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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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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 km² 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 ± 2.9 (mean \pm sd)
137 treatments a year. These treatments included mineral and chemical fungicides (5.7 ± 0.6 and $12.3 \pm$
138 3.3 , respectively), chemical insecticides (7.7 ± 0.3) including broad-spectrum neurotoxic insecticides
139 (3.2 ± 0.6), mating disruption against codling moth (*Cydia pomonella*), and herbicides (2.0 ± 0.6). The
140 average number of treatments in the organic orchards was 27.3 ± 3.4 a year. These treatments included
141 mineral fungicides (14.9 ± 3.1), neem and petrol oils (3.8 ± 0.4), mating disruption, biological
142 selective insecticides against codling moth (5.3 ± 0.7 treatments with granulosis virus and 0.7 ± 0.2
143 treatments with *Bacillus thuringiensis*), and Spinosad (2.5 ± 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 (9th May to 6th July), 2018 (10th May to 10th July), and 2019 (14th May
159 to 8th 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 χ^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 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 ± 6.8
284 and conventional: 53.6 ± 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 ± 11.5 m
294 from their nests. In contrast females from conventional orchards travelled a significantly higher mean
295 distance of 91.9 ± 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 (≤ 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 ± 0.67 ha and 2.12
305 ± 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 ± 17.82 m and 50.49 ± 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

450 **References**

451 Agreste, 2019. Statistique agricole annuelle. Agreste Chiffres Données 4, 5–64.

452 Assandri, G., Bogliani, G., Pedrini, P., Brambilla, M., 2017. Assessing common birds' ecological
453 requirements to address nature conservation in permanent crops: Lessons from Italian vineyards. *J.*
454 *Environ. Manag.* 191, 145–154. doi:10.1016/j.jenvman.2016.12.071

455 Barba, E., Atiénzar, F., Marin, M., Monrós, J.S., and Gil-Delgado, J.A., 2009. Patterns of nestling
456 provisioning by a single-prey loader bird, Great Tit *Parus major*. *Bird Study* 56, 187–197. doi:
457 10.1080/00063650902792049

458 Batáry, P., Matthiesen, T., Tschardtke, T., 2010. Landscape-moderated importance of hedges in
459 conserving farmland bird diversity of organic vs. conventional croplands and grasslands. *Biol.*
460 *Conserv.* 143, 2020–2027. doi. org/ 10. 1016/j. biocon. 2010. 05. 005

461 Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using
462 lme4. *J. Stat. Softw.* 67, 1–48. doi:18637/jss.v067.i01

463 Bengtsson, J., Ahnström, J., Weibull, A. C., 2005. The effects of organic agriculture on biodiversity
464 and abundance: a meta-analysis. *J. Appl. Ecol.* 42, 261–269. doi:10.1111/j.1365-
465 2664.2005.01005.x

466 Bouvier, J.C., Toubon, J.F., Boivin, T., Sauphanor B., 2005. Effects of apple orchard management
467 strategies on the Great tit (*Parus major*) in southeastern France. *Environ. Toxicol. Chem.* 24,
468 2846–2852. doi:10.1897/04-588R1.1

469 Bouvier, J.C., Boivin, T., Charmantier, A., Lambrechts, M., Lavigne, C., 2016. More daughters in a
470 less favourable world: breeding in intensively-managed orchards affects tertiary sex-ratio in the
471 great tit. *Basic Appl. Ecol.* 17, 638–647. doi:10.1016/j.baae.2016.07.003

472 Caccamise, D.F., Hedin, R.S., 1985. An aerodynamic basis for selecting transmitter loads in bird.
473 Wilson Bull. 93, 306–318. <https://www.jstor.org/stable/4162104>

474 Calabrese, J.M., Fleming, C.H., Gurarie, E., 2016. ctm: An R package for analyzing animal
475 relocation data as a continuous-time stochastic process. *Methods Ecol. Evol.* 7, 1124–1132.
476 doi:10.1111/2041-210X.12559

477 Calenge, C., 2006. The package adehabitat for the R software: tool for the analysis of space and
478 habitat use by animals. *Ecol. Model.* 197, 1035. doi:10.1016/j.ecolmodel.2006.03.017

479 Caprio, E., Rolando, A., 2017. Management systems may affect the feeding ecology of great tits *Parus*
480 *major* nesting in vineyards. *Agric. Ecosyst. Environ.* 243, 67–73. doi:10.1016/j.agee.2017.03.013

481 Cooper, T., Arblaster, K., Baldock, D., Farmer, M., Beaufoy, G., Jones, G., Pou, X., McCracken, D.,
482 Bignal, E., Elbersen, B., Washer, D., Angelstam, P., Roberge, J. M., Pointereau, P., Seffer, J.,
483 Galvanek, D., 2007. Final report for the study on HNV indicators for evaluation. Institute for
484 European Environmental Policy, London.

