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

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Highlights

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

Abstract

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

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

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

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

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

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1. Introduction

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

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

The apple is the second most important fruit crop globally (FAO, 2009), accounting for almost 40% of the total area under fruit crops in Europe (Eurostat, 2019). Apple crop intensification has converted traditional, high nature value fruit orchards (Cooper et al., 2007; Myczko et al., 2013) into productivity-oriented plantations of low-stem trees. They are primarily managed through high amounts of inorganic fertilizers, pesticides, and herbicides, with detrimental effects within and surrounding the orchards (Reganold et al., 2001; Simon et al., 2010). In southern France, for instance, conventional production relies on an average of 29 phytosanitary treatments per year, including nine broad spectrum insecticides and 16 fungicides. In contrast, organic farming involves 17 treatments on average, including seven microbiological insecticides and 10 fungicides (Agreste, 2019). Over the past decade, the combination of high environmental impacts of intensification with the development of resistance of target pests to chemical and biological insecticides has promoted ecological intensification in apple orchards across Europe (Simon et al., 2010; Samnegard et al., 2019).

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

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

2. Materials and methods

2.1 Study area

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

Fieldwork was carried out during the springs of 2017, 2018, and 2019 in commercial apple orchards chosen for their similarity regarding both their intrinsic and surrounding vegetation. Among these orchards, four were under conventional management and four under organic management (Table 1). They had similar average areas (mean ± standard deviation (sd): conventional: 1.22 ± 0.36 ha, organic: 0.97 ± 0.28 ha), a plantation density of approximately 1500 trees/ha, and a grassy ground cover. Pest control was carried out from March to October. The management strategies were characterised by the treatment schedules provided by the orchard owners (Supplementary material, Table S1). The conventional orchards were managed with an average of 28.1 ± 2.9 (mean ± sd) treatments a year. These treatments included mineral and chemical fungicides (5.7 ± 0.6 and 12.3 ± 3.3, respectively), chemical insecticides (7.7 ± 0.3) including broad-spectrum neurotoxic insecticides (3.2 ± 0.6), mating disruption against codling moth (*Cydia pomonella*), and herbicides (2.0 ± 0.6). The average number of treatments in the organic orchards was 27.3 ± 3.4 a year. These treatments included mineral fungicides (14.9 ± 3.1), neem and petrol oils (3.8 ± 0.4), mating disruption, biological selective insecticides against codling moth (5.3 ± 0.7 treatments with granulosis virus and 0.7 ± 0.2 treatments with *Bacillus thuringiensis*), and Spinosad (2.5 ± 0.5). All orchards were bordered by hedgerows (mainly poplar or cypress) for protection against the prevailing winds.

2.2 Design and monitoring of nestboxes

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

2.3 Radiotracking

During the springs of 2017 (9th May to 6th July), 2018 (10th May to 10th July), and 2019 (14th May to 8th July), we radiotracked 14 female great tits breeding in the implemented nestboxes; seven females bred in conventional orchards and seven in organic orchards (Table 1). We monitored only females to avoid between-sex variation and because, contrary to males, females return quickly to their nest when disturbed (personal observation). Furthermore, males and females contribute equally to offspring feeding (Smith et al., 1988). To limit pseudoreplication, all females were from different nestboxes and were located, as much as possible, in different orchards each year (two exceptions, Table 1). Females were caught in their nestboxes when nestlings were about 9 days old and they were fitted with a Biotrack Pip Ag317 VHF radiotag (Biotrack Ltd, Wareham, Dorset, UK) (Supplementary material, Fig. S1). The tag weight (0.45 g excluding harness) was well below the recommended 5% of the bird's body weight (Caccamise and Hedin, 1985). The tags were fixed on the birds' backs using biodegradable natural rubber leg harnesses with a diameter of 0.5 mm. Harness length was calculated according to the weight of the birds from the Naef-Daenzer model (2007). The tags were glued to the harnesses with cyanoacrylate Loctite® 454 with Loctite® 7455 activator (Rappole and Tipton, 1991). The tags emitted one signal of 20 milliseconds per second in the 148 MHz frequency with one unique frequency per tag. Their maximum above ground range of 600 m sufficed to locate foraging females in our study sites without disturbing the behaviour of the birds.

