On the breeding ecology of Whinchats Saxicola rubetra in the last Dutch populations

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We studied the breeding ecology of Whinchats *Saxicola rubetra* in four tiny (less than 10 breeding pairs) populations in nature reserves in the Dutch province of Drenthe. We focussed on reproductive rates (laying date, clutch size, hatchling number, breeding success), proportion of unpaired males and nestling diet. Breeding pairs appeared to cluster together, thereby leaving other seemingly suitable parts of the area unoccupied. Clutch size, nest and pair success were similar to or higher than those in other studies. Laying of first eggs peaked during 16–20 May and laying dates had not advanced since the 1950s, in contrast to many other songbirds. We found 34% of the males remained unpaired, limiting the population reproduction rate. Whinchats provided their nestlings primarily with beetles and caterpillars and feeding frequency appeared to depend on prey species. Higher feeding frequencies may lead to a higher risk of nest predation. Being single-brooded, Whinchat populations may be more affected by nest predation than populations of multi-brooded species.

Key words: diet, nest predation, reproduction, phenology, unpaired males, clutch size

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Breeding numbers of Whinchat Saxicola rubetra have declined in Western Europe as a consequence of agricultural intensification (Frankevoort & Hubatsch 1966, Glutz von Blotzheim & Bauer 1988. Bastian & Bastian 1996). Less well understood are declines in more natural areas where factors other than mowing or cutting are limiting population growth. Whinchats prefer a mosaic of different sward heights (Border et al. 2016, Murray et al. 2016) and abandon breeding sites when sward height becomes taller and monotonous, such as after cessation of grazing (Calladine & Jarrett 2021). However, the abundance of suitable habitat does not seem to limit Whinchat numbers in the UK (Stanbury et al. 2021). Equally unclear is why Whinchats abandoned coastal dunes and most of the heathlands in The Netherlands (Sovon 2018), perhaps mostly because their breeding ecology in natural habitats is not studied as extensively as in agricultural areas.

We studied the breeding ecology of Whinchats in four small breeding populations in The Netherlands, all

in designated nature areas, to learn how clutch size, breeding success, number of unpaired males and nestling diet compare to other populations. We also compared breeding phenology with historical data, to test if Whinchats have advanced their breeding, as many other songbirds have (Dunn & Møller 2019). In addition, we discuss whether any of the demographic factors provides evidence of limitations for Whinchats in our study areas.

METHODS

Study species

Whinchats are insectivorous songbirds, weighing about 17 g, which breed at temperate to boreal latitudes from Ireland to Western Siberia (Glutz von Blotzheim & Bauer 1988). They produce one clutch per year of 4–7 eggs in open nests built on the ground, with a replacement clutch after failure. Arthropod prey is caught from

a vantage point whence birds spot their prey in the vegetation or in the air, or they walk on short-grown stretches to pick up prey. Whinchats winter in Africa, in wooded savanna on the south rim of the Sahel but mostly south of the Sahel (Zwarts *et al.* 2023a,b). Although wooded savanna is severely affected by human related activities (Zwarts *et al.* 2023c), there is, as yet, little evidence to suggest that causes of decline are on the African wintering areas (Blackburn & Cresswell 2016). The Dutch breeding population declined by about 80% since the 1970s and is mostly confined to the province of Drenthe, in the northeast of the country, where our study sites are located.

Study sites

We studied Whinchats in four breeding sites: two were characterized by a mixture of (wet) heathlands and raised bogs (Fochteloërveen: FV and Wapserveld: WV) and two were located in meadows and pastures along small brooks (Onlanden: OL and Tempelstukken:TS). Studies were conducted in 2020–2022 in all sites but OL, where we studied Whinchats in 2022. These sites were separated by habitats unsuitable for breeding, namely agricultural land, woodland and villages (Figure 1).

FOCHTELOËRVEEN

The study plot of 116 ha is part of a larger area (1066 ha) that contains the largest population in The Netherlands (maximum 119 territories in 2010, which declined to 60–70 currently; Herman Feenstra pers. obs.). FV is an open desiccated raised bog, compartmentalised by dykes to restore the area to a functional raised bog. The distribution of Whinchats closely follows the dykes or other transitions between wet and dryer situations. The area is grazed by a herded flock of sheep, and small trees (mostly birch *Betula* sp.) are cut down every few years to prevent afforestation. The study plot harbours 8–11 breeding pairs.

WAPSERVELD

In Wapserveld (138.6 ha) the number of breeding pairs peaked in 1990 with 21 territories and in the years following numbers fluctuated between 0 and 6 (van Dijk & Bijlsma 2006). Vegetation is roughly similar to FV, consisting of a mixture of dry heaths on sandy ridges, grass-encroached dry to wet heath and bogs (van Dijk & Bijlsma 2006). The area is grazed by a herded flock of sheep and by several dozen Sayaguesa cattle. During our studies, 3–7 breeding pairs were present.



Figure 1. Overview of the study sites in the province of Drenthe in the Northern Netherlands.

