Searching behaviour of foraging waders: does feeding success influence their walking?

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Predators that feed on clustered prey tend to have an 'area-restricted search' (ARS), characterized by a combination of a slow and tortuous movement in prey-rich areas, and a fast and straight movement in poorer areas. Waders that forage in intertidal areas usually prey upon buried macroinvertebrates, whose distribution is often clustered. However, wader species differ in the strategy used to find their prey: some rely mainly on visual cues, some rely on tactile cues, and others follow a more generalist method, simply sweeping the sediment surface with the bill. We hypothesized that these strategies influence the adoption of an ARS by waders. We analysed this hypothesis by comparing the fine-scale movement of a 'tactile' predator (black-tailed godwit, *Limosa limosa*), with that of a 'visual' predator (redshank, *Tringa totanus*) and a 'sweeper' (avocet, *Recurvirostra avosetta*). We filmed 190 individuals of the three species and, using GIS facilities, obtained more than 12 000 spatial positions, along with detailed records of feeding activity. We analysed several parameters of fine-scale movement of waders, such as foraging and searching speeds, tortuosity, and the relationship between these parameters and foraging success. Only the tactile predator, the black-tailed godwit, followed an ARS, reducing searching speed and increasing spatial turning rate whenever the prey intake was higher. Furthermore, its foraging strategy involved short-term adjustments of movement that maximized the likelihood of finding subsequent prey, suggesting a prior knowledge or an ability to perceive rapidly the distribution pattern of its prey.
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Several studies have shown that species feeding on clustered prey tend to have an 'area-restricted' (or 'area-concentrated') search (ARS; e.g. Thomas 1974; Hill et al. 2000; Nolet & Moij 2002; Fortin 2003). This type of strategy involves an increase in the searching effort after finding a prey, because of the high probability of finding another prey in the vicinity (Benhamou 1992). Two major mechanisms to increase the searching effort are reducing the searching speed and increasing the turning rate of the path (Knoppien & Reddingius 1985; Kareiva & Odell 1987), thus increasing the time spent in that area and, consequently, the likelihood of finding prey. Benhamou (1992) showed that the ARS also maximizes the intake rate when prey items are clustered in continuous patchy environments (i.e. when the patches of prey do not have obvious boundaries, resulting in areas where local density is higher than the average).

Most waders that winter in estuarine areas depend on intertidal flats that are only available during low-tide periods. In these areas they mostly prey upon benthic invertebrates, whose spatial distribution can be considered as continuously patchy (Van de Kam et al. 2004). Wader species differ in the method used to search for food. Some species detect their prey by sight (for example, plovers, genera *Pluvialis* and *Charadrius*, and redshanks, *Tringa totanus*); others use mostly tactile cues (e.g. genus *Limosa*), whereas avocets (genus *Recurvirostra*) sweep their bill and ingest small prey items along with portions of mud (Moreira 1995a, b). Although each species tends to prefer a particular searching technique they can, to some extent, switch from one to another in response to environmental conditions (e.g. Robert & McNeil 1989; Moreira 1995a; Lourenço et al. 2008).

Wintering waders are good models for the study of animal movement, because (1) their feeding behaviour is easy to monitor, (2) they search for food while walking (and not in the air), allowing their movement to be fully described in two dimensions, (3) species with different searching methods coexist in the same areas, allowing a comparison between them, and (4) their time budgets

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are highly constrained by the tidal cycle (Granadeiro et al. 2006), and thus waders need to maximize their immediate intake rate to fulfil their energetic demands (which are among the highest found in birds; Piersma 2002; Rogers et al. 2006). In fact, waders have often been used as models for testing predictions derived from optimal foraging theory (e.g. Goss-Custard 1977a; Piersma et al. 1995; Meire 1996; Stillman 2003; Van Gils et al. 2005a, b). However, these studies mostly focused on optimal diet and patch choice, whereas the analysis of fine-scale movements of waders is still a poorly explored subject (but see Goss-Custard 1970, 1977b; Speakman & Bryant 1993; Wilson & Vogel 1997).

