

Competition and age at first breeding in pied flycatchers

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In short-lived passerines, maximal fitness seems to be obtained by breeding as soon as possible. There are species however in which part of the individuals, does not breed locally the first possible breeding season, suggesting that they do not breed. In pied flycatchers only 26% of the males breeds locally in their first year, for females this is 53%. Lost competition with older earlier arriving birds is seen as the most important cause for this, forcing young birds to make the trade-off between breeding in a low quality territory and skipping the first breeding season. I found a high percentage of one-year-old males outside the nest box plots, areas with less competition. In high density areas the percentage of yearlings is found lower. Among non-breeders the percentage of yearlings was also higher than among breeders. And one-year-old breeding males are darker than non-breeders. These findings all support the competition idea. Less skippers and weaker results in females are possibly because of less competition in females. Skipping the first year of breeding results in a higher lifetime reproductive success, provided that the bird survives it till the second or third year.

Introduction

To maximize fitness, individuals need to get as much offspring as possible which will be able to reproduce. Different species use different strategies to get a high fitness, but in general there is a trade-off between investment in the current breeding season and the ability to produce in future seasons.

Long-lived species are expected to minimize this cost of reproduction to be able to invest in survival. High yearly survival rates within these species make sure many individuals will have many breeding seasons in which they could be reproductively successful. To maximize survival, many long-lived bird species do not invest in reproduction in their first years of life at all. Examples are found in long-lived seabirds (Burger, 1987; Porter, 1988), but also in lekking species (Foster, 1987; Jamieson & Zwickel, 1983) and cooperative breeders (Orians, 1987).

Species that have a higher mortality are expected to invest more in current reproduction at the expense of the future. In these short-lived species, it seems to be most strategic to get as much offspring as possible from the start of their lives, since they have not many years to get offspring. Nevertheless it is also found in some passerine species that part of the birds that physiologically are able to breed do delay their first year of breeding (Cooper, Murphy, Redmond, & Dolan, 2009; Hill, 1988; Lanyon & Thompson, 1986; Samson, 1976). When summarizing these results, it appears that most of these species are long-distance migrants, which travel thousands of kilometers yearly to reach the breeders sites (Table 1). To make this risky journey and not even breed that season does not seem to contribute to a high fitness, but delayed first breeding seems to occur more in migrant species than in residents.

Table 1: First year breeding in different bird species. Overview of ring studies, recaptures are the numbers of individuals ringed as nestling, which were caught back as breeders. 1st year breeding, are the numbers of individuals which were recaptured as breeders when one year old. The percentage is how many of the recaptures were caught as yearling for the first time.

Species	Migration type	Male				Female			Reference
		recaptures	1st year breeding	%		recaptures	1st year breeding	%	
Great tit	resident	764	721	94%	>80%	726	703	97%	(Tinbergen & Ubels, 2015)
Coal tit	resident								(Schmoll, Schurr, Winkel, Epplen, & Lubjuhn, 2009)
Blue tit	resident	73	59	81%		26	21	81%	(Dhondt, 1989)
Kingfisher	resident	74	67	91%		51	48	94%	(Bunzel & Druke, 1989)
Meadow pipit	short distance	49	42	86%		33	31	94%	(Hötker, 1989)
Indigo bunting	intermediate dist.					52	51	98%	(Payne, 1989)
Red-winged blackbird	intermediate dist.	148	11	7%					(Orians & Beletsky, 1989)
Eastern kingbird	long distance	19	12	63%		16	6	38%	(Cooper et al., 2009)
Great reed warblers	long distance	64		70%		65		60%	(Hansson, Bensch, & Hasselquist, 2004)
Pied flycatcher	long distance	273	71	26%		206	109	53%	(Both, 2015)
Pied flycatcher	long distance	21	8	38%		38	13	34%	(von Haartman, 1988)
Pied flycatcher	long distance	68	41	60%		100	70	70%	(Harvey, Stenning, & Campbell, 1985)
Pied flycatcher	long distance	197	72	37%		210	112	53%	(Potti & Montalvo, 1991)
Pied flycatcher	long distance	102	70	69%		99	75	76%	(Lundberg & Alatalo, 1992)
Pied flycatcher	long distance	953	363	38%		1298	777	60%	(Sternberg, 1989)

Pied flycatchers a short-lived long-distance migrants and in the population of my study, it has also been observed that a large fraction of locally born offspring does not breed in their first year as adult (Both, 2015). In males it occurs more than in females, with only 26% of the males are caught as breeders in their first possible breeding season, where this is 53% for females (Both, 2015). Also other pied flycatcher studies showed that many one-year-old birds do not breed (Potti & Montalvo, 1991; Sternberg et al., 2002; von Haartman, 1988) (see table 1). These data even overestimate the breeding probability in the first year, as the individuals that are found breeding for the first time in their second year have one more year of mortality before being observed (Sternberg, 1989). When accounting for this extra mortality and assuming this is similar for breeders and non-breeders, Sternberg estimated that only 20% of the first year males breeding locally, and 37% of the females.

