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1 **Great tits nesting in apple orchards preferentially forage in organic but not conventional**  
2 **orchards and in hedgerows**

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9

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11

12 **Highlights**

- 13 • Female great tits nesting in organic and conventional orchards were radiotracked  
14 • Females from organic orchards foraged mostly in the orchard and travelled less  
15 • Females from conventional orchards foraged mostly outside the orchard  
16 • Nestling survival was lower and fledgling number lower in conventional orchards  
17 • Nestboxes in organic, but not in conventional orchards, may support pest control

18

19 **Abstract**

20 Great tits are insectivorous birds that feed mainly on caterpillars during the breeding season. Their  
21 high pest control potential in apple orchards has been documented. Nestbox provisioning is an  
22 increasingly suggested tool for ecological pest control, but the underlying assumption that birds forage  
23 in intensively managed orchards has never been formally tested.

24 We conducted a fine-scale study of the great tit feeding microhabitat in different orchard  
25 management contexts as pesticide use affects the behaviour and physiology of birds through direct  
26 intoxication and reduced prey abundance. Using radiotracking techniques, we assessed foraging areas  
27 and foraging habitat selection of female great tits breeding in conventional and organic commercial  
28 apple orchards. We also tested whether different orchard-driven foraging strategies could be linked to  
29 differences in reproductive success.

30 We collected 392 foraging locations from seven female great tits nesting in organic orchards and  
31 375 locations from seven females nesting in conventional orchards. Females from organic orchards  
32 mostly searched for food inside the orchard where they bred. This contrasted strongly with females  
33 from conventional orchards ( $54 \pm 10.4\%$  and  $7.1 \pm 3.0\%$  of foraging points inside the orchard,  
34 respectively). Further, females from organic orchards travelled shorter distances. Overall, organic  
35 orchards and hedgerows were the most preferred foraging habitats. Conventional orchard management  
36 was also associated with lower nestling survival and lower fledgling number than organic  
37 management. There were indications that the mean number of fledglings decreased with increasing  
38 mean foraging distance of the female.

39 Our novel insights on the foraging behaviour of great tits in orchards support the benefits of  
40 installing nestboxes in organic but not in conventional orchards. We posit that nestboxes may  
41 encourage feeding activity of insectivorous birds within organic orchards where they may then  
42 contribute to the control of insect pest populations.

43

44 **Key words:** Foraging behaviour; habitat; nestbox; *Parus major*; pest control; radiotracking

45

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54

## 55 1. Introduction

56 In recent decades, agricultural intensification has generated a combination of environmental  
57 hazards and increased production costs that raise major issues for more resilient and sustainable  
58 agricultural production systems (Donald et al., 2006; Tomich et al., 2011; PECBMS, 2020).  
59 Ecological intensification relies on ecosystem services to sustain agricultural production while  
60 minimising adverse effects on the environment (Kleijn et al., 2019). One possible transition to more  
61 environmentally friendly crop production involves the reduction of chemical pesticides and the  
62 enhancement of ecosystem services from natural enemies to suppress pest populations (Losey and  
63 Vaughan, 2006; Samnegard et al., 2019). Farmland insectivorous birds can provide high value pest  
64 control services (Maas et al., 2016; Génard et al., 2017; García et al., 2018). Therefore, enhancing  
65 their breeding or site occupancy opportunities may strengthen crop pest regulation in diverse  
66 agroecosystems (Mols and Visser, 2007; Jedlicka et al., 2014; Rey Benayas et al., 2017; García et al.,  
67 2020; Díaz-Sieffer et al., 2022).

68 Artificial nestboxes are an effective means of increasing densities of insectivorous cavity-nesting  
69 birds, for which natural cavities are an increasingly limiting resource due to the elimination of old  
70 trees (Newton, 1994; Lindell et al., 2018). Bird habitat quality in agroecosystems fundamentally  
71 depends on the nature and quantity of pesticides sprayed for crop protection. This is because of the  
72 lethal and sub-lethal effects of pesticide exposure and the reduced biomass and abundance of  
73 arthropod preys (Genghini et al., 2006; Goulson, 2014; Hallman et al., 2014; Li et al., 2020; Tassin de  
74 Montaignu and Goulson, 2020). Even though nestling provisioning is a crucial and highly energy-  
75 demanding period of bird reproduction (Tinbergen and Ditz, 1994), the influence of pesticide use on  
76 foraging patterns in nesting insectivorous birds has not been a primary focus of study. Novel research  
77 is thus needed to clarify the conditions under which nesting boxes may be a suitable tool for ecological  
78 intensification in different crop management contexts. Such knowledge has strong implications, as  
79 nestboxes are a frequently suggested practice in ecological intensification plans.

80 The apple is the second most important fruit crop globally (FAO, 2009), accounting for almost  
81 40% of the total area under fruit crops in Europe (Eurostat, 2019). Apple crop intensification has

82 converted traditional, high nature value fruit orchards (Cooper et al., 2007; Myczko et al., 2013) into  
83 productivity-oriented plantations of low-stem trees. They are primarily managed through high amounts  
84 of inorganic fertilizers, pesticides, and herbicides, with detrimental effects within and surrounding the  
85 orchards (Reganold et al., 2001; Simon et al., 2010). In southern France, for instance, conventional  
86 production relies on an average of 29 phytosanitary treatments per year, including nine broad spectrum  
87 insecticides and 16 fungicides. In contrast, organic farming involves 17 treatments on average,  
88 including seven microbiological insecticides and 10 fungicides (Agreste, 2019). Over the past decade,  
89 the combination of high environmental impacts of intensification with the development of resistance  
90 of target pests to chemical and biological insecticides has promoted ecological intensification in apple  
91 orchards across Europe (Simon et al., 2010; Samnegard et al., 2019).

92 The great tit (*Parus major*) is a common cavity-nesting bird occurring in a wide range of habitats,  
93 including woodland urban areas and agricultural land, such as orchards (Cramp and Perrin, 1993;  
94 Hinsley et al., 2008). Its tolerance to human disturbance makes it a good candidate species for  
95 ecological intensification. It readily allows for settlement in artificial nestboxes and detailed  
96 measurements of many foraging and breeding parameters (Sanz and Tinbergen, 1999; Naef-Danzer et  
97 al., 2000; Pagani-Núñez et al., 2015). The great tit mainly feeds on caterpillars during the breeding  
98 season. As such, the high pest control potential of the great tit in apple orchards has been largely  
99 documented (Mols and Visser, 2007; García et al., 2020). There is also evidence that apple crop  
100 management practices directly and indirectly affect reproductive parameters of the great tit using  
101 nestboxes through intoxication and lower prey abundance (Bouvier et al., 2005; Bouvier et al., 2016).  
102 The great tit is a single prey loader that feeds nestlings several hundred times a day (Naef-Daenzer et  
103 al., 2000; Barba et al., 2009). This implies both time constraints and energetic costs to search for prey  
104 within the nest surroundings (Rytkönen and Krams, 2003) that may depend on habitat quality (Wilkin  
105 et al., 2009). This allows realistic assumptions of diverging foraging behaviour of the great tit in  
106 conventional and organic apple orchards. Although nestboxes for insectivorous birds, particularly  
107 great tits, are increasingly adopted in European conventional and organic apple orchards to increase  
108 the biological control of insect pests, no study has yet formally assessed whether the birds that use

109 nestboxes in orchards actually feed there. It is thus now essential to highlight the link between the  
110 impact of agricultural management, the ecology of insectivorous bird species, and its implications for  
111 nestbox-aided regulation of agricultural pests.

