

Comparative breeding biology of three insectivorous songbirds in Dutch dune grasslands

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Scholars agree that changes in vegetation have been influencing population sizes of ground-foraging songbirds in Dutch dune grasslands. Due to a lack of knowledge concerning the breeding biology of these species, the mechanisms linking vegetation change and population development remain unclear. Here, I describe the breeding biology of three co-occurring insectivores in Dutch dune grasslands: Meadow Pipit *Anthus pratensis*, European Stonechat *Saxicola torquatus* and Northern Wheatear *Oenanthe oenanthe*. The nestling diet of Meadow Pipits contained many dipterans, such as crane flies (Tipulidae), but almost no beetles and relatively few noctuid caterpillars, whereas beetles and noctuid larvae were important in the diets of both European Stonechat and Northern Wheatear nestlings. Mean brood size was smallest in Meadow Pipit and equal in European Stonechat and Northern Wheatear. Nest depredation was similarly high in the open-nesting Meadow Pipit and European Stonechat, resulting in lower nest success compared to Northern Wheatear, a cavity-breeder. Provisioning rate per nestling was highest in Northern Wheatear, the largest species, with no observed differences between Meadow Pipit and European Stonechat, which resulted in higher per brood provisioning rates for European Stonechat. Since the mean brood size of European Stonechat is larger than that of Meadow Pipit, and since nest depredation generally increases with provisioning rates, one would expect a higher depredation rate in European Stonechat. This suggests that differences in nest site selection between Meadow Pipit and European Stonechat result in relatively lower nest depredation rates in European Stonechat and similar nest success to Meadow Pipit. I suggest that future work should focus on how different vegetation types relate to prey abundance, foraging habitat and vegetation-specific nest depredation, in order to better understand the putative relationships between population growth and vegetation in coastal dune grasslands.

Key words: Meadow Pipit, European Stonechat, Northern Wheatear, diet, clutch size, nest predation, feeding frequency, provisioning frequency, nest success

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Since the end of the 1980s the appearance of Dutch dune grasslands changed due to the encroachment of shrubs and tall nitrophilic grasses such as *Calamagrostis epigejos* and *Carex arenaria* (Ten Harkel & van der Meulen 1995, Veer & Kooijman 1997, Kooijman *et al.* 1998). Encroachment is believed to be a result of excess nitrogen deposition and acidification from agricultural and industrial sources (Veer & Kooijman 1997, Bobbink *et al.* 2010). Furthermore, due to the strong decline of

Rabbit *Oryctolagus caniculus* populations, as a result of viral diseases, the vegetation height increased (Drees & van Manen 2005, Drees *et al.* 2006).

The increased coverage by tall grasses could influence populations of insectivorous songbirds in several ways. Firstly, it affects the (herbivorous) arthropod diversity as a result of declining herb species diversity (Siemann 1998, Koricheva *et al.* 2000, Haddad *et al.* 2001, Otway *et al.* 2005, Schaffers *et al.* 2008). Loss of

herb diversity may therefore lead to dietary constraints for insectivores (Vickery *et al.* 2001, Britschgi *et al.* 2006, Schekkerman & Beintema 2007).

Secondly, although highest prey densities are found in taller vegetation (Morris 2000, Dennis *et al.* 2008, van Oosten *et al.* 2014a), ground-foraging birds prefer short vegetation since tall vegetation is less accessible (Atkinson *et al.* 2004, van Oosten *et al.* 2014a). Increased vegetation height may therefore be detrimental for the feeding success of ground-foraging insectivores.

Lastly, increased vegetation height may also lead to increased depredation rates of nests (Pärt 2001, Low *et al.* 2010, but see Tye 1992) and predation of adult birds (Whittingham & Evans 2004). Mice and voles prefer cover (Pärt 2001, Low *et al.* 2010); their mammalian predators, such as Weasels *Mustela nivalis* and Stoats *M. erminea*, once attracted to this habitat also depredate bird nests as a consequence. This increased rate of predation was shown to lead to a lower nest success of Swedish Northern Wheatears *Oenanthe oenanthe* breeding in tall vegetation compared to those breeding in short vegetation (Pärt 2001, Low *et al.* 2010). Thus, the changes in vegetation composition and structure, caused by deposition of excess nitrogen and cessation of Rabbit grazing, are likely to influence diversity and abundance of ground-foraging and ground-nesting insectivores.

In The Netherlands, the increase of some ground-foraging insectivorous songbirds and the decrease of others in coastal dune grasslands have been attributed to the changes in vegetation structure. The European Stonechat *Saxicola torquatus* for example, strongly increased as a breeding bird and is thought to have profited from the increase in shrubs (Veenstra & Geelhoed 1997, Hustings & Vergeer 2002) since the late 1980s or early 1990s (van der Meer 1996). Meadow Pipits *Anthus pratensis* are also thought to have increased because of grass encroachment in the coastal dunes (Geelhoed *et al.* 1998, Scharringa *et al.* 2010), although longer term trends indicate the species is stable in dune grasslands (Hustings & Vergeer 2002). Other ground-foraging songbirds, such as Northern Wheatears, strongly declined and became rare and local breeding birds (Boele *et al.* 2013), probably due to grass encroachment which rendered the preferred short-grown grasslands unsuitable for foraging (Verstrael & van Dijk 1997, van Oosten 2014a). Finally, some songbirds went locally extinct in the mainland coastal dunes, such as Skylark *Alauda arvensis* (van Reisen 2011) and Whinchat *Saxicola rubetra* (Scharringa *et al.* 2010).