Population studies are always localized, with the potential problem that birds not being observed in a year may in fact be breeding outside the study plot. It is possible that first year birds do breed more often outside the study areas. The rational could be that young individuals are outcompeted at the high density nest box areas, and hence settle in the surrounding low density areas. Indeed removal studies have shown that both sexes were rapidly replaced and for males these were younger individuals (Both, 2015; Sternberg et al., 2002).

The main question this study addresses is: Why do one year old adult birds of short-lived and long-distance migrating species delay first breeding to a later season? The explanations for this could be categorized in strategic/ultimate reasons, and more proximate reasons.

The ultimate reason as often proposed for longer-lived species is the trade-off between investing in the current breeding season and investing in survival. Young individuals are often being faced with this trade-off as consequence of competition with older birds. Individuals migrating for the first time in their life, are possibly not experienced enough to migrate as fast as experienced birds (Sergio et al., 2014) and could arrive too late to breed in that season. Later arrival of one-year-old birds than older birds is observed in many of the migrant passerines in which delayed first breeding was found (Both, 2015; Cooper et al., 2009; Ficken & Ficken, 1967; Hill, 1988; Lanyon & Thompson, 1986; Potti & Montalvo, 1991; Sternberg et al., 2002). Arrival too late in the season could be a reason for skipping a breeding season, because conditions are not optimal anymore then. This is not mentioned in one of the articles however. Most supported reason for skipping the breeding season due to late arrival, is occupation of high quality territories by older earlier arrived birds (Cooper et al., 2009; Ficken & Ficken, 1967; Lanyon & Thompson, 1986). Younger birds are also found breeding in poor habitat (Ficken & Ficken, 1967; Hill, 1988; Lanyon & Thompson, 1986), and in peripheral areas of the population with less competing neighbors (Ficken & Ficken, 1967; Hill, 1988). In case of hole-breeders, shortage of high quality territories could also be caused by a lack of suitable breeding holes or nest boxes. On the other side, also non-breeders are observed without limitation of breeding holes (Potti & Montalvo, 1991). When all high quality territories are already occupied, a trade-off has to be made between breeding in a low quality territory or invest in survival and increase chances in obtaining a high quality territory next year (Lanyon & Thompson, 1986; Zack & Stutchbury, 1992). The decision to minimize reproductive effort in the first possible breeding season could also be made before and be the cause of the late arrival (Hill, 1988; Potti & Montalvo, 1991). However without disadvantage of late arrival, older birds are found to be better competitors (Sternberg et al., 2002). Also other studies have shown that older birds appear to be more dominant and aggressive in competition for high quality territories than one-year-old birds (Cooper et al., 2009; Ficken & Ficken, 1967; Hill, 1988). A loss in the competition for a high quality territory forces the

younger birds to make the trade-off between breeding in a low quality territory or skip the breeding season. Due to site fidelity, the first year of breeding presumably is also location of breeding during next years (Lanyon & Thompson, 1986). Individuals who choose to breed in a low quality territory have one year of reproduction more, but breed there all their life. On the other hand, individuals who choose to skip, have a better chance to get a high quality territory and breed there during the rest of their lives (Zack & Stutchbury, 1992). They have a breeding season less though. Individuals that start breeding in their first possible year are thus expected to have a lower breeding success per year than birds that start breeding later.

A proximate reason is sex bias in the population. An unequal sex ratio in a population could cause that individuals of one sex remain unpaired. If there are for example more males than females in a population, there will be competition for females. When one-year-old males are disadvantaged relative to older males in this competition, their best strategy might be to reduce their reproductive effort in their first year (Hill, 1988). Sex bias could thus be a reason for one-year-old males to skip their first possible breeding season (Samson, 1976). Some studies however showed delay of first breeding in both males and females, indicating no limitations due to sex bias (Both, 2015; Cooper et al., 2009; von Haartman, 1988). Also replacement of both males and females in removal studies shows a surplus in both sexes (Both, 2015; Cooper et al., 2009; Marra & Holmes, 1997).

Another reason could be that birds do not reach the breeding site. Cause could be too low migration experience, but another reason could be that the birds not even leave their wintering area and skip migration and thus breeding for a year.

A low body condition is also a possible proximate reason not to breed. As consequence of hard migration circumstances or harsh conditions on the breeding site, condition of the birds could be too low to breed in that season. Younger birds without migration experience migrate less efficient than older birds (Sergio et al., 2014), which could lead to lower body conditions when arriving at the breeding sites. Body conditions in their first possible breeding year could be dependent on the circumstances the individuals grew up in. Birds that fledged with high body weights probably had higher condition than birds with lower fledging weights. When this difference in body condition between individuals remains during the first year of life, birds with higher fledging weight are likely to skip their first breeding season less often than individuals with lower fledging weights. Date of birth and thereby date of fledging could also cause a difference in body condition, where individuals that were born early should be advantaged. They have more life experience, which could provide advantage in autumn migration and possibly even affects life in wintering areas and during spring migration, resulting in earlier arrival dates or higher body conditions at arrival. In that case, early born individuals are less likely to skip their first breeding season than individuals who are born later. Both fledging weight and birth date related to age at first breeding were not found in other literature.

