Context-dependent conservation of the cavity-nesting European Roller

TOM FINCH,[1][†]* (iD) CLAIRE BRANSTON,[1][§] HARRIET CLEWLOW,[1][¶] JAMIE DUNNING,[2] ALDINA M. A. FRANCO,[3] EDMUNDS RAČINSKIS,[4] TIMOTHÉE SCHWARTZ[5,6,7] & SIMON J. BUTLER[1]

[1]*School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK*
[2]*School of Life Sciences, University of Nottingham, Nottingham NG7 2RD, UK*
[3]*School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK*
[4]*Latvian Ornithological Society, Skolas iela 3, Riga, LV-1010, Latvia*
[5]*A Rocha France, 233 route de Coste Basse, 13200, Arles, France*
[6]*Institut de recherche de la Tour du Valat, Le Sambuc, 13200, Arles, France*
[7]*PSL Research University, CEFE UMR 5175, CNRS, EPHE, Université de Montpellier, Université Paul-Valéry Montpellier, 1919 route de Mende, 34293, Montpellier, France*

To maximize the effectiveness of conservation interventions, it is crucial to have an understanding of how intraspecific variation determines the relative importance of potential limiting factors. For bird populations, limiting factors include nest-site availability and foraging resources, with the former often addressed through the provision of artificial nestboxes. However, the effectiveness of artificial nestboxes depends on the relative importance of nest-site vs. foraging resource limitations. Here, we investigate factors driving variation in breeding density, nestbox occupation and productivity in two contrasting study populations of the European Roller *Coracias garrulus*, an obligate cavity-nesting insectivorous bird. Breeding density was more than four times higher at the French study site than at the Latvian site, and there was a positive correlation between breeding density (at the 1-km^2 scale) and nest-site availability in France, whereas there was a positive correlation between breeding density and foraging resource availability in Latvia. Similarly, the probability of a nestbox being occupied increased with predicted foraging resource availability in Latvia but not in France. We detected no positive effect of foraging resource availability on productivity at either site, with most variation in breeding success driven by temporal effects: a seasonal decline in France and strong interannual fluctuations in Latvia. Our results indicate that the factors limiting local breeding density can vary across a species' range, resulting in different conservation priorities. Nestbox provisioning is a sufficient short-term conservation solution at our French study site, where foraging resources are typically abundant, but in Latvia the restoration of foraging habitat may be more important.

Keywords: foraging resource limitation, France, intraspecific variation, Latvia, nest-site limitation.

Conservation actions tend to focus on manipulating breeding season processes because these are generally the easiest to control, especially for migratory populations which often disperse over distant and disparate non-breeding sites (Finch *et al.* 2017). Understanding the factors which limit the breeding density or productivity of threatened species is therefore often crucial for their

[†]Present address: RSPB Centre for Conservation Science, The Lodge, Sandy SG19 2DL, UK.
[§]Present address: Conservation Ecology Group, Department of Biosciences, Durham University, Durham DH1 3LE, UK.
[¶]Present address: British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK.

*Corresponding author.
Email: tom.finch21@gmail.com
Twitter : @tomfinch89

conservation. Breeding birds are generally limited by the availability of nesting and/or foraging resources (Burke & Nol 1998, Cockle *et al.* 2010, Martin 2015, Vincenzi *et al.* 2015). Reductions in the availability of these resources have been implicated in recent population declines (Franco *et al.* 2005, Thorup *et al.* 2010, Aebischer & Ewald 2012) and efforts to augment them form a key part of many conservation efforts. For example, direct food supplementation is used for the conservation of many vulnerable and endangered species (e.g. Pink Pigeon *Nesoenas mayeri*, Edmunds *et al.* 2008; Stitchbird *Notiomystis cincta*, Ewen *et al.* 2015; European vultures, Moreno-Opo *et al.* 2015), and several European agri-environment schemes aim to increase the quantity and quality of foraging habitat for farmland species of conservation concern (e.g. Cirl Bunting *Emberiza cirlus*, Peach *et al.* 2001; Grey Partridge *Perdix perdix*, Ewald *et al.* 2010; Corn Bunting *Emberiza calandra*, Perkins *et al.* 2011; European Roller *Coracias garrulus* Catry *et al.* 2017). For obligate cavity-nesting species, artificial nestboxes are frequently prescribed where changes in land management have reduced the availability of natural nesting resources (e.g. Echo Parakeet *Psittacula eques*, Tatayah *et al.* 2007; Eurasian Hoopoe *Upupa epops*, Arlettaz *et al.* 2010; Eurasian Wryneck *Jynx torquilla*, Zingg *et al.* 2010). Nestboxes also facilitate monitoring, and may allow competitors or predators to be excluded (Bailey & Bonter 2017).

Conservation interventions are sometimes implemented without an assessment of their necessity or of the likelihood of negative outcomes (Sutherland *et al.* 2004). Supplementary feeding can reduce breeding success at the population level (Plummer *et al.* 2013) and may attract generalist nest predators (Hanmer *et al.* 2017), and artificial nestboxes may present an 'ecological trap' if they attract breeders to suboptimal sites (Klein *et al.* 2007, Bragin *et al.* 2017) or places which could become less suitable under environmental change (Catry *et al.* 2015). Measures that increase the availability of foraging resources will be ineffective in situations where nest-sites are limiting, and vice versa. An added complication is that anthropogenic threats (Olea & Mateo-Tomás 2014), habitat associations (Whittingham *et al.* 2007), population demography (Morrison *et al.* 2016), vulnerability to local extinction (Yackulic *et al.* 2011) and response to conservation interventions (Walker *et al.* 2018) can vary across a species' range, sometimes over relatively small spatial scales. This means that threats and solutions identified in one part of a species' range may not generalize across space (Whittingham *et al.* 2007), and uniform approaches to conservation will often be unsuccessful, or at least inefficient (Kay *et al.* 2016). Instead, to maximize the effectiveness of local conservation interventions, it is important to understand not only the mechanisms underlying resource limitation, but how these vary under different contexts. This requires the use of consistent monitoring across space, allowing explicit intraspecific comparisons. Such intensive multi-site studies are currently rare (Morris *et al.* 2001, but see e.g. Öst *et al.* 2016), with global inventories of threat typically generalizing within species (Birdlife International 2018) and conservation action plans often lacking detailed information on intraspecific variation (e.g. Kovacs *et al.* 2008).

The European Roller (hereafter, 'Roller') is an insectivorous, obligate secondary cavity-nesting bird, breeding in open habitats in warm, lowland regions of Eurasia (Cramp 1985). Rollers principally feed on large invertebrates (grasshoppers, bush-crickets, beetles), as well as small vertebrates and smaller insects (e.g. winged ants) opportunistically (Sosnowski & Chmielewski 1996, Avilés & Parejo 2002, Kiss *et al.* 2014). Their versatile foraging strategies include swallow-like aerial foraging, raptor-like quartering and warbler-like sally-gleaning, but they most often use a 'sit-and-wait' pounce strategy (Cramp 1985, Sosnowski & Chmielewski 1996, Catry *et al.* 2017). The Roller is declining in number and in range (Birdlife International 2015) and reductions in the availability of both food and nesting resources – driven primarily by the intensification of land management, but also land abandonment – have been implicated in this decline (Kovacs *et al.* 2008). Nestbox provisioning has been the primary conservation action, and we estimate there to be a minimum of 7500 nestboxes across Europe targeted specifically at Roller conservation (Appendix S1). In a recent synthesis of conservation evidence, however, the provisioning of artificial nests for Rollers was assessed as 'unknown effectiveness – limited evidence' (Sutherland *et al.* 2015). Nonetheless, nestbox schemes in Spain (Avilés & Sanchez 2000, Václav *et al.* 2011), France (Aleman & Laurens 2013), Hungary (Molnar 1998) and Serbia (Ružić *et al.* 2014) have apparently been successful, achieving high occupation rates and resulting in local

population increases. This suggests that nest-site limitation is potentially widespread across the species' range (Avilés *et al.* 2000), although the failure of other nestbox schemes, particularly towards the north of the range (e.g. Poland, Sosnowski & Chmielewski 1996; Estonia, Lüütsepp *et al.* 2011) suggests other factors may be limiting.

Here, we contrast the drivers of variation in breeding density and productivity for two nestbox schemes, one in France (a stable population, towards the centre of the species' core Mediterranean range) and one in Latvia (a relict population at the northern range limit). This represents the first explicit test of intraspecific variation in the factors limiting breeding density and productivity in this species. Based on 3 years of intensive monitoring of both schemes, we quantify spatial variation in foraging resource availability, and then describe variation in landscape-level breeding density, local-level nestbox occupation and nest-level productivity. Given the lower levels of primary and secondary productivity typical of higher latitudes (Gillman *et al.* 2015), we hypothesize that: (1) foraging resource availability, breeding density and productivity will be lower in Latvia than France; (2) breeding density will be limited by nesting resource availability in France but by foraging resource availability in Latvia; and (3) the effect of foraging resource availability on nestbox occupation and productivity will be stronger in Latvia than in France.

METHODS

Study sites

We collected data on Roller nest-site use, breeding productivity and foraging resource availability for 3 years (2013–2015) for two established nestbox schemes (Fig. 1). The French site (42.81°N, 2.94°E) lies to the north of the Plaine du Roussillon, occupying a gradient from dry vineyard-dominated landscape in the south to orchard- and meadow-dominated landscape on the edge of a brackish lagoon to the north-east. Some 2000 km to the northeast, the Latvian site (57.05°N, 24.47°E) is situated on an ancient sand dune system, where the well-drained soil supports dry Scot's Pine *Pinus sylvestris* forest, with a low understorey of moss, lichen and dwarf ericaceous shrubs, interspersed with patches of open heath and clear-cuts.

