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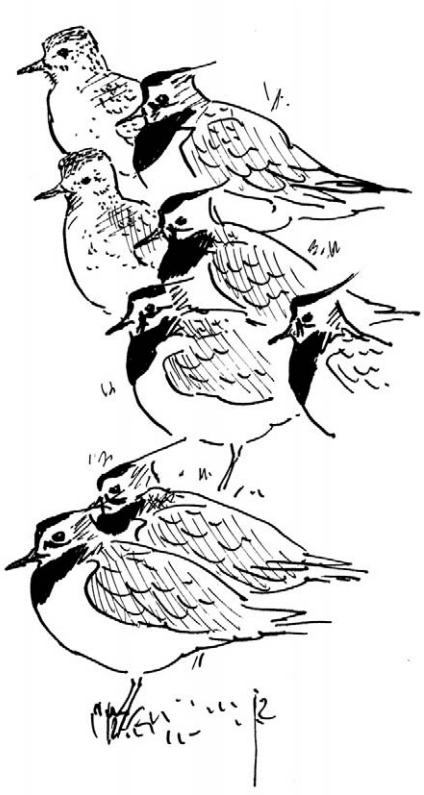
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Comparative diurnal and nocturnal diet and foraging in Eurasian Golden Plovers *Pluvialis apricaria* and Northern Lapwings *Vanellus vanellus* wintering on arable farmland

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Knowledge of diet and intake rates are useful first steps in understanding the distribution and behaviour of foragers. The diet of Golden Plovers and Lapwings feeding on arable farmland has been rarely studied, yet these species increasingly occupy this habitat in winter. They are known to feed at night but little is known about their diet and foraging success at night. This study aimed to describe and compare diurnal and nocturnal foraging behaviour in order to explain spatial and temporal patterns in foraging. Over three winters (1999/2000–2001/02) diurnal and nocturnal observations of focal individuals and collection of faecal samples were used to reconstruct diet and quantify intake rates across a range of arable habitats. Numerically, arthropods (mostly Carabids and millipedes) were the main diurnal prey types but by biomass, small earthworms were the major prey items. Diurnal intake rates were low but comparable with other studies of these species, prompting questions concerning the profitability of feeding on agricultural farmland and the pause–travel foraging mode. Nocturnal intake rates were up to 50% higher due to a greater reliance on catching large earthworms at night. Diurnal intake rates were highest during mild weather and on grass and sugar beet stubble fields; they were lowest on cereal crops, yet this was the habitat most consistently occupied. Current methods for assessing earthworm abundance limit further explanation of foraging behaviour.

Key words: diet, Golden Plover, Lapwing, earthworm, arthropod biometrics, nocturnal

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INTRODUCTION

Describing the diet of an organism is a key step in understanding the factors limiting its distribution. At the simplest level, determining an organism's diet and where those prey may be found reveals basic information about the potential distribution of that organism. However, diets are often complex, varying seasonally, geographically and between individuals and habitats. Moreover, patches

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may differ in the density, availability and profitability of prey items, leading to spatial and temporal variation in patch suitability. An understanding of these processes can enable better explanation of distribution and behaviour patterns. For instance, a thorough knowledge of the digestive constraints of Red Knot *Calidris canutus* allowed greater appreciation of observed prey selection (van Gils *et al.* 2005a) and explanation of forager distribution and movements (van Gils *et al.* 2005b).

We have previously shown marked spatial and temporal patterns in the distribution of foraging Eurasian Golden Plovers *Pluvialis apricaria* and Northern Lapwings *Vanellus vanellus* (Gillings *et al.* 2005, Gillings *et al.* 2007), yet there is only a limited literature on their diet on which to interpret these patterns. Both are predominantly invertebrate feeders (Cramp & Simmons 1983, Wilson *et al.* 1996). Collinge (1927) gave some information on Lapwing diet though it is unclear to which time of year or habitats the information relates. He states that 89% of the diet consists of animal food: 'injurious insects' (to crops) 60%, slugs and snails 10% and earthworms 10%. Vegetable material made up the remaining 11%. Cramp & Simmons (1983) describe the diet of the Golden Plover as "a wide spectrum of invertebrates, but principally beetles and earthworms". Earthworms eaten are largely of the genera *Lumbricus* and *Allolobophora* (Bengtson *et al.* 1978). Barnard & Thompson (1985) made the largest study of wintering plover diurnal foraging behaviour. Their work was undertaken in a largely pastoral landscape in central England where they determined that plover diet consisted almost entirely of earthworms.

No study has critically assessed the diet of Golden Plovers and Lapwings on arable farmland yet there are reasons to expect diets to differ markedly from those in pastoral systems. This is principally because earthworm populations are generally lower in arable farmland than in uncultivated habitats (Edwards & Bohlen 1996, Curry 1998). Earthworm size, biomass, species composition and abundance may be affected by a variety of factors, including: the intensity of tractor traffic (Hansen & Engelstad 1999); the degree of soil compaction (Jégou *et al.* 2002); the type and frequency of ploughing (Curry 1998, Emmerling 2001); application of nitrogen as manure (Curry 1998) versus slurry (Hansen & Engelstad 1999) or agrochemicals; crop type (Edwards & Bohlen 1996); and methods of disposal of crop residues (Edwards & Lofty 1979). For example, ploughing differentially affects the earthworm functional groups. Anecic species (large species with vertical burrows, e.g. *Lumbricus terrestris*) are adversely affected by ploughing whereas endogenic species (typically smaller with horizontal burrows) may benefit from ploughing because it mixes organic material from crop residues into the soil (Curry 1998). The resulting differences in worm abundance and worm size are likely to affect plover foraging decisions and mean that conclusions drawn from other systems where ploughing is infrequent may not apply to arable habitats.

With increasing numbers of Golden Plovers and Lapwings now wintering in the arable zone of eastern Britain (Gillings *et al.* 2006) there is a need to understand how such intensively managed farmland is utilised by these species. One way in which they may do this is by nocturnal foraging. There is mounting evidence that many wader species feed at night, and Golden Plovers and Lapwings do so on most mild nights (Gillings *et al.* 2005). No studies have determined the nocturnal diet of Lapwings or Golden Plovers. This study therefore aims to quantify the diurnal and nocturnal diet and intake rates of Golden Plovers and Lapwings wintering in intensively managed arable farmland. We also present biometric relationships that may be useful for future studies of diet in species that consume earthworms and arthropods in arable fields.

METHODS

The study was conducted in south Norfolk, eastern England (52°25'N, 01°03'E) during October to February of the three winters 1999/2000 to 2001/02. The study area included 213 fields totalling 2063 ha, arranged around four road tran-

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sects from which all fields could be scanned for plovers. The area was low-lying arable farmland and was predominantly used for cereal (65%) and sugar beet (13%) production with less than 5% pasture (see Gillings *et al.* (2007) for full details). On average the area supported 1000–2000 Golden Plovers and c. 1000 Lapwings, which, after accounting for aggregation in only a fraction of fields, gave mean usage densities of 1560 Golden Plover bird-days/ha and 1000 Lapwing bird-days/ha per winter (Gillings *et al.* 2007).

Focal observations and calibration

Focal individuals (Altmann 1973) of both species were observed for 3-min periods to determine the types and sizes of prey consumed. All observations were made from a concealed position in a parked vehicle. During the day, flocks were observed with a Kowa 20–60x83 telescope at a range of less than 200 m. Nocturnal observations were made using an image intensifier (Omega II model and 300 mm variable aperture Nikon SLR camera lens) and 1 million candle power camping lamp with infra red filter. At night it was only possible to record diet for individuals within c. 50 m of the vehicle. All focal observations were performed by one observer (SG) to exclude observer differences in prey size estimation (Lee & Hockey 2001).

