541	0.069	0.945
	DTG (Picea)	−0.490	0.427	1.149	0.251
	DTG (Pinus)	0.044	0.418	0.105	0.917
	DTG (Quercus)	−0.453	0.486	0.933	0.351
	Flycatcher density	0.007	0.010	0.686	0.492
	Geographical location	0.093	0.184	0.505	0.614
(b) Model set 2 with interactions	(Intercept)	1.214	0.643	1.888	0.059
	Nest floor surface	0.010	0.003	2.991	**0.003**
	Predation rate	−0.013	0.079	0.163	0.870
	Temperature	−0.276	0.085	3.246	**0.001**
	DTG (Citrus)	1.988	0.709	2.805	**0.005**
	DTG (Fagus)	−0.767	0.666	1.151	0.250
	DTG (Mixed)	0.094	0.568	0.166	0.868
	DTG (Picea)	−0.482	0.427	1.129	0.259
	DTG (Pinus)	0.091	0.427	0.213	0.831
	DTG (Quercus)	−0.429	0.491	0.875	0.382
	Flycatcher density	0.010	0.026	0.406	0.685
	Geographical location	0.074	0.172	0.429	0.668
	Predation rate: Temperature	0.004	0.006	0.723	0.470
	Flycatcher density: Temperature	0.000	0.002	0.138	0.890
	Flycatcher density: Predation rate	0.000	0.001	0.101	0.920
	Flycatcher density: Predation rate: Temperature	0.000	0.000	0.029	0.977

Note: Bold values indicates statistical significance.

Geographical location = First principal component of altitude, latitude and longitude.

Abbreviation: DTG, dominant tree genus.

TABLE 3 Model-averaged (full average) fixed effects of model sets 3 and 4 explaining clutch coverage in the great tit in study sites where the flycatchers were present. Model set 3 is based on the assumption that temperature, nest predation and information parasitism act additively on clutch coverage, whereas interactive effects of these variables were assumed in model set 4

Model set	Variables	Estimate	Adjusted SE	z value	Pr(>|z|)
(a) Model set 3 without interactions	(Intercept)	−1.241	1.182	1.050	0.294
	Flycatcher density	0.036	0.014	2.591	**0.010**
	Predation rate	0.022	0.014	1.547	0.122
	Temperature	−0.049	0.077	0.634	0.526
	Nest floor surface	0.000	0.002	0.220	0.826
	DTG (Picea)	−0.001	0.217	0.003	0.997
	DTG (Pinus)	−0.026	0.181	0.142	0.887
	DTG (Quercus)	−0.003	0.279	0.010	0.992
	Geographical location	0.009	0.111	0.085	0.932
(b) Model set 4 with interactions	(Intercept)	−1.040	1.942	0.536	0.592
	Flycatcher density	0.033	0.033	1.014	0.310
	Predation rate	0.027	0.134	0.204	0.838
	Temperature	−0.065	0.172	0.378	0.706
	Nest floor surface	0.001	0.003	0.257	0.798
	DTG (Picea)	−0.004	0.219	0.016	0.987
	DTG (Pinus)	−0.032	0.306	0.103	0.918
	DTG (Quercus)	−0.006	0.351	0.018	0.985
	Geographical location	0.010	0.131	0.074	0.941
	Predation rate: Temperature	0.000	0.004	0.049	0.961
	Flycatcher density: Predation rate	0.000	0.002	0.008	0.994
	Flycatcher density: Temperature	0.000	0.003	0.030	0.976

Note: Bold values indicates statistical significance.

Geographical location = First principal component of altitude, latitude and longitude.

Abbreviation: DTG, dominant tree genus.

of averaged models). Bivariate correlations between the study variables are provided in Table S3.

Model set 2 (Table 2b) was derived otherwise similarly to model set 1, but all possible interactions among the nest predation rate, mean spring temperature and flycatcher density were included in the global model (see Table S2b for the set of averaged models).

Model set 3 (Table 3a) was derived otherwise similarly to model set 1, but these models were fitted to data including only areas where the flycatchers were present (flycatcher density > 0, $N_{observations}$ = 169, see Table S4a for the set of averaged models). This was done to reliably estimate the effect of flycatcher density. In the full data the high number of zeros (flycatchers not present) might confound the estimation (underestimation) of flycatcher density effect on great tit egg covering behaviour.

