

Behavioral Strategies and the Spatial Pattern Formation of Nesting

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ABSTRACT: Nesting in dense aggregations is common in central place foragers, such as group-living birds and insects. Both environmental heterogeneity and behavioral interactions are known to induce clustering of nests, but their relative importance remains unclear. We developed an individual-based model that simulated the spatial organization of nest building in a gregarious digger wasp, *Bembix rostrata*. This process-based model integrates environmental suitability, as derived from a microhabitat model, and relevant behavioral mechanisms related to local site fidelity and conspecific attraction. The drivers behind the nesting were determined by means of inverse modeling in which the emerging spatial and network patterns from simulations were compared with those observed in the field. Models with individual differences in behavior that include the simultaneous effect of a weak environmental cue and strong behavioral mechanisms yielded the best fit to the field data. The nest pattern formation of a central place foraging insect cannot be considered as the sum of environmental and behavioral mechanisms. We demonstrate the use of inverse modeling to understand complex processes that underlie nest aggregation in nature.

Keywords: approximate Bayesian computation, habitat selection, integrated nested Laplace approximation (INLA), spatial self-organization, Crabronidae, Hymenoptera.

Introduction

The ideal free distribution predicts that organisms optimally distribute themselves across resource patches to minimize resource competition (Kacelnik et al. 1992). This process leads to the sorting of individuals according to their niche (Hutchinson 1957; Holt 2009) and induces spatial patterns of high densities where the environment is most suit-

able (e.g., in shorebirds; Swift et al. 2017). Animal aggregations are also widely documented in species inhabiting homogeneous environments, not only in social species but also in nonsocial central place foraging wasps, lizards, and birds (Stamps 1988; Tarof and Ratcliffe 2004; Evans and O'Neill 2007). These inherent spatial patterns can emerge from behavioral and internal dynamics, such as the interplay between positive and negative density dependence, and are an example of spatial self-organization (Fortin and Dale 2005; Rietkerk and van de Koppel 2008; Bayard and Elphick 2010; Bradbury and Vehrencamp 2014). The spatial clustering of group-living animals—and more specifically nest clustering—has been explained through several behavioral hypotheses that are intrinsically linked with benefits related to group size (Krause and Ruxton 2002). Groups can provide protection against predation or parasitism (e.g., via a selfish herd; Hamilton 1971; Larsson 1986; supplement S1; supplements S1–S9 are available online) or against climatic extremes (Gilbert et al. 2008), or they can simply increase foraging efficiency (Clark and Mangel 1986). Both environmental and behavioral mechanisms can result in the spatial clustering of individuals or their nests. However, their relative importance remains elusive, especially for invertebrates. Moreover, it is unclear at which level these processes can vary: can mechanisms vary among individuals or even during an individual's lifetime? The relative strengths of environmental and behavioral mechanisms for spatial clustering are expected to vary among systems (e.g., in analogy to bottom-up and top-down regulation of communities; Hunter and Price 1992).

Information use is central to any decision-making and, thus, also to settlement. Information can be personal when individuals directly use cues from the environment or inadvertently social when information is generated by the behavior (e.g., foraging, fighting, mating) of other conspecific individuals (Danchin et al. 2004; Dall et al. 2005). Personal

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information, in addition to self-assessment of the environment, can consist of a female's experience with previous nesting locations, which results in local site fidelity (Hoi et al. 2012; Asís et al. 2014). Variation in information use among individuals may arise from heterogeneity in these strategies, where “producers” rely on personal information and “scroungers” rely on (inadvertent) social information, or from individuals switching between these sources of information (Barnard and Sibly 1981; Coolen et al. 2007).

The spatial clustering of nests is often regarded as a clearly separated and stepwise process where individuals first collectively select suitable environments at larger spatial scales, after which internal dynamics (e.g., competition, attraction, individual and social learning) come into play (Melles et al. 2009; Swift et al. 2017). The prevailing insights are acquired by the analysis of complex spatial patterns and/or from behavioral experiments (e.g., Polidori et al. 2008; Melles et al. 2009; Asís et al. 2014). However, environmental heterogeneity and internal dynamics are anticipated to act simultaneously or even synergistically. Since the emergent patterns of a complex system cannot be predicted from the sum of the underlying components (Bradbury and Vehrencamp 2014), more integrated approaches are needed. Inverse modeling, which can identify the processes that reproduce a set of observed patterns, has been extremely useful from this perspective (Banks et al. 2014; Curtsdotter et al. 2019; Stouffer 2019).

Here, we apply such an inverse approach to understand the contribution of environmental and behavioral mechanisms in nest aggregations of the ground-nesting digger wasp *Bembix rostrata*. We combine a microhabitat suitability model with an individual-based model (IBM) to investigate the processes underlying the spatial dynamics of nest pattern formation as observed in the field. We include three mechanisms in the IBM: (i) environmental suitability, (ii) local site fidelity, and (iii) social cues. The direction and strength of these mechanisms can vary at the population level (uniform for all) as well as between individuals (individually fixed) and within individuals (individually flexible). The simulated spatial point and network patterns are compared with those recorded in the field using approximate Bayesian computation (ABC) to select the most likely combination of environmental and behavioral mechanisms that underlie the observed nesting patterns.

Material and Methods

Study Species

Bembix rostrata (Linnaeus, 1758; Hymenoptera, Crabronidae, Bembicinae) is a specialized, highly philopatric, gregariously nesting digger wasp found in sandy regions of Europe. They inhabit sun-exposed sand dunes with sparse vegetation (Larsson 1986) and are sensitive to trampling (Bonte 2005).

Adults are active from June to August; females construct one nest burrow at a time in which a single larva is progressively provisioned with flies (Nielsen 1945; Field 2005). A female can make a maximum of five nests, each with one offspring (Larsson and Tengö 1989). Several kleptoparasitic fly species (Sarcophagidae) lay their larvae (ovi-larviposition; Piwczyński et al. 2017) on the prey provided by females of *Bembix* species (Nielsen 1945; Evans and O'Neill 2007). A selfish herd pattern has been observed in *B. rostrata* with regard to such brood parasites (Larsson 1986), where the incidence of brood parasitism per nest decreased with higher nest densities (we found a similar pattern in our field data between *B. rostrata* and *Senotainia albifrons*; supplement S1).

Study Site and Sampling

Field data were collected in the summer of 2016 in the De Westhoek nature reserve in De Panne (51°04'38"N, 2°33'37"E; Belgium), in a study plot of approximately 40 × 90 m². Surveys took place on 30 days of favorable (sunny and warm) weather conditions for *B. rostrata* (Schöne and Tengö 1991), between June 28 and August 15. Female wasps were individually tagged with a colored and numbered plastic plate on the thorax (Opalith Zeichenplättchen), and nests were marked with small handcrafted flags. We recorded visually when an individual started a nest or entered the nest with a prey and if the prey was “infected” by kleptoparasitic flies (*Senotainia albifrons*; Miltogramminae, Sarcophagidae). The study area was covered several times per day, to sample each nest aggregate as equally as possible. The position of each nest was measured with a Trimble GPS device (accuracy, 2 cm). Remote-sensing imagery was collected using a drone (Rpaswork.com and Didex.be) equipped with a multispectral camera (red, green, blue, and near infrared bands) at the end of the flight season. These images were processed to create a digital elevation model (pixel size, 2.4 × 2.4 cm²) and to calculate the normalized difference vegetation index (NDVI; pixel size, 1.1 × 1.1 cm²; Pettorelli 2013). The parameter *insolation* (as an indicator of the microclimate; pixel size, 7.2 × 7.2 cm²) was calculated from the digital elevation model using the solar radiation tool and slope (pixel size, 7.2 × 7.2 cm²) with the surface toolset, both extensions of spatial analyst in ArcGIS (ESRI 2011).

Statistical Analyses

The workflow of the analyses is shown in figure 1.

