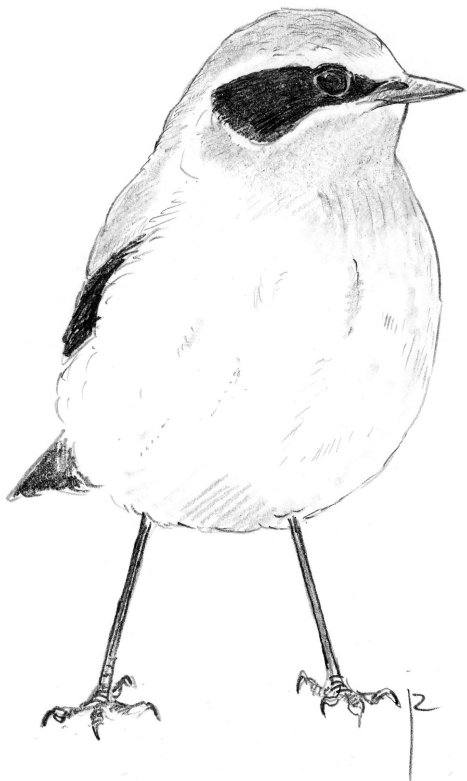


# Habitat selection of brood-rearing Northern Wheatears *Oenanthe oenanthe* and their invertebrate prey

H. Herman van Oosten<sup>1,2,\*</sup>, A.B. van den Burg<sup>3</sup>, R. Versluijs<sup>1</sup> & H. Siepel<sup>2,4</sup>

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Birds consider both variation in prey abundance and accessibility in their decision of where to forage. Acidification and nitrogen deposition affect both prey abundance and accessibility by stimulating growth of nitrophilic grasses at the expense of forbs. Management practises such as mowing or grazing primarily affect vegetation structure which also influences the abundance and accessibility of invertebrates. Hence, for effective management and conservation purposes it is paramount to understand the relationships between vegetation structure, densities of preferred prey and habitat-use of birds. In this study we explore such relationships for the nationally endangered Northern Wheatear *Oenanthe oenanthe* in dune grasslands along the Dutch coast. Our findings support the hypothesis that forager mobility and food accessibility are of greater importance during patch selection than food abundance per se in ground foraging birds. The abundance of all potential prey and three of the four most important actual prey groups was highest in tall grass, but Northern Wheatears foraged preferentially in short grass. Clearly, encroachment by tall grass will diminish habitat suitability for Northern Wheatears due to lowered prey accessibility. We propose that a mixture of short and tall vegetation and landscape management allows for dispersal of arthropods between different (micro)habitats. We provide densities of the important prey in a coastal area where Northern Wheatears still successfully breed. This enables site-managers to efficiently investigate presence and abundance of important prey in seemingly suitable areas but where Northern Wheatears do not breed. Eventually we may be able to discern whether food shortage poses a bottleneck for Northern Wheatears in these uninhabited areas.



Key words: Northern Wheatear, *Oenanthe oenanthe*, dune, grassland, nitrogen, vegetation structure, diet, arthropods, habitat use

<sup>1</sup>Bargerveen Foundation, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands;

<sup>2</sup>Department of Animal Ecology & Ecophysiology, IWWR, Radboud University, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands; <sup>3</sup>Biosphere Science Productions, Berkenlaan 71, 6721 CB Bennekom, The Netherlands;

<sup>4</sup>Dept. Nature Conservation & Plant Ecology, Wageningen University, The Netherlands;

\*corresponding author (h.vanoosten@science.ru.nl)

Only a quarter of the world's temperate grasslands are left undisturbed (Hannah *et al.* 1995) and remaining (semi-)natural grasslands in Europe and North America are under high pressure from deposition of atmospheric nitrogen and acidification (Bobbink *et al.* 2010). The persistence and open character of grasslands is threatened by encroachment of tall, nitrophilic grasses at the expense of abundance and diversity of flowering plants (Stevens *et al.* 2004, Bobbink *et al.* 2010). The result-

ing homogenization of plant communities may well affect arthropod communities (Schaffers *et al.* 2008, Haddad *et al.* 2001, Koricheva *et al.* 2000, Otway *et al.* 2005, Siemann 1998) which, in turn, can be detrimental for vertebrate insectivores occurring in these grasslands.