Model set 4 (Table 3b) was derived otherwise similarly to model set 3, but all two-way interactions among the nest predation rate, mean spring temperature and flycatcher density were included in the global model (the three-way interaction was ignored as the model-fitting failed when it was included in the global model; see Table S4b for the set of averaged models).

Model set 5 ($N_{observations}$ = 74; Table S5) was otherwise similar to model set 1, but it focused on variation in clutch coverage in blue tits (see Table S6 for the set of averaged models). Because of the low number of blue tit observations, we did not conduct any further analyses for this species.

Model sets 6 and 7 tested whether the clutch coverage of great tits or the ecological and abiotic environment explain the number of hatched eggs of great tits by using all great tit data.

In *model set 6* (Table S7), number of hatched eggs was used as a dependent variable and clutch size was added as a covariate in the global model in both model sets to take the effect of clutch size variation into account. In addition to clutch size, fixed effects of the global models included also clutch coverage, mean spring temperature, nest predation rate, flycatcher density, as well as female age and its interaction with clutch size, because female age affects clutch size (Perrins & Mccleery, 1985). Population was set as a random effect. Except clutch size (a non-negative integer), continuous variables were standardized (by subtracting mean from each observation and dividing this difference by standard deviation, see Table S8 for the set of averaged models) to aid model convergence.

Model set 7 (Table S9) was derived otherwise similarly to model set 6, but all possible interactions among the nest predation rate, mean spring temperature and flycatcher density were included in the global model (see Table S10 for the set of averaged models).
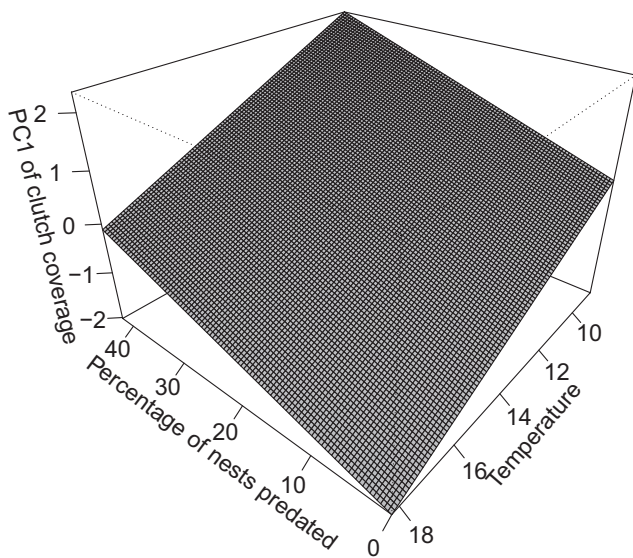
Model sets 8 (Table S11; see Table S12, for the set of averaged models) *and 9* (Table S13; see Table S14, for the set of averaged models)) tested whether the clutch coverage of tits or the ecological and abiotic environment explain the number of fledged offspring of great tits and were derived otherwise similarly to model sets 6 and 7, respectively, but number of fledged offspring was used as a dependent variable. Population was set as a random effect in all models.

Model set 10 (Table S15; see Table S16, for the set of averaged models) was otherwise similar to model set 1, but flycatcher density was replaced with flycatcher presence (binary variable; flycatcher present or not) for checking whether the results are sensitive to the way how flycatcher density is handled (continuous vs. presence/absence).

3 | RESULTS

Model set 1 showed that clutch coverage of great tits was negatively associated with the mean spring temperature, positively associated with nest predation rate and nest floor surface area (Table 2a and Figure 2). Clutch coverage was also affected by the dominant tree genus, being particularly high at sites dominated by genus *Citrus* trees (Table 2a).

Model set 2 showed no evidence of any interactions among the hypothesized mechanisms affecting clutch coverage (Table 2b).