Intake rate was quantified by categorising each peck. Due to distance, obscuring vegetation and the rapidity of the swallowing action, prey items could only be classified as earthworm or non-earthworm. Non-earthworm items were divided into two categories: 'Small' included all items up to half the bill length, and 'Medium' included all consumed items between half and one bill length. Neither small nor medium items could be identified to taxon by field observation and their identity was inferred through a combination of the prey types available in the soil and faecal sample analysis. All items larger than medium were earthworms. Since the energetic content of worms increases exponentially with worm length (Barnard & Thompson 1985), the length of earthworms caught was recorded as multiples of bill length (taken as 24 mm: Golden Plover: 21–26 mm, Lapwing: 22–26 mm, Cramp & Simmons 1983). In addition, whether or not the worm was stretched or unstretched when the length was estimated was recorded. Stretched worm categories were subsequently reassigned to unstretched length using conversions (see below). Plovers rarely failed to extract the whole earthworm. On the few occasions when worms were broken, the fragment length and the estimated size of the original worm were recorded.

Field estimation of the size of consumed prey cannot be considered free from error (Zwarts & Dirksen 1990, Lee & Hockey 2001). Moreover, since mass increases exponentially with length, small errors in size estimation can lead to large errors in intake estimates. A calibration test was performed upon completion of fieldwork to determine the accuracy of field estimates of earthworm sizes and to allow corrections as appropriate. In this blind trial, independent observers determined a frequency distribution and sample size of eight bill-length categories and reproducing these from 3-mm diameter cord. Using forceps a third independent observer held the 'cord worms' up to the bill of a mounted Lapwing in a randomised order for 2-sec periods and SG estimated worm size in multiples of bill length (1x to 8x). The order of the cord worms was randomised, and the procedure repeated a second and third time to give three field estimates of the length of each 'cord worm'. Three matrices of actual size and estimated size were produced containing the percentage of worms falling in each cell. Mean values were calculated across the three matrices to give a matrix of correction factors for each possible combination of estimated size and actual size.

Faecal sample collection and analysis

Faecal samples were collected throughout the winter of 1999/2000 from fields where plovers had been feeding. It was rarely possible to identify droppings to species because most flocks were mixed. Where possible, samples were also obtained from fields where plovers may have been feeding at night by collecting samples from fields that had not been used for daytime feeding.

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Between 10 and 20 samples were collected per field by walking a straight 2 m wide transect through the area where plovers had been feeding. In the laboratory, each sample was spread evenly over a Petri dish marked with lines 8 mm apart and viewed at 6x magnification under a binocular microscope. All identifiable items were counted (e.g. setae, mandibles, arthropod legs, spider chelicari) and lengths and/or widths measured (to nearest 0.1 mm) at 16x magnification. There is wide variation in earthworm seta length for individual worms (Green & Tyler 1989) so seta lengths were not measured. No attempts were made to convert faecal contents into proportional diet due to expected differences in throughput rates and differential digestibility of the various taxa consumed (e.g. Green & Tyler 1989).

Soil sampling and reference material

Previous studies and initial observations suggested measurement of earthworm densities and availability was important. Several reviews have considered techniques for sampling communities or collecting live undamaged specimens for laboratory studies (e.g. Raw 1960, Nordström & Rundgren 1972, Springett 1981, Bouché & Gardner 1984, Daniel *et al.* 1992, Gunn 1992, East & Knight 1998). Use of a chemical vermifuge, formerly formalin and more recently mustard solution, is widely advocated because it is relatively time efficient (Gunn 1992, East & Knight 1998). However, chemical extraction typically underestimates total earthworm biomass (Svendsen 1955, Bouché & Gardner 1984) and is unsuitable for measuring prey abundance for predation studies because the depth sampled cannot be controlled and the penetration of the chemical irritant depends upon soil porosity and water-logging (Nordström & Rundgren 1972). This method is also unsuitable for assessing the abundance of different size classes because the earthworm's escape response is age- and species-specific due to differences in diapause patterns and the direction and stability of burrow systems (Nordström & Rundgren 1972, Bouché & Gardner 1984). Finally, soil cores suffer from avoidance behaviour of earthworms, with potential lateral escape of near-surface dwelling species and vertical escape of deep-burrowing species.

No satisfactory means of assessing earthworm abundance could be identified for this study. Soil coring followed by hand-sorting and washing was selected as the most effective method (Raw 1960, Bouché & Gardner 1984), but was only used for an inventory of available prey types and sizes. Soil cores were 35 mm deep by 200x200 mm square. The depth was selected as c. 1.5 times a plover's bill length (c. 24 mm) because plovers, especially Lapwings, often probe persistently in one spot, enlarging a small hollow allowing access to slightly deeper buried prey than their bill length would initially suggest. Many Lapwings have muddied forehead and loral areas as a result (pers. obs.). Ten cores were taken per field and the material was bagged and taken to the lab. Cores were wet sieved through a 1 mm sieve and a jet of water used to tease apart soil clods and root matter to release invertebrates, ensuring that worms were not broken in the process.

A reference collection of invertebrates encountered on the soil surface of fields was also made and further samples of earthworms were collected for biometric analyses. Where possible, earthworms and their cocoons were identified to species using Gerard (1964). Beetle larvae and adults were identified to family using Chu (1949) and Joy (1932), respectively. Other invertebrates were identified using Chinery (1993).

Reconstructing diet and invertebrate size

Relationships between length and biomass were required to estimate intake rate from field observations of the size of items consumed or arthropod fragments found in faeces. All invertebrates found in soil cores and the reference collection were measured (maximum body length for arthropods, relaxed/unstretched and stretched length for all earthworms) and wet weighed (nearest 0.0001 g). Each arthropod was dissected and the length of mandibles and limb segments recorded. All the fragments of each individual were retained so that the whole organism could then be dried and

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burned to derive ash free dry mass (AFDM). Since some earthworms broke whilst being extracted from the ground by plovers, we calculated the standardised wet mass per mm for different size worms (after Barnard & Thompson 1985). Dry mass was recorded after 2 days drying at 75°C and ash mass was recorded after burning for 2 hours at 550°C, and AFDM was calculated by subtraction. For some very small prey types, items had to be combined into batches of three or more individuals and length–AFDM regressions were performed using the mean length of the items in a batch and the mean AFDM of a single item (AFDM/number of specimens in batch).

Size and size–weight relationships were determined by least-squares regression. Though both the dependent and independent variables may be subject to error, Sokal and Rohlf (2000) suggest that for predictive purposes simple linear regression techniques (Model I) are acceptable. Size–weight relationships were quantified after logging both axes (Sokal & Rohlf 2000). Length-to-length relationships were quantified using untransformed variables and intercepts fixed at zero because visual inspection of the distributions showed that all variables were normally distributed. Due to the exponential relationship between length and AFDM, calculating AFDM based on the mean length of a sample of organism may underestimate the mean AFDM of the sample (Goss-Custard *et al.* 2002). Instead AFDM was calculated for increments of length and the mean calculated by weighting these AFDM values by their relative abundance in the sample.

The size of prey items found in soil cores was compared to those in the diet to determine if plovers preferentially selected certain size classes of prey. Worms broken during soil coring present a problem since large worms are more likely to be cut in half by the core and would cause a bias in estimates of available worms if omitted. Therefore it was necessary to estimate the original size of any worms broken in the coring process. This was done by using the relationship between total length and standardised wet mass (mg/mm) to estimate the original total body length of fragments.

Statistical analysis

All means are presented ± 1 SE. All analyses were performed in SAS (SAS Institute Inc 2001) using either the Genmod or Npar1way procedures. Tests of differences in intake rate between species used a subset of data in which at least five individuals of each species were observed in the same field on the same day, with field being used as a fixed effect. The influence of a series of environmental variables on intake rate (expressed as AFDM or items) was tested using univariate tests. Variables included field habitat, month, hour of observation, weather variables (from a nearby weather station) and percentage moon phase (from US Naval Observatory, http://aa.usno.navy.mil). Analyses using AFDM rates used log(x+1) transformed variables and normal distributed errors but whereas for graphical purposes, the units were mg AFDM s^{-1}, analysis units were mg AFDM min^{-1} to reduce problems associated with adding 1 to a very small number in the transformation. For analyses using the number of prey items, a log link function and Poisson error distribution was used with ln(time) as an offset variable to convert numbers to items per second. For over dispersed models in which deviance divided by degrees of freedom deviated from 1, the scale parameter was estimated by the square root of deviance/df. The effects of independent variables were tested using likelihood ratio tests with significance tested against the chi-squared distribution.

