

Research Article

Palatability of mangrove leaves to invasive apple snails: the relation between feeding electivity and multiple plant characteristics

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Abstract

Mangrove forests worldwide have been subjected to biological invasion. Invasive apple snails (*Pomacea canaliculata*) have established populations in some mangrove forests. The feeding behavior of *P. canaliculata* in mangroves has been unclear until now. The feeding electivity of *P. canaliculata* to mangrove leaves, including leaves from *Acanthus ilicifolius*, *Acrostichum aureum*, *Kandelia candel*, *Aegiceras corniculatum*, and *Sonneratia apetala*, was studied through a selective test, a non-selective test, and a T-tube test. The growth indicators, the feeding ratio, the feeding rate, the feeding amount, the electivity indicator, and the electivity frequency were determined. The weight increase ratios of *P. canaliculata* that consumed leaves of *A. ilicifolius* and *A. aureum* were higher than those that consumed leaves of *K. candel*, *S. apetala*, and *A. corniculatum*. The electivity indicator showed that *P. canaliculata* preferred *A. ilicifolius* leaves and fed little on *A. corniculatum* leaves. *Acrostichum aureum* leaves were the second most preferred food for the apple snails. The feeding electivity of *P. canaliculata* to leaves from five species of mangrove trees was significantly differentiated by cluster analysis, redundancy analysis, and principal component analysis. Eight feeding indicators of the apple snails were positively correlated with the leaf characteristics of nitrogen content, protein content, leaf area, moisture content, and aspect ratio and negatively correlated with the lignin, phenolic, and tannin contents. *Pomacea canaliculata* could discriminate mangrove leaves through physical and chemical characteristics and shift feeding electivity among mangrove leaves under intraspecific competition. Mangrove forests composed mainly of *A. ilicifolius* and *A. aureum* might be at risk of invasion by *P. canaliculata*. A detailed survey on benthic animals is necessary to monitor and prevent *P. canaliculata* invasion in mangroves.

Key words: mangrove wetland, invasive snail, *Pomacea canaliculata*, electivity indicator, leaf characteristic

Introduction

Mangrove wetlands, which are among the most productive ecosystems in the world, provide diverse habitats for terrestrial and aquatic invertebrates, fish, and other wildlife (Alongi 2018; Celis-Hernandez et al. 2020). Mangrove forests play a key role in sustaining ecosystem services. Typically, functions of mangrove forests include the nutrient cycling (Taillardat et al. 2019), environmental protection (Torres et al. 2019),

carbon sequestration (Ouyang et al. 2017), flooding resistance, and erosion prevention (Deb and Ferreira 2017).

Despite the essential roles they play in providing a range of ecosystem services, the conservation of global mangrove forests face severe challenges from anthropogenic activities (Romanach et al. 2018). Exotic invasive species have had a strong negative impact in invaded areas, resulting in economic losses, biodiversity reductions, and the weakening of ecosystem services (Roy et al. 2018). Like many other ecosystems, mangrove forests have also been subjected to exotic species, as these forests provide complex habitats constructed from pneumatophores and sediments for diverse species. Many exotic invasive animals have invaded mangrove forests, including teak defoliator moths (*Hyblaea puera*; Faraco et al. 2019), European shore crabs (*Carcinus maenas*; Garside and Bishop 2014), portunid crabs (*Charyhdis hellerii*) (Dineen et al. 2001), green mussels (*Perna viridis*; Bigatti et al. 2005), Cuban tree frogs (*Osteopilus septentrionalis*; Glorioso et al. 2010), prawns (*Macrobrachium rosenbergii*; Silvaoliveira et al. 2011), black mangrove cichlids (*Tilapia mariae*; Russell et al. 2012), green iguanas (*Iguana iguana*; Burgosrodriguez et al. 2016), and lionfishes (*Pterois volitans/miles*; Sancho et al. 2018). Invasive animals have significantly or potentially influenced mangrove ecosystems through tree defoliation (Faraco et al. 2019), niche competition (Russell et al. 2012), seed germination (Burgosrodriguez et al. 2016), food chain alteration (Glorioso et al. 2010), and habitat shifts (Bigatti et al. 2005).

The apple snail (*Pomacea canaliculata* Lamarck, 1822), which is native to South America, is a harmful gastropod that is listed as one of the 100 worst invasive alien species (Lowe et al. 2000). *Pomacea canaliculata* was introduced into Asian countries in the 1980s for human consumption (Joshi and Sebastian 2006; Lv et al. 2011). However, their economic values plummeted unexpectedly, leading to a failure in the local market. As a result, *P. canaliculata* escaped in various aquatic habitats, including paddy fields, lakes, rivers, canals, and ponds (Kwong et al. 2010; Yang et al. 2018). *Pomacea canaliculata* feeds on rice seedlings and has observably threatened rice productivity (Martín et al. 2008). Furthermore, consuming *P. canaliculata* may transmit rat lungworm disease to humans, as they are a crucial vector of the parasitic nematode (*Angiostrongylus cantonensis*) (Lv et al. 2011).

