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Delayed age at first breeding and experimental removals show large non-breeding surplus in Pied Flycatchers

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Avian breeding populations have been shown to be regulated by territorial behaviour, often creating a surplus of non-breeding individuals. However, most evidence is of a male non-breeder surplus, whereas for a surplus to actually buffer a population both non-breeding males and females should be present. Here, we provide descriptive and experimental evidence for the existence of a population buffer consisting of mostly male and potentially also female Pied Flycatchers using nest box areas. First we show that local recruits often do not breed in their first year, with 23% of all recruiting males observed breeding in their first year, and 51% of females. When accounting for mortality in the years prior to observed first breeding, we estimate that only 9% of all first-year males breed locally, and 29% of first-year females. Similar percentages of first-year flycatchers skipping breeding have been observed in other study populations. We show that in the year of new establishment of our nest box plots, most known-aged flycatchers were first-year birds (77%), whereas after establishment, recruiting immigrants from the same source population were mostly older (28% first-year birds). An experimental removal of paired flycatchers from one study plot in two years (19 and 58 individuals removed) resulted in complete replacement by males and females. Male but not female replacements were younger than removed individuals. These results imply that a non-breeding surplus is present in Pied Flycatcher populations. The average later age at first-breeding in males compared to females, suggests that this non-breeding surplus is strongly male-biased. Skipping breeding in the first year(s) is not just caused by shortage of suitable nesting sites, as we observed on average 12% of males defending a nest box without pairing up with a female. Using stable isotopes ratios, we show that non-breeding first-year individuals do not stay at their African wintering grounds. Competition for nest sites is one cause for refraining from breeding, as shown by our experiments, but cannot be the sole cause, as many nest boxes remain unused in a season, and up to 20% of territorial males defend a nest box without pairing up with a female. We hypothesize that many young flycatchers arrive too late for breeding and are therefore not seen in their first year. Indeed first-year Pied Flycatchers that do breed/defend a nest box arrive on average later at the breeding grounds, and we argue that the non-observed group arrives even later. The causes of their later arrival could be the need for learning, lower quality wintering sites resulting in later departure, and/or a trade-off between low breeding success and the costs of early arrival. These could be general factors in long-distance migrants, and this pleads for a better understanding of how migration develops during ontogeny.

Key words: annual survival, *Ficedula hypoleuca*, population dynamics, floater, age at first breeding

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It has long been recognized that avian breeding populations are to some extent regulated by territorial behaviour, preventing some of the adults from breeding, and thereby creating a surplus of non-breeding individuals (Kluyver & Tinbergen 1953, Brown 1969, Newton 1992, Ens *et al.* 1995). Non-breeders are often difficult to observe, but their presence becomes evident when experimentally removed territorial individuals are rapidly replaced (Krebs 1971, Newton 1992, Marra & Holmes 1997). Most removal experiments have been performed on males (Newton 1992, Sternberg *et al.* 2002), probably because in most species territorial defence is a male activity. The few experiments carrying out female removal showed ambivalent outcomes as to the existence of a non-breeder surplus: it was found in some (Newton 1992, Cooper *et al.* 2009b), but not all studies (Marra & Holmes 1997). For a non-breeding surplus to actually buffer a population, both non-breeding males and females should be present (Marra & Holmes 1997). The generality of a density regulating effect of territoriality by providing such a buffer could be questioned, because the majority of bird populations have male-biased sex ratios (Donald 2007), and the experimental evidence for a non-breed-

ing female surplus is relatively weak, partly because removal studies have concentrated on males.

Delayed maturity has been mostly associated with high adult survival and therefore long life-span (Ricklefs 2000). Short-lived species, such as most passerines from temperate and arctic biomes, are therefore expected to start breeding as young as possible, because they have a large probability of dying before the next breeding season. However, the observed non-breeding surplus in many short-lived passerine species consists mostly of young individuals (Hill 1988, Arcese 1989, Sternberg *et al.* 2002, Cooper *et al.* 2009b). Although this seems paradoxical, these non-breeders are often assumed to attempt to breed, but fail as a result of competition for territories or mates. Alternative explanations for why younger birds skip breeding are more on the strategic side: (1) costs of reproduction are higher for inexperienced individuals, (2) it would be a better strategy to wait to gain a better territory in the future, or (3) they can gain more indirect benefits by extrapair offspring than by reproducing themselves (see Cooper *et al.* 2009b).

In the short-lived Pied Flycatcher *Ficedula hypoleuca* (adult survival rates about 40–50%; Lundberg &

Table 1. Review of ages at first breeding in five long-term population studies of Pied Flycatchers in Europe. For each sex and population combination the accumulated number over all years and proportion of individuals starting to breed at a certain age are given. Also an estimate is made of the percentage of first-year birds that survive and are found breeding (% first yr). These estimates assume an annual survival of 50% for non-breeders, and hence twice as many individuals that start breeding in their second year must have been alive in their first year.

	Age 1 st breeding	Sternberg (1989) Germany 1964–1986		Harvey <i>et al.</i> (1985) England 1948–1964		Lundberg & Alatalo(1992) England 1985–1989		Potti & Montalvo(1991) Spain 1984–1990		This study Netherlands 2007–2016	
		Number	%	Number	%	Number	%	Number	%	Number	%
Males	1	363	38	41	60	70	69	72	37	89	23
	2	408	43	22	32	27	26	72	37	196	50
	3	132	14	3	4	5	5	39	20	68	17
	4	42	4	1	1	0	0	12	6	27	7
	5	8	1	1	1	0	0	2	1	10	3
	Total	953		68		102		197		390	
	% first yr	17		34		49		14		9	
Females	1	777	60	70	70	75	76	112	53	155	51
	2	408	31	20	20	20	20	62	30	108	35
	3	84	6	7	7	4	4	27	13	31	10
	4	25	2	2	2	0	0	8	4	11	4
	5	4	0	1	1	0	0	1	0	0	0
	Total	1298		100		99		210		305	
	% first yr	35		41		56		26		29

Male Pied Flycatcher tries to attract a female into his nest box. The mesh wire functions as a protection measure against martens (photo Richard Ubels, Lhee, 19 April 2013).

Alatalo 1992) many individuals do not breed in their first year(s) (Curio 1959, Lack 1966). Studies reported 24–50% of local female recruits start breeding after their first year, whereas in males this was considerably higher (31–77%, Table 1). Note that these percentages underestimate the proportion of first year birds that actually do not breed, because many of the non-breeders not observed in their first year die before we are able to observe them in their second year. By accounting for this extra year of mortality, Sternberg (1989) estimated the likelihood of a first-year flycatcher being alive in this first year as only 35% for females and a mere 17% for males in his German population. While this seems exceptionally low for a passerine with relatively low annual survival, application of the same method to other population studies indicates

that 26–56% of first-year females actually breed locally, whereas for males estimates range from 9 to 47% (Table 1). Non-breeding males (especially first-year birds) defending nest boxes have been observed in fractions of up to 30%, (Curio 1959), but non-breeding females are seldom observed, even though many females do skip breeding their first year(s) locally.

