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Foraging behavior of the American oystercatcher *Haematopus palliatus pitanay* (Murphy 1925) on the intertidal ascidian *Pyura praeputialis* (Heller 1878) in the Bay of Antofagasta, Chile

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Abstract Oystercatcher foraging behavior has been described for diverse intertidal prey such as limpets, mussels, and oysters. This paper describes foraging behavior of the American oystercatcher, *Haematopus palliatus pitanay*, on attached and wave-dislodged ascidians, *Pyura praeputialis* (prey with a restricted geographic range of 70 km) in the Bay of Antofagasta, Chile. Stabbed holes on the top of the ascidian's tunic, probing excursions, handling time, and five prey-handling sequential stages (striking, hammering, prying, cavity food searching, and swallowing) are described and measured. The need to determine ascidian profitability for oystercatcher species in Australia and Chile is highlighted.

Key words American oystercatcher · *Pyura praeputialis* · Foraging behavior · Chile

Introduction

Oystercatcher (Haematopodidae) foraging behavior has been described on a variety of intertidal benthic prey such as oysters, limpets, mussels, and polychaetes in the northern and southern hemispheres (Hockey 1981; Goss-Custard and Durel 1988; Nol and Humprey 1994). In Australia, sooty oystercatchers also feed on intertidal ascidian (= sea squirt) *Pyura* spp. (Schultz 1989; Chafer 1992), and this food item represents an important food resource. Nevertheless, a description of their foraging behavior is lacking.

In northern Chile, dense intertidal beds of the ascidian *Pyura praeputialis* are common (Castilla 1998; Castilla et al. 2000), and during low tide the American oystercatcher

Haematopus palliatus pitanay (Murphy 1925), known as “pilpilén común,” feeds primarily on them. Information about American oystercatchers (a pied species) feeding on ascidians has not been reported. In Chile, this ascidian is found almost exclusively inside the Bay of Antofagasta, along approximately 60–70 km of coastline (Cerdeira and Oliva 1997; Clarke et al. 1999; Castilla et al. 2000). They aggregate in dense monocultures of individuals that form continuous and cemented units (beds) on rocky intertidal platforms (Paine and Suchanek 1983; Castilla 1998).

Such dense intertidal assemblages of *Pyura* spp. occur only in Australia (Fairweather 1991), South Africa (Fielding 1994), and Chile (Castilla 1998). This article is the first in a series of works examining the ecological importance of oystercatcher foraging behavior on intertidal *P. praeputialis* ascidians from Antofagasta. Here, we describe American oystercatcher foraging behavior on attached and wave-dislodged ascidians in the Bay of Antofagasta and compare it with oystercatcher foraging behavior described for other benthic prey. Additionally, we discuss the potential adaptation of these feeding techniques for oystercatchers foraging on a prey showing such a restricted geographic distribution.

Study area and methods

Adult American oystercatchers were observed and recorded using a video camera between July 1 and October 17, 1997, at the beginning of their breeding season. Field observations were made by one observer during daytime (1000–1800 h) along spring tides ranging between 0.12 and 1.59 m. Age and sex could not be determined. The study took place at the intertidal rocky shore of El Way, Antofagasta (23° 44' S, 70° 26' W), on two horizontal (2°–5° of inclination) platforms (28 m² and 29 m²) that form part of an extensive platform approximately 1 km long and 30 m wide. At El Way, the mid-low intertidal zone is dominated by a dense monoculture of *P. praeputialis* (Castilla 1998). Typically, between three and ten oystercatchers foraged on

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the extensive 1-km platform during each low tide. We observed the oystercatcher *H. palliatus pitanay* through the use of a Bausch and Lomb 15 × 60 mm spotting telescope for a total of 55 h (16 days).

The focal oystercatcher was selected randomly among those foraging and observation was continued to the end of the feeding bout, which usually lasted 5–15 min. The oystercatchers were not banded, so we could not identify individuals and repeated observations were assumed to be independent (Ward 1991). Furthermore, daily observations on three to five oystercatchers (identified by position under continuous recording) were not repeated for individuals. To supplement the direct observations, we used a video camera (Sony Hi-8 TR-910) to record foraging behavior of oystercatchers for a total of 8 h. These observations were conducted from the upper intertidal zone, approximately 20–30 m from the birds. At the end of every observation period (around 1800 h), we examined ascidians and other food items (e.g., sea urchins, keyhole limpets, snails) that had been attacked. We measured the diameter of stabbed (punctured, pierced) holes made by the oystercatchers on attached and wave-dislodged ascidians. Measurements were made with calipers to 0.1 mm precision, and means and standard errors (SE) were calculated.