DE ONLANDEN

The area (131.2 ha) was in agricultural use until 2008 and afterwards declared a natural reserve. The lower parts consist of marshland and the slightly higher parts of dry and open fields, where 8–25 territories were counted in 2012–2022 (Wijnhold *et al.* 2022). The drier area is grazed by cattle and horses year-round. Characteristic plant species include Common Nettle *Urtica dioica*, Broad-leaved Dock *Rumex obtusifolius*, Creeping Thistle *Cirsium arvense* and Marsh Thistle *C. palustre* and grasses, such as softgrass *Holcus* sp. Six out of the total number of breeding pairs bred in the study site in 2022, which does not encompass the total area of De Onlanden.

TEMPELSTUKKEN

Tempelstukken (98.3 ha) consist of pastures, formerly in agricultural use, with characteristic herbs such as Creeping Thistle, Marsh Thistle, Hemp Agrimony *Eupatorium cannabinum* and Common Nettles, in addition to various grasses. The vegetation is less lush and dominated by grasses in the drier parts. Cattle are present year-round. Until 2015 about 15 territories were present, but in 2017 there were only three (Boele *et al.* 2019). During our studies 3–5 pairs were present.

Census, nest searching and nest checks

From the end of April onwards, Whinchats were searched for by visiting every site once or twice a week and observations were registered on (digital) maps, including behaviour. Males are much more visible than females, so considerable effort was put into finding females to every male encountered. This way, we could accurately determine whether a male was paired or not. Unpaired males sang throughout the day until the end of June. Because only a few individuals were colour-ringed, we estimated the number of unpaired males within a population by using the territory mapping method (Bibby *et al.* 1992). The territories of these males were defined by using multiple simultaneous observations of males in territories of paired and unpaired males. During our weekly visits we recorded unpaired males 3–8 (mean: 4.8) times per season. The number of designated territories may have been slightly overestimated.

Nests were found by following females either carrying nesting material or during an incubation pause or by tracking parents while bringing food to their young. Nests were monitored until failure or until young fledged. Although we tried to find all nests, we may have missed some failed nests because of the limited visiting frequency, especially clutches that failed early in the breeding phase. As a consequence, we cannot always be certain whether a nest is a first clutch or a repeat clutch. It is unlikely that we missed successful nests because of the conspicuous and vociferous behaviour of parents with fledged, dependent young.

During the last check of the nest, when young were 6–11 days old, we measured the young by taking maximum wing chord (wing stretched and flattened) to the nearest 0.5 mm and body mass to the nearest 0.25 g.

Clutch size, hatching and nest success

Clutch size is based only on nests during incubation, when clutches were complete. The number of nestlings is only determined for nests of which clutch size was known; when the number of nestlings in the nest was smaller than the number of eggs (including dead eggs), we assumed nestlings disappeared, since unhatched eggs remain in the nests. The number of fledglings is set equal to the number of nestlings counted at the last visit. Broods were assumed to have failed when parents did not utter alarm calls upon approach when nests were empty while eggs or young were in the nest at the last visit.

Date of the first egg for incomplete clutches was determined by assuming one egg is produced every day (Glutz von Blotzheim & Bauer 1988). When nests were found containing young, date of the first egg (day 1 =hatching day) was back-calculated ± 1 day based on maximum wing chord of nestlings of known age, being 7, 8 and 9 days old. The wing growth of nestlings was assumed to be 4 mm per day (based on hundreds of measurements of the related European Stonechat Saxicola rubicola, and also other songbirds, such as Meadow Pipit Anthus pratensis and Northern Wheatear Oenanthe oenanthe; H.H. van Oosten own obs.). Firstegg date was thus calculated for 47 broods with nestlings of $9.0 \pm 1.7 ~(\pm SD)$ days of age.

Nest success is calculated as percentage of successful nests of all nests found, as well as using the Mayfield method to calculate daily survival rates and overall nest success (Mayfield 1961) for all years and study sites combined, because of small sample sizes. We assumed that daily survival was the same for laying, incubating and nestling phases, and we calculated overall nest success using a period of 31 days (five days laying, 13 days incubation and 13 days nestling period; Schmidt & Hantge 1954, Bastian & Bastian 1996). We regarded a nest as successful when at least one nestling fledged.

Nestling diet and provisioning frequency

To determine nestling diet, we filmed provisioning at 11 nests with a video camera on a small tripod (a Sony HDR-CX11, HDR-SR10E, Canon HF 10E or 100E), during 1-28 June 2020-2022: three at WV, five at TS and three at FV (none at OL). Nests were filmed continuously for one day, except for one nest at WV which was filmed for two days. Filming started on average 3.78 h after sunrise (range: 1.57 h– 8.75 h, SD: 1.85) and lasted for 5.95 ± 1.78 h on average during which time 159 \pm 84 (SD) feedings were recorded. In total we recorded 1909 feedings, encompassing 2888 arthropod prey items. Nestling diet was monitored when nestlings were 9.6 days old (range: 6-12). Prey was identified to order level or lower taxonomic level. On average, 9% of all prey remained unidentified, excluding feedings where identification was impossible due to e.g. very rapid feeding or adverse light conditions. Parents always resumed feeding their young quickly after placing the camera, within 15 min.

Provisioning rates were determined from the footage of 13 nests, including two nests filmed exclusively to determine provisioning frequency. The total number of hourly feedings per nest was divided by the number of nestlings to calculate the number of feedings per young.

