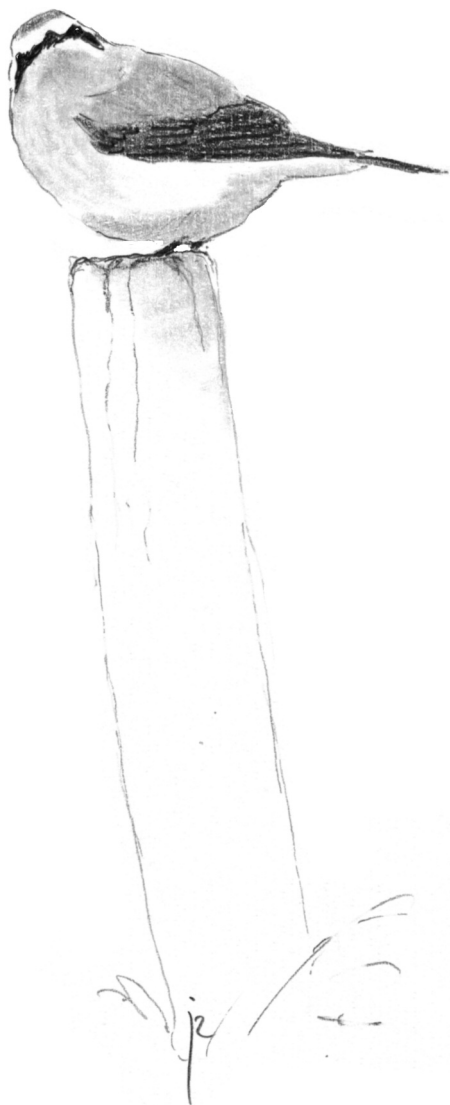


# Female-biased adult sex ratio in relation to sex-specific adult and first-year survival, fledgling sex ratio and dispersal in a migratory passerine

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The relative number of adult males to females in a population, the adult sex ratio (ASR), is an important demographic variable in populations, which plays a role in, for instance, mating systems and viability of populations. The origins of variation in ASR between populations are often unclear. A skewed ASR in a local population may result from a skewed sex ratio among fledglings, sex differences in survival or dispersal or a combination of these. Meta-analyses show that ASRs across bird species are mostly male-biased and that male-biased survival is the main contributor to this bias. Here, we examine the origins of a female-biased ASR in a small population (3–24 breeding females in 2007–2017) of a passerine, the Northern Wheatear *Oenanthe oenanthe*. Because 95% of all fledglings were sexed, 88% of the individuals were colour-banded and because this species is highly philopatric, we could accurately examine: (1) fledgling sex ratio, (2) sex-specific first year and adult apparent survival and (3) sex-specific dispersal. It appeared that survival was not sex-biased for either age cohort but that fledgling sex ratio was male-biased, especially so among late broods. In addition, natal dispersal out of the breeding population was likely male-biased, in contrast to the general pattern of female-bias in avian dispersal. So, perhaps females are more common in our relict population solely because more males disperse from the population than females, without being compensated by male-biased fledgling sex ratio or survival and without compensation from immigrating males. Likely, the population sex ratio (including both adults and young) at the end of the breeding season is male-biased, because of a pronounced male-biased sex ratio among fledglings from late nests. Perhaps this male-bias induces prospecting young males to settle elsewhere to avoid competition next year, but at the same time convinces prospecting females to settle particularly in this area.

Key words: adult sex ratio, ASR, passerine, songbird, adult survival, first-year survival, sex bias, fledgling sex ratio

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Adult sex ratio (ASR) is an important yet somewhat neglected variable in the behavioural and population ecology of birds (Donald 2007). Male-biased adult sex ratios are frequent, especially so in endangered avian species (Donald 2007) or small populations (Zanette 2001, Morrisson *et al.* 2016). This bias could arise as a consequence of demographic processes, such as sex-biased mortality or fledgling sex ratio, but also via behavioural processes, such as sex biased dispersal

(Bessa-Gomes *et al.* 2004, Donald 2007). It seems that in general sex differences in adult survival drive ASR, rather than, for instance, biased hatchling or fledgling sex ratio (Donald 2007), although differences between species may well exist.

Variation in adult sex ratio in populations of wild birds has consequences for population dynamics, demography and behaviour (Donald 2007). Although ASR is an important factor in population biology,

breeding system evolution and conservation (Bessa-Gomes *et al.* 2004, Veran & Beissinger 2009), the origins of variation in ASR between species or populations have been little studied and thus often remain unclear (Donald 2007, Kokko & Jennions 2008, Székely *et al.* 2014), perhaps especially so in small songbirds. Indeed, although sex-biased adult survival is seen as the main driver of skewed ASRs, the ASR of any endangered species or population needs to be determined to be able to properly assess its population dynamics and population viability.