The Microhabitat Suitability Map. We used integrated nested Laplace approximation (INLA; Rue et al. 2009; Lindgren and Rue 2011; Martins et al. 2013) to build the microhabitat suitability model. INLA is a Bayesian approach that allows

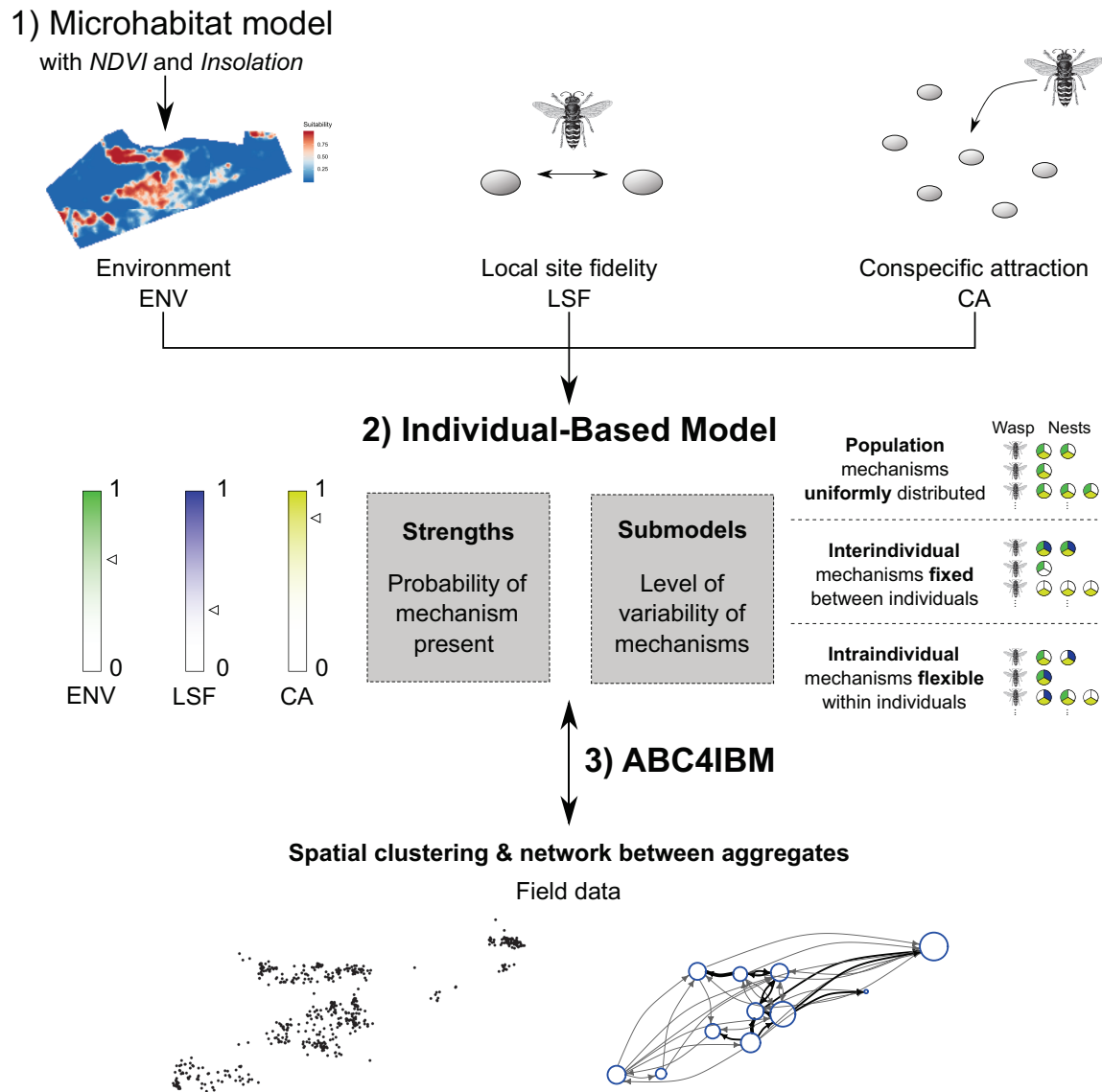


Figure 1: Conceptual figure of the workflow of the analyses. The relation between the nest positions and the environment is investigated by building a microhabitat suitability model with integrated nested Laplace approximation (INLA; panel 1). Because the clustering is much higher than expected based solely on the microhabitat model, the environment and behavioral mechanisms (i.e., local site fidelity and conspecific attraction) are simultaneously modeled with an individual-based model (IBM; panel 2). The simulations differ in strength of the mechanisms. This is implemented through the *strength* parameters, which represent the probability of the mechanisms being present. The presence of the mechanisms can vary on three different levels: population, interindividual, and intraindividual. The simulations from the IBM are compared with the spatial pattern of the field data using approximate Bayesian computation (ABC) to infer which submodels best approach the field data (panel 3).

for spatially autocorrelated residuals of the environmental data related to nest location (Zuur et al. 2017; supplement S6). We used a generalized linear mixed model with a binomial distribution with logit link for the response variable and a spatial dependency structure modeled with the Matérn covariance function (see the code available on Zen-

odo at <https://doi.org/10.5281/zenodo.5212680>). NDVI (vegetation) and *insolation* (microclimate) were used as (normalized) explanatory variables. Every nest was considered as a presence point, and absence/zero data points were generated by selecting an equal number of random points that were at least 1 m from any nest within the study plot. As the study

plot was searched intensely, we considered the generated points to be true absences. Models were compared using the Watanabe-Akaike information criterion (WAIC; Watanabe 2010; Gelman et al. 2014), computed with the *inla* function (Rue and Held 2005; Rue et al. 2009). To confirm our a priori choice of a simple linear model, we considered interactions between both variables and an additional covariate, local slope. WAIC differences for these models with a linear model only including the NDVI and *insolation* parameters were less than 3, so the simple linear model was preferred. The data were split into 70% training and 30% evaluation data. As a cross validation, the final model was run 10 times using different randomly chosen training and evaluation sets each time. To assess the predictive power of the models, the area under the curve (AUC) was calculated using the R package *ROCR* (Sing et al. 2005). Sensitivity (true positive rate; predictive performance of presences), specificity (true negative rate; predictive performance of absences), and balanced accuracy (overall true rate) were calculated using the R package *caret* (Kuhn 2008). To calculate the latter three performance measures, predictions were transformed into 0/1 using the prevalence criterion (Manel et al. 2001; Liu et al. 2005): predictions that are larger than the prevalence threshold (proportion of presences/absences in the evaluation data sets; ± 0.5 in our case) are classified as 1, and the other predictions are classified as 0. The plotting of the spatial field, the spatial residuals that INLA corrects for, shows whether the degree of clustering was higher (hot spots) or lower (cold spots) than expected on the basis of the covariates (NDVI and *insolation*) in the microhabitat model. Different models that considered different spatial scales were compared (each with cross-validation included): buffers between 0.1 and 10 m were drawn around each nest at nine different radii, and the mean of each variable was calculated inside those buffers (QGIS Development Team 2020). The models with buffer scales 0.1, 0.2, 0.5, 1, and 2 m had similar WAIC, AUC, sensitivity, specificity, and spatial field plots. We proceeded with the 1-m scale, as the suitability predictions of this buffer scale were detailed but also smooth, to balance overfitting and poorer estimates (supplement S7). Within each cross validation, predictions of the final model were projected back onto the field study plot within a grid of $0.5 \times 0.5 \text{ m}^2$. A detailed habitat suitability map was created with the average of these predictions (with a 0–1 scale of probability of nest presence). This map was used as an input for the IBM (fig. 1; see also “Inverse Modeling with IBM and ABC” below) to be used as the environmental cue for habitat selection. We did not include the uncertainties of the probabilities in the IBM, as we deem this extra level of stochasticity negligible.

Spatial Point Pattern and Network Analyses. A point pattern analysis was carried out with the R package *Spatstat*

(Baddeley et al. 2015). Spatial clustering of nests was investigated using Ripley’s K at scales between 0 and 40 m, where a higher K than the calculated expected random distribution at a certain scale or radius is indicative of a clustered pattern within that radius and a lower K is indicative of a regular pattern within the radius (Baddeley et al. 2015). Ripley’s K values were transformed to represent the relative change compared with complete spatial randomness (CSR) at a scale r with the formula $K_{\text{rel}}(r) = (K(r) - \text{CSR}(r)) / (\text{CSR}(r))$.