RESULTS

Invertebrates present in arable fields

An inventory of possible prey was made from 170 soil samples plus additional ad hoc searches of fields. Potential prey included earthworms, adult and larval stages of Carabid and Staphylinid beetles, Meloidae beetle larvae, adult weevils, Diptera larvae and pupae, black millipedes (*Cylindroiulus* and *Tachypodoiulus* genera), flat-backed millipedes (*Brachydesmus* and *Polydesmus* genera) and low numbers of slugs, spiders and earthworm cocoons. None of the earthworms sampled from fields were

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identified to species because the majority were immatures and difficult to identify. However, earthworm cocoons extracted from soil cores suggested the presence of the following species (number of cocoons in parentheses): *Lumbricus terrestris* (3), *Allolobophora caliginosa* (2), *A. chlorotica* (4), *A. longa* (3) and possibly *A. rosea* (11).

Biometrics of invertebrates

For all the main invertebrate groups identified there were significant exponential relationships between length and mass (Appendix 1). Stretched worms were on average 69% longer than unstretched worms. When converted to ash, worms weighed only approximately 12% of their original wet mass. These relationships were used in determining the size and biomass of prey items observed in focal observations and faecal samples. Insufficient weevils and spiders were found to perform regressions. For these groups the observed mass of samples from the field was used.

There were strongly significant positive linear relationships between length or width of body parts and total beetle length (Appendix 2). The length of Carabid femurs from fore, mid and hind legs were all positively related to body length. However, since it was rarely possible to ascertain from which leg a femur found in a faecal sample originated, a generic relationship calculated across all legs was determined and this was also a good predictor of body length (Appendix 2).

Diurnal diet: prey type and size

There was a statistically significant difference between species in the broad categories of prey captured by day ($\chi^2_2 = 19.4$, $P < 0.001$) though biologically, the differences were small (Table 1). Despite worms constituting only a small proportion of the number of items, they were likely to have a disproportionate effect on intake due to their relatively high biomass. Focal observations of 16 Golden Plovers (7%) and 25 Lapwings (5%) yielded no prey intake during the 3-min period. In the remainder of focal individuals, earthworms were absent in the intake of 50% of Lapwings and 56% of Golden Plovers and this proportion did not differ between species ($\chi^2_1 = 1.5$, $P > 0.2$).

The identification of small and medium prey items had to be inferred from remains found in faecal samples. In total, 133 faecal samples were collected from diurnal flocks feeding in nine fields (Table 2). These contained the remains of most invertebrates found in soil samples, though in small number. Indeed 32% of diurnal faecal samples contained no identifiable prey remains. By day, the most abundant prey remains were of adult beetles (mostly Carabid and Staphylinid) which occurred in 54% of faecal samples. Earthworm setae were found in 25% of samples and though the number per sample varied from 0 to 29, the overall median was 0.

In the winter of 1999/2000, whether earthworms were stretched or unstretched when consumed was not noted, but across the following two

Table 1. Summary of the prey types captured during day and night by focal Lapwings and Golden Plovers. Sample sizes (number of focal individuals, number of items) are given. Earthworm size distribution is the percentage each worm size made up of the total captured (after applying correction factors from Appendix 1).

Species	Period	Sample size		% prey type			Earthworm size distribution (%)							
		Inds	Items	Small	Medium	Worm	1x	2x	3x	4x	5x	6x	7x	8x
Lapwing	Day	498	3196	80	7	13	19	31	20	15	8	5	2	<1
	Night	25	59	53	8	39	0	0	29	29	24	18	0	0
Golden Plover	Day	223	996	74	11	15	14	30	21	18	11	5	2	<1
	Night	32	67	67	9	24	19	20	17	10	11	10	13	0

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Table 2. Summary of the collection details and contents of plover faecal samples. Period is Day(D) or Night (N) feeding. Habitat codes are CC: cereal crop, CR: oilseed rape crop, GG: grass pasture, EH: harrowed earth, SS: sugar beet stubble. n is number of faecal samples from each field (A – M). Setae: median number of setae per dropping. Content is expressed as the percentage of samples that contained prey items of each type.

Collection details					Setae	Percentage of samples containing:										
	Date	Period	Habitat	*n*		Nothing	Worm	Beetle[a]		Weevil	Millipede	Spider	Diptera			Ant
								Adult	Larva				Larva	Pupa	Adult	
A	09/11/99	D	EH	10	0	20	10	60	10	0	30	0	0	0	0	0
B	09/11/99	D	CC	10	1.5	20	60	60	10	0	0	30	0	0	0	0
C	15/11/99	D	CC	13	0	38	8	62	8	8	8	0	0	0	0	0
D	17/11/99	D	SS	10	0.5	10	50	70	0	0	10	0	0	0	0	0
E	23/11/99	N	SS	10	0	0	40	60	20	0	50	0	50	30	0	0
F	01/12/99	D	EH	20	0	35	30	45	5	5	0	5	0	5	5	0
G	01/12/99	D	GG	20	0	35	10	55	15	0	0	0	5	0	0	0
H	10/12/99	D	GG	20	0	35	10	60	5	5	0	0	0	0	0	0
I	12/12/99	D	CC	20	0	35	35	55	0	10	5	0	0	0	0	5
J	13/02/00	N	CC	10	46.5	0	100	0	0	0	0	0	0	0	0	0
K	18/02/00	D	CC	10	0	40	30	20	20	0	0	0	0	0	0	0
L	25/02/00	N	CR	6	2.5	17	67	17	17	0	0	0	0	0	0	0
M	25/02/00	N	CC	10	0	50	40	0	10	0	0	0	0	0	0	0
Day summary				133	0	32	25	54	8	4	5	3	1	1	1	1
Night summary				36	4.5	17	61	19	11	0	14	0	14	8	0	0

[a]Mostly Carabid and Staphylinid beetles

winters only 7% of all worms captured by plovers were observed in a stretched state. To allow combination of data across winters, all worms lengths from 1999/2000 were assumed to have been estimated when unstretched. After correcting for observer error in size estimation (see Appendix 3) the frequency distribution of worm size categories was right skewed with the modal size class being 2x bill length (Fig. 1, Table 1). There was no significant difference in the size distribution of earthworms captured by day between plover species ($\chi^2_6 = 3.5$, $P > 0.7$, Fig. 1, Table 1). Worm of sizes 1–4x bill length accounted for 80% of worms captured.

For non-earthworm prey, equations from Appendix 2 were used to estimate the original body size of prey items based on fragments found in faecal samples. Where estimates could be made from several different body parts it was necessary to determine which method was least likely to produce biased estimates. Carabid parts were found and measured in the following frequencies: mandible ($n = 3$), femur ($n = 52$), tibia ($n = 45$), elytra width ($n = 12$), and elytra length ($n = 10$). Estimates of beetle length derived from mandibles, femurs and tibias did not differ significantly (5.9 ± 1.8, 5.7 ± 0.3 and 5.2 ± 0.3 mm, respectively, Kruskal-Wallis $\chi^2_2 = 2.1$, $P = 0.34$). Those from elytra width (3.8 ± 0.2 mm) and length (4.7 ± 0.7 mm) differed significantly from those from mandibles, femurs and tibias (Kruskal-Wallis $\chi^2_1 = 10.4$, $P = 0.001$). This was probably because elytra from larger beetles were broken into unidentifiable and/or immeasurable fragments. Therefore, femurs were used to calculate Carabid body size. In contrast Staphylinid beetle length estimates derived from mandibles and elytra did not differ significantly (Kruskal-Wallis $\chi^2_2 = 0.78$, $P > 0.6$).

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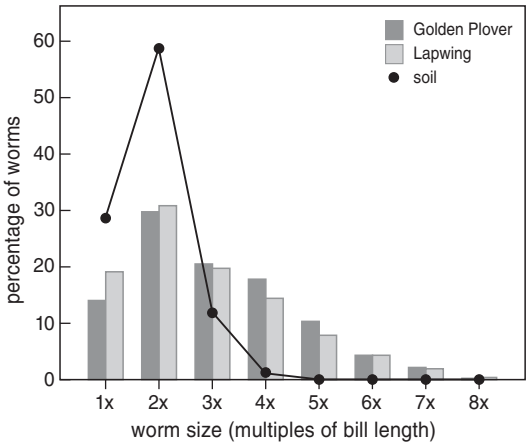


Figure 1. Size distribution of earthworms caught by diurnal foraging Golden Plovers (n = 158), Lapwings (n = 435) and those found in soil cores taken during the day (n = 442).

