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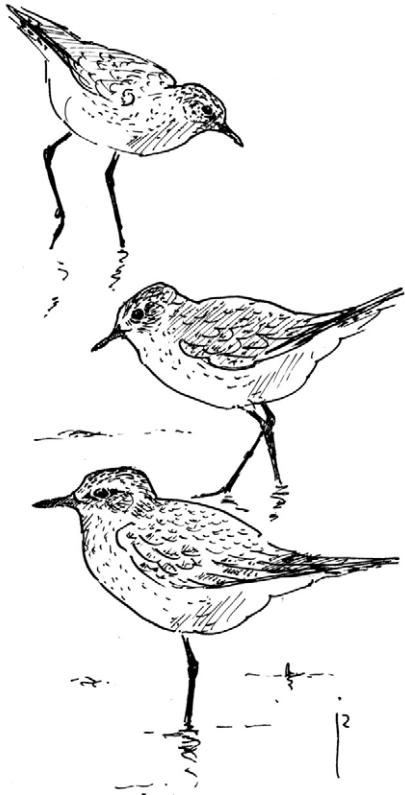
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Behavioural plasticity in foraging mode of typical plovers

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The foraging behaviour of typical plovers is highly stereotyped, and short-billed plovers all forage visually in a run–stop–search manner. To date, the use of a sandpiper-like foraging method by typical plovers is considered anecdotal in non-breeding plovers, since only one study has described Grey Plovers *Pluvialis squatarola* foraging as sandpipers do, striding slowly and pecking at the water surface during short periods. We studied the behaviour and intake rate of Grey and Ringed Plovers *Charadrius hiaticula* foraging like sandpipers on suspended prey items in the water column of hypersaline pans, and investigated factors that may influence their occurrence. The feeding rate was 48.9 ± 18.0 (SD) and 19.1 ± 6.3 prey min^{-1} for Ringed and Grey Plover, respectively. For Ringed Plovers, the net intake rate was 0.23 ± 0.05 kJ min^{-1} , and for Grey Plovers 0.09 ± 0.01 kJ min^{-1} . The sandpiper-like foraging method was particularly important for Ringed Plovers, since up to 24% of the population foraged in this way at high tide. We found that the sandpiper-like foraging method is a common foraging method in Ringed Plover feeding in prey-abundant pans and is occasionally used by Grey Plovers as well. We showed that behavioural plasticity in foraging methods of typical plovers may be greater than has been assumed previously. These results suggest that typical plovers can successfully locate and capture small prey items while walking continuously and without the need to stop to improve visual acuity.

Key words: behaviour, foraging, monocular vision, pecking, plasticity, plovers, waders

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INTRODUCTION

Shorebirds (Charadrii) are an ecologically diverse group of migratory waterbirds found throughout many regions of the world (Piersma *et al.* 1996). The majority of shorebirds belong to two families, the sandpipers (Scolopacidae) and the plovers (Charadriidae), and although there is considerable dietary overlap between these groups, they differ

to a large extent in foraging methods (Turpie & Hockey 1997). In intertidal habitats, sandpipers others than Terek Sandpiper *Xenus cinereus* (Piersma 1986) generally feed by moving over the substrate and either peck prey from the surface or probe in the mud (Paulson 1990). In contrast, the short-billed plovers all forage visually in a run–stop–search manner, and individuals pause to search for prey before moving to capture a prey

item or to search from a new position (Pienkowski 1983, Turpie & Hockey 1997, Byrkjedal & Thompson 1998). The foraging behaviour of typical plovers thus follows a fixed pattern (Baker 1974, Pienkowski 1983, Turpie 1994).

At Cadiz Bay (SW Spain), migrating and overwintering Grey Plovers *Pluvialis squatarola* and Ringed Plovers *Charadrius hiaticula* use intertidal mudflats and adjacent supratidal pans of the saltworks as foraging habitats. During several studies of foraging use of both habitats by shorebirds (Masero *et al.* 2000, Masero & Pérez-Hurtado 2001, Masero 2003), we observed that plovers forage visually in a run-stop-search manner on the intertidal area, while in the water of pans many Grey and Ringed Plovers forage consistently like sandpipers. To date, this foraging method is considered anecdotal in non-breeding plovers, since only one study (Paulson 1990) has documented that Grey Plovers may forage like sandpipers by walking slowly and pecking at the surface during short periods.