When focusing only on sites where flycatchers are present (model set 3), clutch coverage was positively associated with the flycatcher density (Figure 3), but the mean spring temperature and nest predation rate effects disappeared in this smaller subset of the data (Table 3a).
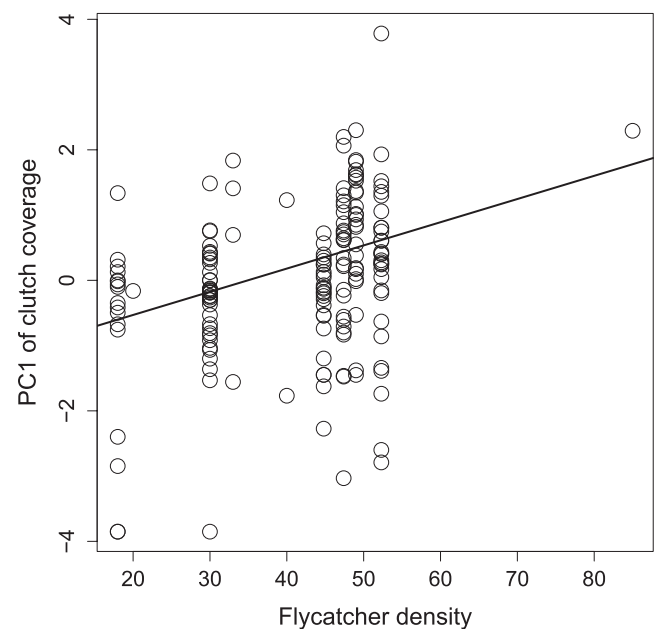
Model set 4 showed no evidence of any interactions among the hypothesized mechanisms affecting clutch coverage on sites where flycatchers are present (Table 3b).

Model set 5 showed that clutch coverage of blue tits was not associated with any of ecological or abiotic factors (Table S5).

Model sets 6 and 8 showed that both the numbers of hatched eggs and fledged offspring were positively associated with clutch size, as expected, and number of fledged offspring was positively associated with mean spring temperature, but neither of them was associated with clutch coverage, predation rate, flycatcher density or female age (Tables S7 and S11 and Figures S2 and S3).

Model sets 7 and 9 showed no evidence of any interactions among the hypothesized mechanisms affecting reproductive success (Tables S9 and S13).

Model set 10 showed that replacing the flycatcher density to flycatcher presence as an explanatory variable did not change the model-averaged results (Table S15).

FIGURE 2 Regression surface illustrating the relationship between the mean spring temperature (°C), nest predation rate and clutch coverage (first principal component of proportion of clutch covered and mass of the cover material) in great tits. The surface was drawn by using model-averaged parameter estimates based on the assumption of additive effects of mean spring temperature, nest predation rate and flycatcher density (Table 2a) for nest predation rate and mean spring temperature effects, setting dominant tree genus to *Betula* and nest floor surface area to its mean value. Variables that, according to model averaging, did not explain clutch coverage were ignored

FIGURE 3 Clutch coverage of great tits in relation to flycatcher density (%) in populations where flycatchers were present. Circles depict data, and the line is a regression line based on model-averaged parameter estimates for flycatcher density effect (Table 3a). Variables that, according to model averaging, did not explain clutch coverage were ignored. The same analysis was repeated without the observation with the highest flycatcher density (>80%). This did not qualitatively change the model-averaged results (see Table S17; see Table S18, for the set of averaged models and Figure S4)

4 | DISCUSSION

The aim of this study was to investigate large-scale geographical variation in great and blue tits' egg covering behaviour in Europe and variables that may explain egg covering behaviour. In particular, we test three hypotheses, *the insulation*, *nest predation and information parasitism hypotheses*, suggested to explain the egg covering behaviour of tits. Our results from 28 different populations across Europe show that the clutch coverage of great tits is more extensive with lower mean spring temperature and higher nest predation rate. The analysis also suggests that the increasing flycatcher density is associated with increased egg covering in great tits. However, this effect was found only in populations where breeding flycatchers were present. Despite flycatchers being absent from some study sites, they were breeding in the vicinity of most of these sites, which means that we may have only tit populations with co-evolutionary history with flycatchers in our data. The hypothesized mechanisms appear to have additive effects on egg covering behaviour. Thus, these results support the mutually non-exclusive hypotheses that have been put forward to explain egg covering behaviour in great tits, suggesting that egg covering may have multiple functions. In blue tits, clutch coverage was not associated with any of ecological or abiotic factors, but one should be careful in interpreting these results due to the limited sample size.

First, clutch coverage may provide thermal insulation against low temperatures in spring during egg-laying, in a period when the females are not staying in the nest for long periods at a time during the day. This is in line with Haftorn and Slagsvold (1995), who found that egg covering tended to be negatively related to the increasing ambient air temperature in great tits. Also, Loukola et al. (2014) found that, in Finland, great tits had 54.5% (0.5 g) more hair on the eggs in Oulu than in Turku. Oulu (latitude 65°) is located over 600 km north of Turku (latitude 60°) and the mean daily spring temperature was 2.4°C cooler (in years 1981–2010) in Oulu (Pirinen et al., 2012).