To test for nestling body mass variation among sites, we computed residual body masses as the difference between the measured and expected body mass, the latter being obtained by fitting a third order cubic regression through all data. A cubic model was used because it provided the best fit, measured as the highest r^2 -value.

Statistics

Differences between sites in proportion of unpaired males, nest success and nestling diet were tested using Pearson's Chi-squared tests. To test for differences in provisioning frequency between sites we used Mann-Whitney U tests. To investigate if provisioning frequency depends on age, we calculated the Pearson correlation coefficient. We tested for possible differences in (residual) body weight of nestlings between the four sites using a one-way ANOVA, after testing and confirming that data were normally distributed by a Kolmogorov-Smirnov test of normality.

RESULTS

Territories

We counted 91 territories of which 31 were occupied by unpaired males (34%) and the remaining 60 by breeding pairs (66%; Table 1). The annual number of breeding pairs was stable during the years, but populations were small (<10 breeding pairs). The proportion of unpaired males did not differ between sites ($\chi^2_3 =$ 5.90, *P* = 0.12). Territories clustered together, covering less than half of the apparently suitable area. Nearestneighbour distances (all sites together) were 38–865 m



Different beetles and their dry-mass fed to nestlings, starting upperleft clockwise: a soldier beetle of 17 mg (*Cantharidae* sp.), two Garden Chafers *Phyllopertha horticola* of 15 mg, a Dune Chafer *Anomala dubia* of 65 mg) and four click beetles *Denticollis linearis* of each 6 mg.

(mean 162 \pm 117 m, \pm SD, n = 91). Unpaired males excluded, distances varied between 60 and 865 m (mean 213 \pm 169 m, n = 72).

Clutch size, hatching and nest success

First eggs were produced between 1 May (2020) and 19 June (2022), peaking in the pentad 16–20 May (Figure 2) and almost 80% of the clutches were produced before the end of May (n = 47 clutches). Known replacement clutches were started on 2, 9 and



Figure 2. The number of nests started per pentad and the contribution of each pentad to the total number of clutches produced.

Table 1. Frequencies of successful and failed breeding pairs, unmated (single) males and success per breeding pair and per territory (which includes the unmated males).

| Area | Year | Success | Failed | Single males | % pairs success | % territory success |
|--------|------|---------|--------|-----------------|-----------------|---------------------|
| FV | 2020 | 11 | 0 | 8 | 100 | 58 |
| | 2021 | 5 | 3 | 6 | 63 | 36 |
| | 2022 | 7 | 1 | 8 | 88 | 44 |
| | Sum | 23 | 4 | 22 | 85 | 47 |
| WV | 2020 | 4 | 3 | 0 | 57 | 57 |
| | 2021 | 2 | 1 | 3 | 67 | 33 |
| | 2022 | 5 | 0 | 1 | 100 | 83 |
| | Sum | 11 | 4 | 4 | 73 | 58 |
| OL | 2022 | 5 | 1 | 2 | 83 | 63 |
| TS | 2020 | 2 | 2 | 0 | 50 | 50 |
| | 2021 | 2 | 3 | 0 | 40 | 40 |
| | 2022 | 2 | 1 | 3 | 67 | 33 |
| | Sum | 6 | 6 | 3 | 50 | 40 |
| Totals | | 45 | 15 | 31 | 75 | 49 |

17 June, but probably most clutches started after the end of May are replacement clutches.

Average clutch size was 6.0 (n = 25 clutches, 4×5 , 17×6 and 4×7 eggs) and for the separate years 5.8 (n = 8), 6.0 (n = 9) and 6.3 (n = 8), respectively. Across the years, nest success was 68% (49/72 nests successful). Mayfield daily survival rate was 0.974 per day (95% CI: 0.963-0.986) and 0.45 for the complete nest period (739.5 nesting days, 19 failed broods). Of all pairs breeding in a year, 75% raised fledglings, replacement clutches included (Table 1) and success per breeding pair did not differ between sites (χ^2_3 = 5.5, P = 0.14). This led to 5.6 fledglings per successful brood (2×3 , 4×4 , 7×5 , 19×6 and 5×7 fledglings), 3.9 fledglings per pair and 2.7 fledglings per territory (single males included). The two nests with three fledglings lost nestlings, which were found dead close to the nests. Nests failed due to predation by unknown animals (a nest was considered depredated if eggs or young were missing when they should have been in the nest) and a nest in OL was destroyed by cattle.

Nestling diet, provisioning frequency and body mass of young

Arthropod species from 12 orders were fed to nestlings (excluding the tail of a Viviparous Lizard *Zootoca vivipara* at WV), mostly imagoes of Coleoptera and larval Lepidoptera (caterpillars) with variation between sites (together 68–76% of prey number). Five other arthropod orders also constituted more than 5% of the diet (Figure 3, Table S1). Nestling diet in FV was less dominated by Coleoptera, whereas more Aranea, Odonata



Figure 3. Diet of nestling Whinchats averaged per site. Only prey families are shown which comprise >5% of the total number of prey fed to nestlings in any site. Miscellaneous: sum of all prey species that per order did not comprise >5% of the diet. The number of prey and site name are shown below each bar. See Table S1 for a detailed overview of the nestling diets.

