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Breeding Dispersal in a Nestbox Population of Collared Flycatchers (*Ficedula albicollis*) on Southern Gotland, Sweden

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Abstract

Dispersal is a fundamental ecological process, and understanding the causes and consequences of dispersal is especially important in light of predicting and facilitating species' distribution shifts in response to environmental change. In this study I aimed to understand dispersal in a nest box population of Collared Flycatchers on the Swedish island of Gotland. I compared an existing nest box population to a new nest box population consisting largely of dispersed individuals. I compared the sizes of the two populations to understand differences in population sizes between old and new breeding sites, and compared the proportions of ringed individuals in order to understand if individuals at the new site dispersed from nearby nest box sites or elsewhere. Additionally, I compared sex- and age-distributions between populations to find out if there are any age- or sex-biases underlying dispersal in this population. Finally, I investigated the consequences of dispersal by comparing laying date, clutch size and hatching success. I found that the initial population size was larger than in the new area. This suggests that dispersal in this population is a fast process, and reaching a full-sized population does not take multiple years. I found no differences in dispersal between individuals of different ages and sexes. Although clutch size and hatching success did not differ between the old and new, dispersed population, laying date was significantly later in the new population. I hypothesise that this is caused by a delay in the onset of breeding due to a longer time having been spent on finding a breeding site by the dispersers. Overall I conclude there does not seem to be any clear age- or sex-biased dispersal in this study, and no clear differences in breeding success. However the significant difference in laying date shows there are some fundamental differences between the old and dispersed populations, and further work is necessary to further explore these differences. Dispersal is a complex ecological process, and if we aim to use knowledge of dispersal in order to predict changes in species distributions and inform conservation, highly detailed studies of focal species will be necessary in order to reach informative conclusions.

Keywords: Collared Flycatcher, *Ficedula albicollis*, dispersal, nest box, breeding success, sex, age

Introduction

Dispersal is a core ecological process. Individuals can disperse to new areas when local population densities are reaching carrying capacity, or when local conditions are no longer suitable (Grant, 1978; Morris et al., 2004). Dispersal thereby allows organisms to cope with changes in environmental conditions. Understanding dispersal is essential in the light of the current global environmental change (Thomas et al., 2004). Climates and habitats are changing rapidly, and in order to persist species will have to adapt to rapidly changing environments (Visser, 2008). As current changes are often too fast to allow local adaptation to new conditions, dispersal to new areas is an essential mechanism by which individuals can cope with environmental change (Parmesan, 2006). It is therefore essential to understand the causes and consequences of dispersal to new areas in order to effectively predict future species distributions and help protect vulnerable species (Heikkinen et al., 2006).

Dispersal behaviour in birds is likely to be driven by a range of different mechanisms, and only part of the population disperses each year (Dobson and Jones, 1985; Pärt and Gustafsson, 1989). In order to fully understand dispersal processes it is necessary to explore differences between populations in existing areas, and populations that have dispersed into new areas. We can for example expect differences in the age-distribution of birds. Young individuals can be at a competitive disadvantage when competing for breeding sites, and might therefore be more likely to disperse (Badyaev et al., 1996; Hetmanski, 2007). Additionally, dispersal distances might differ between individuals of different ages or sexes (Chernetsov et al., 2006; Pärt, 1995). As a result, the newly dispersed population could be different in composition from the source populations, and might show differences in breeding success. Understanding these differences between existing populations and new, dispersed populations will be essential for understanding the causes and consequences of dispersal, and might help us inform effective conservation measures if this knowledge can be applied to species of conservation concern.

Collared Flycatchers (*Ficedula albicollis*) are migratory passerines that breed in parts of Europe and Asia, including the Swedish Island of Gotland (BirdLife International, 2013). Flycatchers readily breed in nest boxes (Gustafsson and Nilsson, 1985), and a long-term dataset has been collected for a large part of the population in Southern Gotland for the past 33 years. Individuals are ringed and breeding success is monitored in a large number of forest plots. Although Collared Flycatchers generally show breeding-site fidelity, small-scale dispersal is shown by part of the breeding population (Pärt and Gustafsson, 1989). This provides us with an ideal system to study dispersal behaviour.

