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20 **Abstract**

21 The need to understand the impacts of land management for conservation, agriculture and
22 disease prevention are driving demand for new predictive ecology approaches that can reliably
23 forecast future changes in population size. Currently, although the link between habitat
24 composition and animal population dynamics is undisputed, its function hasn't been quantified in
25 a way that enables accurate prediction of population change in nature. Here, using 12 house
26 sparrow colonies as proof-of-concept, we apply recent theoretical advances to predict population
27 growth or decline from detailed data on habitat composition and habitat selection. We show, for
28 the first time, that statistical population models using derived covariates constructed from
29 parametric descriptions of habitat composition and habitat selection can explain an impressive
30 92% of observed population variation. More importantly, they provide excellent predictive
31 power under cross-validation, anticipating 81% of variability in population change. These
32 models may be embedded in readily available Generalised Linear Modelling frameworks,
33 allowing their rapid application to field systems. Furthermore, we use optimisation on our
34 sample of sparrow colonies to demonstrate how such models, linking populations to their
35 habitats, permit the design of practical and environmentally sound habitat manipulations for
36 managing populations.

37

38 **Keywords:** habitat engineering, habitat selection, habitats-to-populations (HTP), house sparrow
39 (*Passer domesticus*), population declines, population modelling

40

41

42

43 **Introduction**

44 Accelerating environmental change is driving widespread demand for predictive ecology
45 approaches that are able to make reliable forecasts about our impacts on biological populations
46 (Evans et al. 2011, Mouquet et al. 2015, Dietze et al. 2018). Currently, ecology is particularly
47 successful at explaining the population impacts of measured environmental variables (Mouquet
48 et al. 2015). However, much more needs to be achieved if we are to produce accurate forecasts of
49 how ecological systems will respond to future change (Evans et al 2011, Dietze et al. 2018). The
50 ability to make reliable anticipatory predictions will have widespread applications in species and
51 land management, whether for conservation, environmentally sustainable agriculture, the
52 management of wildlife for food stocks or defence against disease vectors and alien species.

53 A priority focus in such new predictive ecology approaches is the crucial relationship between
54 habitat quality and population growth, a link whose existence is undisputed but whose form and
55 strength are harder to quantify (Morales et al. 2010, Matthiopoulos et al. 2011, Matthiopoulos et
56 al. 2015). The proliferation of spatial modelling in ecology in recent decades is beginning to see
57 data on the spatial distribution of populations being connected to individual aspects of population
58 demography (Johnson et al. 2004, McLoughlin et al. 2006, 2007, Aldridge & Boyce 2007, 2008,
59 Blouin-Demers & Weatherhead 2008, Erickson et al. 2014). By harnessing the predictive power
60 of the link between habitats and populations, such efforts can help build the sort of anticipatory
61 ecological science we urgently need.

62 The growth rate of a population is ultimately driven by a mosaic of spatially heterogeneous
63 habitat covariates representing conditions, resources and risks (Guisan & Zimmermann 2000,
64 Matthiopoulos et al. 2015). To understand and manage population change via habitat
65 composition, we need to identify which habitat variables are likely to be influential. This requires

66 two types of methods, used in tandem. First, transferrable models of habitat selection (Yates et
67 al. 2018) that can successfully capture a species' distribution at both fine and coarse scales and,
68 second, frameworks for connecting habitat use to concurrent population change data. In this
69 paper, we exploit recent developments in both of these directions integrated in a statistical
70 approach recently developed by Matthiopoulos et al. (2015). This framework, henceforth called
71 Habitats-To-Populations (HTP), was derived from first principles, and is thus well supported
72 theoretically, but its utility and power have yet to be tested in a real system. Here, we make the
73 first test in nature of the ability of the HTP framework to predict population change from habitat
74 composition. We do so using a set of house sparrow (*Passer domesticus*) colonies, a species that
75 has experienced rapid, but poorly understood, population declines in parts of its global range,
76 while becoming a highly invasive species elsewhere (Hole et al 2002). Further, we use this
77 quantitative link between habitat composition and change in population size to examine how
78 nascent habitat engineering approaches could be developed to achieve – often elusive –
79 ecological objectives of conservation or pest management.

80 **Materials and Methods**

81 Population change was monitored over a two-year period in a total of 12 sparrow colonies where
82 the colony's nesting area had been identified at the start of monitoring. In these, and a further 20
83 colonies, added to provide a broader representation of habitat scenarios, the composition of all
84 the gardens within each colony's spatial range was documented and observations of habitat use
85 by sparrows were made. Following the paradigm illustrated in Fig. 1 (adapted from
86 Matthiopoulos et al. 2015), our analysis approaches the combined data on habitat use and
87 population change by linking a flexible modelling framework of habitat preferences with a

88 habitat-sensitive model of population growth. In order to test the performance and utility of the
89 HTP theoretical framework for achieving the goals of predictive ecology, we investigated the
90 model's explanatory power, its predictive power under cross-validation and its ability to generate
91 specific, testable recommendations regarding habitat improvements.

