

**1Nonideal nest box selection by tree swallows breeding in farmlands: evidence for an
2ecological trap?**

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13Abstract

14Animals are expected to select a breeding habitat using cues that should reflect, directly or not,
15the fitness outcome of the different habitat options. However, human-induced environmental
16changes can alter the relationship between habitat characteristics and their fitness
17consequences, leading to a maladaptive habitat choice. The most severe case of such nonideal
18habitat selection is the ecological trap, which occurs when individuals prefer to settle in poor-
19quality habitats while better ones are available. Here we studied the adaptiveness of nest box
20selection in a tree swallow (*Tachycineta bicolor*) population breeding over a 10-year period in
21a network of 400 nest boxes distributed along a gradient of agricultural intensification in
22southern Québec, Canada. We first examined the effects of multiple environmental and social
23habitat characteristics on nest box preference to identify potential settlement cues. We then
24assessed the links between those cues and habitat quality as defined by the reproductive
25performance of individuals that settled early or late in nest boxes. We found that tree swallows
26preferred nesting in open habitats with high cover of perennial forage crops, high spring insect
27biomass, and high density of house sparrows, their main competitors for nest sites. They also
28preferred nesting where the density of breeders and their mean number of fledglings during the
29previous year were high. Additionally, we detected mismatches between preference and
30habitat quality for several environmental variables. The density of competitors and conspecific
31social information showed severe mismatches, as their relationships to preference and
32breeding success went in opposite direction under certain circumstances. Spring food
33availability and agricultural landscape context, while related to preferences, were not related to
34breeding success. Overall, our study emphasizes the complexity of habitat selection behavior

35and provides evidence that multiple mechanisms may potentially lead to an ecological trap in
36farmlands.

37**Keywords:** aerial insectivore; ecological trap; habitat preference; habitat quality; house
38sparrow; settlement cue

39 Introduction

40 Breeding habitat selection decisions influence fitness of animals through the costs and benefits
41 of habitat use (Hildén, 1965; Martin, 1998; Morris, 2003). Natural selection should thus favor
42 the evolution of adaptive behavioral responses whereby individuals preferentially use habitats
43 that maximize their fitness (Fretwell and Lucas, 1970; Hale and Swearer, 2016). Because
44 animals cannot always evaluate the quality of habitats in terms of fitness returns due to various
45 constraints such as time and energy, they often rely on cues that reflect, directly or indirectly,
46 the expected fitness outcome of different habitat options (Stamps, 2001; Stamps and Krishnan,
47 2005; Robertson and Hutto, 2006). Those cues include habitat characteristics perceived
48 through personal observation (e.g., landscape features, Bollinger 1995, Hollander et al. 2011;
49 food availability, Burke and Nol 1998) or associated to personal performance in a given
50 environment (Switzer, 1997; Lagrange *et al.*, 2017), or the behavior or performance of other
51 individuals of the same or different species (Mönkkönen *et al.*, 1999; Doligez, 2002; Pärt *et*
52 *al.*, 2011). Social information likely integrates the effect of many environmental factors on
53 expected breeding success via their effects on the distribution and performance of conspecifics
54 and heterospecifics (Doligez *et al.*, 2003). Information can be gathered by prospecting
55 behavior during or at the end of a breeding event, so to be used in future reproduction, and is
56 thought to be a reliable settlement cue if habitat quality is sufficiently predictable (Boulinier
57 and Danchin, 1997; Valone and Templeton, 2002; Doligez *et al.*, 2003).

58 Whichever cues are used, there will necessarily be a temporal gap between the time of habitat
59 selection and the time of breeding, making individuals vulnerable to perturbations that alter

60habitat predictability (Kristan, 2003; Gilroy and Sutherland, 2007). Rapid environmental
61changes, notably human-induced ones, can amplify mismatches between the preferences for
62some habitat characteristics and the fitness outcome of such preferences (Schlaepfer, Runge
63and Sherman, 2002; Robertson and Hutto, 2006). Ecological traps arise from such mismatches
64between expected and realized fitness, and occur when poor-quality habitats are preferred
65although better ones are available (Schlaepfer, Runge and Sherman, 2002; Battin, 2004; Pärt,
66Arlt and Villard, 2007). Ecological traps can result from various mechanisms affecting either
67the attractiveness of habitats, their actual quality or both (Robertson, Rehage and Sih, 2013).
68The consequences of ecological traps on population dynamics depend on the severity of the
69trap, which in turn varies according to the proportion of poor-quality habitats, their relative
70attractiveness and the magnitude of their fitness costs (Delibes, Gaona and Ferreras, 2001;
71Hale, Treml and Swearer, 2015). Maladaptive habitat selection is thus a continuum, with most
72severe cases being attractive sink habitats that could drive population decline and extirpation
73(Delibes, Gaona and Ferreras, 2001; Battin, 2004; Pärt, Arlt and Villard, 2007).

74Among anthropogenically perturbed ecosystems susceptible to creating ecological traps,
75farmlands have received much attention (Hale and Swearer, 2016). Because human activities
76on farmlands are numerous and diversified, as well as temporally unpredictable (e.g. crop
77rotation, soil preparation, harvest, agrochemicals inputs, livestock grazing), many different
78mechanisms have been found to trap various taxa into making bad habitat choices (Hale and
79Swearer, 2016). For example, agricultural practices involving machinery can destroy nests of
80ground-nesting birds or expose them to predators (Bollinger, Bollinger and Gavin, 1990;

81Perlut *et al.*, 2006), decrease prey availability (Catry, Franco and Moreira, 2014; Touihri *et al.*,
822019), directly kill individuals or expose them to predators (Reid, McDonald and
83Montgomery, 2010; Rotem *et al.*, 2013). Pesticide use also has the potential to induce various
84ecological trapping mechanisms, as shown in several taxa (insects: Vonesh and Kraus 2009,
85Duchet *et al.* 2018, Kautz and Gardiner 2019; amphibians: Takahashi 2007, Vonesh and Buck
862007; birds: Gervais *et al.* 2003). Pesticides were shown to affect non-target wildlife both
87directly via lethal or sublethal toxicity (Walker, 2003; Mitra, Chatterjee and Mandal, 2011;
88Eng, Stutchbury and Morrissey, 2019) and indirectly, for instance via trophic effects (e.g.
89decrease in prey quantity and/or quality) or habitat modifications following the use of
90herbicides (Boatman *et al.*, 2004; Morris *et al.*, 2005; Gibbons, Morrissey and Mineau, 2015).
91On a broader scale, changes in landscape structure (i.e., composition and configuration)
92arising from agricultural intensification can also lead to maladaptive habitat selection by, for
93example, creating linear habitats used as travel corridors by predators (Rodenhouse and Best,
941983; Morris and Gilroy, 2008).

95Here we studied the adaptiveness of nest box selection within a tree swallow (*Tachycineta*
96*bicolor*) population breeding along a gradient of agricultural intensification in southern
97Québec, Canada. Our approach followed the two-steps model suggested by Pärt *et al.* (2007)
98to study ecological traps by focusing on individual selection decisions in order to identify
99potential mechanisms of nonideal habitat selection. First, we identified potential cues used by
100tree swallows for nest box selection by determining which environmental and social habitat
101characteristics were associated to preference as determined by nest box occupancy and

102settlement date. Second, we tested if these cues were good predictors of habitat quality as
103defined by two components of reproductive success: (1) number of hatchlings and (2) fledging
104success. We further analyzed the relationship between habitat characteristics and reproductive
105success separately for early and late settlers, who differ in their age structure, body condition
106and breeding phenology (Møller, 1994; Lozano, Perreault and Lemon, 1996; Porlier, Bélisle
107and Garant, 2009), in order to assess whether they experience different constraints that would
108translate into differential habitat selection adaptiveness.

109Although tree swallows are known to breed within or on the edge of patches of open natural
110habitats, especially near wetlands or open water, they can also be attracted by the installation
111of proper nest boxes to various types of anthropogenic landscapes offering open habitat,
112including intensively managed row crops (Ghilain and Bélisle, 2008; Winkler *et al.*, 2011;
113Elgin, Clark and Morrissey, 2020). Despite the fact that it is a well-studied bird species (Jones,
1142003), little is known about the habitat features associated with their nesting site preference
115and the fitness outcome associated with these preferences, especially in agroecosystems. We
116hypothesized that environmental cues such as landscape context and spring food availability
117lead to nonideal breeding habitat selection, while both hetero- and conspecific social
118information provide reliable cues of habitat quality for tree swallows breeding in
119agroecosystems (see Table 1 for rationale).

120**Methods**

121Species and study area

122Tree swallows are small migratory passerines that feed on insects in flight. They breed all over
123North America but, as many other aerial insectivores, have been declining over large portions
124of their breeding range, especially in the north-eastern parts (Nebel *et al.*, 2010; Shutler *et al.*,
1252012; Michel *et al.*, 2016). As an obligate secondary cavity nester, this semi-colonial species
126readily uses nest boxes.

127The study area included 40 farms distributed along a gradient of agricultural intensification
128covering approximately 10,200 km² in southern Québec, Canada (Fig. 1). The eastern part of
129the system was dominated by forests and low-intensity agricultural fields of hay, alfalfa and
130clover, along with pastures and rare natural grasslands, henceforth referred to as “forage
131crops”. Each farm included 10 identical nest boxes mostly arranged in a row along field
132margins and separated by at least 50 meters to limit intra and interspecific competition (see
133Ghilain and Bélisle 2008 for further details on the study system). A Thermochron iButton
134device was fixed on the outside of one nest box on each farm to record hourly ambient
135temperature (model DS1922L; Embedded Data Systems, Lawrenceburg, Kentucky, USA). A
136pluviometer collected precipitation data (millimeters of rainfall) on each farm. We used the
137mean daily temperature, which was correlated with maximum and minimum daily temperature
138($r = 0.89$ and $r = 0.66$, respectively), and mean daily rainfall between May 1 and May 15 to
139characterize spring climate. This time window was chosen to represent the period during
140which swallows are actively selecting nesting sites; 95% of nest boxes that hosted a laying
141event contained nesting material by May 15 and only 10% of laying events occurred before
142this date.

143Nest monitoring

144We monitored nest boxes every other day from 2009 to 2018 starting in early May. We
145recorded the occurrence of nest materials, laying date (first egg), clutch size, number of
146hatchlings, number of fledglings and their fledging date. Only the first breeding attempts of
147each box were kept for the analyses because second clutches are uncommon (11% of all tree
148swallows' breeding attempts between 2009 and 2018) and often result from first clutch failure.
149Focusing on first breeding attempts also allowed us to reduce the potential bias that could arise
150from individuals choosing a nest box that already contained a nest (as in Mingju et al. 2019).
151Monitoring ended when all nestlings had fledged on a given farm. Nest boxes were cleared of
152any nest material and/or dead nestlings every year in October.

153Preference

154Preference for a resource type is the likelihood of it being chosen if offered among equally
155available options (Johnson, 1980), and thus should ideally be assessed by choice experiments
156(Robertson and Hutto, 2006). However, such an approach would have been unrealistic in our
157case considering our large-scale system, yearly variation, and the variety of continuous habitat
158characteristics we tested. We instead evaluated preference using two common surrogates that
159reflect the process of habitat selection: occupancy and settlement patterns (Robertson and
160Hutto, 2006). Preference for each nest box was estimated for each year according to the
161occurrence of a laying event (at least one egg laid) and settlement date (Julian date at which
162nesting material was first observed). However, because some early establishment dates were
163left-censored, i.e., some boxes already contained nest material at the first visit (45% of all

boxes), establishment dates were classified as either “early” or “late” with respect to the annual median establishment date. The category “early” included boxes with settlement dates preceding or equal to the annual median, which comprised nearly all (91.3%) left-censored dates. Overall, the average difference between the annual mean settlement dates categorized as “early” and “late” was 10.4 ± 2.9 days (mean \pm SD). Nest boxes occupied by other species were excluded from analyses ($N = 964$ boxes between 2009 and 2018). The ordinal preference variable featured three categories ranging from least preferred (nest box hosting no laying event during the season) to most preferred nest boxes (early establishment and receiving at least 1 egg; Fig. 2).

Habitat quality

Habitat quality was defined with respect to the fitness outcome resulting from the use of a nest site, as suggested by Johnson (2007). We used two proxies of reproductive success that, when combined, result into the number of fledglings produced during a breeding event, namely (1) the number of hatchlings produced and (2) the proportion of hatchlings that successfully fledged (i.e., fledging success).

Both the number of hatchlings and the fledging success were analyzed separately for breeding attempts of individuals that settled early and late (as defined in Fig. 2), hereafter called early and late settlers, for multiple reasons. First, we know that tree swallows’ breeding success declines during the course of the season (Winkler and Allen 1996, Ghilain and Bélisle 2008, Millet et al. 2015), and that this decline occurs mostly between hatching and fledging (Millet et al., 2015). Because the timing of nest initiation was positively correlated with the date at

185which the first egg was laid ($r = 0.49$), late settlers should have a lower breeding success.
186Early and late settlers likely experience different constraints because factors that are
187susceptible to influence breeding performance (e.g., parasitism, food availability or parent
188condition) may vary seasonally (Grüebler and Naef-Daenzer 2010, Daoust et al. 2012, Rioux
189Paquette et al. 2013). Second, in migratory birds, early arriving individuals are usually more
190experienced and in better conditions (Francis and Cooke, 1986; Møller, 1994, 2003; Lozano,
191Perreault and Lemon, 1996). Separating the effects of habitat characteristics on the breeding
192performance of early and late settlers hence allowed us to investigate, to some extent, the
193potential effects of age and body condition on the adaptiveness of nest site selection. In our
194system, late settlers are younger and thus less experienced (27% of females are second-year in
195late settlers, versus 11% in early settlers; G -test, $p < 0.001$), they are also less genetically
196diversified (i.e., higher internal relatedness), and have a lighter body mass than early settlers
197(Porlier et al. 2009). Finally, the breeding attempts of late settlers are more likely to include
198undetected second clutches, i.e., replacement clutches laid in different nest boxes after a
199failure, which implies that some adults may have already invested energy in a first clutch and
200therefore be more limited for their second breeding attempt (Rooneem and Robertson, 1997).

201Although previous studies found that the age of female tree swallows influences their breeding
202performance (De Steven, 1978; Stutchbury and Robertson, 1988; Rioux Paquette *et al.*, 2014)
203and dispersal behavior (Winkler *et al.*, 2004; Lagrange *et al.*, 2017), we could not directly
204investigate this effect due to the imbalance of age classes ($N = 335$ clutches by second-year
205versus $N = 1501$ by after second-year) within our dataset, leading to a lack of coverage over

the sampling space defined by all predictors as well as to precision and model convergence issues.