To assign the nests to different nest aggregates, a k -means cluster analysis was implemented. The optimal number of nest aggregates was 11, considering an elbow plot (Kassambara and Mundt 2020), visualization of the clusters, and topography of the area (supplement S8).

A network analysis was carried out with the R package *igraph* (Csardi and Nepusz 2006). Nest aggregates from the k -means cluster analysis were considered network nodes in the network analysis, and the consecutive nests of individuals were considered links (or edges) between network nodes. As such, the network nodes are aggregates that are spatially grouped nests, and the individuals moving among (and within) the aggregates to a consecutive nest are the links of the network. Five network metrics were calculated for this directed network, defined according to Farine and Whitehead (2015): (i) the number of loops, which is the total number of links or subsequent nests of individuals; (ii) the number of internal loops, which is the relative number of links that return to the same node, thus signifying individuals that make consecutive nests in the same aggregate; (iii) transitivity (or clustering coefficient), which quantifies how densely nodes are connected (high transitivity indicates that triads [trios of nodes] have a high degree of being mutually linked); (iv) density (or connectance), which is the number of links divided by the total number of possible links between all clusters; and (v) reciprocity, which is the relative number of reciprocal links between nodes.

Inverse Modeling with IBM and ABC. We developed an IBM to simulate and eventually identify the potential drivers behind the species’ nesting dynamics using a pattern-oriented approach (Grimm et al. 2005). Individual wasps, with their different sets of behaviors, are the entities of simulation within a spatially explicit environment. The ODD (overview, design concepts, details) protocol (Grimm et al. 2006, 2010) is added in supplement S2, where a detailed explanation is given and assumptions and parameters are described. Here we briefly discuss the general setup.

The three mechanisms—environment, local site fidelity, and conspecific attraction—were combined in the model using the *strength* parameters: the probabilities of the mechanisms being present. Variation in the presence of the mechanisms was possible at three levels, as modeled in different

submodels or strategies (fig. 1): (1) population level (the mechanisms used are uniform across all of the individuals in the same population); (2) interindividual (the mechanisms can vary among individuals in a population but are fixed for an individual); and (3) intraindividual (the mechanisms can vary within an individual's lifetime and are thus flexible). The null model, in which random locations were chosen within the study area, was used as the fourth submodel. The flow for an individual *Bembix* female when selecting a nesting site was as follows: first, a random position in the area is sampled; then the average suitability according to the focal mechanisms is assessed, after which that position can be stochastically selected according to the calculated suitability (or probability). When the position is not selected, a new one is sampled according to the same procedure (see the ODD protocol in supplement S2).

The habitat suitability map serves as a baseline for the environmental cue: the suitability values are used as probabilities for settling. Local site fidelity is implemented as a Gaussian distribution centered around the previous nest, with one parameter, σ_{sf} , defining the width of the distribution. As such, positions closer to the previous nest have a higher probability of being chosen. Conspecific attraction is coded in two steps. First, the parameter range_{ca} defines the radius of the circle in which the number of other nests are counted. Second, settlement probability is implemented with a sigmoid function (Kun and Scheuring 2006; Broly et al. 2016), with the number of nests counted in the first step as the dependent variable. Two parameters define the sigmoid curve: $\text{mindens}_{\text{ca}}$ is the intercept, and σ_{ca} is the scale parameter of the function. The Boolean parameter *beh-excl* defines whether conspecific attraction and local site fidelity are mutually exclusive: both mechanisms could be strongly present while not jointly determining an individual's nest site selection. To optimize convergence time and remain within reasonable ecological boundaries, we applied uniform priors in a valid parameter space (supplement S2, table S2.1).

To initialize the model and to define boundary conditions, the following properties derived from the field study were used: total number of individuals sampled in the study site (432), total number of days to run a simulation (30), distribution of the number of nests initiated each day, distribution of the number of nests per individual, and distribution of time between subsequent nests. The latter three are used as probability distributions when initializing the *Bembix* population (supplement S1, sec. 3.1; code available on Zenodo at <https://doi.org/10.5281/zenodo.5212680>).

We verified that the priors were not biasing the analysis toward one of the submodels by setting them widely for 100,000 simulations (prior predictive check; supplement S3). Following this analysis, we restricted prior ranges by excluding those ranges where parameters covaried. This step

ensures that certain parameter values are not redundant and improves convergence of the actual simulations.

Each of the four submodels was run 250,000 times with parameters randomly sampled in the prior parameter ranges (supplement S2, table S2.1). Summary statistics for each model simulation were calculated as described above in "Spatial Point Pattern and Network Analyses."

The model was evaluated using ABC (Beaumont 2010; Csilléry et al. 2010; van der Vaart et al. 2016); more specifically, it was evaluated using rejection ABC following van der Vaart et al. (2015) with the R package *abc* (Csilléry et al. 2012). This method is based on the difference between each simulation and the observed field data in the summary statistics of the patterns of interest. As this method cannot compare summary statistics that are continuous functions, such as Ripley's K , values of Ripley's K at a discrete set of distances were chosen as part of the summary statistics. The complete set of summary statistics were six Ripley's K values transformed as described in the previous section (at distances between 2 and 40 m) and five network metrics (number of total loops, number of internal loops, transitivity, density, and reciprocity), also as described in the previous section. The sum of the differences between normalized summary statistics of field and simulation data was calculated. The summation was weighted with the complement of the average Pearson's correlations ($1 - \rho$) for each summary statistic, calculated from all simulations. As such, the summary statistics are corrected for their dependence structure. Minimizing this distance, the 1,000 simulations (0.1%) closest to the observed field data were retained. We calculated the percentage of accepted simulations for each of the three submodels. Pairwise Bayes factors were calculated for each submodel. A Bayes factor of more than 3 for a model comparison implies that the first model is more substantially supported by the data (Kass and Raftery 1995). Since ABC model selection may be vulnerable to bias (van der Vaart et al. 2015), we scrutinized submodel performance via cross validation of the model selection (supplement S4).

The prior and posterior distributions of the summary statistics and parameters were compared as part of the posterior predictive inspection. This allowed us to evaluate how similar the patterns produced by the IBM are to the patterns in the field, estimate parameters, and derive which processes are important to reproduce these patterns.

We derived data from the same data set at the three different steps in our analysis. Generally, using the same data set for parameterization and model evaluation risks overfitting and overconfidence in the focal model (termed "adaptive overfitting" in machine learning; Roelofs et al. 2019). Therefore, independent data sets should ideally be used for input on the one hand and evaluation of the model on the other hand. We argue that the use of complementary or

auxiliary data in the different components of the analysis minimizes the risk of overfitting for the following reasons. First, as the microhabitat model is adjusted for spatial autocorrelation with the use of INLA, the data used here are independent of the clustering of the nests, causing the model predictions to fundamentally represent the effect of environment on nest presence. Second, initialization of the IBM is carried out using auxiliary data or probability distributions from the field data, to have comparable boundary conditions for the simulations. Parameters in the IBM are not derived from the field data and are implemented using wide priors. Third, the ABC compares simulations with field data on the basis of larger-scale emergent patterns of the point pattern: clustering and network metrics.

Results

Field Study

A total of 432 individual digger wasps were tagged, and 561 nests were marked with flags. Test-digging holes (Nielsen 1945) and tagged individuals that were not observed at a nest were excluded. Of those 432 wasps, 330 had one nest, 78 had two, 21 had three, and 3 had four (supplement S9). A total of 150 nests (26.7%) were parasitized by the kleptoparasitic fly *Senotainia albifrons* (supplement S1). Data have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.g79cnp5q8>; Batsleer et al. 2021).