485 Cramp, S., Perrins, C.M., 1993. Handbook of the birds of Europe, the Middle East and North Africa.
486 The birds of the Western Palearctic. Volume VII Flycatchers to shrikes, Oxford University Press,
487 London, UK.

488 Díaz-Sieffer, P., Olmos-Moya, N., Fontúrbel, F. E., Lavandero, B., Pozo, R. A., Celis-Diez, J. L., 2022.
489 Bird-mediated effects of pest control services on crop productivity: a global synthesis. *J. Pest Sci.*
490 95, 567–576. doi:10.1007/s10340-021-01438-4

491 Dib, H., Sauphanor, B., Capowiez, Y., 2016. Effect of management strategies on arthropod
492 communities in the colonies of rosy apple aphid, *Dysaphis plantaginea* Passerini (Hemiptera:
493 Aphididae) in south-eastern France. *Agric. Ecosyst. Environ.* 216, 203–206.
494 doi:10.1016/j.agee.2015.10.003

495 Donald, P.E., Sanderson, F.J., Burfield, I.J., van Bommel, F.P.J., 2006. Further evidence of continent-
496 wide impacts of agricultural intensification on European farmland birds, 1900-2000. *Agric.*
497 *Ecosyst. Environ.* 116,189–196. doi:10.1016/j.agee.2006.02.007

498 Eurostat, 2019. https://ec.europa.eu/eurostat/databrowser/view/orch_total/default/table (accessed 13
499 January 2021).

500 FAO, Food and Agriculture Organization of the United Nations, 2009. Increasing crop production
501 sustainability: the perspective of biological process. FAO, Rome.

502 Fleming, C.H., Fagan, W.F., Mueller, T., Olson K.A., Leimgruber, P., Calabrese, J.M., 2015. Rigorous
503 home range estimation with movement data: a new autocorrelated kernel density estimator.
504 Ecology 96, 1182–1188. doi:10.1890/14-2010.1

505 Fox, J., Weisberg, S., 2019. An R Companion to Applied Regression, Third edition. Sage, Thousand
506 Oaks CA. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.

507 García, D., Miñarro, M., Martínez-Sastre, R., 2018. Birds as suppliers of pest control in cider apple
508 orchards: Avian biodiversity drivers and insectivory effect. Agric. Ecosyst. Environ. 254, 233–
509 243. doi.org/10.1016/j.agee.2017.11.034

510 García, D., Miñarro, M., Martínez-Sastre, R., 2020. Enhancing ecosystem services in apple orchards:
511 Nest boxes increase pest control by insectivorous birds. J. Appl. Ecol. 58, 465–475. doi:
512 10.1111/1365-2664.13823

513 Garcia-Navas, V., Sanz, J.J., 2011. The importance of a main dish: nestling diet and foraging
514 behaviour in Mediterranean blue tits in relation to prey phenology. Oecologia 165:639–649.
515 doi:10.1007/s00442-010-1858-z

516 Génard, M., Bouvier, J.C., Delattre, T., Lavigne, C., Lescourret, F., Toubon, J. F., Boivin, T., 2017.
517 How many insects can a great tit population prey on in apple organic orchards? A modelling
518 bioenergetics study. Acta Hort. 2017, 301–306. doi: 10.17660/ActaHortic.2017.1160.

519 Genghini, M., Gellini, S., Gustin, M., 2006. Organic and integrated agriculture: the effects on bird
520 communities in orchard farms in northern Italy. Biodiv. Conserv. 15, 3077–3094.
521 doi:10.1007/s10531-005-5400-2

522 Goulson, D., 2014. Pesticides linked to bird declines. Nature 511, 295e296. doi.:10.1038/nature13642

523 Hallmann, C.A., Foppen, R.P.B., Van Turnhout, C.A.M., De Kroon, H., Jongejans, E., 2014. Declines
524 in insectivorous birds are associated with high neonicotinoid concentrations. Nature 511, 341e343.
525 doi: 10.1038/nature13531

526 Hartig, F., 2019. DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression
527 models. R package version 0.2.4. <https://CRAN.R-project.org/package=DHARMA>

528 Hinsley, S.A., Hill, R.A., Bellamy, P.E., Harrison, N.M., Speakman, J.R., Wilson, A.K., Ferns, P.N.,
529 2008. Effects of structural and functional habitat gaps on breeding woodland birds: working harder
530 for less. *Landsc. Ecol.* 23, 615–626. doi:10.1006/jema.2000.0360

