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Original article

The energetic importance of night foraging for waders wintering in a temperate estuary

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ABSTRACT

Many species of waders forage extensively at night, but there is very little information on the relevance of this behaviour for the energy budget of waders wintering in estuarine wetlands. Quantitative data on diurnal and nocturnal intake rates can indicate the extent to which birds need to forage at night to supplement their diurnal energetic intake, or rather show a preference for nocturnal foraging.

We compared day and night foraging behaviour, diet, and energy consumption of several wader species in the Tejo estuary, Portugal. There were significant differences between diurnal and nocturnal foraging behaviour. In general, birds moved less at night and scolopacid waders tended to use more tactile foraging methods. Although birds consumed the same type of prey in the two periods, the relative importance of each type changed. Overall, energy consumption was higher during the day except in grey plover, which achieved higher crude intake rates at night.

Our results support the assertion that night foraging is an important part of the energy balance of waders during late winter, but that in most species it is less profitable than diurnal foraging.

1. Introduction

Many species of waders use intertidal areas as feeding grounds during migratory and wintering periods. In these habitats, foraging is limited to the low tide, when invertebrate-rich sediment flats are accessible to birds (e.g. Burger et al., 1977; Tiedemann and Nehls, 1997). Most estuaries have bi-diurnal tides, i.e. there are two low tides and two high tides in each 24 h. Hence, in the winter, over half the period during which intertidal areas are accessible occurs during the night. In fact, several studies have shown that most coastal wintering wader species forage not just during daytime but

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also at night (e.g. Robert and McNeil, 1989; McNeil et al., 1992; Dodd and Colwell, 1998; Sitters et al., 2001). Two hypotheses have been proposed to explain this night time feeding behaviour (McNeil et al., 1992). The *supplementary hypothesis* states that birds will primarily feed during the day, and will only forage at night when they fail to fulfil their daily energetic requirements during the diurnal low tide. Therefore, night foraging would consist of a supplement to diurnal foraging. In contrast, the *preference hypothesis* defends that birds actually prefer to forage at night, because night foraging is either more profitable or safer. Of course, one can also consider different arguments why birds should show no consistent preference between day and night, foraging whenever is better in accordance to proximal ecological and physiological causes (Sitters, 2000).

If the advantages of foraging at night are sufficiently important, then *preference* may be the most parsimonious hypothesis to explain this behaviour. Night foraging seems to be safer (Morrier and McNeil, 1991), as the main predators of waders are raptors (e.g. Page and Whitacre, 1975; Rosa et al., 2006) which mostly hunt during the day. However, owls may also pose a serious threat for waders during the night (Page and Whitacre, 1975; Kus et al., 1984) and areas close to land may be avoided (Mouritsen, 1992; Sitters et al., 2001; Burton and Armitage, 2005) perhaps due to mammalian predators. Some studies have suggested that food resources are more accessible for waders during the night, as some invertebrate prey show increased surface activity at night (Dugan, 1981; Evans, 1987). Human disturbance is greater during daylight hours (Burger and Gochfeld, 1991), and foraging waders frequently suffer kleptoparasitism by gulls at this time (Amat and Aguilera, 1989), which could again favour night foraging.

Conversely, there are also facts supporting the hypothesis of *supplementary* feeding. Several studies have reported higher proportions of birds foraging during the day (Manseau and Ferron, 1991; Dodd and Colwell, 1996), and low light seems to hamper the ability of some species to find prey by sight during the night (Robert and McNeil, 1989; McNeil et al., 2004). Lower temperatures increase the metabolic rates thus increasing energetic demands (Dugan et al., 1981; Kersten and Piersma, 1987), while decreasing the surface activity of suitable prey (Pienkowski, 1983a); however, the heat produced by muscular activity while foraging can also be favourable for thermoregulation (Wilson and Gremillet, 1996). Finally, increases in night foraging during stop-over and pre-migratory periods (Batty, 1988; Zwarts et al., 1990), and also during extreme cold periods in mid-winter (Baker, 1981) when waders need additional energetic intake, also support the supplementary hypothesis.

Few studies have thoroughly quantified the importance of night foraging for the energetic balance of wintering waders (Kalejta, 1992; Turpie and Hockey, 1993). This information is important to understand which of these hypotheses better explains the occurrence of night foraging in waders. Although there are other factors to take into account, namely predation risk, from an energetic point of view a minor energetic contribution of night foraging would validate the supplementary hypothesis, whereas a dominant contribution would instead support the preference hypothesis.

In this study we compared the diet and foraging behaviour of several wader species during the day and during the night, and estimated the energy intake rates in both periods, in an attempt to understand the importance of night foraging for the energetic balance of these birds during the winter. In addition, we evaluated the two main explanatory hypotheses for night forging behaviour in waders in the light of our findings.

2. Materials and methods

2.1. Study site

Field work took place in 13 areas (Hortas [2], Alcochete peer [2], Seixalinho [2], Sarilhos [2], Rosário [2], Moita harbour [2], Coina [1], Arrentela [2], Amora [2]), located throughout the southern bank of the Tejo estuary, in Portugal (Fig. 1). These areas were representative of the different light conditions found in this estuary at night, ranging from near total darkness to highly illuminated. The Tejo estuary is an important wintering and stopover site for several East Atlantic Flyway waders, supporting over 50,000 birds during the winter, mostly dunlin *Calidris alpina*, avocet *Recurvirostra avosetta*, black-tailed godwit *Limosa limosa* and grey plover *Pluvialis squatarola* (e.g. Costa and Rufino, 1997).

2.2. Behavioural observations and counts

Between 21 January and 8 April 2005, birds in the study areas were counted, once per low-tide, both during the day and during the night, in 28 different days balanced over the field season. In each count, we determined the proportion of actively foraging birds. The observations were made everyday in two periods: from 4 days before to 4 days after the new moon

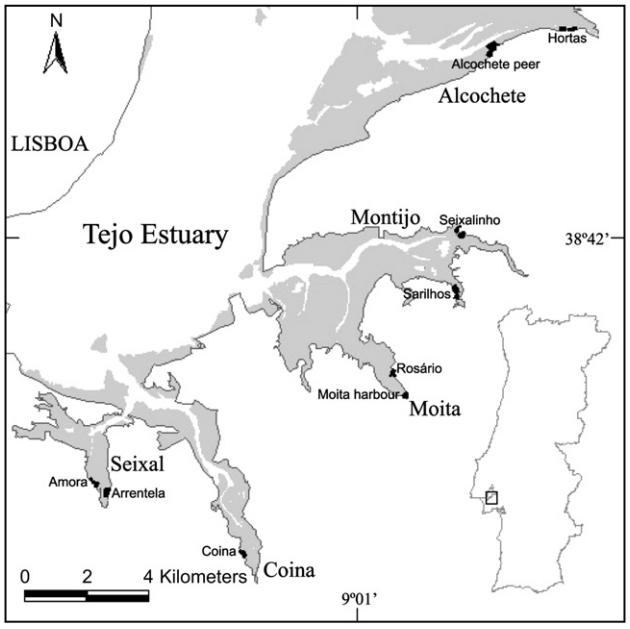

Fig. 1 – Location of the 13 study sites, along the southern bank of the Tejo estuary. Grey areas represent intertidal areas, the study areas are presented in black.