The aim of this study was to understand differences between a population in an older, existing nest box plot, and a population in a new plot area nearby, consisting entirely of dispersed individuals. I aimed to look at the initial size (number of breeding individuals in the new plot area) of the dispersing population, and to find out if there were differences in dispersal between sexes and different age-groups. I hypothesised that the proportion of nest boxes occupied by collared flycatchers would be lower in the new area, since I predicted it would take some years for a full-size population (similar in size to existing nest box areas) to establish in the new area. I hypothesised some differences might be present between sexes in the proportions of birds that are ringed, since dispersal is known to differ between the sexes (Pusey, 1987). As young birds (yearlings, birds in their first breeding season) can be at a competitive disadvantage when competing for nest sites, I hypothesised that they would more likely to disperse to a new area than older birds. I therefore expected to find a higher proportion of yearlings in the new area compared to the old area.

In order to assess the consequences of dispersal, I aimed to find out if dispersal results in differences in laying date or higher breeding success. I hypothesised that birds in the new plot would start laying later compared to birds in the old plot, since they would spend more time searching for suitable breeding sites compared to non-dispersers that simply return to known breeding sites. To compare breeding success, I compared clutch size and hatching success between the two areas. If laying would be found to be delayed in the new plot, I hypothesised that birds will on average lay smaller clutches than in the new plot, since breeding time is restricted (Meijer et al., 1990). Hatching success might then also be reduced in the new area, as birds that have dispersed might be in poorer body condition, and might therefore be less able to successfully incubate (Barbraud and Chastel, 1999).

Methods

Nest box plots

Collared Flycatchers were studied on the Swedish island of Gotland. As part of a long-term study, over one thousand nest boxes have been set up in a range of mixed deciduous forest plots on the south of the island. All existing forest plots used in this study were put up between 3 and 33 years ago. Each year, all birds breeding in these nestboxes are monitored, and each individual receives a leg ring with a unique ringnumber, allowing identification of each known individual in the population.

The smallest distance between 2 of the nest box plots was approximately 0.5 km, the largest distance approximately 50 km. Plots range in size from around 30 to 200 boxes per plot. Boxes are set up in regular grids with approximately 40 m between boxes. Boxes are hung on tree trunks at 1.5 m above ground level. For the purpose of this study, a new nest box plot was set up near the existing plots. The new plot was put up in the last week of April, before the arrival of the Collared Flycatchers for the 2013 breeding season. The plot consisted of a total of 185 boxes, matching the exact set-up of the old nestbox plots. The closest old nest box plot was approximately 1 km away. The old plot that was used as a comparison in this study was situated approximately 5 km away. The new and old plot were very similar in forest structure, containing the same tree and shrub species, and showing the same (variation in) vegetation density. The old plot was similar in size to the newly selected plot, and contained a similar number of nest boxes (173).

Breeding data

During the nest-building, egg-laying and incubation stage, all nest boxes were visited at least once every five days to identify new nests. By counting the number of eggs in the new nests, this therefore gives us the exact timing of laying, as well as a measure of clutch size. Females were caught on the fifth day of incubation to record ringnumber, age (yearling or adult) and weight, as well as a number of size measurements not used in this study (wing-, tail- and tarsus-length). All caught unringed females were ringed. When hatching was due, nests were visited each day to record the exact hatching date and number of hatchlings. Males were caught five days after the chicks hatched to record the same characteristics as for females. Again, unringed caught individuals were ringed. Chicks were ringed and weighed seven days after hatching, and tarsus length and weight were measured for all chicks twelve days after hatching (data not used in this study).

Due to brood manipulations with hatchlings in the old nest box plot (for the purposes of a study that is not discussed in this paper), only hatching success could be used as a measure of breeding success in this study. Fledging success, a useful measure of breeding success, could therefore unfortunately not be included. Unfortunately, as a result of nest predation and nest failure due to unknown causes, full data was not available for all nests. Not all birds were caught, and hatching success measures were missing for those nests that were predated at the incubation stage. Therefore, not all nests could be included in all analyses. The number of nests included and excluded from analyses will be discussed in the results section below.