and caterpillars were provided, and differed from WV ($\chi^2_8 = 20.34$, P = 0.0091). Whinchats in WV and TS provided their young with a similar diet, based on taxonomic orders ($\chi^2_8 = 8.91$, P = 0.35; Figure 3). Prey species differed between sites, depending on habitat and date (Table S1): the beetle *Phyllopertha horticola* (Garden Chafer) peaked in the first half of June and disappeared from mid-June onwards, when other prey were fed to the nestlings, such as click beetles *Denticollis linearis* in FV and WV. In TS *Geotrupidae* beetles and the scarabid beetle *Anomala dubia* (Dune Chafer) were preyed upon, besides caterpillars and the Meadow Plant Bug *Leptopterna dolabrata*. See Table S1 for a detailed overview of the diets per nest.

Median provisioning frequency per young per hour was 5.8 (range:4.0–10.1). Nestlings in WV obtained more feedings (8.1, n = 6 nests) than in TS (5.1, n = 6 nests; U = 1.5, P = 0.011) and nestlings in FV received food with an intermediate frequency (6.3 times per hour). Across all nests and of all 2655 recorded feedings, males provided 50.2% of the feeds and females 49.8% (respectively 1332 and 1323 feeds). Provisioning frequency appeared to increase somewhat with increasing age, but this relation was not significant (r = 0.40, P = 0.17).

Body mass of nestlings did not differ between sites (all nestlings: $F_{3,269} = 2.33$, P = 0.075, n = 273; older nestlings with wing length ≥ 35 mm: $F_{3,154} = 1.98$, P = 0.12, n = 158).

DISCUSSION

From 1998–2000 to 2013–2015, the number of atlas squares (5×5 km) with breeding Whinchats halved in The Netherlands (Sovon 2018). Since 2015 the national trend is unclear, but it seems that the breeding parameters collected in our study are those of a stable population at best.

Reproductive success

Clutch size (6.0 eggs) was in line with other contemporary data (Border *et al.* 2017, Frankiewicz 2008, Müller *et al.* 2005, Shitikov *et al.* 2015), as well as with data collected over 50 years ago in The Netherlands (Koning 2019, Spaans 2021) and in lowland Germany 60–80 years ago (Groebbels 1950, Schmidt & Hantge 1954, Horstkotte 1962). The number of fledglings in successful nests (5.6) was only slightly lower than the clutch size, showing that both egg and chick mortality were low. The nest success of 68% was high compared to the many other studies on Whinchats (Table 2) as were daily survival rates (Table 3). Over a breeding season, 75% of breeding pairs raised at least one young (mostly one brood) successfully, leading to an average productivity of 3.9 fledglings per breeding pair.

Clustered breeding

Breeding Whinchats appeared to congregate (see also Schmidt & Hantge 1954, Parker 1990, Bastian & Bastian 1996), which may be a result of newcomers settling in the vicinity of established males (Schmidt & Hantge 1954, Parker 1990). Other passerines also occur in small clusters of exclusive territories (Stamps 1988, Fletcher & Miller 2006), with neither breeding

 Table 2. Nest success of Whinchats in our and other studies (all as percentage successful nests of all nests found).

| Nest success | Sample size | Country | Year | Source |
|-----------------|----------------|---------|---------|--------------------------|
| 23–35 | _ | UK | 1964–73 | Fuller & Glue 1977 |
| 44 | 57/129 | DE | 1949–52 | Schmidt & Hantge 1954 |
| 46 | 16/35 | UK | 2013-14 | Border et al. 2018 |
| 51 | - | DE | 2015-17 | Evers et al. 2017 |
| 51 | 88/172 | CH | 1980s | Labhardt 1988a |
| 54 | 46/85 | DE | 1972–76 | Bezzel & Stiel 1977 |
| 63 | 49/78 | DE | 1990–94 | Feulner 1995 |
| 63 | 165/253 | RU | 2002-13 | Shitikov et al. 2015 |
| 63 | - | UK | 1966–68 | Gray 1974 |
| 67 | 62/94 | AT | 2008-17 | Uhl 2017 |
| 68 | 49/72 | NL | 2020-22 | current study |
| 68 | 28/41 | CZ | 1996–97 | Pudil 2001 |
| 69 | 74/107 | SLO | 2002–06 | Tome <i>et al</i> . 2020 |
| 75 | 61/81 | AT | 1978–85 | Parker 1990 |
| 76 | 89/117 | PL | 2003-07 | Frankiewicz 2008 |
| 80 | - | CH | 2013 | Brunner et al. 2015 |

Table 3. Nest success measured as daily survival rate and total nest success, as calculated with the nesting period (sum of number of laying days, incubation days and nestling days).

| daily survival rate | total nest success | nesting period (d) | Source |
|---------------------------|--------------------------|-----------------------|--------------------------|
| 0.941 | 0.17 | 29 | Border et al. 2017 |
| 0.958 | 0.25 | 32.29 | Zonneveld 2019 |
| 0.965 | 0.35 | 29.5 | Pudil 2001 |
| 0.970 | 0.38 | 32 | Tome <i>et al</i> . 2020 |
| 0.974 | 0.44 | 31 | current study |

habitat nor food abundance playing a prominent role (Herremans 1993). Perhaps social aspects are important, such as the ease with which potential mates are encountered (Tarof & Ratcliffe 2004). Indeed, clustering may offer the advantage of making it easier to switch partners, if the first breeding attempt fails. This time-saving behaviour may be especially important for single-brooded birds such as Whinchats, which regularly switch partners between first and repeat clutches (Schmidt & Hantge 1954, Bezzel & Stiel 1975, Labhardt 1988a, Parker 1990). Advantages of clustered breeding on an individual level may be stronger in smaller and isolated populations. On a population level, it may result in unoccupied yet high quality areas.