92

93 *Study species*

94 Although increasingly considered as an invasive species in many parts of the world, the house
95 sparrow has been suffering heavy declines in much of its native range in the last decades.
96 Declines have been particularly severe in North-Western Europe and in the UK, where the
97 breeding population has dropped by 71% since the 1970s to 5.1 million today, placing the
98 species on the UK conservation red-list (Robinson et al. 2016). The causes of sparrow declines
99 in urban/suburban environments, where the majority of the population are found, remain
100 uncertain but are probably connected to changing habitat composition of gardens brought on by
101 changes in socioeconomic status and home-improvement trends (Shaw, Chamberlain & Evans
102 2008). It has been suggested that garden paving reduces suitable foraging area, that the use of
103 introduced plants reduces native vegetation and leads to a reduction in invertebrate prey (Chace
104 & Walsh 2004, Shaw et al. 2008, Seress et al 2012), while tidier gardens and modern roofing
105 techniques reduce the availability of cover from predation and the number of nesting sites
106 (Daniels & Kirkpatrick 2006). However, none of these variables have been definitively linked to
107 population change at a landscape scale using population replicates. This requirement, as well as
108 the ease with which sparrows can be observed and their urban and suburban environment can be
109 manipulated, make the species particularly suitable as a test-bed for new modelling ideas and
110 subsequent validation experiments.

111 *Data collection*

112 The set of 32 colonies for our study lay within an area of 200km² in and around the city of
113 Glasgow in Scotland and were chosen to maximise the diversity of structural habitat
114 characteristics and observed colony size.

115 To achieve the fine spatial scales needed for modelling habitat selection, the habitat usage and
116 availability study was carried out by surveying all the individual gardens (150 in total) within the
117 range of each sparrow colony. High-resolution (2x2m grid square size) habitat and space use
118 survey data were collected covering the gardens in each colony. During the habitat usage survey,
119 all the cells in each colony were continually observed until a total of 20 separate sparrow visits to
120 grid cell locations were recorded. We aimed to distribute our observation equally for each unit of
121 area within the complex of gardens belonging to each colony's domain. An additional 20
122 locations were then randomly selected from all the grid squares within the colony. This provided
123 us with a use-availability data set comprising an equal number of ones and zeroes. For our 32
124 colonies, this led to 1280 distinct spatial cell observations of habitat usage. Using Google Earth
125 imagery (GOOGLE EARTH, 2016), for each of the 1280 cells we estimated the percentage
126 covered by hedge, grass, bush, roof, artificial surfaces and trees to the nearest 10%. We also
127 calculated the distance of each cell from the nearest hedge and roof. For 12 focal sparrow
128 colonies, baseline population surveys were available from a citizen science programme, the
129 Glasgow House Sparrow Project, part of a partnership between the Royal Society for the
130 Protection of Birds (RSPB) and the University of Glasgow. This provided data on house sparrow
131 colony size as measured by counting all males present in each colony during the main part of the
132 breeding season (April to July) in 2014. The population surveys were undertaken by trained
133 sparrow surveyors who repeatedly walked every street and back lane in their survey area and

134 counted the total number of adult sparrows in each colony. House sparrows are confident around
135 humans, very vocal and easily identifiable, making exact determination of colony population size
136 in the breeding season straightforward in urban areas. During the breeding season, house
137 sparrows are extremely site faithful to their nest area, with radio tracking showing maximum
138 travel distances of <100m (Shaw 2009). However, even this distance is rare given that 95% of
139 the foraging locations during breeding occur in an area that can be represented by a 16m radius
140 circle (calculated from data in Shaw 2009), allowing precise population counts for each survey
141 area. House sparrows breed in pairs and males are particularly easy to detect and count because
142 they sing for long periods from highly visible song posts next to their nests. We therefore used
143 the maximum number of males recorded in each colony as the measure of colony size.

144 Population growth rates were established as the difference in colony sizes recorded between the
145 years 2014 and 2016 using follow-up colony surveys in the 2016 breeding season based on the
146 same methodology as the first citizen science surveys. The increased sample size (N=32) for the
147 habitat usage survey part of the modelling was chosen to help ensure that the habitat model was
148 provided with adequate data (our habitat use model was particularly data hungry because of the
149 multiple pairwise interactions it contained - see next sub-section).