The Northern Wheatear *Oenanthe oenanthe* is a migratory songbird which has declined strongly as a breeding bird in Northwestern Europe, including The Netherlands. Its decline is mainly due to large scale adverse changes of its preferred habitat. Only a few populations remain in The Netherlands after a decline by more than 90% since the 1980s (van Oosten 2018), three of which have been subject of study since 2007. In the smallest population, polygyny is observed regularly, but not in the other two sites. Since polygyny may be the result of a female-biased ASR, we are curious to learn the demographic origins of the ASR in this relict population using five years of individual-based sex- and stage-specific life history data. We seek to determine which of several demographic factors may cause the local ASR: (1) sex-biased differences in adult yearly survival, (2) sex-biased differences in yearly survival of fledglings, (3) sex-biased differences in fledgling sex ratio and (4) sex-biased differences in emigration outside the study population.

## METHODS

### Study species and study sites

The Northern Wheatear is an insectivorous long-distance migrant breeding from Eastern Canada and Greenland across Eurasia to Western Alaska (Glutz von Blotzheim & Bauer 1988). In The Netherlands, Northern Wheatears occur in heathlands and sandy, oligotrophic grasslands in coastal dunes where they forage on short vegetation (van Oosten *et al.* 2014) and breed in burrows of European Rabbits *Oryctolagus cuniculus* or under tree trunks left after felling of trees (van Oosten 2018). Since 2007 we studied three rather isolated populations of Northern Wheatears in The Netherlands by colour-ringing nestlings and adults (van Oosten *et al.* 2015): the inland population at Aekingerzand (268 ha; 52°55'N, 6°18'E; 11–47 breeding females in 2009–2013), the coastal population at the dune area Vogelduin near Castricum (74 ha; 52°33'N, 4°36'E;

7–24 breeding females in 2009–2013) and the nearby coastal dune population at Den Helder (160 ha; 52°52'N, 4°43'E; 53–67 breeding females in 2009–2013). Together they comprise about half of the total Dutch population. The current study focusses on the population at Vogelduin, because the sex of fledglings is determined (samples collected in 2009–2013) only in this smallest population of the three.

### Adult sex ratio (ASR)

To determine ASR it needs to be ascertained that all adult birds in the population are noted as either involved in the nesting process or present in the population without breeding. In many songbirds this is challenging (Donald 2007, Both *et al.* 2017) because of, for instance, unobtrusive behaviour of the species or because males and females differ in their behaviour and therefore in their visibility (Amrhein *et al.* 2012, Rodrigues *et al.* 2016). Fortunately, Northern Wheatears are very visible because of their habits: they forage conspicuously on short vegetation (mostly < 5 cm; van Oosten *et al.* 2014) in quite open landscapes and are quite vocal in the breeding season. In 2009–2017 we visited Vogelduin on several days per week between early April and the end of July (in 2009 and 2010 until the end of August). Nests with nestlings were easily found by following feeding parents and all nestlings found were (colour) banded when older than five days. The number of non-breeding adults in the population at Vogelduin is very low: if they were present, they should have been noted because of the high visibility of the species, the small size of the population, the fact that on average 88% of all adults were colour-ringed in the period 2009–2017 and because our search-intensity was high, resulting in very high annual resighting probabilities between years (van Oosten *et al.* 2015, 2017). We are therefore confident that we accurately know all adults in the population that primarily aimed to nest in this relict population (see Discussion). Therefore, our annual assessments of ASR (number of adult males per adult female) in the Vogelduin population amount to exact measurements, not samples on which inferences are based for some larger population.

### Polygyny

The fraction of polygynous males among all males present in Vogelduin per year was recorded for the years 2008–2013. The mating status was determined by recording the colour ring combinations and, in one case, by unique feather characteristics of one male which was filmed up close by both its nests.





The dune area Vogelduin, a typical coastal Northern Wheatear-habitat in The Netherlands, where Rabbits provide burrows for Wheatears to nest in, and maintain a short vegetation which is the preferred foraging habitat (photo HHvO, Castricum, 15 May 2008).



A third calendar year male Northern Wheatear at Vogelduin, where it was ringed as nestling on 1 July 2009 (photo Remco Versluijs, Castricum, spring 2011).