531 Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, P.V., Evans, A. D., 2005. Does organic
532 farming benefit biodiversity? *Biol. Conserv.* 122, 113–130. doi:10.1016/j.biocon.2004.07.018

533 Hórak, P., Jenni-Eiermann, S., Ots, I., 1999. Do great tits (*Parus major*) starve to reproduce?
534 *Oecologia* 119, 293–299. doi: 10.1007/s004420050789

535 Jedlicka, J.A., Letourneau, D.K., Cornelisse, T. M., 2014. Establishing songbird nest boxes increased
536 avian insectivores and reduced herbivorous arthropods in a Californian vineyard, USA. *Conserv.*
537 *Evidence.* 11, 34–38.

538 Jedlicka, J. A., Sharma, A. M., Almeida, R. P., 2013. Molecular tools reveal diets of
539 insectivorous birds from predator fecal matter. *Conservation Genet. Resour.* 5, 879-885.
540 doi:10.1007/s12686-013-9900-1

541 Karp, D. S., Judson, S., Daily, G. C., Hadly, E. A., 2014. Molecular diagnosis of bird-
542 mediated pest consumption in tropical farmland. *SpringerPlus* 3, 1-8. doi:10.1186/2193-
543 1801-3-630

544 Kleijn, D., Bommarco, R., Fijen, T.P., Garibaldi, L.A., Potts, S.G., van der Putten, W.H., 2019.
545 Ecological intensification: bridging the gap between science and practice. *Trends Ecol. Evol.* 34,
546 154–166. doi:10.1016/j.tree.2018.11.002

547 Krebs, J.R., 1971. Territory and Breeding Density in the Great Tit, *Parus Major* L. *Ecology* 52, 2–22.
548 [doi:10.2307/1934734](https://doi.org/10.2307/1934734)

549 Li, Y., Miao, R., Khanna, M., 2020. Neonicotinoids and decline in bird biodiversity in the United
550 States. *Nat. Sustain.* doi:10.1038/s41893-020-0582-x

551 Lindell, C., Eaton, R.A., Howard, P.H., Roels, S.M., Shave, M.E., 2018. Enhancing agricultural
552 landscapes to increase crop pest reduction by vertebrates. *Agric. Ecosyst. Environ.* 257, 1–11.
553 doi:10.1016/j.agee.2018.01.028

554 Losey, J.E., Vaughan, M., 2006. The economic value of ecological services provided by insects.
555 BioScience 56, 311–323. doi:10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2

556 Maas, B., Karp, D.S., Bumrungsri, S., Darras, K., Gonthier, D., Huang, J.C.C., Williams-Guillén, K.,
557 2016. Bird and bat predation services in tropical forests and agroforestry landscapes. Biol. Rev. 91,
558 1081–1101. doi: 10.1111/brv.12211

559 Maalouly, M., Franck, P., Bouvier, J.C., Toubon, J.F., Lavigne, C., 2013. Codling moth parasitism is
560 affected by semi-natural habitats and agricultural practices at orchard and landscape levels. Agric.
561 Ecosyst. Environ. 169, 33–42. doi: 10.1016/j.agee.2013.02.008

562 Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. Resource
563 Selection by Animals: Statistical Design and Analysis for Field Studies, 2nd ed. Kluwer Academic
564 Publishers, Dordrecht, The Netherlands.

565 Martínez-Núñez, C., Rey, P.J., Manzaneda, A.J., García, D., Tarifa R., Molina, J.L., 2021.
566 Insectivorous birds are not effective pest control agents in olive groves, Basic Appl. Ecol. 56: 270-
567 280. doi: 10.1016/j.baae.2021.08.006.

568 Mazzia, C, Pasquet, A., Caro, G., Thenard, J., Cornic, J.F., Hedde, M., Capowiez, Y., 2015. The
569 impact of management strategies in apple orchards on the structural and functional diversity of
570 epigeal spiders. Ecotoxicology 24, 616–625. doi: 10.1007/s10646-014-1409-1

571 Mols, C.M.M., Visser, M.E., 2002. Great tits can reduce caterpillar damage in apple orchards. J. Appl.
572 Ecol. 39, 888–899. doi: 10.1046/j.1365- 2664.2002.00761.x.