The aim of this paper is to understand why so many Pied Flycatchers apparently delay breeding, instead of breeding in their first year. We first show how a new study population builds up with individuals of various ages, and then test experimentally whether competition for nest boxes causes individuals to skip breeding at young ages. Furthermore, we test whether individuals skipping their first breeding year may stay at the wintering grounds in Africa. Our results, together with those from other studies (Harvey *et al.* 1985, Sternberg 1989, Potti & Montalvo 1991, Lundberg & Alatalo 1992), showing that females generally start breeding earlier in life, imply that Pied Flycatcher populations are generally male-biased. This male-bias could result from more male offspring being produced, or because males survive better than females. Using our mark-recapture program we investigate whether sex-differences in adult survival rates may explain these male-biased sex ratios.

Finally, we argue that our data are not just specific to Pied Flycatchers and their reliance on nesting holes, but may be more generally applicable to long-distance migrants. We argue that the ontogeny of spring migration may be a reason why so many individuals do not breed in their first year.

METHODS

Pied Flycatchers are cavity-nesting passerines weighing c. 12 g that winter in the Sudan-Guinean zone of West Africa (Ouwehand *et al.* 2016), and breed over most of Europe up to Western Siberia in the east. Males normally arrive about a week earlier than females at the breeding grounds, and first-year birds about five days later than older birds (Lundberg & Alatalo 1992, Potti 1998, Both *et al.* 2016). Pied Flycatchers readily use nest boxes, and males start defending one or more boxes upon arrival. Females choose males defending a nest cavity.

Initial population build-up

Since 2007, we have studied a population of c. 300 breeding pairs of Pied Flycatchers in Drenthe (NL, 52°49'N, 6°22'E) in c. 1100 nest boxes distributed

across nine plots with 100 and three with c. 50 nest boxes each. Study plots of 100 boxes were on average 50 ha in size, the plots with 50 boxes were 20 ha, and were situated in two forested areas (Dwingelderveld and Drents-Friese Wold) some 5 km apart (Figure 1). Distances between adjacent plots ranged from 2.6–7 km, and between the most distant plots 18 km in north-south direction and 12 km east-west. Nest boxes were made of wood (WDH: 9×12×23 cm), had an entrance hole of 32 mm, and were erected in 2007 in areas without nest boxes (except for two plots where boxes had been present for longer periods, but at lower densities). Nest boxes were protected against martens, which did not always prevent predation. Demographic data (Table 2; age at first breeding) are given for all but one of the plots, because one plot ('Ruinen'; Figure 1) located c. 10 km south of the matrix of the other plots, served as experimental area for removals in two years, and was not monitored to the same extent in some of the other years. The occupancy rate of the 1000 nest boxes by any species of breeding bird (based on laying of at least a single egg) for the 11 plots was on average 70%, ranging from 55% in 2007 to 81% in 2012. There was no trend in occupancy rate from 2008–2015 (correlation: $r = 0.18$, $n = 8$, $P = 0.67$).

Before the start of our study in 2007, nest boxes were absent from 10 out of 12 study areas, and we show the effects of nest box addition in some of the plots at Dwingelderveld. In this area breeding bird surveys have been carried out since 1988 by the same observer (Joop Kleine), using the territory mapping method. In 2007, three of his monitoring plots were provided with 100 nest boxes in part of the plot, and we give data on the number of territorial Pied Flycatchers mapped in these plots between 1995–2015.

Demographic data

Nest boxes were checked at least weekly from 10 April – 15 June, and basic reproductive measures were recorded (laying date of first egg, clutch size, number of hatchlings and fledglings). We tried to catch all breeding male and female flycatchers to read their rings, or ring them if unringed. Females were mostly caught during the second half of incubation, and males (and previously uncaught females) when feeding seven-day old chicks. All adults were ringed with unique aluminium rings, and in some years also with a combination of plastic (only on top of an aluminium ring to prevent leg problems) or aluminium colour rings. In most years we caught over 90% of breeding females and over 80% of breeding males (Table 2). The reason why breeding individuals were missed was espe-

cially predation of nests (sometimes including the female) by martens. Capture rates of males were lower than of females because we caught females earlier in the nesting cycle, and we failed to capture some males that either infrequently fed chicks or deserted during the nesting stage. These may include cases of polygyny, with the male concentrating on his primary brood only (Lundberg & Alatalo 1992, Both 2002).

Each year all nestlings were ringed and weighed when seven days old; biometrics were taken when 12 days old (mass, primary 8, tarsus). After fledging we checked for late nestling mortality.

Ageing Pied Flycatchers

Most of the age effects described here are based on captured individuals ringed as nestlings, of which we knew the exact age. However, in one analysis we give the proportion of first-year individuals among breeders that we observed breeding in their first year (i.e. each individual was only included once, Figure 3A). These ages are based on a subsample of the breeding population (20–40%) and were made by one observer (CB) who had previous experience with the species. Age estimation was primarily based on the shape and wear of tail feathers, with additional information of moult, shape and wear of primary coverts, and the outermost greater coverts (Jenni & Winkler 1994). The distinction could only be made between first-year (i.e. born one year ago) and older individuals (called adults), which was done immediately after capture before reading the ring (not to be biased by ring numbers). We checked the accuracy of assignments for individuals which had previously been ringed as nestlings: 87% ($n = 68$) of first-year males, 91% ($n = 212$) of adult males, 76% ($n = 92$) of first-year females, and 94% ($n = 105$) of adult females were aged correctly. This means that in particular, the ages of first-year females were more often incorrectly assigned, and hence their proportion is mostly underestimated.

For the age at first breeding we selected all individuals that were born in our study plots between 2007–2013 and that were found breeding locally in 2008–2016. We excluded one of our plots (Ruinen) because this area was more isolated, used for experimental removals, and with lower capture rates. Individuals were first found breeding between their first and fifth year after birth (Figure 4). A variable fraction of males defending a nest box remained unpaired. Annually we established the fraction of unpaired males based on observations made for quantifying arrival dates. Males that continued singing after 10 May without being chosen by a female were considered as

unpaired. Because most unpaired males frequently enter the box during displays we could catch 55% of these males by putting a spring-trap in the nest box. These males were unlikely to be paired to a female from a different box, because they were not observed

feeding nestlings elsewhere, and continued singing when other males were feeding their nestlings.