Changes in vegetation structure alone could also affect the occurrence of grassland birds. Atkinson *et al.* (2005) found that vegetation structure rather than the

abundance of possible prey determined where birds foraged in agricultural grasslands. Tall grass swards may contain both higher prey species diversity and abundance (Morris 2000, Dennis *et al.* 2008), but, as tall grass vegetation is far less accessible for small ground-foraging birds (Atkinson *et al.* 2004), songbirds appeared to preferentially forage on short swards.

So, birds consider both variation in prey abundance and accessibility in their decisions of where to forage. As acidification and nitrogen deposition (and other forms of fertilisation) affect both prey abundance and accessibility, the suitability of sites as foraging locations may have altered over time. Management practises counteracting the effects of acidification and nitrogen deposition primarily affect vegetation structure, e.g. by mowing or grazing, which also influence the abundance and accessibility of invertebrates. Hence, for effective management and songbird conservation purposes it is paramount to understand the relationships between vegetation structure, densities of preferred prey and habitat-use of birds.

In this study we explore such relationships for the nationally endangered Northern Wheatear *Oenanthe oenanthe* in heterogeneous coastal dune grasslands in The Netherlands. These natural grasslands have been affected by encroachment of tall grass resulting from acidification and nitrogen deposition (Kooijman *et al.* 1998). Northern Wheatears are physically adapted to cursorial locomotion in open habitats (Kaboli *et al.* 2007) where they 'hop-and-peck' on short vegetation (Conder 1989). Therefore, grass encroachment due to atmospheric deposition of nitrogen (Bobbink *et al.* 2010) and declines in grazing by European Rabbits *Oryctolagus cuniculus* due to viral diseases, rendered habitats unsuitable for Northern Wheatears. Remaining populations of Northern Wheatears in The Netherlands breed in structurally heterogeneous habitats where bare sand and low and tall grass swards co-occur on a small spatial scale. We determined the relationships between foraging habitat preference and (1) vegetation type and availability, (2) prey abundance and (3) prey species composition in interaction with vegetation type, and actual bird diet. In particular, we asked whether Northern Wheatears forage predominantly in habitat patches with the highest densities of their preferred prey types, or in patches where these are less abundant but likely to be more accessible.

In relating foraging behaviour to food abundance, a thorough understanding of diet is vital. Knowing a bird's diet is also crucial to optimise arthropod sampling methods for detecting important prey items, since different arthropods require different sampling

methods (Standen 2000). Hence, we will first present results of an extensive Northern Wheatear diet study, performed in the Dutch dune grasslands.

## METHODS

### Study species and study site

Northern Wheatears are small, c. 25 g, insectivorous passerines which breed from Eastern Canada across Eurasia to western Alaska, USA. All birds winter in the African Sahel and Eastern Africa (Glutz von Blotzheim & Bauer 1988), as has recently been shown by the use of geolocators for birds from Alaska and Eastern Canada (Bairlein *et al.* 2012), Germany (Schmaljohann *et al.* 2012) and The Netherlands (van Oosten *et al.* in prep.). Field data for this study were collected during the breeding seasons of 2007–2010 in coastal dunes in the Noord-Hollands Duinreservaat (NHD; 52°33'N, 4°36'E). Here, Northern Wheatears have declined by 90% (from 164 in 1988 to 17 in 2010), as they have elsewhere in the country (Boele *et al.* 2012, Sovon 2002). The study site of 74 ha is located in stabilised grey dunes, within 1 km from the sea. The highly diverse landscape consists of a mosaic of vegetation succession stages with pioneer vegetation around sandy blow-outs (*Phleo-Tortuletum ruraliformisi*), short semi-natural grasslands (*Taraxaco-Galietum veri*), tall grass vegetation (dominated by *Calamagrostis epigejos* and *Carex arenaria*) and bushes such as *Salix repens* and *Hippophae rhamnoides*.