No phenological advances

Many birds show advanced migration and laying phenology in reaction to rising spring temperatures (Crick *et al.* 1997, Crick & Sparks 1999, Jonzén *et al.* 2006, Newson *et al.* 2016, Schmaljohann & Both 2017, the latter also including exceptions). For reasons unknown to us and against the odds, dates of first eggs in our study are similar to those more than half a century ago along the Dutch coast: during 1960–1980 egg laying peaked 11–15 May (n = 172 broods; Koning 2019) and in the period 1947–1961 during 13–17 May along a different part of the coastline (n = 62; Spaans 2021, back-calculation on nestlings ringed per date; assumptions: ring age 9 days, clutch size 5 eggs, incubation 13 days).

Spring arrival times, although having advanced in southern Italy and in Fennoscandia (Jonzén *et al.* 2006), have not advanced in other studies: arrival has not advanced in western Poland since the 1970s (Tryjanowski *et al.* 2002), nor in the UK since the 1960s (Newson *et al.* 2016), in contrast to other longdistance migrants in both studies. Interestingly, Whinchats currently start their autumn migration later, so that their summer-stay is 8.5 days longer (Newson *et al.* 2016), which could increase the opportunity for rare second broods (e.g. Bastian & Bastian 1996).

Nestling diet and implications of increased provisioning frequency

Beetles and caterpillars were the most frequently fed prey to nestlings, albeit percentages varied between years and sites. Others found a variety of prey: beetles, spiders and bugs (Polish abandoned fields; Orłowski *et al.* 2017), caterpillars and butterflies (Polish meadows; Steinfatt 1937), hymenoptera and caterpillars (Czech Republic; Pudil & Exnerová 2015) and diptera, beetles and hymenoptera in alpine meadows



Figure 4. Provisioning frequency per young per hour for our sites and from literature (DE 1996: Bastian & Bastian 1996, CH 2002: Britschgi *et al.* 2006, CH 1981–83: Labhardt 1991, PL 1936: Steinfatt 1937).

(Labhardt 1988b, Britschgi *et al.* 2006). Whinchats appear to have a broad dietary niche and are able to adjust their foraging behaviour, selecting different prey in the course of the season to raise their young.

Beetles contain more indigestible chitin (8% of fresh mass) than caterpillars (3%). Within beetles, differences are also apparent. Garden Chafers of 15 mg contain 6% chitin, whereas click beetles of 6 mg contain 11%, almost twice as much (van Oosten & van den Berg unpubl. data). To provide the nestlings with enough nutrients while providing click beetles, parents fed young up to 10 times per hour, which is frequent as compared to the other nests and to other studies (Figure 4).

Frequent feeding may constrain reproductive outcome in several ways, such as increased energetic costs for adults and increased probability of nest predation. Short flights are energetically costly (e.g. Tatner & Bryant 1986, Nudds & Bryant 2000) and the more frequently nestlings are provided with food, the more energy a female invests in the current brood. As a result, female body mass is lowest during the nestling phase (Labhardt 1984, Flinks & Kolb 1997), and probably decreases in proportion to provisioning frequency (Smith & Roff 1980). After a failed breeding attempt, female body mass increases again until laying of the replacement clutch (Flinks & Kolb 1997), indicating that body reserves must be replenished between clutches (Jones & Ward 1976).

Parental birds may also modulate provisioning rate to avoid the attention of diurnal nest predators, as demonstrated experimentally by Fontaine & Martin (2006). In their study, provisioning frequency increased in the plots without predators compared to the control plots. We did not monitor predators in study plots and control plots without Whinchats, so we cannot confirm nor rule out that Whinchats select breeding areas with low densities of predators.

Nest predation and single broodedness

Single-broodedness could make populations sensitive to nest predation. To maintain stable breeding numbers, nest predation in Whinchats should be lower compared to multi-brooded species. It is of interest that the closely related and common European Stonechat is multi-brooded (Agatho 1961, Bijlsma 1978) and therefore has a greater annual reproductive potential. Stonechats often occur in the same sites as Whinchats and build similar nests on the ground. Annual adult survival is similar: 0.36-0.49 for Whinchats (Fay et al. 2020) and 0.36–0.47 for Stonechats (Gailly et al. 2020; both using Cormack-Jolly-Saber models to estimate survival) and first-year apparent survival may also be similar. Survival being equal, a population of Whinchats needs a higher nest success to persist than a population of Stonechats and, reversely, Stonechats can endure in areas with higher nest predation pressure than Whinchats. Perhaps contemporary populations of Whinchats can only persist in areas with relatively low nest predation pressure, compared to multi-brooded species.

