Detection of earthworm prey by Ruff Philomachus pugnax

Onrust, Jeroen; Loonstra, Anno; Schmaltz, Lucie E.; Verkuil, Yvonne; Hooijmeijer, Joslyn; Piersma, Theun

Published in:
Ibis

DOI:
10.1111/ibi.12467

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Final author's version (accepted by publisher, after peer review)

Publication date:
2017

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):

Copyright
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.
Detection of earthworm prey by Ruff *Philomachus pugnax*

JEROEN ONRUST,1* A. H. JELLE LOONSTRA,1 LUCIE E. SCHMALTZ,1 YVONNE I. VERKUIL,1 JOS C. E. W. HOOLMEIJER1 & THEUNIS PIERSMA1,2

1 Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

2 Department of Coastal Systems and Utrecht University, NIOZ Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg Texel, The Netherlands

Ruff *Philomachus pugnax* staging in the Netherlands forage in agricultural grasslands, where they mainly eat earthworms (*Lumbricidae*). Food intake and the surface availability of earthworms were studied in dairy farmland of southwest Friesland in March–April 2011. Daily changes in earthworm availability were quantified by counting visible earthworms. No earthworms were seen on the surface during daytime, but their numbers sharply increased after sunset and remained high during the night. Nevertheless, intake rates of individual Ruff in different grasslands measured during daytime showed the typical Holling type II functional response relationship with the surfacing earthworm densities measured at night. Radiotagging of Ruff in spring 2007 revealed that most, if not all, feeding occurs during the day, with the Ruff assembling at shoreline roosts at night. This raises the question of why Ruff do not feed at night, if prey can be caught more easily than during daytime. In March–May 2013 we experimentally examined the visual and auditory sensory modalities used by Ruff to find and capture earthworms. Five males were kept in an indoor aviary and we recorded them individually foraging on trays with 10 earthworms mixed with soil under various standardized light and white noise conditions. The number of earthworms discovered and eaten by Ruff increased with light level, but only when white noise was played, suggesting that although they can detect earthworms by sight, Ruff also use auditory cues. We suggest that although surfacing numbers of earthworms are highest during the night, diurnal intake rates are probably sufficient to avoid nocturnal foraging on a resource that is more available but perhaps less detectable at that time.

**Keywords:** foraging, *Lumbricidae*, predator–prey interactions, sensory ecology.

To understand the interactions of predator and prey, it is necessary to know about the sensory ecology of both actors, i.e. how a predator detects and catches its prey and how the availability of the prey changes over time (Zwarts & Wanink 1993, Barbosa & Castellanos 2005, Piersma 2011). Earthworms (*Lumbricidae*) are soil-dwelling organisms that are important food for a wide variety of predators (MacDonald 1983). Earthworms can be caught by probing the soil surface (e.g. the long-billed sandpipers; Burton 1974) or digging through the soil (e.g. Moles *Talpa europaea*; Raw 1966). However, as Darwin (1881) observed, earthworms also come to the soil surface themselves and then are fed upon by visual hunters, including birds (e.g. Golden Plovers *Pluvialis apricaria*: Bengtson *et al.* 1978; Blackbirds *Turdus merula*: Chamberlain *et al.* 1999; reptiles and amphibians: Hamilton 1951, MacDonald 1983).

A migratory sandpiper, the Ruff *Philomachus pugnax*, is virtually extinct as a breeding species in the Netherlands (Boele *et al.* 2016), but still stages there during the migration period (Jukema *et al.*
2001, Verkuil et al. 2010), albeit in greatly diminished numbers (Schmaltz et al. 2015). Ruff use freshwater wetlands and agricultural grasslands, but deterioration of these habitats may have caused declining numbers of staging birds in the Netherlands and a shift towards a more easterly migration route (Verkuil et al. 2012). Ruff are opportunistic feeders and can feed on plant materials as well as invertebrates (Ezealor & Giles 1997, Baccetti et al. 1998). In the Netherlands, Ruff primarily use moist grasslands for feeding (Verkuil & de Goeij 2003, Schmaltz et al. 2016), and their main prey then are earthworms (van Rhijn 1991), sometimes supplemented by leather-jackets (larvae of Tipulidae) (Beintema et al. 1995). When earthworms become less available due to desiccation of the soil and with increasing sward height, Ruff can switch to eating insects by picking them from the foliage if these become available on warm spring days (Verkuil & de Goeij 2003, Schmaltz et al. 2016).