112 In this context, our study aims to assess the extent to which great tits forage in the orchard where  
113 they nest, and we hypothesise that great tits differ in foraging behaviour depending on whether they  
114 nest in conventional or organic orchards. Presented here is the first comparison of foraging home  
115 range and foraging habitat selection of the great tit breeding in conventional and organic apple  
116 orchards. We also tested whether different orchard-driven foraging strategies could be linked to  
117 differences in reproductive success. These issues were addressed in a three-year survey that combined  
118 the radiotracking of female great tits nesting within the studied orchards, an assessment of components  
119 of their reproductive success, and a landscape description of the orchards and their surroundings.

120

## 121 2. Materials and methods

### 122 2.1 Study area

123 The location of the study was in a 50 km<sup>2</sup> pome fruit production area («Basse Vallée de la  
124 Durance», central point: WGS84: 43° 8' N, 3° 9' E) of south-eastern France (Fig. 1). This area is an  
125 agricultural plain (40 to 60 m.a.s.l.) characterised by a dense network of ditches and tree-based  
126 hedgerows, as well as by diverse farming systems. Fruit orchards are the dominant crop in a crop  
127 mosaic that also contains olive orchards, vineyards, vegetables, and cereal crops. Pome fruits represent  
128 87% of all fruit production area in the study area.

129 Fieldwork was carried out during the springs of 2017, 2018, and 2019 in commercial apple  
130 orchards chosen for their similarity regarding both their intrinsic and surrounding vegetation. Among  
131 these orchards, four were under conventional management and four under organic management (Table  
132 1). They had similar average areas (mean  $\pm$  standard deviation (sd): conventional: 1.22  $\pm$  0.36 ha,  
133 organic: 0.97  $\pm$  0.28 ha), a plantation density of approximately 1500 trees/ha, and a grassy ground  
134 cover. Pest control was carried out from March to October. The management strategies were

135 characterised by the treatment schedules provided by the orchard owners (Supplementary material,  
136 Table S1). The conventional orchards were managed with an average of  $28.1 \pm 2.9$  (mean  $\pm$  sd)  
137 treatments a year. These treatments included mineral and chemical fungicides ( $5.7 \pm 0.6$  and  $12.3 \pm$   
138  $3.3$ , respectively), chemical insecticides ( $7.7 \pm 0.3$ ) including broad-spectrum neurotoxic insecticides  
139 ( $3.2 \pm 0.6$ ), mating disruption against codling moth (*Cydia pomonella*), and herbicides ( $2.0 \pm 0.6$ ). The  
140 average number of treatments in the organic orchards was  $27.3 \pm 3.4$  a year. These treatments included  
141 mineral fungicides ( $14.9 \pm 3.1$ ), neem and petrol oils ( $3.8 \pm 0.4$ ), mating disruption, biological  
142 selective insecticides against codling moth ( $5.3 \pm 0.7$  treatments with granulosis virus and  $0.7 \pm 0.2$   
143 treatments with *Bacillus thuringiensis*), and Spinosad ( $2.5 \pm 0.5$ ). All orchards were bordered by  
144 hedgerows (mainly poplar or cypress) for protection against the prevailing winds.

145

## 146 2.2 Design and monitoring of nestboxes

147 The implementation of the nestboxes was designed according to Bouvier et al. (2005). Each  
148 orchard had five nestboxes (Schwegler 1B type with 32 mm diameter entrance) installed in autumn  
149 2015. They were located in apple trees 1.5 m above the ground, 30 m apart, and 20 m from  
150 surrounding hedgerows. The entrances of all nestboxes faced south-east to avoid both the north  
151 prevailing wind and the south prevailing rain. During the 2017, 2018, and 2019 breeding seasons, we  
152 checked all nestboxes weekly from March until the offspring had fledged from the nests. We assessed  
153 several components of reproductive success: the number of pairs per orchard, first laying date, clutch  
154 size, hatching rate, nestling survival, and numbers of fledglings per pair. We cleaned nestboxes in  
155 September each year.

156

## 157 2.3 Radiotracking

158 During the springs of 2017 (9<sup>th</sup> May to 6<sup>th</sup> July), 2018 (10<sup>th</sup> May to 10<sup>th</sup> July), and 2019 (14<sup>th</sup> May  
159 to 8<sup>th</sup> July), we radiotracked 14 female great tits breeding in the implemented nestboxes; seven females  
160 bred in conventional orchards and seven in organic orchards (Table 1). We monitored only females to



161 avoid between-sex variation and because, contrary to males, females return quickly to their nest when  
162 disturbed (personal observation). Furthermore, males and females contribute equally to offspring  
163 feeding (Smith et al., 1988). To limit pseudoreplication, all females were from different nestboxes and  
164 were located, as much as possible, in different orchards each year (two exceptions, Table 1). Females  
165 were caught in their nestboxes when nestlings were about 9 days old and they were fitted with a  
166 Biotrack Pip Ag317 VHF radiotag (Biotrack Ltd, Wareham, Dorset, UK) (Supplementary material,  
167 Fig. S1). The tag weight (0.45 g excluding harness) was well below the recommended 5% of the bird's  
168 body weight (Caccamise and Hedin, 1985). The tags were fixed on the birds' backs using  
169 biodegradable natural rubber leg harnesses with a diameter of 0.5 mm. Harness length was calculated  
170 according to the weight of the birds from the Naef-Daenzer model (2007). The tags were glued to the  
171 harnesses with cyanoacrylate Loctite® 454 with Loctite® 7455 activator (Rappole and Tipton, 1991).  
172 The tags emitted one signal of 20 milliseconds per second in the 148 MHz frequency with one unique  
173 frequency per tag. Their maximum above ground range of 600 m sufficed to locate foraging females in  
174 our study sites without disturbing the behaviour of the birds.