Second, egg covering behaviour might be a protection against nest predators. Yet, it seems unlikely that hair or feather cover could prevent small predators such as weasel (*Mustela nivalis*) or stoat (*Mustela erminea*) from finding the eggs underneath the covering material. Tits also cover eggs in the populations where mustelids are absent, for example on Gotland, Sweden. However, it is possible that covering the eggs may cheat naive predators into believing that there are no eggs in the nest (Perrins, 1979). Also, predators such as woodpeckers (Picidae), that have small olfactory bulbs (Bang & Cobb, 1968), and thus use mostly visual cues when searching for food, could perceive a nest with covered eggs as an empty nest. If egg covering prevents even some of the nest predation attempts by any of the predators, selection for egg covering could be expected. This is because the nest predation is among the most important factors affecting the behaviour and life history traits in birds (Martin & Briskie, 2009). How egg covering affects the behaviour of different predators, remains to be tested.

Third, egg covering could be a defence (counter-adaption) to reduce information parasitism. Hiding the clutch size from flycatchers and other competitors makes sense because the clutch size may provide accurate and reliable inadvertent information about the environment and the quality of the tit parents to prospecting birds. Environmental variation explains a large amount of variance in clutch size (Beldal et al., 1998; Charmantier, Perrins, McCleery, & Sheldon, 2006; McCleery et al., 2004; Tremblay et al., 2003) suggesting that clutch size reliably reflects the quality of the environment and can be readily used as a cue about territory quality. Moreover, the clutch size of tits may reveal their competence in cognition and decision-making (Cauchard et al., 2017; Cole, Morand-Ferron, Hinks, & Quinn, 2012) and the pied flycatchers have been shown to use clutch size of tits as a primary cue of whether to copy or reject observed tit choices, such as a novel nest site feature preference (Loukola et al., 2013). By covering the eggs, tits would hide this information from flycatchers. Without the information about the tits' success, flycatchers may reject the behaviour of the observed tits more frequently and may be less likely to settle in the immediate neighbourhood of a tit nest. Flycatchers breeding close to tits have a negative effect on tit offspring number and condition (Forsman et al., 2007). Consistent with this, a recent study (Loukola et al., 2013) suggested that flycatchers tended to reject the choices of ostensibly successful tits when the clutch was covered. This, in turn, may reduce the costs of interspecific competition (Loukola et al., 2013).

Interspecific exploitation, or eavesdropping (Kroodsma & Miller, 1996) of inadvertent signals is important because it may affect the evolution of extended phenotypes. Usually the evolution of bodily and non-bodily signals are assumed to result from conflicting selection pressures from natural and sexual selection (Schaedelin & Taborsky, 2009). For example, sexual selection may enhance the size and showiness of the nest (Mainwaring et al., 2014; Schaedelin & Taborsky, 2009) while natural selection is expected to reduce the size and the visibility of the nest due to nest predation (Biancucci & Martin, 2010). If information use by other species affects negatively or positively the performance of the species whose extended phenotype is used as a source of information, it brings about coevolution as a potential mechanism affecting the evolution of extended phenotypes. In concert with other recent studies (e.g. Gotelli, Graves, & Rahbek, 2010; Mönkkönen, Devictor, Forsman, Lehikoinen, & Elo, 2017), our results imply that local species interactions can reflect to biogeographical patterns and should also be considered jointly with abiotic factors, which often are solely used to explain large-scale patterns.

Our results also showed that extent of egg covering increased with increasing nest floor surface area. This suggest that the eggs are spread out over a wider area in nest boxes with larger floor area and more material would be then needed to cover the eggs. Clutch coverage was also affected by the dominant tree genus, being particularly high at site (Sagunto, east Spain) dominated by genus *Citrus*, where several nest competitors/predators (black rats [*Rattus rattus*], house sparrows [*Passer domesticus*] and garden dormouse [*Eliomys quercinus*]) occur in high numbers (Barba & Gil-Delgado, 1990; Gil-Delgado, Tamarit, Viñals, Gómez, & Vives-Ferrándiz, 2009). However, leaving the data from Sagunto out from the model set 1 did not change the model-averaged results (Table S19; see Table S20, for the set of averaged models). One explanation for the differences in clutch coverage

among study sites may have been variation in the availability of suitable covering materials. The density and the species composition of local bird and mammal communities, which are linked to various characteristics of the habitat, including tree species, affect the availability of feathers and hairs. The fact that not all tits cover their eggs suggests that some costs are involved. These may include not only the costs of locating and bringing the materials to the nest but also the risk of adult predation when collecting. Egg covering materials (mammal hair, feathers) are usually found on the ground where the risk of predation on the female (only the female builds) may be high at a stage where her body mass is high due to the production of eggs. Also, infestation risk by ticks (Ixodidae) is almost entirely limited to lower levels of the vegetation (Humair, Turrian, Aeschlimann, & Gern, 1993).