### Capture-mark-recapture study

During 2009–2013, we marked (and sexed) 205 nestlings which fledged in Vogelduin with individual combinations of three coloured leg rings and a numbered aluminium ring from the Dutch Centre for Avian Migration and Demography. Fledging success was determined by observing young after fledging and by examining the nest after fledging to check for remaining dead eggs or nestlings. Resightings in 2010–2017 were used to estimate local sex-specific annual apparent survival of fledglings until their first return from the wintering grounds in Africa, and of adult birds (older than 2<sup>nd</sup> calendar year).

We estimated apparent (or local) survival from live resightings of the colour-ringed individuals, using the CJS model option in program MARK v. 9.0 (White & Burnham 1999). Although our data indicated that birds that were alive and returned to the study area were actually all resighted, we still used MARK to use its possibilities to formulate and compare models and to calculate model-averaged apparent survival estimates. Since not a single ‘.01.’ sequence was present in the encounter histories after the year of ringing, a constant value of 1.00 proved the single best model structure for the resighting probability ( $p(.)$ ). For the apparent annual survival rate ( $\Phi$ ), we considered potential effects of age, hatching date (shown to have a significant influence on first-year survival in this population (van Oosten *et al.* 2017)) and sex. With respect to age we distinguished between ‘first year’ (from hatching to 1 July of the next year) and ‘adult’ apparent survival (at all ages  $\geq 1$  year). Note that all birds were marked as fledglings. With respect to hatching date we distinguished between birds hatching ‘early’ (before 5 June) or ‘late’ in the breeding season (at or after 5 June). This date marks the start of a second peak in the distribution of hatching dates in this population (made up mostly of second and replacement broods; van Oosten *et al.* 2017), and also separates broods raised during and after the annual period of peak abundance of Garden Chafer *Phyllopertha horticola*, an important prey species (van Oosten *et al.* 2014). A lower survival of juveniles from late-fledged broods was found in a previous study (van Oosten *et al.* 2017).

Data from 2009–2017 were included in the analysis. A set of 21 candidate models for apparent survival ( $\Phi$ ) was run, defined by all combinations of the three factors mentioned above and their two-way interactions, but omitting combinations including an interaction but not both its constituent main factors, except combinations including age and hatchdate.age, and age and sex.age (an effect of hatch date or sex on first-

year apparent survival only). Given the small size of the dataset and limited number of years we did not include time dependence in the candidate models. Model evaluation was based on Akaike’s Information Criterion corrected for small sample size (AICc; Burnham & Anderson 2002). Using the median  $\hat{c}$  method (Cooch & White 2006), the overdispersion parameter of the full model was estimated at 0.99, hence we used a value of 1 throughout. Model-averaged survival estimates are reported.

### Molecular sex determination to determine fledgling sex ratio

All DNA samples stem from growing feathers of juveniles, collected when colour-ringing the birds in the nest. DNA from feathers was extracted using the QuickExtract DNA Extraction Solution (Epicentre, Madison, WI, USA), with the following particulars: 90  $\mu$ L QE solution, two cut down growing feathers, 1 h of incubation at 65°C, vortexing every 30 min, heat denaturation for 3 min at 95°C and down-spinning twice after denaturation. Sexing primers P2 and P8 (Griffiths *et al.* 1998) were amplified in single PCRs with standard protocols using 20–60 ng DNA, 0.25 U of Taq DNA polymerase (Fermentas), a provided buffer containing  $(\text{NH}_4)_2\text{SO}_4$  and 2 mM  $\text{MgCl}_2$ . Annealing temperature was 50°C for P2P8. PCR product (1.5  $\mu$ L) was mixed with formamide containing the GeneScan 500LIZ size standard, heat-denatured and resolved in POP4 polymer on an ABI 3130xl Genetic Analyzer (all Life Technologies GmbH). In total we sexed 205 fledglings, which is 95.3% of all 215 nestlings that fledged in the period 2009–2013. Therefore, we considered uncertainty about the observed fledgling sex ratio negligible and treated it as an accurately measured feature of the study population.

### Dispersal

Since 88% (in some years 100%) of the breeding adults in Vogelduin and more than 95% of the fledglings were colour-ringed and resighting rates were very high, breeding or natal dispersal between the three breeding sites could be monitored accurately, effectively meaning that half of the Dutch population was checked intensively for immigrants each year. Northern Wheatears dispersing to other sites were less likely to be detected, but were occasionally reported by bird-watchers from the rest of The Netherlands nonetheless. Parts of the most suitable breeding areas in The Netherlands, apart from our study sites, are surveyed annually as a part of the national breeding bird monitoring programme (e.g. Boele *et al.* 2015, Sovon 2018).



In addition, rare breeding birds such as the Northern Wheatear receive much attention from e.g. birders and site-managers. In the current study we are interested in individuals that dispersed between sites, and not individuals that moved within a site.