### Foraging habitat

We studied foraging behaviour of brood-rearing females in five random territories via burst sampling in 2008 (Dunn & Gipson 1977, Swihart & Slade 1997). Males appeared to often be engaged in territorial disputes instead of feeding nestlings which made monitoring of their foraging behaviour less effective. A fix was recorded every 60 seconds, during which period females could transverse their entire territories. A total of 200 fixes were collected per female spread over consecutive days when broods were 4–8 days old, between 17 May and 14 July. Territories were subsequently delineated by a polygon through the outermost fixes (minimum convex polygon, MCP; Mohr 1947) in ArcGIS 9.3 software.

To investigate where females find their food within the MCP territory we performed kernel density estimations (KDE) by using Hawth's Analysis Tools (Beyer 2004) in ArcGIS 9.3 software. To select the best fitting smoothing parameter we inspected kernel density esti-

mates resulting from different smoothing parameters (Kie *et al.* 2010). We applied the same smoothing parameter of value 7 to all five territories. We plotted our chosen utility distribution as isopleths of different values of the likelihood of encountering a foraging female, with 10% increments. As a last step, core foraging areas were delineated by the smallest/shortest density isopleth containing 50% of the fixes.

By describing the vegetation characteristics in the field we determined the cover of three different classes of vegetation structure per MCP, KDE and KDE cores: 'pioneer' (open sand with mosses), 'short' (vegetation <5 cm sward height) and 'tall' (vegetation >5 cm sward height). Northern Wheatears are reported to mainly forage in vegetation shorter than 5 cm (Conder 1989). We stress that 'tall' mostly was much higher than 5 cm sward height, since vegetation appeared either very short due to grazing by European Rabbits *Oryctolagus cuniculus*, or up to 30 cm when ungrazed.

### Nestling diet

To identify prey items, feeding parents were filmed at the nest entrance with automated cameras. During 2008–2010, 11 nests were filmed between 18 May and 10 June. Digital video cameras were mounted on tripods 30 cm from the nest entrance under a camouflaged wire-mesh roof. The camera was activated by two infra-red triggers at the entrance when birds entered the nest. Each feeding video captured 6 seconds. Nests were filmed for a maximum of 5 consecutive days, starting 6 days after hatching. Cameras filmed at least 8 hours per day, between 0700 and 1900. Filmed arthropods were identified to species level when possible, or grouped to higher taxonomic levels as necessary.

Nestlings were weighed and colour banded around day 8 and all nestlings from the filmed nests fledged successfully, indicating that food abundance was not limiting in the nestling phase. After seven years of study we are yet to encounter starved nestlings, in spite of dissecting dead nestlings: stomachs are never empty and birds are not emaciated.

### Prey habitat

Since Northern Wheatears are primarily ground-foragers we determined occurrence and abundance of soil and litter arthropods by taking sod-cuts. In 10 territories samples were taken in 2007, each consisting of three sub-samples. These 10 territories encompassed those in which we determined nestling diet during 2008–2010. The samples were divided according to sward height, similar to foraging habitat: 'pioneer'

( $n = 30$  sub-samples), 'short' ( $n = 30$  sub-samples) and 'tall' ( $n = 30$  sub-samples, Table 1), resulting in  $n = 10$  samples per vegetation type. Each sample was 60 × 60 cm and 7 cm deep to encompass the total organic layer where most soil-arthropods occur. Sward height was determined by placing a dowel vertically into the vegetation of each sod cut (Bibby *et al.* 2000). Sod-cuts were packed individually in plastic containers to prevent arthropods from escaping and were hand-sorted within two days after collecting. Arthropods were stored in 96% ethanol and mostly identified to species-level. We also sampled adult *Phyllopertha horticola* (Coleoptera: Scarabaeidae) which occurred abundantly in late May and early June. In total we established  $n = 10$  plots of 5 × 5 m divided in  $n = 5$  plots per vegetation type 'short' and 'tall'. Each plot was sampled by hand-picking for 10 min in suitable weather during the beetle peak at the end of May.