How Ruff detect the earthworm prey remains unclear. Routinely, deep probing of the soil has been observed (Verkuil & de Goeij 2003, Krupa et al. 2009), which suggests that they can use tactile foraging strategies or that they merely chase retreating prey they had detected in other ways. Indeed, van Rhijn (1991) and Barbosa (1995) identify Ruff as a tactile forager. Hoerschelmann (1970), on the other hand, suggests that the Ruff is a typical visual forager, on the basis of the shape and structure of the bill. Ruff have relatively short bills (30–31 mm for females, 34–35 mm for males; Meissner & Ziecik 2005), and the tip of a Ruff’s bill contains fewer sensory cells than that of more tactile foraging wader species (Ballmann 2004). Nevertheless, Thomas et al. (2006) stated that Ruff use a mixture of both techniques with no bias towards visual or tactile foraging.

Earthworms may come to the surface during the night (Butt et al. 2003) and can then be detected by sight under low illumination. Given their nocturnal surfacing behaviour, at least for visual foragers with good night vision, it would be beneficial to forage nocturnally (McNeil & Rodriguez S. 1996, Lourenço et al. 2008). This seems to be the case for Golden Plovers, which have relatively large eyes and probably also a high rod-to-cone ratio for good night vision (Rojas et al. 1999, Martin & Piersma 2009). Ruff, however, have relatively small eyes (Thomas et al. 2006). Surprisingly, Cramp and Simmons (1983) state that Ruff mainly forage during twilight and at night. It is possible that, depending on ecological context, they switch from being visual hunters by day to tactile feeders by night, as is observed in other shorebird species (Mouritsen 1994, Burton & Armitage 2005). At night, they could also use auditory cues to locate a digging earthworm, as is done by thrushes (Turdidae) during daytime (Montgomerie & Weatherhead 1997) and possibly also by Golden Plovers (Lange 1968).

On the basis of these conflicting statements, we predicted that Ruff use visual cues to catch earthworms, but might switch to using auditory cues in darkness. We used field observations of earthworm-eating Ruff to quantify feeding performance during the day in relation to available prey densities at night, and used radiotelemetry data to establish whether Ruff are indeed diurnal foragers at our study site. We then performed a controlled indoor experiment to examine the capacity of Ruff to use visual and auditory cues in the detection of earthworms.

**METHODS**

**The predator and its prey: field observations**

All fieldwork was conducted in southwest Friesland, the Netherlands (within a radius of about 10 km of 52°55′N, 5°26′E). In this region the total land area consists mainly of grasslands used for dairy farming (Groen et al. 2012). These grasslands are used by Ruff to forage and the numerous lakes and shorelines are used as roosting sites (Verkuil & de Goeij 2003, Schmaltz et al. 2016).

From 21 March to 15 April 2011, foraging Ruff were studied in relation to the earthworm conditions in selected fields. The fields were selected on the basis of the presence of flocks of Ruff (with numbers ranging between 40 and 450 individuals). On 12 different fields (all between 2 and 6.5 ha and all used for dairy farming and with a loamy clay soil), between 6 and 11 different birds each were observed between sunrise and sunset. Bird observations involved the counting of numbers of foraging birds and the scoring of individual prey intake rates. Intake rate was defined as number of eaten earthworms per minute. Intake rates of a focal individual were scored for 5 min using a 20–60× magnification telescope. Intake rates were scored for exactly 100 different Ruff. Although
earthworms could be positively identified as prey (their colour, size and behaviour), not every prey item or swallowing action could be identified and therefore only definitely consumed earthworms were counted. This leads to underestimation of the intake rate. Field observations were stopped when Ruff switched to eating insects. Ruff feeding on insects can clearly be distinguished from earthworm-eating Ruff as their pecking at insects on the foliage results in a very different posture, head movements and gait.