Changes in vegetation as outlined above may indeed be partly responsible for the changes in population size of the songbirds mentioned. However, information on the breeding biology (e.g. nest predation, nestling diet and clutch size) of these songbirds is lacking for the coastal dune grasslands. This is unfortunate, because this information may increase our understanding of the exact nature of the putative link between vegetation changes and changes in songbird populations. To provide this information for some of the songbirds mentioned, I describe here the breeding biology of three co-occurring insectivores in Dutch dune grasslands with different population trends: the Meadow Pipit, the European Stonechat and the Northern Wheatear.

METHODS

Study sites

Meadow Pipit and Eurasian Stonechat data were collected between 7 April and 27 July 2015, in two study sites 25 km apart: part of the Noord-Hollands Duinreservaat (NHD; 52°33'N, 4°36'E) and part of the Amsterdamse Waterleidingduinen (AWD; 52°20'N, 4°30'E). Northern Wheatear data have been collected in the NHD since 2007. Northern Wheatear has not bred in the AWD since the late 1990s or early 2000s.

Both study sites measured approximately 136 ha and consist of hilly, lime-rich, open dune grasslands with scattered sandy blow-outs. The vegetation is dominated by graminoids, such as Wood Small-reed *Calamagrostis epigejos* and Sand Sedge *Carex arenaria*, herbs such as Dune Pansy *Viola curtisii*, mosses, lichens and shrubs, particularly Creeping Willow *Salix repens* and Common Sea-buckthorn *Hippophae rhamnoides*. Rabbits were common in both sites, in roughly equal densities based on droppings (AWD: 19 ± 9.2 and NHD: 20 ± 6.9 droppings per plot (\pm SD), Mann-Whitney *U* test, $U = 250$, $P = 0.23$, $n = 25$ randomly chosen circular plots of 26 cm diameter). Exotic Fallow Deer *Dama dama* are abundant grazers in the AWD but are absent in the NHD, where low-density winter grazing by cattle and horses is used as a nature management tool.

Study species

MEADOW PIPIT

Meadow Pipits (adult body mass c. 18 g) are ground-foraging insectivores which breed at temperate and boreal latitudes from Greenland to Western Siberia. They lay 4–6 eggs, 2–3 times annually in open nests

built on the ground. In Western Europe they nest predominantly between mid-April and July (Glutz von Blotzheim & Bauer 1985). They forage by walking on the ground and picking prey off the ground and vegetation (in Dutch coastal dunes, van Oosten unpubl. data). Dutch breeding birds are migrants, moving south as far as Morocco (Speek & Speek 1984). The breeding population in the Dutch coastal dunes is stable with fluctuations (Hustings & Vergeer 2002).

EUROPEAN STONECHAT

European Stonechats (c. 15 g) are also ground-foraging insectivores. They breed in temperate regions throughout Eurasia (Collar 2005). They lay 3–6 eggs per nest, 2–4 times a year in open nests built on or near the ground. Nesting in Western Europe is predominantly between mid-April and July (Glutz von Blotzheim & Bauer 1988). The Dutch breeding population is migratory and spends the winter mostly in southern Europe and in Africa, north of the Sahara desert while some may cross the Sahara (Speek & Speek 1984, Helm *et al.* 2006). The coastal breeding population in The Netherlands increased considerably since the late 1980s (Hustings & Vergeer 2002). The European Stonechat and Northern Wheatear both belong to the subfamily Saxicolinae.

NORTHERN WHEATEAR

Northern Wheatears (c. 25 g) breed from eastern Canada across Eurasia to western Alaska. They forage mostly on the ground in Dutch coastal dunes (own unpubl. data), where they build nests in abandoned Rabbit burrows and lay 4–7 eggs (NHD, own unpubl. data). Nesting in the NHD is between mid-April and mid-July. Over 95% of all adults and nestlings are individually colour-ringed each year, enabling a detailed overview of how many clutches individual females produce per year. Between 0 and 54% of female Northern Wheatears (>95% individually recognizable by colour-rings) produce a true second brood and 0 to 57% produce a repeat brood after failure of the first brood in the NHD (2007–2014, own unpubl. data). Most birds winter in the Sahel (Bairlein *et al.* 2012, van Oosten *et al.* 2014b, Schmaljohann *et al.* 2015). The Dutch breeding population strongly declined since the late 1980s–early 1990s (Hustings & Vergeer 2002, Boele *et al.* 2013).

Nest searching and nest characteristics

Nest sites were found by following parents carrying nesting material, by following females during an apparent incubation pause or by following parents

bringing food to their broods. Nests were monitored until they failed or until the young fledged. The vegetation in which the nest was built was noted for the two open-nesting species, Meadow Pipit and European Stonechat, and categorized in one out of four different types: (1) grasses (mainly Wood Small-reed, Common Marram *Ammophila arenaria*, Sand Sedge), (2) the shrub Creeping Willow (often to some extent mixed with grasses and *Rubus caesius*), (3) the scrub-like herb Dewberry *Rubus caesius*, and (4) the shrub Common Sea-buckthorn (with Wood Small-reed or Sand Sedge in the undergrowth). Vegetation surrounding the entrance of Northern Wheatear breeding burrows was not recorded in detail during the years 2007–2015, but most of them were located in Rabbit burrows in short (<5 cm sward height) dune grassland.

Clutch size, hatching and Mayfield nest success

During the 2015 breeding season, I determined clutch size and hatching rate of 60 nests of Meadow Pipit (NHD: 45, AWD: 15), 59 of European Stonechat (NHD: 40, AWD: 19) and 13 of Northern Wheatear (all NHD). Of these, 53 nests of Meadow Pipit (NHD: 41, AWD: 12), 53 of European Stonechat (NHD: 34 and AWD: 19) and 147 of Northern Wheatears (2007–2012) were used to calculate nest success.