Data analysis

I carried out a range of different comparisons in order to explore the differences between populations in the old and new plot. Firstly, I compared the proportion of nest boxes that was found to be occupied in the old and new plot. This can give an indication of the rate of dispersal and the speed with which the new, dispersed population could reach the same size as an existing old population. Since the nest boxes were not only occupied by Collared

Flycatchers, but also by a number of other species (Great Tit (*Parus major*), Blue Tit (*Cyanistes caeruleus*) and Eurasian Nuthatch (*Sitta europaea*)), it was necessary to also take the occupancy by these other species into account. This was especially important since these other species start breeding earlier than the Collared Flycatcher. The occupancy of these species could thereby reduce the number of boxes available for Collared Flycatchers. Therefore, I did not only compare the proportion occupancy between the old and new plot for Collared Flycatchers, but also compared the proportion occupancy for the other bird species, and all bird species (including Collared Flycatchers) in total.

Secondly, I compared the proportion of birds that was previously ringed in both old and new areas. This allows me to determine whether the birds in the new area dispersed from the existing nest box plots on the island (individuals ringed in previous years), or from natural cavities elsewhere (unringed individuals). Of course it is possible that a number of pairs were already breeding in natural cavities in the new area, but a survey in a previous year revealed very low numbers of Collared Flycatchers in this new area before boxes were erected (L. Gustafsson pers. comm.). For the purposes of this study, we can therefore assume that the far majority of the breeding population in the new area consists of dispersed individuals.

Furthermore, I compared the proportion of ringed individuals separately for each sex. If a difference in the proportion of ringed individuals would be found between males and females, this would show possible differences in dispersal mechanisms between males and females. Additionally, I compared the ages of the breeding birds between the old and new population, in order to check for an age-bias in dispersal to the new site. I also compared the weights of birds between the old and new site, in order to uncover any differences in body condition (since dispersing birds might spend more energy whilst selecting a new breeding site). Finally, I compared laying date (the date of the first egg), clutch size and hatching success between areas to uncover potential differences in breeding between new and old population.

I analysed all data using R version 2.15.2 (R Core Team, 2012). I used Z-tests (for equality of proportions) to compare the proportions of occupied nest boxes, proportions of previously ringed birds and age distributions of birds. I used Mann-Whitney U tests to compare laying date, clutch size and hatching success between the two areas.

Results

Nest box occupation

In the new area, 58% of all 185 nest boxes were found to be occupied with Collared Flycatchers (see Figure 1). This was a significantly higher proportion of occupied boxes compared to the old area (Z-test for equality of proportions, X^2=12.97, p=0.0003, 95% CI=0.088-0.300), where only 34% of all 173 boxes was found to be occupied. An opposite trend was present for the proportion occupancy by other species (Figure 1). In the new nest box plot, 18% of boxes was found to be occupied with other species, significantly less than the 37% of boxes occupied by other species in the old plot (Z-test for equality of proportions, X^2=15.65, p=$7.6*10^{-5}$, 95% CI=-0.288 - -0.095). When the occupancy proportion of Collared Flycatchers and other species were added, the total occupancy of nest boxes by all species was exactly the same in both areas (71%).

Previously ringed individuals

Due to nest failure in part of the nests it was not possible to catch all breeding individuals. Therefore, when comparing the numbers of ringed individuals between areas, not all breeding birds could be included. However, the majority of birds was caught. More females than males were caught, since females were caught earlier during incubation, whereas males were caught during chick feeding. Therefore, if nests failed during late incubation or early chick feeding, only males were not caught. Out of a total of 98 nests in the new area, 94 females and 71 males were caught. In the old area, out of 58 nests, 53 females and 29 males were caught. All these individuals were included when analysing differences in the proportions of previously ringed birds in