573 Mols, C.M.M., Visser, M.E., 2007. Great tits (*Parus major*) reduce caterpillar damage in commercial
574 apple orchards. PloS One 2: e202. doi:10.1371/journal.pone.0000202

575 Morelli, F., Leszek, J., Tryjanowski, P., 2014. Birds as useful indicators of high nature value (HNV)
576 farmland in Central Italy. Ecol. Indic. 38, 236–242. doi:10.1016/j.ecolind.2013.11.016

577 Myczko, L., Rosin, Z.M., Skorka, P., Wylegala, P., Tobolka, M., Fliszkiewicz, M., Mizera, T.,
578 Tryjanowski, P., 2013. Effects of management intensity and orchard features on bird communities
579 in winter. Ecol. Research 28, 503–5012. doi:10.1007/s11284-013-1039-8

580 Naef-Daenzer, L., Naef-Daenzer, B., Nager, R.G., 2000. Prey selection and foraging performance of
581 breeding Great Tits *Parus major* in relation to food availability. *J. Avian Biol.* 31, 206–214.
582 doi:10.1034/j.1600-048X.2000.310212.x

583 Naef-Daenzer, B., 2007. An allometric function to fit leg-loop harnesses to terrestrial birds. *J. Avian*
584 *Biol.* 38, 404–407. doi:10.1111/j.2007.0908-8857.03863.x

585 Newton, I., 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biol.*
586 *Conserv.* 70, 265–276. doi:10.1016/0006-3207(94)90172-4

587 Nour, N., Currie, D., Matthysen, E., Van Damme, R., Dhondt A.A., 1998. Effects of habitat
588 fragmentation on provisioning rates, diet and breeding success in two species of tit (great tit and
589 blue tit). *Oecologia* 114, 522–530. doi:10.1007/s004420050476

590 Nur, N., 1984. The consequences of brood size for breeding blue tit I. Adult survival, weight change
591 and the cost of reproduction. *J. Anim. Ecol.* 53, 479–496. doi: pdf/10.1111/j.1558-
592 5646.1988.tb04138.x

593 Pagani-Núñez, E., Valls, M., Senar, J.C., 2015. Diet specialization in a generalist population: the case
594 of breeding great tits *Parus major* in the Mediterranean area. *Oecologia* 179, 629–640.
595 doi:10.1007/s00442-015-3334-2

596 Pebesma, E., Bivand, R.S., 2005. S classes and methods for spatial data: the sp package. *R news* 5, 9–
597 13.

598 PECBMS, 2020. European wild bird indicators, 2020 update. Pan-European Common Bird
599 Monitoring Scheme (PECBMS). <https://pecbms.info/european-wild-bird-indicator-2020-update/>

600 R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for
601 Statistical Computing, Vienna, Austria. URL. <https://www.R-project.org/>.

602 Rappole, J.H., Tipton, A.R., 1991. New harness design for attachment of radio transmitters to small
603 passerines. *J. Field Ornithol.* 62, 335–337.

604 Reganold, J.P., Glover, J.D., Andrews, P.K., Hinman, H.R., 2001. Sustainability of three apple
605 production systems. *Nature* 410, 926–930. doi:10.1038/35073574

606 Rey Benayas, J.M., Meltzer, J., de las Heras-Bravo, D., Cayuela, L., 2017. Potential of pest regulation
607 by insectivorous birds in Mediterranean woody crops. PLoS ONE 12, 1–19.
608 doi:10.1371/journal.pone.0180702

609 Rytönen, S., Krams, I., 2003. Does foraging behaviour explain the poor breeding success of great tits
610 *Parus major* in northern Europe? J. Avian Biol. 34, 288–297. doi:10.1034/j.1600-
611 048X.2003.03041.x

612 Samnegård, U., Alins, G., Boreux, V., Bosch, J., García, D., Happe, A.K., Hambäck, P.A., 2019.
613 Management trade-offs on ecosystem services in apple orchards across Europe: Direct and indirect
614 effects of organic production. J. Appl. Ecol. 56, 802–811. doi: 10.1111/1365-2664.13292

615 Sanchez-Bayo, F., 2011. Impacts of agriculture pesticides on terrestrial ecosystems, in: Sánchez-Bayo,
616 F., van den Brink, P.J., Mann, R.M. (Eds.) Ecological Impacts of Toxic Chemicals, Bentham
617 Science Publishers, pp 63–87.

618 Sanz, J.J., Tinbergen, J.M., 1999. Energy expenditure, nestling age, and brood size: an experimental
619 study of parental behavior in the great tit *Parus major*. Behav. Ecol. 10, 598–606.
620 doi :10.1093/beheco/10.5.598

621 Seaman, D.E., Millsbaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J., Gitzen, R.A., 1999.
622 Effects of sample size on kernel home range estimates. J. wildl. Manag. 63, 739–747.