### Statistics

To analyse habitat preferences of Northern Wheatears, we used Jacobs' preference index (Jacobs 1974) calculated as:

$$D = (r-p)/((r+p)-2rp)$$

where  $r$  is the proportional use and  $p$  the proportional availability of each resource class.  $D$  ranges between +1 for maximum preference and -1 for maximum avoidance. In this way we compared vegetation composition of the KDE territory (where the actual foraging occurred) and of the foraging cores to the total available vegetation cover in the MCP territory

To explore covariation between arthropod communities inhabiting different vegetation structures and nestling diets, we performed a Principal Components Analysis (PCA, gradient <3) in Canoco 5, after log-transforming the proportional contribution of each arthropod type to reduce the effect of extreme values. We included all taxa in the analysis for which we deemed the sampling method (sod-cutting) suitable. This meant we excluded, for instance, grasshoppers (Orthoptera) because sod-cutting is an inappropriate method for sampling grasshoppers. Arthropod types excluded for this reason which were actually fed to nestlings were also excluded from the diet in the PCA. Arthropods present in the samples and sampled in a suitable way but not fed to nestlings were included.

For other analyses, data were tested for normality and homogeneity of variances. The data appeared not to meet the assumption of normality; hence we proceeded with non-parametric tests. To determine

whether sampled arthropod densities differed between vegetation types we conducted Kruskal–Wallis tests, followed by Mann–Whitney tests with Bonferroni post-hoc adjustment. To analyse whether abundance of *Phyllopertha horticola* differed between short and tall vegetation we performed a Kolmogorov–Smirnov test, given the higher accuracy at small sample size compared to Mann–Whitney tests (Field 2005).

## RESULTS

### Foraging habitat

MCP territory size was on average  $2.06 \pm 0.34$  (SE) ha (Table 1) of which Northern Wheatears use  $55.9 \pm 6.5\%$  for foraging according to the KDE analysis. Foraging appeared to be highly concentrated in certain parts of the territory:  $51 \pm 2.4\%$  of all foraging actions occurred in  $8.8 \pm 1.7\%$  of the MCP territory and  $16.0 \pm 3.0\%$  of the KDE territory (Table 1).

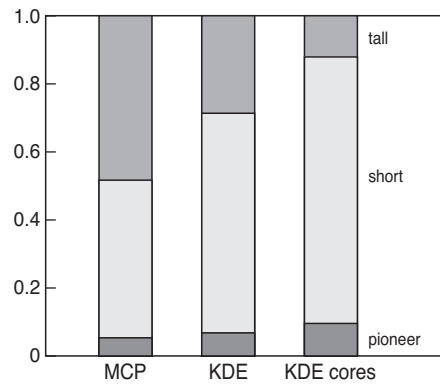
Vegetation composition differed between MCP, KDE and KDE foraging cores (Figure 1), with the amount of pioneer and especially short vegetation increasing from MCP to KDE territory and KDE core. Compared to total

**Table 1.** Size (ha) of territory determined by minimum convex polygon (MCP), kernel density estimations (KDE) and size of the KDE cores where  $51 \pm 2.4\%$  of all foraging actions occurred. Totals and subdivisions per vegetation type are presented. Values are means  $\pm$  SE.

Vegetation type	MCP	KDE	KDE cores
Combined	$2.06 \pm 0.34$	$1.11 \pm 0.09$	$0.18 \pm 0.03$
Pioneer	$0.12 \pm 0.12$	$0.08 \pm 0.08$	$0.02 \pm 0.02$
Short	$0.92 \pm 0.29$	$0.72 \pm 0.20$	$0.14 \pm 0.14$
Tall	$1.02 \pm 0.50$	$0.32 \pm 0.20$	$0.02 \pm 0.02$

**Table 2.** Prey comprising c. 5% or more of the nestling diet,  $n = 11$  broods. Mean and standard error are given in percentages of the total number of prey fed during the diet-study.