## RESULTS

### Polygyny

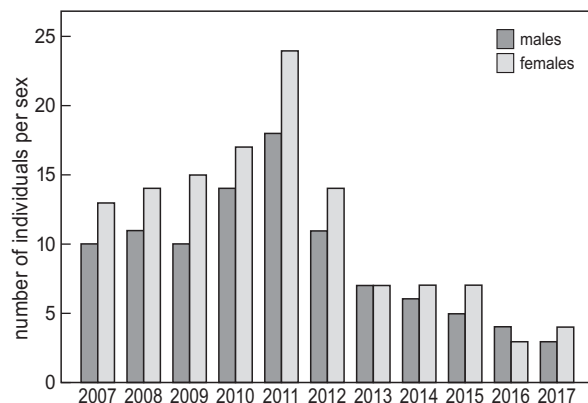
On average,  $30.5\% \pm 14.0$  (SD over years) of the males nesting in 2008–2013 were polygynous (Table 1).

### Adult sex ratio

Females outnumbered males in nine out of eleven years (2007–2017) in the Vogelduin population (Figure 1). Mean ASR (number of adult males per adult female) was  $0.84 \pm 0.19$  (SD over years; range: 0.67–1.33).

**Table 1.** The total number of nesting males, the number of polygynous males and the percentage of polygynous males per year for 2008–2013.

	2008	2009	2010	2011	2012	2013
Total number of males	9	9	14	18	11	6
Number of polygynous males	2	5	3	6	2	2
Percentage polygynous males	22	56	21	33	18	33



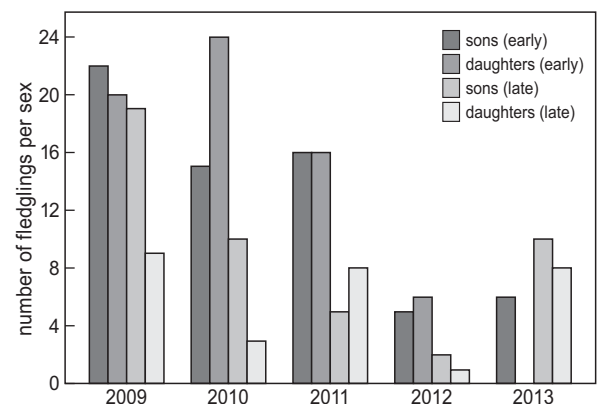
**Figure 1.** Yearly numbers of males and females observed in the breeding season in the study site during 2007–2017, including both colour-ringed and non-ringed individuals. Across all years, 83.5% of all males and 86.3% of all females were colour-ringed (including the starting year 2007 in which only 60% of males and 54% of females were colour-ringed).

These figures exclude birds that dispersed and held a territory elsewhere, but showed up in Vogelduin later in the same season, as they were not available for mating.

### Fledgling sex ratio

Of the 205 fledglings sexed in 2009–2013 (95.3% of all fledglings), 110 were sons and 95 were daughters, resulting in an overall male-biased fledgling sex ratio of  $1.16 \pm 0.47$ , with a range across years of 0.88–2.00. Mean sex ratio among early nests was slightly female biased:  $0.97 \pm 0.21$  (0.63–1.10, 64 sons and 66 daughters) but strongly male-biased among late nests (hatch date  $\geq 5$  June):  $1.59 \pm 1.02$  (0.63–3.33, 46 sons and 29 daughters). When the nestlings are added that did not fledge (because whole broods occasionally succumb due to, for instance, nest predation by Red Foxes *Vulpes vulpes*; van Oosten *et al.* 2015) to enlarge the sample size (total 165 sons, 139 daughters), the results are similar with a male bias across all nestlings:  $1.19 \pm 0.47$  (0.90–2.13). Again, early broods were less male-biased than late broods:  $1.04 \pm 0.19$  (0.86–1.25, 98 sons and 94 daughters) respectively  $1.49 \pm 0.69$  (1.00–2.60, 67 sons, 45 daughters).

Summarising, the overall sex ratio of fledglings (and nestlings) was slightly male-biased, which is foremost a result of a distinct male-bias among late broods.



**Figure 2.** The number of fledglings per sex from early (hatch date  $< 5$  June) and late nests (hatch date  $\geq 5$  June) in 2009–2013. No daughters fledged from early nests in 2013.

### Adult and first-year apparent survival

The model-averaged estimates of apparent survival for males and females are very similar within each age class and hatching date group, with almost completely overlapping confidence intervals (Table 2; e.g. first-year apparent survival early hatched males 0.30, 95%-CI: 0.22–0.40 and females 0.29, 95%-CI: 0.21–0.39).