Visual counts of earthworms were made a day later in the fields where the intake rate observations were made. Surfacing earthworms were counted by lying prone on a robust and simple cart which was gently pushed forward by foot. This cart provided the observer with a good view of the soil (head c. 40 cm above surface) and it created little vibration. Visual counts consisted of counting the surfacing earthworms along two transects of 75 m per grassland. Every earthworm within 50 cm of the central transect line was counted. In this way, about 75 m² was covered per sampling event. One transect took about 45 min to complete. The counts were repeated five times throughout the day at 07:00, 10:00, 14:00, 18:00 and 21:00 h CEST, with the second transect starting an hour after the first. Sunrise during the observation period was between 06:22 and 07:08 h CEST and sunset between 20:08 and 20:44 h CEST. Light intensity during observations was not measured. A head torch (160 Lumens) and a hand-held counter were used to see and count the earthworms after sunset. Earthworms sometimes reacted to the bright light of the head torch, but they retreated into the soil after only 1–3 s (J.O.). As we show below, we never saw any surfacing earthworm during the day and therefore we correlated our measurements of intake rate by Ruff with nocturnal surface availability of visual counts performed after sunset (21:00 and 22:00 h CEST). We used the Type II response model of Holling (1959) to describe the relationship in a biologically sensible way (Duijns et al. 2015).

In spring 2007, 46 male Ruff were caught and applied with 1.8 g radio-transmitters (BD-2 transmitters; Holohil Systems Ltd, Carp, ON, Canada). This was part of a study determining departure dates on migration (Verkuil et al. 2010). Receiver stations were placed at nine roosts throughout the study area (for a map with the roosts locations, see Schmaltz et al. 2016). Data were collected between 25 March and 8 May 2007. As the transmitters had a detection range of about 500 m, the receiver stations could potentially also record nearby foraging birds. To be certain that birds on a roost were not foraging, we only used data of the four offshore roosts where Ruff cannot forage (for locations see the map in Verkuil et al. 2010; the roosts used in this paper are: Bocht fan Molkwar, Makkumer Noardwaard, Makkumer Südwaard and Mokkebank). This selection decreased the number of radiotagged birds to 19. For the whole time period, we calculated the hourly percentage of birds present on a roost from the total number of birds present per hour and the maximum number of birds that were observed at the roosts.

**Sensory capacity: prey detection trials**

Five male Ruff were caught in southwest Friesland by standard wilsternetter procedures (for description and routines, see Rogers & Piersma 2005). To prevent sexual interactions during the experiments, we selected only adult males. After capture, the birds were individually colour-ringed and transported to an indoor aviary of 2 × 2.6 × 4 m (width, height, depth) at the Groningen Institute for Evolutionary Life Sciences in Groningen, the Netherlands, 100 km from the site of capture. To acclimatize the birds to human presence and to reduce the effects of sudden human sounds, a radio station with human voices and music was broadcast continuously. As male Ruff became competitive in spring, wooden dividers were placed in the aviary so that the birds could avoid each other; still, they could move freely through the room and engage in social interactions. During the off-trial days, Ruff were provided ad libitum with commercially obtained live mealworms (Tenebrio molitor larvae), earthworms (Dendrobaena veneta and Eisenia fetida) and fresh water.