150

151 *Statistical analysis of habitat use*

152 Within the broad field of Habitat Selection Functions (HSFs, a term that we use here to describe
153 closely related approaches such as Resource Selection Functions – Manly et al. 2004 – and
154 Maximum Entropy models – Philips, Anderson & Schapire 2006), it is widely recognised that
155 animals respond not merely to the habitat characteristics of their immediate location but also to
156 the overall habitat composition of their surrounding area (e.g., the availability of all habitats

157 within their entire home range). Matthiopoulos et al. (2011) proposed the framework of
 158 Generalised Functional Responses (GFR), which capture nonlinearities in the habitat preferences
 159 of animals by modelling the regression coefficients of an HSF as functions of local habitat
 160 availability. By using data from multiple scenarios of availability (e.g., the different sparrow
 161 colonies in our study) a GFR can interpolate (in environmental space) the response of the species
 162 under as-yet unobserved scenarios of habitat availability. For n explanatory variables
 163 $\mathbf{X} = (X_1, \dots, X_n)$ with $n + 1$ regression coefficients $\beta = (\beta_0, \dots, \beta_n)$, the general HSF takes the
 164 form. h

$$165 \quad h(\mathbf{X}) = \exp(\beta_0 + \sum_{i=1}^n \beta_i X_i) \quad (1)$$

166 These functions can be obtained from statistical models that are fitted equivalently to count, use-
 167 availability or point-process data (Aarts et al. 2012), either via likelihood or maximum entropy
 168 criteria. To extend the HSF framework to account for the regional availability of all habitats
 169 influencing local usage, the Generalised Functional Response writes each beta coefficient as a
 170 function of habitat availability

$$171 \quad \beta_i = \sum_{j=1}^n \sum_{l=1}^k b_{ij} E(X_i^j) \quad (2)$$

172 Where $E(X_i^j)$ is the j^{th} order expectation of the i^{th} covariate. These expectation terms provide
 173 statistical summaries for the distribution of explanatory variables in the neighbourhood of each
 174 spatial point of interest. Their inclusion allows the model to quantify the environmental context
 175 within which utilisation decisions are made by animals (Paton & Matthiopoulos 2016). Including
 176 expectations up to the maximum k^{th} order allows the GFR to account for the average, variance,
 177 skewness, kurtosis etc. of the distribution of variables in surrounding space. However, in the
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178 simplest case (requiring the least amount of usage data to be estimated), only the averages (i.e.
179 1st order expectations) are used. When the coefficients in eq. (2) are placed into the model of eq.
180 (1), they result in interaction terms between local covariate values and their regional
181 expectations.

182 Eq. (2) implies that each sampling scenario (in our study, data within the home range of each
183 sparrow colony) is characterised by a unique response (i.e. a unique regression slope) to each of
184 the covariates, based on characteristics of regional habitat availability. It is, however possible to
185 calculate this unique numerical value of each coefficient for each sampling scenario and to
186 compare the response of animals to covariates between different sampling scenarios. In practice,
187 the GFR takes the form of a generalised linear (or additive) model that comprises all the pairwise
188 interactions between the values of environmental variables at any one sampled location and their
189 (1st, 2nd, etc.) expectations in the vicinity of a location across the sampling scenario
190 (Matthiopoulos et al. 2011, 2015, Aarts et al. 2013, Paton & Matthiopoulos 2016). The specific
191 form of the GLM depends on the data to be analysed (Aarts et al. 2008, Aarts et al. 2012). In our
192 case, the value of use or availability (1 or 0) was used as the response variable in a logit GLM
193 with binomial likelihood, modelling the probability that a cell with particular habitat
194 characteristics contained one of our sparrow detections. To create the GFR, we distinguished
195 between spatially referenced variables (i.e. the characteristics of each 2x2m cell in a garden) and
196 colony/survey-specific variables (e.g. the known size of a colony, or prevailing weather
197 information). Colony size was used as a colony-specific covariate in the habitat model to account
198 for the effect of crowding on apparent habitat suitability (i.e. the possibility that suboptimal
199 habitats are used by birds when they are displaced from optimal habitats by conspecifics).

200 Analysis was performed using R v3.3.0 (R Core Team 2016) with the aid of the R library
201 HaToPo (HABitats-TO-POPulations, available from <https://github.com/JasonMat/HATOPO.git>).