Microhabitat Suitability Model

The microhabitat suitability model has a high predictive performance: AUC \pm SD of the cross-validated final model was $96.0\% \pm 1.3\%$. The sensitivity \pm SD (true positive rate) was $73.9\% \pm 4.1\%$, the specificity \pm SD (true negative rate) was $96.7\% \pm 2.1\%$, and the balanced accuracy \pm SD (overall true rate) was $85.3\% \pm 1.9\%$. The model therefore performed better in predicting nest absences than nest presences. Nevertheless, predictive performance was overall high. High NDVI values decreased and high *insolation* values increased nesting suitability. Thus, sunny sites with a low vegetation cover have a higher probability of containing nests (supplement S6). For every run, zero was excluded from the 95% credibility intervals of the effect sizes, indicating that the signs of the effect sizes were clearly determined (this is a Bayesian approach to evaluating statistical significance at a specified level). The predictions (ranging from 0 to 1) for nest suitability in the whole study plot are shown in figure 2a.

Figure 2b shows the spatial random components (spatial field or “residuals,” which INLA corrects for in the analysis; supplement S6) that had clear hot and cold areas, indicating higher and lower clustering, respectively, than expected based on the NDVI and *insolation* parameters. Such cold

and hot spots indicate unmeasured variables that vary in space or other underlying mechanisms that cannot be attributed to the environment, such as behavior.

Spatial Point Pattern and Network Analyses

Clustering of nests was present up to 10 m (blue circles in fig. 3). Sixty percent of consecutive nests were made in the same aggregate (fig. 3, internal loops, blue line). The network was not densely connected internally (fig. 3, transitivity, blue line), had a low ratio of possible links present (fig. 3, density, blue line), and had a low level of reciprocal connections (fig. 3, reciprocity, blue line). The distances among consecutive nests had a median of 4.30 m, a mean of 11.01 m, and a maximum of 81.53 m (see the histogram in supplement S9).

Inverse Modeling with IBM and ABC

The prior predictive check made it possible to restrict two parameters' prior ranges for the actual simulations (supplement S3). Data from simulations have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.g79cnp5q8>; Batsleer et al. 2021).

The submodel with fixed (interindividual) strategies was substantially better supported than the uniform strategy. ABC analysis showed to a lesser extent the superior performance of the flexible strategy (intraindividual) compared with the uniform one. The fixed and flexible (inter- and intraindividual) submodels perform equally well based on the cross validation of model selection (supplement S4) and Bayes factors (table 1). Similar results were obtained with the 10,000 (1%), 500 (0.05%), and 100 (0.01%) best simulations (supplement S5), indicating that the ABC analysis converged for the number of simulations run.

Both Ripley's *K* values and network metrics calculated from the selected simulations matched the field data well (fig. 3), despite Ripley's *K* having a large range at small distances.

The *strength* parameters for conspecific attraction and local site fidelity were on average 0.739 (median = 0.760, Q_1 = 0.617, Q_3 = 0.895) and 0.674 (median = 0.716, Q_1 = 0.535, Q_3 = 0.853; both distributions skewed toward 1; fig. 4a), respectively, which means that these behavioral mechanisms are strongly present in the population. The *strength* parameter for environment was on average 0.209 (median = 0.174, Q_1 = 0.079, Q_3 = 0.305; distribution skewed toward 0; fig. 4a), which means that the environmental cue is less strongly present—3.5 and 3.2 times weaker on average than conspecific attraction and local site fidelity, respectively.

The estimated range of the conspecific attraction was on average 2.29 m (median = 1.98 m, Q_1 = 1.29 m, Q_3 = 3.05 m; fig. 4a). The two parameters for the sigmoid response

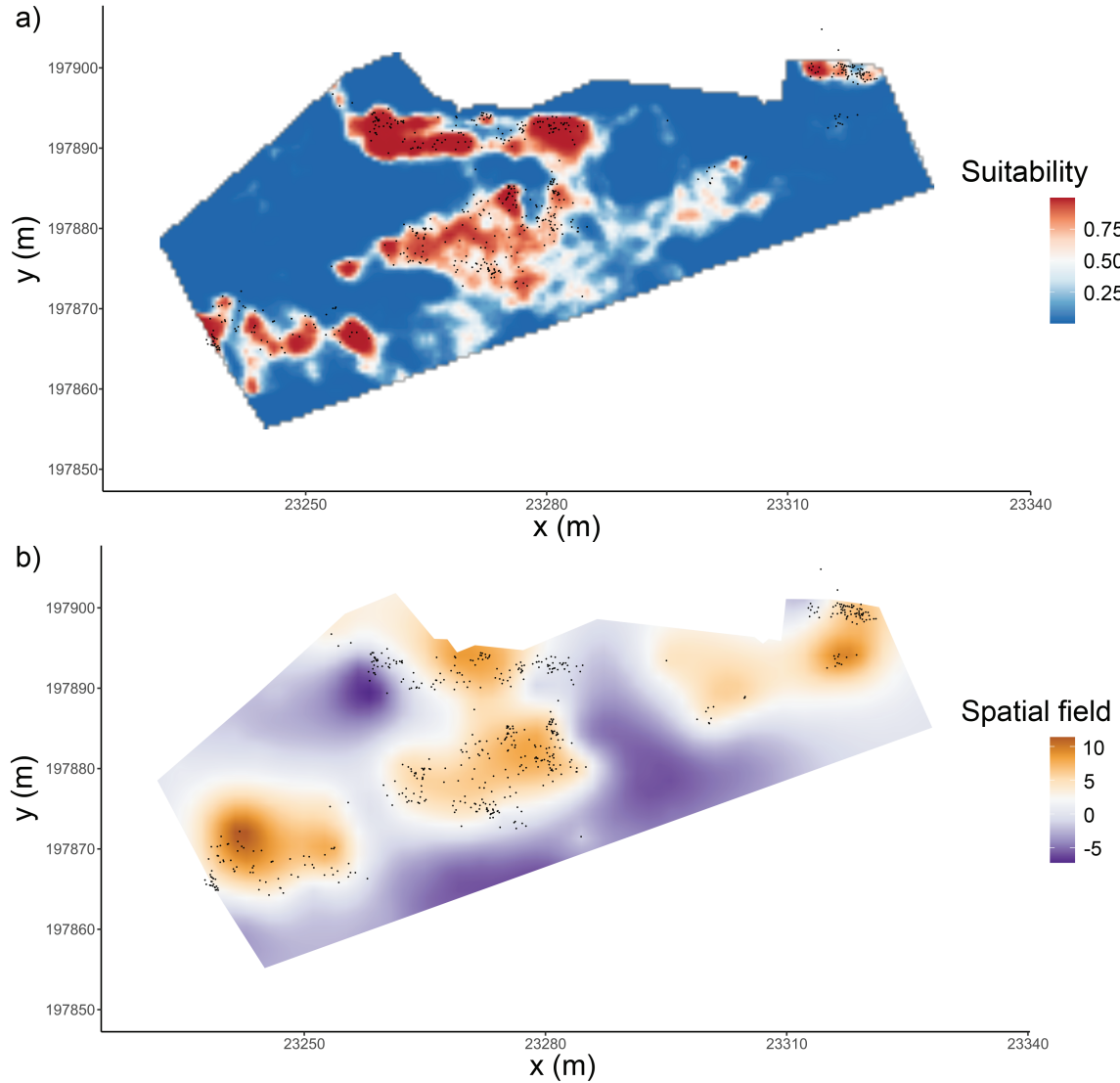


Figure 2: *a*, Predictions for microhabitat suitability (0–1) on the field study plot based on vegetation (the normalized difference vegetation index [NDVI] parameter) and sun irradiance (the *insolation* parameter), mean of all 10 iterations. *b*, Posterior mean values of the spatial field from one of the iterations (others were similar). The spatial field shows where the spatial autocorrelation, corrected for using integrated nested Laplace approximation (INLA), deviated from zero, indicating higher clustering (hot spots; dark orange) or lower clustering (cold spots; dark purple) than expected based on the NDVI and *insolation* parameters. This indicates that other mechanisms must be involved in the clustering of the nests. Black circles indicate nest locations. Pixel size is $50 \times 50 \text{ cm}^2$ on the ground. The Cartesian coordinate reference system used is Belgian Lambert 72, epsg:31370.

function for conspecific attraction were both low (*mindens_{ca}*: mean = -8.13 , median = -8.29 , $Q_1 = -9.25$, $Q_3 = -7.27$; σ_{ca} : mean = 3.16 , median = 1.74 , $Q_1 = 0.69$, $Q_3 = 4.28$; for detailed information about parameter ranges, see supplement 2), indicating that the response function had an intercept very close to zero and a steep slope (fig. 4b)—the probability of nest site selection becomes large at low densities of conspecific nests. The parameter σ_{lsf} for local site fidelity, tended toward a narrow Gaussian distribution,

with a scale up to 10 m (fig. 4b). Of the accepted simulations, 76.5% included the parameter *beh-excl*, indicating that the two behavioral mechanisms are mutually exclusive.