The prey detection trials started when the birds seemed to have fully adjusted to captivity conditions, 2 weeks after capture. Experimental trials were carried out in the mornings. To motivate Ruff to feed during a trial, birds were deprived of food for 12 h before the start of each trial. Fresh water remained available ad libitum. On an experiment day, all birds were caught simultaneously, kept in dark boxes and randomly assigned a sequence number. Trials were carried out in the same aviary in which the Ruff were housed.
Thereafter, Ruff were placed in a small cage (width = 0.8, height = 0.4, depth = 0.4 m), which was divided in two equally sized compartments using a wooden baffle. While the ground layer present in the left side was the same as in the cage (wooden chips) and did not contain prey items, the right side was covered with a shallow layer of 1 cm clean potting soil (ingredients: 70% peat, 20% compost, 10% of an unknown fertilizer) and contained 10 earthworms (length = 50 mm), which were placed in the compartment 10 min before a trial, enabling them to bury themselves in soil and show more or less natural behaviour, but not allowing them to create burrows or casts that might help Ruff in finding them in the field. We chose to use a shallow depth of only 1 cm to be sure that the earthworms presented to the birds in every trial were more or less equally available. Only E. fetida earthworms were used in the experiment, as D. veneta actively jumps upon being touched, a behaviour that could probably make them more available than the more timid earthworm species encountered in the field (J. Onrust unpubl. obs.). After each trial the soil was removed and the number of earthworms left over was scored. Each trial was started with a new set of earthworms.

During a trial, a bird was first placed in the left side of the cage under experimental light and noise conditions. After a habituation period of 5 min we removed the wooden baffle. The bird was then able to feed for 15 min in the experimental compartment. However, full adaptation to darkness often takes about an hour in most animals (Martin 1990, Dusenbery 1992). Therefore, the visual sensitivity of the Ruff under dark conditions was probably not optimal in this experiment. However, the birds were kept for 20–100 min in dark boxes prior to the trials.

A full factorial design with the two factors light and noise was designed to examine the effects of either visual cues or auditory cues (Table 1). In addition, in Treatment 1 all cues were available and in Treatment 6 both types of cues were absent. Treatments were repeated twice for each individual. Treatments were randomly assigned to the birds following the throw of a die. Visual cues were reduced by decreasing the amount of available light; Ruff were allowed to forage under light conditions of 1000, 0.01 and 0 Lux, which correspond to daylight, twilight and complete darkness (Dusenbery 1992).

To exclude auditory cues, we followed Montgomerie and Weatherhead (1997) and Cunningham et al. (2010), and used white noise to mask any sounds made by earthworms moving in the soil. White noise was generated using two speakers (output 100–18 000 Hz) placed on either side of the compartment. The sound level used to generate the white noise was 61 dB. As Ruff did not always consume every prey item they found, we recorded all trials on video (Sony Handycam HDR-SR12E with infrared function) with an extra infrared illuminator (wavelength 850 nm, range 30 m). The camera and illuminator did not create any visible light.

Videos were analysed in Windows Media Player (Windows 10). As we were primarily interested in whether Ruff were able to find earthworms, we noted the number of worms found and eaten (denoted Wf+e). The results were analysed in R version 3.1.2 (R Development Core Team 2014) using generalized linear mixed models with each bird (BirdID) representing a random intercept. The response variable was Wf+e and the explanatory variables were light and noise levels, both categorical. To control for a learning effect between the first and second repetition, we also added repetition as a variable. The package lsmeans was used for a post hoc analysis (Lenth 2016).

Table 1. Overview of the different experimental treatments during tests to examine the visual and auditory sensory modalities used by Ruff to find and capture earthworms.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Background noise</th>
<th>Amount of light</th>
<th>Light level (lux)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Silence</td>
<td>Daylight</td>
<td>1000</td>
<td></td>
</tr>
<tr>
<td>2 White noise</td>
<td>Daylight</td>
<td>1000</td>
<td></td>
</tr>
<tr>
<td>3 Silence</td>
<td>Twilight</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>4 White noise</td>
<td>Twilight</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>5 Silence</td>
<td>Complete darkness</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>6 White noise</td>
<td>Complete darkness</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