202 *Linking habitat to population growth*

203 The second stage of the HTP analysis links population change data to habitat composition and
204 was recently derived by Matthiopoulos et al. (2015). Here, and in Fig. 1, we briefly outline the
205 components of HTP, but the mathematical details can be found in that earlier paper. HTP utilises
206 estimated parameters, generated by two distinct statistical models, namely, a detailed
207 approximation of habitat availability and a species-habitat association model (the HSF/GFR, see
208 previous subsection). Both of these constituent models need to be fitted to multiple *sampling*
209 *scenarios*, to give them the opportunity to learn how the same organisms respond to a diversity
210 of habitat compositions. A sampling scenario corresponds to a definable population or sub-
211 population and its spatial range during a short time window. In this study, it refers to individual
212 house-sparrow colonies. The parameter estimates from these two models are then used in pre-
213 derived mathematical formulae (Matthiopoulos et al. 2015) to construct candidate covariates to
214 be regressed against observations of population change. These new, constructed covariates,
215 although not explicitly spatial, nevertheless contain information about the combinations of
216 habitats experienced by the individuals living in different sampling scenarios. The theoretical
217 motivation behind these new covariates (and consequently, the hypothesis put to the test in the
218 present paper, using real data) is that, by more precisely encompassing the portfolio of habitats
219 exploited by the study individuals, a population model will be better able to retrieve predictive
220 signal from data of population change. This theoretical approach currently entails a set of
221 simplifying assumptions (see also Matthiopoulos et al. 2015), whose relevance to the sparrow
222 system we examine below:

223 1) Accessibility: The entire home range of each colony is assumed equally accessible to each
224 sparrow, such that points are not likely to receive differing degrees of usage due to their distance
225 from the nest. Given the very strong site fidelity of sparrows (see earlier discussion) and
226 resulting short range of movements, this assumption is likely to hold.

227 2) Spatial-pseudoequilibrium: We assume (in a way similar to most habitat analyses - Guisan and
228 Thuiller 2005) that our space-use data come from a population whose distribution is not currently
229 undergoing radical adjustments.

230 3) Negligible individual variation: We assume that habitat use by any one individual is
231 representative of the use of space by the entire colony and that individuals are similar to each
232 other in their behaviour and reproductive potential.

233 4) Non-depletable covariates: Although the approach does take into account secondary effects in
234 distribution and colony growth resulting from crowding and density dependence, we are not
235 explicitly modelling resource depletion. Consequently, our sparrow case study has used habitat
236 characteristics, rather than measurements of prey abundance, as the candidate covariates.

237 5) Exclusion of more sophisticated features: Finally, the model does not currently examine
238 genetic change during the window of observations, formulations with non-additive habitat effects
239 on population fitness, Allee effects in population growth, or saturating responses to
240 superabundant resources.

241 The constructed covariates are employed in a generalised linear model of population change
242 to investigate their impact on population change data in a set of sampling scenarios. This stage of
243 the analysis (corresponding to boxes 3-6 in Fig. 1) relates population growth rates to habitat
244 composition. The deterministic population model used as a platform by Matthiopoulos et al.

245 (2015) has extensive roots in ecology and was most recently proposed by Turchin (2003) as a
 246 convenient starting point for population inference

$$247 \quad \frac{N_{t+1}}{N_t} = \exp(F(\mathbf{f}, \mathbf{N})) \quad (3)$$

248 where F is some function of habitat composition \mathbf{f} and past population densities

249 $\mathbf{N} = \{N_t, N_{t-1}, \dots\}$. The stochastic version of this model takes the form

$$250 \quad \begin{aligned} N_{t+1} &\sim \text{Poisson}(\lambda_t) \\ \lambda_t &= N_t \exp(F(\mathbf{f}, \mathbf{N})) \end{aligned} \quad (4)$$

251 The Poisson distribution is used here purely for illustrative purposes. Alternative distributions
 252 such as the negative binomial may be used to capture over-dispersion in population count data.
 253 Eqs (4) can be conveniently fitted to population count data as a generalised linear model (GLM)
 254 with linear predictor given by

$$255 \quad \ell_t = F(\mathbf{f}, \mathbf{N}) + \ln(N_t) \quad (5)$$

256 In regression terminology, $\ln(N_t)$ is the GLM's offset. Two types of statistical population
 257 models were fitted to the colony growth data. The first, used here as a baseline, we call the
 258 "mean-field" model. It relates population growth to the average values of the habitat variables
 259 across the range of each colony (based on samples from gardens around the nesting colony). This
 260 model ignores the nuances of habitat availability and habitat usage. The second, called here the
 261 "spatial" model was based on the HTP approach and relates population change to the detailed
 262 profile of habitat composition in the domain of each colony. As an example of implementation of
 263 eq. (5) for the two cases, our selected mean-field model in the sparrow analysis (see results
 264 below) was a GLM with linear predictor

$$\ell_t = \alpha_0 + \alpha_1 \langle Bush \rangle + \alpha_2 N_t + \ln(N_t) \quad (6)$$