Both schemes use wooden nestboxes; the design varies slightly between and within schemes, with a typical internal volume of 0.016 m^3 and entrance hole diameter of 6 cm. The mean height ($\pm$sd) from ground to entrance was 3.9 ± 0.95 m in France and 5.1 ± 0.36 m in Latvia. In France, boxes were fixed either to trees ($n = 13$–14, mostly Black Poplar *Populus nigra*), or pylons ($n = 52$–58), whereas in Latvia they were all fixed to Scots Pine ($n = 97$–98). Figure 1 shows the spatial configuration of nestboxes, as well as the location of known natural cavities.

The French Roller population is thought to be increasing (Tron *et al.* 2008), with numbers in the Pyrénées-Orientales département growing substantially following the installation of approximately 150 nestboxes from 1997 onwards (Aleman & Laurens 2013). In contrast, the Roller is 'one of the most rapidly disappearing species' in Latvia (Kerus & Račinskis 2008), with our study site now holding almost all known breeding pairs in the country; the provisioning of approximately 150 nestboxes since 1999 is currently sustaining a population of 20–25 pairs (Račinskis & Mārdega 2011). Since the extirpation of Rollers as a breeding species in Estonia in 2011 (Lüütsepp *et al.* 2011), the relict Latvian population now represents the most northerly known European breeding population.

Foraging resource availability

We first produced a 5 × 5-m resolution land-use map of each study site (Figs S1 and S2). We manually digitized every land parcel (median size = 0.75 ha in France, 1.01 ha in Latvia) within 1 km of a nestbox in QGIS (QGIS Development Team 2015) with reference to aerial photography (BD ORTHO 50 cm, National Geography Institute (IGN); 1:10 000 Orthophotographic Maps, Latvian Geospatial Information Agency). The land-use of each parcel was classified in the field using the definitions in Tables S1 and S2, then converted to a 5 × 5-m raster using the raster R package (Hijmans 2016). Land-use in each parcel was confirmed each year of the study in France but, due to logistical constraints, only in 2014 in Latvia. Although land-use maps were available for only 1 year in Latvia, temporal changes in land-use have been relatively minor at this study site. The only major interannual change arises through clear-felling which, based on the area and
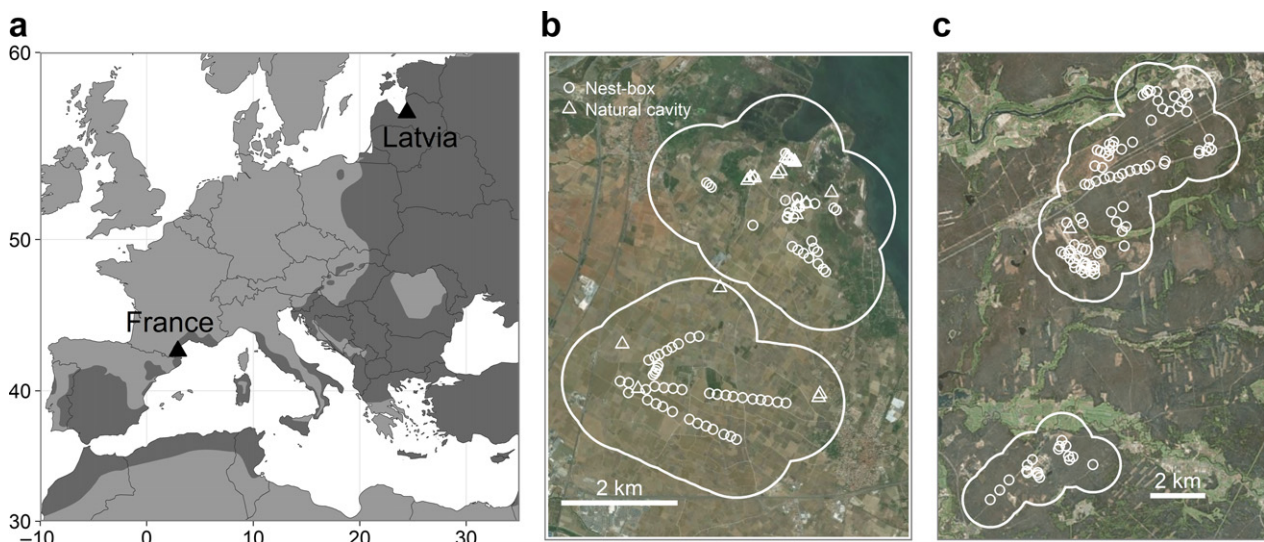
Figure 1. Study sites across Europe. (a) Location of study sites in France and Latvia, with the Roller breeding distribution (Birdlife International & NatureServe 2013) illustrated by the dark grey shading. Detail of (b) French (2015) and (c) Latvian (2014) study sites. Circular points are nestboxes (*n* = 72 in France, 98 in Latvia), triangles are natural cavities (*n* = 24 in France, 1 in Latvia), and the white outline shows the 1-km buffer around all nestbox locations.

approximate age of clear-cuts recorded in 2014, we estimate has affected < 1% of the total study area annually.

The Roller is typically a sit-and-wait, 'pounce' hunter. To mimic broadly the hunting method of the Roller, we used visual transects to quantify the availability of large terrestrial insect prey. We randomly selected 48 (France) and 44 (Latvia) land parcels from a starting pool of all parcels within 250 m of a nestbox, corresponding approximately to the Roller's core foraging range (Avilés & Costillo 1998, Bouvier *et al.* 2014, Catry *et al.* 2017). Surveys were limited to the four main land-use types at each study site to ensure sufficient independent replications: in France, *vine, fallow, orchard* and *hay meadow*, which covered 81% of the total area within 250 m of all nestboxes in 2014, and in Latvia, *pine forest, clear-cut, heath* and *sand*, which covered 80% of the total area within 250 m of all nestboxes in 2014. We stratified this selection process according to the approximate proportional cover of each land-use type, with more transects allocated to the most widespread land-uses, while ensuring a minimum of two transects per land-use type (Table S3). Each 40-m transect started at a random distance (> 40 m) along a randomly selected parcel edge. Each transect was walked perpendicular to the parcel edge at a constant slow pace of approximately 0.3 m/s. A

1.5-m-wide strip was surveyed for large (> 10 mm) terrestrial insects in the orders Coleoptera (beetles), Orthoptera (grasshoppers and bush-crickets), Hemiptera (true bugs, including cicadas) and Mantoidea (mantises), which make up the majority of the Roller's diet (Cramp 1985, Sosnowski & Chmielewski 1996, Avilés & Parejo 2002). Insects were identified, generally to family level, but sometimes to order or genus, then classed into 10-mm bins. Transects were repeated once every 2 weeks throughout the breeding season in Latvia (2014) and France (2015). These counts were then converted into summed per-transect per-visit biomass estimates, using the taxon-specific relationship between body length and ash-free dry weight detailed in Table S4 and Appendix S2. Additional invertebrate surveys using the same methodology were carried out in France in 2014, but over a slightly different time period and by a different observer.

To generate predicted insect biomass in different land-use types across the season, and due to the zero-inflated, non-integer data structure, we used a two-part hurdle model. The first part predicted the probability of recording an insect during a transect (using a generalized linear mixed model (GLMM) with binomial error structure and logit link; 'binomial model'), and the second part predicted the biomass of recorded insects given that

one or more had been recorded during a transect (GLMM with gamma error structure and log link; 'gamma model'). Both model parts were fitted using the R package lme4 (Bates *et al.* 2015) with a random intercept of transect identity to account for the pseudo-replication arising from repeating the same transects through the season. We modelled the fixed effect of land-use type, as well as calendar date and its quadratic effect (both scaled and centred). In France we also included the interaction between land-use and calendar date. However, due to low invertebrate numbers recorded in Latvia, models including the interaction term failed to converge. To identify the best-performing predictive model of insect biomass, candidate models using all combinations of predictor variables were fitted and compared according to corrected Akaike information criterion (AICc) values using the R package MuMIn (Barton 2016). Predictions were model-averaged over the set of 'top' models with ΔAICc < 4 using the 'full' method, in which absent variables are set to zero rather than excluded (Burnham & Anderson 2002).

By multiplying the predictions of the two parts of the hurdle model (i.e. weighting predicted biomass by the probability of observing an insect), we obtained predictions of insect biomass in each land-use type over the course of the season. For rarer land-uses in which insect surveys were not conducted, we assigned insect biomass as detailed in Tables S1 and S2. Briefly, we assume that open water, built-up land and bare ground provide no foraging resources (key prey groups are generally absent from bare ground because of the lack of vegetation). In France, we treated grassy land-uses (wheat and wet grass) as hay meadow, and abandoned or fallow orchard as fallow; all other land-uses (covering just 5.4% of the area within 250 m of all nestboxes) were set to the mean of surveyed land-uses. In Latvia, we treated all forested land-uses as pine forest; all other land-uses (covering just 2.8% of the area within 250 m of all nestboxes) were set to the mean of surveyed land-uses.