RESULTS

Field observations

The intake rate of Ruff showed a slight increase around noon ($F_{2,97} = 3.58$, $R^2 = 0.069$, $P = 0.032$, $n = 100$; Fig. 1a). During 28 h of ‘carting’, covering 0.21 ha of grassland, not a single surfacing earthworm was observed during daytime (Fig. 1b). Earthworms appeared on the surface only after
sunset. However, when plotted per field, the average intake rate of foraging Ruff during the day was a function of the densities of surfacing earthworms measured in darkness (the average of transects at 21:00 + 22:00 h CEST), showing the positive but steadily flattening relationship typical of a Holling type II functional response (Fig. 2, Holling 1959).

At any time of the night, 90–100% of the 19 birds were present at the roost (Fig. 3). By 08:00 h more than 90% of the birds had left the roost for a daytime rest (Schmaltz et al. 2016, Fig. 3). Around 16:00–17:00 h, 80% of birds had left the roost again, but at twilight the majority had returned (Fig. 3).

**Prey detection trials**

The prey detection trials showed that prey intake under daylight was similar at the two noise levels, but in twilight and darkness, earthworms were found and eaten more in the absence of white noise (Fig. 4, Table 2). This indicates that Ruff use auditory cues to find earthworms in twilight and darkness. A post hoc analysis revealed, however, that only the darkness treatment with white noise was significantly different from the two daylight treatments, and twilight with white noise was significantly different from daylight without white noise (Fig. 4). As indicated by an absence of a difference between the first and second repetition of a treatment, there was no significant effect of learning (Table 2).

**DISCUSSION**

To explain how animals maximize their intake rate, we must consider how animals find their prey and sense the availability of prey in the field (MacArthur & Pianka 1966, Piersma 2011). We predicted that Ruff use visual cues to detect and catch earthworms in grasslands, but can switch to using auditory cues at night when food availability is highest in terms of surfacing earthworms (Fig. 1b). However, Ruff still found earthworms during daytime when human observers could not (Fig. 1), and radiotagged Ruff did not forage during the night (Fig. 3). This was unexpected, as we found the expected Holling type II functional response relationship between intake rate measured during daytime and earthworm availability measured at night (Fig. 2). This suggests that earthworms, of which some species surface during the night (Baldwin 1917), remain close to the surface during the day, so that nocturnal measurements of their surface abundance are closely correlated with their daytime availability. For example, Ruff can see parts of the earthworm, use other visual cues such as fresh earthworm casts or, indeed, hear them move. Thus, the most accurate method for measuring earthworm availability for this species should be based on the counting of visible earthworms but also on locating invisible earthworms based on the sound they produce.
The prey detection trials with five birds and two replicates per treatment indicated that Ruff can discover earthworms in twilight and even in total darkness, with a suggestion that white noise reduces performance. This indicates that Ruff find earthworms mainly on the basis of visual and auditory cues, but in principle could also modulate the use of these cues under different light conditions. Such switches between foraging strategies in the day and night have been described previously for several different shorebirds (Hulscher 1976, Robert & McNeil 1989). In the present case, it would be mostly a switch from visual feeding during the day to tactile feeding at night, previously suggested by van Rhijn (1991), Barbosa (1995) and Thomas et al. (2006). However, these studies were based on observations under field conditions, whereas we forced birds to forage in the absence or presence of cues that
limited them to using either a visual or an auditory strategy. Even though our initial experimental setup was not designed to test whether Ruff use tactile cues, Ruff were not able to find worms when both visual and auditory cues were eliminated (treatment 6). This suggests that we successfully eliminated all the cues used by Ruff. Although the difference between white noise in darkness and no white noise is not significant, if Ruff primarily use tactile cues to find prey, they should also have found earthworms in darkness when white noise was played (Fig. 4).