Staphylinids have much reduced elytra which are perhaps less likely to be fragmented. Since no biometric relationships were available for weevils, equations for Carabids were used since they were similarly proportioned and yielded a mean length of 5.0 mm which compared well with the 4.8 mm of weevils found in soil samples.

Nocturnal diet: prey type and size

Nocturnal focal observations were difficult to obtain because plovers were rarely sufficiently close to determine whether pecks were successful so only small sample sizes were achieved (Table 1). There was a suggestion of differences in diet between day and night (Table 1) with a significant difference in the number of small, medium and earthworm prey items eaten by Lapwings between day and night ($\chi^2_1 = 36.7$, $P < 0.01$). For Golden Plover the trend was similar but not significant ($\chi^2_1 = 3.5$, $P > 0.1$). There were insufficient observations of nocturnal worm predation to test critically whether the size of worms eaten differed between day and night though there appeared to be more medium and large sized worms eaten by Lapwings and a more even spread of all sizes by Golden Plovers than was apparent during the day (Table 1).

Thirty-six faecal samples from four fields were thought to originate from nocturnal feeding plovers (Table 2). These contained significantly greater numbers of setae than faecal samples from day feeding (range 0–134, median 4.5, Kruskal-Wallis $\chi^2_1 = 22.9$, $P < 0.0001$). This was largely due to the contents of the ten faecal samples from field J in which the number of setae per sample varied from 16 to 134. Notably these samples were devoid of any other prey items.

Diurnal prey selectivity

Comparisons of the size of daytime consumed versus daytime available prey items were possible for earthworms and carabid beetles; samples sizes of other prey items were insufficient. Though the modal worm size consumed by both species and available in the soil was 2x bill length, consumption of large worms exceeded their apparent availability (Fig. 1). The frequency distribution of worms of different sizes differed significantly between the soil and the combined diet of both species ($\chi^2_3 = 198.6$, $P < 0.001$). Similarly, the frequency distribution of beetle lengths differed significant between captured and available beetles (Kolmogorov-Smirnoff $KSa = 1.45$, $P = 0.03$), with those from faecal samples averaging slightly larger, though not significantly so (Kruskal-Wallis $\chi^2_1 = 3.8$, $P = 0.052$).

Diurnal intake rates

For intake rate calculations, AFDM values for small and medium sized items were taken as 1 mg AFDM and 3 mg AFDM respectively based on figures from Appendix 3. Diurnal AFDM intake rates for Golden Plover and Lapwing were highly variable and highly skewed (skewness 2.6 and 4.5, respectively) (Fig. 2) with mean diurnal intake rates of 0.36 mg AFDM s^{-1} (range 0.00–3.23) and 0.38 mg AFDM s^{-1} (range 0.00–8.28), respectively (Fig. 2). Significantly higher diurnal intake rates were achieved when earthworms were consumed, being 37 times higher in Golden Plover and 17 times higher in Lapwing (Fig. 2, Golden Plover ANOVA LR $\chi^2_1 = 721$, $P < 0.0001$; Lapwing LR $\chi^2_1 = 1164$, $P < 0.0001$). Total diurnal intake rate

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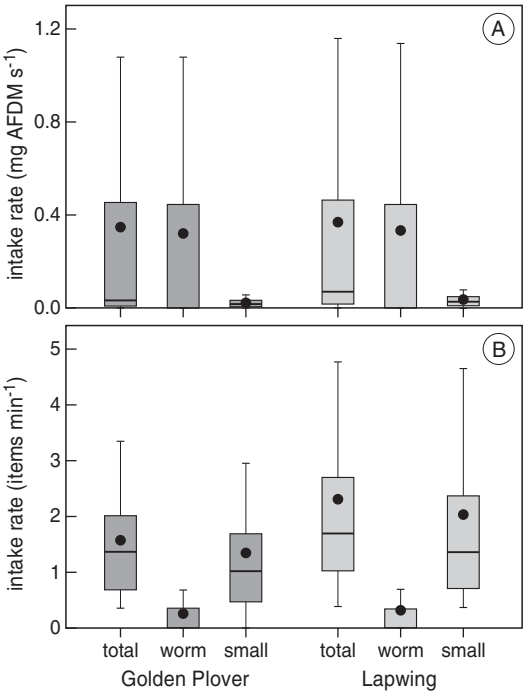


Figure 2. Diurnal intake rates of Golden Plover and Lapwing expressed as A) ash free dry mass per s and B) items consumed per minute (see Table 1 for sample sizes). In each case the total intake is shown along with that arising separately from consumption of earthworms or small and medium size items. Boxes show quartile range, line = median, black dot = mean, whiskers = 10th and 90th percentiles.

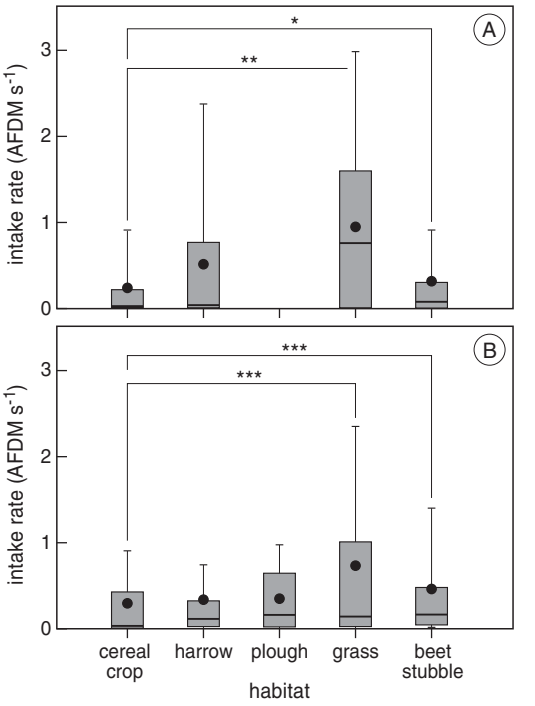


Figure 3. Box plots of diurnal intake rates (AFDM s^{-1}) on different habitat types by A) Golden Plover and B) Lapwing. Boxes represent the quartile range, the line represents the median and the black dot the mean, whiskers show the 10th and 90th percentile of intake rate. Linking lines and asterisks indicate significant difference between linked habitats (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

did not differ significantly between species ($\chi^2_1 = 0.83$, $P = 0.4$).

For both species, most variation in diurnal intake rates was explained by significant differences between habitats (Fig. 3, Table 3), and for Golden Plover also between months (Table 3). Month and habitat were highly correlated and after controlling for habitat type, month explained little extra variation in Golden Plover intake rates ($\chi^2_4 = 11.4$, $P = 0.02$). Intake rates were highest on grass, followed by plough and harrow, sugar beet stubble, and lowest on cereal crop but the only significant pairwise differences were between cereal crop and either sugar beet stubble or grass (Fig. 3). Golden Plover intake rate increased with increasing temperature but only a weak relationship with minimum air temperature was evident for Lapwings (Table 3). These positive temperature effects remained after controlling for habitat differences (Golden Plover $\chi^2_1 = 6.8$, $P = 0.009$; Lapwing, $\chi^2_1 = 4.8$, $P = 0.03$). Golden Plover intake rate also increased with increasing rainfall and decreasing moon phase. The same patterns were found when quantifying intake rate in terms of number of earthworms consumed (Table 3) with the surprising exception of a relationship with rainfall.

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Table 3. Results of univariate regression and ANOVAs relating environmental and temporal variables to (A) log(x + 1) diurnal AFDM intake rates and (B) number of earthworms eaten per second. Symbols represent significance: * for categorical differences, + for positive linear relationships, – for negative linear relationships; one symbol: $P < 0.05$, two symbols: $P < 0.01$, three symbols: $P < 0.001$.