Habitat characteristics

We investigated the effects of several habitat characteristics on nest box preference and reproductive success. These variables were selected based on the breeding ecology of tree swallows and included habitat characteristics describing landscape context, food availability and both hetero- and conspecific social information (see details in Table 1).

Landscape context

We characterized landscape habitat composition by measuring the relative cover of forest, perennial forage crops, as well as of water bodies and wetlands, within radii of 50, 100, 200, 300, 400, 500, 1,000, 5,000, 10,000, and 20,000 m around each nest box. We assessed landscape habitat composition up to the 500-m scale on a yearly basis in the field by visually identifying cultures and marginal habitats and delineating them using orthophotos (1:40,000). Characterization beyond the 500-m scale was based on a mosaic of yearly georeferenced classified optical and radar satellite images taken between 2011 and 2018 (pixel resolution 30 m × 30 m; Agriculture and Agri-Food Canada (AAFC) 2018). Only the year 2018 was used to assess water cover at the above range of scales because it showed better accuracy and water cover should not vary significantly across years (Agriculture and Agri-Food Canada (AAFC), 2018).

225 In order to use the spatial scale most representative of tree swallows' habitat selection
 226 regarding each land cover type, we performed a preference analysis (see Statistical Analysis
 227 section) with candidate models including all control predictors of habitat preference used in
 228 further analyses (Table 1) with focal land cover type at varying spatial scales. We then
 229 compared models on the basis of the second-order Akaike's information criterion (AICc;
 230 Burnham and Anderson 2002). For forest, the 100-m spatial scale clearly had the lowest AICc
 231 score ($w = 0.99$, Fig. A1a). For forage crops, all scales below 500 m were equivalent (Delta
 232 AICc < 1 , Burnham and Anderson 2002) and highly correlated ($0.71 \leq r \leq 0.97$) so we used a
 233 500-m radius to be consistent with previous studies conducted in our system (Fig. A1b). We
 234 considered the interaction between forest cover at 500 m and forage crops at 500 m because
 235 the former was strongly negatively correlated with total agricultural land use, and thus open
 236 habitat ($r = -0.92$, $N = 400$ nest boxes on 40 farms for 10 years). This interaction allowed us to
 237 capture the complexity of landscape contexts specific to the study system by discriminating
 238 the influence of forage crops in open versus forested landscapes. Given that tree swallows'
 239 nest site selection also seemed to respond (yet to a lesser extent) to forage crops at the 5-km
 240 scale (Fig. A1), and that previous studies on our system found an effect of forage crops on
 241 breeding success at that scale (Ghilain and Bélisle 2008, Porlier et al. 2009), we decided to
 242 rerun all analyses with forage crops and forest measured at the 5-km scale. For water bodies
 243 and wetlands, two spatial scales stood out, namely the 2-km and 10-km radii. We used the 10-
 244 km scale as it led to the lower AICc score ($w = 0.20$, Fig. A1c).

245 *Food availability*

Two passive insect traps were installed on each farm around the first and second third of the nest box transect. Traps consisted of ~4-L yellow buckets placed 1.5 m above ground. They were filled with ~2 L of salty detergent solution to reduce surface tension and slow the growth of bacteria and fungi. Two transparent plexiglass screens were mounted perpendicularly to one another above each bucket to intercept flying insects (see Bellavance et al. 2018 and Garrett et al. 2021 for details). We collected the content of each trap on every visit to a farm (i.e., every other day) and conserved arthropods in 70% ethanol until processing. We sorted samples by removing arthropods unlikely to be preyed upon by tree swallows (i.e., bumble bees (*Bombus* spp.: Hymenoptera), June bugs (*Phyllophaga* spp.: Coleoptera), large spiders (Araneae, > 0.5 cm body width), and caterpillars (Lepidoptera); Bellavance et al. 2018). The rest of the sample was dried at 50°C for at least 48 hours before being weighed (Adam Equipment, model AAA250L, ± 0.0001 g). The mean daily dry biomass of arthropods collected between May 1 and May 15 was used as a proxy of yearly food availability on a given farm at the time of nest site selection in further analyses. We compared the average daily insect biomass collected during this period with that collected during the nestling period, defined by the farm's yearly average hatching date and the following 12 days (yearly mean hatching date on the system was used for farms with no nestlings). The correlation between the insect biomass of the two periods was then calculated for each farm in order to assess within-season predictability of this food resource.

Heterospecific social information

266We evaluated the use of heterospecific social information through nest box occupancy of tree
267swallow's main nest-site competitors in our system, house sparrows, which initiate breeding
268before swallows return from their wintering grounds (Robillard, Garant and Bélisle, 2013).
269Occupancy was determined by the presence of at least one house sparrow egg, and only first
270clutches observed in each box were included since a nest box is rarely used by another species
271once house sparrows have built a nest therein.

272*Conspecific social information*

273We defined two sources of social information regarding the future breeding success that an
274individual could expect to experience on a given farm: the density of tree swallows that bred
275on a farm during the previous year and the mean number of fledglings obtained by those
276breeders (Lagrange et al. 2017). This information can be collected directly by an individual
277breeding on the farm during the previous year, or by prospecting individuals that explored
278habitats either during or after the previous breeding season. We worked at the farm level
279because Lagrange et al. (2014) found that fidelity was high at this scale: the probability of a
280female breeding on the same farm for two consecutive years varied between 70% and 94%
281depending on the occurrence of a dispersal event the year before. However, we found that the
282probability of a female reproducing in the same nest box over two consecutive years between
2832009 and 2018 was only 5%. This suggests that a significant component of habitat selection
284occurs at the farm rather than at the nest box level.

285Statistical analyses

286

287To determine if settlement decisions deviate from an ideal habitat selection, we compared the
288relationships linking habitat characteristics to habitat preference and reproductive success.
289Specifically, if the relationship between habitat preference and a given habitat characteristic
290was qualitatively similar to the one linking breeding success to that characteristic, we
291concluded to a case of ideal settlement decision. We identified nonideal decisions when there
292was a mismatch or uncoupling between those two relationships. For example, a habitat
293characteristic that was preferred but that was unrelated to reproductive success suggested a
294case of nonideal selection. Alternatively, a characteristic that was not preferred but that
295influenced reproductive success also suggested a nonideal habitat selection ('equal-preference
296trap'; Robertson and Hutto 2006). Lastly, if both relationships went in opposite directions,
297habitat selection was considered even more maladaptive, and potentially indicating an
298ecological trap (Pärt, Arlt and Villard, 2007).

299*Habitat predictability*

300All analyses were performed in the R environment (v. 3.5.3, R core team 2019). For cues to
301provide information about the expected breeding success of a given nesting site, they must
302show some correlation in time (Doligez *et al.*, 2003). We thus assessed the between-year
303predictability of habitats characteristics by determining the correlation between the current and
304previous year values of habitat characteristics of the 400 nest boxes. For the year 2010 to
3052018, we computed the Pearson's correlation coefficient. We then used the mean of those
306annual correlation coefficients and the standard deviation to assess between-year predictability

307of every habitat characteristics studied, except water bodies and wetlands for which we only
308used the data from 2018.

309*Preference*

310Ordinal logistic regression was used to model the preference for nest boxes with the *ordinal*
311package (v. 4-25, Christensen 2019) using a three-category ordinal response variable based on
312nest box occupancy and settlement date (Fig. 2). The proportional odds assumption, which
313states that the coefficient of each predictor should be constant between all pairs of response
314categories, was found to hold according to the graphical approach suggested by Harrell
315(2015). We built a series of models that included all combinations of the groups of variables
316that characterized landscape context, food availability, and both hetero- and conspecific social
317information, as described and justified in Table 1. All models also included variables
318controlling for geographical position (latitude and longitude) and spring weather. See Table
319A1 for the list of candidate models. We found no evidence of problematic multicollinearity
320among predictors as variance inflation factors (VIFs) were all below three (Zuur *et al.*, 2009).
321See Fig. A2 for the matrix of correlations of all predictors. Predictors were standardized (zero
322mean, unit variance). Random effects included nest box, farm and year identity. We compared
323models based on AICc with the *AICcmodavg* package (v 2.2-2, Mazerolle 2019). Because the
324weight of evidence of the best model for this analysis was strong ($w = 0.88$), we decided to
325base our inferences of nest box preference on that single model (see Table A2 for results of
326model selection).

327 *Habitat quality*

328 All analyses of reproductive success were performed with the *glmmTMB* package (v. 0.2.3,
329 Brooks et al. 2019). We compared the same list of candidate models used for the preference
330 analysis (Table A1) based on AICc in order to assess if the determinants of nest box
331 preference are linked to reproductive success. Because no one model clearly stood out above
332 others, we performed multimodel inference for generating predictions (and unconditional 95%
333 confidence intervals) following Burnham and Anderson (2002). We tested for zero-inflation of
334 both the number of hatchlings and fledging success using the *DHARMA* package (Hartig
335 2019).

336 Number of hatchlings was modeled with zero-inflated generalized linear mixed models
337 (GLMM) using a generalized Poisson distribution with a log link function for the conditional
338 model and a logit link function for the zero-inflated model (Brooks *et al.*, 2019). Both the
339 conditional and zero-inflated models contained the same fixed effects, but not the same
340 random effects. Indeed, we added the identity of the combination of year and farm as a
341 random effect in the zero-inflated model to account for sporadic events that can occur on a
342 farm and lead to the failure of nearly all clutches, and that we may have not detected or
343 measured (e.g., disturbance by a predator causing birds to abandon their clutch). Also, because
344 of convergence issues, we could not keep all random effects and removed those that accounted
345 for very little variance (i.e. $< 1 \times 10^{-7}$ % of the variance explained by random effects). We thus
346 removed the year in the early settlers' conditional model and both nest box and farm identity
347 in the zero-inflation model. For late settlers, we had to remove farm identity in the conditional

and zero-inflation models along with year identity in the zero-inflation model to reach full convergence. Those changes did not affect the magnitude nor the precision of the parameter estimates. We modeled fledging success as a proportion of hatchlings having successfully fledged with generalized linear mixed models using a binomial error distribution and logit link function. Random effects included nest box, farm and year identity.

Results

Habitat predictability

Habitat characteristics were generally predictable between years. Predictability was especially high for forest cover within 100 and 500 m (0.96 ± 0.04 and 0.99 ± 0.01 , mean annual correlation coefficient between current and previous year value \pm SD), forage crop cover within 500 m (0.91 ± 0.10), house sparrow density (0.85 ± 0.04), and tree swallow density (0.85 ± 0.03). Predictability was moderate for spring insect biomass (0.41 ± 0.22) and mean number of fledglings on a farm (0.25 ± 0.15). Finally, we found that the predictability of insect biomass between the time of habitat selection and nestling food provisioning was low ($r = 0.29 \pm 0.34$, mean of all 40 farms \pm SD) and highly spatially variable ($-0.45 \leq r \leq 0.89$, depending on farms).

Preference

On average $64.3\% \pm 7.5$ (mean \pm SD) of our 400 nest boxes were annually occupied by tree swallows, $16.6\% \pm 6.4$ by house sparrows, and $2.3\% \pm 1.5$ by other bird species (i.e., house wrens (*Troglodytes aedon*), eastern bluebirds (*Sialia sialis*), and black-capped chickadees

368(*Poecile atricapillus*)). Each year on average $12.7\% \pm 3.1$ nest boxes received nesting material
369but no laying event, while 6.8 ± 2.5 stayed empty of nesting material throughout the season.

370We found a relationship to preference (Fig. 2) for almost all habitat characteristics describing
371either the landscape context, food availability, and both hetero- and conspecific social
372information (Table 2). Regarding landscape composition, preference decreased with forest
373cover within a 100-m radius and thus the probability of tree swallows laying in highly forested
374habitats was very low (Fig. 3a). The effect of the cover of forage crops within 500 m depended
375on forest cover within 500 m (Fig. 3b), and the same pattern was found when both forage
376crops and forest were measured at the 5-km scale (Fig. A3). Individuals preferred nest boxes
377surrounded by high proportions of forage crops in sparsely forested landscapes. The opposite
378was observed when forest covered reached 50% of the measured area: individuals preferred
379landscapes where open areas were dominated by row crops. The amount of wetlands and open
380water within 10 km was the only landscape composition variable not related to nest box
381preference (Table 2). As expected, nest box preference increased with spring food availability
382(Fig. 3c). Contrarily to our expectations, preference also increased with house sparrow density
383(Fig. 3d). However, because we estimated settlement dates based on the sole observation of
384nest material, we cannot be completely sure that nest was initiated by tree swallows rather than
385another species (e.g., house sparrow), which may add errors in the tree swallow settlement
386dates. We investigated this possibility by classifying early and late settlements using the tree
387swallow laying date rather than nest initiation date as a cutoff. Because the preference still
388increased with house sparrow density, we are confident that this effect was not an artifact of

389nests initiated by house sparrows. As for conspecific social information, preference increased
390with both the density of breeding tree swallows on a farm and their reproductive performance
391in the previous year (Fig. 3e-f).

392Habitat quality

393*Number of hatchlings*

394Overall, 33% of early settlers' clutches experienced complete hatching failure, compared to
39538% for late settlers. Mean number of hatchlings (\pm SD) for early and late settlers that did not
396experience hatching failure was 5.0 ± 1.2 and 4.7 ± 1.3 , respectively.

397The model including both hetero- and conspecific social information best described the
398number of hatchlings produced by early settlers ($w = 0.33$, Table A2). Number of hatchlings
399increased with both tree swallow density on the farm in the previous year and latitude, while
400the probability of hatching failure increased with house sparrow density (Table 2). Those
401effects were also found in the second-best model ($w = 0.22$, Table A2), but the third best
402model ($w = 0.18$, Table A2), which did not include house sparrow density, showed a negative
403effect of the prior year tree swallow density on the probability of hatching failure (Table A3).

404Late settlers' number of hatchlings was best described by the conspecific social information
405model ($w = 0.45$, Table A2). Number of hatchlings increased with the prior year density of
406tree swallows on the farm, while the probability of hatching failure decreased with the mean
407number of fledglings produced on the farm in the previous year (Table 2). The second-best

408model was the null model ($w = 0.26$, Table A2), and the third best model ($w = 0.16$, Table A2)
409showed the same effects as the best one (Table A3). However, when the 5-km scale was used
410to assess the effects of forage crops and forest, the best model included landscape context and
411heterospecific social information ($w = 0.27$, Table A5). This model showed an increase in
412number of hatchlings with forest cover, along with a higher probability of hatching failure on
413farms with high house sparrow density, and where both forage crop and forest covers were
414low (Fig. A3, Table A6).