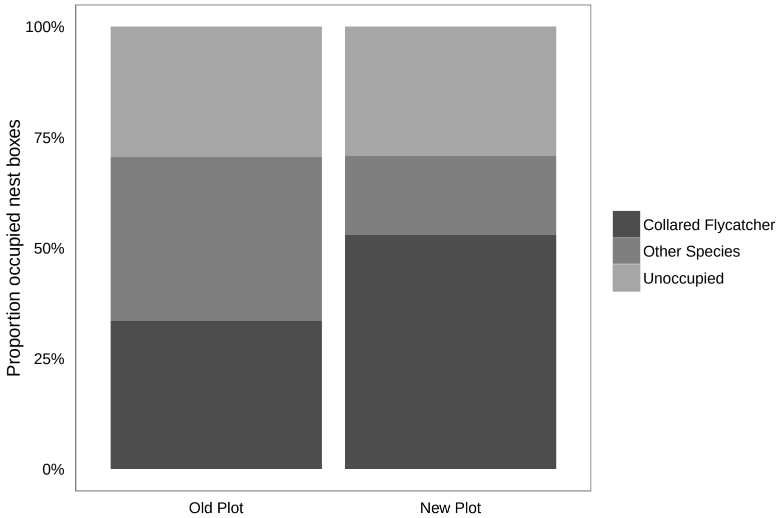

Figure 1. The proportion of nest boxes occupied by Collared Flycatchers (*Ficedula albicollis*) and other species (Great Tit (*Parus major*), Blue Tit (*Cyanistes caeruleus*) and Eurasian Nuthatch (*Sitta europaea*)) in an existing nest box area (Old plot), and a newly erected nest box area (New plot) on Southern Gotland, Sweden.

the old and new area.

In the new area, 38% of all breeding birds had been previously ringed. This was significantly less than in the old nest box plot (Z-test for equality of proportions, X^2=21.94, p=2.8*10^{-6}, 95% CI=-0.458 - -0.193), where 70% of all birds was found to be ringed. In neither of the two plots a significant difference was found in the proportion of ringed females and males (see Figure 2).

Ages

In order to look at age distribution, breeding birds have to be successfully aged. Although males can be easily identified as either yearlings or adults based on plumage characteristics, distinguishing these two age classes in females can be difficult in a proportion of the birds. When looking at differences in age distribution, only birds aged with confidence can be included. Therefore, not all females could be included in the analysis. All 71 males from the new site, and 29 males from the old site were included in the analysis. Out

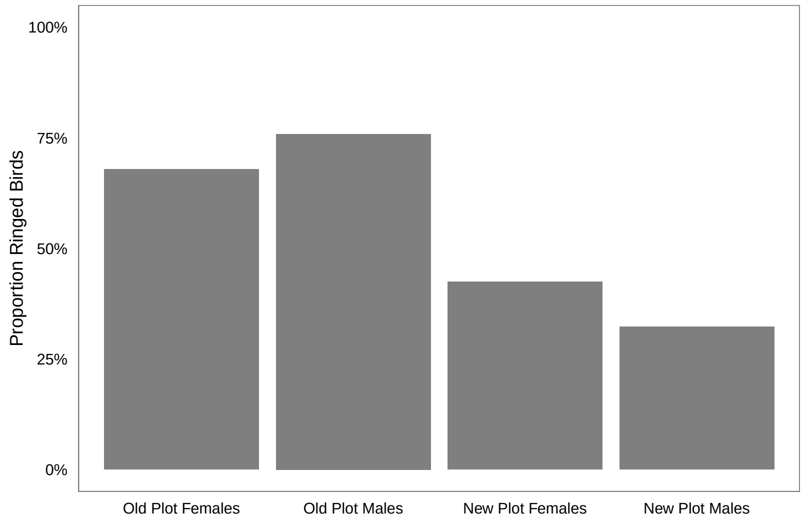

Figure 2. The proportion of ringed Collared Flycatcher (*Ficedula albicollis*) separated by sex. Birds were studied whilst breeding in an existing nest box area (Old Plot), and a newly erected nest box area (New Plot) on Southern Gotland, Sweden. Ringed birds are birds that were ringed in previous breeding seasons, and are therefore known members of the population. Unringed birds are birds that were new to the study population. No significant difference was found between the proportion of ringed males and females in either of the two sites (Z-test for equality of proportions, old site: X^2=0.251, p=0.616, 95% CI=-0.306-0.147; new site: X^2=1.36, p=0.243, 95% CI=-0.059-0.262).

