



Feeding preferences and food searching strategies mediated by air- and water-borne cues in the mud whelk *Terebralia palustris* (Potamididae: Gastropoda)

Sara Fratini*, Marco Vannini, Stefano Cannicci

Dipartimento di Biologia evolutivista "L. Pardi", via Romana 17, 50125 Firenze, Italy

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ABSTRACT

The gastropod *T. palustris* is one of the major species responsible for leaf consumption and degradation within the Indo-Pacific mangrove forests, and it strongly competes with herbivorous sesamid crabs in consuming fallen leaves. This snail feeds at high and low tides and it is able to locate food items by means of chemical cues. The aim of this study was to assess the food preferences of *T. palustris* and to define its feeding strategies at low and high tides, by conducting field trials on water-borne mediated food location at high tide, grazing rate and the chemical attraction exerted by different mangrove leaves. The results showed that *T. palustris* was able to perceive underwater grazed leaves. In addition, we demonstrated that *T. palustris* consumes all the mangrove species (preferentially the Rhizophoraceae leaves) but *Xilocarpus granatum*. Moreover, this snail is differentially attracted to different mangrove species: the major attractive power is wielded by the rhizophoracean species and *Pemphis acidula*, while *X. granatum* does not attract this snail at all. The efficacy and adaptive value of a chemically mediated food searching strategies is unquestionable since by using this ability *T. palustris* can locate and reach the leaves it preferentially consumes. Moreover, *T. palustris* is the only macrobenthic species of East Africa mangroves able to search, detect and consume mangrove leaves at both high and low tides. Such an expanded feeding window permits *T. palustris* to occupy temporal niches left empty by the sesamid crabs.

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1. Introduction

The mud whelk *Terebralia palustris* (Linnaeus) is widespread throughout the Indo-Pacific area and is one of the most abundant inhabitants of mangroves, reaching remarkable densities in some locations, e.g. 150 adults m⁻² in New Caledonia (Plaziat, 1984) and approximately 20 adults m⁻² in Kenya (Fratini et al., 2004). It colonizes the entire mangrove forest, from the lower subtidal fringe to the upper littoral fringe, adapting itself to very different intertidal belts and mangrove microhabitats. Fratini and co-workers (2004) studied the population structure and distribution of this snail in a Kenyan mangrove forest and demonstrated that, in contrast to previous reports (Wells, 1980; Crowe, 1997; Crowe and McMahon, 1997), the snail's zonation depends mainly on the organic content of the soil with the adults (reaching a shell size of 10–12 cm) segregating the juveniles (with a shell size of less than 5–6 cm) into less favourable areas (i.e. those with more acidic soil and less frequently flooded).

This snail has amphibious features and feeds both during low and high tides (Fratini et al., 2004), with the adults grazing on fallen mangrove leaves and the juveniles eating mud and leaf debris (Nishihira, 1983; Houbrick, 1991; Dahdouh-Guebas et al., 1998; Fratini et al., 2004). Although classically the role of *T. palustris* and of other

mangrove gastropods in nutrient dynamics has been largely overlooked, recent studies have demonstrated their central ecological role. Adult *T. palustris* contribute massively to leaf degradation and consumption: Fratini et al. (2004) showed that, when fed *ad libitum*, this whelk is able to consume a huge amount of fallen leaves, much more than is naturally available in the wild. Moreover, thanks to analyses of carbon and nitrogen isotope ratios in various mangrove macroinvertebrates, it has been shown that molluscs massively contribute to entrapping primary production within the mangrove ecosystem, since they ingest a much higher amount of mangrove leaves than sesamid crabs (Bouillon et al., 2002a,b, 2003).

As widely recognised for many gastropods (Croll, 1983), *T. palustris* uses olfaction to locate suitable food resources. In particular, in its food search it relies on chemical cues released by broken (scraped) mangrove leaves or propagules, as experimentally demonstrated by Fratini et al. (2001). This means that this snail is able to locate a mangrove leaf feeder thanks to the cues released by the leaves when grazed, while conversely it is not attracted to snails that are not feeding nor to food items that have not been scraped (Fratini et al., 2001). As a result of this feeding recruitment process, *T. palustris* actively competes with the leaf feeding sesamid crabs. When the crabs encounter a leaf on which a substantial number of snails have settled, they are not able to grasp and capture the leaf for themselves (Fratini et al., 2000). Moreover, while at low tide this snail bases its food-finding ability on air-borne cues (Fratini et al., 2001), it can

* Corresponding author. Tel.: +39 0552288204; fax: +39 055222565.
E-mail address: sarafatini@unifi.it (S. Fratini).

probably use water-borne cues as well since it has been shown that foraging activity also occurs during high tide (Fratini et al., 2004). Finally, while no data are available on the existence of a preference towards specific mangrove plants, *T. palustris* is known to discriminate between different food items, being more attracted to fresh mangrove leaves than to senescent or fallen leaves or propagules (Fratini et al., 2001).

Within this conceptual framework, the main aim of this study was to use field trials to test the possible feeding preferences of *T. palustris* and the attraction exerted by different leaves via air-borne cues. In addition, we also investigated whether at high tide (i.e. under water) the food searching strategy of *T. palustris* is chemically mediated as it is at low tide.