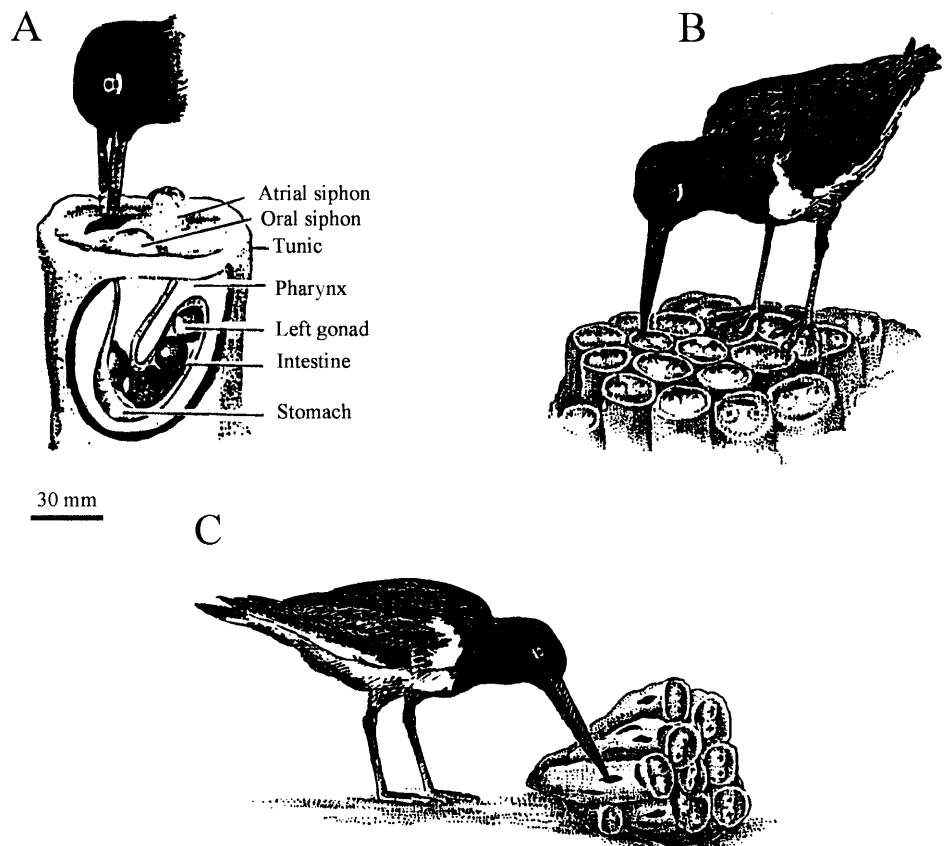
Videotapes were used to characterize specific and fast movements during oystercatcher foraging bouts. Foraging behavior was divided into probing (sensu Del Hoyo et al. 1996) and handling. Probing was defined as an unsuccessful

feeding attempt and handling as a successful attempt. Handling was subdivided into five sequential stages: (1) striking (= single or multiple thrusts by the bill against an ascidian), where the bird raises its head; (2) hammering (= repetitive thrusts by the bill on a selected point of the ascidian tunic leading to perforation), where the bird does not raise its head; (3) ascidian body cavity searching (= the use of the bill for food searching inside the body of the ascidian); (4) bill prying movements, used to expand the stabbed hole; and (5) swallowing. These stages were timed in nine bouts, corresponding to 3 oystercatchers, and the results are presented as the time duration of each stage and frequency. Probing times, mean duration of probing excursions (= exploration) and mean handling time, were calculated in 12 oystercatcher feeding excursions on *Pyura* beds. These measurements were calculated from films analyzed on a frame-by-frame basis (Sony STV 3000 time-lapse video recorder) and digitized video sequences (Media 100 v. 2.6 digital video system; Bio-Analysis program NIH 1.61 for Macintosh).