In this study I mainly aim at the possible trade-off between breeding in low quality territories and skipping the breeding season in the first year of life, which has to be made as consequence of competition. Therefore I will examine the age distribution of pied flycatchers in different ecological conditions, compare the natal dispersal between individuals that start breeding in their first year of life or later and I will examine the potential fitness consequences of starting breeding in the first year of life or later. This may help to explain why such a high proportion of individuals apparently starts breeding later in life. Furthermore, I will examine individual differences, e.g. fledging weight, between first year breeders and later starters, which may make it possible to predict whether a individual will or will not breed in his first year of life.

Methods

Pied flycatchers are small (ca 12 g) short-lived (adult annual survival ca 40%) and long distance migrants with a breeding range from southern Europe till West-Siberia and wintering areas in West-Africa. Location of this study is the Dwingelderveld (52°48'11"N, 6°23'56"E) in Drenthe, Netherlands. Since 2007 a population study is going on with 12 nest box plots, 10 plots with 100 nest boxes and 2 plots with 50 nest boxes. My study area is situated in and around four of these nest box plots at the north side of the Dwingelderveld, with a maximum distance of around 1.7 km to the nearest nest box plot (Appendix 1).

Searching and catching outside nest box plots

From April 21, 2015 I visited the study area almost daily to search for singing pied flycatchers outside the nest box plots. At that moment already most males had arrived within the nest box areas. The blue areas on the map (Appendix 1) are the areas I came almost daily till the beginning of June; the yellow areas I visited less, but I also came there once in three days during that period. To catch the singing males a nest box was placed at their locations, with the aim that the males would check it. First my aim was only to catch ringed birds, but soon I placed boxes at every singing bird, because it saved time not to check if he was ringed before and even though he was not ringed, he could get a ringed female. A spring trap was placed in the entrance and when a bird entered, the trap closed the entrance. Birds were then easy to take out the box. These traps were only placed in nest boxes when I was in the neighborhood, to avoid the chance that the birds were captive for more than half an hour. In some of the nest boxes the male was already caught within half an hour, but there were also nest boxes in which I placed a trap several days in vain, while the singing bird was still present. When a bird was caught, I read the ring or ringed the bird and measured wing length, tarsus length, body weight and I scored his plumage. That score is the Drost score, which ranges from 1 to 7, with 1 dark black and 7 only brown feathers (von Haartman, 1988). The scores outside the nest box plots ranged from 4 to 7, and most birds scored 7. After that a wing and tail feather were taken for analysis apart from this study, and the bird was released. I left the nest box in place, so that if the male got a female and nested in the nest box, I was also able to catch the female. I did not place traps in nest boxes where I caught a male already, except if there was another bird singing with another appearance or without ring or with the ring on the other leg. When a pair started to breed, I also caught the female while incubating and I ringed and measured the nestlings the way it is done in the nest box plots.

Other catching methods

When the singing male was not attracted by the nest box, I tried another method to catch him. I used a mist net and played the sound of a singing pied flycatcher next to it, but because I did not catch any bird that way, I also tried to attract the bird to the net by placing mealworms next to it and also play alarm calls of pied flycatchers. That did also not work out. This method did work in two of the three cases where a pair was feeding young in a natural hole. In both these cases both male and females were caught. It possibly did work here because of ants that were dragging the mealworms towards their anthill attracted attention of the birds.

Besides catching birds outside the nest box plots another method was tried to catch non-breeding birds inside the plots, not very successful though. A stuffed owl surrounded by mist nets was installed with alarm calls playing from the audio system. It was tried two times next to nest boxes occupied by pied flycatchers in the nestling phase. In both cases the adults gave

no reaction at all and only one flew in the net, but that was not because he was flying towards the owl. In the second attempt however, after more than half an hour without any movement, an unringed and thus non-breeding young male was caught. Partly because of lack of time and little reaction towards the owl, I decided to stop trying to catch this way, but this method could perhaps have fetched more useful captures.

To catch non-breeding birds inside nest box plots, traps are placed in nest boxes where males were singing, but still were unpaired at the end of the spring. This method is used every year.

At the beginning of the breeding season, arriving birds were tried to catch with mist nets and a sound system with singing pied flycatchers. Aim of this was to observe whether young birds arrive later than older birds or not. The catching sessions started an hour before dawn, because pied flycatchers migrate at night and therefore we expected that they would be attracted by sound the most at the end of the night. To not disturb the study area and because the birds migrated from the south, the mist nets were installed south of a nest box plot. It was not successful though, with only one catch in three morning sessions, so we decided to stop trying this.

Age estimation

Based on wear and shape of greater coverts and tail feathers age of pied flycatchers can be estimated as one-year-old bird or older bird. Age of ringed individuals is known and by comparing age estimations with real ages, the accuracy of the age estimation can be determined. I estimated 93% of the males correct ($n=27$), but for females this part was only 61% ($n=18$).