A AFDM of prey

Variable	Golden Plover			Lapwing		
	df	Dev	LR test	*df*	Dev	LR test
Habitat	210	463	$\chi^2_3 = 14.5$**	490	994	$\chi^2_4 = 20.1$***
Month (Oct–Feb)	209	459	$\chi^2_4 = 16.4$**	490	1017	$\chi^2_4 = 8.9$
Hour	212	490	$\chi^2_1 = 2.1$	493	1031	$\chi^2_1 = 1.7$
Minimum air temperature	212	478	$\chi^2_1 = 7.6$++	493	1027	$\chi^2_1 = 4.1$+
Maximum air temperature	212	487	$\chi^2_1 = 3.6$	493	1032	$\chi^2_1 = 1.6$
Soil temperature (20 cm)	212	477	$\chi^2_1 = 8.0$++	493	1029	$\chi^2_1 = 2.7$
Windrun	212	492	$\chi^2_1 = 1.5$	493	1031	$\chi^2_1 = 2.1$
Rainfall	212	483	$\chi^2_1 = 5.7$+	493	1034	$\chi^2_1 = 0.6$
Moon phase	212	477	$\chi^2_1 = 8.2$––	493	1034	$\chi^2_1 = 0.6$

B Number of worms eaten

Variable	Golden Plover			Lapwing		
	df	Dev	LR test	*df*	Dev	LR test
Habitat	210	263	$\chi^2_3 = 13.0$**	490	708	$\chi^2_4 = 22.3$***
Month (Oct–Feb)	209	251	$\chi^2_4 = 23.3$***	490	728	$\chi^2_4 = 8.5$
Hour	212	279	$\chi^2_1 = 0.5$	493	729	$\chi^2_1 = 7.2$++
Minimum air temperature	212	262	$\chi^2_1 = 14.0$+++	493	740	$\chi^2_1 = 0.3$
Maximum air temperature	212	272	$\chi^2_1 = 5.3$+	493	740	$\chi^2_1 = 0.0$
Soil temperature (20 cm)	212	262	$\chi^2_1 = 13.4$+++	493	739	$\chi^2_1 = 0.7$
Windrun	212	276	$\chi^2_1 = 2.7$	493	739	$\chi^2_1 = 0.5$
Rainfall	212	275	$\chi^2_1 = 3.3$	493	740	$\chi^2_1 = 0.3$
Moon phase	212	270	$\chi^2_1 = 7.4$––	493	738	$\chi^2_1 = 1.5$

Nocturnal intake rates

As during the day, nocturnal intake rates for Golden Plover and Lapwing were highly variable and highly skewed with mean intake rates of 0.37 mg AFDM s^{-1} (range 0.00–3.66) and 1.13 mg AFDM s^{-1} (range 0.00–5.37) respectively. After combining data across species, nocturnal intake rates were 50% higher than diurnal intake rates ($\chi^2_1 = 5.5$, $P = 0.02$). There were insufficient nocturnal data to perform species tests or paired day-night analyses to control for effects of habitat and season.

DISCUSSION

Through a combination of focal observations and faecal sampling this study describes the main components of the diurnal and nocturnal diet of Golden Plovers and Lapwings on arable farmland. As with other studies, earthworms are important, but we also find appreciable predation of beetles. These results suggest that plovers achieved higher intake rates at night, probably through greater reliance on captures of large earthworms.

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Prey type and prey size

During the day, Golden Plovers and Lapwings captured similar sized earthworms, mostly 1–3× bill length (<72 mm) in agreement with earlier studies on pastoral farmland (Bengtson *et al.* 1978, Barnard & Thompson 1985). Large earthworms were captured more often than expected based on their availability in the soil. A caveat must be added that the sampling technique may have missed large worms (escaping down their vertical burrows) whilst still capturing smaller surface dwelling worm species. Small adult and larval Carabid and Staphylinid beetles and millipedes accounted for the majority of the remaining 85% of prey items. However, without controlled laboratory experiments to quantify differential digestibilities of these arthropods (e.g. Green & Tyler 1989) it is impossible to determine their relative importance.

Consumed adult Carabids were less than 5–6 mm in length and millipedes approximately 10 mm in length. There was no clear directional difference in the size of Carabid beetles in the soil and those consumed by plovers as there was for earthworms. It is difficult to obtain information from other studies on the importance of non-earthworm prey in the diet of wintering plovers since earthworms are usually considered the sole important prey type (e.g. Barnard & Thompson 1985, Byrkjedal & Thompson 1998). There is some justification for this in that although earthworms accounted for only 13–15% of items eaten by plovers, they accounted for the majority of energetic intake because all other prey were of low biomass: even a 2× bill earthworm (36 mm) weighed 20 mg AFDM which was six times more than a typical Carabid.

Which earthworm species do plovers consume? Cramp and Simmons (1983) list the main species as being from the genera *Allolobophora* and *Lumbricus*. Golden Plovers collected in Iceland in spring had *Allolobophora caliginosa* and *Lumbricus rubellus* in their stomachs, with the former being more abundant (Bengtson *et al.* 1978). Based on cocoons, at least five earthworm species were present in the arable fields but the relative abundance of different earthworm species cannot be inferred from these data because different species produce cocoons at different depths (Gerard 1964). It is likely that during the day the main plover prey are *A. caliginosa* and *A. chlorotica* which are unpigmented topsoil feeders and are usually the two most abundant earthworm species in arable soils (Edwards & Bohlen 1996). At night probably these two species are supplemented by the availability of the larger *L. terrestris* which forms vertical burrows and only comes up to the soil surface at night (Edwards & Bohlen 1996). This may explain the suggestion that more large earthworms were consumed at night than during the day.

These estimates of dietary composition are not free from biases. Compared to their numeric abundance in soil samples Diptera larvae and slugs were the main invertebrate groups that were scarce or lacking in faecal samples. Both these soft-bodied invertebrates are unlikely to leave identifiable remains in faecal samples yet are probably present in the diet (perhaps especially slugs at night). It is notable that the one batch of faecal samples (E) in which Diptera larvae and pupae were numerous was from a sugar beet stubble field and this is the habitat in which these items were most abundant in soil samples (pers. obs.). Also, the likelihood of detection of beetles in faecal samples is high due to large number of highly characteristic fragments per individual (2 elytra, 2 mandibles, multiple antenna segments, 18+ limb parts).

Diurnal and nocturnal intake rates

Diurnal intake rate achieved by Golden Plovers and Lapwing feeding on a variety of agricultural fields were highly variable, and depended on the inclusion of earthworms in the diet. The highest intake rates were only achieved if earthworms were consumed during the focal period. Variance might be partly attributable to individual differences although aggressive encounters and conspecific kleptoparasitism of the type seen in Oystercatchers (Ens & Cayford 1996) were rare. Individuals may differ in their skill at finding and capturing earthworms and measures of pause–travel

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Table 4. Estimates of diurnal intake rate (mg AFDM s^{-1}) for Golden Plovers (GP) and Lapwings (L) on a range of habitat types. For comparison, intake rates are also given for Black-tailed Godwit *Limosa limosa* (BG). Intake rate was determined empirically in sources b and d. For sources a and c, intake rate (mg AFDM s^{-1}) was estimated from other intake parameters presented by the authors and allometric relationships from this paper.