The reproductive success of great tits was not significantly associated with clutch coverage. This suggests that egg covering had limited fitness consequences for the tits in the year of study. Year 2013 was phenologically an extremely late year for nesting of forest passerines in most parts of Europe (Glądalski et al., 2016; Wesołowski, Cholewa, Hebda, Maziarz, & Rowiński, 2016; F. Adriaensen, unpublished data) and it may have affected the reproductive investment decisions of tits in general. Long-term data and manipulative experiments, such as adding/removing covering of eggs or manipulation of temperature within nests (see e.g. Bleu, Agostini, & Biard, 2017) or nest predation risk perception (see e.g. Doligez & Clobert, 2003) could be the next step to test whether the egg covering behaviour is an adaptive trait.

5 | CONCLUSION

Egg covering most likely serves multiple functions in great tits. It provides thermal insulation against cold temperatures and hides the eggs from the nest predators looking for an egg meal and from information parasites searching for clutch-size information. The interactions among the nest predators, information parasites and tits are expected to result in a series of adaptations and counter-adaptations, egg covering having a function in hiding the eggs. Hence, our results suggest that interspecific interactions also shape extended nest phenotypes of birds, resulting in geographical variation in nest characteristics, depending on the co-occurrence of interacting species. Social information use as a mechanism shaping the extended phenotypes in general has gone unnoticed (Schaedelin & Taborsky, 2009) but is likely to be common in nature. Many extended phenotypes are long-lasting and readily available for coexisting animals that can use them as indicators of food resources or as a source of social information in own decision-making. If other species' utilization of extended phenotypes has negative consequences for the species whose extended phenotype is utilized, the information content of the extended phenotype is expected to evolve in a direction that reduces such costs. Changing the information content of the extended phenotype, such as egg covering, is costly in terms of time and energy and there is a lot of variation in this behaviour, both within and among populations. The pattern of geographical variation in tits' egg covering behaviour is in line with the geographical mosaic

of coevolution theory that predicts that interspecific interactions occur at the population scale and may result in different outcomes in different localities (Thompson, 2005). Therefore, geographical variation in species co-occurrences should be taken into account when studying how interspecific interactions affect (co)evolution.

ORCID

Olli J. Loukola https://orcid.org/0000-0002-9094-2004
Peter Adamik https://orcid.org/0000-0003-1566-1234
Emilio Barba https://orcid.org/0000-0003-2882-9788
Blandine Doligez https://orcid.org/0000-0003-3015-5022
Tapio Eeva https://orcid.org/0000-0002-0395-1536
Sami M. Kivelä https://orcid.org/0000-0002-6844-9168
Toni Laaksonen https://orcid.org/0000-0001-9035-7131
Chiara Morosinotto https://orcid.org/0000-0002-9172-894X
Raivo Mänd https://orcid.org/0000-0002-0878-1775
Petri T. Niemelä https://orcid.org/0000-0002-7518-4057
Vladimir Remeš https://orcid.org/0000-0001-8919-1496
Jelmer M. Samplonius https://orcid.org/0000-0002-8700-4041
Manrico Sebastiano https://orcid.org/0000-0002-9186-0772
Juan Carlos Senar https://orcid.org/0000-0001-9955-3892
Tore Slagsvold https://orcid.org/0000-0003-2410-3269
Barbara Tschirren https://orcid.org/0000-0003-4806-4102
János Török https://orcid.org/0000-0002-4799-5522
Jukka T. Forsman https://orcid.org/0000-0002-4156-7930

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BIOSKETCH

Olli J. Loukola is a post-doctoral researcher at University of Oulu, Finland. He is a behavioural ecologist and his research focuses on the information use within and among species and its ecological and evolutionary implications. Read more at: https://www.researchgate.net/profile/Olli_Loukola2

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.