Analysis

Because of the high percentage correct estimated ages for males, I used the estimated ages to compare the distribution with the age distribution inside the nest box plots, because that provided a bigger sample size. Outside the nest box plots it was not always clear if a bird was a breeder or a non-breeder and therefore I included both breeders and non-breeders inside the nest box plots to create the age distribution. My age estimates for females were not good enough to use for the analysis, so there I only used the age distributions of ringed individuals. Females are caught during incubation, so all caught females are breeders. Age distributions from outside the plots are only compared with age distributions inside the plots in 2015, to prevent that significant effects are found due to a possible exceptional year.

Also age distributions between breeding males and non-breeding males inside the nest box plots were compared. Only known ages were used here, because that provided high enough sample sizes and is the most accurate. The research started in 2007, so in 2008 only one-year-old birds could be caught, therefore I only included years after 2008.

A general linear mixed model was used to analyze the percentage of older than one-year-old breeders dependent on the density. As measure for density the number of occupied nest boxes where egg laying started before May 20 was taken. This number was both taken for all species and for only pied flycatchers. Only nest box plots with 100 nest boxes were included in the analysis. May 20 was taken to include as much pied flycatchers as possible, but to prevent that second broods of tits were included. The analysis was run with density as fixed factor and nest box plot as random factor. The percentage of older birds was based on the estimated ages. Besides running the model with every year included, it was also run with starting year 2007 excluded.

For comparing natal dispersal distances between sexes and between individuals that started breeding at different ages were used, also a general linear mixed model was used. Sex and age at first breeding were included as fixed factors and nest box plots as random factor. Age at first breeding was divided in 3 groups, namely age=1, age=2 and age>2 and the logarithm of distance in meters was used. Distances between nest boxes were calculated with Pythagoras, since X- and Y-coordinates are known for all nest boxes.

Site fidelity was checked by comparing distances from birth location to first breeding location, to distances from first to second breeding location and second to third breeding location. A Kruskal-Wallis test was used for this and the sexes were separated. The logarithm of distance in meters was used to create the graph, but not to do the statistics because some values were zero.

To examine whether sex, birthday and fledging weight were determining factors for a bird to start in their first possible year with breeding or not, generalized mixed models with a binary response were used, with a 0 for non-breeding at one-year-old age and 1 for breeding. Models with all possible combinations of the three factors were run. The model with the lowest AIC-value explains the data the best.

Some characteristics were also compared between one-year-old breeding and non-breeding males. Birth date, fledging weight, wing length and tarsus length were normally distributed and thus analyzed with a t-test, while for drost score a Mann-Whitney U test was used.

The lifetime reproductive success is calculated for both males and females, the sum of all their broods. Only birds that started breeding before 2011 are included, to prevent incomplete numbers due to still reproducing birds. Birds which started at different ages with breeding are compared with a Kruskal-Wallis test. Also the average number of fledglings per nest and the number of nests is calculated and analyzed.

Survival rates to a certain age are calculated by dividing the number of individuals of the researched group alive at that age by the number of individuals of that group alive in the year before. A bird is registered alive when it is caught in that year. Because of low sample sizes in other groups, only survival of both males and females is calculated for birds that started breeding at an age of 1 or 2, to their second or third year. Birds that started breeding when two years old, are not caught in their first year and thus only survival from their second to their third year could be calculated.

Results

Age distribution in and outside nest box plots

Males caught outside the nest box plots were predominantly first year, both in the group with known ages and for all 28 males caught (Table 2). In the larger group or all males, 64% was young outside, whereas inside the nest box plots we only found 15% of the males of known age being first year (Yates corrected $\chi^2=11.4$, $p=0.0007$). For the group that was ringed and hence of known age, the difference was even bigger: 70% vs. 15% (Yates corrected $\chi^2= 7.74$, $p=0.0054$). In contrast, for females we found no difference in age composition outside and inside the nest box areas: 0% vs. 17% first year breeders (Fisher Exact test, $p=0.603$).

The three older ringed males, aged 2, 3 and 8, were all born in the same nest box plot, nearest to where they were caught and were never seen back as adult in previous years. One of them bred in one of my nest boxes. Of the 7 one-year-old birds, 4 were born in the nearest two nest

box plots. Two were born inside a nest box plot at a distance of around 16 km and the last was not born in a nest box of this study, but born and ringed in a forest about 22 km from where caught. He did breed in one of my nest boxes even as two of the other young birds.

From 3 of the 4 ringed females birth places are known, all in the nearest nest box plot, one in 2010 and two in 2013. The first one was found breeding in nest box plots in the two previous years about 8 km from this year, the others were not caught back till now. The remaining one was caught as breeder in 2013 for the first time in a nest box plot about 9 km from this year.

Table 2: Age composition of male and female pied flycatchers caught in Drenthe in 2015, divided in three groups: Inside ringed are ringed individuals caught inside the main nest box areas with known age, Outside estimated are individuals caught outside the nest box areas where age is estimated and Outside ringed, are the individuals caught outside the nest box areas which were ringed and thus with known ages.

	Males			Females		
	Inside ringed	Outside estimated	Outside ringed	Inside ringed	Outside estimated	Outside ringed
1 year	4	18	7	3	4	0
> 1 year	22	10	3	15	9	4
Total	26	28	10	18	13	4

Among the unpaired males caught in the nest box plots, the percentage one-year-old birds was higher than among breeding males, 37% vs. 17% ($\chi^2=26.5$, $p<0.001$) (Table 3).