In addition to their high fecundity and strong resistance, *P. canaliculata* exhibit a voracious appetite for macrophytes in invaded wetlands, which constitute a major part of the daily diet of apple snails, irrespective of seasonal changes (Kwong et al. 2010; Yang et al. 2018). Over fifty plant species served as food sources for *P. canaliculata*, and the electivity of snails varied greatly (Horgan et al. 2014). The amount of elephant-head amaranth (*Amaranthus gangeticus*) consumed daily by *P. canaliculata* contributed 22% to the weight of individuals (Wong et al. 2010). The

grazing rates of *P. canaliculata* on diverse macrophytes were closely related to nutrient traits, including nitrogen, phenolic contents (Qiu and Kwong 2009), and dry matter (Wong et al. 2010).

The distribution range of *P. canaliculata* was estimated to be between 40°N–40°S globally, and the species is known to have devastating effects in Asia, North America, and Oceania (Hayes et al. 2008). To clarify the invasion strategy leading to population establishment, many researchers have assessed the resistance of *P. canaliculata* to abiotic stressors, such as low temperature, pH, dissolved oxygen level, desiccation, and salinity (Seuffert and Martin 2009; Bernatis et al. 2016; Yang et al. 2017). As a freshwater gastropod, apple snails can grow in brackish water (5‰) (Yang et al. 2017). A *P. canaliculata* population was reported in brackish water (1–2.1‰) in a Chilean lagoon (Letelier et al. 2016). This finding demonstrated that *P. canaliculata* could survive brackish waters and its potential to invade estuarine habitats.

These fears recently became a reality following the discovery of *P. canaliculata* in mangrove forests. A routine benthic investigation reported that *P. canaliculata* had established populations in six mangrove wetlands in a coastal area (Ma et al. 2018). Here we report for the first time the presence of *P. canaliculata* in a mangrove wetland in Guangzhou, China. Given the voracious appetites of *P. canaliculata* for macrophytes in freshwater wetlands, we hypothesized that the mangrove leaves might provide a consistent food source for *P. canaliculata* in mangrove wetlands. Mangrove leaves contain complex secondary metabolites, including tannins, alkaloids, and diverse bioactive compounds (Behbahani et al. 2018). However, little is known regarding the feeding behavior of *P. canaliculata* on mangrove leaves. Therefore, to identify the mechanisms involved in food consumption by *P. canaliculata* in recently invaded mangrove forests, we asked two questions: 1) What was the electivity of *P. canaliculata* to mangrove leaves? 2) Was the feeding electivity of *P. canaliculata* influenced by the physical and chemical characteristics of the mangrove leaves? The study puts forward a new perspective to understand the influence of a recently invaded snail in mangrove wetlands. Answering these questions is beneficial for predicting the further spread of *P. canaliculata* in mangrove wetlands and assess the risk of *P. canaliculata* in diverse mangrove forests.

Materials and methods

P. canaliculata and plant materials

Apple snails were collected from mangrove wetlands in Guangzhou, China (22°62'N; 113°66'E) in February 2019 (Supplementary material Figure S1). The species in the mangrove included *Acanthus ilicifolius* L. (Acanthaceae, holy mangrove shrub), *Acrostichum aureum* L. (Pteridaceae, Mangrove fern),

Kandelia candel L. (Rhizophoraceae, Narrow-Leaved Kandelia), *Aegiceras corniculatum* L. (Primulaceae, Black mangrove), and *Sonneratia apetala* Buch.-ham (Sonneratiaceae, Mangrove apple). The mean air temperature in this region was 22.4 °C, and the annual precipitation was 1667.6 mm, according to the China Meteorological Data Sharing Service System (<http://data.cma.cn/>). In 2018 water temperature, salinity, and pH ranged from 15.5 to 25.5 °C, 2.0 to 6.2‰, and 7.2 to 7.8, respectively, at the sampling location.