Mayfield daily nest success (henceforth: daily nest success) was determined per species per study site, for nests with known fate (Mayfield 1975), with the 95% confidence interval (CI) calculated following Beintema (1992). Furthermore, Mayfield total nest success (henceforth: nest success) was calculated for the summed incubation-plus-nestling period, set to 27 days for all three species (Meadow Pipit: Halupka 1998, European Stonechat and Northern Wheatear: Cramp 1988). Data from 2007–2012 was used to calculate nest success of Northern Wheatear; data of 2013 onwards was not used because of nest-protection measures.

The total number of nest days (the number of days a nest is under observation, until nestlings fledged or the nest failed) used to calculate nest success was: Meadow Pipit, NHD: 268.5 and AWD: 57, European Stonechat, NHD: 357 and AWD: 111.5, and Northern Wheatear, NHD: 2440 nest days. Nests were scored as being depredated when eggs or nestlings should have been present, based on their age, but were absent. Premature fledging of nestlings was easily ascertained by incessant alarm calls from parental birds in the nest perimeter. In a few cases ($n = 3$) nests of Meadow Pipits were abandoned during the egg phase (recognized by the eggs being cold when they should be warm because of incubation).

Growth rates of nestlings

To obtain data on nestling growth rates, we aimed for measuring body mass and maximum wing length daily, and always by the same observer. Growth-curves were constructed for nestlings of known age. In passerines, the wing feathers normally continue to grow in times of dietary constraints (Nilsson & Svensson 1996, Nilsson & Gårdmark 2001), hence wing length is a good indicator of nestling age. With the assumptions that (1) all three species lay one egg per day, (2) start incubating on the day the last egg is laid and that (3) incubation takes 13 days (Glutz & Bauer 1985, 1988), the date of first egg was back-calculated for each nest with day 1 = hatching day.

Nestling diet

To determine nestling diets of Meadow Pipit and European Stonechat, feeding parents were filmed continuously at the nest if the vegetation surrounding the nest permitted placement of a handy-cam video camera on a small tripod. The camera (either a Sony HDR-CX11 or HDR-SR10E or Canon HF 100E) was placed under a plastic camouflage cover. All nests filmed were classified as 'early' (between mid-May and mid-June) or 'late' (between late-June and mid-July), analogous to a previous study on Northern Wheatears (van Oosten *et al.* 2015; based on mean laying date of first versus second and repeat clutches).

I filmed a total of 205 feeds at six early nests of Meadow Pipits and 219 feeds at four early nests of European Stonechats. Dietary data from eleven early nests (6039 feedings) of Northern Wheatears are from the years 2008–2010 and were also obtained in a similar fashion as mentioned above (reported in van Oosten *et al.* 2014a; the results of which are also shown here in order to facilitate comparison with the two other insectivores). Furthermore, using similar methods I filmed a total of 190 feeds at three late nests of European Stonechat, 951 feeds at seven late nests of Northern Wheatear (which are from the years 2008–2010 and were also obtained from video-recorded feeding parents) but no feeds of late Meadow Pipits.

Each nest was filmed continuously for one morning, starting on average 3 h and 50 min after sunrise (varying between 35 min and 5 h plus 35 min after sunrise, depending on the exact moment the nest was found and also depending on the weather conditions). A nest was filmed for 4 h and 40 min on average (SD: 2 h and 3 min). When parents had not resumed feeding their young after 45 min, the video-camera was removed. Meadow Pipits appeared much more sensitive

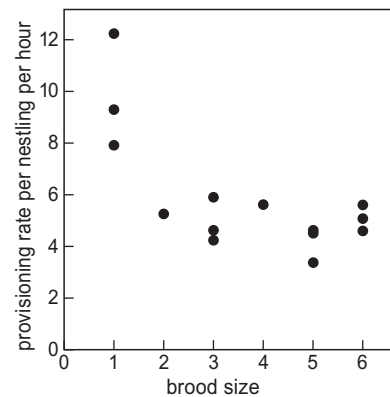


Figure 1. The average number of feeds per nestling per hour for the Northern Wheatear. Solitary nestlings obtain more feeds than nestlings from brood sizes of 2–6. Data from 19 nests during 2008–2010, 7.5 ± 0.7 observation hours per nest.

to the presence of the video-camera than European Stonechats, resulting in fewer filmed nests of Meadow Pipits (Table S1 and S2). Nestling diet was monitored when nestlings were 5–10 days old, when they were capable of handling chitinous prey. Prey was identified to species level if possible but mostly to genus or family. A large but varying fraction of prey remained unidentified, especially for Meadow Pipit (37%) but more prey were identified for European Stonechat and Northern Wheatear (both 6–15% unidentified prey).

Prey per feeding and provisioning rates

The number of prey per feed was determined from the same footage as was used to determine the nestling diet. Provisioning rates for Meadow Pipit and European Stonechat were determined from the diet footage and from 5 additional nests filmed solely to monitor provisioning frequency. Provisioning frequency of Northern Wheatears was determined by visual monitoring of 19 nests for 6 to 11 h per nest in 2008–2010. In addition to the data collected in 2015, I also added (unpublished) provisioning data from 4 nests of Meadow Pipit collected in 2009. This way, I determined feeding frequencies for 11 nests of Meadow Pipit, 13 of European Stonechat and 19 of Northern Wheatear. I did not use nests of Northern Wheatears with only one nestling in the analysis because single nestlings obtained more feeds per hour than nestlings in nests of 2–6 young (Figure 1), and because broods of both other species were never found to contain one nestling. Between 2007 and 2015, only 5 nests of Northern Wheatear were found with one nestling, out of a total of 157 nests with known brood size.

Statistics

Differences in nest location and in nestling diet were tested using Pearson's Chi-squared tests. I tested for differences in laying date, clutch size, the number of prey per feeding and the number of feedings per nestling per hour among the three species using ANOVAs with Tukey post-hoc tests (critical $P = 0.016$). All analyses were performed in SPSS 21.0 (IBM, USA).