Many migratory shorebird populations are declining (Morrison *et al.* 2001), and a growing number of theoretical models on foraging behaviour provides a basis to assess and predict the habitat loss or human disturbance effects on these populations (e.g. Stillman *et al.* 2000, Caldow *et al.* 2004). These models rest on the assumption that we have knowledge on the behavioural plasticity of the shorebirds' foraging method, and have insight in the range of potential foraging habitats available to birds. Therefore, it is necessary to understand the behavioural plasticity of foraging methods in order to make a realistic assessment of the likely effects of habitat loss and disturbance on migratory shorebirds such as typical plovers.

In this study we analysed the behaviour and intake rate (ingested biomass per unit time) of Grey and Ringed Plovers foraging like sandpipers on pelagic prey items. The plover eyes are placed on the sides of the head, allowing them to see objects on each side at the same time (monocular vision). Monocular vision provides plovers with a wide field of view, but they may have a harder time judging distances and have poorer depth per-

ception. This visual limitation could explain the necessity of their run-stop-search method of foraging, since they must stop moving in order to locate prey before running in the direction where it was sighted (Turpie 1994). Here, we also addressed the question about this possible visual limitation of typical plovers.

METHODS

Study area

The study was carried out at Cádiz Bay Natural Park (36°23'N, 6°8'W; SW Spain), a Ramsar area (10 000 ha) with large areas of intertidal mudflats and adjacent saltworks and fishponds. Cadiz Bay is an internationally important area for overwintering Grey and Ringed Plovers, supporting 2000 and 2700 individuals, respectively (Pérez-Hurtado *et al.* 1993). Both plover species mainly feed on the intertidal mudflats at low tide, and use adjacent active and inactive saltworks as roosting and/or foraging areas at high tide. The foraging areas used during high tide are shallow waters (<5 cm depth) of hypersaline pans bounded by gently sloping dikes and wide shores, as well as muddy surfaces after pans have been emptied during the process of salt production.

Foraging behaviour and intake rate

Data were collected during winter (December – early February) 1995–96, 1996–97 and summer (August – early September) 2005. Grey and Ringed Plovers foraging actively in the shallow water of the pans were observed for 1-min periods through a 20x60 telescope. Most observations (>90%) were made at <25 m during high tide periods, usually from a hide placed on the shore of a pan at low tide. To avoid pseudoreplication (Hulbert 1984), we carefully selected 1–3 different individuals at random per pan. After observations, we measured water depth of each foraging site with a ruler.

During the focal observations, we recorded the number of failed and successful attempts to capture prey. It was not possible to visually identify

the small prey items and/or to collect faeces from the bottom of the pans, so potential prey items were identified by taking qualitative reference samples from the water column with a zooplankton net (150 μm mesh; 3–5 randomly transects of 5 m each) following observations. Analysis of these samples showed that the potential prey items were the adult crustacean Brine Shrimp *Artemia* spp., and larvae of the pelagic beetle *Ochthebius* spp., larvae and nymphs of the Chironomid *Chironomus salinarius*, as well as larvae of the alkaline fly *Ephydra* spp.

To estimate the intake rate of plovers foraging like sandpipers on small prey items, we analysed data from overwintering birds foraging on hypersaline pans (the saltworks named 'La Tapa') where the only available prey was Brine Shrimp. For this purpose, the ash free dry mass (AFDM) of the mean sized Brine Shrimp in the pans was multiplied by the number of prey taken per minute (see details in Masero 2002, 2003). Brine Shrimps had a small variability in biomass during winter ($<2 \times 10^{-5}$ g AFDM), thus making estimations of energy intake rates precise. Each peck was assumed to be successful because observations of plovers at close range showed that each peck was followed by swallowing movements. An assimilation efficiency of 70% for Brine Shrimp was assumed to estimate the net intake rate (Masero 2003).

Data from Masero *et al.* (2000) about the use of saltworks at Cadiz Bay by foraging shorebirds were used to determine the occurrence of the sandpiper-like foraging method in Grey and Ringed Plovers throughout the annual cycle. That study was carried out in an area (La Tapa) where intertidal mudflats and adjacent saltworks function as a closed system, and included several counts per month (a count per week during January–March, and two/three counts per month, at least a week apart, during the rest of the annual cycle) of the number of foraging birds at high tide in hypersaline pans, noting whether plovers used the sandpiper-like foraging method or the run–stop–search method.

RESULTS

Ringed Plovers generally foraged along the shore of the pans, either alone or amongst loose flocks along with small-sized sandpiper species, showing a strong preference ($>75\%$ individuals) for foraging in shallow water (0.5–2 cm depth). They foraged by pecking from the water column while walking slowly, and we did not observe the typical stances of plovers (see illustrations in Pienkowski 1983) while foraging. The mean feeding rate in winter and summer was 47.0 ± 15.3 prey min^{-1} ($n = 18$) and 51.7 ± 21.1 prey min^{-1} ($n = 12$), respectively, and no seasonal variation could be detected (Mann-Whitney U test: $Z = 0.48$, $P = 0.63$).