We used DNA Genomic Extraction Kits (AxyPrep) to extract total genomic DNA from the foot tissue of collected snails. The cytochrome oxidase subunit I gene was amplified by polymerase chain reaction (PCR) using the primers (LCO1490 and HCO2198) (Folmer et al. 1994). The reaction system (30 µL) composed of 2×PowerTaqPCRMasterMix 15 µL, 1 µL each of forward and reverse primers, ddH₂O 12 µL, and 1 µL template DNA. Purified PCR product was sequenced using an ABI-3730xl (USA). Nucleotide sequences obtained were assembled and edited using BioEdit [7.2.6.1] (Hall 1999). The collected snails were identified as *Pomacea canaliculata* by sequencing of mitochondrial cytochrome oxidase I (GenBank Accession number: MW799954; MW799955). The apple snails were reared in a laboratory to obtain the eggs. Hatched snails were reared in artificial seawater (2.0‰) for two weeks before they were transferred in four sets of aquaria (80 cm × 60 cm × 60 cm) filled with artificial seawater (4.0‰). The salinity was monitored using a salinity meter (SX5051, Shanghai) and manipulated by adding artificial sea salt (Yanzhibao, Guangdong) to aerated tap water. The salinity (4.0‰) and pH (7.3–7.5) of the seawater were adjusted according to the water quality determined in the sampling locations and described in previous studies (Yang et al. 2017). *Pomacea canaliculata* were fed with lettuce (*Lactuca sativa* L.) daily at room temperatures (25 ± 2 °C). The water in the aquaria was changed with aerated seawater every three days. Healthy snails, characterized by smooth and intact shells and active movement in the aquaria, were used in further experiments. Before use in an experiment, the snails were starved for 24 h. All experiments were conducted at room temperature using artificial seawater at 4‰ with a 1:1 ratio of male and female snails.

Mangrove leaves, including those from *A. ilicifolius*, *A. aureum*, *K. candel*, *A. corniculatum*, and *S. apetala*, were tested to determine the feeding indicators of the apple snails. Fresh mangrove leaves were collected directly from the sampling sites, and their physical and chemical characteristics were determined. At the end of the non-selective/selective feeding and electivity experiments, the remaining mangrove leaves were cleaned using purified water to remove adhered salt. The tests were both performed in 6 replicates. Additionally, leaves used in the non-selective/selective feeding tests were oven-dried at 105 °C (4 h) and 80 °C (48 h) to obtain a constant weight.

Non-selective feeding test of P. canaliculata on mangrove leaves

Cleaned fresh leaves were used in the non-selective feeding test. Fresh leaves from each species (49.4–50.0 g) were placed separately in a chamber (40 cm × 30 cm × 23 cm). Ten healthy snails (height: 3.2 ± 0.2 cm) were randomly selected for each chamber, and their weights were recorded for further calculation. The snails were placed together with fresh leaves in a plastic chamber filled with artificial seawater (6 L). All the snails were alive at the end of the 120 h test.

The artificial seawater in the chambers was changed daily to maintain water quality. The feeding amount per snail weight (Fa), absolute feeding ratio (Ra), feeding rate per day (Rt), and Ivlev's electivity indicator (E), hereinafter referred to as the electivity indicator, were calculated to assess the feeding behavior of the snail (Ivlev et al. 1961, equations 1 to 6).

$$Fa_i = \frac{(FW_i \times m_i - DW_i)}{W_i} \quad (\text{equation 1})$$

$$Ra_i = \frac{(FW_i \times m_i - DW_i)}{FW_i \times m_i} \quad (\text{equation 2})$$

$$Rt_i = \frac{Fa_i}{10} \times \frac{1}{T} \quad (\text{equation 3})$$

$$R_i = \frac{(FW_i \times m_i - DW_i)}{\sum_{i=1}^5 (FW_i \times m_i - DW_i)} \quad (\text{equation 4})$$

$$P_i = \frac{FW_i}{\sum_{i=1}^5 FW_i} \quad (\text{equation 5})$$

$$E_i = \frac{R_i - P_i}{R_i + P_i} \quad (\text{equation 6})$$

$i=1-5$, representing five mangrove leaves;

m_i was the moisture of a type of leaf;

FW_i was the initial fresh weight of a type of leaf (g);

DW_i was the final dry weight of a type of leaf (g);

Fa_i was the feeding amount (dry weight) per individual weight (g g^{-1});

W_i was the total weight of ten snails (g);

Ra_i was the absolute feeding ratio;

Rt_i was the feeding rate (dry weight) per day per individual weight ($\text{g d}^{-1} \text{g}^{-1}$);

10 was the number of individuals;

T was the experimental duration (d);

E_i was the Ivlev's Electivity indicator; $E_i > 0$ means the plant was selected,

$E_i = 0$ means random selection, $E_i < 0$ means the plant was non-selective;

P_i was the ratio of weight of a type of leaf to total leaves weight;

R_i was the ratio of intake of snails on a type of leaf to total intake.