of 92 females from the new site, 70 were included in the analysis. For the old site, 41 out of 44 females were included in the analysis. Figure 3 shows the proportion of yearling and adult birds in the two plots. No significant difference was found between the old and new plot (Z-test for equality of proportions, X^2=0.610, p=0.435, 95% CI=-0.086-0.221).

Body Weight

No significant difference was found in body weight between the two areas for either males and females. The mean body weight for males in the old site was 13.02 grams, compared to 12.92 grams at the new site (Mann-Whitney U test, W=896.5, p=0.362). For females, the mean weight at the old site

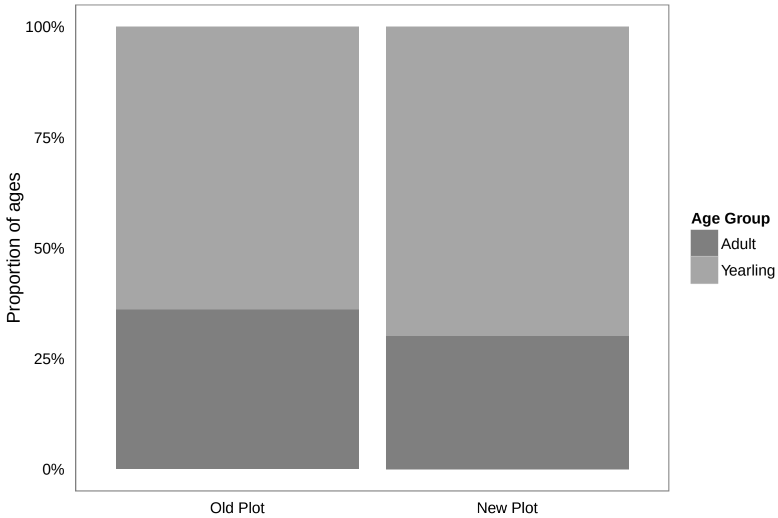

Figure 3. The proportions of yearling and adult Collared Flycatcher (*Ficedula albicollis*) in an existing nest box area (Old plot), and a newly erected nest box area (New plot) on Southern Gotland, Sweden. No significant difference was found in the proportions of ages between the two areas (Z-test for equality of proportions, X^2=0.610, p=0.435, 95% CI=-0.086-0.221)

was 14.94 grams, and 14.86 grams at the new site (Mann-Whitney U test, W=2109, p=0.541).

Breeding measures

Laying date (day of first egg) was available for all nests, therefore all 98 nests for the new area and 58 nests for the old area were included in the analysis. Figure 4 shows the days of first eggs for both plots, with counting starting with day 1 on the 1st of May. Mean laying date of the first egg was significantly earlier in the old nestbox plot (day 20), compared to the new nestbox plot (day 23) (Mann-Whitney U text, W=3974.5, p=$2.9*10^{-5}$).

A count of the total number of eggs (clutch size) was available for all nests, so again all nests were included in this analysis. In both plots, clutch sizes ranged from 4 to 7 eggs. The mean number of eggs per nest was very similar between plots (old plot: 5.9, new plot: 6.1), and no significant difference was found (Mann Whitney U test, W=3225.5, p=0.103).