To avoid potential behavioural biases resulting from stress of capture or an adjustment period inherent to carrying the radiotag equipment, the tracking of the birds began approximately 24 hours after they were equipped. Tracking lasted from 7.30 am to 1.30 pm and from 3.00 pm to 5.30 pm. It was performed for all birds by the same two observers, each equipped with a directional Yagi-Uda antenna, a VHF receiver (Sika, Biotrack Ltd.), and a walkie-talkie. The positions of the observers were chosen so as not to lose signals due to the orchard configuration or landscape elements, such as hedgerows. The azimuths of the foraging females were obtained from the directional antennas and magnetic compasses of each observer, complemented with visual observations. The observers simultaneously recorded the foraging female's azimuth. The female's position was determined as the intersection of two azimuths, according to the principle of triangulation defined by White and Garrott (1990). Upon visual inspection of the birds, each azimuth was annotated according to the observed behaviour (i.e., resting, foraging, and going back to the nest) and only foraging points were used for further analyses. Females were tracked for 1.5 days, as a trade-off between equivalence between the numbers of recorded female positions in organic and conventional orchards (Table 2) and the necessity to remove the tag early enough to avoid premature fledgling in response to the handling of the mother in the nestbox. As a result, the net tracking duration, i.e., sum of durations during which each female could be monitored while feeding, was on average 4h41min (range: [2h14, 7h45], Table 2). Females were recaptured in nestboxes for tag removal after the radiotracking scheme.

2.4 Landscape feature description

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

2.5 Statistical analysis

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

2.5.1 Foraging distances

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

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

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

2.5.2 Foraging areas

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

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

2.5.3 Foraging habitat selection

Foraging habitat selection was analysed by comparing habitats located at the foraging relocations with the composition of the habitats available in the 400 m radius around the nest, using Manly’s selectivity measure (third-order selection; Manly et al., 2002). To account for location uncertainties inherent to the radiotracking equipment and methodology, the composition of the habitat used was measured as the proportion of all habitats in a 5 m buffer around each original relocation. Habitat selection was tested at the population level with log-likelihood Khi2 (Manly et al., 2002). The differences between selection ratios were computed and tested using the widesIII R function (“adehabitatHS” package, Calenge, 2006).

2.5.4 Reproductive success

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

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

3. Results

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

3.1 Foraging distance

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

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

3.2 Foraging area

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

3.3 Habitat selection

Foraging female great tits showed a significant habitat selection behaviour (Manly's Khi2L = 3299.06, p < 0.0001, Manly et al., 2002). We observed two preferred habitat types amongst those available in the landscape surrounding their nests (Fig. 5). Organic orchards and hedgerows were present in higher proportions at foraging locations than in the buffer zone surrounding the female's nest. Urban areas, annual crops and woods were present in lower proportions. The selection ratios for the other habitats, including conventional orchards, did not show a significant deviation from random use. Organic orchards showed the highest of all selection ratios, significantly higher than any other habitats. Conventional orchards showed lower selection ratio than organic orchards and wooded fallow lands. Their selection ratios were not significantly different from habitats below the random use threshold. Woods were never used by any individual during the study and annual crops were used only once.

3.4 Reproductive success

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

Considering only pairs involving tagged females, the mean number of fledglings decreased with increasing mean foraging distance of the female (Chi2 = 8.15, $P = 4.3\ 10^{-3}$, Fig. 7). However, this effect was not significant when accounting for orchard management (Management Chi2 = 5.44, P = 0.019; Distance Chi2 = 1.52, P = 0.218).