Selective feeding test of P. canaliculata on mangrove leaves

Fresh mangrove leaves were treated in the same way as for the non-selective feeding test. Each species of mangrove leaf weighed from 9.9 to 10.9 g. Leaves (50 g) from five species were placed together with healthy apple snails in a chamber (40 cm × 30 cm × 23 cm) filled with artificial seawater (6 L). The apple snails included in the test were 3.5 ± 0.1 m in height. The feeding test lasted for 120 h, and all the snails were alive in the chamber after the test. The artificial seawater in the chamber was changed daily to maintain water quality. Feeding amount per apple snail weight (Fa), absolute feeding ratio (Ra), feeding rate per day (Rt), and Electivity indicator (E) were used to assess the difference in food intake by the apple snails among the leaves from the five species of mangrove.

Electivity of P. canaliculata on mangrove leaves in a T-shaped Tube

The feeding electivity of the apple snail on leaves from five mangrove species was measured using a modified T-shaped tube (Takeichi et al. 2007; Figure S2). Six healthy snails 3.4 ± 0.2 cm in height were placed at one end of the tube, and mangrove leaves (9.8–10.4 g) were placed at the other two ends (right and left). Artificial seawater was added to the T-shaped tube before the test. Leaves from the five species of mangrove were placed in pairs on the left and right ends of the tube. Ten combinations were used in the test, including I (*A. ilicifolius* vs *A. aureum*, *A. ilicifolius* vs *K. candel*, *A. ilicifolius* vs *A. corniculatum*, *A. ilicifolius* vs *S. apetala*), II (*A. aureum* vs *K. candel*, *A. aureum* vs *A. corniculatum*, *A. aureum* vs *S. apetala*), III (*K. candel* vs *A. corniculatum*, *K. candel* vs *S. apetala*), and IV (*A. corniculatum* vs *S. apetala*). Paired combinations of leaves from the same mangrove species were also assessed in the T-shaped tube. After each test, the T-shaped tube was cleaned with purified water to remove leaf residue and snail metabolites to prevent possible interference with the next test. Each test lasted for 24 h. The electivity frequency (Ef) was the ratio of the number of snails recorded at one end to the total number of snails. The average Ef was used to measure the choices of snails between the same species of mangrove leaves.

Growth of P. canaliculata after feeding on mangrove leaves

The growth of *P. canaliculata* with mangrove leaves was assessed by examining the following indicators: weight increase ratio, survival ratio, and egg mass quantity. The fresh leaves were cleaned with a filter paper before the experiment. Each species of fresh leaf was placed separately in a plastic chamber (40 cm × 30 cm × 23 cm) together with ten healthy snails (height: 3.4 ± 0.2 cm). The growth test was performed in 6 replicates for

Table 1. Measurement of plant characteristics.

Plant characteristics	Measurement
Crude fiber content	National Standards of China GB/T 5009.10-2003
Protein and total nitrogen content	National Standards of China GB 5009.5-2016
content, lignin content	the Klason method (Fukushima et al. 2015)
Tannin and total phenol content	EDTA method (Nierop and Verstraten 2006)
Wax content	chloroform volatilization method (Kitagami et al. 2013)
Chlorophyll content	ethanol extraction method (Li et al. 2000)
Leaf hardness	hardness meter (SHORE-A, China)
Leaf thickness	thickness gauge (YHT127, China)
Leaf shape (width, length, and area)	leaf area analyzer (LG16T-LI-3000C)

each kind of leaf. The tested leaves (49.8–50.5 g) and the artificial seawater (6 L) in each chamber were replaced daily. The initial live weight (W_1) and the final live weight (W_2) of the snails were determined using an electronic balance, and the experiment lasted for 30 days. The weight increase ratio was calculated as $(W_2 - W_1) / W_1 \times 100\%$. Dead snails were removed from the chamber, and the final quantity (S) of dead snails was recorded (Martín et al. 2008). The survival ratio of the snails was calculated after 30 days using the equation of $(10 - S) / 10 \times 100\%$. The egg masses of the snails were collected every day, and the total quantity of egg masses was recorded as the total number of the clutches.

Determination of the chemical and physical characteristics of mangrove leaves

The contents of crude fiber, protein, total nitrogen, lignin, tannin, total phenol, wax, and chlorophyll were determined according to the published methods (Table 1). The hardness, thickness, and shape characteristics of mangrove leaves were measured using standard devices (Table 1). The hardness, thickness, and leaf shape characteristics were repeatedly measured 20 times on each leaf. Twenty mangrove leaves in total were used for each leaf characteristic.