RESULTS

Nest characteristics

Mean Julian laying dates up to mid-May differed between the three species ($F_2 = 80.76$, $P < 0.001$), with Meadow Pipit (117 ± 7 days (\pm SD), range 103–130) laying later in the year than European Stonechat (110 ± 7 days, range 102–123; $P < 0.01$), and Northern Wheatear (2007–2015; 129 ± 9 , range 108–145) laying later on average than both other species (both $P < 0.01$).

Nest locations of Meadow Pipit and European Stonechat differed with respect to the vegetation-types ($\chi^2_3 = 30.58$, $P < 0.0001$; Table 1), with Meadow Pipit mostly building nests in grassy vegetation and European Stonechat in scrubby vegetation (Figure 2). Northern Wheatears built their nests in abandoned Rabbit burrows, with the nest placed between 0.20 and 1.7 m from the entrance.

Clutch size, hatching and nest success

Average clutch-size differed among the three songbirds ($F_2 = 58.84$, $P < 0.0001$), with Meadow Pipit having smaller clutches than either European Stonechat ($P < 0.01$) or Northern Wheatear ($P < 0.01$; Table 2). European Stonechat and Northern Wheatear had clutches of similar size ($P = 0.18$; Table 2). The fraction of unhatched eggs in nests where at least one egg hatched did not differ between Meadow Pipit and European Stonechat (Mann-Whitney U test, $U = 1490$, $P = 0.77$), whereas hatching rate was lower for Northern Wheatear than for both other species combined (Table 2; $U = 6799$, $P = 0.022$). Daily nest success for Meadow Pipit and European Stonechat was higher in the NHD than in the AWD and daily nest success of Northern Wheatears was higher than for

Table 1. Vegetation in which nests of Meadow Pipits ($n = 50$) and European Stonechats ($n = 54$) were built. The table shows the fraction of nests built in each vegetation type by each bird species. European Stonechat selects more scrubby vegetation than Meadow Pipits. Northern Wheatears nested in Rabbit burrows.

	grasses	<i>Salix repens</i>	<i>Rubus caesius</i>	<i>Hippophae rhamnoides</i>
Meadow Pipit	0.54	0.40	0.04	0.02
European Stonechat	0.07	0.59	0.17	0.17



Figure 2. Typical nest locations of (A) Meadow Pipit (AWD, 23 July 2015) and (B) European Stonechat (NHD, 14 July 2015), in the study sites. Note the grassy vegetation surrounding the Meadow Pipit nest, whereas the European Stonechat nest is constructed amidst scrubby *Salix repens* and *Rubus caesius*. The white arrows indicate the nest location.

Table 2. Clutch size, hatching and nest success. Species names (number of nests used to calculate nest success); clutch size and hatching (fraction of hatched eggs) given as average \pm SD during the whole season; daily nest success and nest success (both with 95% CI) for the incubating and nestling period. Clutch size and hatching is based on a larger data set, see: Clutch size, hatching and Mayfield nest success.

NHD	Clutch size	Hatching	Daily nest success	Total nest success
Meadow Pipit ($n = 41$)	3.8 ± 0.7	0.95 ± 0.11	0.940 (0.926–0.954)	0.19 (0.13–0.28)
European Stonechat ($n = 34$)	5.4 ± 0.7	0.95 ± 0.11	0.944 (0.932–0.956)	0.21 (0.15–0.30)
Northern Wheatear ($n = 147$)	5.2 ± 1.0	0.80 ± 0.07	0.969 (0.961–0.976)	0.43 (0.34–0.52)
AWD				
Meadow Pipit ($n = 12$)	4.1 ± 0.9	0.97 ± 0.11	0.877 (0.834–0.920)	0.03 (0.01–0.11)
European Stonechat ($n = 19$)	5.5 ± 0.8	0.91 ± 0.16	0.883 (0.853–0.914)	0.04 (0.01–0.09)

both other songbirds, resulting in higher nest success rates (Table 2). Almost all failed nests are due to nest depredation (see Methods).

Growth rates of nestlings

Nestlings from the different species reached their differing maximum body mass at a partly different age (Figure 3). Nestling Meadow Pipits reached their maximum average weight of 17.4 g on day 12, European Stonechats 15.5 g on day 12 and Northern Wheatears reach 24.6 g on day 14.

Nestling diet

For the early nests, the proportions of prey in the diets differed among the three songbirds ($\chi^2_{12} = 103.25$, $P < 0.001$): diets of Meadow Pipit and European Stonechat differed ($\chi^2_6 = 49.68$, $P < 0.001$) as did diets of European Stonechat and Northern Wheatear ($\chi^2_6 = 13.81$, $P = 0.032$; Figure 4A). European Stonechat and Northern Wheatear often fed beetles and their larvae (Coleoptera) as well as caterpillars (Lepidoptera) to their nestlings (Figure 4, Table S1). Meadow Pipits, in contrast, fed almost no beetles to their nestlings. They also fed fewer Noctuid larvae to their nestlings compared to both chat species; Figure 4, Table S1). Instead, Meadow Pipits fed their young more often with adult crane flies (Tipulidae) compared to European Stonechats and Northern Wheatears.

In late nests, the proportions of prey species did not differ between European Stonechat and Northern Wheatear ($\chi^2_6 = 9.10$, $P = 0.17$; Figure 4B, Table S2). Diets of late broods of European Stonechat and Northern Wheatears contained partly different prey compared to early nests due to phenology of the prey. The Garden Chafer *Phyllopertha horticola*, most notably, disappeared from the diet and from the field,

whereas imagoes of another scarab beetle, the Dune Chafer *Anomala dubia*, appear from mid-June onwards, in the field and in the diet (Table S1 and S2). As for early nests, Noctuid caterpillars were important prey (Figure 4B, Table S1 and S2).