4. Discussion

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

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

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

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

The importance of landscape scale effects on bird biodiversity and avian-mediated pest-control have been well recognised (Tscharntke et al., 2005). This supported the development of hedgerows and other habitat enhancements that are beneficial to both wildlife and sustainable farming in intensively managed agricultural landscapes (Batáry et al., 2010). However, the foraging area for insectivorous birds in agricultural landscapes was still unknown despite its basic implications for considering the provision of pest control services by birds in farm management. For the first time, our results unequivocally show that female great tits can feed in the orchard where they nest under organic farming. Such behaviour is consistent with overall evidence that organic farming is far more beneficial to arthropod diversity and abundance than conventional farming (Bengtsson et al., 2005; Hole et al., 2005; Stein-Bachinger et al., 2021), including apple orchards (Maalouly et al., 2013; Mazzia et al., 2015; Dib et al., 2016). This relies on the three main farming practices acknowledged to benefit biodiversity: (i) the exclusion of chemical pesticides and fertilisers, (ii) the appropriate management of non-crop habitats and field margins, and (iii) the preservation of mixed farming that provides greater habitat structural heterogeneity (Hole et al., 2005). Of these practices, pesticide use most differentiates organic from conventional farming in our study and likely explains the observed effects on great tit behaviour. As all organic orchards result from the conversion of former conventional orchards, all studied orchards were of similar size and planting structure. Adverse effects of pesticide use on arthropod populations were less prominent in organic orchards due to the use of more selective compounds for pest control. In south-eastern France, the main apple insect pest is the codling moth. In organic farming, it is controlled by the very specific granulosis virus as well as pheromonal male mating disruption, while conventional farming involves chemical insecticides with broad-spectrum efficiency among arthropod communities.

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

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

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

4.2 Interferences between pest management and great tit reproductive success

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

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

5. Conclusions

In the present study, the preferred feeding habitats used by great tits were organic orchards (mainly apple, pear, and olive), followed by hedgerows. Our results provide guidelines to farmers wishing to increase the level of ecosystem services provided by insectivorous bird species in intensively-managed orchards. Females nesting in organic apple orchards largely foraged within the orchard, which strongly supports the benefit of installing nestboxes in an environment that apparently meets the ecological requirements of great tits. Conversely, nestboxes in conventional orchards likely increase mortality risks in nestlings, they should thus not be advised. By installing nestboxes for insectivorous birds, which generally lack natural cavities for breeding, it is thus possible to encourage their feeding activity within organic orchards where they may then contribute to the control of insect pest populations (Mols and Visser, 2002; Garcia et al., 2020 in apple orchards but see Martínez-Núñez et al., 2021, in olive groves).

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Figure captions

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

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

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

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

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

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

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

Table 1: Distribution of monitored great tit pairs and radio-tracked females among study orchards 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
		212	2	3	0
	2018	88	2	4	0
		122	2	4	1
		200	3	4	1
		212	2	3	2
	2019	88	3	4	1
		122	1	2	1
		200	3	4	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
		230	3	4	0
	2019	11	4	6	1
		194	1	1	0
		230	3	4	1

Table 2: Characteristics of radiotracking sequences for each individual female great tit: Year, number 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

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

Local			Landscape							
Management	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

Table 4: Components of great tit reproductive success in organic and conventional orchards in 2017, 2018 and 2019 [number of orchards, mean (± standard error) numbers of breeding pairs per orchard, 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 ± 0.00	6.4 ± 0.31	6.07 ± 0.58	5.40 ± 0.61
	2018	4	4.25 ± 0.25	6.48 ± 0.27	6.41 ± 0.24	5.88 ± 0.22
	2019	3	3.67 ± 1.45	6.03 ± 0.66	5.86 ± 0.51	5.56 ± 0.47
Conventional						
	2017	4	4.25 ± 1.03	6.17 ± 0.45	5.83 ± 0.64	2.50 ± 0.25
	2018	4	3.75 ± 0.25	6.10 ± 0.28	5.23 ± 0.71	1.31 ± 0.66
	2019	4	3.00 ± 0.58	5.69 ± 0.24	5.25 ± 0.48	1.75 ± 0.32

Table 5: Analysis of the variation in components of great tit reproductive success in response to 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