Land-use-specific values were then mapped onto the 5 × 5-m land-use raster for two time windows; the 7-day period starting 23 May, corresponding to the pre-egg-laying period (approximately 1 week prior to the median first egg date), and the 7-day period starting 27 June, corresponding to the 'chick-rearing period' (approximately 1 week after the median hatching date). Predicted insect biomass (summed at the nest-level across a 250-m buffer) in the preceding and following 7-day periods was strongly correlated in France ($r_{72} > 0.84$, $P < 0.001$), and in Latvia predicted insect biomass was strongly correlated among all 7-day periods ($r_{95} > 0.99$, $P < 0.001$).

As intensive insect surveys were only conducted in 1 year at each site, subsequent analyses assume that these relative differences in insect biomass between land-use types change little from year to year. Comparison of 2015 French survey data with pilot data collected in 2014 supports this assumption (Fig. S3), although absolute biomass was lower in 2015, perhaps due to observer differences and an earlier survey window. Despite slight inter-annual differences in relative insect biomass among land-uses, when aggregated to the 1-km-square level, predicted relative insect biomass was similar when based on 2014 or 2015 survey data (Fig. S4). In both years, biomass in France was substantially higher than in Latvia in 2014.

Nest monitoring

Potential Roller nest-sites (both artificial nest-boxes and suitable cavities in trees and buildings) were monitored throughout the 2013–2015 breeding seasons in France and Latvia (Table S5). Although an intensive search of suitable natural cavities was beyond the scope of this study, Roller nests were found in Iberian Green Woodpecker *Picus sharpei* nest hollows, decaying tree hollows and rural buildings in France, and Black Woodpecker *Dryocopus martius* nest hollows in Latvia. Nest contents were observed either directly or with an inspection camera (Rigid CA-100 with 360-cm extension) attached to a telescopic pole.

We categorized nest-sites as 'Roller' (Roller eggs or nestlings observed during a season), 'empty' (no eggs or nestlings of any species observed during a season) or 'competitor' (eggs or nestlings of another bird species observed during a season, most commonly Western Jackdaw *Coloeus monedula* or Little Owl *Athene noctua* in France, and Common Redstart *Phoenicurus phoenicurus*, Eurasian Hoopoe or Great Tit *Parus major* in Latvia), and recorded parameters relating to the circumstances, timing and success of breeding (Table S6). Note that the 'Roller' and 'competitor' categories are not mutually exclusive; some nests were occupied by a competitor followed by a Roller (in that order, without exception).

Analysis: landscape-level breeding density

To compare the relative importance of nest-site and food availability in predicting landscape-level breeding density, we divided each site into a regular 1000-m grid (following UTM gridlines) and calculated for each square, or 'landscape': (1) the number of nestboxes, as a measure of nest-site availability; (2) the mean predicted insect biomass during the chick-rearing period, as a measure of foraging resource availability; and (3) the number of Roller breeding attempts in nestboxes (but not natural cavities), as a measure of breeding density. In France, 12 squares contained nestboxes in 2013 and 2014, and 13 squares in 2015. In Latvia there were 24 squares in all years.

We compared five nested models designed to test our hypothesis that the effects of nestbox density and foraging resource availability on breeding density should differ between the two countries, controlling for interannual variation. All models were GLMMs (with Poisson error structure and log link) with Roller nest density as the dependent variable and a random intercept grouping each unique grid cell (surveyed in multiple years). Independent variables were either: (1) the four-way interaction of nestbox density, foraging resource availability (both scaled and centred separately for each country), year (a three-level factor) and country (a two-level factor); (2) the three-way interaction of nestbox density, foraging resource availability and country; (3) the two-way interactions between nestbox density and country and foraging resource availability and country; (4) the additive effects of nestbox density and foraging resource availability; or (5) an intercept-only model (Table 1). These competing models were ranked according to AICc and, for the purposes of plotting fitted relationships (Fig. 4), we averaged model predictions over the set of models with ΔAICc < 4 (Burnham & Anderson 2002).

We also tested the sensitivity of this analysis to grid size (comparing 500- and 1000-m grids) and placement (comparing 500 random origin coordinates) by fitting two Poisson GLMMs for each resolution, origin and country, with either nestbox density or foraging resource availability as the independent variable and a random intercept grouping each grid cell.

Table 1. Model selection for landscape-scale breeding density analysis.

Model (n = 109)	k	AICc	Δ_i	w_i
Nestbox density × Country + Foraging resource availability × Country	6	230.9	0.00	0.84
Nestbox density × Foraging resource availability × Country	8	234.2	3.32	0.16

Five competing models are ranked in order of AICc. k = number of parameters, Δ_i = difference in AICc between ith model and 'best' model, w_i = Akaike model weight. Parameter estimates are not shown. Only models with Δ_i < 4 are shown, although w_i is calculated across all models.

Analysis: local-level nest-site selection

To test whether Rollers selected nestboxes based on the availability of surrounding foraging resources, we calculated mean predicted prey biomass within 250 m of each nestbox based on land-use in the appropriate year for the pre-laying and chick-rearing periods. We also calculated the distance to the next-nearest known Roller nest (including those in natural cavities) based on occupancy patterns in the appropriate year. Additionally, to test whether Rollers avoided the approximately 12% of French nestboxes with missing lids (through disrepair), we generated a two-level factor describing whether the lid was present (1) or absent (0).

We constructed GLMMs (with binomial error structure and logit link) separately for France and Latvia, because we include slightly different independent variables in each country (see below). Nestboxes which were empty but checked only once during a season were excluded, as were nestboxes occupied by competitors but not Rollers. The dependent variable was a binary outcome distinguishing whether, in a particular year, a nest was occupied by a Roller (1) or was empty (0). For France, the model included predicted prey biomass for laying- and chick-rearing periods, distance to nearest neighbour and lid presence/absence. There was no variation in nestbox condition in Latvia, so lid presence/absence was not considered in the model. Furthermore, due to strong correlations between predicted prey biomass for laying- and chick-rearing periods (r_{95} > 0.99, P < 0.001) in Latvia, only the latter was included in this model. A random intercept grouping nests into 1-km grid cells was included to account for spatial

non-independence, and continuous variables were centred and scaled. As above, we ranked several competing models (testing all combinations of additive effects as well as an intercept-only model, Table 2) according to AICc, with the expectation that models including the effect of foraging resource availability would receive more support in Latvia than in France.

This modelling approach assumed that only empty nestboxes were available to Rollers. We repeated these analyses under the alternative assumption that competitor nests were also available to Rollers, with the binary variable distinguishing Roller (1) from empty or competitor (0) nestboxes (Table S9).

Analysis: reproductive parameters

To compare differences between France and Latvia across all years in the mean number of eggs (excluding clutches which were possibly incomplete at the time of failure, assuming a 2-day laying interval), hatchlings and fledglings, we used a generalized linear model (with Poisson error structure and log link) with the single fixed effect of country. In France, there were four apparent instances of repeat laying following the failure of a previous breeding attempt. We excluded the initial failures from analysis, but because we cannot be certain that these consecutive attempts involved the same individual birds, our measures should be interpreted as number of eggs per cavity, rather than per pair. Equivalently, 'breeding density' measures occupied cavity density rather than breeding pair

density; it is not possible to rule out the possibility of two pairs using the same cavity in the same year.

We then tested whether fecundity (clutch size) and success (fledglings per egg) varied according to surrounding foraging resource availability. As above, we constructed separate models for each country. Variation in the number of eggs per cavity (excluding nests which had incomplete clutches at the time of failure) was modelled using a Poisson error structure with log link, and variation in fledglings per egg (excluding nests which were discovered after hatching) was modelled using a binomial error structure with logit link. Data from nestboxes and natural cavities were combined over 2013–2015. Fixed effects were year (a factor), lay date, nearest-neighbour distance and predicted prey biomass (for the pre-egg-laying period for the clutch size model, and both pre-egg-laying and chick-rearing period for the breeding success model in France, and the chick-rearing period only for the breeding success model in Latvia), with a random intercept grouping nests into regular 1-km grid cells. As above, continuous variables were scaled and centred, and we compared several competing models using AICc, fitting combinations of spatial (nearest-neighbour distance and/or prey biomass) and temporal predictors (year and lay date), as well as an intercept-only model (Tables 3 and 4), with the expectation that models including the effect of foraging resource availability would receive more support in Latvia than in France. For the purposes of plotting fitted relationships (Fig. 5), predictions were averaged across the set of models with ΔAICc < 4.

Table 2. Model selection for nestbox occupation (Roller–empty model).

	Neighbour distance	Nestbox condition	Foraging resource availability (laying)	Foraging resource availability (chick-rearing)	k	AICc	Δ_i	w_i
France (n = 148)	0.622*	●*	○	0.554	5	166.8	0.00	0.296
	0.798*	●*	0.536	0.585	6	166.9	0.03	0.292
	0.842*	●*	0.606	○	5	168.2	1.38	0.148
	0.674*	●*	○	○	4	168.4	1.61	0.132
	○	●*	○	0.595*	4	169.6	2.77	0.074
Latvia (n = 206)	−0.462			0.473*	4	185.1	0.00	0.403
	○			0.559*	3	185.2	0.12	0.380
	−0.583			○	3	187.2	2.15	0.138
	○			○	2	188.3	3.23	0.080

● = categorical factor present; ○ = continuous variable or categorical factor absent from model; k = number of parameters in model; Δ_i = difference in AICc between ith model and 'best' model; w_i = Akaike model weight. Intercept, although not shown, is present in all models. Parameter estimates marked with * have 95% confidence intervals which do not overlap 0. Parameter estimates are not shown for categorical factors. Only models with Δ_i < 4 are shown, although w_i is calculated across all models.