Table 3: Age composition of males caught as breeders and non-breeders in nest box plots from 2009 till 2014.

	Breeding	Non-breeding
1 year	89	51
> 1 year	438	87
Total	527	138

Breeding density and age composition

Plots with low numbers of pied flycatchers in a year had a higher proportion of young males and with increasing flycatcher numbers the proportion of older males increased (Figure 1; GLMM, $F=12.350$, $df1=1$, $df2=70$, $p=0.001$). A similar effect was found for females, although the effect was weaker (Figure 1; $F=4.109$, $df1=1$, $df2=70$, $p=0.046$). The effect was mostly driven by the start of the population study in 2007, when numbers of flycatchers were low and the proportion of young individuals was high. When excluding 2007, the effect was weaker and not significant anymore for both males ($F = 3.440$, $df1=1$, $df2=61$, $p=0.068$) and females ($F = 2.360$, $df1=1$, $df2=61$, $p=0.130$).

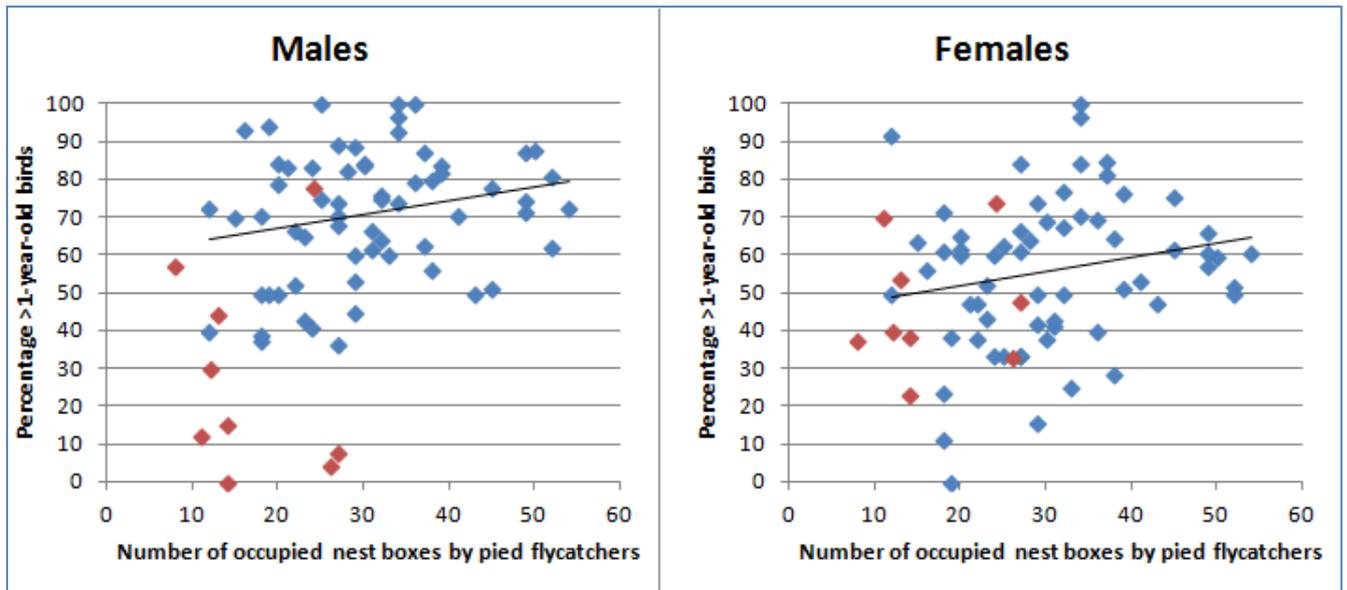


Figure 1: Scatter plot of percentage of older males and females against the number of occupied nest boxes by pied flycatchers which started egg laying before May 20, each point represents one nest box plot per year. The linear trend line is also shown. Red dots are the 2007 data points.

Natal dispersal and age at first breeding

Natal dispersal distances were not influenced by the age at which individuals bred for the first time ($F=0.923$, $df1=2$, $df2=597$, $p=0.398$), but they were by sex ($F=7.376$, $df1=1$, $df2=597$, $p=0.007$). Natal dispersal distances of females were on average bigger than those of males: 3674 ($n=277$) vs. 2782 ($n=324$) meters (Kruskal-Wallis=6.059, $N=593$, $df=1$, $p=0.014$).

The distances between different breeding locations of individuals are smaller than the natal dispersal distances (Figure 2) for both females (Kruskal-Wallis=77.720, $N=342$, $df=2$, $p=0.000$) and males (Kruskal-Wallis=98.835, $N=386$, $p=0.000$).