Figure 1

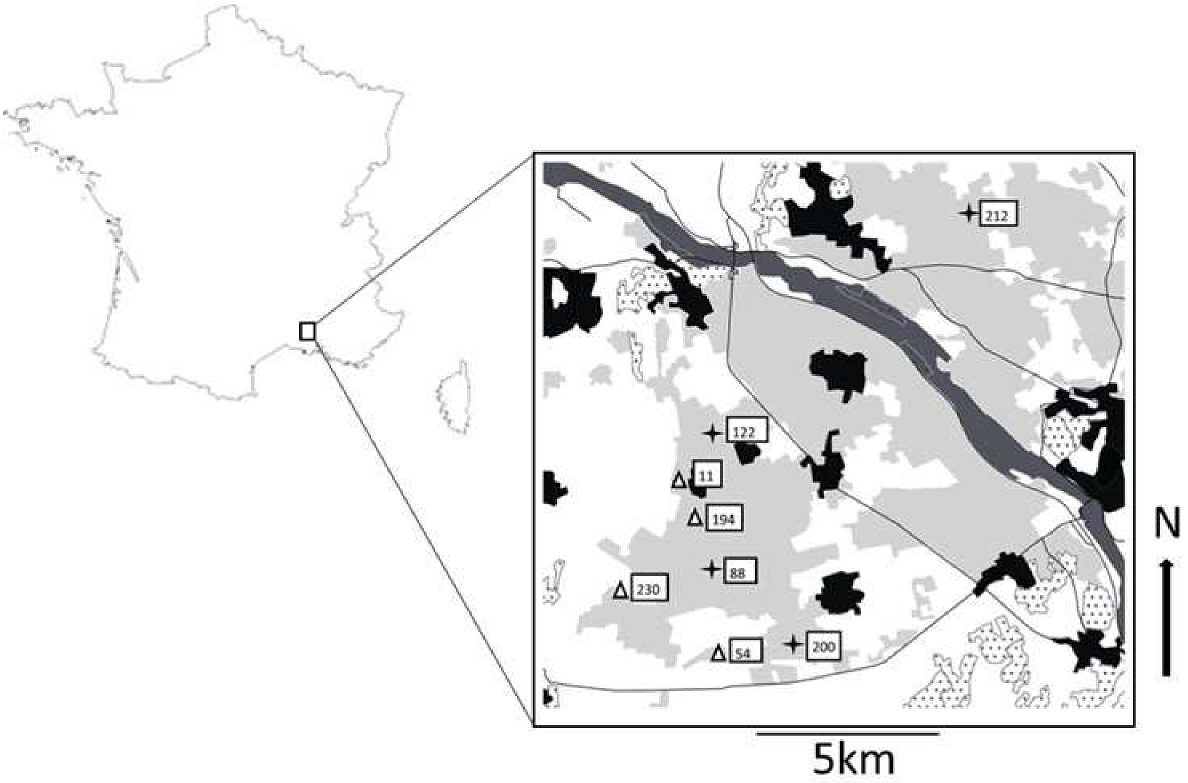


Figure 2

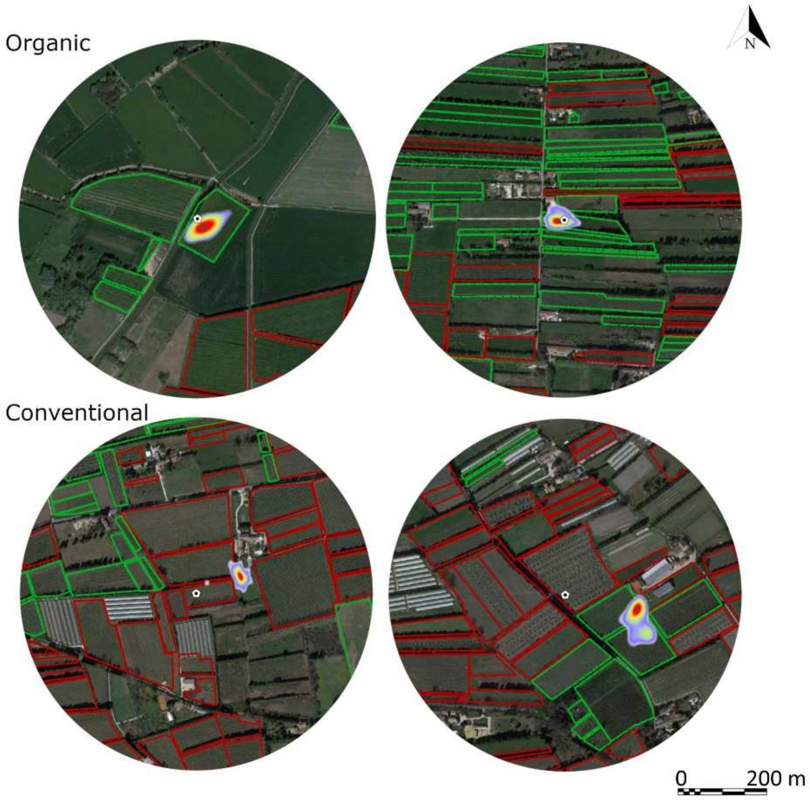


Figure 3

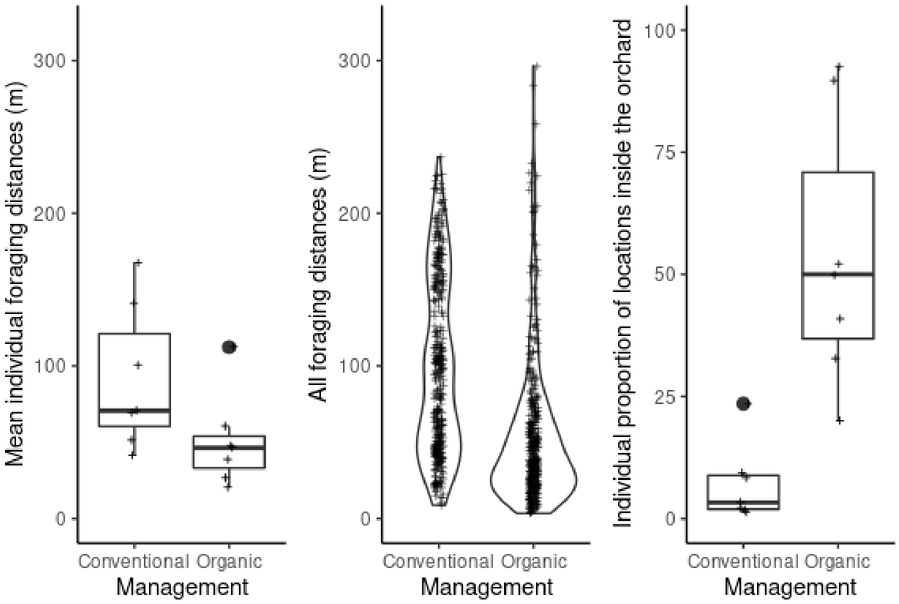

Mean individual foraging distances (m)
All foraging distances (m)
Individual proportion of locations inside the orchard
0
100
200
300
0
25
50
75
100
Conventional
Organic
Management