For all analyses we tested for spatial autocorrelation by calculating Moran's *I* on raw residuals (from the best performing model across each analysis) at a range of different spatial lag distances, using the Moran.I function in the ape package in R (Paradis *et al.* 2004).

RESULTS

Foraging resource availability

Insect biomass varied substantially between countries, land-use types and across the course of the breeding season (Fig. 2). Most striking were the differences in biomass between France (mean ± se biomass per transect = 0.25 ± 0.025 g) and Latvia (0.05 ± 0.006 g), indicating a fundamental disparity in the availability of large terrestrial insects.

There was strong support for the fixed effect of land-use in both the binomial and gamma models in France (Table S7), but only in the binomial model in Latvia (Table S8). In France, insect biomass was more than twice as high in hay meadow and fallow than in orchard and vine, and in Latvia, insect biomass was substantially higher in open (sunny) habitats (clear-cut, heath and sand) than in pine forest (Fig. 2).

Temporal patterns were more complex, but there was a general increase in insect biomass across the season with a peak in late June (corresponding approximately to the start of the chick-rearing period), except in hay meadows in France, which saw a decline in biomass after harvesting in early June (Fig. 2). Towards the end of the breeding season, insect biomass declined in most land-use types.

Landscape-level breeding density

Despite the density of nestboxes being similar between sites (France: mean ± se = 5.4 ± 0.66/km², range 1–17; Latvia: 4.0 ± 0.38/km², range 1–15), the mean density of Roller-occupied nestboxes was more than four times higher in France (2.2 ± 0.43 pairs/km², range 0–11) than in Latvia (0.5 ± 0.09 pairs/km², range 0–3).

The importance of nestbox density and foraging resource availability in predicting variation in landscape-level breeding density varied strongly between countries, with strong support for interaction terms (Table 1). Breeding density was strongly positively related to nestbox availability in France but not in Latvia (Fig. 3a,c); conversely, it was strongly positively related to foraging resource availability in Latvia but not in France (Fig. 3b,d).

These patterns were insensitive to the resolution and placement of the grid used to calculate density (Fig. S5). In France, the relationship between nestbox density and breeding density was positive (lower 95% confidence bound > 0) for 100% of 500 random origin points at both grid sizes, whereas the effect of foraging resource availability was positive for only 1 and 20% of random origin points at 500- and 1000-m grid sizes, respectively. In Latvia, the effect of foraging resource availability was positive for 96 and 75% of random origin points, whereas the effect of nestbox density was positive for only 6 and 24% of random origin points at 500- and 1000-m grid sizes, respectively.
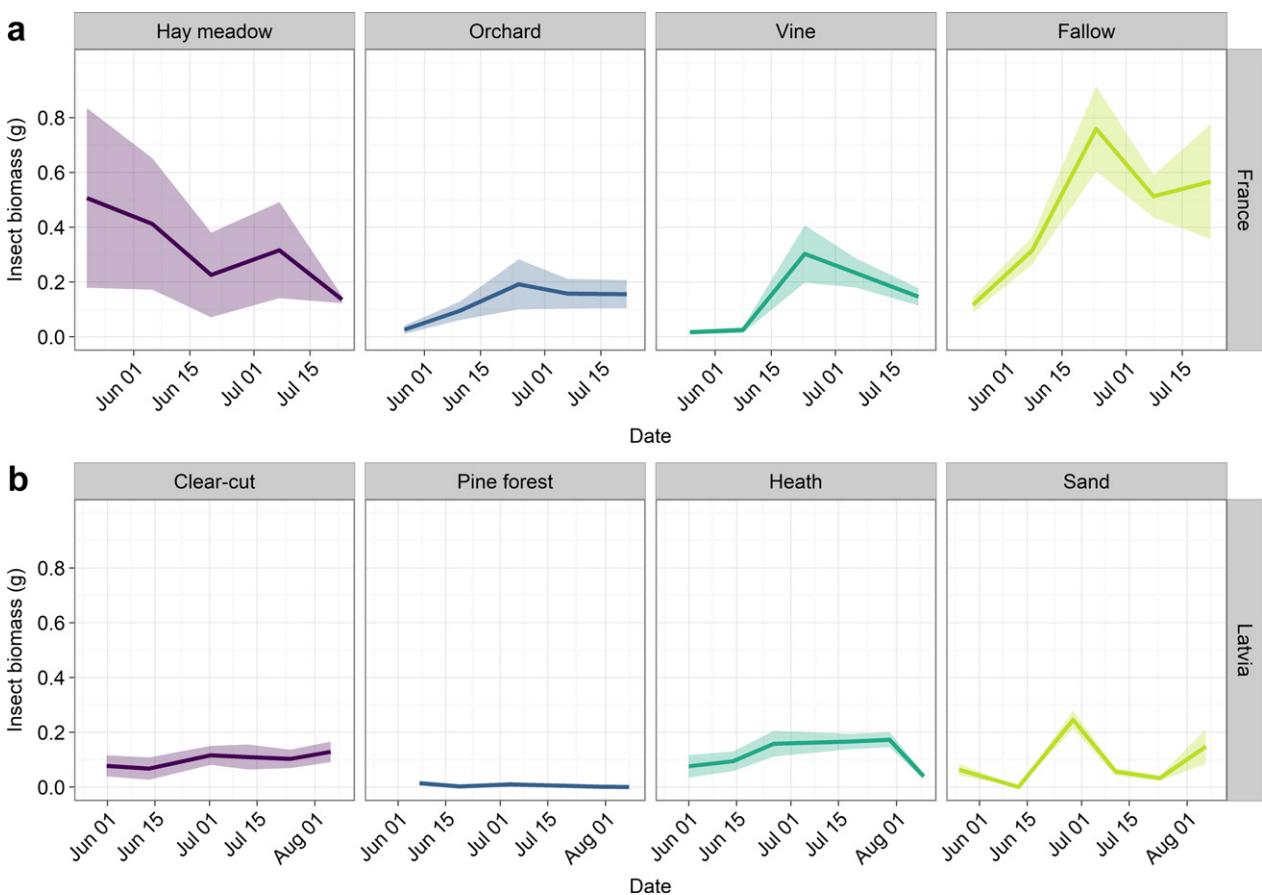
Table 3. Model selection for clutch size.

	Neighbour distance	Foraging resource availability (laying)	Year	Lay date	*k*	AICc	Δ_i	w_i
France (*n* = 87)	○	○	○	○	2	317.4	0.00	0.363
	○	0.064	○	○	3	317.9	0.47	0.286
	−0.020	○	○	○	3	319.4	2.00	0.133
	−0.018	0.064	○	○	4	319.9	2.54	0.102
Latvia (*n* = 39)	○	○	○	○	2	136.7	0.00	0.540
	○	0.043	○	○	3	138.8	2.06	0.193
	0.021	○	○	○	3	139.0	2.28	0.172

● = categorical factor present; ○ = continuous variable or categorical factor absent from model; *k* = number of parameters in model; Δ_i = difference in AICc between *i*th model and 'best' model; w_i = Akaike model weight. Intercept, although not shown, is present in all models. Parameter estimates are not shown for categorical factors. Only models with $\Delta_i < 4$ are shown, although w_i is calculated across all models.

Table 4. Model selection for breeding success.

	Neighbour distance	Foraging resource availability (laying)	Foraging resource availability (chick-rearing)	Year	Lay date	k	AICc	Δ_i	w_i
France ($n = 79$)	○	0.180	−0.648*	●*	−0.508*	7	299.7	0.00	0.756
	−0.004	0.181	−0.647*	●*	−0.508*	8	302.1	2.48	0.219
Latvia ($n = 39$)	○		○	●*	0.390	5	110.1	0.00	0.484
	○		−0.296	●*	0.331	6	111.4	1.28	0.256
	−0.191		○	●*	0.407	6	112.3	2.18	0.163
	−0.256		−0.341	●*	0.344	7	113.3	3.21	0.097

● = categorical factor present; ○ = continuous variable or categorical factor absent from model; k = number of parameters in model; Δ_i = difference in AICc between ith model and 'best' model; w_i = Akaike model weight. Intercept, although not shown, is present in all models. Parameter estimates marked with * have 95% confidence intervals which do not overlap 0. Parameter estimates are not shown for categorical factors. Only models with $\Delta_i < 4$ are shown, although w_i is calculated across all models.

Figure 2. Insect biomass (g per transect) as a function of calendar date and land-use in (a) France and (b) Latvia. Lines show mean observed biomass per transect ±se.