Grey plovers also foraged in loose flocks (<10 individuals) or alone, but tended to forage away from the pan's shore, apparently avoiding other foraging shorebirds (especially small-sized sandpipers), and using much of the shallow water surface (1–4 cm) available in each pan. Similarly to Ringed Plovers, they foraged by pecking small prey items from the water column while walking slowly, and they also did not use the typical stances of plovers while foraging. The mean feeding rate was similar in both seasons (winter: 19.8 ± 6.03 prey min^{-1} , $n = 13$; summer: 17.1 ± 7.2 , $n = 7$; Mann-Whitney U test: $Z = -1.1$, $P = 0.27$).

The percentage of plovers using this sandpiper-like foraging method in hypersaline pans ranged between 0–24.1% and 0–4.5% for Ringed and Grey Plover, respectively (Fig. 1). The intake rate for both plovers foraging like sandpipers on the crustacean *Artemia* is shown in Table 1. For comparative purposes, we also show data from other studies about intake rates by typical plovers on intertidal areas using the highly characteristic run–stop–search behaviour.

DISCUSSION

We found that the sandpiper-like foraging method is a common foraging method in Ringed Plovers feeding in prey-abundant pans and is occasionally

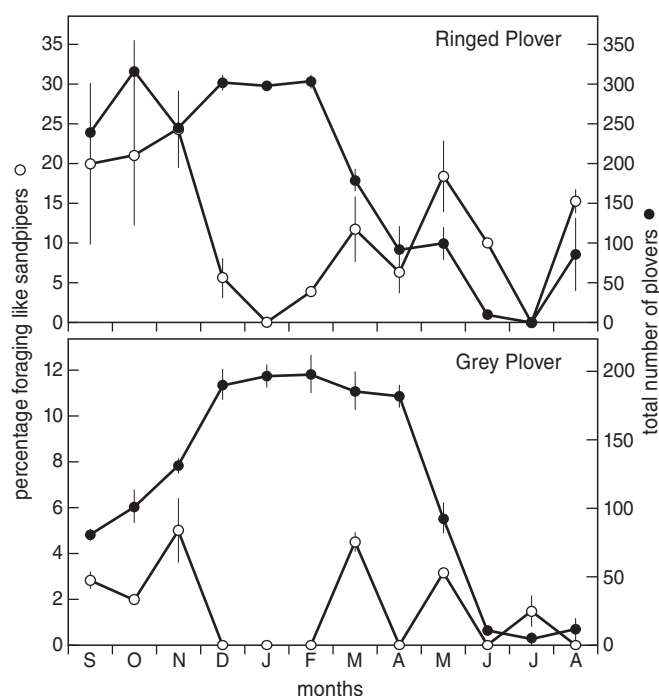


Figure 1. Percentage (\pm SD) of Grey and Ringed Plovers foraging like sandpipers during the season, and the total number foraging at high tide in the same salt pans. Data were taken in an industrial saltworks located in SW Spain.

Table 1. Mean (\pm SD) net energy intake rates (kJ min^{-1}) of Grey and Ringed Plovers using the sandpiper-like foraging (SF) and the run-stop-search (RSS) method.

Habitat (main prey type)	Grey Plover	Ringed Plover	Foraging mode	Reference
Hypersaline pans (Brine shrimp <i>Artemia</i> spp.)	0.1 ± 0.0	0.2 ± 0.0	SF	This study
Intertidal mud and sandflats (crustacea – polychaete worms)	0.9 ± 0.2	0.3 ± 0.0	RSS	Pienkowski 1982 ^a
Intertidal mudflats (benthic invertebrates)	1.1 ± 0.5	-	RSS	Turpie 1995 ^b
Intertidal mudflats (benthic invertebrates)	1.2 ± 0.1	-	RSS	Turpie & Hockey 1993 ^c
Intertidal mudflats (benthic invertebrates)	0.9 ± 0.3	-	RSS	Turpie & Hockey 1997 ^d

^aAverage values from Table VIII and IX; ^bAverage value from Table 2; ^cAverage value from Table 5; ^dAverage value from Table 4.

used by Grey plovers as well. This shows that behavioural plasticity of the foraging methods of typical plovers may be greater than previously assumed. A foraging repertoire that exploits disparate prey types may lead to the expansion of the