Estimating the proportion of individuals that is not breeding for a certain age class should take into account mortality until the first year of breeding. To

Figure 1. Location of the nest box plots in Drenthe, The Netherlands. Black areas are the major wooded plots, and circles our nest box areas. Plots with letters contain 100 nest boxes each, and plots with numbers 50 boxes.

make an estimate of the actual non-breeding population size, we assumed that annual survival rates of non-breeding individuals were a bit higher than for breeding individuals (i.e. 50% (for both sexes), compared to 46% for breeding males and 35% for breeding females, see Table 2). This higher survival rate for presumed non-breeders is likely to occur, because they do not pay a cost of reproduction (Gustafsson & Sutherland 1988). We consider it likely that this cost is higher for females than males, as adult females have a fair chance of predation during incubation (pers. obs.). We performed the same calculations as Sternberg (1989) to calculate the total non-breeding population. For this we made the simplifying assumption that all birds start breeding not later than in their third year (although males in particular were sometimes found breeding for the first time at higher ages). The population of individuals alive in their first year was calculated as: number observed first year + number first observed second year/survival rate + number first observed after second year/(survival rate)², where survival rate = 0.50.

Removal experiment

The experimental removal of breeding pairs was part of a translocation experiment meant to force pairs to breed at an unfamiliar place. Most of our removals were done from the 'Ruinen' plot and here we only analyse data on replacement after removal from this plot. In 2009 we removed nine pairs plus a single female, and from those nine pairs, two were already replacements from a nest box after we first removed another pair from that box (Burger & Both 2011). In 2010 we removed 20 of the original pairs, plus 16 more individuals that replaced these birds after removal from the same nest box (Burger *et al.* 2013). We removed birds between 23 April and 5 May in both years, with 80% between 23–30 April, coinciding with the peak female arrival in both years (Both *et al.* 2016).

Our comparison of the age composition of the original population and the replacements is based on individuals that were caught in the experimental plot. For the birds in the experimental plot we distinguish individuals that were initial breeders which were removed, the replacement individuals settling in the nest boxes after removal and a group of breeders that were unmanipulated either because we failed to catch them for translocation or because they settled later in boxes where no birds were removed.

In the experiment we only considered real ages based on individuals ringed as nestlings, as birds were caught by observers with varying experience in ageing.

MARK analysis

We used capture-mark-recapture analyses to investigate sex differences in adult survival, which may explain the apparent male-bias in our adult breeding population. Adult survival between breeding seasons was calculated using the program MARK v. 6.1 (White & Burnham 1999) only for breeding adults that were not part of any manipulation in any year (neither translocation nor delayed hatching of more than two days (Samplonius *et al.* 2016), nor individuals equipped with geolocators (Ouweland & Both 2017)). Note that in the adult category we also included individuals breeding in their first year, as they formally become adults after their first complete moult just after, or even overlapping breeding. In this analysis, males that were caught as non-breeders were not considered to be caught, because our focus is on breeder survival. Exclusion of these captures either may decrease capture rate or survival rate. This simplifies comparison with females; most other studies also did not sample non-breeders. We perform model-selection to see which model describes survival best, and report on year- and sex-specific capture and survival rates (Table 2). Captures up to 2016 were included, but survival estimates of adults breeding up to 2014 are given, since for 2015 these were rather uninformative because for individuals breeding in 2015 and not seen in 2016 we do not know yet whether they were dead, or missed while alive.

Stable isotope analysis

To find out whether young flycatchers that skip breeding in their first year stayed in Africa, we analysed stable isotope profiles of their feathers. Pied Flycatchers moult their tail once a year after the breeding season at the breeding grounds, and their tertials twice a year: after the breeding season at the breeding grounds, and prior to migration from the wintering grounds (Jenni & Winkler 1994). Birds caught during the breeding season thus have feathers grown the previous June/July (tail feathers, primaries and secondaries), and a new generation of body feathers grown in February/March in Africa (including tertials and sometimes one or more secondaries).

From each individual we collected one of the central tail feathers, and one of the middle tertials, and stored them in paper envelopes for later analysis. If the birds that forgo breeding stayed in Africa during the breeding season, we expect the isotope ratios of tail feathers and winter moulted tertials to be similar, whereas if they do return to the breeding grounds the isotope ratios of the two types of feathers will differ, as

is the case in breeding individuals that moulted their tail feathers at the breeding site.

Feathers were cleaned of organic contaminants using hexane and were then air dried. The feather tip was cut into small fragments and kept in tin cups. Samples (350–700 mg) were analysed for their stable carbon ($^{13}\text{C}/^{12}\text{C}$) and stable nitrogen isotope ratio ($^{15}\text{N}/^{14}\text{N}$) at the NIOZ Royal Netherlands Institute for Sea Research, The Netherlands. The stable isotope ratios were determined with a Thermo Scientific Flash 2000 Elemental Analyser coupled to a Thermo Scientific Delta V Advantage isotope ratio mass spectrometer. Results were expressed in standard δ -notation relative to Pee Dee Belemnite (v PDB) for $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$ values. The maximum recorded deviations as determined using laboratory standards calibrated by certified international reference samples were in all cases $<0.2\text{‰}$ for $\delta^{13}\text{C}$ and $<0.3\text{‰}$ for $\delta^{15}\text{N}$ values.

RESULTS

Initial population build-up

In the first year of our nest box study, 162 Pied Flycatcher pairs were breeding in 950 available nest boxes, and the numbers gradually increased to around 310 in 2011–2015, with a notable drop in 2014 (Table 2).

Prior to the provision of nest boxes in 2007, Pied Flycatchers were not abundant in the area: the number of territorial males mapped tripled from 17 in 2006 to 50 in 2007 in three of our study plots situated in long-term bird monitoring plots (Figure 2A). In the first four years the density of territorial males increased locally up to seven-fold (compared to levels prior to 2007), and levelled off afterwards (Figure 2A). This increase may even be an underestimate, because our nest box plots were considerably smaller than the size of the monitoring plots, and the number of nests in our nest boxes sometimes outnumbered the territorial males mapped (Figure 2B).

In our first year, 2007, we caught 284 adult breeders of which 13 (5%, 4 males, 9 females) had been ringed somewhere else as nestlings (all within 25 km of our study sites). In this first year, a majority of these ringed immigrants were one-year olds (77%; Figure 3B). In subsequent years, the number of previously ringed new immigrants from outside of our own study sites proportionally dropped (see Table 2), and the overall percentage of one-year old immigrants in 2008–2015 was 28% (Figure 3B; significant difference between 2007 and later years: Yates corrected $\chi^2 = 9.79$, $P = 0.018$).

Figure 2. (A) Number of territorial Pied Flycatchers per year in three subareas of Dwingelderveld 7, 8 and 10; Figure 1), before and after the provision of 100 nest boxes per plot. (B) Number of Pied Flycatcher nests in these subareas. Note that census plots were about 2–3 times larger than nest box plots. Territory mapping data was kindly provided by Joop Kleine.

Ringed immigrants born in other areas were more often female (63 individuals) than male (29 individuals), and there was a tendency that within this group of immigrants more females were in their first year (females: 41% ($n = 63$), males: 21% ($n = 26$): Yates corrected $\chi^2 = 2.86$, $P = 0.091$).