Nestbox occupation

Consistent with differences in nestbox density relative to landscape-level breeding density, nestbox occupation rates were much higher in France than in Latvia; on average, Roller breeding attempts were recorded in 42% of nestboxes in France but in only 13% in Latvia. In France, only 21% of nestboxes were empty – the remainder being occupied by other avian species – compared with 58% in Latvia.
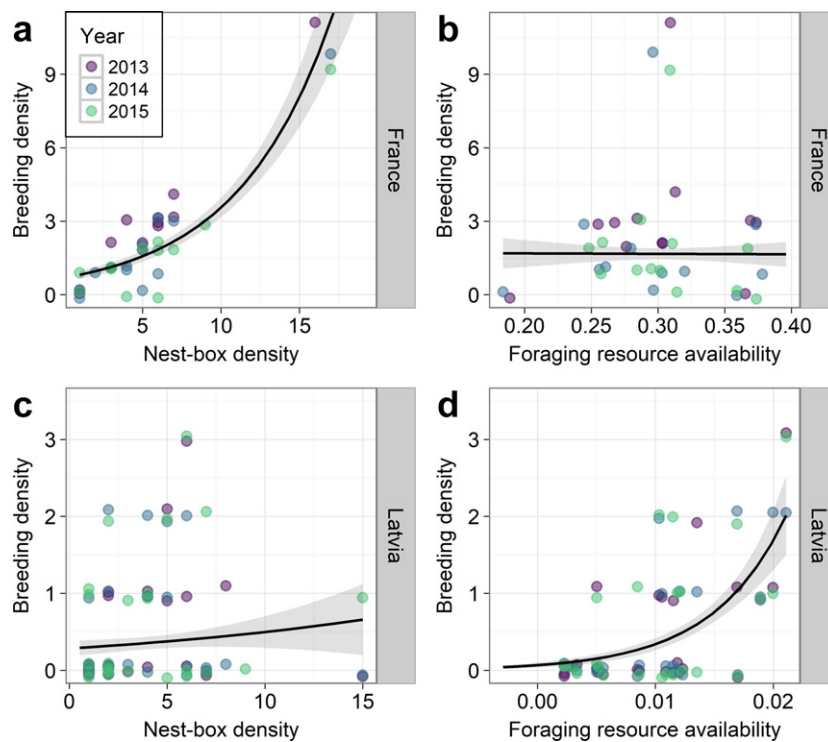
Figure 3. Local breeding density correlates with nestbox density in France (a) but not Latvia (c), and estimated foraging resource availability in Latvia (d) but not France (b); these results are consistent across years. Each point represents one 1 × 1-km square. Points are semi-transparent, coloured by year, and vertically jittered to reduce overlap. Dashed lines and shaded regions represent predictions (±se) of the best-fitting model.

Models describing the probability of a nestbox being occupied by a Roller had relatively low explanatory power (France best model: $R^2_m = 0.29$, $R^2_c = 0.43$; Latvia best model: $R^2_m = 0.13$, $R^2_c = 0.29$). In both France and Latvia, no model stood out as having especially strong support, although the majority of models outperformed the intercept-only model (Table 2). In France, the only variable appearing in all top models ($\Delta AICc < 4$) was nestbox condition (Table 2), with intact boxes more likely to be occupied than those without lids. On average, 57% (13/23) of nestboxes without lids were empty, compared with only 26% (33/125) of nests with lids (Fig. 4e). There was also a positive effect of nearest breeding neighbour distance such that, compared with empty boxes, Roller nests tended to be farther away from other Roller nests (Table 2, Fig. 4a). In Latvia, there was a positive effect of foraging resource availability during the chick-rearing period, with empty nestboxes concentrated in areas with lower predicted prey biomass (Fig. 4b, d). The 95% confidence intervals of these

parameters did not overlap 0, suggesting that they represent reliable effects (Table 2).

The above results are based on the 'Roller-empty' model, in which nestboxes occupied by competitors were assumed to be unavailable. Models assuming that competitor nests were also available yielded similar results in Latvia, but slightly different results in France, where support for the effects of nestbox condition and foraging resource availability was reduced (Table S9).

Reproductive parameters

Although there were differences in reproductive parameters between France and Latvia (Fig. 5a), none of these were significant (chi-square likelihood ratio test, $P > 0.05$). Losses in France primarily occurred due to partial and complete failures during the egg stage (mean ± se = 0.68 ± 0.04 hatchlings per egg, with 15% of clutches producing no chicks at all), whereas chick survival was high (0.92 ± 0.02 fledglings per hatchling). In Latvia, losses were higher during the chick stage
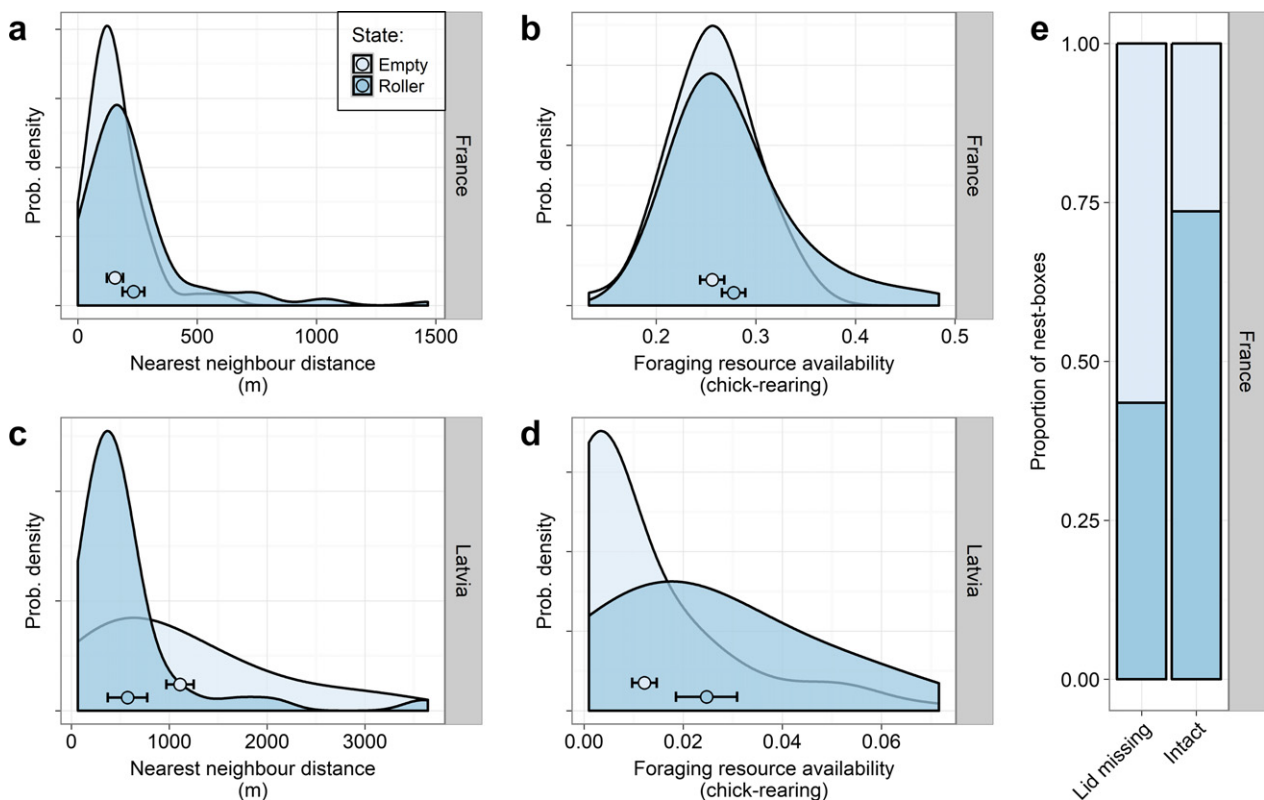
Figure 4. Probability density distributions for nearest-neighbour distance (a, c) and estimated foraging resource availability (b, d) of empty nestboxes (pale blue) and those occupied by Rollers (dark blue). Points and horizontal bars show mean ± 95% confidence interval. (e) Proportion of intact and lid-less nestboxes which are empty or occupied by Rollers (France only). Data are combined across all years 2013–2015.

(0.84 ± 0.03 hatchlings per egg, 0.68 ± 0.06 fledglings per hatchling), with several complete post-hatching losses (20% of broods produced no fledglings).

Models predicting variation in fecundity (clutch size) performed poorly; in both France and Latvia, the best model was the intercept-only model (Table 3). Models predicting variation in breeding success (fledglings per egg) performed better, with R^2_m values of 0.21 and 0.34 for the best models in France and Latvia, respectively. Contrary to our expectations, there was little support for an effect of foraging resource availability on breeding success in Latvia (Table 4). Instead, temporal predictors appeared in all top models, with strong interannual variations driven by particularly low productivity in 2014 compared with 2013 (Fig. 5c). In France there was a significant seasonal decline in breeding success (Fig. 5b), as well as a surprising negative effect on breeding success of foraging resource availability during the chick-rearing period (Table 4).