Species	Habitat	Prey type	Intake rate	Source
GP	Young pasture	Earthworms	0.02–0.30	a
	Old pasture	Earthworms	0.23–0.40	a
L	Pastures	Earthworms	0.07–0.52	a
L	Wet grass	Mixed (inc. earthworms)	0.01–1.31 (mean 0.48)	b
GP	Grass	Mixed (inc. earthworms)	0.02	c
	Plough	Mixed (inc. earthworms)	0.01	c
	Estuary	Mixed (inc. *Nereis*)	0.04	c
L	Grass	Mixed (inc. earthworms)	0.02	c
	Plough	Mixed (inc. earthworms)	0.01	c
	Cereal stubble	Mixed (inc. earthworms)	0.06	c
	Harvested potato	Mixed (inc. earthworms)	0.03	c
	Estuary	Mixed (inc. *Nereis*)	0.01	c
BG	Wet grass	Earthworms	4–5	d

Sources:
a: Barnard and Thompson (1986). Calculated as follows: captures per second from Fig. 6.6 therein, worm length from Table 6.5 therein, and length–AFDM relationship from Appendix 1 of this paper.
b: S. Gillings, unpublished data, Gaast, Netherlands, November 2002.
c: S.R. Baillie (1976). Calculated as follows: mm of worm eaten per hour divided by worms eaten per hour from Table 20 therein, converted to mg AFDM using length–AFDM relationships in Appendix 1 of this paper (also applied to Nereis). AFDM value for small and median prey items assumed as 1 mg and 3 mg as herein. Intake summed across prey categories and converted from hours to seconds.
d: J.A. Gill, unpublished data, Hampshire, England.

foraging suggested that individuals differed in the distances at which they could detect prey (Gillings 2003).

The majority of diurnal intake rates observed were low: 90% were less than 1 mg AFDM s^{-1}, 50% were less than 0.1–0.2 mg AFDM s^{-1}. Such high skew in diurnal intake rates has also been shown for Whimbrel *Numenius phaeopus* (Zwarts & Dirksen 1990). Table 4 gives diurnal intake rates estimated from other studies of Golden Plovers and Lapwings. The estimates calculated from Baillie (1976) are likely to be underestimates since mean worm length was used to calculate AFDM, and any wide variance in worm length will yield disproportionately high AFDM values due to the exponential worm–AFDM relationship. Nonetheless, given the variety of methods used by different authors and the crude methods needed to convert figures to common units, it is striking that most plover diurnal intake rates were less than 0.5 mg AFDM s^{-1}, many were an order of magnitude lower, and all were in the same range as those calculated in this study. They were also two orders of magnitude lower than diurnal intake rates achieved by Black-tailed Godwits *Limosa limosa* feeding on earthworms in wet grassland. Are these low intake rates typical for waders feeding in agricultural habitats? Comparable intake rates of godwits and plovers in the same location would be informative. Alternatively, are low intake rates typical of pause–travel foragers such as plovers? Such species spend significant portions of 'foraging time' motionless, either scanning for prey or engaged in vigilance. Thus estimates of intake rate could be artificially low if vigilance time was inadvertently incorporated in the calculations. Also, in this study

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plovers walked the equivalent of 4–7 m on average for each prey capture (Gillings 2003). This is a much greater distance than suggested by Metcalfe (1985) for Lapwings on mudflats and might go towards explaining the low intake rate. A comparative study of pause–travel foragers and their intake rates on farmland and intertidal habitats but would be interesting.

Weak positive relationships were detected between temperature and diurnal intake rate for both species as already shown by Barnard & Thompson (1985). These are to be expected since cold weather causes earthworms to retreat deeper into the soil (Edwards & Bohlen 1996) where they cease to be available to foraging plovers. Similar relationships between temperature and intake rate mediated by prey behaviour are apparent in intertidal systems (Goss-Custard 1969, Pienkowski 1983a, 1983b). It is not clear why Golden Plover diurnal intake rates were lowest when the moon was full. Since diurnal intake rates were lowest on cereal crops and highest on grass. it is surprising that these plovers feeding on arable farmland spend up to 70% of their diurnal foraging time on cereal crops and virtually ignore grass (Gillings *et al.* 2007). Harrow, plough and sugar beet stubbles were ephemeral in nature and present for few days. These fields, with their recently disturbed soil may provide suitable feeding conditions for short periods of time and may be used opportunistically by plover flocks.

Nocturnal intake rates were up to 50% greater than diurnal intake rates. McLellan (1979) also found that Lapwing's nocturnal intake rates were twice as high as diurnal intake rates. High intake rates at night are to be expected for several reasons. Darkness does not hinder foraging plovers since they have specialised night vision (Rojas de Azuaje *et al.* 1993, Rojas *et al.* 1999) and may be capable of locating prey through auditory cues (Lange 1968). The absence of gulls at night frees plovers from kleptoparasitism, potentially allowing them to eat large earthworms that were unprofitable due to the risk of theft during the day. Finally, larger 'anecic' earthworm species (e.g. *Lumbricus terrestris* and *Allolobophora longa*) forage on the soil surface at night in addition to the smaller earthworm species normally present near the soil surface. More setae in faecal samples from nocturnal feeding areas and nocturnal focal observations showing capture of larger average worm size confirm that high nocturnal intake rates are achieved through predation of large earthworms.

Conclusions

Golden Plovers and Lapwing feeding on arable farmland in winter have a diet dominated by earthworms and beetles which yields low diurnal intake rates. Nocturnal foraging may allow plovers to exploit alternative more profitable prey types, yielding higher intake rates that may be essential for successfully balancing energy budgets. Indeed nocturnal foraging may be the preferred strategy. More work is required to understand the functional relationships between prey density and intake rates for explaining patterns of habitat selection and day–night activity. However, there is a clear need for a repeatable and efficient method for assessing earthworm abundance for predation studies such as this.

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Appendices are available at www.ardeajournal.nl

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REFERENCES

Altmann J. 1973. Observational study of behaviour: sampling methods. Behaviour 49: 227–267.

Baillie S. 1976. The utilisation of estuarine and agricultural habitats by Lapwings (*Vanellus vanellus* L.) and Golden Plover (*Pluvialis apricaria* L.). Unpublished BSc thesis, University of Aberdeen.

Barnard C.J. & Thompson D.B.A. 1985. Gulls and plovers: the ecology and behaviour of mixed-species feeding groups. Croom Helm, London.

Bengtson S.A., Rundgren S., Nilsson A. & Nordström S. 1978. Selective predation on lumbricids by golden plover *Pluvialis apricaria*. Oikos 31: 164–168.

Bouché M.B. & Gardner R.H. 1984. Earthworm Functions .VIII. Population Estimation Techniques. Revue D Ecologie et de Biologie Du Sol 21: 37–63.

Byrkjedal I. & Thompson D. 1998. Tundra plovers: the Eurasian, Pacific and American Golden Plovers and Grey Plover. T. & A.D. Poyser, London.

Chinery M. 1993. Insects of Britain and Northern Europe. Third edition. Collins, London.

Chu H.F. 1949. How to know the immature insects. WM. C. Brown Co. Publishers, Dubuque, Iowa.

Collinge W.E. 1913. The food of some British wild birds: a study in economic ornithology. Dulau, London.

Cramp S. & Simmons K.E.L. 1983. Handbook of the birds of Europe, Middle East and North Africa: the birds of the western palearctic, Vol. III, Waders to Gulls. Oxford University Press, Oxford.

Curry J.P. 1998. Factors affecting earthworm abundance in soils. In: Edwards C.A. (ed) Earthworm ecology: 37–64. St. Lucie Press, London.

Daniel O., Jager P., Cuendet G. & Bieri M. 1992. Sampling of *Lumbricus terrestris* (Oligochaeta, Lumbricidae). Pedobiologia 36: 213–220.

East D. & Knight D. 1998. Sampling soil earthworm populations using household detergent and mustard. J. Biol. Education 32: 201–206.

Edwards C.A. & Bohlen P.J. 1996. Biology and ecology of earthworms. Third edition. Chapman & Hall, London.

Edwards C.A. & Lofty J.R. 1979. The effects of straw residues and their disposal on the soil fauna. In: Grossbard E. (ed) Straw decay and its effect on disposal and utilization: 37–44. Wiley, New York.

Emmerling C. 2001. Response of earthworm communities to different types of soil tillage. Appl. Soil Ecol. 17: 91–96.

Ens B.J. & Cayford J.T. 1996. Feeding with other oystercatchers. In Goss-Custard J.D. (ed) The oystercatcher: from individuals to populations: 77–104. Oxford University Press, Oxford.

Gerard B.M. 1964. The Linnean Society of London synopses of the British fauna: No 6. Lumbricidae (Annelida). Second edition. The Linnean Society of London, London.