**Table 2.** Model-averaged estimates (with 95% confidence intervals) for apparent survival ( $\Phi$ ) and resighting probability ( $p$ ) of Northern Wheatears by age class, hatching period and sex.

Par.	Group	Age class	Estimate	95%-CI
$\Phi$	males, early-hatched	first year	0.30	0.22–0.40
$\Phi$	females, early-hatched	first year	0.29	0.21–0.39
$\Phi$	males, late-hatched	first year	0.21	0.12–0.34
$\Phi$	females, late-hatched	first year	0.21	0.12–0.35
$\Phi$	males, early-hatched	adult	0.40	0.29–0.52
$\Phi$	females, early-hatched	adult	0.40	0.29–0.53
$\Phi$	males, late-hatched	adult	0.39	0.24–0.57
$\Phi$	females, late-hatched	adult	0.41	0.25–0.58
$p$	all	all	1.00	1.00–1.00

These estimates also show the lower first-year apparent survival, which differs more between early- and late-hatched birds than within the adult age class.

The three most parsimonious models for apparent survival included effects of age and hatching date, but not of sex (Table S1). In the top-ranking model, apparent survival was lower in first year birds than in adults, and lower in late-hatched than early hatched young in the first year but not thereafter, as adults. There was little support for a sex effect, as the most parsimonious model containing sex as a variable (interacting with age, affecting first-year survival only) was ranked 4<sup>th</sup> at slightly less than 2 AICc units more than the top model. The best model including sex as a main effect ranked 7<sup>th</sup>, at 3.65 AICc units below the top model. To conclude, apparent survival does not differ between the sexes for either age class.

### Dispersal

From the small Vogelduin population 10 out of a total of 368 ringed and fledged juveniles (2007–2016) were noted elsewhere, either as breeding birds or as unpaired territorial birds. Of these ten, eight were males and two were females. This ratio does not significantly differ from parity ( $\chi^2_1 = 3.60$ ,  $P = 0.06$ ), however. In summary, males seem to be the more dispersive sex in this isolated population of Northern Wheatears.

## DISCUSSION

Male-biased adult sex ratios are frequent in populations of wild birds, especially so in endangered species (Donald 2007) or small populations (Zanette 2001, Morrisson *et al.* 2016). Nevertheless, we report a female-bias in a small relict population of the Northern

Wheatear. Our study suggests that the female-biased ASR is not caused by sex-biases in adult or first-year apparent survival. Instead, male-biased dispersal away from the natal site may cause the female-biased ASR, a finding which contrasts with the general pattern of female bias in avian dispersal (Greenwood & Harvey 1982, Clarke *et al.* 1997). Moreover, male-biased dispersal probably occurs more frequently than our results indicate, because the sex ratio among fledglings is male biased and because we found no sex biases in survival.

Females outnumbered males in nine out of eleven years; males were more common only in 2016, and in 2013 the number of both sexes was equal. It is quite remarkable that almost every year more females were present than males, even though the population was very small with 3–24 breeding females in 2007–2017. Males would be expected to occasionally be the more common sex just by chance, for instance if more females were predated during autumn and spring migration. Yet, males were the more numerous sex in one year only, in spite of the fact that males are often the more conspicuous sex, which may lead to (male-) biased estimates of the ASR (Bessa-Gomes *et al.* 2004). If males are also the more visible sex in Northern Wheatears, it would follow that, if anything, the ASR may in fact have been even more female biased than we found. A possibility to account for the apparent lack of males is the presence of non-breeding, non-territorial males. While such individuals may roam about the population and may go largely unnoticed in songbirds inhabiting denser habitat and having more furtive habits, such as Pied Flycatchers *Ficedula hypoleuca* (Both *et al.* 2017), this is not so likely in Northern Wheatears which are very visible and conspicuous birds because of their habits and their habitat. Together with the small population inhabiting a small area, plus the fact that most (in some years all) adults and fledglings were colour-banded, we are confident that the local ASR as we report here is accurate.

A female-biased ASR in Vogelduin is not seen in other populations of Northern Wheatears, nor is the frequent occurrence of polygynous males. The Northern Wheatear is generally known as a monogamous species, although occasional instances of polygyny were reported from the populations at Den Helder and Aekingerzand, and from outside The Netherlands (Cramp 1988, Glutz von Blotzheim & Bauer 1988). Given the observation that polygyny is not a widespread mating system in this species, the high frequency of polygynous males in Vogelduin may be a consequence, rather than the cause, of a female-biased

ASR. Indeed, mating systems vary with ASR in several passerine species, where males are more often polygynous in years with a female-biased sex ratio (e.g. Smith *et al.* 1982, Neergaard & Arvidson 1995, Wiktander *et al.* 2000, Mulvihill *et al.* 2002, Kus *et al.* 2017).