During the population build-up, the estimated age of first-time breeders was strongly biased towards young birds, especially in males where 89% of breeders were first-year birds in 2007, and this dropped to a mere 9% in 2015 (Figure 3A; Spearman rank correlation on percentage first-year breeders in males against year: $r_s = -0.90$, $n = 9$, $P = 0.003$). In contrast, we found only 59% of females were first-year birds in 2007, and also there was no trend over the years, with rather stable percentages between 40–55% ($r_s = -0.22$, $n = 9$, $P = 0.58$). Note that first-year females were more difficult to age correctly, and this may have affected this result.

Nine years after the provision of nest boxes, it is still very much an open population, with at least 40% of

Figure 3. (A) Annual percentage of first-time breeders estimated as first-year birds in our population. All age estimates were made by the same experienced observer. (B) Percentage of first-year Pied Flycatchers among immigrants ringed as nestlings outside our study population breeding in their first year in our study plots in Southern Drenthe. Numbers on top are sample sizes. Individual males that were caught as non-breeders are included, and an individual is only included the first time it was caught.

female and 30% of male breeders each year being unringed individuals of unknown origin (either immigrants, or young born in natural cavities in the surrounding forest), and 15–30% being locally born first-year breeders (Table 2).

Age at first breeding

For the cohorts born locally in 2007–2013 we have records of 305 females and 390 males returning to the breeding area until 2016 as breeders (in total 9322 nestlings ringed, recruitment rate: 7.5%). In addition, 40 locally born males were caught as non-breeders and not seen later in life as breeders.

Females and males were recorded first breeding between their first and fifth year (Figure 4A, B), and in females the proportion observed breeding in the first year (51%, $n = 305$, cohorts 2007–2013) was higher than for males (23%, $n = 390$, Yates corrected $\chi^2 = 57.67$, $P < 0.0001$). The mean age at first breeding for

females was 1.57, for males 2.02 (cohorts 2007–2013). In males (but not females) the proportion breeding in the first year declined between 2007–2013 (Pearson correlation: $r = -0.88$, $n = 7$, $P = 0.01$), whereas in females there was an increase in the proportion of individuals starting breeding in the second year ($r = 0.87$, $n = 7$, $P = 0.01$). Note that these proportions of individuals skipping breeding years are likely to be highly biased, because individuals observed for the first-time breeding in their second year had one more year of mortality before starting to breed, individuals starting to breed in their third year two additional years of pre-breeding mortality, etc. If we assume that their survival is about similar to or somewhat higher than that of breeders (c. 50%, see also next paragraph), we arrive at even higher proportions of individuals skipping several breeding years: based on the combined data from 2007–2013, we estimate that for the females the proportion breeding in the first year drops to 29% whereas for males it drops to a mere 9% (Table 1).

Males first caught during their first year were more often non-breeding (33%, $n = 134$) than when caught first later in life (9%, $n = 292$), which was a highly

Figure 4. Observed age at first local breeding in locally born Pied Flycatchers in SW-Drenthe. For each cohort (2007–2013) the percentage of individuals for each first age at breeding is plotted.

significant difference (Yates corrected $\chi^2 = 43.34$, $P < 0.0001$). Of all locally born males first caught as non-breeders, 64% were in their first year ($n = 69$). Local return rates were higher for males that were not breeding in their first return year (49%, $n = 65$) than males breeding in their first return year (42%, $n = 309$), but this was not a significant difference (Yates corrected $\chi^2 = 0.94$, $P = 0.33$).

Experimental removal and replacement

Our removal experiments in 2009 and 2010 resulted in almost complete replacement of both sexes (Figure 5). For this we compared number of nests after removal with the previous year's population size in experimental and control plots. After removal of 19 (10 females, 9 males) individuals in 2009 and 54 (28 females, 26 males) individuals in 2010 from the Ruinen

plot, we found no reduction of local breeding population size relative to the previous year (Figure 5). Removed breeding pairs were replaced within a couple of days, and in some cases a third pair took over after two replacement pairs had been removed from the same box. In 2009 we observed replacement in 8/8 removals, and in 2010 in 16/23 removals. Replacements did not just occur early in the season, as for the 23 females removed before 30 April we found replacements in 87% boxes, whereas after 30 April this was still 75% ($n = 12$, sample size also includes nest boxes with double removals). Within the removal study plot, only one out of the 98 nest boxes remained unused in 2009, and in 2010 only five boxes were unused, suggesting strong competition for the available boxes.

Among replacements, we knew the real age of only 11 males and 14 females because they had been ringed

Table 2. Statistics of origin of adult breeding Pied Flycatcher since population establishment in Drenthe plots in 2007. Nests where parental identity was unknown are either failed nests (most likely through predation) or where a parent could not be caught (died, or males not providing food to young, potentially because they are polygynous). For a subset of study plots (excluding the Ruinen plot) we give the total number of males that were singing each year, and the proportion of these males that remained unpaired. Individual males that sung for some days before they disappeared are not included, and males were considered unpaired when they were still singing after 10 May and did not pair up with a female. Survival and recapture rates are estimates from a mark-recapture model in program MARK, using only individuals that were not manipulated during their entire life. This model was a full sex $\times$ year model, with both survival and recapture rates being sex and year dependent. Survival rates are from the mentioned year to the next year, whereas recapture rates are for the year mentioned in the column. All captures until 2015 were included, but we do not give survival rates from 2014–2015 because recapture rates for 2015 cannot be estimated. This analysis is based on 1187 individual females of which 289 were recaptured at least once and 865 males of which 340 were recaptured at least once.

	2007	2008	2009	2010	2011	2012	2013	2014	2015
Number of nests	162	252	281	279	306	293	311	246	307
Female number caught	150	221	237	275	280	270	280	240	277
Nests female ID known (%)	93	88	84	99	92	92	90	98	90
Unringed immigrants (%)	94	76	59	55	43	54	49	42	47
Ringed immigrants (%)	6	5	5	3	4	1	1	1	2
Locally 1st time breeders (%)	0	7	14	17	15	18	17	20	20
Experienced breeders (%)	0	12	22	26	38	27	34	37	31
Survival estimate	0.23	0.22	0.31	0.45	0.35	0.36	0.35	0.40	
Recapture rate		0.57	0.54	0.73	0.68	0.59	0.73	0.83	0.88
Male number caught	122	182	209	252	263	258	252	226	250
Nests male ID known (%)	75	72	74	90	86	88	81	92	81
Unringed immigrants (%)	97	71	47	44	34	34	38	29	33
Ringed immigrants (%)	3	3	1	2	0	2	1	1	1
Locally 1st time breeders (%)	0	6	15	17	23	24	25	29	26
Experienced breeders (%)	0	20	37	37	43	40	36	41	39
Survival estimate	0.43	0.40	0.51	0.48	0.46	0.40	0.54	0.49	
Recapture rate		0.60	0.68	0.70	0.66	0.69	0.76	0.74	0.82
Total arriving males	119	229	269	268	292	350	338	308	321
Proportion non-breeders (%)	12.6	9.6	15.6	5.2	7.2	12.0	7.1	20.8	15.6