415*Fledging success*

416The average proportion of nestlings that fledged was 0.75 ± 0.37 and 0.69 ± 0.41 (mean \pm SD)
417for early and late settlers, respectively. The conspecific social information model best
418described the fledging success of early settlers ($w = 0.36$), which decreased with the mean
419number of fledglings produced on the farm in the previous year (Fig. 4a). That effect was also
420found in the second and third best models ($w = 0.25$ and 0.13 ; Table A4). When investigating
421the effects of forage crops and forest at the 5-km scale, the best model also included landscape
422context ($w = 0.42$, Table A5) and showed a positive effect of forage crops within 5 km and
423water bodies and wetlands within 10 km, along with a negative effect of the mean number of
424fledglings produced in the previous year (Fig. A3, Table A6).

425Fledging success of late settlers was best described by the model including both landscape
426context and conspecific social information ($w = 0.31$, Table A2). Fledging success decreased
427with forest cover within 100 m (Fig. 4b), the prior year density of tree swallows (Fig. 4c), and

latitude. On the other hand, it increased with the mean number of fledglings produced on the farm in the previous year (Fig. 4a). Those effects, albeit variable or uncertain given the width of confidence intervals, were also found in the second and third best models ($w = 0.27$ and 0.22 ; Table A4).

Discussion

We investigated the links between several environmental and social habitat characteristics, nest box preference, and annual reproductive success in a tree swallow population breeding along a gradient of agricultural intensification. We found multiple mechanisms that may lead to an ecological trap, which took two forms : (1) a habitat characteristic that was associated with preference, but not with reproductive success; and, more severely, (2) a habitat characteristic for which the relationship between preference and reproductive success went in opposite directions. While landscape context and spring food availability led to nonideal habitat choices of the first form, both hetero- and conspecific social information promoted mismatches of the second form. Our results suggest that both environmental and social cues can lead to maladaptive habitat choices, which contradicts our hypothesis stipulating that, within farmlands, environmental cues are poorer predictors of habitat quality than social ones. Overall, our study highlights settlement decisions that drive our tree swallow population further away from an ideal distribution. Our results have implications for declining farmland birds as well as for the use of nest boxes as a conservation tool.

Landscape

448As expected, nest boxes surrounded by high forest cover within 100 m were less attractive to
449tree swallows and led to a lower fledging success in late settling individuals. Previous studies
450found that tree swallows avoid breeding near forest, both in a nest box grid and in natural tree
451cavities (Rendell and Robertson, 1990; Robles and Martin, 2013). Breeding near forest edges
452may be avoided because it (1) requires individuals to travel farther to forage (Bruun and
453Smith, 2003), and/or (2) impedes nest defense against predators (Rendell and Robertson,
4541990), which may be more active and/or abundant along forest edges (Lahti, 2001; Chalfoun,
455Thompson and Ratnaswamy, 2002). These limitations may be more important for late settlers
456because they are on average less experienced and in worse condition than early settlers, and
457thus potentially less able to cope with increased foraging costs (Frey-Roos, Brodmann and
458Reyer, 1995). Flying insects may also be less abundant as the season progresses, making
459foraging more costly for late settlers (Rioux Paquette *et al.*, 2013; Bellavance *et al.*, 2018).
460Alternatively, predation on eggs, nestlings and adults does occur in our system, notably by
461animals associated to forest such as raccoons (*Procyon lotor*) and red squirrels (*Tamiasciurus*
462*hudsonicus*). Predation events accounted for 25% of broods that failed to produce at least one
463fledgling, and 11% ($N=825$) of late settlers experienced brood predation as compared to 8%
464for early settlers ($N=1195$). Late settlers may thus be more at risk if nest predation increases
465throughout the breeding season, as previously observed for cavity-nesting birds (Fisher and
466Wiebe, 2006; Robles and Martin, 2013), or if they are less able to deter predator attacks.

467Perennial forage crops influenced preference differently in forested versus open landscapes at
468both the 500-m and 5-km scales. Tree swallows preferred forage crops in landscapes that

469 offered more open fields over which to forage, but the opposite was true in forested
470 landscapes. This effect may partly result from the landscape structure inherent to the gradient
471 of agricultural intensification that spans our study system where forage crops and pastures are
472 generally cultivated over much smaller areas and within more forested areas than intensive
473 row crops (Bélanger and Grenier, 2002). Tree swallows may thus simply prefer less
474 fragmented open landscapes for reasons discussed above and find themselves attracted to the
475 permanent cover of forage crops that green up earlier and that may harbor higher insect
476 densities in early spring (Thorup *et al.*, 2017). This being said, wind-protected vegetated
477 boundaries like forest edges often support higher insect densities (John P. McCarty and
478 Winkler, 1999; Gruebler, Morand and Naef-Daenzer, 2008) and can provide prime foraging
479 opportunities to aerial insectivores (Evans, Bradbury and Wilson, 2003; Stanton, Morrissey
480 and Clark, 2016). Forage crops within 5 km are also positively associated to breeding
481 performance of tree swallows in our study area (Ghilain and Bélisle, 2008; Porlier, Bélisle and
482 Garant, 2009; Daoust *et al.*, 2012). While neither forage crops nor forest at a 500-m scale
483 influenced the number of hatchlings or fledging success, forage crops within 5 km increased
484 early settlers' fledging success and decreased late settlers' probability of hatching failure
485 within open landscapes, suggesting an adaptive habitat selection (Figure S3, Tables S5 and
486 S6). Overall, as breeding success is likely to depend on the amount and type of open areas, as
487 well as on how these mingle with treed habitats at 5 km, we conclude that the amount of
488 forage crops or forest within 500 m, on their own, are not providing ideal settlement cues in
489 our agricultural context.

Surface water and wetland cover within 10 km was not a determinant of nesting site preference nor breeding performance. This result was surprising because tree swallows are known to breed near water (Winkler et al. 2011) and feed on insects with an aquatic larval stage, even in our study area (John P. McCarty and Winkler, 1999; Bellavance *et al.*, 2018; Michelson, Clark and Morrissey, 2018; Elgin, Clark and Morrissey, 2020). Yet, when running our analyses with forage crops and forest at the 5-km scale we detected an increased fledging success with water and wetland cover for early settlers (Table A6). As our ability to detect such an effect was limited by the low availability of these habitats in our study area (range: 1-11% within 10 km), this result highlights the importance of water for tree swallows breeding in agricultural landscapes. These once abundant wetlands were drained and are now a rare resource for tree swallow (Jobin *et al.*, 2003; Blann *et al.*, 2009).

Food availability

Some studies found that prey availability affect breeding habitat selection in insectivorous birds (Petit and Petit, 1996; Burke and Nol, 1998), including aerial insectivores (Brown and Brown, 1996; Forsman *et al.*, 1998; English *et al.*, 2017). Tree swallows were found to settle preferentially in habitats showing higher spring insect availabilities and this, despite that insect biomass during nest site selection was poorly correlated to that of the food provisioning period. The fact that spring insect availability was a poor indicator of future foraging conditions within an agricultural context is not surprising given that pesticide applications and other farming activities can unpredictably disrupt insect phenology and abundance (Pisa *et al.*, 2015; Mulé *et al.*, 2017; Botías *et al.*, 2019). This observation concords with previous studies

511that found important between-year and within-season differences in Diptera and total insect
512abundance patterns along the agricultural intensification gradient of our study area (Rioux
513Paquette *et al.*, 2013; Bellavance *et al.*, 2018). Given its low within-season predictability, it is
514thus not surprising that we observed no relationship between spring insect availability and the
515breeding performance metrics we considered. While our result does not by any means
516downplay the importance of food availability for feeding nestlings (John P McCarty and
517Winkler, 1999; Nooker, Dunn and Whittingham, 2005), it nevertheless leads us to conclude
518that food availability at the time of nest site selection is a nonideal settlement cue for these
519birds when breeding in current agroecosystems.

520Heterospecific social information

521In contrast to previous observations showing a negative association between TRES nest box
522occupancy and HOSP density, (Robillard *et al.* 2013), we found that tree swallows were
523attracted to farms presenting high house sparrow densities, their main competitors for nest sites. This
524was unexpected given that swallows that settled on such farms were indeed more likely to experience
525hatching failure, an effect seen in early settlers when assessing forage crop and forest covers at a 500-
526m scale, and in both early and late settlers when using a 5-km scale (Table A6). Such an increased
527hatching failure probably results from competition for nest boxes between these two species often
528leading to lethal interactions, nest usurpation and destruction of swallows' eggs (Winkler *et al.*, 2011).
529Given the significant fitness costs imposed by such agonistic interactions, we may expect tree
530swallows to use the abundance of house sparrows for detecting breeding habitat and assessing its
531quality, as information provided by heterospecifics is often used for such purposes (Mönkkönen, Helle
532and Soppela, 1990; Forsman, Seppänen and Mönkkönen, 2002; Thomson, Forsman and Mönkkönen,

5332003; Parejo *et al.*, 2008; Kivelä *et al.*, 2014). For time-limited species such as migrants, the presence
534of a resident species sharing some ecological requirements or mortality factors, like house sparrows for
535tree swallows, could be a useful indicator of habitat quality (Mönkkönen *et al.*, 1999; Thomson,
536Forsman and Mönkkönen, 2003; Parejo, Danchin and Avilés, 2005; Seppänen *et al.*, 2007). Unlike
537conspecific social information, it is often available upon arrival on the breeding grounds and also
538available for individuals who had no access to previous year information (i.e., dispersers) (Doligez,
5392002; Kivelä *et al.*, 2014). Moreover, heterospecific attraction is more likely to occur when search
540costs are high, which is likely the case for cavity users due to the scarcity of nest sites, but only when
541the costs of competition are low (Mönkkönen *et al.*, 1999; Stamps, Krishnan and Reid, 2005; Seppänen
542*et al.*, 2007).

543Given the above, it is thus surprising that tree swallows were attracted to sites where they
544incurred greater costs from house sparrows. One potential explanation for this result is that
545tree swallows' habitat preferences likely evolved with competing resident species for which
546the use of heterospecific information have represented lower costs (e.g., black-capped
547chickadees). House sparrows were introduced from Europe to the United States in the 1850's
548(Lowther and Cink, 2006), and competition with tree swallows was likely exacerbated by
549agricultural intensification over the last decades through their access to farm buildings for
550nesting sites and grains as a food resource (Robillard *et al.* 2013). Although competitors for
551cavities are generally more abundant in natural environments partly due to the larger entrance
552of natural cavities as compared to nest boxes (Robertson and Rendell, 1990; Norris *et al.*,
5532018), they may also be less aggressive than house sparrows (Winkler *et al.*, 2011).

554Conspecific social information

555 We found that tree swallows used conspecific social information as settlement cues, and both
556 the density of conspecifics and their breeding success in the previous year were generally good
557 predictors of the number of hatchlings produced. However, they were not good predictors of
558 fledging success, which decreased with previous-year breeding success and conspecific
559 density for early and late settlers, respectively. Both early and late settlers were thus
560 susceptible to being trapped into breeding on farms where their capacity to raise nestlings until
561 fledgling was lowered, yet based on different sources of social information.

562 Many studies have shown that individuals could be attracted to habitats occupied by
563 conspecifics (e.g., Nocera *et al.*, 2006; Stamps, 1988; Ward and Schlossberg, 2004).
564 Conspecific attraction, by causing individuals to breed in aggregation, has many potential
565 benefits, including: increased detectability of both nesting and foraging habitat patches
566 (Brown, 1988; Barta and Giraldeau, 2001; Stamps, 2001; King and Cowlshaw, 2007),
567 increased mating and extra-pair copulation opportunities (Griffith, Owens and Thuman,
568 Katherine, 2002; Lessard *et al.*, 2014), and increased detectability and defense against
569 predators (Smith, 1986; Turner and Pitcher, 1986). Breeding in aggregation can also bring
570 density-dependent costs such as aggressive interactions and competition for resources
571 (Fretwell and Lucas, 1970; Sutherland, 1996; Newton, 1998; Winkler *et al.*, 2011), and
572 increased predation and parasitism (Møller, 1989). Here we found that these costs might
573 overcome the benefits of cueing on conspecifics density for late settlers, who experienced a
574 lower fledging success on (previously) densely populated farms. Late settlers may thus be
575 more vulnerable to density-dependent costs of breeding aggregations because of their inferior

576experience or body condition. Alternatively, those costs could increase in severity during the
577course of the season and be more damaging to late settlers (Fisher and Wiebe, 2006; Robles
578and Martin, 2013).

579Two previous studies in our system showed the importance of public information on
580settlement decisions by finding that a given nest box occupancy was positively correlated to
581the fledging success experienced in the same box in the previous year (see Ghilain and Bélisle
5822008; Robillard et al. 2013). In this study, we showed that this trend also occurred at the farm
583level, even though the predictability of breeding success was moderate. Public information
584regarding reproductive success is thought to be the most robust and integrative form of social
585information about the consequences of local environmental factors on this fitness component
586(Valone and Templeton, 2002; Doligez *et al.*, 2003; Seppänen *et al.*, 2007). Yet we found that
587public information led to a slight but significant mismatch between habitat preference and
588quality in early settlers, whose fledging success decreased with the mean number of nestlings
589fledged on the farm in the previous year. Nevertheless, early settlers' fledging success
590remained higher than that of late settlers and this potential ecological trap may only have a
591limited impact on population dynamics. The mechanism underlying this putative trap is
592unclear but is likely to result from one or more factors that were not measured in this study
593and that are correlated to past breeding success rather than to breeding success itself, or from a
594statistical artifact whereby high annual breeding success estimates punctually "regress to the
595mean" (Barnett, 2004).

596Temporal constraints

Relationships between cues and breeding success varied according to the timing at which tree swallows settled in nest boxes, which underlines the relevance of considering different behavioral adaptive outcomes for individuals that may experience different constraints when studying habitat selection. Indeed, we showed that early and late settlers faced different selective pressures along the breeding season likely due to differential experience, body condition or timing (breeding phenology). At our latitudes, time constraints can induce such interindividual disparity because breeding conditions peak in quality over a short period and may thereby lead to phenological mismatches (Bourret *et al.*, 2015; Visser and Gienapp, 2019). Moreover, individuals that settle later benefit from less nest site options and, assuming they arrive later on breeding grounds, may also have less time for exploration which can lead to decisions based on poor or incomplete knowledge (Orians and Wittenberger, 1991). While late settlers often make poorer habitat choices due to time constraints, we also detected mismatches between preference and habitat quality in early settlers due to heterospecific competition. Our results emphasize the ecological importance of phenological (Visser and Gienapp, 2019) and phenotypic (Edelaar, Siepielski and Clobert, 2008; Matthysen, 2012) (mis)matches and support the hypothesis that there may be costs to breed either too early or too late.