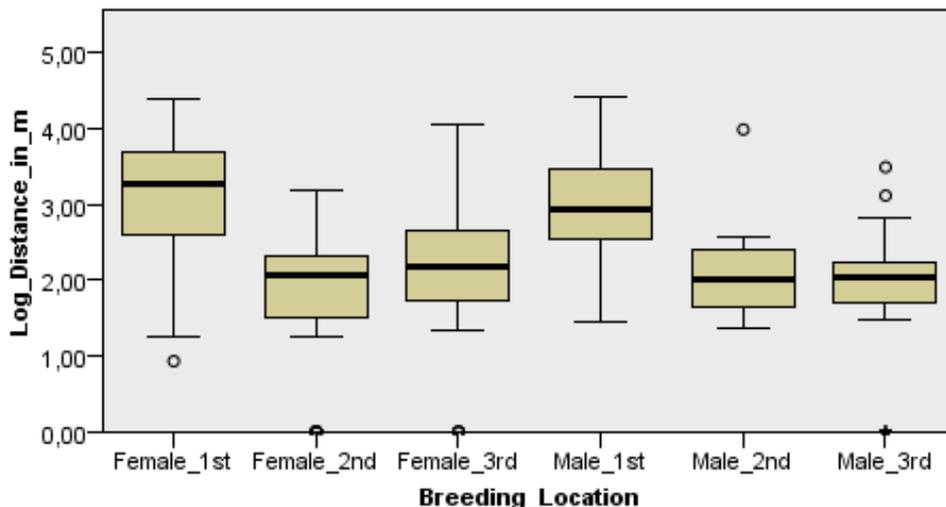


Figure 2: Box plot of logarithm of distances between breeding locations in different years. The 1st distance is the distance from birthplace to first breeding location, 2nd and 3rd are the distances from 1st to 2nd breeding location and 2nd to 3rd breeding location. When data points were 0, they are also included as 0 in the logarithmic data for this figure.

Can initial differences explain age at first breeding?

The model without sex, birth day and fledging weight included explained the variation in first year breeders the best (Table 4) and the model with only sex included second best.

Table 4: Generalized linear models with binary response, 0 for not breeding at when one year old and 1 for breeding when one year old, that explain first year breeding data best, based on AIC-value.

Model	1	2	3	4	5
Sex	-	x	-	x	-
Birth day	-	-	x	x	-
Fledging weight	-	-	-	-	x
AIC-value	8.614	15.637	143.503	197.139	208.688

Among the one-year-old males, breeders are darker than non-breeders, with average drost score of respectively 6.5 and 6.8 (Mann-Whitney U=877.00, N=98, p=0.042). Birthday, fledging weight, tarsus length and wing length did not differ between both groups (Table 5).

Table 5: Test-results of the comparison between one-year-old breeding males vs. one-year-old non-breeding males

	breeding	non-breeding	t	df	p
Birthday (in Aprilday)	53.79	54.03	0.200	96	0.842
Fledging weight (in gram)	14.27	14.40	0.805	96	0.423
Tarsus length (in mm)	17.45	17.55	0.994	96	0.323
Wing length (in mm)	60.22	60.66	1.474	94	0.144

Fitness consequences of variation of age at first breeding

The lifetime reproductive success is higher for birds that bred at an age of 2 or 3 for the first time than birds that started breeding in their first year, in both males and females (Table 6). The average number of fledglings per nest is not significant higher in those groups, but the number of nests is.

Table 6: Average lifetime reproductive success numbers per pied flycatcher which bred for the first time before 2011.

		Age at first breeding			Kruskal-Wallis	df	significance
		1	2	3			
Male	# of fledged young	8.3	10.6	12.6	9.961	2	0.007
	fledged young per nest	5.3	5.5	5.5	0.953	2	0.621
	# of nests	1.7	2.0	2.3	7.764	2	0.021
	N	32	39	15			
Female	# of fledged young	6.9	9.3	8.8	11.482	2	0.003
	fledged young per nest	5.0	5.6	5.7	2.969	2	0.227
	# of nests	1.4	1.7	1.6	6.986	2	0.030
	N	72	24	5			

Survival after first breeding seems higher when this is at a two-year-old age, in both males ($\chi^2=0.595$, p=0.44) and females ($\chi^2=2.45$, p=0.12) (Table 7). In males survival from second to third year seems also to be higher in individuals that started breeding in their second year ($\chi^2=0.300$, p=0.58) in females the difference is even smaller ($\chi^2=0.018$, p=0.89).

Table 7: Survival of individual pied flycatchers from the previous age to the next age, divided in sex and age at first breeding

Age at first breeding	Survival to age	
	2	3
Male	1	0.34
	2	0.33
Female	1	0.26
	2	0.39

Discussion

A large fraction of pied flycatchers delays the start of first breeding to their second or even third year, which seems to contradict the life-history strategy of a short-lived species. In this study I show that the age composition of males is different between the nest box areas and the surrounding area, suggesting that young males may be outcompeted in the higher breeding densities of the nest box areas. The negative correlation between local breeding density and proportion of young males is consistent with this notion of competition. However, in females I did not find a difference in age composition, and the correlation with breeding density was weak. Delaying first breeding to avoid competition and get a higher quality territory next year, would suggest those birds to breed closer to their birth place than birds that started in their first year, I did not find this however. Their first breeding location is important because I showed strong site fidelity in the next years, where females have a higher natal dispersal than males. Most initial differences between individuals like birthday, fledging weight, tarsus length and wing length were no measure for a bird to breed or skip in their first year. Sex had an influence, while more females started breeding in their first year than males do. And darker males more often start to breed in their first year, possibly because this provides an advantage in competition. I showed that both males and females that delayed first breeding raised on average more young during their lives than birds that bred in their first year. Most obvious cause for this is that these birds raised more nests, which could be caused by the low survival rates of first year breeders. Survival to the second year of birds that did not breed in their first year is not known however.