Order	Family	Species	Mean $\pm$ SE
Araneae			$4.9 \pm 1.0$
Coleoptera			$40.0 \pm 5.0$
	Elateridae (larvae)		$13.8 \pm 4.6$
	Scarabaeidae	<i>Phyllopertha horticola</i>	$17.2 \pm 3.7$
Lepidoptera (larvae)			$33.4 \pm 1.9$
Diptera (imagos)			$6.6 \pm 1.7$
	Asilidae	<i>Philonicus albiceps</i>	$5.7 \pm 1.5$
Unidentified arthropods			$5.9 \pm 1.1$



**Figure 1.** The proportional cover of three different vegetation types (tall, short and pioneer vegetation) differs between total territory size (MCP: Minimum Convex Polygon), the actual part used for foraging (KDE: Kernel Density Estimation) and distinct foraging cores in which 51% of all foraging events occurred (KDE cores).

vegetation availability within the MCP borders, Jacob's (D) preference index indicates that females preferred to forage on short (+0.36) and pioneer (+0.11) vegetation but avoided tall vegetation (−0.40). Within the foraging cores where 50% of all foraging actions took place preferences become even more pronounced: +0.61 (short), +0.30 (pioneer) and −0.74 (tall).

### Nestling diet

In total, 6039 feeds were investigated in 11 nests, i.e.  $549 \pm 311$  per nest. These feeds contained 10,291 detected prey items, i.e.  $936 \pm 553$  per nest. Prey types which comprised >5% of the nestling diet by number were deemed important; these belonged to just four orders (excluding the unidentified arthropods, Table 2), out of 14 orders recorded on film. Important prey were Araneae, larvae of Lepidoptera (especially Noctuidae

like *Cerapteryx graminis*, *Mythimna* sp., *Agrotis* sp. but also Nymphalidae, mainly *Issoria lathonia*) and Elaterid beetle larvae (especially *Melanotus punctolineatus*), imagines of the scarabid beetle *Phyllopertha horticola* and Diptera (Asilidae, mainly *Philonicus albiceps*). These four important groups comprised  $73.0 \pm 2.85\%$  of the total diet fed to nestlings. Variance in diet composition between nests was considerable: caterpillars (Lepidoptera) were fed between 24.5 and 42.3% of a diet, for instance. A complete overview of the diet is provided in Appendix 1.

**Prey habitat**

We sampled on average 80.4% of all arthropod taxa fed to the filmed broods. Flying insects such as Odonata and Diptera were not sampled, nor was Orthoptera for which sod-cutting is not a suitable sampling method. Unidentified prey fed to nestlings was also counted as not-sampled. The number of arthropod taxa differed significantly between types of vegetation structure (Table 3;  $H(2) = 67.490, P < 0.001$ ) and was highest in tall and lowest in pioneer vegetation. Pioneer vegetation harboured fewer taxa than short ( $U = 49.000, P < 0.001$ ) and short fewer than tall vegetation ( $U = 54.000, P < 0.001$ ).

**Table 3.** Species richness and arthropod abundance differs per vegetation type. Values are means  $\pm$  SE. Different superscripted letters denote significant differences among groups (see Results).

	Vegetation type		
	Pioneer	Short	Tall
Number of taxa	3.6 $\pm$ 0.5 <sup>a</sup>	12.3 $\pm$ 0.6 <sup>b</sup>	21.7 $\pm$ 1.2 <sup>c</sup>
Arthropod abundance	6.6 $\pm$ 1.0 <sup>a</sup>	25.8 $\pm$ 2.1 <sup>b</sup>	84.2 $\pm$ 7.4 <sup>c</sup>

The total abundance of arthropods also differed significantly between vegetation types (Table 3;  $H(2) = 67.933, P < 0.001$ ). Pioneer vegetation showed lowest abundance and tall the highest. Abundance in pioneer vegetation was lower than in short ( $U = 49.000, P < 0.001$ ) and in short lower than in tall vegetation ( $U = 54.000, P < 0.001$ ).