Figure 5. Relationship between local number of Pied Flycatcher nests within study plots for two consecutive years, and the effect of removal and addition of pairs. Each dot represents a study plot with 100 nest boxes. In one plot (Ruinen) pairs were removed for translocation in 2009 and 2010, and the number of final breeding pairs after translocation is given. In one plot in 2010 numbers were reduced strongly after 2009, probably due to making boxes predator-proof.

as nestlings, preventing sensible statistical analysis. For these individuals, there was a tendency in males that replacement individuals were more often first-year birds (2 first-year out of 5 males = 40%) than in the original population (0 out of 6 = 0%). In females no such bias was found, with 3/7 (43%) original females being first-year, and 1/6 (17%) among replacement females. Furthermore, replacement males were less often individuals that had bred in previous years (5/18 = 28%) than in the original population (10/27 = 37%). Again, in females we found no indication of differences among replacement (9/27 = 33%) and original breeders (8/28 = 29%) in the likelihood that they had been breeders in previous years. These experiments suggest that removed individuals were (almost) completely replaced, and that new settlers were possibly younger or less experienced in males but not in females.

Additional observations on unpaired males

The idea that a surplus of male and female non-breeders exists because of competition for nesting holes, logically would mean that any male defending a suitable nest box would become paired. However, this was not the case. The proportion of males that remained unpaired but were advertising at a nest box fluctuated between 5 and 21% per year (see Table 2). Especially in 2014 when there was a high percentage of unpaired males, plots varied in the proportion of unpaired males: with five plots having at least 25% of males unpaired, whereas three plots had less than 10% of males unpaired.

How do the observed numbers of unpaired males compare to the estimated 90% first-year individuals that refrain from local breeding? Over all years, we observed on average 33 males (including older individuals and immigrants) per year that sang without pairing up with a female. Based on our demographic analysis, 116 locally born first-year males per year should be present without breeding. Hence, the observed number of non-breeding territorial males is only a fraction of those present.

No evidence for staying in Africa

We found no evidence that flycatchers that skip breeding stay at their wintering site during their first summer, as stable isotope ratios of tail feathers did not differ between individuals that were observed breeding in their first year and that skipped the first year (Figure 6). A comparison of tail feathers of ten locally born individuals that recruited in their first year with eight locally born individuals that skipped the first breeding season (and for which we thus do not know their moulting site), showed no difference in $\delta^{15}\text{N}$ ($F_{1,16} = 0.59$, $P = 0.46$), but a hint for a difference in $\delta^{13}\text{C}$ ($F_{1,16} = 4.10$, $P = 0.060$). Because these feathers could only be collected once they recruit as breeders, the tail feathers were grown respectively in the nest (for first-year breeders) or when adult (skipped breeders). The observed difference in $\delta^{13}\text{C}$ may well be an age effect because the timing, conditions under and way in which feathers assimilate isotopes can differ in nestlings compared to full-grown birds (Hobson & Wassenaar 2008). We indeed found a similar difference in $\delta^{13}\text{C}$ (but not $\delta^{15}\text{N}$) for paired observations of individuals sampled in their first and second year (first year $\delta^{13}\text{C}$: -24.41 ; second year: -23.68 ; $t_7 = -2.86$, $P = 0.024$), although their tail feathers must have been grown on the same breeding grounds.

When comparing two-year old individuals, of which eight were observed breeding in their first-year and

Figure 6. Isotope profiles of Pied Flycatcher feathers that were (triangles) or were not (dots) skipping their first breeding season. Above the diagonal: profiles for tertials (moulted at the wintering grounds). Below the diagonal: profiles for tail feathers (moulted after the breeding season, normally at the breeding sites). Filled dots are individuals that recruited in their first year and open dots the same individuals in their subsequent year ($n = 8$). Filled triangles are individuals breeding for the first time in their second year, and open triangles the same individuals in subsequent breeding seasons ($n = 10$).

eight others not, we found no difference in tail feather $\delta^{15}\text{N}$ ($F_{1,14} = 0.00$, $P = 0.95$) or $\delta^{13}\text{C}$ ($F_{1,14} = 1.30$, $P = 0.27$). For eight individuals that were not found breeding in their first year, but bred in the second and third year, the tail feathers in the second year (referring to the first breeding year) should have been moulted in Africa if they stayed there over summer, but the tail feathers of the third year must come from the breeding grounds. However, a paired t -test did not show any difference in $\delta^{15}\text{N}$ ($t_7 = -1.22$, $P = 0.27$) or $\delta^{13}\text{C}$ ($t_7 = -1.35$, $P = 0.22$) between the years. A comparison with tertials that are moulted in Africa prior to migration shows clear differences with tail feathers in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Figure 6), and therefore we had enough power to detect a stay, if any, in Africa.

Demographic summary

The later age at first breeding in males compared to females implies a male-biased sex ratio, and our question here is whether sex differences in adult survival may explain this?

Overall, local annual survival for breeding females was lower than for breeding males (females: 0.35, 95%-CI: 0.33–0.38; males: 0.46, CI: 0.44–0.49; mark-recapture model from MARK, with year + sex specific recapture rates, and only sex-specific survival rates; for year-specific survival rates see Table 1). As permanent breeding dispersal inflates survival downwards, and

females disperse more frequently than males, the lower apparent female survival may in reality be the result of dispersal. The best MARK model (lowest AIC) was with year (but not sex) specific recapture rates, and an additive effect of year and sex on survival.

Annual recapture rates of adults with at least one year breeding experience (estimate for two sexes combined 72%) were considerably lower than the proportion of nests with known adults (Table 1). The difference between these two metrics was larger for females than for males (average for 2008–2015 for females: 92% nests had a known female, whereas capture rate was 67%; for males these were 82% and 69%; paired t -test on within-year differences in these values between the sexes, $t_6 = 2.49$, $P = 0.047$). The best estimate of the proportion of adult individuals alive that are not breeding locally is 13% for males (difference between the 31% not-observed in Mark analysis and the 18% of breeders not captured), and 25% for females. These data show that also within experienced breeders, a considerable fraction of individuals remain undetected, even when accounting for the fact that not all parents are identified (often through nest failure before catching). These individuals either refrain from breeding in such a year, or have been breeding outside our study areas. The latter is not unlikely, as breeding dispersal between our subareas in adults is considerable (Burger 2014: females: 17% ($n = 307$); males: 11% ($n = 392$)), and thus individuals are also likely to disperse to areas outside our plots. The larger discrepancy in females compared to males between the proportion of individuals caught and recapture rate could thus be caused by the higher breeding dispersal rate.