Prey per feed and provisioning rates

All three passerines provided different numbers of prey per feed ($F_2 = 150.28$, $P < 0.001$): Meadow Pipits (2.5 ± 1.2 , $n = 510$ prey in $n = 205$ feeds) delivered more prey per feed than European Stonechats (1.2 ± 0.4 , $n = 470$ prey in $n = 409$, $P < 0.01$) and Northern Wheatears (1.7 ± 1.0 , $n = 11\ 919$ prey in $n = 6990$, $P < 0.01$). The average number of feeds per nestling

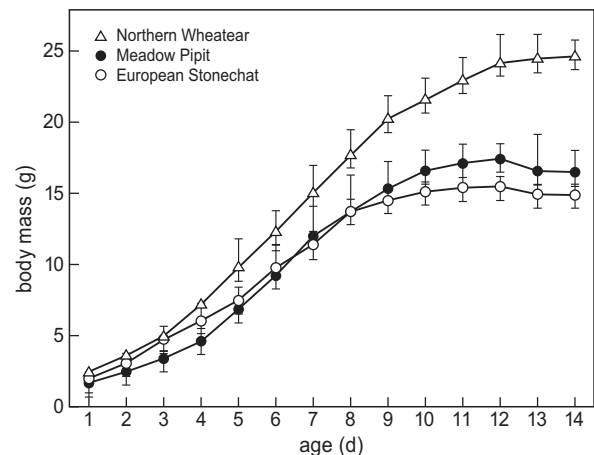


Figure 3. Average body mass (\pm SD) of nestlings as function of age (accuracy ± 1 day), day 1 = hatching day. Number of measurements, including repeat-measurements: Meadow Pipit 358 measurements on 149 nestlings and European Stonechat 654 on 189 nestlings. Northern Wheatear: collected data 2008–2015, 322 nestlings. Masses of Northern Wheatear on days 1–5 originate from Glutz & Bauer 1988.

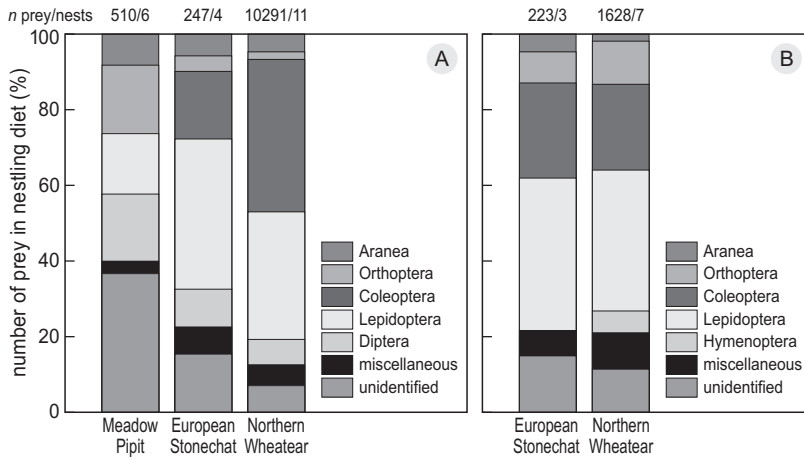


Figure 4. Diet of nestling Meadow Pipit, European Stonechat and Northern Wheatear for early nests (A) and European Stonechat and Northern Wheatear for late nests (B). Only prey families are shown which comprise > 5% of the total number of prey fed to nestlings. Unidentified: prey which were not identifiable. Miscellaneous: sum of all prey species that per species did not comprise > 5% of the diet. The number of prey and the number of broods is shown above each bar. The diets are presented in more detail in Tables S1 and S2.

per hour (Table 3) differed among the three species ($F_2 = 22.71$, $P < 0.001$), with Meadow Pipit and European Stonechat feeding their young at lower rates than Northern Wheatears ($P < 0.001$). Provisioning frequency per nestling per hour did not differ between Meadow Pipit and European Stonechat ($P = 0.85$). Per hour, a European Stonechat nestling received about half of the number of prey items a nestling Meadow Pipit or Northern Wheatear received: Meadow Pipit 8.3 prey items/h, European Stonechat 4.0 prey items/h and Northern Wheatear 8.7 prey/h.

DISCUSSION

I explored the breeding biology of Meadow Pipit, European Stonechat and Northern Wheatear which co-occur in Dutch dune grasslands. These three ground-foraging insectivores differed in several aspects of their breeding biology, such as nestling diet, clutch size, nest predation and food provisioning rates.

Diet and provisioning

The diet of Meadow Pipits included many adult dipterans such as adult crane flies, which has also been

commonly observed in other studies (Cragg 1961, Evans *et al.* 2005, Douglas *et al.* 2008). European Stonechats and Northern Wheatears, in contrast, often fed beetles and Noctuid caterpillars to their nestlings, which Meadow Pipits did much less often. Composition of diet often changes with increasing nestling age in songbirds. Spiders (Aranea), for instance, are often reported to be predominantly fed to young nestlings (e.g. in tits *Paridae*; Royama 1970, Török 1986), Willow Warblers *Phylloscopus trochilus* (Krupa 2004) and Green Woodhoopoes *Phoeniculus purpureus* (Radford 2008)), allegedly because of the high concentration of specific amino acids necessary for growth at an early age (Ramsay & Houston 2003). Whether diet also changes with increasing age in the three species of this study remains unknown because of the small sample size and lack of data on within-brood changes in diet with increasing nestling age. Hence, observed dietary differences may also be due to, for example, site differences. A larger sample size and repeated observations of the same broods at different ages are needed to meaningfully study the relation between diet and nestling age.

Meadow Pipits supplied their nestlings with more prey items per feed than European Stonechats but prey

Table 3. Provisioning strategies of Meadow Pipit, European Stonechat and Northern Wheatear. *n* is number of nests monitored to determine provisioning frequency; monitoring time is time spent monitoring the nest to determine the provisioning rate, number of observed feeding events is given for the total observation time.