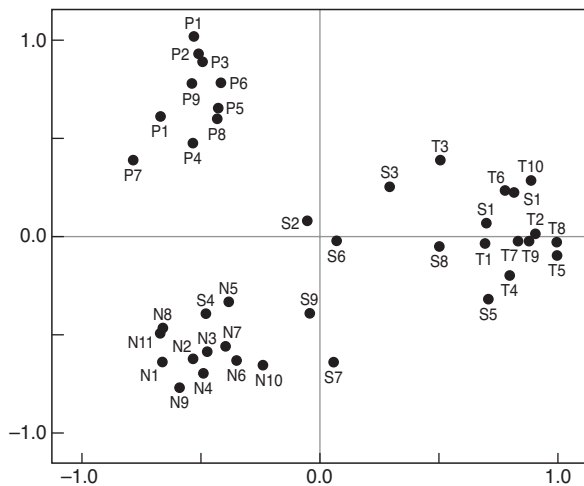
Vegetation structure also strongly affected abundance of preferred prey (Table 4; Araneae ( $H(2) = 56.96, P < 0.001$ ), which were more common in tall than in short ( $U = 26.00, P = 0.013$ ) and occurrence in short did not differ from pioneer vegetation ( $U = 71.00, P = 0.382$ ). Abundance of *Elateridae* larvae ( $H(2) = 49.87, P < 0.001$ ) was greater in short than in pioneer ( $U = 62.00, P < 0.001$ ) and in tall than in short vegetation ( $U = 301.50, P = 0.011$ ). *Phyllopertha horticola* was found more abundantly in tall than in short vegetation ( $Z = 1.581, P = 0.013$ ). *Lepidoptera* larvae ( $H(2) = 14.35, P = 0.001$ ) were found more in short than in both pioneer ( $U = 218.50, P = 0.001$ ) and tall ( $U = 277.50, P = 0.006$ ) vegetations.

**Relative composition of prey species**

PCA analysis explained 63% of total variance with two axes: first axis 36.9% and second axis 26.1%. The analysis revealed that the species composition differed strongly between samples from the three vegetation types and the actual birds' diet (Figure 2). Samples from pioneer habitat clustered together, as did those from tall habitats. Interestingly, the faunal composition in short grass habitat (the intermediate stage considering vegetation height) did not bridge the gap between pioneer and tall grass communities. Most short grassland samples resembled those from tall grass, but some were much more like the preferred diet samples from Northern Wheatear nests. The latter (and thus some of the short grassland samples) were relatively rich in

**Table 4.** Abundance of sampled important prey per vegetation type. Values are means  $\pm$  SE. Different superscripted letters denote significant differences among groups (see Results).

Order	Family	Genus	Vegetation type		
			Pioneer	Short	Tall
Araneae			0.21 <sup>a</sup> $\pm$ 0.11	1.13 <sup>a</sup> $\pm$ 0.19	5.20 <sup>b</sup> $\pm$ 0.60
Coleoptera	Elateridae		1.75 <sup>a</sup> $\pm$ 0.48	4.89 <sup>b</sup> $\pm$ 0.58	8.37 <sup>c</sup> $\pm$ 1.13
	Scarabaeidae	Phyllopertha	–	6.00 <sup>a</sup> $\pm$ 1.21	96.00 <sup>b</sup> $\pm$ 22.18
Lepidoptera			0.39 <sup>a</sup> $\pm$ 0.17	4.97 <sup>b</sup> $\pm$ 1.44	0.63 <sup>a</sup> $\pm$ 0.18



**Figure 2.** Principal Component Analysis (PCA) indicates separate clustering of arthropod samples from pioneer vegetation (P1–P10), samples of arthropods fed to nestlings (diet data of 11 nests, N1–N11) and arthropod samples from tall vegetation (T1–T10). Samples from short vegetation (S1–S10) are widely scattered, bridging the gap between tall vegetation and the diet samples, indicating the existence of different types of short vegetation. Eigenvalue axis 1: 0.37, Eigenvalue axis 2: 0.26.

caterpillars, weevils and larvae of elaterid beetles. Pioneer vegetation was relatively rich in darkling beetles (and relatives) and tall grasslands in millipedes, centipedes, isopods and ground beetles.