175 To avoid potential behavioural biases resulting from stress of capture or an adjustment period  
176 inherent to carrying the radiotag equipment, the tracking of the birds began approximately 24 hours  
177 after they were equipped. Tracking lasted from 7.30 am to 1.30 pm and from 3.00 pm to 5.30 pm. It  
178 was performed for all birds by the same two observers, each equipped with a directional Yagi-Uda  
179 antenna, a VHF receiver (Sika, Biotrack Ltd.), and a walkie-talkie. The positions of the observers were  
180 chosen so as not to lose signals due to the orchard configuration or landscape elements, such as  
181 hedgerows. The azimuths of the foraging females were obtained from the directional antennas and  
182 magnetic compasses of each observer, complemented with visual observations. The observers  
183 simultaneously recorded the foraging female's azimuth. The female's position was determined as the  
184 intersection of two azimuths, according to the principle of triangulation defined by White and Garrott  
185 (1990). Upon visual inspection of the birds, each azimuth was annotated according to the observed  
186 behaviour (i.e., resting, foraging, and going back to the nest) and only foraging points were used for  
187 further analyses. Females were tracked for 1.5 days, as a trade-off between equivalence between the

188 numbers of recorded female positions in organic and conventional orchards (Table 2) and the necessity  
189 to remove the tag early enough to avoid premature fledgling in response to the handling of the mother  
190 in the nestbox. As a result, the net tracking duration, i.e., sum of durations during which each female  
191 could be monitored while feeding, was on average 4h41min (range: [2h14, 7h45], Table 2). Females  
192 were recaptured in nestboxes for tag removal after the radiotracking scheme.

193

#### 194 *2.4 Landscape feature description*

195 We characterised the landscape within 400 m surrounding the nestboxes of the 14 female great tits  
196 we tracked. The 400 m buffer zones around the nests included the largest distances covered by  
197 foraging great tits in the present study. The landscape was mapped using a Geographic Information  
198 System (ArcGis V. 10.3). Particular attention was paid to orchards and wooded areas because great tits  
199 are known to forage in tree canopies. Organic orchards, conventional orchards, annual crops, woods,  
200 wooded fallow land, grassland, hedgerows, and built areas within the buffer zones were manually  
201 digitalised based on aerial photographs (BD ORTHO®, IGN 2017) and field surveys. The apple  
202 orchards in the study were mainly surrounded by agricultural land covers including orchards, both  
203 organic and conventional except in one situation, and annual crops (Table 3). Orchards produced  
204 mainly apples and to a lesser extent pears and olives. There were hedgerows (representing from 2.6%  
205 to 8.5% of total area) in all buffer zones. Landscapes surroundings conventional study orchards  
206 differed from those surrounding organic study orchards by their higher proportion of conventional  
207 orchards ( $P = 0.006$ , supplementary material, Table S2).

208

#### 209 *2.5 Statistical analysis*

210 All statistical analyses were performed with software R 3.6.3 (R Core Team, 2020) using RStudio  
211 1.3.1056.

212

213 *2.5.1 Foraging distances*

214 The distance covered by individuals searching for food was computed as the Euclidean distance  
215 between each foraging relocation and the nestbox GPS coordinates (with the `spDists` R function,  
216 package “`sp`”, Pebesma and Bivand, 2005). Variation in (square root transformed) distances between  
217 organic and conventional orchards was analysed using linear mixed models, which included the  
218 orchard management strategy and the year as the fixed independent variables and the female’s identity  
219 as the random factor (R package `lme4`, Bates et al., 2015). It was tested for significance with Wald  
220  $\chi^2$  tests (Anova in package `car`, Fox and Weisberg, 2019). Model residuals were inspected for  
221 dispersion using a quantile-quantile (QQ) plot of standardised residuals, as well as for uniformity and  
222 outliers using a plot of residual versus predicted values. Associated statistical tests were also  
223 performed with the `DHARMA` R package (Hartig, 2019).

224 The proportion of foraging relocations located inside and outside a nestbox orchard was estimated  
225 with an overlay analysis in ArcGis. The very few ambiguous attributions, when both inside and  
226 outside areas were present in a 5 m radius around the point, were discarded. Variations in these  
227 proportions between organic and conventional orchards were analysed using generalised linear mixed  
228 models for binomial data with the orchard management strategy and the year as the fixed independent  
229 variables and the female’s identity as the random factor (R package `lme4`, Bates et al., 2015).  
230 Significance and model residuals were analysed as above.

231 The relationship between reproductive success of tracked females and foraging distance was  
232 analysed using generalised linear models for Poisson data with the number of fledglings as the  
233 dependent variable and the orchard management and mean foraging distance as fixed independent  
234 variables (R package `lme4`, Bates et al., 2015). Significance and model residuals were analysed as  
235 above.

236

237 *2.5.2 Foraging areas*

238 The locations of foraging points were used to calculate the foraging area: a maximum of 80 and a  
239 minimum of 23 foraging relocations were obtained for each individual, with more than the 40  
240 locations recommended for robust estimates of home-range areas (Seaman et al., 1999) for all but two  
241 individuals (32 and 23 foraging relocations) (Table 2).

242 The foraging area was calculated with a 95% kernel density estimator (Worton, 1989). We  
243 calculated foraging areas using the continuous-time movement modelling package (ctmm; Calabrese et  
244 al., 2016). This was done via auto-correlated kernel density estimation (Fleming et al., 2015) to deal  
245 with temporal autocorrelation between data points. The function `variogram.fit` in the `ctmm` package  
246 allowed for automatically choosing the model parameters with better fit. We compared the area  
247 covered by foraging females between organic and conventional orchards using linear models that  
248 included the year and the management strategy as fixed independent variables (R package `lme4`, Bates  
249 et al., 2015). Model residuals were analysed as above.

250

251 *2.5.3 Foraging habitat selection*

252 Foraging habitat selection was analysed by comparing habitats located at the foraging relocations  
253 with the composition of the habitats available in the 400 m radius around the nest, using Manly's  
254 selectivity measure (third-order selection; Manly et al., 2002). To account for location uncertainties  
255 inherent to the radiotracking equipment and methodology, the composition of the habitat used was  
256 measured as the proportion of all habitats in a 5 m buffer around each original relocation. Habitat  
257 selection was tested at the population level with log-likelihood  $\text{Khi}^2$  (Manly et al., 2002). The  
258 differences between selection ratios were computed and tested using the `widesIII` R function  
259 ("`adehabitatHS`" package, Calenge, 2006).

260

#### 261 2.5.4 Reproductive success

262 We investigated the factors affecting great tit reproductive success at the nest level with generalised  
263 linear mixed models. These included management strategy and study year as fixed independent  
264 variables (R package lme4, Bates et al., 2015). We included orchard identity as a random factor in all  
265 models to account for the non-independence of nests within orchards. Variance inflation factors were  
266  $< 2$  for all models, confirming the low levels of multicollinearity between independent variables (Zuur  
267 et al., 2010). Model residuals were inspected for dispersion using a quantile-quantile (QQ) plot of  
268 standardised residuals and for uniformity and outliers using a plot of residual versus predicted values.  
269 Associated statistical tests were also performed with the DHARMA R package (Hartig, 2019). Based  
270 on the type of data and on residual analyses, the log-transformed number of eggs was modelled using a  
271 Gaussian distribution. The number of fledglings was modelled using a Poisson distribution. Egg  
272 mortality was calculated considering the presence or absence of non-hatched eggs among those that  
273 were laid. Nestling survival was calculated based on the number of dead and live nestlings. Egg  
274 mortality and nestling survival were modelled using a binomial distribution.

275 At the orchard level, we investigated the factors affecting the number of breeding pairs and the first  
276 laying date with linear mixed models, including management strategy and the study year (Year) as  
277 fixed independent variables (R package lme4, Bates et al., 2015) and a random 'orchard identity'  
278 factor. Model fit and significance of independent variables were assessed as above.