It is worth mentioning that our estimate of nest site preference is imperfect. Indeed, settlement patterns may not directly represent habitat preference if there are alternative selection strategies among individuals, for example within and among age classes (Robertson and Hutto 2006). Yet, our three-category estimate of preference, integrating two rather than just one

618commonly used surrogates of habitat preference, should allow a good understanding of the
619habitat selection process used by tree swallows as it discriminates the choice of occupying a
620nest site and the timing of that choice. Interestingly, it is not excluded that the preference
621patterns we observed have a genetic component, especially since a previous study found some
622evidence of spatial genetic structure across our study area for a candidate gene that is related
623to the timing of migration in passerines. Thus the settlement patterns observed here may have
624a genetic basis (Bourret and Garant, 2015).

625Our proxies of habitat quality, that is the number of hatchlings and fledging success, only
626represent the reproductive success at the nesting stage. Because we did not investigate adult
627survival, post-fledging survival or recruitment rate, our habitat quality proxies are not
628perfectly representative of fitness experienced by individuals using a given habitat (Johnson,
6292007), especially since post-fledging and adult survival likely depends on physiological,
630phenological and environmental factors (Naef-Daenzer, Widmer and Nuber, 2001; Greño,
631Belda and Barba, 2007; Clark *et al.*, 2018; Boynton, Mahony and Williams, 2020; Evans *et*
632*al.*, 2020). Nonetheless, fledging success and number of fledglings are among the most
633important determinants of population growth and lifetime reproductive success in this species
634(Cox *et al.*, 2018; Berzins *et al.*, 2020). More research is needed to determine the demographic
635consequences of the nonideal behaviors we identified and their potential impact on long-term
636population growth. For instance, assessing demographic rates associated with different habitat
637types in order to investigate whether local tree swallow populations of our study area are

638subjected to a source-sink dynamic resulting from an ecological trap would be a valuable
639complement to the current study.

640We found that landscape context, spring food availability and social information from both
641hetero- and conspecifics influence tree swallows' nest site preference. Relying on multiple
642cues for assessing habitat quality may render this species less susceptible to making bad
643habitat choices and fall into a severe ecological trap (Valone and Templeton, 2002; Pärt *et al.*,
6442011; Hale, Treml and Swearer, 2015). Yet, by investigating the relationships between habitat
645characteristics and quality, we also identified several settlement decisions suggestive of
646ecological traps. Contrary to our hypothesis, we found the most severe mismatches between
647nest site preference and fitness outcome to be associated with the use of hetero- and
648conspecific social information. Given these results, there is thus evidence that farmlands can
649potentially lead to an ecological trap via different mechanisms, including landscape
650modifications, low within-season insect predictability, the presence of house sparrows as nest
651site competitors, and nest boxes creating supra-optimal densities. This has some implications
652regarding the decline of farmland birds, which has been attributed to habitat loss and
653alteration, interference with farming equipment, direct (toxicological) and indirect (trophic)
654effects of pesticide use (Stanton, Morrissey and Clark, 2018). Moreover, our study has
655implications for the use of nest boxes as a conservation and research tool (Møller and Møller,
6561992; Lambrechts *et al.*, 2010). Indeed, natural cavities are often limited in numbers, and
657artificial ones can be provided with the potential consequence of attracting birds into novel or
658improper breeding habitats (Holt and Martin, 1997; Newton, 1998; Maicas *et al.*, 2012).

659Although the implementation of nest boxes is an interesting tool to manipulate a species and
660assess its response to different ecological conditions, care must also be taken regarding the
661generality of conclusions obtained in such studies and their use to understand the fundamental
662ecology of species under natural conditions.

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665References

666Agriculture and Agri-Food Canada (AAFC) (2018) *Annual Crop Inventory*,

667<https://open.canada.ca/data/en/dataset/>.

668Barnett, A. G. (2004) 'Regression to the mean: what it is and how to deal with it', *International Journal*

669*of Epidemiology*, 34(1), pp. 215–220. doi: 10.1093/ije/dyh299.

670Barta, Z. and Giraldeau, L. A. (2001) 'Breeding colonies as information centers: a reappraisal of

671information-based hypotheses using the producer-scrourer game', *Behavioral Ecology*, 12(2), pp.

672121–127. doi: 10.1093/beheco/12.2.121.

673Battin, J. (2004) 'When good animals love bad habitats: Ecological traps and the conservation of

674animal populations', *Conservation Biology*, 18(6), pp. 1482–1491. doi: 10.1111/j.1523-

6751739.2004.00417.x.

676Bélanger, L. and Grenier, M. (2002) 'Agriculture intensification and forest fragmentation in the St.

677Lawrence valley, Québec, Canada', *Landscape Ecology*, 17(6), pp. 495–507. doi:

67810.1023/A:1021443929548.

679Bellavance, V. *et al.* (2018) 'Influence of agricultural intensification on prey availability and nestling

680diet in Tree Swallows (*Tachycineta bicolor*)', *Canadian Journal of Zoology*, 96(9), pp. 1053–1065. doi:

68110.1139/cjz-2017-0229.

682Benton, T. G., Vickery, J. A. and Wilson, J. D. (2003) 'Farmland biodiversity: Is habitat heterogeneity

683the key?', *Trends in Ecology and Evolution*, 18(4), pp. 182–188. doi: 10.1016/S0169-5347(03)00011-9.

684Berzins, L. L. *et al.* (2020) 'The relative contribution of individual quality and changing climate as

685drivers of lifetime reproductive success in a short-lived avian species', *Scientific Reports*, 10(1), pp. 1–
68612. doi: 10.1038/s41598-020-75557-w.

687Blann, K. L. *et al.* (2009) 'Effects of Agricultural Drainage on Aquatic Ecosystems: A Review', *Critical*
688*Reviews in Environmental Science and Technology*, 39(11), pp. 909–1001. doi:
68910.1080/10643380801977966.

690Boatman, N. D. *et al.* (2004) 'Evidence for the indirect effects of pesticides on farmland birds', *Ibis*,
691146(Suppl. 2), pp. 131–143. doi: 10.1111/j.1474-919X.2004.00347.x.

692Bollinger, E. K. (1995) 'Successional Changes and Habitat Selection in Hayfield Bird Communities', *The*
693*Auk*, 112(3), pp. 720–730. doi: 10.1093/auk/112.3.720.

694Bollinger, E. K., Bollinger, P. B. and Gavin, T. A. (1990) 'Effects of Hay-Cropping on Eastern Populations
695of the Bobolink', *Wildlife Society Bulletin*, 18(2), pp. 142–150.

696Botías, C. *et al.* (2019) 'Impact of pesticide use on the flora and fauna of field margins and
697hedgerows', in *The ecology of hedgerows and field margins*. Routledge, New York, USA, pp. 90–109.

698Boulinier, T. and Danchin, E. (1997) 'The use of conspecific reproductive success for breeding patch
699selection in terrestrial migratory species', *Evolutionary Ecology*, 11(5), pp. 505–517. doi:
70010.1007/s10682-997-1507-0.

701Bourret, A. *et al.* (2015) 'Multidimensional environmental influences on timing of breeding in a tree
702swallow population facing climate change', *Evolutionary Applications*, 8(10), pp. 933–944. doi:
70310.1111/eva.12315.

704Bourret, A. and Garant, D. (2015) 'Candidate gene-environment interactions and their relationships

705with timing of breeding in a wild bird population', *Ecology and Evolution*, 5(17), pp. 3628–3641. doi:
70610.1002/ece3.1630.

707Boynton, C. K., Mahony, N. A. and Williams, T. D. (2020) 'Barn Swallow (*Hirundo rustica*) fledglings use
708crop habitat more frequently in relation to its availability than pasture and other habitat types', *The*
709*Condor*, 122(2), p. duz067. doi: 10.1093/condor/duz067.

710Brooks, M. E. *et al.* (2019) 'Statistical modeling of patterns in annual reproductive rates', *Ecology*,
711100(7), pp. 1–7. doi: 10.1002/ecy.2706.

712Brown, C. R. (1988) 'Enhanced Foraging Efficiency Through Information Centers: A Benefit of
713Coloniality in Cliff Swallows', *Ecology*, 69(3), pp. 602–613. doi: 10.2307/1941009.

714Brown, C. R. and Brown, M. B. (1996) *Coloniality in the Cliff Swallow: The Effect of Group Size on Social*
715*Behavior*. University of Chicago Press.

716Bruun, M. and Smith, H. G. (2003) 'Landscape composition affects habitat use and foraging flight
717distances in breeding European starlings', *Biological Conservation*, 114(2), pp. 179–187. doi: 10.1016/
718S0006-3207(03)00021-1.

719Burke, D. M. and Nol, E. (1998) 'Influence of Food Abundance, Nest-Site Habitat, and Forest
720Fragmentation on Breeding Ovenbirds', *The Auk*, 115(1), pp. 96–104. doi: 10.2307/4089115.

721Burnham, K. P. and Anderson, D. R. (2002) *Model Selection and Multimodel Inference: A Practical*
722*Information-Theoretic Approach*. 2nd edn, Springer. 2nd edn. New York: Springer. doi:
72310.1177/0049124104268644.

724Catry, I., Franco, A. M. A. and Moreira, F. (2014) 'Easy but ephemeral food: exploring the trade-offs of

725agricultural practices in the foraging decisions of Lesser Kestrels on farmland', *Bird Study*. Taylor &
726Francis, 61(4), pp. 447–456. doi: 10.1080/00063657.2014.953031.

727Chalfoun, A. D., Thompson, F. R. and Ratnaswamy, M. J. (2002) 'Nest predators and fragmentation: A
728review and meta-analysis', *Conservation Biology*, 16(2), pp. 306–318. doi: 10.1046/j.1523-
7291739.2002.00308.x.

730Clark, R. G. *et al.* (2018) 'Geographic variation and environmental correlates of apparent survival rates
731in adult tree swallows *Tachycineta bicolor*', *Journal of Avian Biology*, 49(6), pp. 1–13. doi:
73210.1111/jav.01659.

733Cox, A. R. *et al.* (2018) 'Demographic drivers of local population decline in Tree Swallows (*Tachycineta*
734*bicolor*) in Ontario, Canada', *The Condor*, 120(4), pp. 842–851. doi: 10.1650/CONDOR-18-42.1.

735Cox, A. R. *et al.* (2019) 'Rainy springs linked to poor nestling growth in a declining avian aerial
736insectivore (*Tachycineta bicolor*)', *Proceedings of the Royal Society B: Biological Sciences*, 286(1898),
737p. 20190018. doi: 10.1098/rspb.2019.0018.

738Daoust, S. P. *et al.* (2012) 'Direct and indirect effects of landscape structure on a tri-trophic system
739within agricultural lands', *Ecosphere*, 3, pp. 1–19. doi: 10.1890/ES12-00300.1.

740Delibes, M., Gaona, P. and Ferreras, P. (2001) 'Effects of an Attractive Sink Leading into Maladaptive
741Habitat Selection', *The American Naturalist*, 158(3), pp. 277–285.

742Doligez, B. (2002) 'Public Information and Breeding Habitat Selection in a Wild Bird Population',
743*Science*, 297(5584), pp. 1168–1170. doi: 10.1126/science.1072838.

744Doligez, B. *et al.* (2003) 'When to use public information for breeding habitat selection? The role of

environmental predictability and density dependence', *Animal Behaviour*, 66(5), pp. 973–988. doi: 10.1006/anbe.2002.2270.

Duchet, C. *et al.* (2018) 'Pesticide-mediated trophic cascade and an ecological trap for mosquitoes', *Ecosphere*, 9(4), pp. 498–513. doi: 10.1002/ecs2.2179.

Dunn, P. O. and Winkler, D. W. (1999) 'Climate Change Has Affected the Breeding Date of Tree Swallows', *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 266(1437), pp. 2487–2490.

Edelaar, P., Siepielski, A. M. and Clobert, J. (2008) 'Matching habitat choice causes directed gene flow: A neglected dimension in evolution and ecology', *Evolution*, 62(10), pp. 2462–2472. doi: 10.1111/j.1558-5646.2008.00459.x.

Elgin, A. S., Clark, R. G. and Morrissey, C. A. (2020) 'Tree Swallow selection for wetlands in agricultural landscapes predicted by central-place foraging theory', *The Condor*, 122(4), p. duaa039. doi: 10.1093/condor/duaa039.

Eng, M. L., Stutchbury, B. J. M. and Morrissey, C. A. (2019) 'A neonicotinoid insecticide reduces fueling and delays migration in songbirds', *Science*, 365, pp. 1177–1180.

English, P. A. *et al.* (2017) 'Habitat and food supply across multiple spatial scales influence the distribution and abundance of a nocturnal aerial insectivore', *Landscape Ecology*. Springer Netherlands, 32(2), pp. 343–359. doi: 10.1007/s10980-016-0454-y.

Evans, D. R. *et al.* (2020) 'Individual condition, but not fledging phenology, carries over to affect post-fledging survival in a Neotropical migratory songbird', *Ibis*, 162(2), pp. 331–344. doi: 10.1111/ibi.12727.

766Evans, K. L., Bradbury, R. B. and Wilson, J. D. (2003) 'Selection of hedgerows by Swallows *Hirundo*
767*rustica* foraging on farmland: the influence of local habitat and weather', *Bird Study*, 50(1), pp. 8–14.
768doi: 10.1080/00063650309461284.

769Fisher, R. J. and Wiebe, K. L. (2006) 'Nest site attributes and temporal patterns of northern flicker nest
770loss: effects of predation and competition', *Oecologia*, 147(4), pp. 744–753. doi: 10.1007/s00442-005-
7710310-2.

772Forsman, J. T. *et al.* (1998) 'Heterospecific attraction and food resources in migrants' breeding patch
773selection in northern boreal forest', *Oecologia*, 115(1–2), pp. 278–286. doi: 10.1007/s004420050517.

774Forsman, J. T., Seppänen, J.-T. and Mönkkönen, M. (2002) 'Positive fitness consequences of
775interspecific interaction with a potential competitor', *Proceedings of the Royal Society of London.*
776*Series B: Biological Sciences*, 269(1500), pp. 1619–1623. doi: 10.1098/rspb.2002.2065.

777Francis, C. M. and Cooke, F. (1986) 'Differential Timing of Spring Migration in Wood Warblers
778(*Parulinae*)', 103(3), pp. 548–556.