Male-biased population sex ratio

Reproductive success of 75% and 3.9 fledglings per pair as found in our study, could be sufficient for a stable or increasing population of Whinchats (Bastian & Bastian 1996). However, taking into account the unpaired males, territory success sinks to 49% and the number of fledglings to 2.7 per territory, which might be insufficient to maintain a stable population (Bastian & Bastian 1996). Unpaired males are a well-known phenomenon in songbirds (Price 1936, Nice 1937, Mayr 1939, Stewart & Aldrich 1951), and have also been observed in Whinchats, but their occurrence varies (Table 4). The sex ratio may be male-biased in small populations (Dale 2001, Woolfenden et al. 2001) and the proportion of males may increase with decreasing populations size (Morrison et al. 2016), but explanations for this are various (Donald 2007). One possibility is that nestling sex ratio is male-biased, as found in Northern Wheatears (van Oosten & Schekkerman 2021); alternatively, maternal care may lead to higher mortality if predation rate is higher in incubating females (Bastian & Bastian 1996), or if maternal care is more energetically costly (Donald 2007). However, the available evidence does not conclusively show that survival of female Whinchats is lower than that of males (Blackburn & Cresswell 2016, Fay et al. 2020). Although Fay et al. (2020) calculated a lower apparent survival for females, they suggest that this could be explained by a greater tendency for dispersal in females and in fact the sexes may have similar survival rates. The absence of populations with more equal or even female-biased sex ratios may be a result of low detectability of unpaired females. Whinchats may indeed show strong natal dispersion, based on low return rates to study areas (Schmidt & Hantge 1954, Shitikov et al. 2012, 2015). Evidence is as erratic as it is impressive: one nestling ringed on 23 July 1930 in Germany was found breeding in France the next year, 1051 kilometres away (Bastian 1992)! It is noteworthy that sex ratio in a wintering population near Jos, Nigeria is not male-biased (408 sexed Whinchats in 2011-2014, 207 males, 201 females, data collected and kindly provided by E. Blackburn, A. Risely and W. Cresswell).

To conclude, it remains unclear which factors currently limit the remaining Dutch populations. Neither habitat availability nor breeding success appears to be limiting. It seems worthwhile to focus further work on the causes of the male-biased sex ratio in the breeding populations.

| Table 4. Average proportion of unpaired males in our four stud | dy |
|--|----|
| sites and comparison with published estimates from other pop | u- |
| lations. | |

| % Unpaired | Country | Source |
|------------|---------|---------------------|
| 2.0 | DE | Fischer et al. 2013 |
| 5 | DE | Schmidt & Hantge |
| 1954 | | |
| 8.7 | CH | Brunner et al. 2015 |
| 10 | CH | Müller et al. 2005 |
| 12.1 | DE | Bezzel & Stiel 1975 |
| 16.7 | DE | Luick et al. 2004 |
| 22.7–28.4 | DE | Evers et al. 2017 |
| 23 | NL | Oosterveld 1999 |
| 25.0 | DE | Feulner 2016 |
| 34 | NL | current study |
| 37.6 | PL | Orłowski 2004 |
| 37.0 | PL | Frankiewicz 2008 |
| 43 | DE | Ranftl et al. 1988 |
| | | |

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SAMENVATTING

Het Paapje Saxicola rubetra is een karakteristieke zangvogel van extensief gebruikte, weinig gemaaide wei- en hooilanden. Door deze voorkeur is de soort sterk achteruitgegaan in Nederland en elders in West-Europa. Hoewel het Paapje in de schijnwerper staat van onderzoekers in Europa, heeft er maar weinig onderzoek naar zijn broedbiologie plaatsgevonden buiten het agrarisch gebied. In Nederland broeden Paapjes met name nog in natuurgebieden, in de provincie Drenthe, waar de populaties vaak kleiner zijn dan 10 broedparen. In vier van deze populaties hebben we de broedbiologie bestudeerd om vast te stellen welke eigenschappen de soort in de problemen brengt. Paapjes bleken geclusterd in de onderzochte terreinen voor te komen, waardoor geschikte terreindelen onbezet bleven. Legselgrootte, nest- en paarsucces waren hetzelfde of hoger dan in andere studies van recente datum en van langer geleden. De meeste legsels werden tussen 16 en 20 mei gestart, wat nagenoeg hetzelfde tijdstip is als meer dan een halve eeuw geleden. In tegenstelling tot veel andere zangvogels hebben Paapjes hun legdatum dus niet vervroegd in deze opwarmende wereld. In hoeverre hun datumvastheid een evolutionair voordeel biedt weten we niet; we weten wel dat het paarsucces hoog is en er veel jongen uitvliegen. Paapjes voeren in Drenthe vooral kevers en rupsen, waarbinnen de soortensamenstelling veranderde in de loop van het seizoen. Aan de randen van het Wapserveld werden Rozenkevers Phyllopertha horticola (15 mg, 6% chitine) begin juni gevoerd, maar half juni werden Smalle Kniptorren Denticollis linearis (6 mg, 11% chitine) gevoerd: laatstgenoemde kever wordt veel vaker aangevoerd dan Rozenkevers, met als tweeledig verwacht effect dat dagactieve predatoren een nest eerder zullen vinden en dat vrouwtjes meer energie besteden aan het broedsel, waardoor de kans op een vervolglegsel kleiner wordt. Het is dus zaak om in dit terrein begin juni jongen in het nest te hebben. Nestsucces is bij Paapjes van groot belang, omdat ze maar één nest per jaar maken. Hierdoor zal een populatie eerder afnemen bij een toenemende mate van nestpredatie vergeleken met soorten die meerdere nesten per jaar maken, maar met dezelfde jaarlijkse overleving - zoals de Roodborsttapuit Saxicola rubicola. Ten slotte bleek 34% van de mannetjes ongepaard te zijn om vooralsnog onbekende redenen. De oorzaak kan liggen in grotere dispersieneigingen of grotere sterfte van vrouwtjes, of bijvoorbeeld door de door mannen gedomineerde seksratio onder nestjongen.