623 Sekercioglu, C.H., 2006. Increasing awareness of avian ecological function. Trends Ecol. Evol. 21,
624 464–471. doi :10.1016/j.tree.2006.05.007

625 Seki, S.I., Takano, H., 1998. Caterpillar abundance in the territory affects the breeding performance of
626 great tit *Parus major minor*. Oecologia 114, 514–521. doi:10.1007/s004420050475

627 Simon, S., Bouvier, J.C., Debras, J.F., Sauphanor, B., 2010. Biodiversity and pest management in
628 orchard systems. A review. Agron. Sustain. Dev. 30, 139–152. doi:10.1051/agro/2009013

629 Smith, G.S., Kallander, H., Fontell, K., Ljungström, M., 1988. Feeding frequency and parental
630 division of labour in the double-brooded great tit *Parus major*. Behav. Ecol. Sociobiol. 22, 447–
631 453. doi:10.1007/BF00294983

632 Stauss, M.J., Burkhardt, J.F., Tomiuk, J., 2005. Foraging flight distances as a measure of parental
633 effort in blue tits *Parus caeruleus* differ with environmental conditions. *J. Avian Biol.* 36, 47–56.
634 doi:10.1111/j.0908-8857.2005.02855.x

635 Stein-Bachinger, K., Gottwald, F., Haub, A., Schmidt, E., 2021. To what extent does organic farming
636 promote species richness and abundance in temperate climates? A review. *Org. Agric.* 11:1–12.
637 doi:10.1007/s13165-020-00279-2

638 Tassin de Montaigu, C., Goulson, D., 2020. Identifying agricultural pesticides that may pose a risk for
639 birds. *PeerJ* 8:e9526. doi:10.7717/peerj.9526

640 Tschardtke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives
641 on agricultural intensification and biodiversity-ecosystem service management. *Ecol. Lett.* 8, 857–
642 874. doi: 10.1111/j.1461-0248.2005.00782.x

643 Tinbergen, J.M., Ditz, M.W., 1994. Parental energy expenditure during brood rearing in the great tit
644 (*Parus major*) in relation to body mass, temperature, food availability and clutch size. *Funct. Ecol.*
645 563–572. doi:10.2307/2389916

646 Tomich, T.P., Brodt, S., Ferris, H., Galt, R., Horwath, W.R., Kebeab, E., Yang, L., 2011.
647 Agroecology: A review from a global-change perspective. *Annu. Rev. Environ. Resour.* 36, 193–
648 222. doi:10.1146/annurev-environ-012110-121302

649 van Noordwijk, A.J., McCleery, R.H., Perrins, C.M., 1995. Selection for the timing of great tit
650 breeding in relation to caterpillar growth and temperature. *J. Anim. Ecol.* 64, 451–458.
651 doi:10.2307/5648

652 Walker, C.H., 2002. Neurotoxic pesticides and behavioral effects upon birds. *Ecotoxicology* 12, 307–
653 316. doi:10.1023/A:1022523331343

654 Wenny, D.G., DeVault, T.L., Johnson, M.D., Kelly, D., Sekercioglu, C.H., Tomback, D.F., Whelan,
655 C.J., 2011. The need to quantify ecosystem services provided by birds. *Auk*, 128, 1–14. doi:
656 10.1525/auk.2011.10248

657 Whelan, C.J., Sekercioglu, C.H., Wenny, D.G., 2015. Why birds matter: from economic ornithology to
658 ecosystem services. *J. Ornithol.* 156, 227–238. doi:10.1007/s10336-015-1229-y

659 Wilkin, T.A., King, L.E., Sheldon, B.C., 2009. Habitat quality, nestling diet, and provisioning
660 behaviour in great tits *Parus major*. *J. Avian Biol.* 40, 135–145. doi: 10.1111/j.1600-
661 048X.2009.04362.x

662 White, G. C., Garrott, R.A., 1990. Analysis of wildlife radio-tracking data. Academic Press eds, San
663 Diego.

664 Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies.
665 *Ecology* 70, 164–168. doi:10.2307/1938423

666 Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common
667 statistical 635 problems. *Methods Ecol. Evol.* 1, 3–14. doi:10.1111/j.2041-210X.2009.00001.x
668

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
Conventional	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	
Organic	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
Organic						
	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
Conventional						
	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	34.75	2.8 × 10⁻⁸
	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	62.77	2.3 × 10⁻¹⁵	2	2.75	0.253
	Number of fledglings	1	49.79	1.7 × 10⁻¹²	2	0.84	0.656