DISCUSSION

A large proportion of male and female Pied Flycatchers was found not to be breeding in their first year of life. We estimated that about 90% of male and 70% of female first-year flycatchers did not breed in our study areas. This suggests a large non-breeding surplus of especially younger birds, which was supported by a large increase in (initially first-year) breeding flycatchers after the provision of large numbers of nest boxes. Removal experiments of male and female breeders resulted in rapid replacement, again supporting the presence of a surplus non-breeding population of both sexes. Skipping breeding in the first years may partly be caused by competition for (high quality) breeding territories/nest boxes, but the high rate of

skipping breeding during the years of population growth, the availability of at least 200 unused boxes per year and the existence of a large fraction of non-breeding males is inconsistent with the competition hypothesis as the sole explanation.

Population establishment

As shown in many previous experiments on hole breeders (Newton 1994), Pied Flycatcher breeding densities in our study areas were, prior to the provision of nest boxes, strongly limited by nest sites. It is surprising (but not unprecedented) how quickly the flycatchers found the newly provided nest boxes, and in the first year most of the breeding birds using the boxes were young individuals (Figure 3), although many older (especially) females were observed as well. We have only limited knowledge of where these birds came from, as only a fraction of the birds were ringed in a large nest box area around 25 km south of our plots. Other potential sources of unringed birds are the large recreational areas where people provide nest boxes around their houses and caravans, and the birds breeding in natural cavities (Bijlsma & Both 2014). Furthermore, it is important to note that the period of rapid population increase coincided with a large-scale outbreak of Geometrid caterpillars in 2007–2009, which may have attracted birds to settle, and local reproduction to be high.

It is puzzling that in the first year of our study we had mostly first-year immigrants, and that in the second year most ringed immigrants coming from the same known source were older. Why did we in 2007 not find breeders born in 2005 or before, as many of these must not have bred in 2007? Actually, in 2008 most ringed new immigrants had been born in 2006, not in 2007, whereas the population was still growing. The lack of older (especially male) immigrants in 2007 suggests that older individuals do not search for new breeding sites when they just arrive in spring from Africa, but do so later in the season, possibly when other pairs have offspring. They could have found the newly created nest box sites and made an informed habitat choice for these sites with high reproductive success (Doligez *et al.* 2002). In contrast, first-year individuals that are known to be more dispersive (Winkel & Hudde 2001) do find new breeding areas when they arrive in spring, and their habitat choice may be more based on the heterospecific information provided by relatively high local densities of tits (Monkkonen *et al.* 1999).

Why do flycatchers not breed at younger ages?

Consistent with our data, earlier studies have reported large proportions of Pied Flycatchers not breeding locally in their first year, these were generally larger in males than in females (Table 1). Our value for females is similar to those obtained in Spanish (Potti & Montalvo 1991) and German studies (Sternberg 1989), but notably lower than in two British studies (Harvey *et al.* 1985, Lundberg & Alatalo 1992). Males in our study had the lowest likelihood of breeding in their first year, this was highest in the British studies. A potential explanation for these population differences is that (temporal) emigration (i.e. young birds first breeding outside study plots, before moving in) varies between habitats, and is lower for the British populations than the others. This seems unlikely, as the Spanish population is located on a mountain, and alternative breeding sites are not in close proximity (Potti & Montalvo 1991). As a result, local recruitment rates are relatively high (22%), as are parental return rates (55%; own mark-recapture analysis based on data provided by Canal *et al.* 2014), and these values are clearly higher than in Britain (Lundberg & Alatalo 1992). It is also unlikely that population differences result from variation in adult survival, as female survival is relatively low in our population (35%) compared to the British (44%) and Spanish populations. Despite geographic differences, a high proportion of non-breeding first-year birds are present in all populations. If we account for the extra mortality of individuals that first appear as breeders later in life, at least 50% of first year birds do not breed locally, and in our population we estimated that only 10% of males alive in their first year do breed locally. Although this estimate depends on the estimated (and unknown) survival rate of non-breeders, even if we assume an exceptionally high survival rate of 80% (instead of 50%), we still estimate that 83% of males and 56% of females are not breeding locally in their first year.

Where could all these non-breeders be? As stable isotope ratios of feathers moulted during the non-breeding year are very similar to ratios found in the first breeding year, it is unlikely that they stayed in Africa. Young birds could breed locally outside the study plots, and with age move into the nest box areas. This would imply that young individuals are outcompeted from nest box areas, or may prefer breeding at lower densities than normal in most managed forests (Lundberg & Alatalo 1992). The quick and complete replacement after our experimental removal of breeding pairs indeed suggested that individuals are excluded from breeding by competition. Earlier experi-

ments had shown competition to be important for male Pied Flycatchers (Sternberg *et al.* 2002), but we also found that females were quickly replaced. Consistent with the local competition hypothesis and earlier studies on male replacement, younger males seemed to suffer more from local competitive exclusion for breeding sites than older males, and hence this could in part explain why males do not breed locally in their first year. In contrast, we found no indication of younger females being more common in the replacement group, although sample size of known-aged individuals was small. It also must be noted that the removal experiment was performed in a plot with high nest box occupancy, and in most of our other plots a larger fraction of nest boxes remains unused in any year. Therefore, the role of competition for nesting sites as cause for delayed age at first breeding may have been overestimated, and will depend on the availability of nest sites. Given that over the entire study area at least 190 boxes per year remained unused for breeding (and on average 300 boxes), the competition hypothesis must only be part of the explanation, although we cannot rule out that high quality nest sites are highly competed for (see also Cooper *et al.* 2009b).

All our data support the idea that many young males are not breeding, and do not even defend a nest box in their first year, as they remain unnoticed before being observed at a later age. As in other flycatcher populations (Huhta *et al.* 1998, Dale 2001), we do observe males that fail to pair up with a female despite defending an empty nest box, but their numbers are far too low to explain the 90% skipping breeding in the first year. Given that the age at first breeding in females is younger than in males, it must be that indeed many males do not breed. It is also unlikely that all these males behave territorially in the forest surrounding the nest boxes, as local densities of territorial males defending natural cavities are low in most areas without boxes (monitoring data Joop Kleine; see however Bijlsma & Both (2014) for local higher densities). Interestingly, while catching adults who are provisioning nestlings, a third or fourth adult is regularly observed around the nest box that is not entering the box. In theory these can be neighbours (see Thomson *et al.* 2013), but given that most neighbours are busy provisioning their own brood, this seems unlikely. We do not know for sure whether these extra individuals are mostly males.

We do not have evidence that non-breeding females are present. The question is whether females are in short supply, causing the high proportion of young males skipping breeding, or whether non-breeding

females are present as well. The data are ambiguous, because the removal study clearly showed replacement of females over a prolonged part of the season (Burger & Both 2011), but the presence of a large proportion of non-breeding males that defend a nest box in certain years (up to 20%) suggests that non-breeding females are absent. If so many young females are present without breeding, why then do these bachelor males not find a mate? They can breed outside the study plots when younger, and move into the plots with age. Female flycatchers are indeed more dispersive than males, which is also true after the first year. However, in Russia immigrant females had a lower local survival rate (due to permanent emigration?) than locally born females (Chernetsov *et al.* 2009).