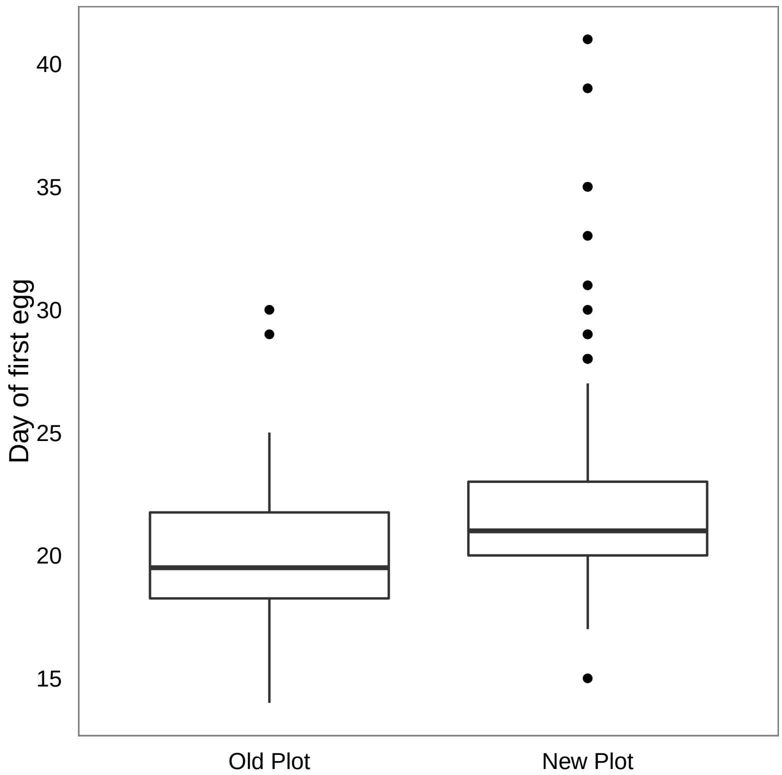

Figure 4. The laying day of the first egg in Collared Flycatcher (*Ficedula albicollis*) nests in an existing nest box area (Old plot), and a newly erected nest box area (New plot) on Southern Gotland, Sweden. Counting of days started with day 1 on the 1st of May 2013. Mean laying date of the first egg was significantly earlier in the old nestbox plot (Mann-Whitney U test, W=3974.5, $p=2.9*10^{-5}$).

In order to compare hatching success between plots, nests that had been predated at the incubation stage were excluded. This was the case for four nests in the new plot. No nests in the old plot had been predated. As a result, 94 nests from the new plot, and all 58 nests from the old plot were included in the analysis. As with clutch size, mean number of hatchlings was very similar between plots (old plot: 5.8, new plot: 5.4). Again, no significant difference was present (Mann Whitney U test, W=2674.5, p=0.830).

Discussion

Nest box occupation

A significantly higher proportion of nest boxes was found to be occupied by Collared Flycatchers in the new nest box area compared to the existing area. This is in contrast with the hypotheses. I expected the population of nesting Collared Flycatchers in the new area to be lower than in the old, established population. I predicted a small initial population of Collared Flycatchers, which would grow to a full-size population over time through additional dispersal and reproduction. However, a full-sized population (defined as a population similar or larger in size compared to the existing nest box area) seems to have established in this first year of the set-up of a new nest box site. Although there are studies focussing on fluctuations in population sizes in Collared Flycatchers in peripheral areas (see for example Thingstad et al. (2006)), to my knowledge there are no studies looking at the initial populations sizes in a new nest box breeding area within the existing range of Collared Flycatchers. Therefore, studies in other areas confirming these results would be useful. Collared Flycatchers seem to readily disperse to a new breeding site when conditions at that locality are suitable for their needs. This is a promising result in the light of protection from habitat change. If local conditions change, the set-up of a new breeding area nearby can attract large numbers of individuals within one year of the start of such a project, even though Collared Flycatchers are birds that are generally known to show breeding site-fidelity (Von Haartman, 1949). Although Collared Flycatchers are currently not a species of any conservation concern, this knowledge can still be useful for local-scale projects, or could be useful to inform projects involving other species.