Spatial autocorrelation

Across all models and most spatial lag distances, Moran's I was low and not significantly different from 0 (Fig. S6). For the nestbox occupation model in Latvia, Moran's I was significant and positive at the smallest spatial lag ($I = 0.184$, $P = 0.018$; Fig. S6c), and for the clutch size analysis in France, Moran's I was significant and positive at lag distances ≥ 900 m ($I < 0.08$, $P < 0.05$; Fig. S6d). The spatial autocorrelation observed in the France clutch size model is weak and of little concern. Spatial autocorrelation was stronger for the Latvia occupation model (but still relatively weak), suggesting that high and low residuals are clustered in space, at least over small (50-m) spatial scales. Fitting separate models to data from each year in turn reduced Moran's I close to 0
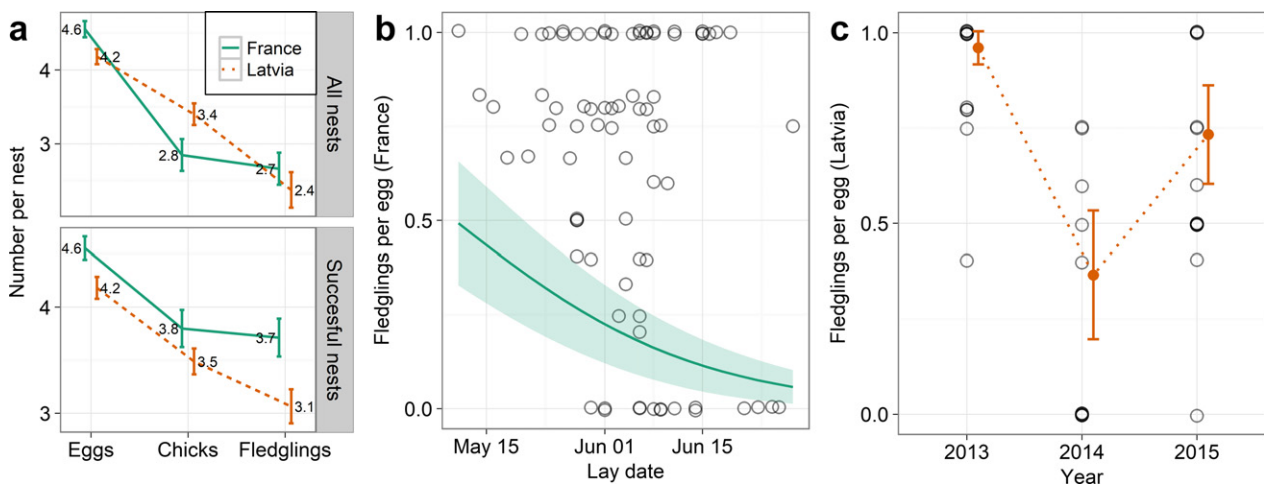
Figure 5. Variation in productivity between and within study sites. (a) Mean (±se) number of eggs, chicks and fledglings per nest (top panel) and successful nest (bottom panel) in France and Latvia. Numbers beside points indicate the mean value. (b) Model-averaged relationship (±se) between lay date and survival of eggs to fledging in France. (c) Model-averaged relationship (±se) between year (a fixed factor) and survival of eggs to fledging in Latvia. Points are vertically jittered in (b) and (c) to reduce overlap.

($P > 0.05$), with no effect on the sign, and little effect on the magnitude, of the estimated model coefficients.

DISCUSSION

To maximize the effectiveness of conservation interventions, an understanding of between-population variation in the relative importance of different limiting factors, and the mechanisms underpinning these, is crucial. The effectiveness of nestboxes is likely to be maximized in areas where foraging resource availability is not currently limiting, whereas other interventions may be necessary where populations are limited by foraging resource availability. By testing which factors drive variation in breeding density and nestbox occupation at two contrasting study populations, we provide evidence to improve the efficacy of conservation interventions at both sites.

Nest cavity limitation

At our French study site, variation in landscape-level breeding density was strongly driven by nest-site availability. The linear relationship between nestbox density and Roller breeding density was striking, with almost half of all nestboxes being occupied by breeding Rollers even at high nestbox densities of 15 per km². This result corroborates observed population increases following the provisioning of nestboxes in this region (Aleman & Laurens 2013). Although our inventory of natural cavities was not comprehensive, when we included the availability and use of these natural cavities (in addition to nestboxes), our conclusions remained unchanged; breeding density increases with cavity availability in France but not in Latvia.

Given the *ad hoc* distribution of nestboxes, we were unable to test whether Roller density continues to increase beyond nestbox densities of 15 per km². However, over small areas, natural cavities can reach very high densities in our French study site, especially in poplar hedges surrounding fruit orchards. These areas of high cavity availability have correspondingly high breeding density, and more extreme instances of 'semi-coloniality' have been reported elsewhere (Butler 2001, Václav et al. 2011). Nonetheless, we did find a slightly negative density-dependent effect (i.e. a positive effect of nearest-neighbour distance) on nestbox occupation probability, suggesting that at the territory-scale, Rollers tend to avoid conspecifics (Kiss et al. 2017).

Nestboxes have become a central tool for Roller conservation (Kovacs et al. 2008), in part because they facilitate monitoring, but also because of their apparent effectiveness, as indicated by high occupation rates and increases in local population size (e.g. Ružić et al. 2014). However, the long-term viability of these schemes must be borne in mind. Our results

suggest that nestboxes with damaged lids (making up approximately 12% of all nestboxes at our French study site in 2015) are twice as likely to remain empty compared with intact boxes. If sufficient funds cannot be secured to ensure maintenance and replacement, then the conservation gains attributable to nestbox schemes may be short-lived. The negative density-dependent effect on nestbox occupation probability suggests that Rollers avoid proximity to conspecifics. High nestbox densities may force Rollers into inter- and intraspecific competition, and we suspect that the high egg loss rates observed in France may be due as much to competition as to predation. Additionally, evidence from Spain suggests that exposed (i.e. unconcealed) nestboxes may present an ecological trap by attracting Rollers to nest-sites in which breeding success is depressed (Rodríguez *et al.* 2011), and in Portugal, wooden nestboxes offer poorer insulation from high temperatures compared with traditional cavities in rural mudbrick buildings (Catry *et al.* 2015). Nestbox provisioning should therefore be accompanied by longer-term solutions such as planting and protecting suitable tree species (Lindenmayer *et al.* 2009) and supporting populations of primary excavators (Blanc & Walters 2008).

The high local densities observed in France may not necessarily translate into wider population increases if nestboxes draw breeders away from neighbouring breeding sites. Nestboxes – usually placed on pylons or exposed tree trunks – are conspicuous and potentially attractive (Rodríguez *et al.* 2011, Kiss *et al.* 2017), so increases in local density may reflect the abandonment of natural cavities, perhaps re-enforced through conspecific attraction (Václav *et al.* 2011). In France, our observations of high natural cavity occupation within the study site suggest that this is not the case, although we cannot rule out that nestboxes cause a redistribution (rather than an augmentation) of breeding pair numbers at the regional scale. At our Latvian study site, there has been gradual redistribution of Roller nests from natural cavities to nestboxes, which has facilitated the protection of nests against predation by Pine Martens *Martes martes*. In addition, the narrow entrance hole diameter excludes Stock Doves *Columba oenas*, which otherwise compete with Rollers for natural cavities.

Foraging resource limitation

In Latvia, we found no relationship between the availability of nestboxes and the density of breeding Rollers, with many nestboxes remaining empty. This suggests that, here, Rollers have reached a carrying capacity set by some other factor. Previous studies have demonstrated associations between insect-rich habitats (as opposed to more intensively managed ones) and Roller nest-site use in Spain, Portugal and France (Avilés & Costillo 1998, Catry *et al.* 2011, 2017, Rodríguez *et al.* 2011, Bouvier *et al.* 2014) but not Hungary (Kiss *et al.* 2017). There is also evidence that variation in breeding productivity can be explained by surrounding foraging habitat (e.g. Avilés & Parejo 2004, Kiss *et al.* 2014), although this is not always the case (e.g. Rodríguez *et al.* 2011).

In Latvia, we found positive relationship between predicted insect biomass and both Roller breeding density and nestbox occupation. The availability of insect prey in Latvia is low and restricted mainly to open habitats (open heaths and clear-cuts); even the richest land-use types in Latvia had a lower insect biomass than the poorest types in France. The clustered distribution of open habitats and the slight negative effect of nearest-neighbour distance on nestbox occupation probability suggest that Rollers are aggregating in patches of high-quality foraging habitat. In France, there was no support for an effect of foraging resource availability on breeding density, and only a weak effect on nestbox occupation. Clearly, our ability to detect such an effect depends on there being sufficient variation in habitat quality at an appropriate spatial scale, and the fine-scale mosaic of land-use types in France may result in most nestboxes being within a few hundred metres of insect-rich habitat. Alternatively, the higher rates of occupation by medium-sized resident avian competitors (Jackdaws and Little Owls) in France compared with Latvia may prevent higher quality breeding sites being immediately available to Rollers on arrival. When we assumed that nestboxes occupied by competitor species were available to Rollers (i.e. the Roller–other model), the weak positive effect of foraging resource availability on nestbox occupation disappeared, suggesting that competitor species may indeed be tending towards higher quality breeding sites.

We also detected no positive correlation between foraging resource availability and breeding

productivity. In Latvia, contrary to our expectation, there was no association, and in France the effect was surprisingly negative. In Latvia, variation in breeding success was primarily driven by inter-annual variations in weather, perhaps swamping any effects of foraging resource availability (which may be small anyway, given that most nests were located near areas of open habitat). In France, the negative relationship between breeding success and predicted prey biomass during the chick-rearing period is surprising. One hypothesis which deserves further attention is that inter- and intraspecific nest-site competition is elevated in areas of high foraging habitat quality, with despotic interactions resulting in the loss of eggs (or, we speculate, in some cases in the death of breeding adults).

Although our visual transects were coarsely analogous to the foraging mode of the Roller, it is possible that some important taxa went under-recorded. Beetles, for instance, were poorly represented in Latvia (28% of biomass) despite being known to contribute an important part of the Roller's diet in central and northern Europe (Cramp 1985, Sosnowski & Chmielewski 1996). Beetles were patchily distributed, often around piles of dung or dead wood; this low encounter rate does not lend itself to our relatively short transects. Similarly, in France we may have under-estimated cicada abundance (also 28% of biomass), which can form an important part of Roller nestling diet (Christof 1991). Cicadas tend to aggregate around taller vegetation (e.g. poplar and cypress *Cupressus sempervirens* hedges, but also vines, scrub and rank vegetation), often towards field edges. In addition to this taxonomic-bias, encounter rates may have varied between habitats and across the course of the season (e.g. lower detectability in denser vegetation). All invertebrate survey methods have their biases, however (Doxon *et al.* 2011), and our visual transects at least provide a quantification of general terrestrial insect activity. Although we surveyed insects in only 1 year in each country, comparable data from 2 years in France suggest that relative differences between land-uses were relatively consistent between 2014 and 2015, and unlikely to influence our findings.