779Fretwell, S. D. and Lucas, H. L. (1970) 'On territorial behavior and other factors influencing habitat
780distribution in birds', *Acta Biotheoretica*, 19(1), pp. 16–36. doi: 10.1007/BF01601953.

781Frey-Roos, F., Brodmann, P. A. and Reyer, H.-U. (1995) 'Relationships between food resources,
782foraging patterns, and reproductive success in the water pipit, *Anthus sp. Spinoletta*', *Behavioral*
783*Ecology*, 6(3), pp. 287–295. doi: 10.1093/beheco/6.3.287.

784Gervais, J. A., Rosenberg, D. K. and Anthony, R. G. (2003) 'Space Use and Pesticide Exposure Risk of
785Male Burrowing Owls in an Agricultural Landscape', *The Journal of Wildlife Management*, 67(1), p.
786155. doi: 10.2307/3803071.

787 Ghilain, A. and Bélisle, M. (2008) 'Breeding success of Tree Swallows along a gradient of agricultural
788 intensification', *Ecological Applications*, 18(5), pp. 1140–1154. doi: 10.1890/07-1107.1.

789 Gibbons, D., Morrissey, C. and Mineau, P. (2015) 'A review of the direct and indirect effects of
790 neonicotinoids and fipronil on vertebrate wildlife', *Environmental Science and Pollution Research*,
791 22(1), pp. 103–118. doi: 10.1007/s11356-014-3180-5.

792 Gilroy, J. J. and Sutherland, W. J. (2007) 'Beyond ecological traps: perceptual errors and undervalued
793 resources', *Trends in Ecology and Evolution*, 22(7), pp. 351–356. doi: 10.1016/j.tree.2007.03.014.

794 Giroux, I. (2019) *Présence de pesticides dans l'eau au Québec : Portrait et tendances dans les zones de*
795 *maïs et de soya – 2015 à 2017, Québec, ministère de l'Environnement et de la Lutte contre les*
796 *changements climatiques, Direction générale du suivi de l'état de l'environnement*. doi: .1037//0033-
797 2909.126.1.78.

798 Greño, J. L., Belda, E. J. and Barba, E. (2007) 'Influence of temperatures during the nestling period on
799 post-fledging survival of great tit *Parus major* in a Mediterranean habitat', *Journal of Avian Biology*,
800 39, pp. 41–49. doi: 10.1111/j.2007.0908-8857.04120.x.

801 Griffith, S. C., Owens, I. P. F. and Thuman, Katherine, A. (2002) 'Extra pair paternity in birds : a review
802 of interspecific', *Molecular Ecology*, 11, pp. 2195–2212.

803 Gruebler, M., Morand, M. and Naef-Daenzer, B. (2008) 'A predictive model of the density of airborne
804 insects in agricultural environments', *Agriculture, Ecosystems & Environment*, 123(1–3), pp. 75–80.
805 doi: 10.1016/j.agee.2007.05.001.

806 Hale, R. and Swearer, S. E. (2016) 'Ecological traps: current evidence and future directions',
807 *Proceedings of the Royal Society B: Biological Sciences*, 283(1824), p. 20152647. doi:

80810.1098/rspb.2015.2647.

809Hale, R., Tremblay, E. A. and Swearer, S. E. (2015) 'Evaluating the metapopulation consequences of
810ecological traps', *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 282(1804),
811p. 20142930. doi: <http://dx.doi.org/10.1098/rspb.2014.2930>.

812Hallmann, C. A. *et al.* (2014) 'Declines in insectivorous birds are associated with high neonicotinoid
813concentrations', *Nature*. Nature Publishing Group, 511(7509), pp. 341–343. doi:
81410.1038/nature13531.

815Harrell, F. E. (2015) *Regression Modeling Strategies*. Cham: Springer International Publishing (Springer
816Series in Statistics). doi: 10.1007/978-3-319-19425-7.

817Hildén, O. (1965) 'Habitat selection in birds : A review', *Annales Zoologici Fennici*, 2(1), pp. 53–75.

818Hollander, F. A. *et al.* (2011) 'Maladaptive Habitat Selection of a Migratory Passerine Bird in a Human-
819Modified Landscape', *PLoS ONE*, 6(9), p. e25703. doi: 10.1371/journal.pone.0025703.

820Holt, R. F. and Martin, K. (1997) 'Landscape Modification and Patch Selection : The Demography of
821Two Secondary Cavity Nesters Colonizing Clearcuts', *The Auk*, 114(3), pp. 443–455.

822Jobin, B. *et al.* (2003) 'Landscape changes and ecological studies in agricultural regions, Québec,
823Canada', *Landscape Ecology*, 18(6), pp. 575–590. doi: 10.1023/A:1026047625427.

824Johnson, D. H. (1980) 'The Comparison of Usage and Availability Measurements for Evaluating
825Resource Preference', *Ecology*, 61(1), pp. 65–71. doi: 10.2307/1937156.

826Johnson, M. D. (2007) 'Measuring Habitat Quality : a Review', *The Condor*, 109(3), pp. 489–504.

827Jones, J. (2003) 'Tree Swallows (*Tachycineta bicolor*): A New Model Organism?', *The Auk*, 120(3), pp.

828591–599. doi: 10.2307/4090091.

829Kautz, A. R. and Gardiner, M. M. (2019) 'Agricultural intensification may create an attractive sink for
830Dolichopodidae, a ubiquitous but understudied predatory fly family', *Journal of Insect Conservation*.
831Springer International Publishing, 23(3), pp. 453–465. doi: 10.1007/s10841-018-0116-2.

832King, A. J. and Cowlshaw, G. (2007) 'When to use social information: the advantage of large group
833size in individual decision making', *Biology Letters*, 3(2), pp. 137–139. doi: 10.1098/rsbl.2007.0017.

834Kivelä, S. M. *et al.* (2014) 'The past and the present in decision-making: the use of conspecific and
835heterospecific cues in nest site selection', *Ecology*, 95(12), pp. 3428–3439. doi: 10.1890/13-2103.1.

836Kristan, W. B. (2003) 'The Role of Habitat Selection Behavior in Population Dynamics : Source-Sink
837Systems and Ecological Traps', *Oikos*, 103(3), pp. 457–468.

838Lagrange, P. *et al.* (2017) 'Assessment of individual and conspecific reproductive success as
839determinants of breeding dispersal of female tree swallows: A capture–recapture approach', *Ecology*
840*and Evolution*, 7(18), pp. 7334–7346. doi: 10.1002/ece3.3241.

841Lahti, D. C. (2001) 'The “edge effect on nest predation” hypothesis after twenty years', *Biological*
842*Conservation*, 99(3), pp. 365–374. doi: 10.1016/S0006-3207(00)00222-6.

843Lambrechts, M. M. *et al.* (2010) 'The Design of Artificial Nestboxes for the Study of Secondary Hole-
844Nesting Birds: A Review of Methodological Inconsistencies and Potential Biases', *Acta Ornithologica*,
84545(1), pp. 1–26. doi: 10.3161/000164510X516047.

846Lessard, A. *et al.* (2014) 'Individual and environmental determinants of reproductive success in male
847tree swallow (*Tachycineta bicolor*)', *Behavioral Ecology and Sociobiology*, 68(5), pp. 733–742. doi:

84810.1007/s00265-014-1686-y.

849Lowther, P. E. and Cink, C. L. (2006) *House Sparrow* (*Passer domesticus*), *The Birds of North America*
850Online. Edited by A. F. Poole. doi: 10.2173/bna.12.

851Lozano, G. A., Perreault, S. and Lemon, R. E. (1996) 'Age, Arrival Date and Reproductive Success of
852Male American Redstarts *Setophaga ruticilla*', *Journal of Avian Biology*, 27(2), pp. 164–170.

853Maícas, R. *et al.* (2012) 'Nest-site selection, territory quality and breeding performance in a Blue Tit
854*Cyanistes caeruleus* population', *Acta Oecologica*, 39, pp. 43–50. doi: 10.1016/j.actao.2011.11.004.

855Martin, T. E. (1998) 'Are microhabitat preferences of coexisting species under selection and
856adaptive?', *Ecology*, 79(2), pp. 656–670. doi: 10.1890/0012-9658(1998)079[0656:AMPOCS]2.0.CO;2.

857Matthysen, E. (2012) 'Multicausality of dispersal: a review', in Clobert, J. *et al.* (eds) *Dispersal Ecology*
858*and Evolution*. Oxford University Press, pp. 3–18. doi: 10.1093/acprof:oso/9780199608898.003.0001.

859McCarty, John P. and Winkler, D. W. (1999) 'Foraging Ecology and Diet Selectivity of Tree Swallows
860Feeding Nestlings', *The Condor*, 101(2), pp. 246–254.

861McCarty, John P and Winkler, D. W. (1999) 'Relative importance off environmental variables in
862determining the growth of nestling Tree Swallows *Tachycineta bicolor*', *Ibis*, 141(1 999), pp. 286–296.
863doi: 10.1111/j.1474-919X.1999.tb07551.x.

864Michel, N. L. *et al.* (2016) 'Differences in spatial synchrony and interspecific concordance inform guild-
865level population trends for aerial insectivorous birds', *Ecography*, 39(8), pp. 774–786. doi:
86610.1111/ecog.01798.

867Michelson, C. I., Clark, R. G. and Morrissey, C. A. (2018) 'Agricultural land cover does not affect the

868diet of Tree Swallows in wetland-dominated habitats', *The Condor*, 120(4), pp. 751–764. doi: 10.1650/
869CONDOR-18-16.1.

870Millet, A. *et al.* (2015) 'Patterns of Fluctuating Selection on Morphological and Reproductive Traits in
871Female Tree Swallow (*Tachycineta bicolor*)', *Evolutionary Biology*, 42(3), pp. 349–358. doi:
87210.1007/s11692-015-9333-8.

873Mingju, E. *et al.* (2019) 'Old nest material functions as an informative cue in making nest - site
874selection decisions in the European Kestrel (*Falco tinnunculus*)', *Avian Research*. BioMed Central,
87510(43), pp. 1–8. doi: 10.1186/s40657-019-0182-5.

876Mitra, A., Chatterjee, C. and Mandal, F. B. (2011) 'Synthetic Chemical Pesticides and Their Effects on
877Birds', *Research Journal of Environmental Toxicology*, 5(2), pp. 81–96. doi: 10.3923/rjet.2011.81.96.

878Møller, A. P. (1989) 'Parasites, Predators and Nest Boxes: Facts and Artefacts in Nest Box Studies of
879Birds?', *Oikos*, 56(3), p. 421. doi: 10.2307/3565628.

880Møller, A. P. (1994) 'Phenotype-dependent arrival time and its consequences in a migratory bird',
881*Behavioral Ecology and Sociobiology*, 35(2), pp. 115–122. doi: 10.1007/BF00171501.

882Møller, A. P. (2003) 'Extrapair paternity in relation to sexual ornamentation, arrival date, and
883condition in a migratory bird', *Behavioral Ecology*, 14(5), pp. 707–712. doi: 10.1093/beheco/arg051.

884Møller, A. P. and Moller, A. P. (1992) 'Nest Boxes and the Scientific Rigour of Experimental Studies',
885*Oikos*, 63(2), pp. 309–311. doi: 10.2307/3545393.

886Mönkkönen, M. *et al.* (1999) 'Evolution of heterospecific attraction: using other species as cues in
887habitat selection', *Evolutionary Ecology*, 13(1), pp. 93–106. doi: 10.1023/A:1006590215306.

888Mönkkönen, M., Helle, P. and Soppela, K. (1990) 'Numerical and behavioural responses of migrant
889passerines to experimental manipulation of resident tits (*Parus* spp.): heterospecific attraction in
890northern breeding bird communities?', *Oecologia*, 85(2), pp. 218–225. doi: 10.1007/BF00319404.

891Montiel-León, J. M. et al. (2019) 'Widespread occurrence and spatial distribution of glyphosate,
892atrazine, and neonicotinoids pesticides in the St. Lawrence and tributary rivers', *Environmental*
893*Pollution*, 250, pp. 29–39. doi: 10.1016/j.envpol.2019.03.125.

894Morris, A. J. et al. (2005) 'Indirect effects of pesticides on breeding yellowhammer (*Emberiza*
895*citrinella*)', *Agriculture, Ecosystems & Environment*, 106(1), pp. 1–16. doi:
89610.1016/j.agee.2004.07.016.

897Morris, A. J. and Gilroy, J. J. (2008) 'Close to the edge: predation risks for two declining farmland
898passerines', *Ibis*, 150(SUPPL.1), pp. 168–177. doi: 10.1111/j.1474-919X.2008.00857.x.

899Morris, D. W. (2003) 'Toward an Ecological Synthesis : A Case for Habitat Selection', *Oecologia*,
900136(1), pp. 1–13.

901Morrissey, C. A. et al. (2015) 'Neonicotinoid contamination of global surface waters and associated
902risk to aquatic invertebrates: A review', *Environment International*. Elsevier Ltd, 74, pp. 291–303. doi:
90310.1016/j.envint.2014.10.024.

904Mulé, R. et al. (2017) 'Systematic Review of the Effects of Chemical Insecticides on Four Common
905Butterfly Families', *Frontiers in Environmental Science*, 5(JUN), pp. 1–5. doi:
90610.3389/fenvs.2017.00032.

907Naef-Daenzer, B., Widmer, F. and Nuber, M. (2001) 'Differential post-fledging survival of great and
908coal tits in relation to their condition and fledging date', *Journal of Animal Ecology*, 70(5), pp. 730–

909738. doi: 10.1046/j.0021-8790.2001.00533.x.

910Nebel, S. *et al.* (2010) 'Declines of Aerial Insectivores in North America Follow a Geographic Gradient',

911*Avian Conservation and Ecology*, 5(2). doi: 10.5751/ACE-00391-050201.

912Newton, I. (1998) *Population Limitation in Birds*. San Diego, California: Academic Press. doi:

91310.1016/B978-0-12-517365-0.X5000-5.

914Nocera, J. J., Forbes, G. J. and Giraldeau, L. A. (2006) 'Inadvertent social information in breeding site

915selection of natal dispersing birds', *Proceedings of the Royal Society B: Biological Sciences*, 273(1584),

916pp. 349–355. doi: 10.1098/rspb.2005.3318.

917Nooker, J. K., Dunn, P. O. and Whittingham, L. a (2005) 'Effects of food abundance, weather, and

918female condition on reproduction in tree swallows (*Tachycineta bicolor*)', *The Auk*, 122(4), pp. 1225–

9191238. doi: 10.1642/0004-8038(2005)122[{}1225:EOFAWA]2.0.CO;2.