266 Here, log-linear population growth is predicted by the average availability of bushes across the
 267 domain of each colony, with the added effect of the colony's size (representing density
 268 dependence). Such a model, employing average conditions across the domain of a colony, may
 269 be able to capture coarser aspects of habitat dependence but it ignores the fact that members of
 270 the population are exposed to combinations of covariates spatially, and they can modulate that
 271 exposure (whether beneficial or otherwise) by differentiating their use of different habitat types
 272 within their range. This is where information from the habitat model can extend the predictive
 273 reach of mean-field models such as eq. (6). The effect of habitat availability and habitat use on
 274 population growth was estimated via the HTP model, implemented in the HaToPo library for R
 275 (R-Core 2016). HaToPo yields a set of constructed candidate covariates of population change,
 276 each of which is a function of previously estimated parameters from the models of habitat
 277 availability and habitat use. Furthermore, it captures the spatial features of conspecific
 278 interference to create a constructed covariate for density dependence. Our final spatial model
 279 was, once again, a GLM of the form of eq. (5) but this time, the linear predictor comprised
 280 constructed covariates in bush, grass, roof and density dependence (see results, below).

$$\ell_t = \alpha_0 + \alpha_1 Bush + \alpha_2 Grass + \alpha_3 Roof + \alpha_4 f(N_t) + \ln(N_t) \quad (7)$$

282 *Model fitting and selection*

283 It was possible to subject our habitat model (the GFR) to autonomous selection via the Akaike
 284 Information Criterion (AIC – e.g. Burnham and Anderson, 2002). This would lead to the most
 285 parsimonious model of habitat preference and use. However, we found that this approach led to
 286 habitat models that were over-parameterised for the later purposes of population prediction. Thus

287 far, this is a unique problem in the literature, because previous studies on habitat preferences did
288 not historically need to consider predictions of population growth. We decided to perform a
289 search for parsimonious habitat models evaluating each candidate GFR on the basis of how well
290 it ultimately enabled the population model to predict population change. This was done by means
291 of leave-one-out cross-validation on our 12 colonies for which population change data were
292 available.

293 Our model fitting and model selection protocol was as follows (the full R-code is provided in
294 the Appendix, subdivided in sections): We first specified a candidate model (Section 2 of R-
295 code) and fitted it to the aggregate space-use data from all 32 colonies (Section 3 of R-code). The
296 `gfr()` function in the `HaToPo` library automatically extends the dataframe to include habitat
297 availability expectations and specifies the necessary interaction terms for the fully expanded
298 GFR model formula. Using the functions `favail()` and `ga.gfr()` in the `HaToPo` library, we obtained
299 two objects containing 1) parametric approximations of habitat availability for each colony and
300 2) the colony-specific habitat selection coefficients. These two objects were then passed to the
301 `pop.covariates()` function in `HaToPo` (Section 5 in R-code) which constructed a set of candidate
302 covariates for population growth. Population growth was regressed against these constructed
303 covariates (Section 5 in R-code). Since we only had population data for 12 colonies, we
304 subjected this population GLM to model selection by AIC. The ability of the combined habitat
305 (HSF/GFR) and population (HTP) model to explain population data was evaluated by the
306 percentage deviance explained in the final population model. The ability of the combined models
307 to predict new data was evaluated by the Sum of Squared Residuals (SSR) under leave-one-out
308 cross validation applied to the entire modelling workflow (Section 6 in R-code). We selected the

309 combined habitat and population model based on predictive ability (all the habitat models
310 examined are listed at the final section of the R-code).

311 *Optimising population growth via habitat manipulation*

312 The resulting fully fitted spatial population model (in eq. (7)) connects habitat composition to
313 population growth. To evaluate how responsive the species might be to conservation actions
314 through changes in gardening practices, we carried out the following optimisation protocol
315 (Section 8 in R-code). We perturbed the non-structural aspects of different garden cells in our
316 data set (i.e. the percentages of grass, tree, hedge and bush), until we obtained the maximum
317 improvement in predicted growth rates in all 12 of our colonies. However, we constrained our
318 optimisation so that we only accepted proposed landscaping improvements if the confidence
319 intervals associated with the predicted growth rates did not also include a wide range of possible
320 deteriorations (specifically, no proposed improvement was accepted if its lower confidence
321 interval was less than 70% of the previously accepted mean improvement). There is considerable
322 precedent in the reserve design literature for such constrained optimisation that incorporates
323 objective functions constructed from combinations of point and interval model estimates
324 (Moilanen & Wintle 2006). As part of our optimisation, we sought to understand 1) whether all
325 colonies could benefit from such manipulations, 2) how much improvement we might expect and
326 3) how drastic a manipulation would be required to generate these improvements.