2. Materials and methods

2.1. Study site

The research was conducted at Dabaso shore, within Mida Creek (03° 21' S; 39° 59' E), North Kenya Coast, in February 2005 and July 2007. This mangrove forest is characterised by a very narrow landward *Avicennia marina* belt followed by an extended *Rhizophora mucronata* - *Ceriops tagal* forest. In particular, the experiments were performed in the muddy small creeks within the *R. mucronata* dominated forest. In these creeks the density of adult *T. palustris* is about 5 individuals/m² (Fratini et al., 2001, 2004).

2.2. Field experiments

The goal of assessing the feeding preferences and strategies of *T. palustris* was achieved by means of four different sets of experiments, designed to address three specific issues.

2.2.1. Is the perception of the food items chemically mediated underwater?(experiment 1)

In order to verify whether at high tide, the snail's attraction towards food items was chemically mediated as it is at low tide, we tested the underwater attraction power of minced *R. mucronata* green leaves. The minced leaves were placed into net bags thus avoiding the scattering of leaf debris by the tidal currents, but allowing the odours to disperse. The bags were fixed with an iron wire to the muddy soil, in order to prevent them from being transported away by the tide. During each trial, we used five bags with leaves and five empty net bags as controls, randomly distributed approximately 5 m apart along a 50 m transect. The transect was parallel to the direction of the current. Four trials were performed at diurnal high tides close to the spring tide, on different days, in February 2005. The trials began as the tide was entering the creek and the snails were covered by at least 10 cm of water. We counted the numbers of snails present within a 30 cm radius around the bags as soon as they were placed in position and one hour later. The difference between the final and initial snail number (ΔN) represents the number of snails attracted towards the bags.

2.2.2. Do the leaves of various mangrove species promote different grazing rates?(experiment 2 and 3)

In order to assess whether the snails consume different amount of the different mangrove plants we performed two experiments: experiment 2 established the grazing rate in "free conditions", i.e. the snails (at least the first one per leaf) encountered the leaf by chance moving within the experimental area, while experiment 3 measured the leaf grazing rate in "obliged" conditions, i.e. a fixed number of snails was offered the different mangrove species. The grazing rate as calculated by experiment 2 is affected by the feeding recruitment process, and the number of snails on a single leaf was not established *a priori*.

Expt. 2: a total of 480 fresh green leaves collected among the branches of the eight mangrove species present in the study area were placed on the ground at the beginning of a diurnal low tide and left in place for 3 hours. The species used were: *R. mucronata*, *C. tagal* and *Bruguiera gymnorrhiza* (Rhizophoraceae), *A. marina* (Avicenniaceae), *Sonneratia alba* (Sonneratiaceae), *Pemphis acidula* (Lythraceae), *Lumnitzera racemosa* (Combretaceae) and *Xylocarpus granatum* (Meliaceae).

The trials were performed six times close to a spring tide on different not consecutive days, three during the dry season (February 2005) and three during the wet season (July 2007). The leaves had been previously marked with a red numbered tag tied to the petiole. They were photographed with a digital camera, immediately before and after the trial in order to estimate the percentage of leaf consumed by the snails (Fratini et al., 2004). We also counted the number of snails grazing on a single leaf at the end of each trial. The smaller size of the *A. marina*, *P. acidula*, *L. racemosa* and *X. granatum* leaves compare with the rhizophoracean and *S. alba* leaves could affect the probability of a snail finding the leaf. In order to compensate for this size difference we joined together 2–4 leaves using adhesive tape and in the calculation of grazing rate we treated these combined leaves as a single leaf.

Expt. 3: fifteen fresh leaves of the 8 mangrove species (for a total of 120 leaves) were put within experimental cages, distributed 20 cm one from each other on the mud platform in front of the *Rhizophora* fringe. The cages were plastic cylinders about 30 cm high and of 20 cm in diameter, open up and down, thus the leaves were put down on the mud. Two adult snails (with a shell size of 8–10 cm), taken within the experimental area, were led, at random, on each leaf. Before each trial the leaves were marked with a tag and weighted using an electric precision balance (± 0.01 gr.). After two hours, the snails were removed and the leaves were gently collected, washed (for removing the mud), dried and then weighted. The difference between the weight before and after each trial represents the amount (in percentage) consumed by the snails.

The trials were performed 3 times around spring tide, in different not consecutive days, during the wet season (July 2007). As in experiment 2, we compensated the minor size of *A. marina*, *P. acidula*, *L. racemosa* and *X. granatum* leaves joining together 2–4 leaves.

2.2.3. Are there differences in the attractiveness of the leaves of various mangrove species?(experiment 4)

In order to test whether *T. palustris* was differentially attracted by the various mangrove plants, we tested the attraction effect of green leaves belonging to the above-cited eight mangrove species. To answer this question, we used the "cylinder experiment" approach as performed by Fratini et al. (2001). Briefly, this method consists of putting the potentially attractive cues (i.e. the different mangrove leaves, minced) on a petri dish placed inside opaque plastic cylinders, about 30 cm high and 20 cm in diameter. The cylinders were raised about 0.5 cm above the soil in order to exclude the visual component

Table 1

A two factor mixed-model ANOVA based on the number of snails found around the two different treatments (control and minced mangrove leaves) at different times

Experiment 1					
Source	SS	DF	MS	F	P
Treatment	846.4	1	846.4	15.50	0.03
Time	218.6	3	72.87	2.40	0.09
Time X Treatment	163.8	3	54.6	1.80	0.17
RES	971.6	32	30.36		
TOT	2200.4	39			

Data (ΔN : the difference between the final and the initial number of snails around the tested cues) were not transformed (Cochran's Test: $C=0.3672$, $P=n.s.$)

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