ASR was determined for individuals that established territories in Vogelduin. We did not include the six Northern Wheatears that were first seen nesting or defending territories without acquiring a mate elsewhere, before showing up in Vogelduin later in the breeding season. Whereas Northern Wheatears return to Vogelduin during the first half of April, the six initially dispersing individuals eventually returned to their natal grounds mostly in June (interval between first observation elsewhere and first observation in Vogelduin:  $44 \pm 14$  days,  $\pm$ SD). These males failed to acquire a partner in Vogelduin, whereas the single initially dispersing female nested in Vogelduin as a secondary female to a polygynous male, after unsuccessfully having nested 6 km north of Vogelduin.

### Adult survival

Male-biased survival is regarded as the factor most often causing a male-biased ASR (Donald 2007), at least more frequently so than either a male-biased offspring sex-ratio or female dispersal does (Székely *et al.* 2014). Yet, detailed case studies are needed since assessments of how several factors, operating simultaneously, may influence ASR in a local population are still rarely reported (Donald 2007, Eberhart-Phillips *et al.* 2017).

We previously reported higher adult male survival for our three populations of Northern Wheatears in The Netherlands across four years (van Oosten *et al.* 2015), as did others for the same species, although differences between the sexes were slight (Seward *et al.* 2013, Henry & Ollivier 2015) or only marked in less suitable, tall vegetation (Low *et al.* 2010). Variation in survival between years was considerable and females enjoyed a higher survival than males in some years (van Oosten *et al.* 2015). No sex differences in apparent survival were found in the current study, which is based partly on different years (2010–2017) than in van Oosten *et al.* (2015; 2008–2011). So, even if adult male survival is higher on average than female survival, effects on ASR are small since sex-bias in adult survival is not consistently large. Moreover, this should lead to a male-biased instead of female-biased ASR in the breeding population, especially since the fledgling sex ratio is male-biased but first-year survival is not sex-biased.

The observation that sex-specific adult survival has no clear effects on the local ASR is interesting, since

“ASRs in wild bird populations are significantly predicted by sex-biased adult mortality rates” (Székely *et al.* 2014), across 187 bird species. Given the multitude of lifestyles, degrees of sexual size dimorphism, and life-histories among bird species, it may not be surprising that different patterns are observed in some species or populations.

### Fledgling sex ratio and first-year survival

Sex-biases in fledgling sex ratio and first-year survival may result in a skewed ASR (Veran & Beissinger 2009, Eberhart-Phillips *et al.* 2017, Kus *et al.* 2017), although few studies have investigated the contribution of fledgling sex ratio to ASR (Donald 2007, Kus *et al.* 2017). We colour-ringed and sexed 95% of all fledglings during five years, which enabled us to accurately determine whether fledgling sex-ratio and first-year apparent survival relate to ASR, helped by the fact that Northern Wheatears in this population show high degrees of natal philopatry (van Oosten *et al.* 2015, 2016). In contrast to some studies (Donald 2007), but in line with others (Rosivall *et al.* 2004, Cichon *et al.* 2005, Kus *et al.* 2017, Morandini *et al.* 2019) we did find a sex-biased sex ratio among all fledglings, a result of a greater proportion of fledged sons. The overall male-biased sex ratio among fledglings is mostly due to a pronounced male bias among fledglings of late broods. First-year apparent survival, on the other hand, was not sex-biased but we found, as previously for partly different years (van Oosten *et al.* 2017), that survival of fledglings from late nests is lower than that of early fledglings. Why this is so in Northern Wheatears and if it relates to the distinct male-bias among fledglings from late broods, is as yet unknown, but food availability and competition may play a role.

### Dispersal

An alternative explanation for the often strongly male-biased ASR in small breeding populations is dispersal of females to areas without breeding populations. For instance, the ASR in remaining populations of Ortolan Buntings *Emberiza hortulana* in Norway is strongly male-biased, which is attributed to female-biased dispersal (Dale 2001, Steifetten & Dale 2006), although the potential effect of fledgling sex-ratio and sex-specific first-year survival on ASR have been not been examined.

A different dispersal pattern exists in the Northern Wheatears from Vogelduin, for which we found indications of a male-biased dispersal between populations and into areas without a breeding population (although the total detected number of dispersed individuals was

low). Unpaired male Northern Wheatears that dispersed to sites without a breeding population were discovered by their territorial behaviour, e.g. singing, during breeding bird censuses. However, single females outside the breeding areas may be noticed less readily, since they may not sing or show other conspicuous behaviours. It is therefore possible that dispersed females may go unnoticed and cause a male bias in dispersal records. We doubt that this is the case, however, since more males also dispersed between the study sites (where resighting rates for both sexes are close to 1) and to other sites where Northern Wheatears are much sought after.