279

### 280 3. Results

281 We analysed 392 foraging locations of seven female great tits in organic orchards as well as 375  
282 locations of seven female great tits in conventional orchards (Table 2). The average number of  
283 locations did not differ between females from organic and conventional orchards (organic:  $56.0 \pm 6.8$   
284 and conventional:  $53.6 \pm 5.7$ ,  $F_{(1,12)} = 0.075$ ,  $P = 0.79$ ) and it was not significantly correlated to the net  
285 tracking duration (Spearman  $r = 0.41$ ,  $p = 0.15$ ).

286

287 *3.1 Foraging distance*

288 Females from organic orchards frequently searched for food inside the orchard where they bred (54  
289  $\pm 10.4\%$  of foraging points), whereas females from conventional orchards mainly searched for food  
290 outside ( $7.1 \pm 3.0\%$ ,  $\text{Chisq} = 23.99$ ,  $P = 9.7 \cdot 10^{-7}$ , Fig. 2 and 3), regardless of the year ( $\text{Chisq} = 0.53$ ,  $P$   
291  $= 0.76$ ).

292 This difference in the location of foraging points was associated with a difference in distances that  
293 females travelled. Females breeding in organic orchards travelled a mean distance of  $50.5 \pm 11.5$  m  
294 from their nests. In contrast females from conventional orchards travelled a significantly higher mean  
295 distance of  $91.9 \pm 17.8$  m (Fig. 2,  $\text{Chisq} = 5.29$ ,  $P = 0.022$ ). Density curves (Fig. 3) show a typically  
296 skewed distribution in females from organic orchards, strongly dominated by short-distance ( $\leq 40$  m)  
297 movements with rare long-distance movements. Meanwhile, in females from conventional orchards,  
298 density curves show a slight preference for short movements around 50 m, but with an almost equally  
299 strong presence of long (100 m) and very long (200 m) movements. The distribution of distances was  
300 narrower in organic than in conventional orchards, regardless of the year ( $\text{Chisq} = 1.00$ ,  $P = 0.61$ ).

301

302 *3.2 Foraging area*

303 On average, the area covered by individual foraging females from organic orchards did not differ  
304 significantly from that of foraging females from conventional orchards (Fig. 4;  $1.88 \pm 0.67$  ha and  $2.12$   
305  $\pm 0.50$  ha, respectively,  $F_{(1,12)} = 0.046$ ,  $P = 0.83$ ), regardless of the year ( $F_{(2,12)} = 0.66$ ,  $P = 0.54$ ).

306 *3.3 Habitat selection*

307 Foraging female great tits showed a significant habitat selection behaviour (Manly's  $\text{Khi2L} =$   
308  $3299.06$ ,  $p < 0.0001$ , Manly et al., 2002). We observed two preferred habitat types amongst those  
309 available in the landscape surrounding their nests (Fig. 5). Organic orchards and hedgerows were  
310 present in higher proportions at foraging locations than in the buffer zone surrounding the female's  
311 nest. Urban areas, annual crops and woods were present in lower proportions. The selection ratios for  
312 the other habitats, including conventional orchards, did not show a significant deviation from random

313 use. Organic orchards showed the highest of all selection ratios, significantly higher than any other  
314 habitats. Conventional orchards showed lower selection ratio than organic orchards and wooded  
315 fallow lands. Their selection ratios were not significantly different from habitats below the random use  
316 threshold. Woods were never used by any individual during the study and annual crops were used only  
317 once.

318

### 319 *3.4 Reproductive success*

320 A total of 87 great tit breeding pairs was monitored for components of reproductive success in the  
321 study orchards from 2017 to 2019. The number of breeding pairs per orchard, clutch size, egg  
322 mortality, nestling survival, and the number of fledglings per pair did not differ among years (Tables 4  
323 and 5). Conventional orchard management was associated with lower nestling survival and lower  
324 fledgling number than organic management (Fig. 6, Tables 4 and 5).

325 Considering only pairs involving tagged females, the mean number of fledglings decreased with  
326 increasing mean foraging distance of the female ( $\text{Chi}^2 = 8.15$ ,  $P = 4.3 \cdot 10^{-3}$ , Fig. 7). However, this  
327 effect was not significant when accounting for orchard management (Management  $\text{Chi}^2 = 5.44$ ,  $P =$   
328  $0.019$ ; Distance  $\text{Chi}^2 = 1.52$ ,  $P = 0.218$ ).

329

## 330 4. Discussion

### 331 *4.1 Foraging behaviour of female great tits depends on apple orchard management*

332 Sustainable solutions to pest management in agroecology are increasingly relying on natural pest  
333 control by a wide range of organisms including insectivorous birds (Sekercioglu 2006; Wenny et al.  
334 2011; Díaz-Sieffer et al., 2022). Birds can contribute to 20-70% reduction in arthropod biomass  
335 (Sekercioglu 2006; Jedlicka et al., 2014; García et al., 2020), consume agricultural pests (Jedlicka et  
336 al., 2013; Karp et al., 2014), and lower pest damage to plants with subsequent higher crop yield or  
337 fruit production (Whelan et al., 2015). Further, there is evidence that predation pressure on apple pests  
338 can increase in orchards with nest boxes (García et al., 2020). Nestboxes are thus increasingly used in

339 European conventional and organic apple orchards for pest control. This raised the need to establish  
340 whether great tits nesting in an orchard actually feed there, and whether orchard management practices  
341 influence their foraging behaviour. The main findings of our study are that female great tits nesting in  
342 organic apple orchards frequently foraged in the orchard where they nested, whereas females in  
343 conventional apple orchards primarily foraged outside the orchard where they nested, most notably in  
344 organic orchards. Furthermore, the area used by these females for foraging (approximately 1.5 ha) was  
345 the same regardless of the type of orchard in which they nested, but females in conventional orchards  
346 travelled almost twice as far as those in organic orchards to forage ( $91.93 \pm 17.82$  m and  $50.49 \pm 11.48$   
347 m, respectively).

348 Radiotracking in intensively managed environments such as orchards requires operating within  
349 narrow time windows defined by minimising disturbance to birds and their offspring, in addition to  
350 avoiding pesticide spraying. Our sample has been limited to a small number of individuals because we  
351 chose to observe the tagged birds as intensively as possible during a short period, but with a large  
352 number of collected locations. Despite these limitations, we obtained similar tracking durations and  
353 numbers of locations in organic and conventional orchards. We found significant differences in the  
354 distances travelled and the proportion of locations within the orchard between individuals nesting in  
355 organic and conventional orchards. This is consistent with the fact that organic orchards were the most  
356 highly selected foraging habitat, regardless of the nesting site.