Lost competition with older birds

Late arrival (Both, 2015; Cooper et al., 2009; Ficken & Ficken, 1967; Hill, 1988; Lanyon & Thompson, 1986; Potti & Montalvo, 1991; Sternberg et al., 2002) and less competitive abilities (Cooper et al., 2009; Ficken & Ficken, 1967; Hill, 1988; Sternberg et al., 2002) are often mentioned as causes for lost competition of young birds with respect to older birds. And this loss forces them to make the trade-off between skipping their first breeding season and breeding in a lower quality territory (Lanyon & Thompson, 1986; Zack & Stutchbury, 1992). The trade-off could also have to be made because of avoidance of competition, instead of loss. My results support the idea that competition is cause for young birds to skip the breeding season or breed anywhere else, because I found lower proportions of young birds in higher density areas. This relation is not found when first year of study, 2007, is excluded. But this is the only year with really low densities, which provides important data points for this analysis. That younger birds are often found in peripheral and less quality territories as consequence of lost competition (Ficken & Ficken, 1967; Hill, 1988; Lanyon & Thompson, 1986), is also supported by my results, with a high proportion of young males outside the nest box plots. The weaker relation between young birds and density in females and the lower percentage young birds outside the nest box plots in females may be not that surprising, because there is possibly less direct competition in females than in males. The proportion of first year skippers

is also lower among females, compared to males (Both, 2015). That the proportion of young birds among caught non-breeding males is found higher than among breeding males is a sign of lower competitive abilities, which is mentioned more often (Cooper et al., 2009; Ficken & Ficken, 1967; Hill, 1988; Sternberg et al., 2002). That competition is an important reason for skipping the first breeding season is also reflected in the finding that darker males breed more often in their first year, which makes them possibly more attractive for females and provides them thus advantage in competition.

Choosing for skipping the first year of breeding should increase chances to get a higher quality territory next year (Lanyon & Thompson, 1986; Zack & Stutchbury, 1992). In terms of natal dispersal I would have expected that this distance would have been smaller among skippers, but I did not find any difference. This analysis may not be that valuable however, because high quality territories are not necessarily as close as possible to the birth place of the bird. When choosing for breeding in a low quality territory, the bird should due to site fidelity breed there also the rest of his life and skippers should in this way breed in a high quality territory their whole life (Lanyon & Thompson, 1986; Zack & Stutchbury, 1992). In this study I found indeed strong site fidelity, indicating that the first territory location is important for the success during the rest of life.

Consequences for lifetime reproductive success

I found that first year breeders raised less young than first year skippers during their lives. This difference is mainly caused by the higher number of broods in individuals that started breeding at an age of 2 or 3 years, indicating that the survival is higher when starting at a later age. And that is also what my analysis on survival suggests. The difference in survival from year 2 to 3 is especially in females not that big that it would make an impact on the lifetime reproductive success though. The average number of fledglings is namely almost equal for birds that started breeding at different ages. The low survival after breeding in the first year is apparently the cause for the low number of broods in these first-year-breeders. Skipping the first year of breeding seems to be the best strategy for obtaining the highest lifetime reproductive success, but survival to the second breeding year is not taken into account for the skippers. This survival should be about 0.8 or higher, to make the lifetime reproductive success of skippers higher. Survival rates are not known for non-breeding individuals, but a survival of 0.8 seems to be higher than possible. Therefore start breeding in the first season seems to be a better strategy than delaying it, but every individual has to deal with different conditions.

Delaying of first breeding in other species

It is hard to compare these results with other species, because age at first breeding is not researched in many species that well, especially in combination with the lifetime reproductive success. Based on the species in which delaying of first breeding is known (Table 1), it seems to occur in long distance migrants in particular. Which could to a great extent be declared by competition. Less migratory experience and therefore later arrival, maybe even in lower condition, is something resident species do not have to deal with. During the winter they can explore the breeding areas and get to know vacant territories. Direct competition could be avoided that way.

I would expect that delaying of first breeding occurs in more migratory passerines. It depends on the densities and breeding opportunities however. In populations of hole breeders with high densities and few suitable holes I would expect more delaying of first breeding than in populations of open nest breeders with low densities and big suitable areas.