Context-dependent conservation

Our results point towards context-dependent priorities for Roller conservation. In France, the maintenance and expansion of the nestbox scheme appears sufficient to increase local population size. If all 1-km^2 landscapes in our study area contained 15 nestboxes, we would expect breeding density to increase to approximately 8 pairs/km^2 (a substantial increase on the current average of 2.2 pairs/km^2). In Latvia, although the erection of nestboxes has almost certainly prevented the extinction of this relict population – in part because they facilitate active protection against nest predation – we suggest that efforts should also focus on protecting, improving and expanding the open habitats which provide important foraging resources.

We suspect that our findings will extend to other parts of the Roller's range, with northerly populations tending to be the most sensitive to foraging resources and southerly populations to nesting resources. Many southern populations have expanded into suitable foraging habitat following the provisioning of nestboxes over the last few decades (Rodríguez *et al.* 2011, Václav *et al.* 2011, Aleman & Laurens 2013), whereas the provisioning of nestboxes has had limited success in Poland (Sosnowski & Chmielewski 1996), and the small and isolated population in Estonia became extinct despite the provisioning of nestboxes (Lüütsepp *et al.* 2011).

Although our results point to the factors currently limiting local breeding density, they do not necessarily explain historical changes in Roller numbers. We found no evidence of nest-site limitation in Latvia, indicating that availability is currently sufficient. However, prior to the installation of nestboxes, nest-site availability may have been a limiting factor, and probably still is, in suitable foraging habitats away from the nestbox scheme. Black Woodpecker holes are few and far apart, and often far from appropriate Roller foraging habitat. Our Latvian study population is somewhat atypical of the historical national population, which was until recently widely distributed across the farmed landscape (Kerus & Račinskis 2008). The cause of this decline was probably a location-specific combination of loss of suitable foraging habitat and, through the removal of large old trees as well as the decline of the Green Woodpecker *Picus viridis* (Birdlife International 2015), loss of nest-sites.

Nestboxes represent the primary conservation intervention for the European Roller, and probably account for the 'actions in several countries [which] have contributed to national recoveries', resulting in the recent down-listing of the species

from Near Threatened to Least Concern (Birdlife International 2017). The extent to which the estimated 7000–10 000 breeding pairs in Europe (Birdlife International 2015) are dependent on artificial nestboxes is unclear, but taking our estimate of 7500 boxes and an occupation rate of 27.5% (the mean across our two study sites), the numbers could be significant. Our results suggest that the efficacy of nestbox installation might vary across the species' range, and highlights the need for longer-term solutions.

REFERENCES

Aebischer, N. & Ewald, J.A. 2012. The Grey Partridge in the UK: population status, research, policy and prospects. *Anim. Biodivers. Conserv.* **35**: 353–362.

Aleman, Y. & Laurens, J. 2013. Répartition et effectifs du Rollier d'Europe (*Coracias garrulus*) dans les Pyrénées-Orientales en 2011. *La Mélano* **13**: 1–11.

Arlettaz, R., Schaub, M., Fournier, J., Reichlin, T.S., Sierro, A., Watson, J.E.M. & Braunisch, V. 2010. From publications to public actions: when conservation biologists bridge the gap between research and implementation. *Bioscience* **60**: 835–842.

Avilés, J.M. & Costillo, E. 1998. Selection of breeding habitats by the Roller (*Coracias garrulus*) in farming areas of the southwestern Iberian peninsula. *Die Vogelwarte* **39**: 242–247.

Avilés, J.M. & Parejo, D. 2002. Diet and prey type selection by Rollers *Coracias garrulus* during the breeding season in southwest of the Iberian Peninsula. *Alauda* **70**: 227–230.

Avilés, J.M. & Parejo, D. 2004. Farming practices and Roller *Coracias garrulus* conservation in south-west Spain. *Bird Conserv. Int.* **14**: 173–181.

Avilés, J.M. & Sanchez, A. 2000. Avian responses to nestbox installation in steppes of the south-west of the Iberian Peninsula (Extremadura). *Avocetta* **241**: 51–54.

Avilés, J.M., Sanchez, J.M. & Parejo, D. 2000. Nest-site selection and breeding success in the Roller (*Coracias garrulus*) in the Southwest of the Iberian peninsula. *J. Ornithol.* **141**: 345–350.

Bailey, R. & Bonter, D. 2017. Predator guards on nest boxes improve nesting success of birds. *Wildl. Soc. Bull.* **41**: 434–441.

Barton, K. 2016. *MuMIn: Multi-Model Inference. R package version 1.15.6.*

Bates, D., Mächler, M. & Bolker, B. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**: 1–48.

Birdlife International 2015. *European Red List of Birds.* Cambridge: Birdlife International.

Birdlife International 2017. *Coracias garrulus* (amended version published in 2016). The IUCN Red List of Threatened Species 2017. Cambridge: Birdlife International. e.T22682860A111884908.

Birdlife International 2018. *State of the World's Birds.* Cambridge: Birdlife International.

Birdlife International & NatureServe 2013. *Bird Species Distribution Maps of the World.* Cambridge: BirdLife International; Arlington: NatureServe.

Blanc, L.A. & Walters, J.R. 2008. Cavity-nest webs in a longleaf pine ecosystem. *Condor* **110**: 80–92.

Bouvier, J.-C., Muller, I., Génard, M., Lescourret, F. & Lavigne, C. 2014. Nest-site and landscape characteristics affect the distribution of breeding pairs of European Rollers *Coracias garrulus* in an agricultural area of Southeastern France. *Acta Ornithologica* **49**: 23–32.

Bragin, E.A., Bragin, A.E. & Katzner, T.E. 2017. Demographic consequences of nestbox use for Red-footed Falcons *Falco vespertinus* in Central Asia. *Ibis* **159**: 841–853.

Burke, D. & Nol, E. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. *Auk* **115**: 96–104.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*, 2nd edn. New York, NY: Springer.

Butler, S.J. 2001. *Nest-site selection by the European roller (Coracias garrulus) in southern France.* MSc Thesis.

Catry, I., Silva, J.P., Cardoso, A., Martins, A., Delgado, A., Sanches, A.R., Santos, A., Estanque, B., Cruz, C.M., Pacheco, C., Leitao, D., Pereira, E., Matilde, E., Moital, F., Romba, F., Sequeira, N., Monteiro, P., Rocha, P., Correia, R., Alcazar, R., Congarato, R., Heleno, R., Catry, T., Silva, T. & Ferro, T. 2011. Distribution and population trends of the European Roller in pseudo-steppe areas of Portugal: results from a census in sixteen SPAs and IBAs. *Airo* **21**: 3–14.

Catry, I., Catry, T., Patto, P., Franco, A.M.A. & Moreira, F. 2015. Differential heat tolerance in nestlings suggests sympatric species may face different climate change risks. *Clim. Res.* **66**: 13–24.

Catry, I., Marcelino, J., Franco, A.M.A. & Moreira, F. 2017. Landscape determinants of European Roller foraging habitat: implications for the definition of agri-environmental measures for species conservation. *Biodivers. Conserv.* **26**: 553–566.

Christof, A. 1991. *Le rollier d'Europe.* Puteaux: Point Vétérinaire.

Cockle, K.L., Martin, K. & Drever, M.C. 2010. Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. *Biol. Cons.* **143**: 2851–2857.

Cramp, S. 1985. *The Birds of the Western Palearctic, Vol. 4: Terns to Woodpeckers.* Oxford: Oxford University Press.

Doxon, E.D., Davis, C.A. & Fuhlendorf, S.D. 2011. Comparison of two methods for sampling invertebrates: vacuum and sweep-net sampling. *J. Field Ornithol.* **82**: 60–67.

Edmunds, K., Bunbury, N., Sawmy, S., Jones, C.G. & Bell, D.J. 2008. Restoring avian island endemics: use of supplementary food by the endangered Pink Pigeon (*Columba mayeri*). *Emu* **108**: 74–80.

Ewald, J.A., Aebischer, N., Richardson, S.M., Grice, P.V. & Cooke, A.I. 2010. The effect of agri-environment schemes on grey partridges at the farm level in England. *Agr. Ecosyst. Environ.* **138**: 55–63.

Ewen, J.G., Walker, L., Canessa, S. & Groombridge, J.J. 2015. Improving supplementary feeding in species conservation. *Conserv. Biol.* **29**: 341–349.

Finch, T., Butler, S., Franco, A. & Cresswell, W. 2017. Low migratory connectivity is common in long-distance migrant birds. *J. Anim. Ecol.* **86**: 662–673.

Franco, A.M.A., Marques, J.T. & Sutherland, W.J. 2005. Is nest-site availability limiting Lesser Kestrel populations? A multiple scale approach. *Ibis* **147**: 657–666.

Gillman, L.N., Wright, S.D., Cusens, J., McBride, P.D., Malhi, Y. & Whittaker, R.J. 2015. Latitude, productivity and species richness. *Glob. Ecol. Biogeogr.* **24**: 107–117.

Hanmer, H.J., Thomas, R.L. & Fellowes, M.D.E. 2017. Provision of supplementary food for wild birds may increase the risk of local nest predation. *Ibis* **159**: 158–167.