357 The importance of landscape scale effects on bird biodiversity and avian-mediated pest-control  
358 have been well recognised (Tschardt et al., 2005). This supported the development of hedgerows  
359 and other habitat enhancements that are beneficial to both wildlife and sustainable farming in  
360 intensively managed agricultural landscapes (Batáry et al., 2010). However, the foraging area for  
361 insectivorous birds in agricultural landscapes was still unknown despite its basic implications for  
362 considering the provision of pest control services by birds in farm management. For the first time, our  
363 results unequivocally show that female great tits can feed in the orchard where they nest under organic  
364 farming. Such behaviour is consistent with overall evidence that organic farming is far more beneficial  
365 to arthropod diversity and abundance than conventional farming (Bengtsson et al., 2005; Hole et al.,



366 2005; Stein-Bachinger et al., 2021), including apple orchards (Maalouly et al., 2013; Mazzia et al.,  
367 2015; Dib et al., 2016). This relies on the three main farming practices acknowledged to benefit  
368 biodiversity: (i) the exclusion of chemical pesticides and fertilisers, (ii) the appropriate management of  
369 non-crop habitats and field margins, and (iii) the preservation of mixed farming that provides greater  
370 habitat structural heterogeneity (Hole et al., 2005). Of these practices, pesticide use most differentiates  
371 organic from conventional farming in our study and likely explains the observed effects on great tit  
372 behaviour. As all organic orchards result from the conversion of former conventional orchards, all  
373 studied orchards were of similar size and planting structure. Adverse effects of pesticide use on  
374 arthropod populations were less prominent in organic orchards due to the use of more selective  
375 compounds for pest control. In south-eastern France, the main apple insect pest is the codling moth. In  
376 organic farming, it is controlled by the very specific granulosis virus as well as pheromonal male  
377 mating disruption, while conventional farming involves chemical insecticides with broad-spectrum  
378 efficiency among arthropod communities.

379 Another central finding of this study was that female great tits that nested in conventional orchards  
380 also frequently foraged in organic orchards, which was the most strongly selected habitat in this  
381 agricultural landscape. These females preferentially selected different types of organic orchards (apple  
382 but also olive and pear) and hedgerows. To a much lesser extent, they selected other available habitats  
383 in the surroundings of their nests, i.e., conventional orchards, isolated trees, meadows, urban areas,  
384 annual crops, and woods. As great tits forage in the tree canopy and mainly prey on tree-dwelling  
385 caterpillars to feed their young (Nour et al., 1998; Wilkin et al., 2009; Caprio and Rolando, 2017;  
386 Garcia et al., 2020), we expected preferential selection of tree-based habitats. Our results thus provide  
387 valuable support to the demonstrated value of hedgerows for bird conservation (Morelli et al., 2014;  
388 Assandri et al., 2017).

389 The non-selection of surrounding woods was unexpected as they constitute a common habitat for  
390 great tits (Krebs, 1971; Naef-Daenzer, 2000) and likely provide more food resources than hedgerows  
391 (Krebs, 1971). In a similar study, male great tits nesting in vineyards foraged preferentially in a wood  
392 habitat when they travelled far from the nest (Caprio and Rolando, 2017). Krebs (1971) showed great

393 tit individuals breeding in hedgerows avoided woods because of the strong territoriality that  
394 characterises this species, as well as intraspecific competition with wood-resident pairs. In this study,  
395 woods may have been avoided by females because of competition with resident pairs. Organic  
396 orchards, in contrast, provided food resources but no nesting cavities and were thus less likely to host  
397 competing individuals. Additionally, feeding adults factor distance in their selection of foraging areas  
398 to limit the time and energy expenditures of repeated feeding round trips. Woods may have been  
399 ignored in our study simply because closer resources were available. The average area foraged by  
400 female great tits covered approximately 2 ha, which did not depend on whether their nestboxes were in  
401 an organic or conventional orchard. This foraging area is larger than foraging areas observed in oak  
402 forests (0.33 to 1.34 ha), which are considered optimal food sources for this species (Krebs, 1971;  
403 Naef-Daenzer, 2000). This suggests a lower availability of caterpillar preys in agricultural landscapes  
404 than in natural landscapes. This forces birds to increase their foraging range to compensate for lower  
405 prey density (Krebs, 1971; Stauss et al., 2005). Such compensation remains lower than in vineyard  
406 landscapes, where great tits can expand their foraging areas to 10 ha (K95 in Caprio and Rolando,  
407 2017).

408 Finally, we found that the distances travelled to reach appropriate feeding areas were greater and  
409 more variable for the females nesting in conventional orchards. Note that travel distance differences  
410 between females from organic and conventional orchards may have been exacerbated by the larger  
411 percent area of conventional orchards in the landscape surrounding conventional compared to organic  
412 orchards. The females that nest in conventional orchards might have to travel larger distances once  
413 they leave their nesting orchard due to higher food limitation in the neighbouring conventional  
414 orchards. One likely implication is a stronger necessity to search for food outside the orchard and a  
415 greater dependency on the landscape surrounding the orchard.

416

#### 417 *4.2 Interferences between pest management and great tit reproductive success*

418 We found that the main differences in reproductive success components between orchard  
419 management strategies were due to nestling mortality as nestling survival was significantly affected

420 but not clutch size nor egg mortality. The average number of fledglings per pair was three times lower  
421 in conventional than in organic orchards due to significantly lower pre-fledging nestling survival in  
422 conventional orchards (Fig. 6 A - E). A direct effect of pesticide toxicity on nestling survival is one  
423 likely explanation for this result. Great tits synchronise laying and nestling hatching periods with  
424 abundance peaks of insect prey (van Noordwijk et al., 1995; Seki and Takano, 1998; Garcia-Navas  
425 and Sanz, 2011), which also coincides with peaks of insecticide treatment activity in orchards  
426 (Bouvier et al., 2016). In conventional orchards, these treatments involve broad-spectrum chemical  
427 neurotoxins (avermectin, neonicotinoid, pyrethroid and oxydiazine families) with a low persistence  
428 (Sanchez-Bayo, 2011), but a high toxicity linked to death or behavioural disorders in non-target  
429 organisms, such as birds (Walker, 2002; Sanchez-Bayo, 2011; Li et al., 2020).

430 Collecting large amounts of food is costly. The excessive expenditure of energy may affect the  
431 future condition and survival of the parents (Nur, 1984; Hōrak et al., 1999). It is possible that the need  
432 for longer trips affected the feeding rate of nestlings in conventional orchards. It should be noted that  
433 our results on the link between reproductive success and distance travelled by females are uncertain  
434 and that this question deserves further investigation, possibly focusing on a larger number of females  
435 from conventional orchards.

436

## 437 5. Conclusions

438 In the present study, the preferred feeding habitats used by great tits were organic orchards (mainly  
439 apple, pear, and olive), followed by hedgerows. Our results provide guidelines to farmers wishing to  
440 increase the level of ecosystem services provided by insectivorous bird species in intensively-managed  
441 orchards. Females nesting in organic apple orchards largely foraged within the orchard, which strongly  
442 supports the benefit of installing nestboxes in an environment that apparently meets the ecological  
443 requirements of great tits. Conversely, nestboxes in conventional orchards likely increase mortality  
444 risks in nestlings, they should thus not be advised. By installing nestboxes for insectivorous birds,  
445 which generally lack natural cavities for breeding, it is thus possible to encourage their feeding activity

446 within organic orchards where they may then contribute to the control of insect pest populations (Mols  
447 and Visser, 2002; Garcia et al., 2020 in apple orchards but see Martínez-Núñez et al., 2021, in olive  
448 groves).