If not competition, what else may explain why so many individuals delay breeding? It is well known that in many migratory species first-year individuals arrive later at the breeding grounds than older individuals, a pattern also observed in Pied Flycatchers (Lundberg & Alatalo 1992, Potti 1998, Both *et al.* 2016). Later arrival may cause the first breeding season to be skipped, but could also be a consequence, as low prospects for successful breeding may relax the pressure for early arrival. Relatively little is known about ontogeny of migration, but a longitudinal study on satellite-tagged Black Kites *Milvus migrans* showed clear improvements in migration timing and efficiency over the first five years of life (Sergio *et al.* 2014). Also, juvenile White Storks *Ciconia ciconia* migrate less efficiently in terms of energy and time expenditure than adults during their first autumn migration, and take longer to reach the wintering sites (Rotics *et al.* 2016). In Wood Thrushes *Hylocichla mustelina*, first-year birds tracked in spring from the Central American wintering grounds departed 8 days later than older individuals, migrated with lower speed, and subsequently arrived about 14 days later at their breeding grounds (McKinnon *et al.* 2014). The reason why young individuals depart later and migrate at a slower speed could be due to them wintering in lower quality habitat, which adversely affects their body condition and subsequently delays their departure date from the wintering grounds (Studds & Marra 2005, 2011). These studies may imply that young migrants forego breeding because they arrive (too) late in spring, which could result from wintering in lower quality habitat, the need for learning to migrate, or age-dependent costs and benefits of arriving early.

In our Pied Flycatcher population, first-year individuals arrived on average five days later than second year individuals, and in males arrival advanced up to the

fourth year of life (seven days earlier than first year males; Both *et al.* 2016). This may not seem an impressive difference, but this arrival is just for the individuals that were observed, whereas individuals arriving even later may refrain from singing because the breeding season is almost over, and thereby remain unnoticed. Also in other migrant species there is evidence of young individuals arriving later than older ones, and that a proportion of the first-year males and females do not breed (Hansson *et al.* 2004, Cooper *et al.* 2009a), although a causal link needs to be established. Given the fact that young individuals must learn many behaviours in early life, including migration, it is rather likely that young individuals in particular arrive too late for breeding, especially if the breeding season is short. Our flycatcher population is indeed characterized by a relatively short breeding season of 19 days (i.e. the average time interval between the 5–95% of the laying date distribution within years). If we assume that after this period breeding becomes unprofitable (Drent *et al.* 2003, Visser *et al.* 2015) an arrival delay of on average 14 days (see McKinnon *et al.* 2014) would result in many individuals arriving too late, given their large variation in departure from Africa (Ouwehand & Both 2017).

If a large proportion of first-year birds arrive too late for successful breeding, could adults also skip breeding if they encounter detrimental conditions during migration? It was striking that adult recapture rates based on mark-recapture analyses were only 72% for both sexes, whereas a notably higher percentage of all breeding adults were caught every season. Again, breeding dispersal may cause individuals to not be recorded breeding locally for a year, and thus breeding dispersal may actually be more common than is often considered, even for adult males. However, some adults may be delayed during migration due to poor body and/or environmental conditions, resulting in late arrival and skipping of the short breeding season. For two more isolated mountainous populations of Spanish flycatchers, Sanz (2001) also gave recapture rates of around 70%, in contrast to the 92% of breeding females each year being identified. Skipping breeding years thus could be a consequence of a long-distance migratory life-style, especially if the ecological time window for successful breeding is short.

Demography: how high must first-year survival be?

If so many Pied Flycatcher skip breeding in their first year, how high must first-year survival then be to maintain population numbers? Given our demographic data (Table 2), we can give a range of the required first-year

survival by demographic balancing, assuming that the regional population is stable (Ricklefs 1973, Redmond & Murphy 2012). We applied this method for several estimates of adult survival and the proportion of first-year individuals that do breed, assuming constant reproductive output and a probability of (successful) breeding after the first year of 90% (Figure 7). Using mean estimated adult survival rates (males: 46%, females: 35%) and probability of breeding in the first year (males: 10%, females: 30%), the required first-year survival should be 38% for males and 42% for females. These estimates seem to be unrealistically high, especially because in females first-year survival exceeds the estimated adult survival. The initially low estimate of adult female survival in our population may be partly attributed to a population establishment effect. In the first years most individuals were immigrants (Table 2), and earlier work showed that consistent (and genetically determined) individual differences in dispersal propensity exist (Chernetsov *et al.* 2009, Doligez *et al.* 2009), and as a consequence these immigrants likely permanently emigrated after breeding, resulting in low local survival rates in females in especially the first two years (22–23%). Given the higher estimates in more recent years, and the higher breeding dispersal rate of females, we regard an adult female survival estimate of 45% more likely (see also similar estimates by Sanz (2001) for Spain, and Lundberg & Alatalo (1992) for England). Given this 45% adult survival rate and 30% first-year breeding probability, we estimate first-year survival to be 32% in females. Males have breeding dispersal, albeit lower than females, and if we estimate their adult survival at 50% (instead of 46%), the corresponding first-year survival would be 33%. Any underestimate in the probability of breeding at younger ages would reduce the estimated first-year survival (Figure 7). The same is true for underestimating adult survival, but there are hardly higher values reported for the various studies estimating adult survival in Pied Flycatchers (Lundberg & Alatalo 1992, Sanz 2001). The biggest unknown is the survival probability of individuals that do not breed, and if their survival is substantially higher than for breeders the estimated required first-year survival also drops.

Our first-year survival estimates still seem rather high relative to adult survival rates, and are indeed lower than estimates based on mark-recapture analyses using CJS in Spanish Pied Flycatchers (22%; Canal *et al.* 2014), or other long-distance migrating passerines (reviewed by Redmond & Murphy 2012). However, all these estimates are underestimates, as they do not

Figure 7. Estimated first-year survival required for a stable population, given various estimates of adult survival (different lines) and probability of breeding in the first year. For this model we used a breeding success of six fledglings and a probability of adult (second year onwards) breeding of 90% (the remaining 10% refrained from breeding, or failed). Adult survival is assumed similar for all individuals after their first year onwards, including individuals that do not breed. The dot gives an estimate for males, and the triangle for females (see text).

include permanent emigration. Moreover, it is not clear how these studies dealt with the potential of a large fraction of young individuals skipping breeding. Using demographic balancing, estimated first-year survival rates in Eastern Kingbirds *Tyrannus tyrannus* rose from 29% (CJS) to 38% (Redmond & Murphy 2012). For the more isolated Spanish flycatcher population with 55% adult survival and the estimated proportion of first-year breeding (Table 1), the expected first-year survival comes close to what is actually observed (24–26% expected vs 22% observed). If these estimated high first-year survival rates are correct, it is an intriguing question to ask whether this is mostly so for migrants wintering in the tropics (and resembling more tropical residents). One can hypothesize that this migration strategy comes with the cost of frequently skipping the first breeding season, as part of the population needs to learn migration behaviour. Alternatively, the high survival rates in the first year are the result of skipping the first breeding year and the birds not taking the risk of arriving early with the associated mortality cost.