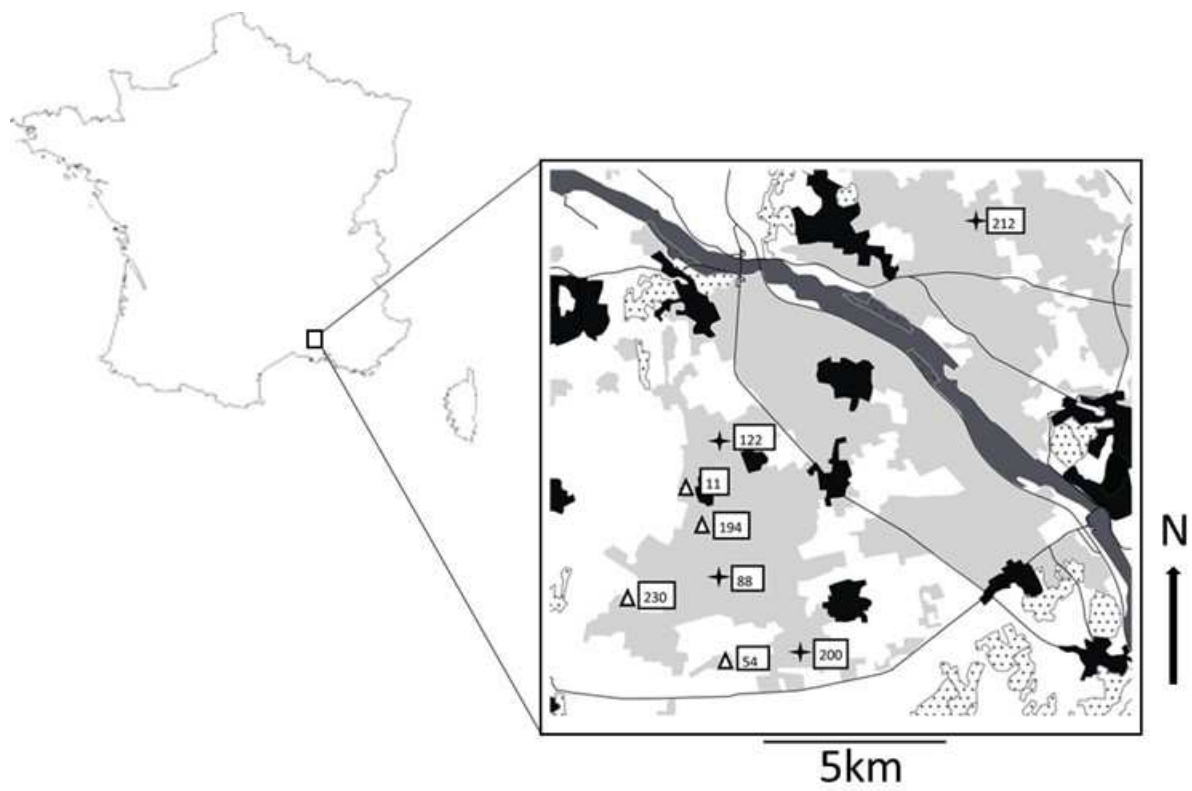
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715 **Figure 1**

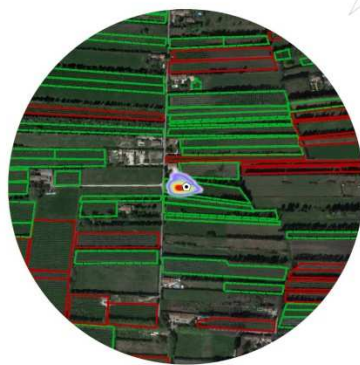
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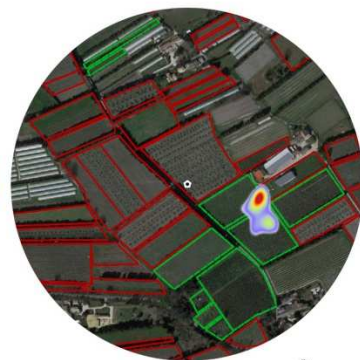
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718 **Figure 2**
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Organic