Hijmans, R.J. 2016. *raster: Geographic Data Analysis and Modeling. R package version 2.5-8.*

Kay, G.M., Barton, P.S., Driscoll, D.A., Cunningham, S.A., Blanchard, W., McIntyre, S. & Lindenmayer, D.B. 2016. Incorporating regional-scale ecological knowledge to improve the effectiveness of large-scale conservation programmes. *Anim. Conserv.* **19**: 515–525.

Kerus, V. & Račinskis, E. 2008. The second Latvian Breeding Bird Atlas 2000–2004: preliminary results. *Rev. Catalana Ornitol.* **24**: 100–106.

Kiss, O., Elek, Z. & Moskat, C. 2014. High breeding performance of European Rollers *Coracias garrulus* in heterogeneous farmland habitat in southern Hungary. *Bird Study* **61**: 496–505.

Kiss, O., Tokody, B., Ludnai, T. & Moskát, C. 2017. The effectiveness of nest-box supplementation for the conservation of European Rollers (*Coracias garrulus*). *Acta Zool. Acad. Scie. Hung.* **63**: 123–135.

Klein, Á., Nagy, T., Csörgő, T. & Mátics, R. 2007. Exterior nest-boxes may negatively affect Barn Owl *Tyto alba* survival: an ecological trap. *Bird Conserv. Int.* **17**: 263–271.

Kovacs, A., Barov, B., Orhun, C. & Gallo-Orsi, U. 2008. *International Species Action Plan for the European Roller Coracias garrulus garrulus.*

Lindenmayer, D.B., Welsh, A., Donnelly, C., Crane, M., Michael, D., Macgregor, C., McBurney, L., Montague-Drake, R. & Gibbons, P. 2009. Are nest boxes a viable alternative source of cavities for hollow-dependent animals? Long-term monitoring of nest box occupancy, pest use and attrition. *Biol. Cons.* **142**: 33–42.

Lüütsepp, G., Kalamees, A. & Lüütsepp, O. 2011. European Roller *Coracias garrulus* in Estonia 2000–2011. *Hirundo* **24**: 61–72.

Martin, T.E. 2015. Consequences of habitat change and resource selection specialization for population limitation in cavity-nesting birds. *J. Appl. Ecol.* **52**: 475–485.

Molnar, G. 1998. Breeding biology and foraging of Rollers (*Coracias garrulus*) nesting in nest-boxes. *Ornis Hungar.* **8** (Suppl. 1): 119–124.

Moreno-Opo, R., Trujillano, A., Arredondo, Á., González, L.M. & Margalida, A. 2015. Manipulating size, amount and appearance of food inputs to optimize supplementary feeding programs for European vultures. *Biol. Cons.* **181**: 27–35.

Morris, A.J., Whittingham, M.J., Bradbury, R.B., Wilson, J.D., Kyrkos, A., Buckingham, D.L. & Evans, A.D. 2001. Foraging habitat selection by Yellowhammers (*Emberiza citrinella*) nesting in agriculturally contrasting regions in lowland England. *Biol. Cons.* **101**: 197–210.

Morrison, C.A., Robinson, R.A., Butler, S.J., Clark, J.A., Gill, J.A. & Morrison, C.A. 2016. Demographic drivers of decline and recovery in an Afro-Palaearctic migratory bird population. *Proc. R. Soc. B* **283**: 20161387.

Olea, P.P. & Mateo-Tomás, P. 2014. Living in risky landscapes: delineating management units in multithreat environments for effective species conservation. *J. Appl. Ecol.* **51**: 42–52.

Öst, M., Ramula, S., Lindén, A., Karell, P. & Kilpi, M. 2016. Small-scale spatial and temporal variation in the demographic processes underlying the large-scale decline of eiders in the Baltic Sea. *Popul. Ecol.* **58**: 121–133.

Paradis, E., Claude, J. & Strimmer, K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**: 289–290.

Peach, W.J., Lovett, L.J., Wotton, S.R. & Jeffs, C. 2001. Countryside stewardship delivers Cirl Buntings (*Emberiza cirlus*) in Devon, UK. *Biol. Cons.* **101**: 361–373.

Perkins, A.J., Maggs, H.E., Watson, A. & Wilson, J.D. 2011. Adaptive management and targeting of agri-environment schemes does benefit biodiversity: a case study of the *corn bunting Emberiza calandra*. *J. Appl. Ecol.* **48**: 514–522.

Plummer, K.E., Bearhop, S., Leech, D.I., Chamberlain, D.E. & Blount, J.D. 2013. Winter food provisioning reduces future breeding performance in a wild bird. *Sci. Rep.* **3**: 2002.

QGIS Development Team 2015. *QGIS Geographic Information System*. Beaverton: Open Source Geospatial Foundation Project.

Račinskis, E. & Mārdega, I. 2011. *Conservation and population status of the European Roller in Latvia. Poster at 8th Conference of the European Ornithologists' Union, Riga.*

Rodríguez, J., Avilés, J.M. & Parejo, D. 2011. The value of nestboxes in the conservation of Eurasian Rollers *Coracias garrulus* in southern Spain. *Ibis* **153**: 735–745.

Ružić, M.M., Szekeres, O., Ágoston, A., Balog, I & Brdarić, B. 2014. *The recovery of the European Roller Coracias garrulus population in Vojvodina Province, Serbia. Proceedings of the Second Adriatic Flyway Conference.*

Sosnowski, J. & Chmielewski, S. 1996. Breeding biology of the Roller *Coracias garrulus* in Puszcza Pilicka Forest (Central Poland). *Acta Ornithol.* **31**: 119–131.

Sutherland, W.J., Pullin, A.S., Dolman, P.M. & Knight, T.M. 2004. The need for evidence-based conservation. *Trends Ecol. Evol.* **19**: 305–308.

Sutherland, W.J., Dicks, L.V., Ockendon, N. & Smith, R.K. 2015. *What Works in Conservation*. Cambridge: Open Book Publishers.

Tatayah, R.V.V., Malham, J., Haverson, P., Reuleaux, A. & Van de Wetering, J. 2007. Design and provision of nest boxes for Echo Parakeets *Psittacula eques* in Black River Georges National Park, Mauritius. *Conservat. Evid* **4**: 16–19.

Thorup, K., Sunde, P., Jacobsen, L.B. & Rahbek, C. 2010. Breeding season food limitation drives population decline of the Little Owl *Athene noctua* in Denmark. *Ibis* **152**: 803–814.

Tron, F., Zenasni, A., Bousquet, G., Cramm, P. & Beesnard, A. 2008. Réévaluation du statut du Rollier d'Europe [*Coracias garrulus*] en France. *Ornithos* **15**: 84–89.

Václav, R., Valera, F. & Martínez, T. 2011. Social information in nest colonisation and occupancy in a long-lived, solitary breeding bird. *Oecologia* **165**: 617–627.

Vincenzi, S., Hatch, S., Merkling, T. & Kitaysky, A.S. 2015. Carry-over effects of food supplementation on recruitment and breeding performance of long-lived seabirds. *Proc. Roy. Soc. B Biol. Sci.* **282**: 20150762.

Walker, L.K., Morris, A.J., Cristinacce, A., Dadam, D., Grice, P.V. & Peach, W.J. 2018. Effects of higher-tier agri-environment scheme on the abundance of priority farmland birds. *Anim. Conserv.* **21**: 183–192.

Whittingham, M.J., Krebs, J.R., Swetnam, R.D., Vickery, J.A., Wilson, J.D. & Freckleton, R.P. 2007. Should conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. *Ecol. Lett.* **10**: 25–35.

Yackulic, C.B., Sanderson, E.W. & Uriarte, M. 2011. Anthropogenic and environmental drivers of modern range loss in large mammals. *Proc. Natl Acad. Sci. USA* **108**: 4024–4029.

Zingg, S., Arlettaz, R. & Schaub, M. 2010. Nestbox design influences territory occupancy and reproduction in a declining, secondary cavity-breeding bird. *Ardea* **98**: 67–75.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Land-use categories and definitions for France.

Table S2. Land-use categories and definitions for Latvia.

Table S3. Number of insect transects conducted in each major land-use in France and Latvia.

Table S4. Modelled ash-free dry weight (g) according to insect taxon (rows) and size class (columns).

Table S5. Nest control effort across the study period in France and Latvia. Median values per nest (25th–75th percentiles).

Table S6. Definitions of parameters calculated for each Roller breeding attempt.

Table S7. Model summaries for models predicting variation in (a) the probability of observing an insect on a transect and (b) the biomass of observed insects in France. Results are presented only for models with $\Delta_i < 4$, but w_i is calculated across all models.

Table S8. Model summaries for models predicting variation in (a) the probability of observing an insect on a transect and (b) the biomass of observed insects in Latvia. Results are presented only for models with $\Delta_i < 4$, but w_i is calculated across all models.

Table S9. Model selection table for nest-box occupation (Roller–other model).

Figure S1. 5×5-m land-use map of the French study site (2015).

Figure S2. 5×5-m land-use map of the Latvian study site (2014).

Figure S3. Predicted insect biomass per land-use type over 2 years in France.

Figure S4. Relationship between predicted insect biomass within each 1-km grid square derived from either 2014 (*x*-axis) or 2015 (*y*-axis) insect survey data.

Figure S5. Sensitivity of breeding density analysis to grain size and grid origin.

Figure S6. Spatial auto-correlation.

Appendix S1. Estimating the number of European Roller nestboxes.

Appendix S2. Converting insect counts to biomass estimates.