920Norris, A. R. *et al.* (2018) 'Nest boxes increase reproductive output for Tree Swallows in a forest

921grassland matrix in central British Columbia', *PLOS ONE*, 13(10), p. e0204226. doi:

92210.1371/journal.pone.0204226.

923Orians, G. H. and Wittenberger, J. F. (1991) 'Spatial and Temporal Scales in Habitat Selection', *The*

924*American Naturalist*, 137, pp. S29–S29.

925Parejo, D. *et al.* (2008) 'Do great tits rely on inadvertent social information from blue tits? A habitat

926selection experiment', *Behavioral Ecology and Sociobiology*, 62(10), pp. 1569–1579. doi:

92710.1007/s00265-008-0586-4.

928Parejo, D., Danchin, E. and Avilés, J. M. (2005) 'The heterospecific habitat copying hypothesis: can

929competitors indicate habitat quality?', *Behavioral Ecology*, 16(1), pp. 96–105. doi:

93010.1093/beheco/arh136.

931Pärt, T. *et al.* (2011) 'Prospectors combine social and environmental information to improve habitat

932selection and breeding success in the subsequent year', *Journal of Animal Ecology*, 80(6), pp. 1227–

9331235. doi: 10.1111/j.1365-2656.2011.01854.x.

934Pärt, T., Arlt, D. and Villard, M. A. (2007) 'Empirical evidence for ecological traps: A two-step model

935focusing on individual decisions', *Journal of Ornithology*, 148(Suppl. 2), pp. S327–S332. doi:

93610.1007/s10336-007-0226-1.

937Perlut, N. G. *et al.* (2006) 'Grassland songbirds in a dynamic management landscape: behavioral

938responses and management strategies.', *Ecological applications : a publication of the Ecological*

939*Society of America*, 16(6), pp. 2235–47. doi: 10.1890/1051-0761(2006)016[2235:gsiadm]2.0.co;2.

940Petit, L. J. and Petit, D. R. (1996) 'Factors Governing Habitat Selection by Prothonotary Warblers: Field

941Tests of the Fretwell-Lucas models', *Source: Ecological Monographs Ecological Monographs*, 66(663),

942pp. 367–387. doi: 10.2307/2963523.

943Pisa, L. W. *et al.* (2015) 'Effects of neonicotinoids and fipronil on non-target invertebrates',

944*Environmental Science and Pollution Research*, 22(1), pp. 68–102. doi: 10.1007/s11356-014-3471-x.

945Porlier, M., Bélisle, M. and Garant, D. (2009) 'Non-random distribution of individual genetic diversity

946along an environmental gradient', *Philosophical Transactions of the Royal Society B: Biological*

947*Sciences*, 364(1523), pp. 1543–1554. doi: 10.1098/rstb.2009.0010.

948Reid, N., McDonald, R. A. and Montgomery, W. I. (2010) 'Homogeneous habitat can meet the discrete

949and varied resource requirements of hares but may set an ecological trap', *Biological Conservation*,

950143(7), pp. 1701–1706. doi: 10.1016/j.biocon.2010.03.041.

951Rendell, W. B. and Robertson, R. J. (1990) 'Influence of Forest Edge on Nest-Site Selection by Tree
952Swallows', *The Wilson Bulletin*, 102(4), pp. 634–644.

953Rioux Paquette, S. *et al.* (2013) 'Seasonal patterns in Tree Swallow prey (Diptera) abundance are
954affected by agricultural intensification', *Ecological Applications*, 23(1), pp. 122–133. doi: 10.1890/12-
9550068.1.

956Rioux Paquette, S. *et al.* (2014) 'Severe recent decrease of adult body mass in a declining
957insectivorous bird population', *Proceedings of the Royal Society B: Biological Sciences*, 281(May), p.
95820140649. doi: 10.1098/rspb.2014.0649.

959Robbins, C. S. (1981) 'Bird Activity Levels Related to Weather', *Studies in Avian Biology*, (6), pp. 301–
960310.

961Robertson, B. A. and Hutto, R. L. (2006) 'A Framework for Understanding Ecological Traps and an
962Evaluation of Existing Evidence', *Ecology*, 97(2), pp. 302–312. doi: 10.1890/07-1861.1.

963Robertson, B. A., Rehage, J. S. and Sih, A. (2013) 'Ecological novelty and the emergence of
964evolutionary traps', *Trends in Ecology and Evolution*. Elsevier Ltd, 28(9), pp. 552–560. doi:
96510.1016/j.tree.2013.04.004.

966Robertson, R. J. and Rendell, W. B. (1990) 'A comparison of the breeding ecology of a secondary
967cavity nesting bird, the Tree Swallow (*Tachycineta bicolor*), in nest boxes and natural cavities',
968*Canadian Journal of Zoology*, 68(5), pp. 1046–1052. doi: 10.1139/z90-152.

969Robillard, A., Garant, D. and Bélisle, M. (2013) 'The Swallow and the Sparrow: How agricultural

970intensification affects abundance, nest site selection and competitive interactions', *Landscape*
971*Ecology*, 28(2), pp. 201–215. doi: 10.1007/s10980-012-9828-y.

972Robles, H. and Martin, K. (2013) 'Resource Quantity and Quality Determine the Inter-Specific
973Associations between Ecosystem Engineers and Resource Users in a Cavity-Nest Web', *PLoS ONE*,
9748(9), p. e74694. doi: 10.1371/journal.pone.0074694.

975Rodenhouse, N. L. and Best, L. B. (1983) 'Breeding Ecology of Vesper Sparrows in Corn and Soybean
976Fields', *American Midland Naturalist*, 110(2), p. 265. doi: 10.2307/2425268.

977Rooneem, T. M. and Robertson, R. J. (1997) 'The potential to lay replacement clutches by tree
978swallows', *The Condor*, 99(1), pp. 228–231.

979Rotem, G. *et al.* (2013) 'Wheat fields as an ecological trap for reptiles in a semiarid agroecosystem',
980*Biological Conservation*. Elsevier Ltd, 167, pp. 349–353. doi: 10.1016/j.biocon.2013.08.028.

981Schlaepfer, M. A., Runge, M. C. and Sherman, P. W. (2002) 'Ecological and evolutionary traps', *Trends*
982*in Ecology and Evolution*, 17(10), pp. 474–480. doi: 10.1016/S0169-5347(02)02580-6.

983Seppänen, J.-T. *et al.* (2007) 'Social information use is a process across time, space, and ecology,
984reaching heterospecifics', *Ecology*, 88(7), pp. 1622–1633. doi: 10.1890/06-1757.1.

985Shutler, D. *et al.* (2012) 'Spatiotemporal Patterns in Nest Box Occupancy by Tree Swallows Across
986North America', *Avian Conservation and Ecology*, 7(1), p. 3. doi: 10.5751/ACE-00517-070103.

987Smith, R. J. F. (1986) 'Evolution of Alarm Signals: Role of Benefits of Retaining Group Members or
988Territorial Neighbors', *The American Naturalist*, 128(4), pp. 604–610. doi: 10.1086/284591.

989Stamps, J. A. (1988) 'Conspecific Attraction and Aggregation in Territorial Species', *The American*

990 *Naturalist*, 131(3), pp. 329–347. doi: 10.1086/284793.

991 Stamps, J. A. (2001) 'Habitat selection by dispersers : intergrating proximate and ultimate
992 approaches', in *Dispersal*, pp. 230–242.

993 Stamps, J. A., Krishnan, V. V. and Reid, M. L. (2005) 'Search Costs and Habitat Selection by Dispersers',
994 *Ecology*, 86(2), pp. 510–518. doi: 10.1890/04-0516.

995 Stamps, J. and Krishnan, V. V. (2005) 'Nonintuitive Cue Use in Habitat Selection', *Ecological Society of*
996 *America*, 89(11), pp. 2850–2861. doi: 10.1890/1.

997 Stanton, R. L., Morrissey, C. A. and Clark, R. G. (2016) 'Tree Swallow (*Tachycineta bicolor*) foraging
998 responses to agricultural land use and abundance of insect prey', *Canadian Journal of Zoology*, 94(9),
999 pp. 637–642. doi: 10.1139/cjz-2015-0238.

1000 Stanton, R. L., Morrissey, C. A. and Clark, R. G. (2018) 'Analysis of trends and agricultural drivers of
1001 farmland bird declines in North America: A review', *Agriculture, Ecosystems & Environment*. Elsevier,
1002 254(254), pp. 244–254. doi: 10.1016/j.agee.2017.11.028.

1003 De Steven, D. (1978) 'The influence of age on the breeding biology of the Tree Swallow *Iridoprocne*
1004 *Bicolor*', *Ibis*, 120(4), pp. 516–523. doi: 10.1111/j.1474-919X.1978.tb06817.x.

1005 Stutchbury, B. J. and Robertson, R. J. (1988) 'Within-season and age-related patterns of reproductive
1006 performance in female tree swallows (*Tachycineta bicolor*)', *Canadian Journal of Zoology*, 66(4), pp.
1007 827–834. doi: 10.1139/z88-122.

1008 Sutherland, W. J. (1996) *From Individual Behaviour to Population Ecology*. New York: Oxford
1009 University Press.

1010Switzer, P. V (1997) 'Past reproductive success affects future habitat selection', *Behavioral Ecology*
 1011*and Sociobiology*, 40(5), pp. 307–312. doi: 10.1007/s002650050346.

1012Takahashi, M. (2007) 'Oviposition site selection: Pesticide avoidance by gray treefrogs', *Environmental*
 1013*Toxicology and Chemistry*, 26(7), pp. 1476–1480. doi: 10.1897/06-511R.1.

1014Thomson, R. L., Forsman, J. T. and Mönkkönen, M. (2003) 'Positive interactions between migrant and
 1015resident birds: testing the heterospecific attraction hypothesis', *Oecologia*, 134(3), pp. 431–438. doi:
 101610.1007/s00442-002-1140-0.

1017Thorup, K. *et al.* (2017) 'Resource tracking within and across continents in long-distance bird
 1018migrants', *Science Advances*, 3(1), p. e1601360. doi: 10.1126/sciadv.1601360.

1019Touihri, M. *et al.* (2019) 'Effects of agricultural lands on habitat selection and breeding success of
 1020American kestrels in a boreal context', *Agriculture, Ecosystems & Environment*. Elsevier,
 1021272(November 2018), pp. 146–154. doi: 10.1016/j.agee.2018.11.017.

1022Turner, G. F. and Pitcher, T. J. (1986) 'Attack Abatement: A Model for Group Protection by Combined
 1023Avoidance and Dilution', *The American Naturalist*, 128(2), pp. 228–240.

1024Twining, C. W. *et al.* (2016) 'Omega-3 long-chain polyunsaturated fatty acids support aerial
 1025insectivore performance more than food quantity', *Proceedings of the National Academy of Sciences*
 1026*of the United States of America*, 113(39), pp. 10920–10925. doi: 10.1073/pnas.1603998113.

1027Twining, C. W., Shipley, J. R. and Winkler, D. W. (2018) 'Aquatic insects rich in omega-3 fatty acids
 1028drive breeding success in a widespread bird', *Ecology Letters*, 21(12), pp. 1812–1820. doi:
 102910.1111/ele.13156.

1030Valone, T. J. and Templeton, J. J. (2002) 'Public information for the assessment of quality: A
 1031widespread social phenomenon', *Philosophical Transactions of the Royal Society B: Biological*
 1032*Sciences*, 357(1427), pp. 1549–1557. doi: 10.1098/rstb.2002.1064.

1033Visser, M. E. and Gienapp, P. (2019) 'Evolutionary and demographic consequences of phenological
 1034mismatches', *Nature Ecology and Evolution*. Springer US, 3(6), pp. 879–885. doi: 10.1038/s41559-019-
 10350880-8.

1036Vonesh, J. R. and Buck, J. C. (2007) 'Pesticide alters oviposition site selection in gray treefrogs',
 1037*Oecologia*, 154(1), pp. 219–226. doi: 10.1007/s00442-007-0811-2.

1038Vonesh, J. R. and Kraus, J. M. (2009) 'Pesticide alters habitat selection and aquatic community
 1039composition', *Oecologia*, 160(2), pp. 379–385. doi: 10.1007/s00442-009-1301-5.

1040Walker, C. H. (2003) 'Neurotoxic pesticides and behavioural effects upon birds', *Ecotoxicology*, 12(1–
 10414), pp. 307–316. doi: 10.1023/A:1022523331343.

1042Ward, M. P. and Schlossberg, S. (2004) 'Conspecific Attraction and the Conservation of Territorial
 1043Songbirds', *Conservation Biology*, 18(2), pp. 519–525.

1044Winkler, D. W. et al. (2004) 'Breeding Dispersal and Philopatry in the Tree Swallow', *The Condor*,
 1045106(4), p. 768. doi: 10.1650/7634.

1046Winkler, D. W. et al. (2011) *Tree Swallow (Tachycineta bicolor)*, *The Birds of North America Online*.

1047Winkler, D. W. and Allen, P. E. (1996) 'The seasonal decline in tree swallow clutch size: Physiological
 1048constraint or strategic adjustment?', *Ecology*, 77(3), pp. 922–932. doi: 10.2307/2265512.

1049Zuur, A. F. et al. (2009) *Mixed effects models and extensions in ecology with R*, *Statistics for biology*

1050*and health*. New York, NY: Springer New York (Statistics for Biology and Health). doi: 10.1007/978-0-1051387-87458-6.

1052

Table 1. Justification of the explanatory variables used to assess the determinants of habitat preference and their impact on the reproductive success of tree swallows in a nest box network in southern Québec, Canada, between 2009 and 2018.