327 *Results*

328 *Habitat usage*

329 Following model selection, the preferred model of habitat use contained three main effects
330 (percentage of grass, bush and roof in each cell) and 16 other terms representing average habitat

331 values across the colony and interactions between the model's main terms and colony-specific
332 averages. The combination of main effects and interactions in the GFR allows the construction of
333 colony-specific coefficients of habitat selection arising from the response of the animals to the
334 particular habitat configuration in the vicinity of each colony, a phenomenon, known in the
335 literature as a functional response in habitat selection (Arthur et al. 1996, Mysterud & Ims 1998,
336 Mauritzen et al. 2003, Matthiopoulos et al. 2011, Aarts et al 2013). We examined the histograms
337 and pairwise correlations between different habitat-selection coefficients, estimated for different
338 colonies (Fig. 2). Looking at the single-coefficient histograms (on the diagonal of Fig. 2) we see
339 that sparrows predominantly avoid areas with grass (histogram centred at negative values in Fig.
340 2aa) and prefer areas with bush cover (histogram centred at positive values in Fig. 2bb). The
341 histogram of coefficients for roof (Fig. 2cc) does not present a predominantly positive or
342 negative bias, indicating that in different colonies (depending on habitat composition) sparrows
343 may use roofs more, or less than expected by chance. However, the variable has been retained by
344 model selection because it lends the habitat model explanatory power. The off-diagonal plots in
345 Fig. 2 also provide evidence of strong pairwise correlation between modelled responses to all
346 three environmental variables. The specific coefficient values estimated are determined by the
347 existence of trade-offs and synergies between coefficients for different variables. Trade-offs
348 (negative correlations) would indicate that these covariates are substitutable. Synergies, shown
349 by a positive relationship between coefficients, indicate that the associated covariates operate in
350 a complementary way, increasing each-other's apparent preference.

351 The habitat usage model explained a modest percentage (33%) of the null deviance,
352 suggesting either an inherently high noise-to-signal ratio in habitat use by sparrows (e.g.
353 individual variation), or that not all relevant features (e.g. direct measures on availability of food)

354 were included in the analysis. The parameters of the GFR model were next embedded in the HTP
355 approach (see next section), to represent the expected frequency of interactions between
356 sparrows and different features of their environment.

357 *Linking habitat to population growth*

358 The 12 focal house sparrow colonies at which we measured population growth varied in size
359 from 2 to 24 pairs, with a mean colony size in the 2014 breeding season of 6.5 ± 1.7 pairs
360 increasing to a mean colony size of 8.2 ± 1.7 pairs in the breeding season of 2016.

361 Cross-validation served as the ultimate arbiter for the best spatial and mean-field models (Table
362 S1). Despite using such a numerically greedy approach to model selection, computational
363 requirements were very low (in the order of seconds) because HTP is based on pre-derived
364 mathematical expressions (Matthiopoulos et al. 2015) and generalised linear models. Both the
365 mean-field and spatial models found relationships between population change and their
366 respective bush covariates, as well as evidence for density dependence. The spatial model
367 additionally found links with grass and roof. The best-performing spatial model explained 92%
368 of the deviance in the observed population growth rates ($r^2 = 0.9$ - Fig. 3a) and was able to
369 retain high performance under prediction, where it achieved an r^2 of 0.81 (Fig. 3b). The spatial
370 model (Table S1) was characterised by a large, positive intercept, expressing a tendency for
371 population growth, which was moderated strongly by too much exposure to grass and roof
372 structures, but also (to a lesser extent) exposure to bushes. This was somewhat unexpected since
373 the habitat model indicated an overall preference for bushes. The mean-field model explained a
374 comparatively lower but still respectable percentage of deviance (72% with $r^2 = 0.68$ - Fig. 3c)
375 but suffered a greater drop when tested for predictive ability under cross-validation ($r^2 = 0.5$ -

376 Fig. 3d). The mean-field model was also poorer at detecting factors linked to population growth
377 with the overall availability of bushes and density dependence the only main explanatory
378 variables identified as important.

379 Therefore, the HTP approach was able to extract considerably more explanatory and
380 predictive power by looking at the exact composition of habitats and whether they were over- or
381 under-used by sparrows, rather than the average of single environmental variables on which most
382 existing modelling approaches would be based. We also observed a difference in specificity
383 between mean-field and spatial models. In particular, whereas several of the mean-field
384 candidate models had similar cross-validation scores to the best model of that category, the
385 spatial model category comprised highly variable cross-validation scores (therefore, it strongly
386 differentiated between the high-performance model selected, and several others that were similar
387 in structure but poorer in performance than the mean-field equivalents).