References

- Both, C. (2015). *Unpublished data of the pied flycatcher research in Drenthe*. Unpublished manuscript.
- Bunzel, M., & Druke, J. (1989). Kingfisher. *Lifetime Reproduction in Birds*, , 107-116.
- Burger, J. (1987). Foraging efficiency in gulls: A congeneric comparison of age differences in efficiency and age of maturity. *Studies in Avian Biology*, 10(225), 83-89.
- Cooper, N. W., Murphy, M. T., Redmond, L. J., & Dolan, A. C. (2009). Density-dependent age at first reproduction in the eastern kingbird. *Oikos*, 118(3), 413-419.
doi:10.1111/j.1600-0706.2008.16997.x
- Dhondt, A. (1989). Blue tit. *Lifetime Reproduction in Birds*, , 15-33.
- Ficken, M. S., & Ficken, R. W. (1967). Age-specific differences in breeding behavior and ecology of american redstart. *Wilson Bulletin*, 79(2), 188-&.
- Foster, M. S. (1987). Delayed maturation, neoteny, and social system differences in 2 manakins of the genus chiroxiphia. *Evolution*, 41(3), 547-558. doi:10.2307/2409256
- Hansson, B., Bensch, S., & Hasselquist, D. (2004). Lifetime fitness of short- and long-distance dispersing great reed warblers. *Evolution*, 58(11), 2546-2557.
doi:10.1111/j.0014-3820.2004.tb00883.x
- Harvey, P. H., Stenning, M. J., & Campbell, B. (1985). Individual variation in seasonal breeding success of pied flycatchers (*ficedula-hypoleuca*). *Journal of Animal Ecology*, 54(2), 391-398. doi:10.2307/4486

- Hill, G. E. (1988). The function of delayed plumage maturation in male black-headed grosbeaks. *Auk*, *105*(1), 1-10.
- Hötker, H. (1989). Meadow pipit. *Lifetime Reproduction in Birds* (I. Newton, Ed.). Academic Press, London, , 119-133.
- Jamieson, I. G., & Zwickel, F. C. (1983). Spatial patterns of yearling male blue grouse and their relation to recruitment into the breeding population. *Auk*, *100*(3), 653-657.
- Lanyon, S. M., & Thompson, C. F. (1986). Site fidelity and habitat quality as determinants of settlement pattern in male painted buntings. *Condor*, *88*(2), 206-210.
doi:10.2307/1368917
- Lundberg, A., & Alatalo, R. (1992). The pied flycatcher. *Poyser, London*,
- Marra, P., & Holmes, R. (1997). Avian removal experiments: Do they test for habitat saturation or female availability? *Ecology*, *78*(3), 947-952.
- Orians, G., & Beletsky, L. (1989). Red-winged blackbird. *Lifetime Reproduction in Birds*, , 183-197.
- Orians, G. H. (1987). Helping and communal breeding in birds - ecology and evolution - brown,jl. *Nature*, *330*(6144), 121-122. doi:10.1038/330121c0
- Payne, R. (1989). Indigo bunting. pages 153—172 in lifetime reproduction in birds (I. Newton, ed.).
- Porter, J. M. (1988). Prerequisites for recruitment of kittiwakes *rissa-tridactyla*. *Ibis*, *130*(2), 204-215. doi:10.1111/j.1474-919X.1988.tb00971.x

- Potti, J., & Montalvo, S. (1991). Return rate, age at 1st breeding and natal dispersal of pied flycatchers *ficedula-hypoleuca* in central Spain. *Ardea*, 79(3), 419-428.
- Samson, F. B. (1976). Territory, breeding density, and fall departure in Cassin's finch. *Auk*, 93(3), 477-497.
- Schmoll, T., Schurr, F. M., Winkel, W., Epplen, J. T., & Lubjuhn, T. (2009). Lifespan, lifetime reproductive performance and paternity loss of within-pair and extra-pair offspring in the coal tit *periparus ater*. *Proceedings of the Royal Society B-Biological Sciences*, 276(1655), 337-345. doi:10.1098/rspb.2008.1116
- Sergio, F., Tanferna, A., De Stephanis, R., Lopez Jimenez, L., Blas, J., Tavecchia, G., . . . Hiraldo, F. (2014). Individual improvements and selective mortality shape lifelong migratory performance. *Nature*, 515(7527), 410-+. doi:10.1038/nature13696
- Sternberg, H. (1989). Pied flycatcher. *Lifetime Reproduction in Birds*, , 55-74.
- Sternberg, H., Grinkov, V., Ivankina, E., Ilyina, T., Kerimov, A., & Schwarz, A. (2002). Evaluation of the size and composition of nonbreeding surplus in a pied flycatcher *ficedula hypoleuca* population: Removal experiments in Germany and Russia. *Ardea*, 90(3), 461-470.
- Tinbergen, J., & Ubels, R. (2015). *Unpublished data of great tit research in the Lauwersmeer*. Unpublished manuscript.
- von Haartman, L. (1988). *The biological significance of the nuptial plumage of the male pied flycatcher* L. von Haartman.

Zack, S., & Stutchbury, B. J. (1992). Delayed breeding in avian social-systems - the role of territory quality and floater tactics. *Behaviour*, *123*, 194-219.

doi:10.1163/156853992X00020

Appendix 1: Study area in Drenthe, the Netherlands.

Red areas: nest box plots, blue areas: well searched areas, yellow areas: less searched areas.