449

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#### 669 **Figure captions**

670 **Figure 1.** Map of the study area providing the locations of the 8 study orchards, together with their id  
671 number. Cross: conventional; Triangle: organic. The landscape background is schematic (from corine  
672 land cover 2012). Orchards are represented in light grey, woodlands as dotted areas and artificialized  
673 areas in black. Dark grey: The Durance river. See table 1 for details on orchards characteristics.

674 **Figure 2.** Examples of 95% kernels for foraging areas of four female great tits nesting in organic (top)  
675 and conventional (bottom) orchards. The nestbox is represented by a white symbol. Organic orchards  
676 are delineated with green lines and conventional orchards with red lines.

677 **Figure 3.** Effect of organic vs. conventional management on the foraging behaviour of female great  
678 tits. **Left:** Mean individual foraging distances; **Middle:** Density plots of all foraging distances; **Right:**  
679 Individual proportion of foraging points inside the breeding orchard. Crosses: actual data points. Plain  
680 circles: boxplots outliers.

681 **Figure 4.** Individual foraging areas (based on 95% kernels estimated by CTMM), as a function of  
682 orchard management. Circles: boxplot outliers. Crosses: actual data points.

683 **Figure 5.** Habitat selection by foraging female great tits breeding in organic and conventional  
684 orchards. Habitat selection is estimated by Manly's third order habitat selection ratio (means and 95 %  
685 confidence intervals) based on relocation data with a 5 m user error. A significant habitat selection or  
686 avoidance is indicated by a deviation from random use (horizontal dotted line). Letters indicate the  
687 significance of differences between habitats.

688 **Figure 6.** Five components of great tit reproductive success (A-E) in south-eastern France apple  
689 orchards under conventional and organic management. N=87 clutches (A, C-E) and 22 orchards (B).

690 **Figure 7.** Number of fledglings per pair as a function of the female's mean foraging distance. Black  
691 squares indicate nestboxes in organic orchards and crossed squares indicate nestboxes in conventional  
692 orchards. The relation was significant when distance was the only independent variable in the model,  
693 i.e., all birds were pooled (black line and grey area: mean model prediction and its standard error,  
694 respectively), but not when orchard management was also included as independent variable in the  
695 model.  
696

697 **Table 1:** Distribution of monitored great tit pairs and radio-tracked females among study orchards  
 698 each year.

Orchard type	Year	Orchard identification number	Number of great tit pairs	Number of great tit clutches	Number of tracked females
<b>Conventional</b>	2017	88	4	6	0
		122	2	2	0
		200	4	6	1
	2018	212	2	3	0
		88	2	4	0
		122	2	4	1
		200	3	4	1
		212	2	3	2
		88	3	4	1
	2019	122	1	2	1
		200	3	4	0
		212	1	2	0
212		1	2	0	
<b>Organic</b>	2017	11	4	5	1
		54	3	5	1
		194	4	5	1
	2018	11	4	4	0
		54	3	4	0
		194	3	5	2
	2019	230	3	4	0
		11	4	6	1
		194	1	1	0
		230	3	4	1

699

700

701 **Table 2:** Characteristics of radiotracking sequences for each individual female great tit: Year, number  
 702 of foraging locations, and net tracking duration.

Management	Organic							Conventional						
Individual	1	2	4	9	10	12	14	3	5	6	7	8	11	13
Year	2017	2017	2017	2018	2018	2019	2019	2017	2018	2018	2018	2018	2019	2019
Foraging locations	52	65	58	48	23	66	80	51	32	54	48	48	82	60
Duration (h:mn)	06:24	07:45	06:56	02:35	02:14	03:26	03:09	04:27	03:05	04:30	05:55	04:45	05:29	04:51

703

704 **Table 3:** Characteristics of the study orchards: area and landscape mean % area of each considered landcover in 400 m radius buffer zones.

Management	Local		Landscape							
	Orchard identification number	Area (ha)	Organic orchard	Conventional orchard	Hedgerows	Woods	Grassland	Annual crops	Built areas	Wooded fallow land
Conventional	88	0.91	5.4	25.5	8.5	4.2	29.2	10.3	5.2	11.7
	122	2.26	12.3	37.9	6.6	4.5	7.5	12.7	15.1	3.3
	200	0.85	0	45.2	6.4	0	18.6	24.7	3.8	1.3
	212	0.51	12.1	42.8	6.1	2.9	17.2	1.6	12.9	4.4
Organic	11	0.52	12.1	13.7	7.8	4.6	19.8	8.4	28.6	4.9
	54	0.47	37.7	1.0	2.6	0	1.2	24.3	33.2	0
	194	0.55	23.6	16.4	8.7	3.6	15.8	9.4	14.5	7.9
	230	1.36	10.8	10.9	3.0	4.1	9.4	61.2	0.5	0.2

705



706 **Table 4:** Components of great tit reproductive success in organic and conventional orchards in 2017,  
 707 2018 and 2019 [number of orchards, mean ( $\pm$  standard error) numbers of breeding pairs per orchard,  
 708 and eggs, nestlings, and fledglings per pair].

		Number of orchards	Number of pairs	Clutch size	Number of nestlings	Number of fledglings
<b>Organic</b>						
	2017	3	5.00 $\pm$ 0.00	6.4 $\pm$ 0.31	6.07 $\pm$ 0.58	5.40 $\pm$ 0.61
	2018	4	4.25 $\pm$ 0.25	6.48 $\pm$ 0.27	6.41 $\pm$ 0.24	5.88 $\pm$ 0.22
	2019	3	3.67 $\pm$ 1.45	6.03 $\pm$ 0.66	5.86 $\pm$ 0.51	5.56 $\pm$ 0.47
<b>Conventional</b>						
	2017	4	4.25 $\pm$ 1.03	6.17 $\pm$ 0.45	5.83 $\pm$ 0.64	2.50 $\pm$ 0.25
	2018	4	3.75 $\pm$ 0.25	6.10 $\pm$ 0.28	5.23 $\pm$ 0.71	1.31 $\pm$ 0.66
	2019	4	3.00 $\pm$ 0.58	5.69 $\pm$ 0.24	5.25 $\pm$ 0.48	1.75 $\pm$ 0.32

709

710 **Table 5:** Analysis of the variation in components of great tit reproductive success in response to  
 711 orchard management and year. df: degrees of freedom; P-values < 0.05 are in bold.