Over the last two decades the numbers of staging Ruff have declined considerably in the Netherlands (Jukema et al. 2001, Verkuil et al. 2010, 2012). Agricultural intensification has resulted in grasslands that are less attractive for feeding. Although earthworms can profit from higher manure input (Hansen & Engelstad 1999), earthworm availability for Ruff might have declined because of generally drier conditions (Ausden & Bolton 2012). To avoid the drought, earthworms in drained grasslands retreat deeper into the soil (Gerard 1967). Furthermore, tipulid larvae are also susceptible to desiccation and avoid drained grasslands (Pritchard 1983, Carroll et al. 2011). This may provide part of the reason why Verhulst et al. (2007) found a positive relationship between groundwater level and meadow bird numbers and prey density. High groundwater levels also have a positive effect on the penetrability of the soil for a bird’s bill, making it easier to catch earthworms (Green et al. 1990, Duckworth et al. 2010, Ausden & Bolton 2012).

In staging areas, food conditions need to be sufficient to allow migrants to gain the fuel stores for onward migration and breeding (Piersma & Baker 2000). Biometric data of Ruff that were caught as part of a long-term study monitoring the population of Ruff staging in southwest Friesland (Hooijmeijer 2007) indicated that the fuelling rates of male Ruff declined between 2001 and 2008.

Figure 4. Results of the prey detection trials. Boxplots represent the data of five captive male Ruff under three light conditions (darkness, twilight and daylight, which correspond to 0, 0.01 and 1000 Lux, respectively) and with or without white noise. Per bird, all treatments were repeated twice. Significant differences between treatments are indicated with an asterisk (*P ≤ 0.05).

Table 2. Coefficient estimates β, standard errors, se (β), associated Wald's z-score (= β/SE(β)) and significance level P for all predictors in the analysis derived from a generalized linear mixed model (GLMM) with number of earthworms found and eaten as the response variable and light conditions and white noise (Y/N) as explanatory variables (fixed effects). Bird identity is fitted as a random effect. Reference level for white noise was ‘no noise’, for light levels it was darkness, and for the interaction terms it was no noise*darkness.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Coef. β</th>
<th>se (β)</th>
<th>z-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-0.140</td>
<td>0.651</td>
<td>-0.214</td>
<td>0.830</td>
</tr>
<tr>
<td>Repetition</td>
<td>0.189</td>
<td>0.271</td>
<td>0.697</td>
<td>0.486</td>
</tr>
<tr>
<td>White noise</td>
<td>-2.906</td>
<td>1.081</td>
<td>-2.689</td>
<td>0.007</td>
</tr>
<tr>
<td>Twilight</td>
<td>0.067</td>
<td>0.458</td>
<td>0.146</td>
<td>0.884</td>
</tr>
<tr>
<td>Daylight</td>
<td>0.903</td>
<td>0.428</td>
<td>2.109</td>
<td>0.035</td>
</tr>
<tr>
<td>White noise*Twilight</td>
<td>2.362</td>
<td>1.191</td>
<td>1.984</td>
<td>0.047</td>
</tr>
<tr>
<td>White noise*Daylight</td>
<td>2.702</td>
<td>1.144</td>
<td>2.361</td>
<td>0.018</td>
</tr>
</tbody>
</table>
feeding are suf
implies that food conditions during the daytime
therefore, rarely if ever forage nocturnally. This
migratory staging in southwest Friesland, Ruff,
use of auditory cues to exploit an abundant
hearing. However, our data showed that Ruff are
already close to the surface.
and auditory cues to detect earthworms that are
during the night, Ruff predominantly fed during
insects (i.e. supplementary hypothesis), or because
food conditions at night are better and predation
risk is lower (i.e. preference hypothesis). After
sunset, food conditions for Ruff should be better,
as earthworms start to surface then (Fig. 1b). Ruff
can still find earthworms in darkness, probably by
hearing. However, our data showed that Ruff are
not nocturnally active and therefore rarely make
use of auditory cues to exploit an abundant
resource during the night (Fig. 4). During their
migratory staging in southwest Friesland, Ruff,
therefore, rarely if ever forage nocturnally. This
implies that food conditions during the daytime
feeding are sufficient.