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Table S1. Composition of nestling diets of Whinchats per nest and per date. The number per prey type is the percentage of each prey-type in the diet. One nest was filmed for two consecutive days in site WV, which is indicated by an asterisk.

| Sita | | | EV | EV | ΕW | INTA | W/1/* | 10/1/× | 1A/A7 | ot L | υĽ | Ъ | L | L F |
|----------------------|----------------|--------------------------|------------|----------|----------|--------|------------|------------|------------|-------------|-----------|-----------|---------|------|
| | | | > С ц \ | л с | л ц С | ^ ^ ^ | | | > ~ ~ | 0.1 1 | | 01 | CI OF | |
| # prey # feedings | | | 61 1 | 87 20 | 190 | 181 | 340 200 | 498 253 | 307 307 | 334 945 | 129 78 | 197 | 48 | |
| age nestlings | | | 10 | c/ 1 | 9,4 | 0 | 10 | 11 | 100 | 2 2 1 | 5 | 11 | 0 | |
| # nestlings | | | 9 | ν | 9 | | 9 | 9 | Ω | 9 | ν Ω | Ω | 6 | |
| Film date | | | 8/6/21 | 14/6/21 | 24/6/21 | 2/6/22 | 15/6/20 | 16/6/20 | 16/6/20 | 1/6/20 | 1/6/22 | 14/6/21 2 | 24/6/21 | 28/6 |
| Order | Family | Species | % | % | % | % | % | % | % | % | % | % | % | |
| Aranea | | | 14.7 | 6.1 | 7.5 | 4.7 | 2.9 | 3.0 | 1.5 | 0.3 | 15.5 | 1.1 | 0.0 | |
| Isopoda | | | 0.0 | 0.0 | 3.0 | 9.3 | 3.5 | 2.6 | 5.0 | 0.0 | 1.6 | 4.0 | 0.0 | |
| Diplopoda | | | 0.0 | 2.0 | 0.0 | 0.8 | 0.3 | 0.0 | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 | |
| Odonata | | | 0.0 | 6.1 | 8.6 | 6.2 | 2.1 | 2.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| | Coenagrionidae | | 0.0 | 2.0 | 6.0 | 2.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| | | Pyrrhosoma nymphula | 0.0 | 0.0 | 0.0 | 1.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| | Corduliidae | Cordulia aenea | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| | Lestidae | | 0.0 | 0.0 | 0.4 | 0.0 | 0.6 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| | Libellulidae | | 0.0 | 3.1 | 0.4 | 3.1 | 0.9 | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | - |
| | | Libellula quadrimaculata | 0.0 | 0.0 | 0.0 | 2.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | - |
| Orthoptera | | | 0.0 | 4.1 | 1.9 | 0.0 | 2.6 | 0.6 | 0.6 | 1.2 | 0.8 | 0.0 | 0.0 | |
| | Acrididae | | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 0.0 | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 | - |
| Heteroptera | | | 0.0 | 0.0 | 0.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 | 0.0 | õ |
| | Miriidae | Leptopterna dolabrata | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | õ |
| Coleoptera | | | 8.8 | 60.2 | 27.2 | 89.1 | 55.6 | 62.2 | 55.1 | 73.1 | 29.5 | 83.3 | 68.8 | 1 |
| | Carabidae | | 0.0 | 0.0 | 0.0 | 0.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| | Cantharidae | | 4.4 | 18.4 | 0.7 | 5.4 | 0.3 | 0.4 | 0.6 | 15.0 | 2.3 | 4.6 | 2.1 | - |
| | Cerambycidae | | 0.0 | 2.0 | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.9 | 1.6 | 0.0 | 0.0 | - |
| | Chrysomelidae | | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.9 | 0.0 | 0.0 | 0.0 | - |
| | Coccinellidae | | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | - |
| | Curculionidae | | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.4 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | |
| | Elateridae | Denticollis linearis | 0.0 | 0.0 | 14.9 | 3.9 | 45.0 | 49.8 | 37.7 | 0.0 | 0.0 | 0.0 | 4.2 | |
| | | sp. | 0.0 | 0.0 | 0.4 | 3.1 | 0.0 | 4.4 | 0.7 | 5.7 | 1.6 | 0.0 | 0.0 | |
| | Geotrupidae | | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 35.4 | |
| | Scarabeidae | Phyllopertha/Anomala | 0.0 | 0.0 | 0.0 | 0.0 | 2.4 | 2.2 | 0.7 | 0.0 | 0.0 | 3.4 | 0.0 | |
| | | Phyllopertha horticola | 0.0 | 9.2 | 3.0 | 67.4 | 2.4 | 0.0 | 1.7 | 42.8 | 19.4 | 71.3 | 0.0 | |
| | | Anomala dubia | 0.0 | 0.0 | 0.4 | 0.0 | 0.6 | 0.8 | 9.3 | 0.0 | 0.0 | 0.6 | 8.3 | |
| | | Melolontha melolontha | 0.0 | 0.0 | 0.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |

Table S1. Continued.

| Site | | | FV | FV | FV | MV | WV* | WV* | M | TS | ST | TS | TS | TS |
|----------------------|----------------|------------------------------|----------|----------|---------|------------|---------|------------|---------|------------|--------|---------|----------------------|---------|
| | | | 60 | 00 | 096 | 000 | 01.0 | 007 | | 100 | 120 | 174 | 10 | 1 50 |
| # prey # feedings | | | 00 19 | 07 05 | 190 | 722 181 | 040 | 470 253 | 307 | 745 745 | 78 | 177 | 0 1 44 | 119 |
| age nestlings | | | 10 | 12 | 9 | 6 | 10 | 11 | 10 | 11 | 2 | 11 | 6 | 6 |
| # nestlings | | | 9 | 5 | 9 | 7 | 9 | 9 | 5 | 9 | S | S | 9 | 4 |
| Film date | | | 8/6/21 | 14/6/21 | 24/6/21 | 2/6/22 | 15/6/20 | 16/6/20 | 16/6/20 | 1/6/20 | 1/6/22 | 14/6/21 | 24/6/21 | 28/6/22 |
| Order | Family | Species | % | % | % | % | % | % | % | % | % | % | % | % |
| | Silphidae | | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | Staphylinidae | Staphylinus olens | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 0.8 | 0.6 | 0.0 | 0.0 |
| Hymenoptera | | | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 0.0 | 0.6 | 0.3 | 0.0 | 0.6 | 0.0 | 1.6 |
| | Apidae imago | Antophila sp. | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | Formicidae | | 0.0 | 0.0 | 0.0 | 1.6 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | Tenthredinidae | | 0.0 | 0.0 | 0.0 | 1.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Lepidoptera | | | 69.1 | 13.3 | 36.6 | 30.2 | 13.8 | 13.9 | 27.2 | 3.9 | 31.8 | 1.7 | 22.9 | 37.2 |
| | Erebidae im. | Spilosoma lubricipeda | 0.0 | 3.1 | 0.0 | 0.0 | 0.9 | 0.6 | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | Geometridae | | 1.5 | 6.1 | 5.2 | 1.6 | 0.6 | 0.4 | 3.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | Noctuidae | imago | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| | | caterpillar | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.7 | 0.0 | 0.0 | 0.0 | 2.1 | 0.8 |
| | Nymphalidae | | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 3.9 | 0.0 | 14.6 | 17.8 |
| | | Inachis io caterpillar | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.8 | 0.0 | 14.6 | 14.0 |
| | | Aglais urtica caterpillar | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.1 | 0.0 | 0 | 1.6 |
| | Saturniidae | Saturnia pavonia caterpillar | r 0.0 | 0.0 | 4.5 | 0.0 | 3.5 | 2.0 | 2.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 'brown moth' | | 57.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Diptera | | | 5.9 | 5.1 | 3.7 | 11.6 | 4.4 | 6.2 | 2.8 | 6.9 | 10.1 | 4.0 | 8.3 | 7.8 |
| | Asilidae | | 0.0 | 1.0 | 0.0 | 0.8 | 1.5 | 0.6 | 0.7 | 0.3 | 2.3 | 0.0 | 2.1 | 1.6 |
| | Rhagionidae | | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 0.2 | 0.4 | 5.7 | 3.9 | 1.7 | 0.0 | 0.8 |
| | Syrphidae | | 0.0 | 0.0 | 0.0 | 0.8 | 0.3 | 0.2 | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 | 2.3 |
| | Tabanidae | | 1.5 | 2.0 | 1.5 | 6.2 | 0.0 | 3.2 | 0.7 | 0.0 | 0.8 | 0.0 | 0.0 | 1.6 |
| | Tipulidae | | 4.4 | 0.0 | 0.4 | 0.0 | 0.0 | 0.4 | 0.0 | 0.3 | 2.3 | 0.6 | 6.3 | 0.0 |
| Neuroptera | Myrmeleonidae | | 0.0 | 0.0 | 0.4 | 0.0 | 0.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Crassiclitellata | ۱ Lumbricidae | | 0.0 | 0.0 | 0.0 | 0.0 | 0.9 | 0.2 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Gastropoda | | | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.8 |
| Vertebrata | Lacertidae | Zootaca vivipara | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| larva sp. | | | 0.0 | 0.0 | 0.0 | 3.9 | 0.3 | 0.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.6 |
| unidentified p | rey | | 1.5 | 3.1 | 10.4 | 19.4 | 12.6 | 8.2 | 6.8 | 14.1 | 10.9 | 5.2 | 0.0 | 14.0 |