	Monitoring time (h)	Observed feeding events (<i>n</i>)	feeds/h	feeds/nestling/h
Meadow Pipit (<i>n</i> = 11)	51.0	617	12.1	3.3 ± 1.1
European Stonechat (<i>n</i> = 13)	48.8	869	17.8	3.3 ± 0.9
Northern Wheatear (<i>n</i> = 19)	158.4	3354	21.2	5.1 ± 0.8

often seemed smaller (prey size was not measured). The large fraction of unidentified prey in the diets of Meadow Pipits is due to prey of very small size, hampering identification. Individual nestlings of Meadow Pipit and European Stonechat obtained similar number of feeds per hour, yet a Meadow Pipit nestling gains 12% more weight over the same nestling period. It is possible that the nutritional value per feed is larger in Meadow Pipit than in European Stonechat, in spite of smaller mean prey size for the former.

Species composition of the nestling diets of European Stonechat and Northern Wheatear was quite similar, especially in late broods. This is somewhat surprising, since one would expect prey size to increase with the size of the insectivorous predator (Hespenheide 1971, Kaspari & Joern 1993, Brandl *et al.* 1994). Instead of feeding larger prey (which may be unavailable or occurring in too low densities to be profitable), nestlings of Northern Wheatear were being fed 50% more frequently in order to gain 60% extra weight, as compared to European Stonechat. Also, parental Northern Wheatears bring more prey items per feed (1.7) than European Stonechats (1.2). Perhaps Northern Wheatears can hold more prey items in their bills than European Stonechats because their bills are 1.6–2.9 mm longer (measured from skull, Glutz von Blotzheim & Bauer 1988).

The main difference in foraging behaviour between Meadow Pipit and the chats is that the two chats also dig in the soil when foraging, which I never observed in Meadow Pipit. This precludes Meadow Pipits from finding large soil-dwelling prey, such as wire worms (Coleoptera, larval Elateridae) and Noctuid larvae which are mainly found just underneath sheets of moss and at the basal stems of grasses in the NHD.

Nest success

Ground-nesting birds of open landscapes are prone to high levels of nest predation (Martin 1993), which results in low nest success. For instance, nest success is between 0.43–0.48 for ground-nesting passerines in shrub and grassland habitat in North America (Martin 1993).

Nest success of Meadow Pipit was low in the NHD compared to this general estimate of nest success rate, and especially so in the AWD (0.19 and 0.03, respectively). Other studies in Germany (Hötker & Sudfeldt 1982) and Poland (Halupka 1998) measured a nest success of 0.29–0.48 for Meadow Pipit, with variation between years. Nest success of European Stonechats was also low in the NHD (0.21) and especially in the AWD (0.04), compared to 0.45 in England (Fuller &

Glue 1977). Nest success of Northern Wheatear was higher than both open nesters (average 0.43 for 2007–2012), yet other studies in Sweden (Moreno 1989, Pärt 2001), England (Tye 1992) and Germany (Buchmann 2001) found a nest success of 0.53–0.9 (as fraction of nests found since no Mayfield nest success is reported).

Thus, nest success appears (somewhat) lower in all three species compared to the findings of other studies. An explanation may be that my data are from one year only (except for the Northern Wheatear), which may have been a particularly poor year. Furthermore, the number of predators may have been higher in my study sites than in other sites, whether or not in combination with a low availability of prey in 2015. The lower nest success of Northern Wheatear compared to other studies may be a result of different methodology: nest success as determined by the number of nests that failed as a fraction of the total number of nests found, often leads to a higher nest success than when using Mayfield nest success (Snow 1955). Future work may shed light on the regularity of the low nest success rates in the Dutch coastal dunes.

The difference in nest success between both study sites is remarkable, but the cause is uncertain. Perhaps the low number of nests found in the AWD may have led to spurious results. Alternatively, suitable nesting sites probably occur in smaller patches in the AWD, because the large number of Fallow Deer in the AWD probably strongly diminishes the size of grassy plots in which Meadow Pipits nest, as well as the grassy undergrowth of shrubs, in which European Stonechats nest. Nests in these small patches of suitable vegetation may be more prone to predation since they are easier found by, and more accessible to, predators.

Nest success of the open-nesting Meadow Pipit and European Stonechat was less than half of that found for Northern Wheatear, a cavity-nester. This is in line with the notion that predation pressure on broods is generally higher for open-nesting species than for hole-nesting birds (Skutch 1949, Martin & Li 1992). Open-nests are probably depredated by a larger number of different predator species than cavity nests, and may well include avian predators. Information on predator species is limited for both open-nesters in the research sites. A Common Kestrel *Falco tinnunculus* depredated a brood of Meadow Pipit, and Red Fox *Vulpes vulpes* a brood of European Stonechats while these broods were being video-recorded, and Carrion Crows *Corvus corone* were observed depredating a nest of Meadow Pipits. In 2016, Red Foxes appeared to be the only nest predator for nine depredated nests of Meadow Pipit and

European Stonechat in the NHD, as determined by using infra-red camera-traps (van Oosten, in press). Red Foxes are the main nest predator for Northern Wheatear in the NHD (van Oosten *et al.* 2015), being the only animal in the Dutch dunes capable of excavating the nests. These observations fit with other studies where Carrion Crows, mustelids and Red Foxes were the main predators, such as in farmland areas (MacDonald & Bolton 2008, Teunissen *et al.* 2008) but also in semi-natural habitat, such as heathlands (Praus *et al.* 2014).