## DISCUSSION

Our findings support the hypothesis that forager mobility and food accessibility are of greater importance during patch selection than food abundance *per se* in ground foraging birds (Fuller *et al.* 2003, Atkinson *et al.* 2005, Vandenberghe *et al.* 2009). The abundance of all potential prey and of three of the four most important actual prey groups was highest in tall grass patches, but Northern Wheatears taking care of nestlings foraged preferentially in short grass and even preferred pioneer vegetation, with low food abundance, over tall vegetation (cf. Brooke 1979, Conder 1989, Tye 1992). Clearly, encroachment by tall grass species resulting from nitrogen deposition and acidification will diminish habitat suitability for Northern Wheatears, due to lowered prey accessibility.

In habitat management, consolidating (and expanding) short grass vegetation will benefit Northern Wheatears most. However, most short grassland sites resemble the fauna community of tall grass vegetation. Based on the dominant species groups in these tall and

short grass vegetations, their faunal similarity probably reflects the development of organic layers in the top-soil, and associated detritivore-driven fauna community make-up. Because conditions in the top-soil are similar and many potential prey species can occur in both vegetation types, we hypothesize that the arthropod-rich tall grass patches may serve as a source of potential food items, and thus be beneficial to the birds indirectly (Bonte *et al.* 2002, Butterfield *et al.* 1995). As such, the mosaic of tall and short grass vegetations may be a preferable habitat lay-out compared to continuous short grassland (Morris 2000, Cole *et al.* 2010), but this requires further research.

Interestingly, some fauna communities of short grassland closely resembled the diet of Northern Wheatear nestlings. These sites were particularly rich in caterpillars, weevil and click-beetle larvae. The diversity in faunal communities in short grasslands was large and it is not known by which factors this variation has arisen. However, we expect the short grasslands to fall into two broad categories: (1) a stage in succession following pioneer grassland and (2) well-developed grassland, which is kept short by grazing activity by European Rabbits and ungulates. It remains unclear whether a closer resemblance of the fauna community of a site to the birds' actual diet will relate directly to a higher foraging efficiency and breeding success.

Pioneer vegetations were also preferred by females taking care of nestlings, but, as the density of possible food items proved low here, the significance of pioneer grassland for the foraging birds is likely less than that of short grassland. However, pioneer grasslands are a necessary predecessor to short grasslands without a thick organic top-soil.

We also emphasize that demands of arthropod prey during their complete life-cycle should be subject of attention in grassland management and restoration. Larval stages of *Anomala dubia*, for example, occur in dynamic foredunes (van Duinen *et al.* 2005) where we did not observe Northern Wheatears to either forage or breed. Yet, *Anomala dubia* appeared to be a major component of the nestling diet of late broods (van Oosten unpubl.). It appeared that adult beetles fly inland towards secondary dunes, where they become important prey for Northern Wheatears. This indicates that well-intended conservation measures may be more successful if not solely aimed at restoration of breeding habitat *per se* but at restoration on a wider scale.

We show that only few prey groups are important prey for nestlings of the threatened Northern Wheatear. Other dietary studies show that these prey groups are important components of the diet in many locations

across Europe (Tye 1992, Exnerova *et al.* 1992, Moreno 1987). Differences between studies in relative contribution may be partly site-specific or depending on phenology of the prey or sampling method.

We provide densities of those prey in a coastal area where Northern Wheatears still successfully breed. This enables site-managers to efficiently investigate presence of important prey and their abundance in areas which seem very suitable for Northern Wheatears but where they do not occur as breeding birds. Eventually, we may be able to discern whether food shortage poses a bottleneck for Northern Wheatears in areas where they do not breed.