The fact that the proportion of nest boxes occupied was not only the same, but even higher than in the old nest box population, was an unexpected result. However, when other species were also included in the analysis, the total proportion of nest boxes occupied in each area was the same (Figure 1). I suspect that this higher proportion of Collared Flycatchers in the new site might be an artefact of the methods. Nest boxes in the new area were put up at the end of April, after the Great Tits, Blue Tits and Nuthatches have already started selecting breeding sites. Therefore, we might see relatively lower numbers of these other species, and higher numbers of Collared Flycatchers through reduced interspecific competition. This is a likely explanation, since Gustafsson (1986) showed that the number of nest boxes occupied by Collared Flycatchers increased significantly when Great Tit occupancy was experimentally reduced. A future study where nest boxes are installed well in advance of the breeding season would be useful to further evaluate whether this result was an artefact of the methods.

Although not the main focus of this study, it is worth noting that despite the differences in the relative proportions of breeding species, the total proportion of boxes occupied by all species is the same (71%) for both areas. This might indicate that regardless of species, a maximum carrying capacity of breeding birds is possible in a forest, despite an over-abundance of breeding sites (nest boxes). It would be interesting to find out if a similar trend is found in other areas where proportions of species differ between area, and what is driving this. Potential drivers could be territory size or resource availability in the forest area.

Previously ringed individuals

Significantly fewer birds were found to be previously ringed in the new plot compared to the old plot. In the old plot only 30% of birds were new, in the new area this was 62%. This means that a larger than average number of birds comes from outside the known study population, even though many nest box plots are found in the close vicinity of the new site. It is difficult to pinpoint exactly where these birds have dispersed from. A number of them might be adults that previously bred in natural holes in the new nest box plot, as well as returning yearlings that were born there in the previous breeding season. However, these forests normally only support a very low number of natural holes, and a large part of the birds in the new plot is therefore likely to have dispersed from elsewhere. Whether this is from natural populations nearby on the island, or from more distant sites is not possible to distinguish at the moment. Most likely, there will be a mix of both local and long-distance migrants, as was shown for Pied Flycatchers by Thomson et al. (2003). Overall, we can conclude now that the new population is made up of a mix of individuals from different localities. Results from next years' breeding seasons can focus on finding out where these individuals came from, and how many years it will take for the population to reach a stable number of ringed individuals, and if this number is similar to other sites.

No significant difference was found in the proportion of ringed males and females. A difference would have indicated differential dispersal for males and females, since it would have indicated that females and males dispersed from different source populations. However, the absence of a difference in the proportion of ringed males and females does not allow us to say no such differential dispersal is present. Since the nest box plots where birds are ringed are spread out across the southern part of the island, ringed males and females could still have dispersed from different source populations. Future work could focus on exploring these more subtle differences.

Ages

In contrast to the hypothesis, no significant difference was found in the age-composition of the new and old plot. I expected a higher proportion of yearlings in the new plot, as yearlings are often at a competitive disadvantage compared to adults, so might be more likely to disperse from their natal site into the new area. However, based on the data from this study, this does not seem to be the case. Von Haartman (1949) found that in the closely related Pied Flycatcher nearly all breeding adults returned to their previous breeding areas, whereas only 7% of male and 2% of female yearlings return to their natal sites. If a similar trend would hold true for the Collared Flycatcher, we could have therefore expected a relatively higher proportion of yearling birds in this new nest box site. However, a more detailed study is needed to exclude the possibility that these yearling birds have dispersed to other new breeding areas. With the data from this study, we cannot yet conclude that there is no aged-biased dispersal present in this study area.

Breeding measures

As dispersing birds might spend more time looking for suitable nesting sites than individuals that simply return to previously known breeding sites, I hypothesised laying to begin later at new sites. This was shown to be the case, since mean laying date of the first egg was significantly later in the new plot compared to the old plot. Breeding started an average of 3 days later at the new site. A relationship between dispersal distance and laying date has been found in other species, as Newton and Marquiss (1983) showed in the Sparrowhawk (*Accipiter nisus*). However, it is not a trend that is found in all species, as no such relationship was present in for example Great Tits (*Parus major*) and Tree Swallows (*Tachycineta bicolor*) (Winkler et al., 2005; Greenwood et al., 1979). The difference in laying date shows that although numbers of Collared Flycatchers in the new area are high, there are some fundamental differences between the old population and the new, dispersed population. A difference in the timing of laying might result in differences in food availability in the forest, since there are clear, narrow peaks of insect availability that are important for chick feeding. A small shift might result in a significant difference in offspring survival or body condition. Future studies at this site can focus on seeing if there are any differences between offspring raised in this new site, and offspring raised at the old site.