388 *Optimising population growth via habitat manipulation*

389 Our optimisation exercise aimed at using the HTP approach to predict how colony growth rates
390 might be increased by judiciously manipulating habitat composition. We arrived at
391 recommendations for improving growth for 10 out of 12 colonies (Fig. 4). Our results suggested
392 that six out of seven colonies with currently zero or negative growth rates could be pushed to
393 positive growth. Notably, the recommended changes (increases or decreases in any one type of
394 habitat) were not proportional across colonies, underlining the point that joint availability of all
395 habitats is important for determining habitat use and population impacts. For the specific set of
396 colonies we focused on, a reduction in the amount of grass was the most frequently
397 recommended habitat manipulation (suggested as a way to increase population growth rate in 11
398 out of the 12 colonies, colonies in Fig. 4). The other habitat manipulations were more colony-

399 specific but involved offsetting the reduction in grass with recommended increases to the various
400 habitat variables that represent potential cover from predators (bushes, hedges or trees depending
401 on the specific colony). All these increases were achievable with low potential for unpleasant
402 surprises (i.e. the confidence intervals shown as rhombuses in the proposed growth rates of Fig. 4
403 did not encompass the possibility of population declines).

404 **Discussion**

405 Here, we have exploited new theoretical developments in statistical ecology to demonstrate, for
406 the first time, that predictive modelling of population growth in nature is possible based on
407 habitat composition. Further, we have demonstrated an early example of an optimisation process
408 for habitat composition that shows how a predictive ecology modelling approach can be used to
409 derive tailored land management recommendations that could be used to promote, or control
410 population growth for conservation, sustainable agriculture, wildlife stock management and
411 defence against disease vectors.

412 In our study species, habitat selection was noisy. Our habitat model was able to account for
413 only 33% of the variability in the space use data. Its modest explanatory power could be because
414 important covariates of usage were absent. Examples might include the actual (Barnard 1980,
415 Gotmark & Post 1996), or perceived (Brown & Kotler 2004, Zanette et al. 2011) risk of
416 predation. Alternatively, sparrow behaviour in response to habitat could be genuinely very noisy
417 due to unmodelled individual variation or due to the time of year at which habitat usage was
418 being measured (the survey was carried out during a period when resources are less constrained
419 than they would be in winter (MacLeod et al. 2006)). Despite this, inclusion of habitat use and
420 availability into our statistical model of colony growth rates pushed explanatory power from

421 72% to 92% (compare Figs. 3c and 3a) with even greater gains (50% to 81%) in predictive
422 power (compare Figs 3d with 3c). To our knowledge this is the first modelling approach to
423 successfully predict the majority of population growth variation across replicate populations
424 based on habitat composition and usage.

425 It should be noted that this is a proof-of-concept study on a relatively small sample of 12
426 populations, and the above metrics of predictive performance are based on the same cross-
427 validation procedure used to carry out model selection. More work will be needed to examine if
428 the high percentages of predictive power can be sustained for other species and out-of-data
429 predictions for larger samples of independent populations. It is nevertheless possible to evaluate
430 our results based on a comparison between the spatial and mean-field approaches. Our
431 constructed covariates, based on habitat availability and expected use, had much greater
432 predictive power than the average availability of habitat variables. The conclusion therefore is
433 that, even if the animals' usage of the different components of their habitat has elements of
434 randomness (as the noisy GFR seems to suggest), the signal of habitat composition may remain
435 strong within population growth data.

436 The HTP framework in its current form is particularly suited to the life history of house
437 sparrows. However, future research could be directed to make the HTP approach applicable to
438 populations with variable accessibility constraints, non-equilibrium distributions, population age-
439 or stage-structure, depletable covariates, genetic change, non-additive habitat effects on
440 population fitness, Allee effects in population growth, or saturating responses to superabundant
441 resources. From the point of view of statistical inference, in future implementations, the two
442 model components of habitat selection and population growth would ideally be implemented as
443 simultaneous (or, at least connected) inference, so that uncertainty from both models is

444 propagated through the full workflow to the final results. Such joint inference is, as yet
445 unavailable in the literature. Our cross-validation approach in the present paper (applied to the
446 full workflow) was a step in this direction.

447 Our garden habitat composition manipulation exercise (Fig. 4) is mainly a sensitivity analysis
448 used to illustrate the extent of garden modifications required to improve colony viability and the
449 improvements that might be possible. Even though we chose a simplistic algorithm that altered
450 garden cells independently of each other (an approach that is too fragmented from a garden
451 landscaping point of view), our analysis does demonstrate that habitat manipulation can have
452 large impacts on expected population growth, in several cases even reversing population
453 declines. Such emerging exemplars of the possibilities for habitat engineering for the purposes of
454 management have considerable future potential, and deserve further algorithm development and
455 experimental testing. Since the habitat modifications suggested here were achieved by focusing
456 just on changing vegetation types in gardens, rather than changes to more fixed structural
457 elements of the landscape, the predictions from these types of models should be practical to test.
458 Ultimately, this type of testing could enable conservation organisations, such as the Royal
459 Society for the Protection of Birds in the UK, to provide bespoke guidance to individual
460 homeowners and other land owners who wish to enhance the wildlife potential of their
461 properties.