There seems to be a discrepancy between our results that there was a sex-bias among individuals shown to disperse away from our study area, while the estimates of apparent (local) survival based on live resightings in the study area, being the product of true survival and  $(1 - \text{permanent emigration})$ , did not show a sex difference. We consider two likely explanations for this. First, the mark-recapture dataset may well have been too small to statistically show a difference in apparent survival between males and females. Note that the confidence intervals around the apparent survival estimates were large (see Table 2), and that because only a minority of all birds emigrate from the Vogelduin area, a sex difference in emigration rate will generate a much smaller difference in the apparent survival estimate than an equally large sex difference in true survival, that will be difficult to discern with our small sample size. Second, temporary emigration rather than permanent emigration may be the driving force causing the female-biased ASR. This explanation is supported by the fact that several males were observed to return to Vogelduin later in the season, after initially moving elsewhere. These males were not included in the ASR estimates as they were not available for mating, but they were included in the survival estimates.

Many studies report a higher dispersal distance for females than for males within breeding populations (Greenwood & Harvey 1982, Clarke *et al.* 1997) and this also applies to Northern Wheatears in a Swedish population (Arlt & Pärt 2008). In songbirds, males arrive before females do, also in Northern Wheatears (Schmaljohann *et al.* 2016) and attract returning females or females passing by towards their breeding sites by song and distinctive displays. But how do females that decide to settle solitary outside the breeding population attract males? It is difficult to envision why females would disperse from the few remaining breeding sites, especially when territories are vacant (Arlt & Pärt 2008), to try their luck elsewhere:

chances to successfully breed elsewhere must be very slim since females normally do not make their presence known by singing or otherwise attracting behaviour. In addition, philopatry is strongly selected for in declining populations (e.g. Brown & Kodric-Brown 1977, Weatherhead & Forbes 1994, Heino & Hanski 2001), as a likely result of the higher number of offspring from females that did return to the remaining isolated population, compared to no offspring from females that did not return. Perhaps longer-distance movements, as we report here, will appear to be generally male-biased once more detailed studies have been published, in contrast to female-biased dispersal within breeding populations (Greenwood & Harvey 1982, Clarke *et al.* 1997). Indeed, results of Both *et al.* (2012) suggest that long-distance dispersal in Pied Flycatchers could well be male-biased.

Male-biased dispersal out of our small, relict population is intriguing when considering that polygyny is frequent (annual average 31% of the males in 2008–2013), which means that the local population is short of males. So, perhaps polygyny is frequent just because males disperse more frequently than females. We do not know why males choose to settle in other areas, where chances of finding a female are likely smaller than in Vogelduin. Perhaps the solution is related to age and perhaps condition of those dispersing individuals: all were in their second calendar-year, suggesting that these birds decide not to waste their energy in fruitless fights with older males over territories and females, and instead try their luck elsewhere.

Another possibility to explain the female-biased sex ratio is that Northern Wheatears often choose the site where they will set-up territories next year by using cues from the current year: Pärt *et al.* (2011) found that 79% of returning adults established territories at sites they had been prospecting the preceding years as non-breeding adults. Since fledglings from early nests largely leave the area before those hatched from late nests (van Oosten *et al.* 2017), there may be a surplus of males at the end of the breeding season because the sex ratio among fledglings hatched in late nests is male-biased. This, in turn, could cause prospecting juvenile males to decide to settle elsewhere the next year, whereas prospecting females may deem the Vogelduin to be an excellent area for the very same reason.

To conclude, our results suggest that the female-biased ASR among Northern Wheatears inhabiting Vogelduin may be a result of male-biased dispersal, because neither first-year nor apparent adult survival was sex-biased, and because the fledgling sex ratio was, if anything, male-biased. This male-biased



dispersal may be driven by the male-biased sex ratio (including both adults and fledglings) at the end of the season as a result of the strongly male-biased fledgling sex ratio among late broods.