Conventional

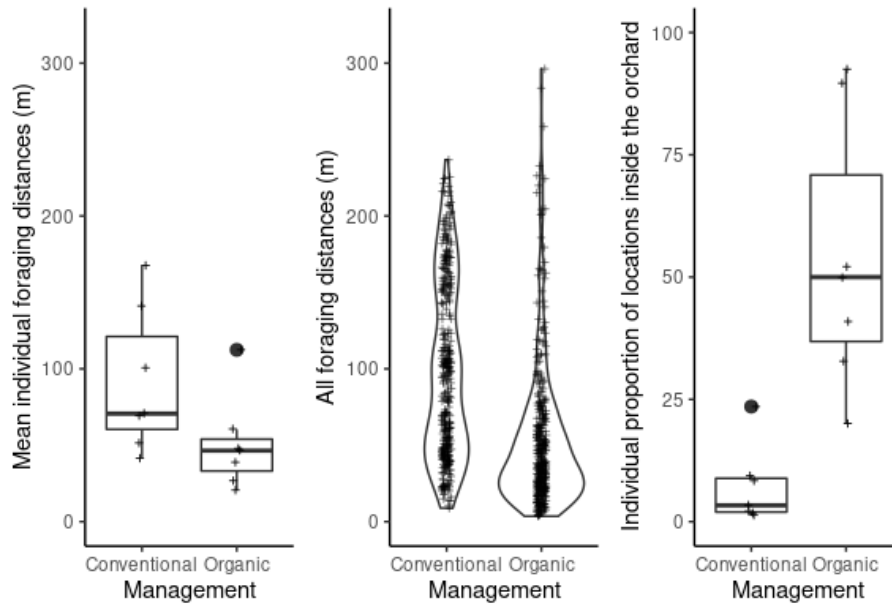


0 200 m

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.

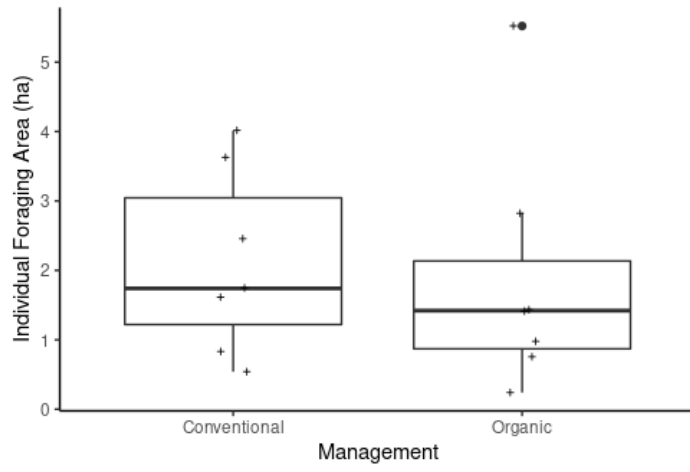
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723 **Figure 3**
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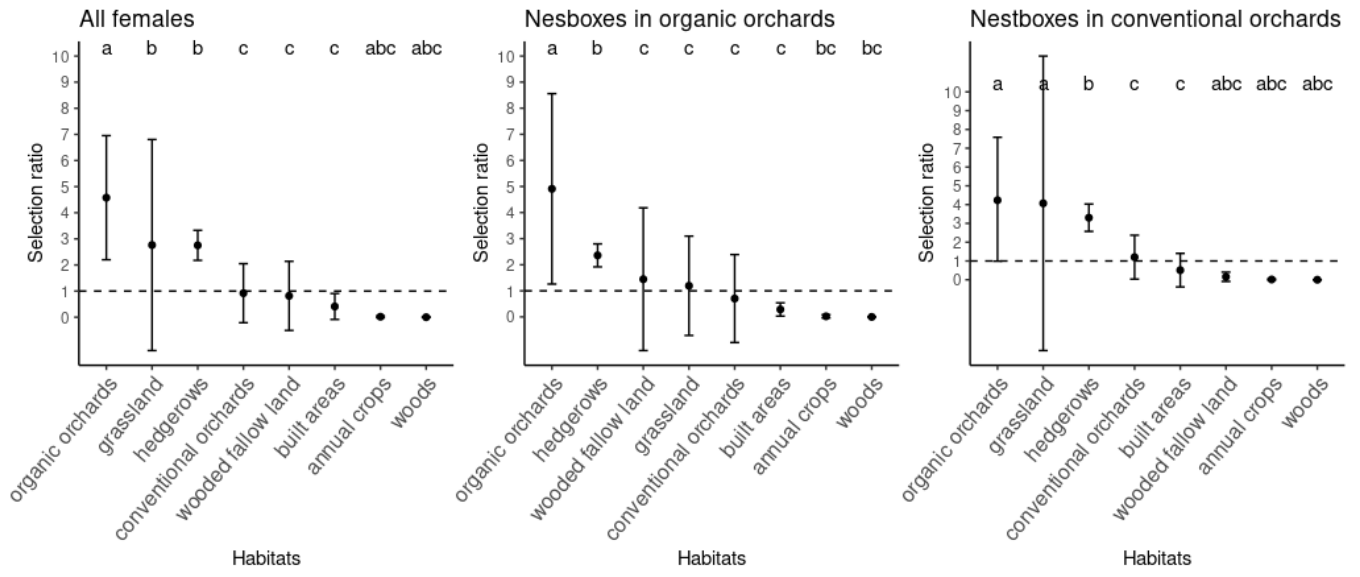
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727 **Figure 4**