Clutch size and nest depredation

The possibility of nest predation increases with increasing provisioning rates (Skutch 1949, Lima 1987) because feeding parents may attract predators to the nest (Martin *et al.* 2000). Northern Wheatears fed their young more frequently than both open nesting species, because their broods need more food since they are larger in terms of total brood mass. Yet, their nest success is the highest of the three species. The increased attraction of predators by frequent feeding in Northern Wheatear is likely off-set by the relative safety of the breeding hole. Even though mammalian predators enter the holes (e.g. mustelids) or excavate the nest (Red Foxes), avian predators are less likely to get into the nesting burrows of Northern Wheatears.

Northern Wheatear parents can frequently provide food without incurring the costs of increased nest predation, as a result of their hole-nesting habits (Martin *et al.* 2000). This raises the question of whether bird species with at least a similar feeding frequency as Northern Wheatears could maintain their populations in the study sites when nesting in the open, or whether they would succumb due to theoretically high levels of nest depredation. An example may be the Whinchat *Saxicola rubetra*. Although food provisioning rates in the Dutch dunes are unknown, Britschgi *et al.* (2006) report that Swiss Whinchats provision individual nestlings 7.9 times per hour (clutch size on average 5.3 eggs, resulting in 42 visits per nest per hour). If the provisioning frequency were equally high in the Dutch dunes, I suspect very few broods would escape the attention of predators – compare to 3.4 times per nestling per hour for the closely related European Stonechat. Whinchats breed once a year (with re-nesting after failure; Frankevoort & Hubatsch 1966), compared to up to three times per year for European Stonechats (Frankevoort & Hubatsch 1966). Under current predation pressure the combination of a potentially high provisioning rate and single-broodedness may have proven to be an unsuccessful one.

Nest success of both open-nesters, Meadow Pipit and European Stonechat, was similar despite broods of European Stonechat being larger. The frequency with which an individual nestling was fed was similar for Meadow Pipit and European Stonechat. As a result, the larger brood of the latter was visited more frequently and European Stonechat should be more prone to nest predation than Meadow Pipit (Martin *et al.* 2000). Yet, predators are not attracted more often to nests of European Stonechats, as shown by the similar nest success. (At least in 2015, nest predation appeared to be the main cause for nest failure and not a lack of food, since no emaciated nestlings were encountered.) This may be an effect of different nest locations, since nest location clearly affects the chance of nest depredation (Burhans & Thompson 2001, Martin *et al.* 2000). The relatively dense scrub vegetation where European Stonechats breed is physically perhaps less accessible for potential (avian) predators, compared to the grassy habitat where Meadow Pipits nest. As a consequence, if Meadow Pipits had a larger clutch size than currently observed (e.g. similar in size to European Stonechats) this would possibly result in higher nest predation rates (Slagsvold 1982, Martin 1995, McCleery *et al.* 1996), which could substantially lower the probability of successfully raising a brood.

Concluding remarks

Here, basic information on the breeding biology of three insectivorous songbirds breeding in Dutch dune grasslands is provided. Although these songbirds all breed and forage on the ground, they appeared to differ in several aspects of their breeding biology, such as clutch size, nestling diet, nest predation and food provisioning rates. Differences in population trends for the different bird species may be linked to the observed differences in their breeding biology, but that causal link remains to be studied. To further improve our understanding of the putative relationships between population growth and vegetation in coastal dune grasslands, future work should focus on the interaction between different vegetation types in dune grasslands and prey abundance, foraging habitat and vegetation-specific nest depredation, both in a descriptive and experimental way.

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SAMENVATTING

Algemeen wordt aangenomen dat recente veranderingen in de vegetatie van duingraslanden langs de Nederlandse kust effect hebben gehad op de populatiegrootte van verschillende zangvogels die in deze graslanden broeden en daar hun voedsel zoeken. De precieze mechanismen van deze veronderstelde relatie zijn echter niet duidelijk door gebrek aan voldoende kennis over de broedbiologie van deze soorten. In dit artikel worden de resultaten van een onderzoek naar de broedbiologie gepresenteerd voor drie soorten die in deze graslanden broeden, namelijk Graspieper *Anthus pratensis*, Roodborsttapuit *Saxicola torquatus* en Tapuit *Oenanthe oenanthe*. Het onderzoek vond plaats in het Noord-Hollands Duinreservaat (NHD) en de Amsterdamse Waterleidingduinen (AWD). Het voedsel van nestjongen van Graspiepers (5 nesten) bevatte veel Diptera (18%), zoals langpootmuggen (Tipulidae), en slechts weinig kevers (1%) en rupsen van uiltjes (Noctuidae, 7%). Rupsen van uiltjes en kevers vormden wel een belangrijk deel van het voedsel van jonge Roodborsttapuiten (NHD 18%, AWD 35%, 4 nesten) en Tapuiten (NHD 40%, AWD 21%, 11 nesten). Legselgrootte was het kleinst bij Graspiepers ($3,8 \pm 0,7$, 41 nesten) en even groot voor Roodborsttapuit ($5,4 \pm 0,7$, 34 nesten) en Tapuit ($5,2 \pm 1,0$, 147 nesten). De mate van nestpredatie was voor Graspieper en Roodborsttapuit (die beide open nesten maken) even groot (Mayfield nestsucces in NHD voor de twee soorten 0,19 respectievelijk 0,21 voor ei- en jongenfase gezamenlijk). Nestpredatie was voor Tapuiten (die in holen van Konijnen *Oryctolagus cuniculus* broeden) veel kleiner (Mayfield nest-