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## SAMENVATTING

De geslachtsverhouding onder volwassen vogels is een belangrijke demografische variabele in populaties. Deze verhouding speelt bijvoorbeeld een rol in paarsystemen en de levensvatbaarheid van populaties. Desondanks wordt deze geslachtsverhouding maar weinig bestudeerd, waardoor de oorzaken van een scheve ratio binnen populaties vaak onbekend zijn. Onbalans in de geslachtsverhouding kan bijvoorbeeld een gevolg zijn van een scheve verhouding bij de uitgevlogen jongen of een hogere overleving van een van beide geslachten. Uit meta-analyses blijkt dat vogelpopulaties in de regel relatief meer mannen bevatten en dat een hogere overleving onder mannen hiervan de oorzaak is. In dit artikel zijn we op zoek naar de oorsprong van een door vrouwen gedomineerde geslachtsverhouding in een relictpopulatie van Tapuiten *Oenanthe oenanthe* in het Vogelduin bij Castricum (3–24 broedende vrouwen in 2007–2017). Omdat 88% van de individuen gekleurd was, van 95% van alle uitgevlogen jongen het geslacht bekend was en omdat Tapuiten zeer plaatstrouw zijn, konden we de volgende parameters nauwkeurig bepalen: de geslachtsafhankelijke (1) volwassenoverleving, (2) overleving van uitgevlogen jongen, (3) emigratie uit de onderzoekspopulatie en (4) de geslachtsverhouding bij uitgevlogen jongen. Het blijkt dat de volwassenoverleving noch de jongenoverleving hoger is voor mannen dan wel vrouwen maar wel dat er meer zonen uitvliegen dan dochters, vooral uit late nesten. Misschien zijn vrouwen algemener slechts doordat meer mannen dan vrouwen uit de populatie zich elders vestigen, zonder dat het mannenoverschot onder uitgevlogen jongen, een eventuele hogere overleving van mannen of immigratie van mannen voor deze emigratie compenseert. Mogelijk speelt een mannenoverschot aan het einde van de broedtijd een rol (door een groter aandeel mannen uit de late broedsels): van jonge Tapuiten is bekend dat zij de keuze waar volgend jaar te broeden al in hun geboortjaar maken; dan zou een mannenoverschot aan het eind van het broedseizoen mannen kunnen doen besluiten zich elders te vestigen, terwijl vrouwen zich juist aangetrokken voelen door een mannenoverschot.

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## SUPPLEMENTARY MATERIAL

**Table S1.** Model selection results for apparent annual survival ranking 21 candidate models according to their AICc-values. Factor abbreviations: *A* = age (1<sup>st</sup> year or older), *S* = sex (male or female), *D* = hatch date (early or late). All models had a single parameter for recapture probability  $p(\cdot)$ , estimated at 1.00.

nr	Model for $\Phi$	AICc	$\Delta$ AIC	AIC Weights	Model Likelihood	N. Par	Deviance	$-2\log(L)$
1	<i>A+D.A</i>	364.85	0.00	0.248	1.000	4	60.916	355.64
2	<i>D+A+D.A</i>	366.47	1.62	0.110	0.446	5	60.463	355.19
3	<i>A</i>	366.53	1.68	0.107	0.433	3	64.647	359.36
4	<i>A+S.A+D.A</i>	366.61	1.76	0.103	0.415	5	60.607	355.34
5	<i>D+A</i>	367.19	2.34	0.077	0.310	4	63.258	357.98
6	<i>A+S.A</i>	368.48	3.62	0.040	0.163	4	64.540	359.26
7	<i>S+A</i>	368.51	3.65	0.040	0.161	4	64.570	359.29
8	<i>S+D+A+D.A</i>	368.54	3.69	0.039	0.158	6	60.454	355.18
9	<i>D</i>	368.59	3.73	0.038	0.155	2	68.746	363.45
10	<i>D+A+S.A</i>	369.07	4.22	0.030	0.122	5	63.063	357.78
11	<i>S+D+A</i>	369.22	4.37	0.028	0.112	5	63.219	357.94
12	<i>S+D+A+S.A+D.A</i>	369.55	4.69	0.024	0.096	7	59.359	354.09
13	<i>S+D+A+S.D+D.A</i>	369.93	5.08	0.020	0.079	7	59.741	354.47
14	<i>S+D+A+S.A</i>	370.31	5.45	0.016	0.065	6	62.217	356.94
15	.	370.42	5.57	0.015	0.062	2	70.583	365.28
16	<i>S+D+A+S.D</i>	370.44	5.58	0.015	0.061	6	62.347	357.07
17	<i>S+D+A+S.D+S.A+D.A</i>	370.97	6.11	0.012	0.047	8	58.667	353.40
18	<i>S+D+A+S.D+S.A</i>	371.43	6.58	0.009	0.037	7	61.240	355.97
19	<i>S</i>	372.36	7.51	0.006	0.023	3	70.481	365.18
20	<i>S+D</i>	372.63	7.78	0.005	0.020	4	68.699	363.40
21	<i>S+D+S.D</i>	373.57	8.72	0.003	0.013	5	67.567	362.27