Explanatory variable	Type	Abbreviation	Justification
% Forest within 100 m of nest box	Landscape	Forest 100 m	Tree swallows settle first in nest sites far from forest edges to avoid interspecific competition and nest predation and to maximize flight area (Rendell and Robertson, 1990).
% Forage crops within 500 m of nest box		Forage crops 500 m	Nest box occupancy decreases with intensive cultures, while both number of fledglings and fledging probability increase with forage crops (hay, alfalfa and clover), pastures and natural grasslands (Ghilain and Bélisle, 2008).
Interaction % Forest within 500 m or 5 km × % Forage crops within 500 m or 5 km of nest box		Forest 500 m or 5 km × Forage crops 500 m or 5 km	Relative use and suitability of an open habitat may depend on its amount as well as on the amount and suitability of alternative habitats, and how they are arranged in space as this affects functional connectivity (Mysterud and Ims 1998, Sutherland 1996, Bruun and Smith 2003).
% Water + wetlands within 10 km of nest box		Water 10 km	Tree swallows are known to breed near water and wetlands over which they forage for insects of better nutritional quality (Winkler <i>et al.</i> , 2011; Twining <i>et al.</i> , 2016; Bellavance <i>et al.</i> , 2018; Twining, Shipley and Winkler, 2018). Agricultural intensification in southern Québec reduced wetlands (Bélanger and Grenier, 2002; Benton, Vickery and Wilson, 2003; Jobin <i>et al.</i> , 2003), and strongly contaminated surface waters with pesticides (Giroux 2019, Montiel-León <i>et al.</i> 2019), which may negatively affect swallows either directly through toxic effects or indirectly by reducing the availability of aquatic insects (Hallmann <i>et al.</i> , 2014; Gibbons, Morrissey and Mineau, 2015; Morrissey <i>et al.</i> , 2015).
Mean spring insect dry biomass on farm (g/day)	Food	Insects	Migrant aerial insectivores may be constrained to assess the quality of habitats based on the information available upon their arrival on breeding grounds, yet insect prey availability and quality can be modulated by an unpredictable use of pesticides in both space and time (Rioux Paquette <i>et al.</i> , 2013; Pisa <i>et al.</i> , 2015; Mulé <i>et al.</i> , 2017; Botías <i>et al.</i> , 2019). Prey availability is typically positively correlated to multiple reproductive success components in tree swallows (John P McCarty and Winkler, 1999; Nooner, Dunn and Whittingham, 2005).
Density of house sparrows on farm (no. nest boxes occupied)	Heterospecific social information	Competitor density	Tree swallow occupancy is negatively associated with house sparrow abundance, likely because of competition for nesting sites (Robillard, Garant and Bélisle, 2013).
Density of tree swallows on farm (no. nest boxes occupied) in the previous year	Conspecific social information	Density @ <i>t</i> -1	Cues associated to the location and breeding performance of conspecifics may act as reliable information integrating multiple environmental effects on breeding success (Boulinier and Danchin 1997, Valone and Templeton 2002). Conspecific aggregations may thus be attractive, inasmuch as they could also provide breeding benefits (Lombardo 1987; Lagrange <i>et al.</i> 2017; Pegan <i>et al.</i> 2018).
Mean no. fledglings on farm in the previous year		Success @ <i>t</i> -1	Individuals may use previous year breeding success cues at the farm or nest box level to guide settlement decisions (Lagrange <i>et al.</i> 2017).
Mean spring temperature on farm (°C)	Control		Higher spring temperatures are associated with earlier timing of breeding (Dunn and

Mean spring precipitations on farm (mm)	Winkler, 1999; Bourret <i>et al.</i> , 2015). Higher precipitations reduce insect and bird activity (Robbins, 1981; Gruebler, Morand and Naef-Daenzer, 2008; Cox <i>et al.</i> , 2019).
Longitude of nest box	Tree swallows settle earlier in the western part of the study system, possibly because they use the St. Lawrence River and some of its main tributaries as migratory routes (Porlier, Bélisle and Garant, 2009).
Latitude of nest box	Tree swallows arrive in the study system by the south, and breeding phenology is known to depend on latitude in our study system (Bourret <i>et al.</i> , 2015).

1053

Explanatory variables	Estimates (95% confidence intervals)						
	Preference <i>N</i> = 2915	Number of hatchlings				Fledging success	
		Early settlers <i>N</i> = 1268		Late settlers <i>N</i> = 891		Early settlers <i>N</i> = 953	Late settlers <i>N</i> = 644
		Conditional	Zero-inflated	Conditional	Zero-inflated		
Forest 100 m	-0.60 (-0.73, -0.48)						-0.45 (-0.69, -0.21)
Forest 500 m	0.03 (-0.18, 0.24)						-0.25 (-0.58, 0.08)
Forage crops 500 m	-0.03 (-0.22, 0.16)						-0.16 (-0.47, 0.16)
Forest 500 m × Forage crops 500 m	-0.30 (-0.49, -0.11)						-0.15 (-0.46, 0.16)
Water 10 km	-0.04 (-0.30, 0.21)						-0.11 (-0.51, 0.29)
Insect biomass	0.13 (0.02, 0.24)						
Competitor density	0.25 (0.13, 0.36)	-0.01 (-0.03, 0.01)	0.20 (0.01, 0.39)				
Density @ t-1	0.69 (0.56, 0.82)	0.02 (0.00, 0.04)	-0.16 (-0.36, 0.03)	0.02 (0.00, 0.04)	-0.10 (-0.28, 0.08)	-0.08 (-0.24, 0.09)	-0.44 (-0.62, -0.25)
Success @ t-1	0.40 (0.31, 0.50)	-0.01 (-0.02, 0.01)	-0.16 (-0.33, 0.01)	0.02 (0.00, 0.04)	-0.20 (-0.39, -0.01)	-0.24 (-0.36, -0.11)	0.42 (0.28, 0.57)
Temperature	0.00 (-0.13, 0.12)	-0.01 (-0.03, 0.00)	0.24 (-0.07, 0.56)	-0.02 (-0.05, 0.01)	0.04 (-0.15, 0.23)	0.26 (-0.05, 0.58)	-0.17 (-0.65, 0.30)
Precipitations	-0.14 (-0.23, -0.05)	0.01 (0.00, 0.03)	0.01 (-0.17, 0.19)	0.02 (0.00, 0.04)	-0.13 (-0.31, 0.05)	0.08 (-0.03, 0.19)	-0.02 (-0.15, 0.11)
Longitude	-0.13 (-0.38, 0.12)	0.01 (-0.01, 0.03)	0.09 (-0.09, 0.28)	0.01 (-0.01, 0.04)	0.03 (-0.16, 0.21)	0.23 (-0.10, 0.56)	0.18 (-0.19, 0.56)
Latitude	-0.15 (-0.35, 0.04)	-0.02 (-0.04, 0.00)	0.03 (-0.14, 0.20)	0.01 (-0.01, 0.03)	0.02 (-0.17, 0.21)	-0.17 (-0.48, 0.14)	-0.48 (-0.79, -0.18)

1054 **Table 2. Determinants of nest box preference in tree swallows and their effect on**
1055 **the reproductive success of early and late settlers in a nest box network in**
1056 **southern Québec, Canada, between 2009 and 2018.**

1057 Coefficients come from an ordinal logistic mixed regression for preference, a zero-inflated
1058 GLMM using generalized Poisson distribution and log link function for the number of
1059 hatchlings and GLMM using binomial error distribution and logit link function for fledging
1060 success. Predictors were standardized (zero mean, unit variance). For each analysis we present
1061 the coefficients of the model that ranked best in terms of AICc, their 95% confidence intervals
1062 and the sample size. See Table 1 for definitions the variables and Table A2 for results of the
1063 model selection. Estimates for which the confidence interval excludes zero are in bold.

1064 **Figure captions**

1065 **Figure 1. Distribution of the 40 farms in southern Québec, Canada, where nest box**
1066 **preference and breeding ecology of tree swallows were monitored between**
1067 **2009 and 2018 along a gradient of agricultural intensification. Land cover**
1068 **types are based on a mosaic of classified satellite images (Agriculture and**
1069 **Agri-Food Canada (AAFC) 2018). The study system is characterized by a**
1070 **gradient of intensive agriculture in the West (yellow) which shifts to a less**
1071 **intensive and more forested landscape in the East (light and dark green).**
1072 **Each farm is represented by a circle.**

1073 **Figure 2.** Decision tree leading to the classification of tree swallow's nest boxes in order
1074 of preference according to the presence of a laying event and the settlement
1075 date. Sample sizes (*N*) are presented for each category of preference for 400
1076 nest boxes between 2009 and 2018, for a total of 2735 observations.

1077 **Figure 3.** Predicted probabilities of a tree swallow nest box being classified in low,
1078 intermediate or high preference level (as defined in Fig. 2) in southern Québec,
1079 Canada, between 2009 and 2018, as a function of a) forest cover near nest box,
1080 b) cover of perennial forage crops and openness of landscape, c) food
1081 availability in spring, d) competitor density, e) density of breeders on a farm in
1082 the previous year and f) mean performance of breeders (number of fledglings)
1083 in the previous year. Inference was based on an ordinal mixed logistic
1084 regression (model #16 in Table A1). See Table A2 for details on model
1085 selection. Other variables in the model were kept at their average value. Shaded

1086 areas represent 95% confidence intervals. $N = 2915$ potential breeding attempts
1087 along 10 years on 40 farms.

1088 Figure 4. Averaged predicted fledging success of early and late settlers as a function of a)
1089 mean performance of breeders on a farm in the prior year forest, b) forest cover
1090 near the nest box and c) density of breeders on a farm in the prior year, for tree
1091 swallows in a nest box network in southern Québec, Canada between 2009 and
1092 2018. Multimodel inference was made on the list of models presented in Table
1093 A1, see Table A2 for the Akaike weights. Other variables in the model were
1094 kept at their average value. The points represent raw data and shaded areas are
1095 95% confidence intervals. Blue = early settlers, green = late settlers. $N=953$ for
1096 early settlers, $N= 644$ for late settlers.

1097 Figure A1. Results of the model selection by AICc aiming to identify key spatial scale at
1098 which the cover of a) forest, b) forage crops, and c) water bodies and wetlands
1099 most affect nest box preference in a tree swallow population breeding in
1100 farmlands in southern Québec, Canada, between 2009 and 2018.

1101 Figure A2. Correlation matrix of the explanatory variables used to assess the determinants
1102 of habitat preference and their impact on the reproductive success of tree
1103 swallows in a nest box network in southern Québec, Canada, between 2009 and
1104 2018. See Table 1 for the description and justification of the variables.

1105 Figure A3. The effect of agricultural intensity and openness of landscape within 5 km
1106 around nest box on a) nest box preference, b) probability of hatching failure of
1107 late settlers, and c) fledging success of early settlers for tree swallows in a

1108 gradient of agricultural intensification in southern Québec, Canada, between
1109 2009 and 2018. Preference predictions were based on an ordinal mixed logistic
1110 regression (model #16 in Table A1). $N = 2915$ potential breeding attempts.
1111 Probability of hatching failure model-averaged predictions were made on the
1112 list of models presented in Table A1. $N = 891$ clutches. Fledging success model-
1113 averaged predictions were made on the list of models presented in Table A1.
1114 $N = 953$ broods. See Table A5 Akaike weights of each analysis. Other variables
1115 in the models were kept at their average value. Shaded areas represent 95%
1116 confidence intervals.

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1121**Data Accessibility Statement**

1122Full dataset will be archived in Dryad upon acceptance.

1123

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1132Appendix

1133

1134Some of our explanatory variables, notably landscape-related ones, showed correlations (Fig.
1135A2). High forest cover within 500 m was associated with high forest cover within 100 m ($r =$
11360.42) and high cover of water bodies and wetland within 10 km ($r = 0.45$), which in turn was
1137associated with high cover in forage crops in 500 m ($r = 0.54$). Those landscape variables were
1138also associated with a longitudinal gradient, with more forest within 500 m, forage crops
1139within 500 m and water within 10 km in the eastern part of the system ($r = 0.46, 0.60$ and
11400.63). Water in 10 km also followed a latitudinal gradient, being more abundant in the South (r
1141 $= -0.51$). Finally, a high density of house sparrow on a farm was associated with a low density
1142of tree swallow in the previous year ($r = -0.46$).

1143

1144**Table A1. List of the candidate models used to assess the determinants of habitat**
1145**preference and their impact on the reproductive success of tree swallows in**
1146**a nest box network in southern Québec, Canada, between 2009 and 2018.**

#	Candidate model
0	~ Null
1	~ Control
2	~ Landscape + Control
3	~ Food + Control
4	~ Heterospecific social information + Control
5	~ Conspecific social information + Control
6	~ Landscape + Food + Control
7	~ Landscape + Heterospecific social information + Control
8	~ Landscape + Conspecific social information + Control
9	~ Food + Heterospecific social information + Control
10	~ Food + Conspecific social information + Control
11	~ Heterospecific social information + Conspecific social information + Control
12	~ Landscape + Food + Heterospecific social information + Control
13	~ Landscape + Food + Conspecific social information + Control
14	~ Landscape + Heterospecific social information + Conspecific social information + Control
15	~ Food + Heterospecific social information + Conspecific social information + Control
16	~ Landscape + Food + Heterospecific social information + Conspecific social information + Control

1147Landscape, food, heterospecific and conspecific social information and control refer to the
1148categories of predictors presented in Table 1.

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Table A2. Results of the model selections made on the candidate models presented in
Table A1 for the different response variables: nest box preference, number

of hatchlings and fledging success of tree swallows in southern Québec, Canada, between 2009 and 2018.