succes 0,43 voor ei- en jongenfase gezamenlijk). Een jonge Tapuit, de grootste van de drie soorten, werd vaker gevoerd per uur ($5,1 \pm 0,8$ keer, 18 nesten) dan jongen van de beide andere soorten. Het feit dat een jonge Graspieper per uur ($3,3 \pm 1,1$, 11 nesten) even vaak werd gevoerd als een jonge Roodborsttapuit ($3,3 \pm 0,9$ keer, 13 nesten) zou eigenlijk moeten resulteren in frequentere nestpredatie van Roodborsttapuitnesten, omdat de kans dat een nest wordt gepredeerd over het algemeen toeneemt met de voerfrequentie, die een functie is van de broedselgrootte. Dat nesten van Roodborsttapuitnesten toch niet vaker worden gepredeerd, wordt mogelijk bepaald door een andere nestplaatskeuze van deze soort. Hoewel de drie onderzochte zangvogels naast elkaar voorkomen, alle op de grond broeden en daar ook hun voedsel zoeken, blijken ze toch (deels) van elkaar te verschillen in een aantal aspecten van hun broedbiologie, zoals legselgrootte, het voedsel dat voor de jongen wordt aangebracht, voerfrequentie en mate van nestpredatie. De verschillende populatietrends van de drie zangvogels houden mogelijk verband met de hier gerapporteerde verschillen in broedbiologie. Om de mogelijke relatie tussen populatieontwikkeling van op de grond foeragerende zangvogels van duingraslanden en de vegetatie beter te begrijpen moet toekomstig werk zich richten op de verschillende vegetatietypen in duingraslanden in relatie tot talrijkheid en beschikbaarheid van prooi, foerageerhabitat en vegetatiespecifieke nestpredatie.

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SUPPLEMENTARY MATERIAL

Table S1. Composition of nestling diets of Meadow Pipit, European Stonechat and Northern Wheatear, per site. Only nests found between mid-May and mid-June are included ('early nests'). The number per prey type is the numerical fraction of each prey type in the diet. Only prey families are shown which comprise > 5% of the total number of prey fed to nestlings. Unidentified: prey which were not identifiable. Miscellaneous: sum of all prey species that per species did not comprise > 5% of the diet. Northern Wheatear data originate from van Oosten *et al.* (2014). Averages are shown \pm SD.

	Meadow Pipit		European Stonechat		Northern Wheatear		
	NHD	AWD	NHD	AWD	NHD		
Site							
Number of filmed nests	5	1	1	3	11		
Number of prey	248	262	162	85	10291		
Number of feeds	96	109	144	75	6039		
Prey per feed	2.6	2.4	1.1	1.1	1.7		
Average age of nestlings (min–max)	7.5 (5–10)	8	9	7.3 (6–8)	8.1 (6–10)		
Film date	13–20/5	27/5	22/5	8–26/5	18/5–10/6		
Order	Family	Species					
Aranea			0.03 \pm 0.03	0.15	0.01	0.17 \pm 0.04	0.05 \pm 0.03
Orthoptera			0.04 \pm 0.09	0.31	0.06	0	0.02 \pm 0.01
Coleoptera			0.01 \pm 0.03	0	0.18	0.18 \pm 0.08	0.40 \pm 0.17
	Elateridae		0	0	0.07	0.05 \pm 0.05	0.14 \pm 0.15
	Scarabeidae	<i>Phyllopertha horticola</i>	0	0	0.08	0.09 \pm 0.15*	0.17 \pm 0.12
	Carabidae / Staphylinidae		0.01 \pm 0.03	0	0.01	0.01 \pm 0.01	0.01 \pm 0.01
Lepidoptera			0.28 \pm 0.18	0.13	0.40	0.45 \pm 0.05	0.33 \pm 0.06
	Noctuidae		0.19 \pm 0.18	0.03	0.29	0.37 \pm 0.04	0.21 \pm 0.09
	Nymphalidae		0	0.02	0	0	0.06 \pm 0.07
Diptera			0.18 \pm 0.19	0.10	0.15	0.01 \pm 0.01	0.07 \pm 0.06
	Asilidae		0.04 \pm 0.07	0.05	0.13	0.01 \pm 0.01	0.06 \pm 0.05
	Tipulidae		0.08 \pm 0.09	0.02	0	0	0
Miscellaneous prey			0.03 \pm 0.03	0.04	0.03	0.06 \pm 0.03	0.05 \pm 0.01
Unidentified larva			0.03 \pm 0.05	0.02	0.09	0.05 \pm 0.05	0.03 \pm 0.01
Unidentified other prey			0.39 \pm 0.07	0.24	0.09	0.08 \pm 0.08	0.06 \pm 0.04

**Phyllopertha horticola* (Coleoptera: Scarabeidae) occur abundantly in both sites between late May–mid June. One nest was filmed 26 May when *Phyllopertha* were commonly fed (27% of all prey were *Phyllopertha*). The other two nests were filmed 6 May, when *Phyllopertha* were not yet available (0% of all prey was *Phyllopertha*).

Table S2. Composition of nestling diets of Meadow Pipit, European Stonechat and Northern Wheatear, per site. Only nests found between late-June and mid-July are included ('late nests'). The number per prey type is the numerical fraction of each prey type in the diet. Only prey families are shown which comprise > 5% of the total number of prey fed to nestlings. Unidentified: prey which were not identifiable. Miscellaneous: sum of all prey species that per species did not comprise > 5% of the diet. Averages are shown \pm SD.

	European Stonechat		Northern Wheatear
	NHD	AWD	NHD
Site			
Number of filmed nests	1	2	7
Number of prey	79	144	1628
Number of feeds	69	121	951
Prey per feed	1.1	1.2	1.7
Average age of nestlings (min-max)	11	10 (9-11)	8.2 (7-10)
Film date	24/6	23/6-07/7	19/6-08/7
Order	Family	Species	
Aranea			0.03
Orthoptera			0.03
Coleoptera			0.30
	Elateridae		0.03
	Scarabeidae	<i>Anomala dubia</i>	0.25
Lepidoptera			0.37
	Noctuidae		0.15
	Pyralidae		0.05
	'small white caterpillar'		0.03
Hymenoptera			0
	Formicidae		0
Miscellaneous prey			0.03
Unidentified larva			0.08
Unidentified other prey			0.18