462 Quite apart from its applied importance, our study contributes several conceptual
463 developments relating to habitat. For example, it casts a critical light on the implicit assumption
464 (pervading the broad class of applied habitat models) that hotspots in spatial usage are indicative
465 of fitness-conferring habitats. Although it is understood that, biologically, the relationship
466 between space use and population growth may not be straightforward (Pulliam 2000, Morales et

467 al. 2010, Peterson et al. 2011), high-usage and high-fitness are often conflated in contemporary
468 literature (e.g. Stockwell, 2006), in order to provide solutions to urgent applied problems.
469 However, the fact that usage is observed and modelled directly, but fitness is not, leaves open the
470 possibility of mismanaging wildlife whose distribution does not directly reflect habitat
471 suitability. The predictive ecology modelling approach we demonstrate here shows how such
472 problems could be overcome by the generation of fully estimable population models, able to
473 predict how populations would change under specific management and environmental change
474 scenarios.

475 Packaging habitat selection and population fitness in simple qualitative rules of thumb will
476 continue to be a challenge long into the future, because such rules cannot apply indiscriminately
477 across different species or even subpopulations. This challenge means that models, such as the
478 one presented here, could prove valuable in the design of conservation and landscape
479 management strategies, particularly when it is imperative to exploit efficiencies in management
480 to navigate human-wildlife conflicts, where only narrow strips of common ground can reconcile
481 conservation with human exploitation (Redpath et al. 2013). Much work remains to be done
482 before habitat manipulations can be designed with regularity and without the close supervision of
483 ecological experts. However, such efficiencies now appear more achievable, given our finding
484 that, at least in this study system, moderate manipulations in habitat are predicted to have large
485 effects on population growth, even reversing ongoing declines.

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620

621 **Figure legends**

622 **Figure 1:** The six building blocks of the Habitats-To-Populations framework (HTP, modified
623 from Matthiopoulos et al. 2015) can be divided into categories: Three steps (in blue background)
624 modelling habitat use, and three steps (in white background) accounting for the effects of habitat
625 on population growth. The environment can be characterised by the availability of different
626 habitat types (Step 1). Animals have habitat preferences (Step 2) which may lead them to use
627 habitats disproportionately to their availability. Together, the combination of habitat availability
628 and habitat preferences are assumed to give rise to the observed spatial distribution of a
629 population (Step 3). These first three steps comprise the Habitat Selection Model and they
630 determine the exposure of individuals to different habitat types that influence their fitness (Step
631 4), which, in turn, determines the collective capability of a population to grow (Step 5).
632 Processes of population growth determine current population density (Step 6), which has the
633 opportunity to mould habitat availability but also the potential to feed back directly into
634 population growth and habitat preferences (via density dependent and spatial crowding). The key
635 advantage of this approach is that all six processes can be estimated from field data. Statistical
636 inference for the steps in dark blue requires spatial data on habitat availability and use. The steps
637 shown in white require additional temporal data on population change.

638

639 **Figure 2:** Analysis of the colony-specific habitat selection coefficients obtained via the GFR
640 model, incorporating main effects and relevant interactions for each covariate. The histograms on
641 the diagonal summarise the coefficient values obtained for each environmental covariate (green

642 curves are smoothed versions of the same information). The pairwise scatter-plots, off the
643 diagonal show the correlations (in this example, all synergistic) between regression coefficients.

644

645 **Figure 3:** Goodness-of-fit and predictive ability for the spatial model (a and b, respectively) and
646 for the mean-field model (c and d, respectively). The spatial model uses information extracted
647 from models of habitat availability and use in each garden cell around the colonies. The mean
648 field model only uses average availability. For the goodness of fit plots (a & c), the regression
649 line and corresponding prediction intervals come from a linear model fitted to the observations
650 against the population model fit. For the prediction plots, each dot represents an iteration of our
651 leave-one-out cross-validation algorithm.

652

653 **Figure 4:** Results of the garden improvement optimisation. The black line segments show the
654 improvements possible in each of our 12 colonies (sorted in order of low-to-high observed
655 growth rate). The pie charts show the alterations in composition of the gardens around each
656 colony in terms of six habitat categories (explained in the key), two of which (artificial surface
657 and roof) were constrained to starting conditions and four of which (bush, grass, hedge and tree)
658 were allowed to be varied to optimise population growth. The confidence intervals of the
659 predicted growth rates are represented as the top and bottom vertices of the grey rhombuses
660 surrounding each line segment.

661