Figure 4

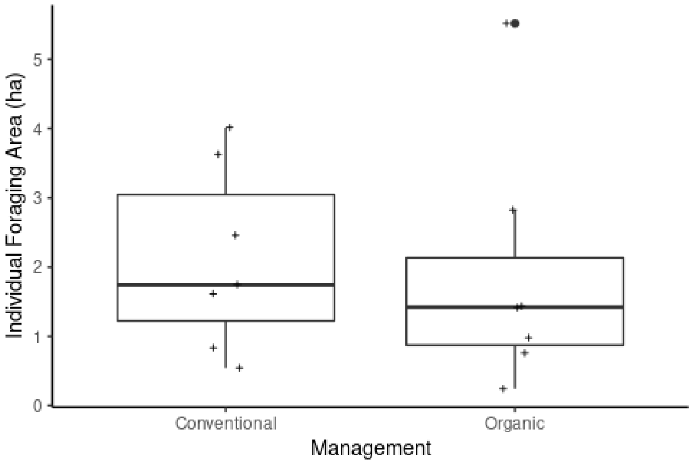

Individual Foraging Area (ha)
0
1
2
3
4
5
Conventional
Organic
Management

Figure 5

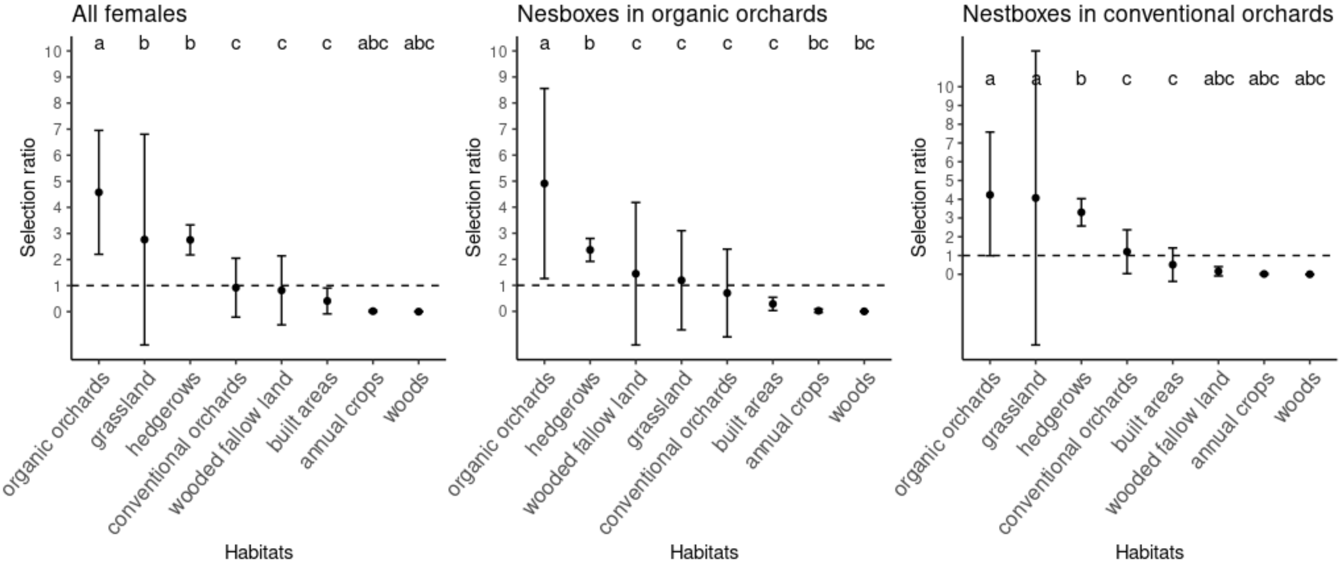

All females
Nesboxes in organic orchards
Nestboxes in conventional orchards
Selection ratio
Habitats
0
1
2
3
4
5
6
7
8
9
10
a
b
c
bc
abc
organic orchards
grassland
hedgerows
conventional orchards
wooded fallow land
built areas
annual crops
woods