The ARS hypothesis predicts that, in patchy environments, waders should increase their searching effort after ingesting a prey, owing to the higher likelihood of finding another prey nearby. This strategy has been recorded in red knots, *Calidris canutus*, and great knots, *Calidris tenuirostris*, feeding in intertidal areas (Van Gils 2004). However, other waders do not search in this way (e.g. the semipalmated sandpiper, *Calidris pusilla*; Wilson & Vogel 1997), presumably because they use a 'visual' searching method. In fact, for a mostly visual predator, prey detectability is highly dependent on the activity of prey, which is often depressed by the presence of predators. Most benthic invertebrates tend to retract into their burrows or cease their activity when predators are foraging nearby (Van de Kam et al. 2004). Consequently, visual predators may not benefit from long residence periods in the same spot, because disturbed invertebrates will remain retracted deep in the sediment or inactive until they leave. On the other hand, an increase in the searching effort after prey ingestion is only to be expected when there is a clear relationship between prey intake rate and prey density. This relationship is probably the norm in most predators, but does not seem to be the case for some waders, such as avocets, *Recurvirostra avosetta*, which 'sweep' the sediment and ingest

indiscriminately small items along with some mud (e.g. Moreira 1995b). Therefore, we predict that waders that rely mostly on tactile cues to find their prey are the most likely to adopt an ARS. We tested this prediction using model species with different searching methods: a 'tactile predator' (black-tailed godwit, *Limosa limosa*), a 'visual predator' (redshank) and a 'sweeper' (avocet). We also provide a detailed characterization of several parameters of the fine-scale movement of foraging waders.

METHODS

Study Area

We conducted the study in an intertidal flat located in the southern margin of the Tagus estuary, Portugal (38°45′N, 09°50′W), one of the largest and most important wetlands in the Iberian Peninsula. The study area constitutes a regular feeding ground for several wader species (Lourenço et al. 2005; Dias et al. 2008), including those we focused on in this study: avocet, black-tailed godwit and redshank. Flocks in excess of 100 individuals of each species are regularly observed here. Previous surveys of benthic fauna (unpublished data) have shown that prey density is unevenly distributed, but richer patches have gradual boundaries, thus forming a 'continuous patchy environment' (sensu Benhamou 1992). Two areas (100 × 50 m² and 60 × 50 m²) were defined in the study site, each consisting of 5 × 10 m grid plots, marked with canes in the corners (Fig. 1). The canes were buried in the sediment 1 month before the study, to allow the sediment to be flattened by the tides, eliminating our footprints. The exact position of one of the canes was recorded with GPS (horizontal accuracy = 4 m), and all the other canes were placed using a tape measure and
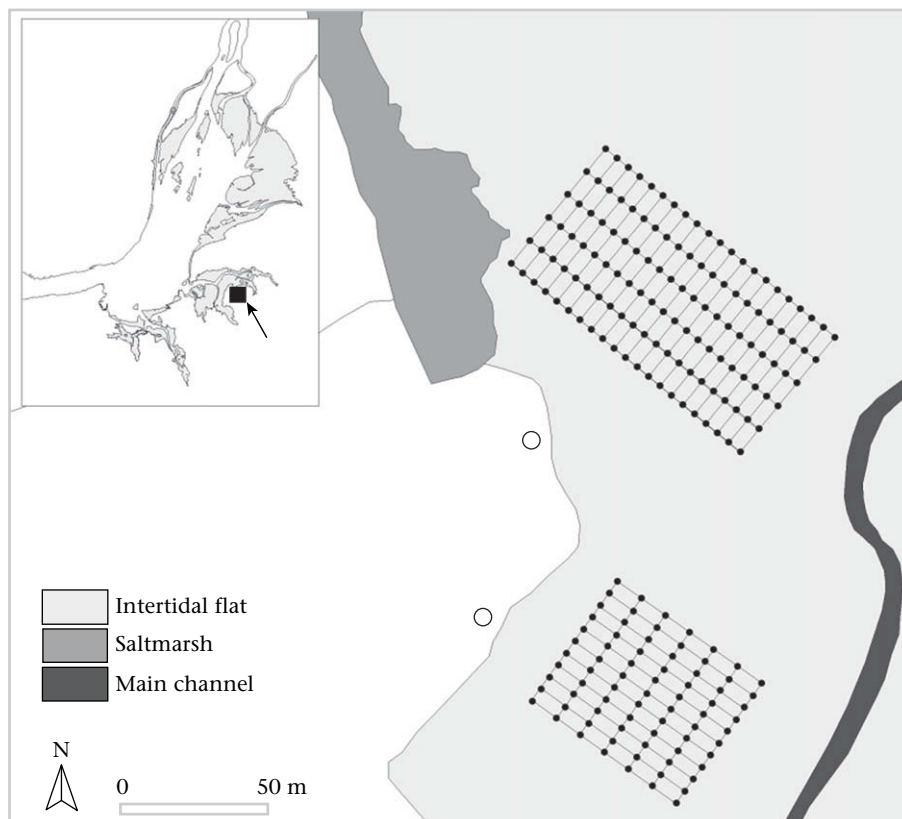

Figure 1. Study area. Small dots represent the location of the canes placed on the sediment, delimiting the plots (rectangles); open circles represent the location of videocameras.