		Management			Year		
		df	Chisq	P	df	Chisq	P
Per orchard	First laying date	1	0.008	0.931	2	<b>34.75</b>	<b>2.8 × 10<sup>-8</sup></b>
	Pairs	1	2.19	0.139	2	2.70	0.260
Per pair	Clutch size	1	1.50	0.220	2	0.48	0.788
	Egg mortality	1	1.47	0.225	2	0.11	0.945
	Nestling survival	1	<b>62.77</b>	<b>2.3 × 10<sup>-15</sup></b>	2	2.75	0.253
	Number of fledglings	1	<b>49.79</b>	<b>1.7 × 10<sup>-12</sup></b>	2	0.84	0.656

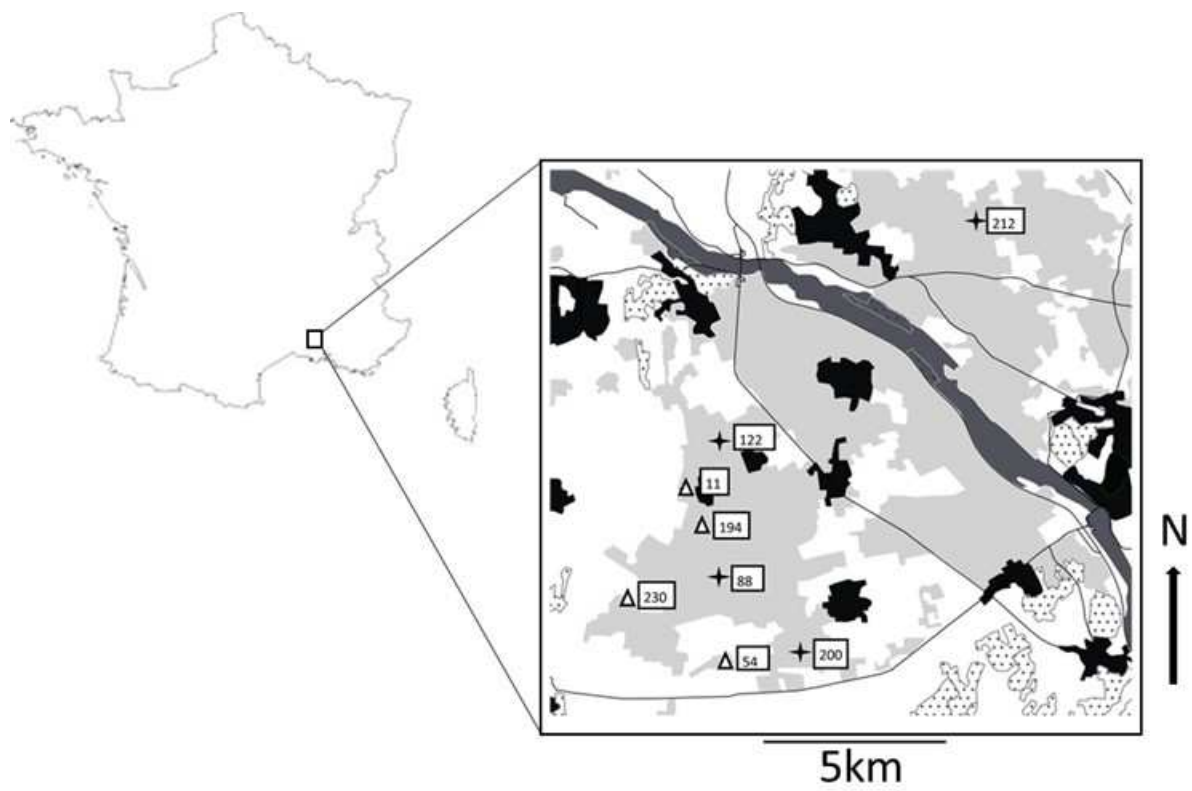
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715 **Figure 1**

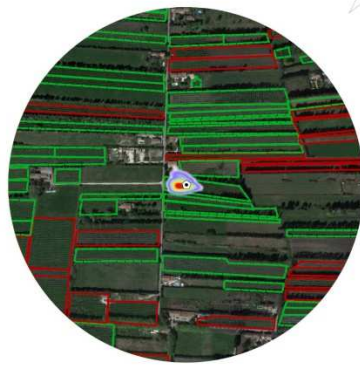
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718 **Figure 2**  
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Organic



Conventional

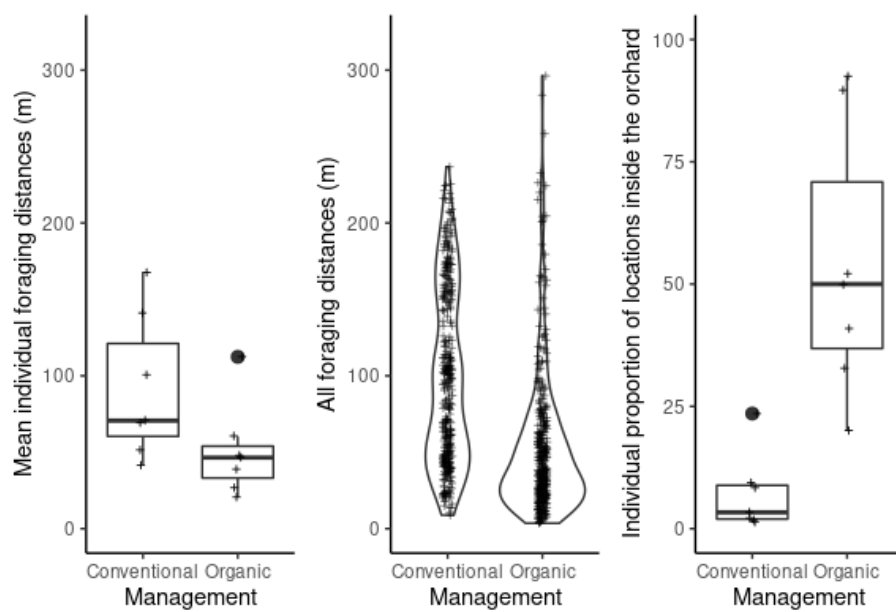


0 200 m

A horizontal scale bar with a black outline, showing a length of 200 meters. The bar is divided into four equal segments of 50 meters each.