Gillings S. 2003. Diurnal and nocturnal ecology of Golden Plovers *Pluvialis apricaria* and Lapwings *Vanellus vanellus* wintering on arable farmland. Unpubl. PhD thesis, University of East Anglia, Norwich, UK.

Gillings S., Austin G.E., Fuller R.J. & Sutherland W.J. 2006. Distribution shifts in wintering Golden Plovers *Pluvialis apricaria* and Lapwings *Vanellus vanellus* in Britain. Bird Study 53: 274–284.

Gillings S., Fuller R.J. & Sutherland W.J. 2005. Diurnal studies do not predict nocturnal habitat choice and site selection of Eurasian Golden Plovers *Pluvialis apricaria* and Northern Lapwings *Vanellus vanellus*. Auk 122: 1249–1260.

Gillings S., Fuller R.J. & Sutherland W.J. 2007. Winter field use and habitat selection by Eurasian Golden Plovers *Pluvialis apricaria* and Northern Lapwings *Vanellus vanellus* on arable farmland. Ibis 149: 509–520.

Goss-Custard J.D. 1969. The winter feeding ecology of the Redshank. Ibis 111: 338–356.

Goss-Custard J.D., Clarke R.T., McGrorty S., Nagarajan R., Sitters H.P. & West A.D. 2002. Beware of these errors when measuring intake rate in waders. Wader Study Group Bull. 98: 30–37.

Goss-Custard J.D. 1977. The energetics of prey selection by redshank, *Tringa totanus* (L.), in relation to prey density. J. Anim. Ecol. 46: 1–19.

Green R.E. & Tyler G.A. 1989. Determination of the diet of the stone curlew (*Burhinus oedicnemus*) by faecal analysis. J. Zool. 217: 311–320.

Gunn A. 1992. The use of mustard to estimate earthworm populations. Pedobiologia 36: 65–67.

Hansen S. & Engelstad F. 1999. Earthworm populations in a cool and wet district as affected by tractor traffic and fertilisation. Appl. Soil Ecol. 13: 237–250.

Jégou D., Brunotte J., Rogasik H., Capowiez Y., Diestel H., Schrader S. & Cluzeau D. 2002. Impact of soil compaction on earthworm burrow systems using X-ray computed tomography: preliminary study. Eur. J. Soil Biol. 38: 329–336.

Joy N.H. 1932. A practical handbook of British beetles. H.F. & G. Witherby, London.

Lange G. 1968. Über Nahrung, Nahrungsaufnahme und Verdaungstrakt Mitteleuropäischer Limikolen. Beitr. Vogelkd. 13: 225–334.

Lee N.M. & Hockey P.A.R. 2001. Biases in the field estimation of shorebird prey sizes. J. Field Ornithol. 72: 49–61.

McLellan J.A. 1979. The formation and function of mixed species wader flocks in fields. Unpubl. PhD thesis, University of Aberdeen.

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Metcalfe N. 1985. Prey detection by intertidally feeding lapwing. Zeitschr. Tierpsychol. 67: 45–57.
Nordström S. & Rundgren S. 1972. Methods of sampling lumbricids. Oikos 23: 344–352.
Pienkowski M.W. 1983a. Changes in the foraging pattern of plovers in relation to environmental factors. Anim. Behav. 31: 244–264.
Pienkowski M.W. 1983b. Surface activity of some intertidal invertebrates in relation to temperature and the foraging behaviour of their shorebird predators. Mar. Ecol. Progr. Ser. 11: 141–150.
Raw F. 1960. Earthworm population studies: a comparison of sampling methods. Nature 187: 257.
Rojas de Azuaje L.M., Tal S. & McNeil R. 1993. Comparison of rod/cone ratio in three species of shorebirds having different nocturnal foraging strategies. Auk 110: 141–145.
Rojas L.M., McNeil R., Cabana T. & Lachapelle P. 1999. Diurnal and nocturnal visual capabilities in shorebirds as a function of their feeding strategies. Brain Behav. Evol. 53: 29–43.
SAS Institue 2001. SAS/STAT user's guide, version 8.02. Cary, North Carolina.
Sokal R.R. & Rohlf F.J. 2000. Biometry: the principles and practice of statistics in biological research. Freeman & Co, New York.
Springett J.A. 1981. A new method for extracting earthworms from soil cores, with a comparison of 4 commonly used methods for estimating earthworm populations. Pedobiologia 21: 217–222.
Svendsen J.A. 1955. Earthworm population studies: a comparison of sampling methods. Nature 175: 864.
van Gils J.A., de Rooij S.R., van Belle J., van der Meer J., Dekinga A., Piersma T. & Drent R. 2005. Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. I. Prey choice. J. Anim. Ecol. 74: 105–119.
van Gils J.A., Dekinga A., Spaans B., Vahl W.K. & Piersma T. 2005. Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. II. Patch choice and length of working day. J. Anim. Ecol. 74: 120–130.
Wilson J.D., Arroyo B.E. & Clark S.C. 1996. The diet of bird species of lowland farmland: a literature review. Royal Society for the Protection of Birds, Sandy.
Zwarts L. & Dirksen S. 1990. Digestive bottleneck limits the increase in food intake of Whimbrels preparing for spring migration from the Banc D'Arguin, Mauritania. Ardea 78: 257–278.
Zwarts L. & Wanink J.H. 1993. How the food-supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body-weight, biomass, burying depth and behaviour of tidal-flat invertebrates. Neth. J. Sea Res. 31: 441–476.

SAMENVATTING

Gedurende de winter foerageren Goudplevier *Pluvialis apricaria* en Kievit *Vanellus vanellus* steeds vaker op bouwland, maar tot dusver is vooral het voedsel van in graslanden overwinterende Goudplevieren en Kieviten beschreven. De auteurs vergeleken het foerageergedrag overdag en 's nachts van overwinterende Goudplevieren en Kieviten op bouwland in oostelijk Engeland gedurende drie winters (1999–2002). De prooiopnamesnelheid, het voedsel en de prooibeschikbaarheid werden gekwantificeerd voor verschillende typen bouwland. In vorige Britse studies uitgevoerd in graslanden werd geconcludeerd dat overwinterende plevieren bijna uitsluitend regenwormen aten. De auteurs stelden echter vast dat op bouwland overdag grote aantallen geleedpotigen (vooral loopkevers en miljoenpoten) werden gegeten. Uitgedrukt in vleesgewicht vormden regenwormen wel de belangrijkste voedselcomponent. De auteurs benadrukken echter dat van prooien als muggenlarven en slakken bijna geen sporen in de uitwerpselen achterblijven, terwijl deze prooien wel talrijk aanwezig waren, vooral in akkers met bietenresten. Overdag waren de gevangen wormen klein van formaat (1–3 keer de snavellengte, en gemiddeld kleiner dan 72 mm). Deze kleine regenwormen zijn de pigmentloze *Allolobophora caliginosa* en *A. chlorotica*, soorten die algemeen voorkomen in de toplaag van landbouwgronden. Nachtelijk foerageren leek heel belangrijk voor de overwinterende plevieren: de waargenomen opnamesnelheden lagen tot 50% hoger, waarschijnlijk omdat de plevieren dan ook in staat zijn de grotere Rode Worm *Lumbricus rubellus* te vangen. Plevieren aten gemiddeld grotere regenwormen dan dat er beschikbaar waren. De auteurs benadrukken echter dat de gebruikte methode om regenwormdichtheden te bepalen, onvoldoende nauwkeurig is. Vergeleken met andere studies aan bijvoorbeeld de Grutto *Limosa limosa* waren de waargenomen opnamesnelheden overdag laag, wat vragen oproept over de profijtelijkheid van foerageren op bouwland, maar wat ook gevolg kan zijn van de stop-en-kijk foerageertechniek. Overdag bereikten de vogels de hoogste opnamesnelheden met zacht weer, en op grasland en akkers met bietenresten. De opnamesnelheden waren op graanakkers lager dan op grasland. Akkers werden echter wel consistent vaker bezocht, terwijl graslanden zelfs vermeden werden. Naast de voedselopnamesnelheid zijn er dus nog andere factoren die de verspreiding van deze plevieren op bouwland bepalen. (YIV)

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Appendix 1. Results of regression analyses of length and mass for invertebrates. *S*: stretched worm length (mm), *U*: unstretched worm length (mm), *L*: body length (mm), *W*: wet mass (g), *A*: AFDM (mg), *D*: standardised wet mass (mg/mm). * $P < 0.05$, ** $P < 0.01$, **** $P < 0.0001$. *n*: sample size. In cases where items were too small to burn individually and had to be grouped, two sample sizes are given: the total number of items and the number of groups in parentheses.