Candidate model	Preference			Number of hatchlings						Fledging success					
				Early settlers			Late settlers			Early settlers			Late settlers		
	K	$\Delta AICc$	w	K	$\Delta AICc$	w	K	$\Delta AICc$	w	K	$\Delta AICc$	w	K	$\Delta AICc$	w
0	5	288.95	0.00	7	23.34	0.00	7	1.13	0.26	4	7.14	0.01	4	55.86	0.00
1	9	280.91	0.00	15	19.24	0.00	15	7.94	0.01	8	10.69	0.00	8	58.51	0.00
2	14	168.94	0.00	25	33.50	0.00	25	15.21	0.00	13	15.04	0.00	13	50.17	0.00
3	10	282.33	0.00	17	19.32	0.00	17	10.69	0.00	9	11.08	0.00	9	55.57	0.00
4	10	280.73	0.00	17	2.88	0.08	17	7.74	0.01	9	12.71	0.00	9	60.56	0.00
5	11	121.05	0.00	19	1.24	0.18	19	0.00	0.45	10	0.00	0.36	10	13.08	0.00
6	15	170.05	0.00	27	33.90	0.00	27	18.85	0.00	14	15.31	0.00	14	49.48	0.00
7	15	170.11	0.00	27	17.44	0.00	27	15.20	0.00	14	17.02	0.00	14	52.26	0.00
8	16	15.91	0.00	29	16.26	0.00	29	10.88	0.00	15	3.20	0.07	15	0.00	0.31
9	11	282.11	0.00	19	4.32	0.04	19	10.40	0.00	10	13.04	0.00	10	57.63	0.00
10	12	120.14	0.00	21	1.39	0.16	21	2.06	0.16	11	0.74	0.25	11	12.41	0.00
11	12	103.90	0.00	21	0.00	0.33	21	3.42	0.08	11	2.03	0.13	11	14.09	0.00
12	16	171.11	0.00	29	19.29	0.00	29	18.75	0.00	15	17.15	0.00	15	51.57	0.00
13	17	14.17	0.00	31	16.60	0.00	31	14.11	0.00	16	3.87	0.05	16	0.72	0.22
14	17	4.05	0.12	31	15.48	0.00	31	13.82	0.00	16	5.24	0.03	16	0.32	0.27
15	13	100.43	0.00	23	0.85	0.22	23	5.38	0.03	12	2.79	0.09	12	13.28	0.00
16	18	0.00	0.88	33	16.56	0.00	33	16.96	0.00	17	5.83	0.02	17	0.89	0.20

1153 In bold are the best models ($\Delta AICc = 0$) for each analysis.

1154 K = number of parameters

1155 w = Akaike weight

1157**Table A3. Effect of habitat characteristics on the number of hatchlings of early and late tree swallow settlers in a nest box**
1158**network in southern Québec, Canada, between 2009 and 2018, according to the second and third best models in**
1159**terms of AICc (Table A2).**

Explanatory variable	Estimate (95% confidence interval)							
	Early settlers				Late settlers			
	2nd best $w = 0.22$		3rd best $w = 0.18$		2nd best $w = 0.34$		3rd best $w = 0.12$	
	Conditional	Zero-inflated	Conditional	Zero-inflated	Conditional	Zero-inflated	Conditional	Zero-inflated
Forest 100 m								
Forest 500 m								
Forage crops 500 m								
Forest 500 m × Forage crops 500 m								
Water 10 km								
Insects	0.01 (0.00, 0.03)	0.02 (-0.20, 0.23)					0.02 (-0.01, 0.04)	0.04 (-0.15, 0.22)
Competitor density	-0.01 (-0.03, 0.01)	0.20 (0.01, 0.39)						
Density @ t-1	0.02 (0.00, 0.04)	-0.16 (-0.36, 0.03)	0.03 (0.01, 0.04)	-0.28 (-0.44, -0.12)			0.03 (0.01, 0.05)	-0.10 (-0.28, 0.08)
Success @ t-1	0.00 (-0.02, 0.01)	-0.16 (-0.33, 0.01)	-0.01 (-0.02, 0.01)	-0.17 (-0.34, 0.00)			0.02 (0.00, 0.04)	-0.20 (-0.39, 0.00)
Temperature	-0.02 (-0.03, 0.00)	0.24 (-0.09, 0.56)	-0.01 (-0.03, 0.00)	0.24 (-0.09, 0.57)			-0.02 (-0.06, 0.01)	0.03 (-0.17, 0.22)
Precipitations	0.01 (0.00, 0.03)	0.01 (-0.17, 0.19)	0.01 (0.00, 0.03)	0.03 (-0.15, 0.21)			0.01 (-0.01, 0.03)	-0.13 (-0.31, 0.05)
Longitude	0.01 (-0.01, 0.03)	0.09 (-0.10, 0.28)	0.02 (0.00, 0.03)	0.05 (-0.13, 0.23)			0.01 (-0.01, 0.03)	0.02 (-0.18, 0.21)
Latitude	-0.02 (-0.04, 0.00)	0.03 (-0.14, 0.20)	-0.02 (-0.04, 0.00)	0.04 (-0.13, 0.21)			0.01 (-0.01, 0.03)	0.01 (-0.18, 0.20)

1160 Predictors were standardized (zero mean, unit variance). The Akaike weight of each model is presented along with
1161 the estimates and their 95% confidence intervals. Estimates for which the confidence interval excludes zero are in
1162 bold.

Explanatory variable	Estimate (95% confidence interval)							
	Early settlers				Late settlers			
	2nd best $w = 0.25$		3rd best $w = 0.13$		2nd best $w = 0.27$		3rd best $w = 0.22$	
	Conditional	Zero-inflated	Conditional	Zero-inflated	Conditional	Zero-inflated	Conditional	Zero-inflated
Forest 100 m			-0.45 (-0.68, -0.21)	-0.45 (-0.69, -0.21)			-0.45 (-0.68, -0.21)	-0.45 (-0.69, -0.21)
Forest 500 m			-0.27 (-0.60, 0.06)	-0.23 (-0.57, 0.12)			-0.27 (-0.60, 0.06)	-0.23 (-0.57, 0.12)
Forage crops 500 m			-0.15 (-0.46, 0.17)	-0.16 (-0.48, 0.16)			-0.15 (-0.46, 0.17)	-0.16 (-0.48, 0.16)
Forest 500 m × Forage crops 500 m			-0.17 (-0.48, 0.14)	-0.16 (-0.47, 0.15)			-0.17 (-0.48, 0.14)	-0.16 (-0.47, 0.15)
Water 10 km			-0.13 (-0.53, 0.27)	-0.12 (-0.53, 0.28)			-0.13 (-0.53, 0.27)	-0.12 (-0.53, 0.28)
Insects	0.09 (-0.06, 0.23)			-0.11 (-0.29, 0.07)	0.09 (-0.06, 0.23)			-0.11 (-0.29, 0.07)
Competitor density		-0.01 (-0.17, 0.15)	-0.14 (-0.34, 0.06)			-0.01 (-0.17, 0.15)	-0.14 (-0.34, 0.06)	
Density @ t-1	-0.08 (-0.24, 0.09)	-0.08 (-0.26, 0.09)	-0.48 (-0.68, -0.28)	-0.45 (-0.64, -0.26)	-0.08 (-0.24, 0.09)	-0.08 (-0.26, 0.09)	-0.48 (-0.68, -0.28)	-0.45 (-0.64, -0.26)
Success @ t-1	-0.23 (-0.36, -0.11)	-0.24 (-0.36, -0.11)	0.42 (0.27, 0.56)	0.41 (0.26, 0.56)	-0.23 (-0.36, -0.11)	-0.24 (-0.36, -0.11)	0.42 (0.27, 0.56)	0.41 (0.26, 0.56)
Temperature	0.22 (-0.10, 0.55)	0.26 (-0.05, 0.58)	-0.17 (-0.64, 0.30)	-0.14 (-0.62, 0.33)	0.22 (-0.10, 0.55)	0.26 (-0.05, 0.58)	-0.17 (-0.64, 0.30)	-0.14 (-0.62, 0.33)
Precipitations	0.07 (-0.04, 0.18)	0.08 (-0.03, 0.19)	-0.01 (-0.14, 0.12)	-0.01 (-0.14, 0.12)	0.07 (-0.04, 0.18)	0.08 (-0.03, 0.19)	-0.01 (-0.14, 0.12)	-0.01 (-0.14, 0.12)
Longitude	0.21 (-0.13, 0.54)	0.23 (-0.11, 0.56)	0.17 (-0.20, 0.55)	0.21 (-0.18, 0.60)	0.21 (-0.13, 0.54)	0.23 (-0.11, 0.56)	0.17 (-0.20, 0.55)	0.21 (-0.18, 0.60)
Latitude	-0.17 (-0.49, 0.14)	-0.17 (-0.48, 0.14)	-0.48 (-0.79, -0.18)	-0.47 (-0.78, -0.16)	-0.17 (-0.49, 0.14)	-0.17 (-0.48, 0.14)	-0.48 (-0.79, -0.18)	-0.47 (-0.78, -0.16)

1163 **Table A4. Effect of habitat characteristics on the fledging success of early and late tree swallow settlers in a nest box**
1164 **network in southern Québec, Canada, between 2009 and 2018, according to the second and third best models**
1165 **in terms of AICc (Table A2).**

1166 Predictors were standardized (zero mean, unit variance). The Akaike weight of each model is presented along with
1167 the estimates and their 95% confidence intervals. Estimates for which the confidence interval excludes zero are in
1168 bold.

Table A5. Results of the model selections made on the candidate models presented in Table A1 for the different response variables: nest box preference, number of hatchlings and fledging success of tree swallows in southern Québec, Canada, between 2009 and 2018, using a 5-km rather than 500-m scale for forage crops and forest cover.

Candidate model	Preference			Number of hatchlings						Fledging success					
				Early settlers			Late settlers			Early settlers			Late settlers		
	K	$\Delta AICc$	w	K	$\Delta AICc$	w	K	$\Delta AICc$	w	K	$\Delta AICc$	w	K	$\Delta AICc$	w
0	5	289.72	0.00	7	24.39	0.00	7	2.49	0.08	4	23.02	0.00	4	54.63	0.00
1	9	281.68	0.00	15	20.30	0.00	15	9.30	0.00	8	26.57	0.00	8	57.28	0.00
2	14	151.51	0.00	25	27.96	0.00	25	3.53	0.05	13	11.70	0.00	13	45.91	0.00
3	10	283.09	0.00	17	20.37	0.00	17	12.05	0.00	9	26.96	0.00	9	54.34	0.00
4	10	283.18	0.00	17	1.42	0.16	17	7.50	0.01	9	28.59	0.00	9	59.33	0.00
5	11	121.81	0.00	19	2.30	0.10	19	1.36	0.14	10	15.88	0.00	10	11.84	0.00
6	15	152.81	0.00	27	28.41	0.00	27	5.87	0.01	14	12.01	0.00	14	44.33	0.00
7	15	153.47	0.00	27	12.56	0.00	27	0.00	0.27	14	13.50	0.00	14	47.99	0.00
8	16	14.40	0.00	29	14.65	0.00	29	2.23	0.09	15	0.00	0.42	15	0.00	0.26
9	11	284.56	0.00	19	2.63	0.09	19	10.18	0.00	10	29.00	0.00	10	56.40	0.00
10	12	120.90	0.00	21	2.44	0.10	21	3.42	0.05	11	16.62	0.00	11	11.18	0.00
11	12	102.71	0.00	21	0.00	0.33	21	3.64	0.04	11	17.63	0.00	11	12.31	0.00
12	16	154.75	0.00	29	13.92	0.00	29	1.71	0.11	15	13.97	0.00	15	46.42	0.00
13	17	13.84	0.00	31	15.58	0.00	31	4.78	0.02	16	0.93	0.27	16	0.13	0.24
14	17	2.74	0.20	31	13.17	0.00	31	2.48	0.08	16	1.52	0.20	16	0.07	0.25
15	13	99.15	0.00	23	0.81	0.22	23	5.49	0.02	12	18.53	0.00	12	11.50	0.00
16	18	0.00	0.80	33	14.69	0.00	33	4.24	0.03	17	2.66	0.11	17	0.03	0.25

1170

1171 In bold are the best models ($\Delta AICc = 0$) for each analysis.

1172 K = number of parameters

1173 w_i = Akaike weight

1174

Table A6. Determinants of nest box preference in tree swallows and their effect on the reproductive success of early and late settlers in a nest box network in southern Québec, Canada, between 2009 and 2018, using a 5-km rather than 500-m scale for forage crops and forest cover.

Explanatory variable	Estimate (95% confidence interval)						
	Preference <i>N</i> = 2915	Number of hatchlings				Fledging success	
		Early settlers <i>N</i> = 1268		Late settlers <i>N</i> = 891		Early settlers <i>N</i> = 953	Late settlers <i>N</i> = 644
		Conditional	Zero-inflated	Conditional	Zero-inflated		
Forest 100 m	-0.58 (-0.70, -0.46)			-0.01 (-0.03, 0.01)	0.12 (-0.04, 0.29)	0.10 (-0.07, 0.28)	-0.49 (-0.71, -0.27)
Forest 5 km	0.21 (-0.07, 0.48)			0.05 (0.01, 0.08)	-0.07 (-0.39, 0.25)	-0.44 (-0.93, 0.06)	0.06 (-0.35, 0.48)
Forage crops 5 km	0.15 (-0.04, 0.34)			0.00 (-0.04, 0.03)	-0.21 (-0.51, 0.09)	0.53 (0.26, 0.80)	-0.03 (-0.33, 0.27)
Forest 5 km× Forage crops 5 km	-0.28 (-0.50, -0.06)			-0.03 (-0.06, 0.01)	0.61 (0.27, 0.95)	-0.58 (-0.90, -0.26)	-0.16 (-0.48, 0.16)
Water 10 km	-0.11 (-0.37, 0.15)			-0.01 (-0.04, 0.02)	-0.16 (-0.47, 0.15)	0.57 (0.13, 1.01)	-0.20 (-0.60, 0.20)
Insect biomass	0.12 (0.01, 0.24)						
Competitor density	0.26 (0.13, 0.38)	-0.01 (-0.03, 0.01)	0.22 (0.02, 0.41)	-0.01 (-0.03, 0.01)	0.24 (0.06, 0.42)		
Density @ t-1	0.69 (0.55, 0.82)	0.02 (0.00, 0.04)	-0.15 (-0.35, 0.05)			-0.02 (-0.19, 0.15)	-0.45 (-0.64, -0.26)
Success @ t-1	0.39 (0.30, 0.48)	-0.01 (-0.02, 0.01)	-0.16 (-0.33, 0.02)			-0.25 (-0.38, -0.13)	0.40 (0.25, 0.55)
Temperature	-0.01 (-0.15, 0.14)	-0.01 (-0.03, 0.00)	0.24 (-0.08, 0.56)	-0.01 (-0.05, 0.02)	-0.04 (-0.23, 0.16)	0.25 (-0.04, 0.55)	-0.16 (-0.63, 0.31)
Precipitations	-0.15 (-0.24, -0.07)	0.01 (0.00, 0.03)	0.01 (-0.17, 0.19)	0.01 (-0.01, 0.03)	-0.16 (-0.34, 0.02)	0.05 (-0.06, 0.16)	-0.02 (-0.15, 0.10)
Longitude	-0.24 (-0.53, 0.04)	0.01 (-0.01, 0.03)	0.10 (-0.09, 0.28)	-0.01 (-0.05, 0.03)	0.26 (-0.09, 0.61)	-0.19 (-0.68, 0.30)	0.07 (-0.36, 0.50)
Latitude	0.00 (-0.22, 0.21)	-0.02 (-0.04, 0.00)	0.04 (-0.13, 0.21)	0.03 (0.00, 0.05)	-0.21 (-0.46, 0.04)	0.22 (-0.15, 0.59)	-0.39 (-0.73, -0.05)

Coefficients come from an ordinal logistic mixed regression for preference, a zero-inflated GLMM using generalized Poisson distribution and log link function for the number of hatchlings and GLMM using binomial error distribution and logit link function for fledging success. Predictors were standardized (zero mean, unit variance). For each analysis we present the coefficients of the model that ranked best in terms of AICc, their 95% confidence intervals and the sample size. See Table 1 for definitions the variables and Table A5 for results of the model selection. Estimates for which the confidence interval excludes zero are in bold