Figure 6

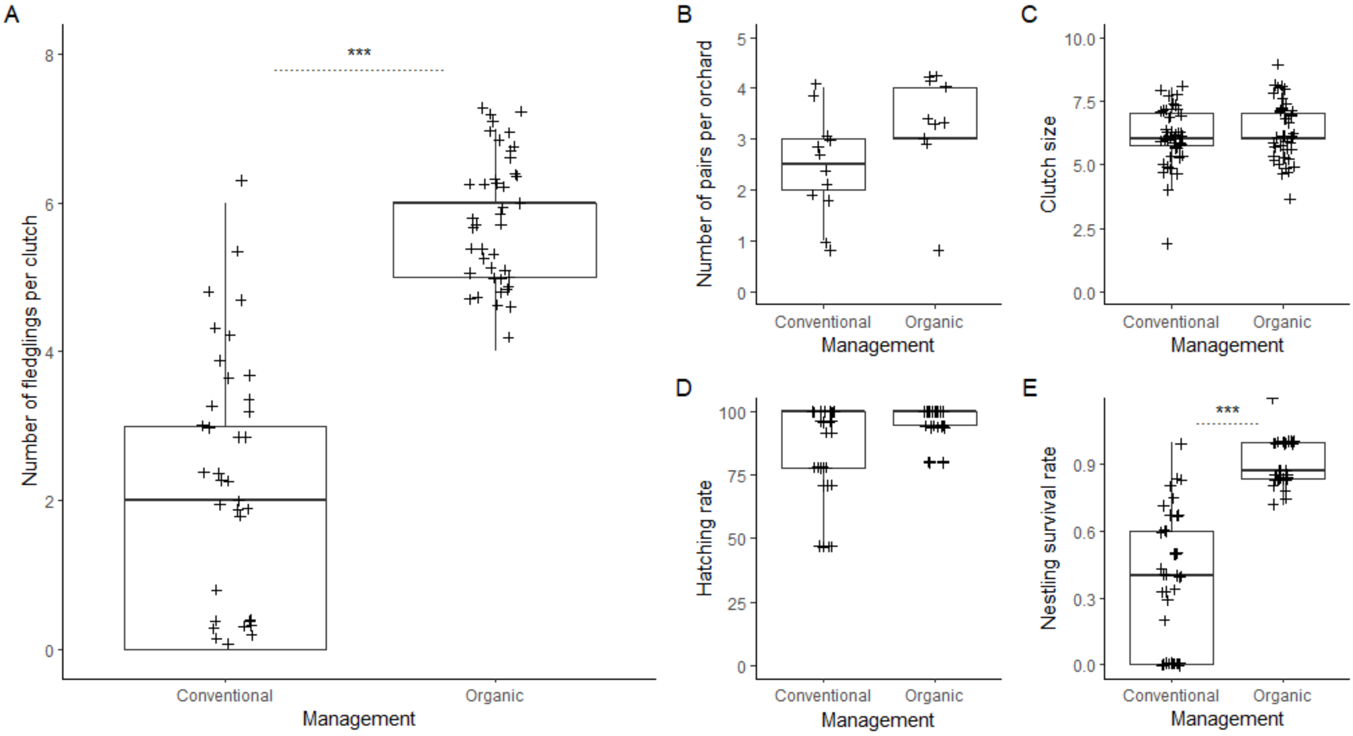
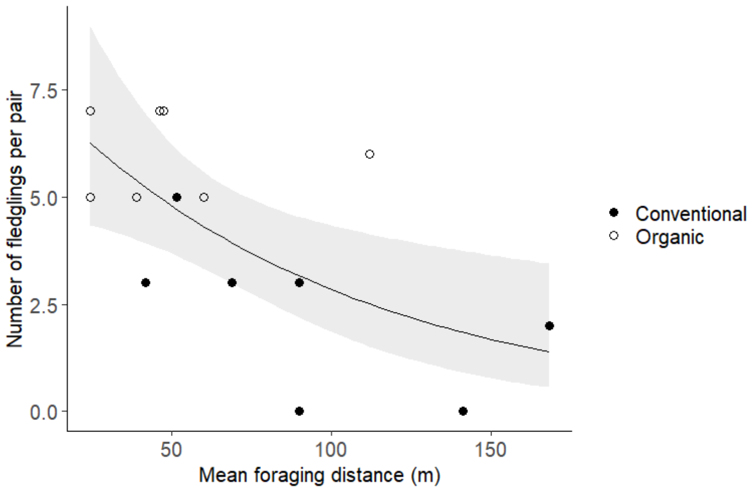

A
***
Number of fledglings per clutch
0
2
4
6
8
Conventional
Organic
Management
B
Number of pairs per orchard
0
1
2
3
4
5
Conventional
Organic
Management
C
Clutch size
0.0
2.5
5.0
7.5
10.0
Conventional
Organic
Management
D
Hatching rate
0
25
50
75
100
Conventional
Organic
Management
E
***
Nestling survival rate
0.0
0.3
0.6
0.9
Conventional
Organic
Management

Figure 7


Number of fledglings per pair
7.5
5.0
2.5
0.0
50
100
150
Mean foraging distance (m)
● Conventional
○ Organic