Discussion

We used an inverse modeling approach to study the processes underlying the aggregative nest pattern formation in the digger wasp *Bembix rostrata*. The observed patterns

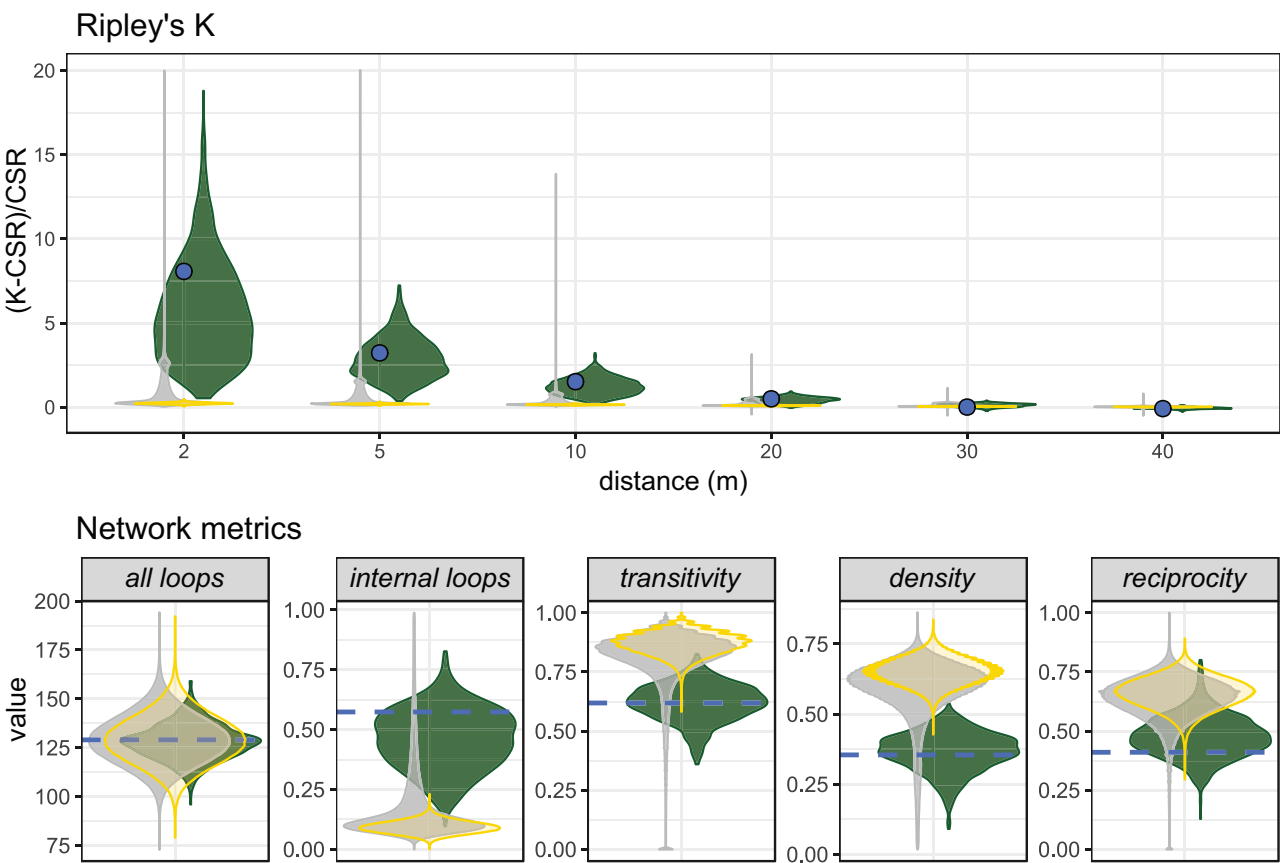


Figure 3: Violin plots of the distribution of prior summary statistics of all 1,000,000 simulations (gray), the distribution of the posterior summary statistics of the 1,000 (0.1%) best models (green), and field data (blue circles or lines). Yellow distributions are from the null model (submodel random). Summary statistics are of two types: spatial clustering (Ripley's K ; relative change compared with complete spatial randomness [CSR]) and network metrics (all and internal loops, transitivity, density, and reciprocity).

in nature were best predicted by simultaneously considering the effects of the environment, conspecific attraction, and local site fidelity. We found that nest pattern formation cannot be decomposed into a stepwise process of environmental filtering and behavioral effects. Rather, it represents a complex system with varying nest choice strategies that rely on the simultaneous integration of environmental and behavioral mechanisms with differing strengths. The spatial patterns of

nesting are primarily explained by models with individual differences in behavior, including that an individual uses either personal information or inadvertent social information.

Conspecific attraction is widespread in digger wasps (Evans and O'Neill 2007). Individuals can be attracted to conspecifics, as their presence provides an honest cue for habitat suitability. In such situations, the use of social information may have adaptive payoffs by reducing the investment

Table 1: Bayes factors (BFs) and proportions of accepted models for model selection with approximate Bayesian computation (ABC) analysis

	Random	Population	Interindividual	Intraindividual	% accepted simulation
Random	–	.00	.00	.00	0
Population	∞	1.00	.31	.36	14.3
Interindividual	∞	3.20	1.00	1.14	45.7
Intraindividual	∞	2.80	.88	1.00	40.0

Note: The ABC analysis retained the 1,000 best simulations of 1,000,000 (0.1%). The submodels represent at which level the mechanisms can vary: population, interindividual, or intraindividual. BFs are the ratios of the posterior probabilities of two models, indicating the strength of evidence for model M_1 (rows) relative to model M_0 (columns), given the data. Evidence categories according to Kass and Raftery (1995) are as follows: $BF < 1$ indicates more evidence for M_0 than M_1 , $1 < BF < 3$ indicates weak evidence for M_1 compared with M_0 , and $3 < BF < 10$ indicates substantial evidence for M_1 compared with M_0 .