How good is our fitness estimate?

In our population, only 7.5% of the ringed fledglings return as breeders; can we estimate what proportion this is of the estimated total number surviving? Unfortunately, we do not know the sex of offspring at fledging, and thus have no idea how much this differs between the sexes, but we have observed 390 male and 305 female local recruits (of any age at first breeding),

suggesting more female dispersal. Assuming equal sex-ratio at fledging, we find 8.3% (390/4661) of males recruit as breeders, and 6.5% (305/4661) of females. If we assume first-year survival for males to be 33%, adult survival 50%, proportion breeding in the first-year 10%, second-year 80% and later 90%, we expect 16% of the juveniles to be observed as breeders at least once in any year of their life. This is about twice the observed proportion, suggesting that half of the males disperse permanently out of our study plots. For females a corresponding estimate would be that we only observe one third of the surviving females in our population. If we overestimated first-year survival (see above), this would mean that we actually sample a higher percentage of the surviving offspring within our study plots.

It has long been recognized that natal dispersal in particular is an important component in the demography of long-distance migrants (Paradis *et al.* 1998, Winkler *et al.* 2005), although it is hard to quantify where these emigrants go for breeding. Most dispersing offspring may breed at short distances from their natal area outside our study plots, but we also have several records of individuals dispersing to sites at more than 200 km, and long-distance dispersal may be more common in this species than is often assumed (see also Both *et al.* 2012). Little is known of whether these dispersing individuals are a biased sample of the population, and if they are, they could potentially affect fitness estimates that are based on local recruits only. Furthermore, long-distance dispersers may be especially important in the process of adapting to large-scale environmental change, as they may adaptively disperse to areas with a better phenotype-habitat matching (Edelaar *et al.* 2008), and/or introduce new alleles into their final breeding populations to boost the potential for selection. Our study emphasized that there is a large group of surviving young flycatchers that remain undetected, and both for population and evolutionary dynamics we need to improve our understanding of the composition of this group.

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SAMENVATTING

Broedpopulaties van vogels worden soms gereguleerd door territoriaal gedrag, waarbij individuen niet tot broeden komen omdat ze geen territorium kunnen bemachtigen. Hierdoor ontstaat een groep niet-broeders, die een zogenaamde buffer vormen voor als broedvogels verdwijnen. Het meeste bewijs hiervoor komt van experimenten waarbij mannelijke territoriumeigenaren werden weggevangen, en de vrijgekomen territoria werden vaak snel opgevuld door niet-territoriale mannen. Het is echter onduidelijk hoe algemeen vrouwelijke niet-broeders zijn, terwijl voor een regulerend effect van een dergelijke bufferpopulatie mannen én vrouwen noodzakelijk zijn. In deze studie laten we zien dat bij Bonte Vliegenvangers veel mannelijke en vrouwelijke niet-broeders aanwezig zijn. Een groot deel van de Bonte Vliegenvangers die wij als nestjong in onze broedpopulatie in ZW-Drenthe ringden, broedde niet in hun eerste levensjaar: slechts 23% van de mannelijke rekruten begon in het eerste jaar te broeden, en 51% van de vrouwelijke rekruten. Vogels die pas in het tweede of derde jaar voor het eerst tot broeden komen hebben al een aantal jaar kans gehad om dood te gaan. Als we rekening houden met de mortaliteit van deze niet-broedvogelpopulatie, dan schatten we dat slecht 9% van alle eerstejaarsmannen die in leven zijn lokaal tot broeden komt, en 29% van de eerstejaarsvrouwen. Dit lijkt onwaarschijnlijk weinig, maar vergelijkbare percentages werden ook in andere Bonte Vliegenvangerpopulaties gevonden. De vraag is waar al deze niet-broeders zijn, en of ze een bufferpopulatie vormen die wel tot broeden kan komen indien de mogelijkheid zich voordoet? We laten zien dat in het eerste jaar nadat we de nestkasten ophingen vooral eerstejaars vliegenvangers broeden (77% van geringde immigranten), terwijl in de jaren daarna de geringde immigranten minder vaak eerstejaars waren (28%). Dit wijst op competitie voor broedplaatsen, en een experiment in twee jaar waarbij we paartjes wegvingen liet zien dat deze plekken snel weer werden opgevuld, en dat het wegvangen van een aanzienlijk deel van de populatie geen effect had op de uiteindelijke broedpopulatiegrootte. In dit experiment waren de nieuwe mannen vaker eerstejaars dan de weggevangen mannen, maar bij vrouwen was er geen leeftijdsverschil. Het experiment laat duidelijk zien dat Bonte Vliegenvangers een niet-broedende populatiebuffer hebben van mannen en vrouwen. Onze bevinding dat vrouwen gemiddeld op jongere leeftijd beginnen te broeden dan mannen, wijst er wel op dat er meer niet-broedende mannen dan vrouwen zijn. De volgende vraag is of al die jonge vogels die niet tot broeden komen, uitgesloten worden door competitie met oudere vogels? Dit lijkt niet het geval: in alle jaren waren mannen aanwezig die een nestkast verdedigden en zongen, maar geen vrouw kregen (gemiddeld 12% van de mannen, maar in sommige jaren wel 20%). Dus hoewel er veel vrouwen hun eerste broedjaar lijken over te slaan, zouden ze met deze mannen kunnen paren. We kunnen uitsluiten dat deze vogels in hun eerste voorjaar in Afrika blijven, want analyse van stabiele isotopen in hun staartveren laat zien dat die niet in Afrika gegroeid zijn. We suggereren dat veel van de jonge Bonte Vliegenvangers in hun eerste jaar te laat op de broedgebieden arriveren om nog succesvol te kunnen broeden. Eerder onderzoek heeft inderdaad laten zien dat jongen vijf dagen later aankomen dan ouderejaars. Omdat dit leeftijdsverschil alleen kon worden gemeten aan de vogels die of wel tot broeden kwamen, of een nestkast bezetten, denken we

dat de (jonge) niet-broeders nog later arriveren. Waarom jongen zoveel later arriveren is onbekend, maar mogelijkwerwijs moeten ze hun trekroute leren, overwinteren ze op slechtere plekken in Afrika om op te vetten voor vertrek, of zijn de kosten van een vroege aankomst relatief hoog in vergelijking met de opbrengst aan broedmogelijkheden. Het is mogelijk dat dit voor veel soorten lange-afstandstrekkingen geldt en we pleiten daarom voor een beter begrip van hoe trekgedrag van vogels zich ontwikkelt gedurende het leven, om beter te begrijpen waarom veel vogels hun eerste broedjaar overslaan.

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