Ringed and Grey Plover's ecological niche, which potentially has a competitive advantage in nutrient acquisition (Lowry *et al.* 2005). Although the sandpiper-like foraging method was associated with an opportunistic behaviour (most plovers fed

in the hypersaline pans only at high tide, when their preferred foraging grounds on intertidal areas were unavailable; Masero *et al.* 2000), the food obtained using this foraging method could significantly contribute to the daily energy intake of plovers (up to 5% and 24% of the total population of migrating Grey and Ringed Plovers fed at high tide, respectively). The theoretical daily energy requirement of Grey and Ringed Plover using Nagy's (1987) equation (body masses from birds captured at Cadiz Bay) is 130 and 311 kJ day⁻¹, respectively (see calculation details in Masero & Pérez-Hurtado 2001). According to our estimates of intake rates at high tide and assuming that the duration of the high tide period in the saltworks is 4 hours on average, the food obtained using the sandpiper-like foraging method contributed up to 37 and 8% of the daily energy requirement of Ringed and Grey Plover, respectively, in the periods when it was used most. The proportion of plovers foraging like sandpipers at high tide peaked in November, and was greater during the migration periods than during the winter. In November the foraging conditions at the intertidal flats were especially bad (strong western winds) and there was a high food availability in the saltworks (Masero *et al.* 2000). Accordingly, we suggest that this foraging method is a supplement to meet their energy requirements when environmental factors at the intertidal foraging grounds were adverse and/or to meet the high energy demands associated with the long-distance migration.

The intake rates of Grey and Ringed Plovers were similar, and lower than those of birds feeding with the run-stop-search method (especially Grey Plover). It is possible that the intake rates of birds using the sandpiper-like foraging mode to feed on Brine Shrimps is limited by the speed they can peck, so this foraging method may be more profitable for small species than for large ones. Presumably, this would not apply so much to birds hunting with the run-stop-search method, as they are targeting larger prey items.

The ability of plovers to use the sandpiper-like foraging method may be a reminiscence of the ancient pecking behaviour of birds. Following a

deductive method, Zweers and co-workers showed how bird foraging behaviour evolved from an ancestral feeding system (i.e. pecking; Zweers 1991, Zweers & Gerritsen 1997, Zweers & Vanden Berge 1997). This theory is based on the premise that pecking is a general feeding mechanism present in all Neornithes, which shares common elements with the feeding mechanisms in lower tetrapods (Zweers 1991). In fact, the common ancestor of modern birds was described as a Stone-curlew-like shorebird (Zweers & Gerritsen 1997). Therefore, it is not unexpected that plovers use a pecking foraging mode.

Turpie (1994) speculated that typical plovers foraging on intertidal mudflats are less able to see their prey while they are moving than when they are standing still, and that might be the reason that they frequently run towards prey with their head held sideways in an attempt to improve visual acuity (this head movement would help to compensate visual problems such as a harder time judging distances and worse depth perception). Most plovers foraged on the crustacean Brine Shrimp, a prey type that swims in the water without showing any escape behaviour from predatory birds (see discussion in Masero 2003). Our observations suggest that typical plovers can successfully locate and capture small prey items suspended in the water column by uninterrupted walking and without the need to stop to spot a prey with a single eye. As birds with monocular vision do have a limited field of binocular vision directly in front of them (Fernández-Juricic *et al.* 2004), we suggest that plovers using the sandpiper-like foraging method could successfully locate these small prey items in front of them with binocular vision.

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SAMENVATTING

Plevieren staan bekend om hun typische manier van voedsel zoeken waarbij ze afwisselend rennen en stil staan. Het voorkomen van voedselzoeken zoals strandlopers dat doen – langzaam lopen en tegelijkertijd pikkend – is voor plevieren amper beschreven. In dit artikel wordt het gedrag en de opnamesnelheid beschreven van Bontbekplevieren en Zilverplevieren die in zoutpannen in het zuidwesten van Spanje als strandlopers in het water zwevende prooien pakken. De twee soorten pakten respectievelijk 48.9 ± 18.0 en 19.1 ± 6.3 prooien per minuut (gemiddelde met standaardafwijking), resulterend in een netto opname snelheid van 0.23 ± 0.05 en 0.09 ± 0.01 kJ min⁻¹ wanneer rekening wordt gehouden

met een voedselvertering van 70%. Tot 24% van de Bontbekplevieren zocht op de strandlopermanier voedsel, en vooral in voedselrijke zoutpannen volgden de plevieren deze tactiek. Zilverplevieren deden dat ook maar in veel mindere mate. Dit onderzoek onderstreept dat plevieren meer variatie in de wijze van voedselzoeken kunnen vertonen dan voorheen aangenomen. Hoewel verondersteld wordt dat plevieren stil moeten staan om prooien voldoende scherp te zien, blijken ze ook in staat voedsel te ontdekken en pakken terwijl ze zonder onderbreking lopen. (CB)

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