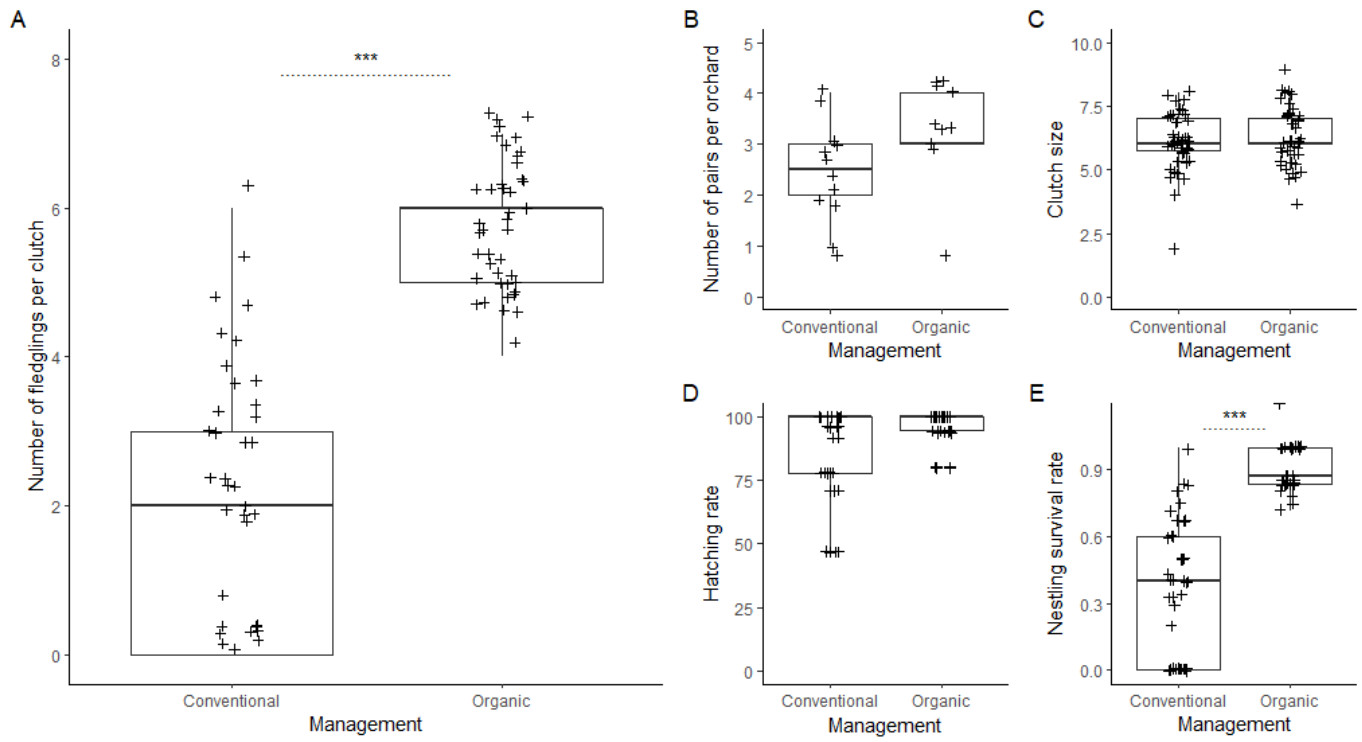
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731 **Figure 5**
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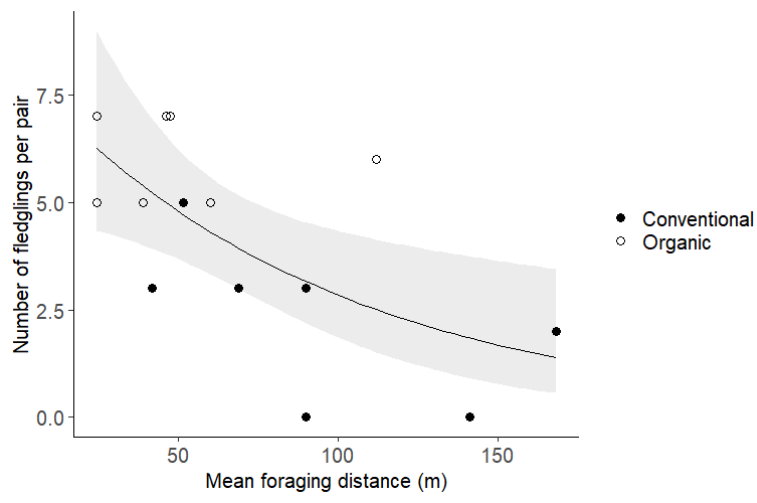
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735 **Figure 6**
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740 **Figure 7**
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