Prey type	*n*	Least-squares	R^2	Equation
Beetle larva	9	$F_{1,7} = 25.3$**	0.78	$A = 0.0124L^{2.40}$
Carabid adult	38 (15)	$F_{1,13} = 102.8$****	0.89	$A = 0.0164L^{2.90}$
Diptera larvae	95 (9)	$F_{1,7} = 12.8$**	0.64	$A = 0.0077L^{2.57}$
Diptera pupae	68 (5)	$F_{1,3} = 13.6$*	0.82	$A = 0.019L^{2.80}$
Earthworm	70	$F_{1,69} = 2716.4$***	0.98	$S = 1.69U$
	437	$F_{1,435} = 2811.3$***	0.86	$W = 0.000095U^{2.00}$
	124	$F_{1,122} = 701.3$***	0.85	$A = 0.009U^{2.13}$
	455	$F_{1,453} = 663.9$***	0.59	$U = 26.58 \times \mathrm{Ln}(D) + 8.21$
Earthworm cocoon	30 (4)	$F_{1,2} = 181.4$**	0.51	$A = 0.33L^{1.81}$
Millipede	65 (15)	$F_{1,13} = 13.6$**	0.51	$A = 0.00318L^{2.60}$
Staphylinid adult	14 (5)	$F_{1,3} = 65.3$**	0.96	$A = 0.0478L^{1.78}$
Slug	28 (15)	$F_{1,13} = 232.8$****	0.95	$A = 0.038L^{2.19}$

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Appendix 2. Regression results and equations relating body part dimensions to total body length in a reference sample of adult Carabid and Staphylinid beetles and larval beetles (Carabidae, Staphylinidae and Meloidae). These equations were used to calculate the size of beetles consumed from the dimensions of fragments found in faecal samples. In each case x is length or width of body part and L is body length. **** $P < 0.0001$. n: sample size.

Relationship	n	Regression	R^2	Equation
Carabid adult				
Mandible length	29	$F_{1,28} = 1226.0$****	0.98	$L = 9.45x$
Foreleg femur length	29	$F_{1,28} = 2704.1$****	0.99	$L = 5.33x$
Foreleg tibia length	29	$F_{1,28} = 1811.3$****	0.98	$L = 5.91x$
Midleg femur length	29	$F_{1,28} = 3614.6$****	0.99	$L = 5.18x$
Midleg tibia length	29	$F_{1,28} = 2072.5$****	0.99	$L = 5.33x$
Hindleg femur length	28	$F_{1,27} = 2536.6$****	0.99	$L = 4.03x$
Hindleg tibia length	28	$F_{1,27} = 1714.5$****	0.98	$L = 3.97x$
Generic femur length	86	$F_{1,85} = 3174.5$****	0.97	$L = 4.70x$
Generic tibia length	86	$F_{1,85} = 1845.9$****	0.96	$L = 4.79x$
Elytra length	25	$F_{1,24} = 4354.6$****	0.99	$L = 1.66x$
Elytra width	23	$F_{1,22} = 1630.9$****	0.99	$L = 4.43x$
Staphylinid adult				
Mandible length	13	$F_{1,12} = 372.0$****	0.97	$L = 12.8x$
Foreleg femur length	13	$F_{1,12} = 681.4$****	0.98	$L = 7.93x$
Foreleg tibia length	13	$F_{1,12} = 427.4$****	0.97	$L = 9.46x$
Midleg femur length	13	$F_{1,12} = 451.6$****	0.97	$L = 7.62$v
Midleg tibia length	13	$F_{1,12} = 453.2$****	0.97	$L = 8.55x$
Hindleg femur length	13	$F_{1,12} = 370.0$****	0.97	$L = 7.18x$
Hindleg tibia length	13	$F_{1,12} = 246.9$****	0.95	$L = 6.88x$
Generic femur length	41	$F_{1,40} = 1513.5$****	0.97	$L = 7.58x$
Generic tibia length	42	$F_{1,41} = 900.4$****	0.96	$L = 8.09x$
Elytra length	13	$F_{1,12} = 207.9$****	0.95	$L = 4.60x$
Elytra width	13	$F_{1,12} = 88.7$****	0.88	$L = 8.45x$
Beetle larva				
Mandible length	17	$F_{1,16} = 250.3$****	0.94	$L = 13.44x$

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Appendix 3. Calibration of focal observations. The independently created sample of artificial cord 'worms' consisted of 80 'worms', ten of each size class 1x to 8x bill length. The percentage of worms assigned to an incorrect size class (error rate), was 37%, 36% and 35% in the three trials. In all but one case, misclassifications were of just plus or minus one size class. Error was directional – across all three trials (240 worms) the size of only four worms (1.7%) was over-estimated whereas the size of 83 worms (34.6%) was under-estimated. There was a tendency for worms towards the lower bound of each size class to be incorrectly assigned into the next smallest size class and this tendency was greater for large worms ($r = 0.76$). The table gives mean correction percentages for converting observed frequencies of worm sizes to true estimates of worm size. These values are means across the three trials of the percentage of worms classified to each class. For instance, the true total number of size 2x worms is equal to 11.6% of the observed number of size 1x worms plus 81.9% of observed size 2x worms.

Estimated size class	Actual size class							
	1	2	3	4	5	6	7	8
1	88.4	11.6	0	0	0	0	0	0
2	0	81.9	18.1	0	0	0	0	0
3	0	0	60.0	40.0	0	0	0	0
4	0	0	0	52.4	47.6	0	0	0
5	0	0	0	0	44.4	53.0	2.6	0
6	0	0	0	0	5.6	35.6	58.9	0
7	0	0	0	0	0	6.1	56.4	37.5
8	0	0	0	0	0	0	4.8	95.2

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Appendix 4. Estimated length (mean ± SE, mm) of prey items found in faecal samples and AFDM (mg) values calculated by applying the regression equations in Appendix 1 to estimated lengths then calculating a mean across individuals. Method refers to the body part used to estimate prey size; M: mandible, F: femur, T: tibia, E: Elytra, L: length. For comparison, the AFDM of different size earthworms is also given based on the equation in Appendix 1 applied to 1 mm increments and taking a mean within each size class.

Prey type		Length Mean ± SE	*n*	Method	AFDM Mean ± SE
Beetle larva		13.5 ± 3.3	8	M	11.1 ± 4.8
Carabid adult		5.7 ± 0.3	52	F	3.4 ± 0.5
Diptera larva		6.5 ± 1.3	7	L	1.4 ± 0.6
Diptera pupa		2.6 ± 0.2	3	L	0.3 ± 0.1
Millipede[a]		c.10	10	-	c.1.3
Staphylinid adult		10.6 ± 1.5	11	M, E	3.6 ± 0.3
Weevil[b]		5.0 ± 0.0	35	F, T	2.5
Earthworm[c]	1x	(1–24)		L	2.7 ± 0.5
	2x	(25–48)		L	20.0 ± 1.6
	3x	(49–72)		L	57.0 ± 2.9
	4x	(73–96)		L	115.3 ± 4.2
	5x	(97–120)		L	195.8 ± 5.5
	6x	(121–144)		L	299.2 ± 6.9
	7x	(145–168)		L	426.2 ± 8.4
	8x	(169–192)		L	577.2 ± 9.8

[a]Measurement error prevented calculating the size and AFDM of dietary millipedes from fragments. Size is estimated visually in comparison with known reference samples and AFDM calculated from allometric relationships.
[b]Insufficient samples or size range to calculate a regression equation. AFDM is taken directly from burnt weevils.
[c]No sample sizes for earthworms because these values are based on allometric relationships from Appendix 1 and calculated using the method of Goss-Custard *et al.* (2002).

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