Results

A total of 18 h of foraging observation were completed on 48 oystercatchers feeding on the midintertidal *P. praeputialis* beds during low tide. Of the 48 birds, 40 (83%) were feeding on attached ascidians, and 8 (17%) were prey-

Fig. 1. **A** Schematic of an American oystercatcher hammering on a sessile sea squirt at the top of the tunic shows external structure (siphon and tunic). **B** Main internal structures seen through an opening. Single perforations are usually made next to one of the siphons. **C** Oystercatcher hammering on wave-dislodged sea squirt and puncturing multiple holes on the lateral portion of the tunic



ing on keyhole limpets (*Fissurrella crassa*, *F. limbata*, *F. pulcra*, *F. maxima*), the snail *Tegula atra*, and the black sea urchin *Tetrapygyus niger*. Oystercatchers always attacked attached ascidians on the top of their tunic near the siphon (Fig. 1A,B). Stabbed holes produced on the top of the ascidian's tunic by the oystercatcher were 18.90 ± 0.88 mm in diameter (54 observations). Oystercatchers probed 0 to 16 times ($X = 4.45 \pm 1.4$), where zero represents searching time without ascidian tunic probing before a successful attack (= when the ascidia is perforated). The mean duration of probing excursions (12 observations) was 11.97 ± 3.34 s (range, 0–34.5 s). Mean handling time per ascidian was 144.46 ± 16.59 s (range, 66.87–303.70 s). Duration times of the five handling sequential stages (nine bouts) were (1) strike: 2.19 ± 0.30 s (0.90%); (2) hammering: 31.56 ± 5.74 s (13.01%); (3) prying: 18.94 ± 10.47 s (7.81%); (4) ascidian body cavity food searching: 175.21 ± 30.50 s (72.23%) and (5) swallowing: 14.67 ± 2.72 s (6.05%). Every sequence took more than 500 head movements, including up to 25 swallows per ascidian.

During high tide (8.3 h of observation), 28 oystercatchers were observed at the upper part of the beach: 19 were feeding on wave-dislodged ascidians and 9 were performing self-maintenance activities. Wave-dislodged ascidians (stranded in the upper and supralittoral intertidal zone) were punctured, one to four holes, mainly on the lateral portion of the tunics (Fig. 1C). These holes were 19.01 ± 0.64 mm in diameter (46 observations).

Discussion

Oystercatchers forage on a variety of prey using different feeding techniques (Nol and Humprey 1994). These techniques may be taken as evidence for their feeding behavior flexibility on the prey item consumed. Until now, ascidian species had not been included as prey items consumed by the American oystercatcher *Haematopus palliatus pitanay* (Goodall et al. 1957; Nol and Humprey 1994). In our study, the species fed on attached ascidians during low tides and on wave-dislodged ascidians during high tide. In both cases the oystercatchers used a combination of feeding techniques. Examples are (a) probing, which has been described as the main oystercatcher feeding technique for searching marine worms in intertidal mudflats; (b) hammering, frequently used by oystercatchers to remove mussels from clumps on rocks; (c) stabbing, used to open bivalves; and (d) prying, used to detach limpets (Nol and Humprey 1994).

In Chile, *Pyura praeputialis* has a very restricted distribution of about 70 km of coastline. It is interesting to note that a prey with such a restricted distribution can influence the foraging behavior of a bird species distributed along most of the South American coast (Goodall et al. 1957). There is no information about how long *P. praeputialis* has been present in the Bay of Antofagasta, making it difficult to develop an evolutionary adaptive argument (but see Castilla and Guíñez, 2000). We suggest that the feeding technique adaptation described may be a consequence of a learning

process. In fact, in June 1998 we observed one juvenile American oystercatcher attempting to puncture ascidians while accompanied by two adults.

On the other hand, in Antofagasta, the American oystercatcher forages mainly on ascidians, even though other prey, such as limpets, snails, and black sea urchins, are also consumed. The reason for this preference could be rocky shore ascidian abundance or profitability. If the oystercatcher preference for sea squirts is related to their abundance, then the birds may adapt so as to reduce, or even to eliminate, competition with other bird species by the use of the feeding techniques described (Welty 1975). Also, ascidian profitability needs to be evaluated.

The American oystercatcher handling and bill movements while feeding on ascidians are similar to the foraging behavior reported by Lauro and Nol (1995) for the sooty oystercatcher *H. fuliginosus* and the pied oystercatcher *H. longirostris* when foraging in mudflats in Australia. The size of the perforations made by sooty oystercatchers on the tunics of wave-dislodged *P. stolonifera* (Kott 1997; Fairweather 1991) in New South Wales, Australia (Chafer 1992), ranged between 15 and 20 mm and therefore are similar to that reported here (10–35 mm). Further observations of oystercatchers preying on *Pyura* spp. in Chile, Australia, and South Africa are needed to compare their feeding behavior and foraging strategies. Moreover, the understanding of ecological and behavioral interactions with other shorebird species may also give insight into community interactions modulated by oystercatchers.

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