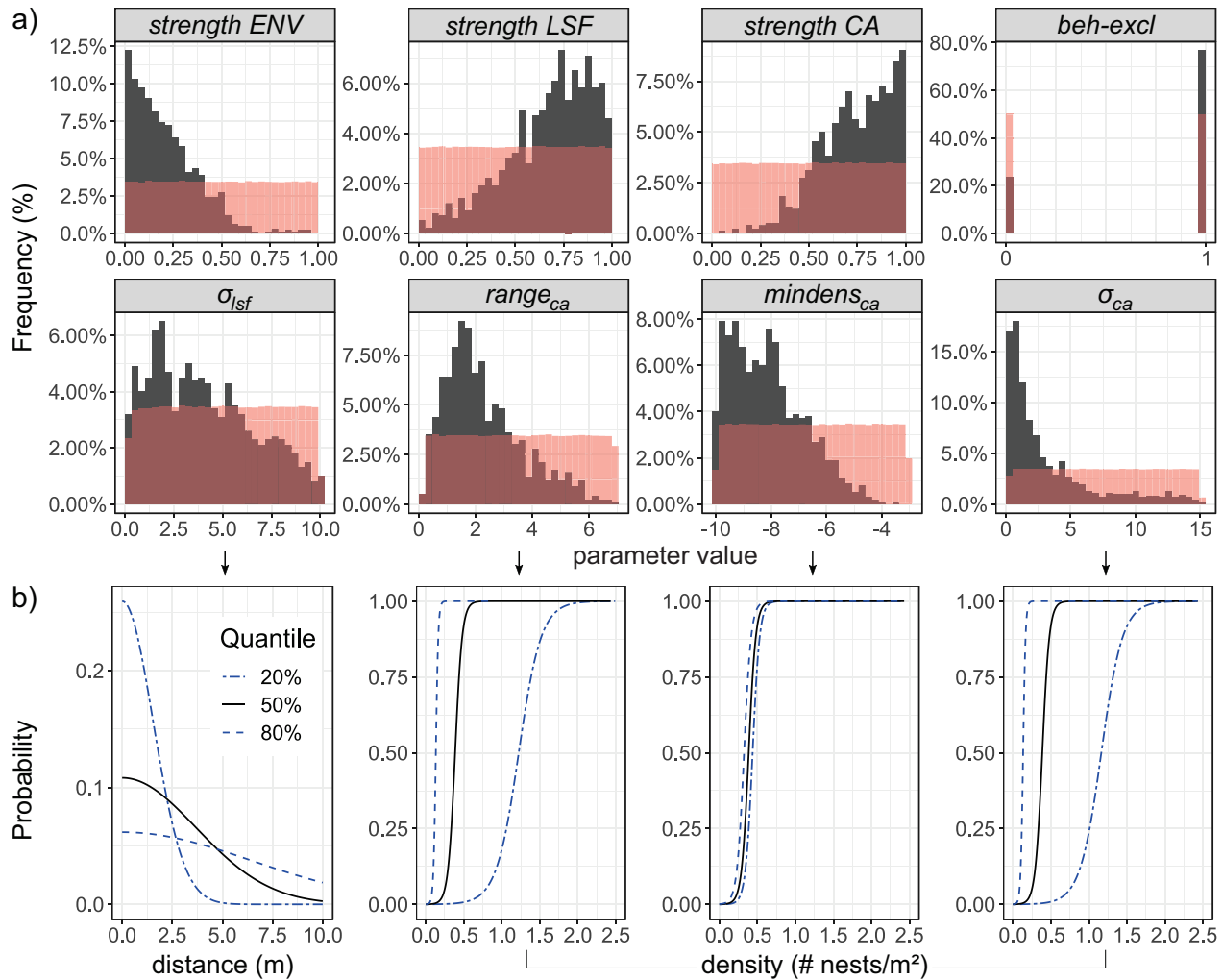


Figure 4: a, Priors (transparent red) and posteriors (dark gray) of the *strength* parameters (of the mechanisms: ENV = environment; LSF = local site fidelity; CA = conspecific attraction) and parameters of the behavioral mechanisms. The parameter *beh-excl* defines whether conspecific attraction and local site fidelity are mutually exclusive (1) or not (0). b, Effect of the posteriors on the response functions, defined by the bottom four parameters, plotted for the median (50% quantile), the 20% quantile, and the 80% quantile of the corresponding parameter. Parameters other than the focal are held constant at the median of the posterior distributions. Local site fidelity (first graph in b) is implemented with a Gaussian curve with the center at the previous nest. Conspecific attraction is implemented with a sigmoid curve (three graphs on the right in b), with the dependent variable the density of nests (number of nests within *range_{ca}*). See the main text and supplement S2 for further details on parameter definitions and ranges.

of time and energy in sampling of the environment (Dall et al. 2005). Conspecific attraction strongly affects nest site selection in the studied population (Buxton et al. 2020), while environmental cues appear to have a weaker effect. While the use of social information is best known in vertebrates and social insects, nonsocial insects also possess individual and even social learning abilities that eventually contribute to higher fitness (Coolen et al. 2005). *Bembix rostrata* is known to perform test-digging behavior, in which individuals seem to sample the environment by digging shallow burrows in the sand across the nesting area before

starting to dig an actual nest (Nielsen 1945). The use of social cues for habitat suitability is therefore likely adaptive, as it reduces the time and energy spent on this behavior. The large contribution of social attraction in predicting nest patterning likely explains the high levels of philopatry in *B. rostrata* (Nielsen 1945; Larsson 1986; Blösch 2000), that is, their tendency to remain in the same nesting area for several consecutive generations.

The selfish herd hypothesis states that individuals within a population attempt to reduce their predation or parasitism rate by putting other conspecifics between themselves and

predators or parasites (Mooring and Hart 1992). This theory has been invoked to explain the aggregation of *B. rostrata* (Larsson 1986) and another closely related digger wasp, *Crabro cribrellifer* (Wcislo 1984). These studies, along with our data (supplement S1), show that the incidence of parasitism per nest decreases with nest density. In our system, the presence of *Senotainia albifrons* brood parasites is anticipated to convey information to the wasps and to induce conspecific attraction. However, how much the actual presence of these brood parasites contributes to the overall conspecific attraction is uncertain. Since we lack more information on the dynamics of these parasites, such mechanisms were not directly incorporated in the model but were instead included as part of the primary process of attraction. Several nests nevertheless occurred at quite low densities, where the parasitism rate, and especially its variation, is higher (supplement S1, fig. S1.2). Potential reasons for this more risky behavior could include, nonexhaustively, spatial bet hedging (Philippi and Seger 1989), imperfect information on parasitism risk (Koops and Abrahams 1998), or avoidance of perceived intraspecific competition (Polidori et al. 2008). Regarding the last mechanism, conspecific kleptoparasitism (wasps that steal prey from neighboring individuals) has been observed in five other *Bembix* species but not (yet) in *B. rostrata* (Evans and O'Neill 2007).

The most likely nest selection strategy identified by our model is one with individually consistent but mutually exclusive behaviors (parameter *beh-excl*): when local site fidelity is used, conspecific attraction is not used simultaneously for nest site selection. Consistent individual variation in movement behavior, with individuals relying on either personal or social information, can be responsible for the emergence of ecological patterns at larger spatial scales (Spiegel et al. 2017). Such heterogeneity in behavior due to individual specialization may be especially relevant in populations experiencing high levels of intraspecific competition (Araújo et al. 2011). The second-most probable but slightly less supported model considered individual behavioral flexibility during an individual's lifetime. Shifts in individual behavior have been found across taxa in, for example, foraging in heterogeneous environments (Newlands et al. 2004; Webber et al. 2020), mating (Perrill et al. 1982), migration (Eggeman et al. 2016), and seasonal aggregation (Bonar et al. 2020). These shifts arise from plasticity in response to environmental and demographic changes (e.g., density, competition, predation). We modeled behavioral shifts as a stochastic process, since any information on the potential conditionality of such shifts was lacking. Explicitly considering thresholds that underlie movement changes is nevertheless important to explain larger-scale patterns (Morales and Ellner 2002; Newlands et al. 2004; Goossens et al. 2020). In our study, a flexible strategy is not clearly distinguishable from a consistent one in explaining the spatial nest pattern. Therefore, our results

show that there are clear behavioral differences between individuals, but it is not conclusive if these behaviors vary over time. Moreover, in some species (e.g., caribou [*Rangifer tarandus*]), both consistent and flexible strategies can be present in a population depending on the sociospatial position of individuals (Bonar et al. 2020). The relative importance of different strategies can change within and among populations or seasons or with different levels of parasitic pressure (Spiegel et al. 2017). More fine-scaled individual studies or experiments are therefore required to explore the importance of consistent and flexible strategies.

The joint contributions of the environment and internal dynamics to predict spatial nest patterns in our system suggest synergism among multiple processes underlying spatial pattern formation. These mechanisms are often studied in isolation, as behavioral and landscape ecologists traditionally work on very different scales and units of research (Lima and Zollner 1996). These research fields have accordingly developed their specific analytical methods that can be regarded as separate approaches to explain spatial pattern formation of nests in a stepwise manner (Melles et al. 2009). Such combined approaches have been applied in insect (Polidori et al. 2008; Asís et al. 2014) and bird-oriented (Brown and Brown 2000; Perry and Andersen 2003; Melles et al. 2009) research, most often from a conservation perspective (Etterson 2003; Ward and Schlossberg 2004; Bayard and Elphick 2010; Swift et al. 2017). Spatial pattern analysis of point data from homogeneous landscapes allows inference of putative feedbacks that eventually lead to spatial self-organization (Rietkerk and van de Koppel 2008). The assumption of environmental homogeneity is not always valid. We likewise first decoupled environment from behavior by building the microhabitat model with INLA but integrated both types of mechanisms again in the IBM. IBMs are ideal for bridging and integrating these seemingly separate processes at different scales and enable quantifying their relative importance and synergism. This inverse approach has much to offer for understanding behavioral mechanisms underlying spatial organization, including identifying its own methodological limits. Spatial organization processes are inherently stochastic, and replications are hard to obtain as the strength or shape of processes are likely to change with space and time (Wagner and Fortin 2005). The general approach we illustrate here could thus be applicable in teasing apart coexisting, context-dependent processes, which are pervasive in ecological systems.