In conclusion, a combination of field and experi-
mental indoor observations on the relationships
between Ruff and earthworms indicated that
although we measured only surfacing earthworms
during the night, Ruff predominantly fed during
the day. We propose that they use indirect visual
and auditory cues to detect earthworms that are
already close to the surface.

Special thanks go to the friendly and helpful Frisian
dairy farmers who allowed us to carry out fieldwork
on their fields. We gratefully thank the Frisian ‘wilsteflapp-
ers’ for catching the Ruff. This work is part of the
research programme financed by the Province of Friesian
(University of Groningen/Campus Frysland support for
J.O. through the Waddenacademie, and direct grant
help for LES to T.P.). The prey detection trials com-
plied with the Dutch Law on Experimental Animals and
were approved by the Experimental Animals Ethics
Committee, DEC: 6351C. The radio-transmitter study
was financed by the GUF-Gratama Foundation (project
04.05) and by grants of the Schure-Beijerinck Popping
Foundation (SBP/JK2006-39 and SBP/JK2007-34). We
acknowledge the help of Jen Smart, Ruedi Nager and
the anonymous referees in improving the article.

REFERENCES

Ausden, M. & Bolton, M. 2012. Breeding waders on wet
grasslands: factors influencing habitat suitability. In Fuller,
R.J. (ed.) Birds and Habitat: Relationships in Changing
Landscapes: 278–306. Cambridge: Cambridge University
Press.

Preliminary data on the diet of migrating Ruff Philomachus

Baldwin, F.M. 1917. Diurnal activity of the earthworm. J.

from the Middle Miocene of the Nördlinger Ries. Bonn. Zool.

Barbosa, A. 1995. Foraging strategies and their influence on
26: 182–186.


Atlas van de Nederlandse Weidevogels. Haarlem: Schuyt &
Co.

Bengtson, S.A., Rundgren, S., Nilsson, A. & Nordström, S.
1978. Selective predation on Lumbricids by Golden Plover

Boele, A., van Bruggen, J., Hustings, F., Koffijberg, K.,
Vergeer, J.W. & van der Meij, T. 2016. Broedvogels in

Burton, P.J.K. 1974. Feeding and the Feeding Apparatus in
Waders. London: British Museum (Natural History).

diurnal and nocturnal use of intertidal feeding grounds by

distribution and surface activity of adult Lumbricus terrestris

Carroll, M.J., Dennis, P., Pearce-Higgins, J.W. & Thomas,
C.D. 2011. Maintaining northern peatland ecosystems in
a changing climate: effects of soil moisture, drainage and
drain blocking on craneflies. Glob. Change Biol. 17: 2991–
3001.

Importance of feeding ecology to the reproductive success
of Blackbirds Turdus merula nesting in rural habitats. Ibis

Cram, S. & Simmons, K.E.L. (eds.) 1993. Handbook of the
Birds of Europe the Middle East and North Africa: The Birds
of the Western Palearctic vol. III. Waders to Gulls. Oxford:
Oxford University Press.

Cunningham, S.J., Alley, M.R., Castro, I., Potter, M.A.,
Cunningham, M. & Pyne, M.J. 2010. Bill morphology of
ibises suggests a remote-tactile sensory system for prey

Darwin, C. 1881. The Formation of Vegetable Mould Through
the Action of Worms With Observations on Their Habits.
London: John Murray.

limits foraging: a possible mechanism for the range
dynamics of the Hadeda Ibis in southern Africa. Divers.
Distrib. 16: 765–772.

Field measurements give biased estimates of functional
response parameters, but help explain foraging distributions.

Acquire and Respond to Information. New York: Freeman.

© 2017 British Ornithologists’ Union


R Development Core Team. 2014. R: A language and environment for statistical computing. Available at http://www.R-project.org/


© 2017 British Ornithologists’ Union


Received 9 September 2015; revision accepted 31 January 2017.
Associate Editor: Jen Smart.