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## SAMENVATTING

Grondbewonende vogels laten zich in hun keuze om op een bepaalde plek te gaan foerageren zowel door het aanbod als de toegankelijkheid tot hun prooien leiden. Door verzuring en vermeting verdringen snelgroeiende grassen de oorspronkelijke vegetatie waardoor de insectenfauna verandert. Het beheer met betrekking tot vergrassing grijpt met name in op de vegetatie door bijvoorbeeld maaien en begrazing, wat ook effecten heeft op de insectenfauna. Voor effectieve bescherming is het dus van groot belang de relaties tussen vegetatiestructuur, prooidichtheid en habitatgebruik van de vogels te doorgronden. In dit artikel ontrafelen wij deze relaties voor de Tapuit *Oenanthe oenanthe* in Nederlandse duingraslanden. Onze resultaten ondersteunen de hypothese dat de toegankelijkheid tot prooien van groter belang is dan prooidichtheid *per se*. De abundantie van zowel alle gevonden evertrebraten als drie van de vier belangrijkste prooisoorten was het hoogst in hoog gras, maar Tapuiten foerageerden bij voorkeur in kort gras. Vergrassing leidt dus duidelijk tot een verminderde toegankelijkheid tot prooien voor Tapuiten. Door dichtheden van belangrijke prooien te berekenen geven we beheerders de mogelijkheid de aanwezigheid en abundantie van deze prooien te onderzoeken in terreinen die ogenschijnlijk prima lijken, maar waar de Tapuit niet (meer) voorkomt. Uiteindelijk kan zo getoetst worden of voedselbeschikbaarheid voor Tapuiten een probleem kan vormen in deze terreinen.

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**Appendix 1.** Relative nestling diet of 11 nests, filmed between 18 May and 10 June. L = (mainly) larva, I = (mainly) imago. Values are mean percentage  $\pm$  SE.

Order	Family	Genus / species	L/I	mean $\pm$ SE
Haplotaxida			–	0.05 $\pm$ 0.03
Araneae				4.92 $\pm$ 1.03
Diplopoda			–	0.35 $\pm$ 0.14
Isopoda				0.87 $\pm$ 0.31
Odonata		<i>Enallagma, Orthetrum cancellatum</i>	I	0.03 $\pm$ 0.01
Orthoptera	mainly Acrididae		–	1.61 $\pm$ 0.44
Dermaptera			I	0.01 $\pm$ 0.01
Hemiptera			–	0.49 $\pm$ 0.24
Coleoptera				40.02 $\pm$ 5.04
	Alleculidae / Tenebrionidae		L	0.98 $\pm$ 0.25
	Carabidae		L	0.2 $\pm$ 0.13
	Chrysomelidae		I	0.06 $\pm$ 0.06
	Curculionidae	mainly <i>Philopedon plagiatus</i>	I	3.32 $\pm$ 1.03
	Elateridae			13.76 $\pm$ 4.64
		<i>Agrypnus murina</i>	L	4.39 $\pm$ 1.59
		<i>Melanotus punctolineatus</i>	L	8.85 $\pm$ 3.01
	Lagriidae		I	0.06 $\pm$ 0.04
	Scarabaeidae			17.28 $\pm$ 3.75
		<i>Phyllopertha horticola</i>	I	17.19 $\pm$ 3.73
	Staphylinidae		I	0.85 $\pm$ 0.23
Lepidoptera				33.38 $\pm$ 1.92
	Arctiidae		I	0.21 $\pm$ 0.08
	Geometridae		L	0.7 $\pm$ 0.37
	Hesperiidae	<i>Hesperia comma</i>	L	0.01 $\pm$ 0.01
	Lasiocampidae		I	0.2 $\pm$ 0.07
	Lycaenidae		I	0.01 $\pm$ 0.01
	Noctuidae	mainly <i>Cerapteryx, Agrotis, Mythimna</i>	L	21.4 $\pm$ 2.62
	Nymphalidae	mainly <i>Issoria lathonia</i>	L	5.68 $\pm$ 2.14
	Pyrilidae	probably <i>Synaphe punctalis</i>	L	0.51 $\pm$ 0.28
Diptera				6.59 $\pm$ 1.72
	Asilidae	mainly <i>Philonicus albiceps</i>	I	5.66 $\pm$ 1.53
	Therevidae		I	0.18 $\pm$ 0.11
	Tipulidae		I	0.16 $\pm$ 0.11
Hymenoptera				1.1 $\pm$ 0.39
	Apidae			0.05 $\pm$ 0.05
	Formicidae		I	0.97 $\pm$ 0.39
	Ichneumonidae		I	0.04 $\pm$ 0.03
Neuroptera			I	0.01 $\pm$ 0.01
Gastropoda			–	2.48 $\pm$ 0.36
larva spec			–	5.95 $\pm$ 1.06
unidentified spec			–	1.18 $\pm$ 0.47