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Statement of Authorship

All three authors conceived the ideas and designed methodology. F.B. collected and analyzed the data, developed the model, and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data and Code Availability

Data have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.g79cnp5q8>), and code has been deposited in Zenodo (<https://doi.org/10.5281/zenodo.5212680>).

Literature Cited

- Araújo, M. S., D. I. Bolnick, and C. A. Layman. 2011. The ecological causes of individual specialisation. *Ecology Letters* 14:948–958.
- Asís, J. D., Y. Ballesteros, J. Tormos, L. Baños-Picón, and C. Polidori. 2014. Spatial nest-settlement decisions in digger wasps: conspecifics matter more than heterospecifics and previous experience. *Ethology* 120:340–353.
- Baddeley, A., E. Rubak, and R. Turner. 2015. Spatial point patterns: methodology and applications with R. Chapman & Hall/CRC, Boca Raton, FL.
- Banks, H. T., S. Hu, and W. C. Thompson. 2014. Modeling and inverse problems in the presence of uncertainty. Chapman & Hall/CRC, Boca Raton, FL.
- Barnard, C. J., and R. M. Sibly. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour* 29:543–550.
- Batsleer, F., D. Maes, and D. Bonte. 2021. Data from: Behavioral strategies and the spatial pattern formation of nesting. *American Naturalist*, Dryad Digital Repository, <https://doi.org/10.5061/dryad.g79cnp5q8>.
- Bayard, T. S., and C. S. Elphick. 2010. Using spatial point-pattern assessment to understand the social and environmental mechanisms that drive avian habitat selection. *Auk* 127:485–494.
- Beaumont, M. A. 2010. Approximate Bayesian computation in evolution and ecology. *Annual Review of Ecology, Evolution, and Systematics* 41:379–406.
- Blösch, M. 2000. Die Grabwespen Deutschlands—Tierw. Deutschl. 71. Goecke & Evers, Keltern.
- Bonar, M., K. P. Lewis, Q. M. R. Webber, M. Dobbin, M. P. Laforge, and E. Vander Wal. 2020. Geometry of the ideal free distribution: individual behavioural variation and annual reproductive success in aggregations of a social ungulate. *Ecology Letters* 23:1360–1369.
- Bonte, D. 2005. Anthropogenic induced changes in nesting densities of the dune-specialised digger wasp *Bembix rostrata* (Hymenoptera: Sphecidae). *European Journal of Entomology* 102:809–812.
- Bradbury, J. W., and S. L. Vehrencamp. 2014. Complexity and behavioural ecology. *Behavioral Ecology* 25:435–442.
- Broly, P., Q. Ectors, G. Decuyper, S. C. Nicolis, and J.-L. Deneubourg. 2016. Sensitivity of density-dependent threshold to species composition in arthropod aggregates. *Scientific Reports* 6:1–13.
- Brown, C. R., and M. B. Brown. 2000. Nest spacing in relation to settlement time in colonial cliff swallows. *Animal Behaviour* 59:47–55.
- Buxton, V. L., J. K. Enos, J. H. Sperry, and M. P. Ward. 2020. A review of conspecific attraction for habitat selection across taxa. *Ecology and Evolution* 10:12690–12699.
- Clark, W., and M. Mangel. 1986. The evolutionary advantages of group foraging. *Theoretical Population Biology* 30:45–75.
- Coolen, I., O. Dangles, and J. Casas. 2005. Social learning in non-colonial insects? *Current Biology* 15:1931–1935.
- Coolen, I., L. A. Giraldeau, and W. Vickery. 2007. Scrounging behavior regulates population dynamics. *Oikos* 116:533–539.
- Csardi, G., and T. Nepusz. 2006. The igraph software package for complex network research. *InterJournal, Complex Systems* 1695.
- Csilléry, K., M. G. B. Blum, O. E. Gaggiotti, and O. François. 2010. Approximate Bayesian computation (ABC) in practice. *Trends in Ecology and Evolution* 25:410–418.
- Csilléry, K., O. François, and M. G. B. Blum. 2012. abc: an R package for approximate Bayesian computation (ABC). *Methods in Ecology and Evolution* 3:475–479.
- Curtisdotter, A., H. T. Banks, J. E. Banks, M. Jonsson, T. Jonsson, A. N. Laubmeier, M. Traugott, et al. 2019. Ecosystem function in predator–prey food webs—confronting dynamic models with empirical data. *Journal of Animal Ecology* 88:196–210.
- Dall, S. R. X., L. A. Giraldeau, O. Olsson, J. M. McNamara, and D. W. Stephens. 2005. Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution* 20:187–193.
- Danchin, E., L. A. Giraldeau, T. J. Valone, and R. H. Wagner. 2004. Public information: from nosy neighbours to cultural evolution. *Science* 305:487–491.
- Eggeman, S. L., M. Hebblewhite, H. Bohm, J. Whittington, and E. H. Merrill. 2016. Behavioural flexibility in migratory behaviour in a long-lived large herbivore. *Journal of Animal Ecology* 85:785–797.
- ESRI (Environmental Systems Research Institute). 2011. ArcGIS desktop: release 10. ESRI, Redlands, CA.
- Etterson, M. A. 2003. Conspecific attraction in loggerhead shrikes: implications for habitat conservation and reintroduction. *Biological Conservation* 114:199–205.
- Evans, H. E., and K. M. O'Neill. 2007. The sand wasps: natural history and behavior. Harvard University Press, Cambridge, MA.