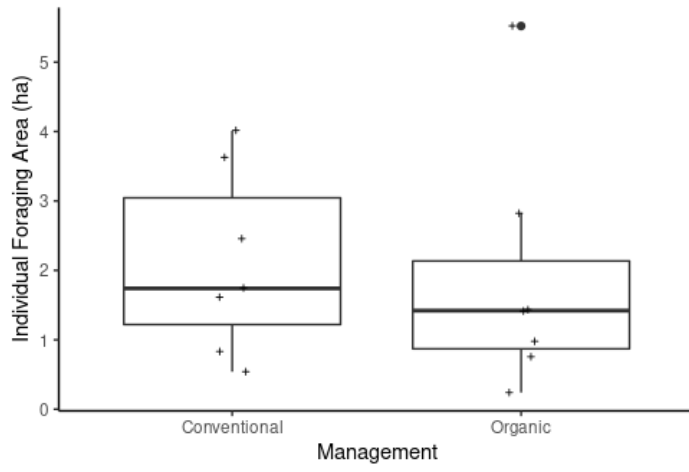
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723 **Figure 3**  
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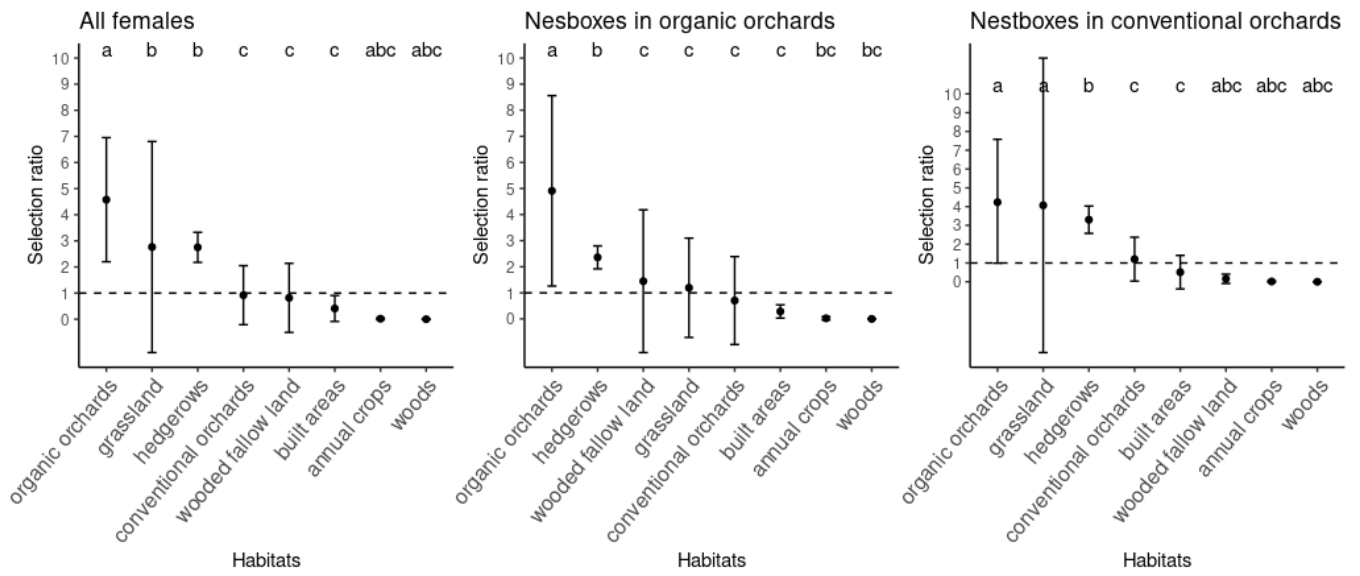
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727 **Figure 4**



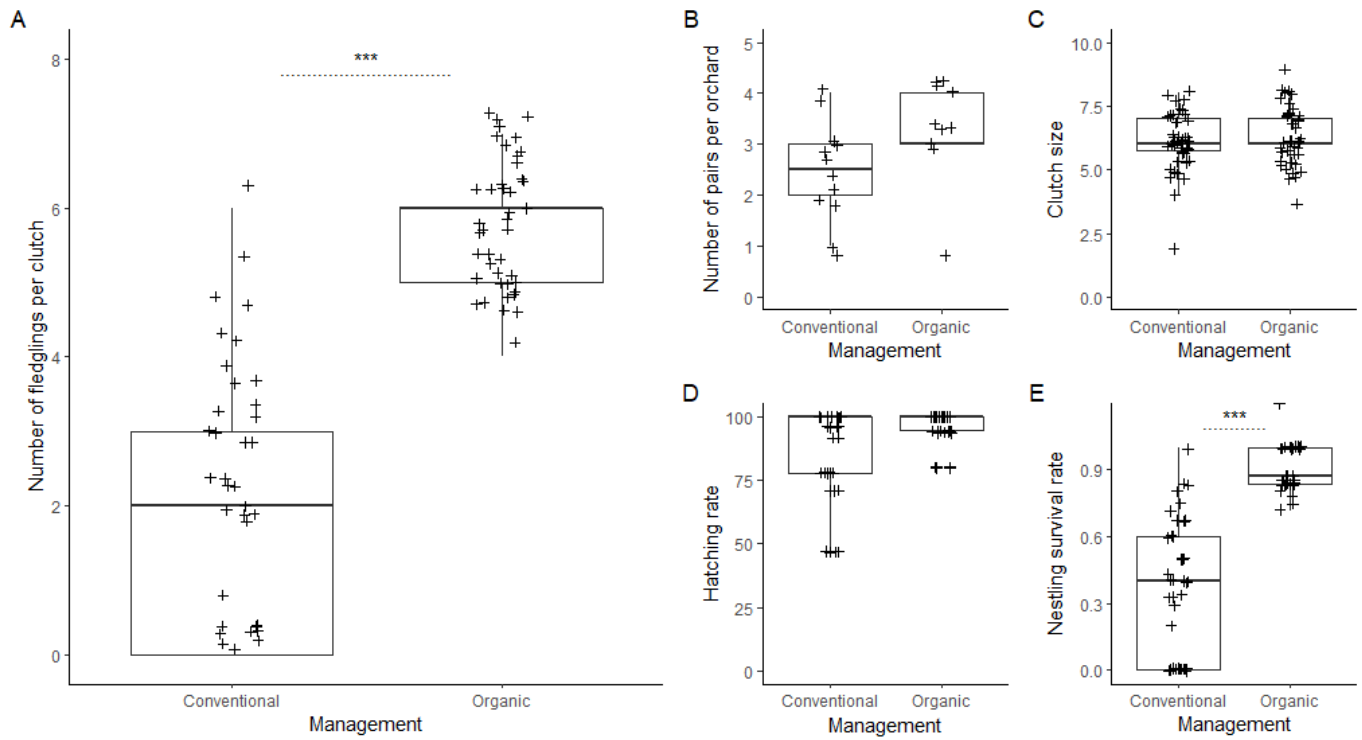
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731 **Figure 5**  
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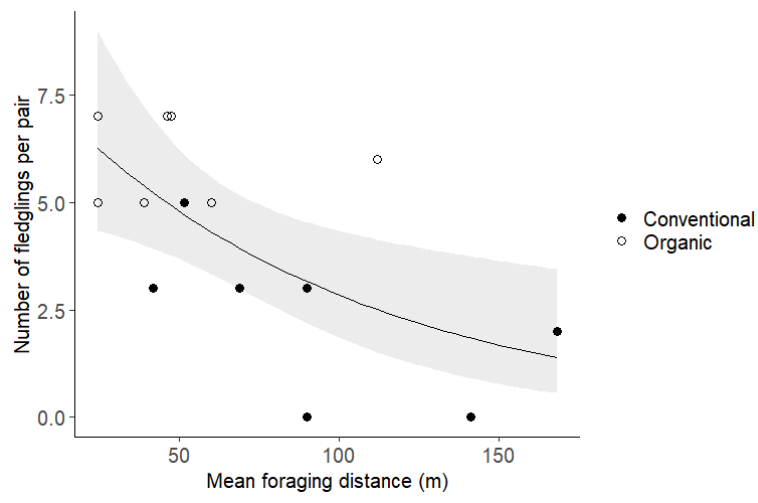
735 **Figure 6**  
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740 **Figure 7**  
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