No significant difference was found in clutch size and hatching success between plots. This suggests that up to the hatching stage, there is no difference in reproductive success between the old population and the dispersing population. As with laying date, this trend seems to differ between species. For Sparrowhawk females that dispersed further clutch sizes were significantly larger (Winkler et al., 2005). In Great Tits clutch sizes did not differ depending on dispersal distance (Greenwood et al., 1979). Dow and Fredga (1983) found that Goldeneyes (*Bucephala clangula*) that moved to other nest boxes had significantly smaller clutch sizes. Whether a relationship between dispersal and clutch size or hatching success is found might depend on the differences in resources between the source areas and the new site. An extensive study in a range of new nest box sites with differing distance and habitat from the source population could give a clearer idea of these relationships in Collared Flycatchers. As mentioned before, no fledgling success data is available for this study. Chick feeding is the most energetically expensive phase of the breeding season, and if dispersing adults are in worse condition due to the costs associated with selecting a new breeding site, fledging success might be significantly reduced. We could find no indication of lower body weight in dispersing birds compared to birds at the old site, however, a measure of fledgling success or a measure of survival to the following breeding season is necessary to say with certainty that breeding success does not differ between new and old populations.

Conclusion

The aim of this study was to understand differences between an existing nest box population, and a population in a new nest box plot that consists largely of dispersed individuals. I aimed to compare the sizes of populations, and find out if there are differences in dispersal between sexes and different age-groups. Additionally, I aimed to find out if dispersal resulted in differences in laying date, clutch size or hatching success.

It can be concluded that the initial population size in the new area was surprisingly large, even larger than the old population used for comparison. In this specific case of the Collared Flycatcher on Gotland, settlement in new areas does not seem to be a slow, multi-year process where the population slowly grows, but an instant settlement of a full-sized population. Although this is a useful finding, it is necessary to repeat this work in other areas and follow the progress of the population over the next years to see how population dynamics develop further. It is especially important to ensure nest boxes are installed in advance of the breeding seasons of all species, to capture the settlement of all species in the areas, thereby preventing an unnatural advantage for the relatively late-breeding Collared Flycatchers.

No differences in dispersal mechanisms between sexes or age-groups could be found based on this data, but further work is necessary to make definite conclusions, as the scope of this work was very limited. A population-based approach was taken, but in order to get a better idea of dispersal it will be necessary to follow the movements of birds at the level of the individual. In that way, it will be possible to get a measure of the direction and distance of dispersal by members of the population, which will allow us to draw more confident conclusions about potential differences in dispersal between sexes and age groups.

Egg laying was found to be significantly later in the new area. I hypothesise that this is the result of all individuals having dispersed into this new population, thereby having spent more time than average looking for a new breeding site. Therefore, these trends are likely to only be present during the first few years of settlement in a new area. After some years, timing of breeding will be likely to be synchronous with the other areas on the island. However, long-term monitoring of this population is necessary to confirm if this is the case. Clutch size and hatching success were not found to differ between the old and new site, however, a measure of fledging success is necessary to effectively compare breeding success.

Due to the small size and limited scope of this study, it is not possible to draw any general conclusions about the causes and consequences of dispersal. Sex- or aged-biased dispersal could not be shown to be a driver of dispersal in this study. However, overall this study illustrates that dispersal is a highly complex process, with many potential causes and consequences. Dispersal patterns will differ not only depending on the species, but also on the presence of competitors and available resources. In areas (or times) where competition is high and resources limited, dispersal might be a much faster process than in areas (or times) where resources are plentiful. In order to effectively protect species against changing environments, it will be extremely difficult to use general rules. Highly detailed, long-term studies about the ecology of focal species will be necessary before responses to changing environmental conditions can be predicted. Therefore, general habitat protection, both within and outside a focal species' range, is of vital importance when protecting vulnerable species and their ecosystems.

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