- Farine, D. R., and H. Whitehead. 2015. Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology* 84:1144–1163.
- Field, J. 2005. The evolution of progressive provisioning. *Behavioral Ecology* 16:770–778.
- Fortin, M. J., and M. R. T. Dale. 2005. *Spatial analysis: a guide for ecologists*. Cambridge University Press, Cambridge.
- Gelman, A., J. Hwang, and A. Vehtari. 2014. Understanding predictive information criteria for Bayesian models. *Statistics and Computing* 24:997–1016.
- Gilbert, C., S. Blanc, Y. Le Maho, and A. Ancel. 2008. Energy saving processes in huddling emperor penguins: from experiments to theory. *Journal of Experimental Biology* 211:1–8.
- Goossens, S., N. Wybouw, T. Van Leeuwen, and D. Bonte. 2020. The physiology of movement. *Movement Ecology* 8:5.
- Grimm, V., U. Berger, F. Bastiansen, S. Eliassen, V. Ginot, J. Giske, J. Goss-Custard, et al. 2006. A standard protocol for describing individual-based and agent-based models. *Ecological Modelling* 198:115–126.
- Grimm, V., U. Berger, D. L. DeAngelis, J. G. Polhill, J. Giske, and S. F. Railsback. 2010. The ODD protocol: a review and first update. *Ecological Modelling* 221:2760–2768.
- Grimm, V., E. Revilla, U. Berger, F. Jeltsch, W. M. Mooij, S. F. Railsback, H.-H. Thulke, et al. 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science* 310:987–991.
- Hamilton, W. D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31:295–311.
- Hoi, H., A. Kristin, F. Valera, and C. Hoi. 2012. Traditional versus non-traditional nest-site choice: alternative decision strategies for nest-site selection. *Oecologia* 169:117–124.
- Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences of the USA* 106:19659–19665.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724–732.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–427.
- Kacelnik, A., J. R. Krebs, and C. Bernstein. 1992. The ideal free distribution and predator-prey populations. *Trends in Ecology and Evolution* 7:50–55.
- Kass, R. E., and A. E. Raftery. 1995. Bayes factors. *Journal of the American Statistical Association* 90:773–795.
- Kassambara, A., and F. Mundt. 2020. factoextra: extract and visualize the results of multivariate data analyses. <https://cran.r-project.org/web/packages/factoextra/>.
- Koops, M. A., and M. V. Abrahams. 1998. Life history and the fitness consequences of imperfect information. *Evolutionary Ecology* 12:601–613.
- Krause, J., and G. D. Ruxton. 2002. *Living in groups*. Oxford University Press, Oxford.
- Kuhn, M. 2008. Building predictive models in R using the caret package. *Journal of Statistical Software* 28:1–26.
- Kun, Á., and I. Scheuring. 2006. The evolution of density-dependent dispersal in a noisy spatial population model. *Oikos* 115:308–320.
- Larsson, F. K. 1986. Increased nest density of the digger wasp *Bembix rostrata* as a response to parasites and predators. *Entomologia Generalis* 12:71–75.
- Larsson, F. K., and J. Tengö. 1989. It is not always good to be large; some female fitness components in a temperate digger wasp, *Bembix rostrata* (Hymenoptera: Sphecidae). *Journal of the Kansas Entomological Society* 62:490–495.
- Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* 11:131–135.
- Lindgren, F., and H. Rue. 2011. An explicit link between Gaussian fields and Gaussian Markov random fields: the stochastic partial differential equation approach. *Journal of the Royal Statistical Society B* 73:423–498.
- Liu, C., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28:385–393.
- Manel, S., H. C. Williams, and S. J. Ormerod. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* 38:921–931.
- Martins, T. G., D. Simpson, F. Lindgren, and H. Rue. 2013. Bayesian computing with INLA: new features. *Computational Statistics and Data Analysis* 67:68–83.
- Melles, S. J., D. Badzinski, M. J. Fortin, F. Csillag, and K. Lindsay. 2009. Disentangling habitat and social drivers of nesting patterns in songbirds. *Landscape Ecology* 24:519–531.
- Mooring, M. S., and B. L. Hart. 1992. Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. *Behaviour* 123:173–193.
- Morales, J. M., and S. P. Ellner. 2002. Scaling up animal movements in heterogeneous landscapes: the importance of behavior. *Ecology* 83:2240–2247.
- Newlands, N. K., M. E. Lutcavage, and T. J. Pitcher. 2004. Analysis of foraging movements of Atlantic bluefin tuna (*Thunnus thynnus*): individuals switch between two modes of search behaviour. *Population Ecology* 46:39–53.
- Nielsen, E. T. 1945. *Moeurs des Bembex*. 7th ed. Spoolia Zool Mus Haun, København.
- Perrill, S. A., H. C. Gerhardt, and R. E. Daniel. 1982. Mating strategy shifts in male green treefrogs (*Hyla cinerea*): an experimental study. *Animal Behaviour* 30:43–48.
- Perry, E. F., and D. E. Andersen. 2003. Advantages of clustered nesting for least flycatchers in north-central Minnesota. *Condor* 105:756–770.
- Pettorelli, N. 2013. *The normalized difference vegetation index*. Oxford University Press, Oxford.
- Philippi, T., and J. Seger. 1989. Hedging one's evolutionary bets, revisited. *Trends in Ecology and Evolution* 4:41–44.
- Piwczyński, M., T. Pape, E. Deja-Sikora, M. Sikora, K. Akbarzadeh, and K. Szpila. 2017. Molecular phylogeny of Miltogramminae (Diptera: Sarcophagidae): implications for classification, systematics and evolution of larval feeding strategies. *Molecular Phylogenetics and Evolution* 116:49–60.
- Polidori, C., P. Mendiola, J. D. Asis, J. Tormos, J. Selfa, and F. Andrietti. 2008. Female–female attraction influences nest establishment in the digger wasp *Stizus continuus* (Hymenoptera: Crabronidae). *Animal Behaviour* 75:1651–1661.
- QGIS Development Team. 2020. QGIS geographic information system. Open Source Geospatial Foundation. <http://qgis.osgeo.org>.
- Rietkerk, M., and J. van de Koppel. 2008. Regular pattern formation in real ecosystems. *Trends in Ecology and Evolution* 23:169–175.
- Roelofs, R., S. Fridovich-Keil, J. Miller, V. Shankar, M. Hardt, B. Recht, and L. Schmidt. 2019. A meta-analysis of overfitting in machine learning. *Advances in Neural Information Processing Systems* 32:9179–9189.

- Rue, H., and L. Held. 2005. Gaussian Markov random fields: theory and applications. Chapman & Hall/CRC, Boca Raton, FL.
- Rue, H., S. Martino, and N. Chopin. 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society B* 71:319–392.
- Schöne, H., and J. Tengö. 1991. Homing in the digger wasp *Bembix rostrata* - release direction and weather conditions. *Ethology* 87:160–164.
- Sing, T., O. Sander, N. Beerenwinkel, and T. Lengnauer. 2005. ROCr: visualizing classifier performance in R. *Bioinformatics* 21:3940–3941.
- Spiegel, O., S. T. Leu, C. M. Bull, and A. Sih. 2017. What's your move? movement as a link between personality and spatial dynamics in animal populations. *Ecology Letters* 20:3–18.
- Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. *American Naturalist* 131:329–347.
- Stouffer, D. B. 2019. All ecological models are wrong, but some are useful. *Journal of Animal Ecology* 88:192–195.
- Swift, R. J., A. D. Rodewald, and N. R. Senner. 2017. Environmental heterogeneity and biotic interactions as potential drivers of spatial patterning of shorebird nests. *Landscape Ecology* 32:1689–1703.
- Tarof, S. A., and L. M. Ratcliffe. 2004. Habitat characteristics and nest predation do not explain clustered breeding in least flycatchers (*Empidonax minimus*). *Auk* 121:877–893.
- van der Vaart, E., M. A. Beaumont, A. S. A. Johnston, and R. M. Sibly. 2015. Calibration and evaluation of individual-based models using approximate Bayesian computation. *Ecological Modelling* 312:182–190.
- van der Vaart, E., A. S. A. Johnston, and R. M. Sibly. 2016. Predicting how many animals will be where: how to build, calibrate and evaluate individual-based models. *Ecological Modelling* 326:113–123.
- Wagner, H. H., and M. J. Fortin. 2005. Spatial analysis of landscapes: concepts and statistics. *Ecology* 86:1975–1987.
- Ward, M. P., and S. Schlossberg. 2004. Conspecific attraction and the conservation of territorial songbirds. *Conservation Biology* 18:519–525.
- Watanabe, S. 2010. Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *Journal of Machine Learning Research* 11:3571–3594.
- Wcislo, W. T. 1984. Gregarious nesting of a digger wasp as a “selfish herd” response to a parasitic fly (Hymenoptera: Sphecidae; Diptera: Sacrophagidae). *Behavioral Ecology and Sociobiology* 15:157–160.
- Webber, Q., M. Laforge, M. Bonar, A. Robitaille, C. Hart, S. Zabihi-Seissan, and E. Vander Wal. 2020. The ecology of individual differences empirically applied to space-use and movement tactics. *American Naturalist* 196 E1–E15.
- Zuur, A., E. N. Ieno, and A. A. Saveliev. 2017. Beginner's guide to spatial, temporal and spatial-temporal ecological data analysis with R-INLA. Volume 1: using GLM and GLMM. Highland Statistics, Newburgh.

References Cited Only in the Online Enhancements

- Asís, J. D., J. Tormos, and S. F. Gayubo. 2004. Nesting behaviour and provisioning in *Bembix merceti* and *Bembix zonata* (Hymenoptera: Crabronidae). *Journal of Natural History* 38:1799–1809.
- Python Software Foundation. 2001. Python language reference, version 3.4. <http://www.python.org>.

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Bembix rostrata resting at the closed entrance of a nest. Photo by Femke Batsleer.