Statistical analyses

All statistical analyses were performed in SPSS 19.0 (SPSS Inc., USA) and R software 4.0.3 (R Core Team 2020). A Levene test and Kolmogorov-Smirnov test were used to assess the homogeneity of variances and normality of the data. To compare the growth, feeding indicators (R_a , R_t , F_a , E , E_f) of *P. canaliculata* and leaf characteristics, we used ANOVAs (Duncan's or Tamhane's T_2), nonparametric tests (Kruskal-Wallis with Dunn-Bonferroni), and T-test. To analyze the relationship between feeding indicators and leaf characteristics, we used linear fit through the function "lm" in the R package of "stats" (R Core Team 2020). To analyze correlations between typical feeding indicators and plant characteristics, we used Redundancy analyses (RDA) through the R packages of "vegan", "ggplot2", and "ggrepel" (Wickham 2009; Oksanen et al. 2019; Slowikowski 2020; R Core Team 2020).

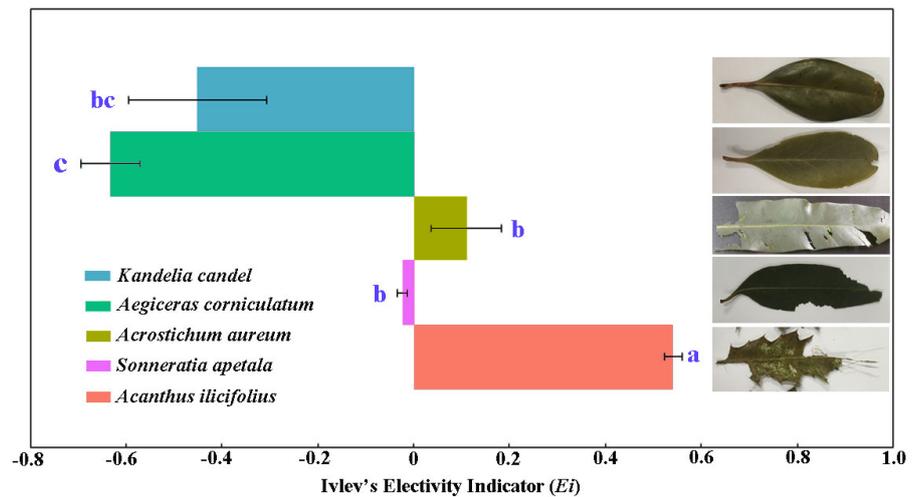


Figure 1. Ivlev's Electivity indicator of *Pomacea canaliculata* on mangrove leaves. ANOVA (Tamhane's T2) was used in comparisons.

To detect the collinearity among the explanatory variables, we performed a collinearity test through the function "ordistep" of R packages "vegan" (Blanchet et al. 2008; Oksanen et al. 2019; R Core Team 2020). To analyze the differentiation of feeding electivity of *P. canaliculata* on mangrove leaf, we used Principal component analysis (PCA) through the function PCA, fviz_eig, in R packages of "FactoMineR" and "factoextra" (Lê et al. 2008; Kassambara and Mund 2017; R Core Team 2020).

Results

T-tube test electivity of P. canaliculata on the mangrove leaves

The *P. canaliculata* exhibited significantly different values of electivity indicator (E) among the mangrove leaves (Figure 1), with E value being highest for *A. ilicifolius* compared with *A. aureum* ($p = 0.009$), *S. apetala* ($p < 0.001$), *K. candel* ($p = 0.006$), and *A. corniculatum* ($p < 0.001$). The E value for *A. corniculatum* was lower than that of *A. ilicifolius* ($p < 0.001$), *S. apetala* ($p < 0.001$), and *A. corniculatum* ($p < 0.001$). The *P. canaliculata* showed a negative E value for the leaves of *K. candel* and *A. corniculatum*. The E value of *P. canaliculata* for *S. apetala* was nearly zero.

A distinct difference existed in the average electivity frequency (E_f) and pairwise E_f of *P. canaliculata* in the T-tube test (Figure 2). The average E_f value of *P. canaliculata* decreased as follows: *A. ilicifolius* > *A. aureum* > *S. apetala* > *A. corniculatum*, *K. candel*. There was a significant pairwise E_f value for *A. ilicifolius* leaves than for leaves of other species. The lowest E_f value was observed between *K. candel* and *A. ilicifolius*.

Cluster analysis showed the similarity in food electivity of *P. canaliculata* to the mangrove leaves (Figure 3). The five species of mangrove leaves were divided into three groups: *A. ilicifolius* and *A. aureum*; *S. apetala*; and *A. corniculatum* and *K. candel*. *Acanthus ilicifolius* and *A. aureum* leaves

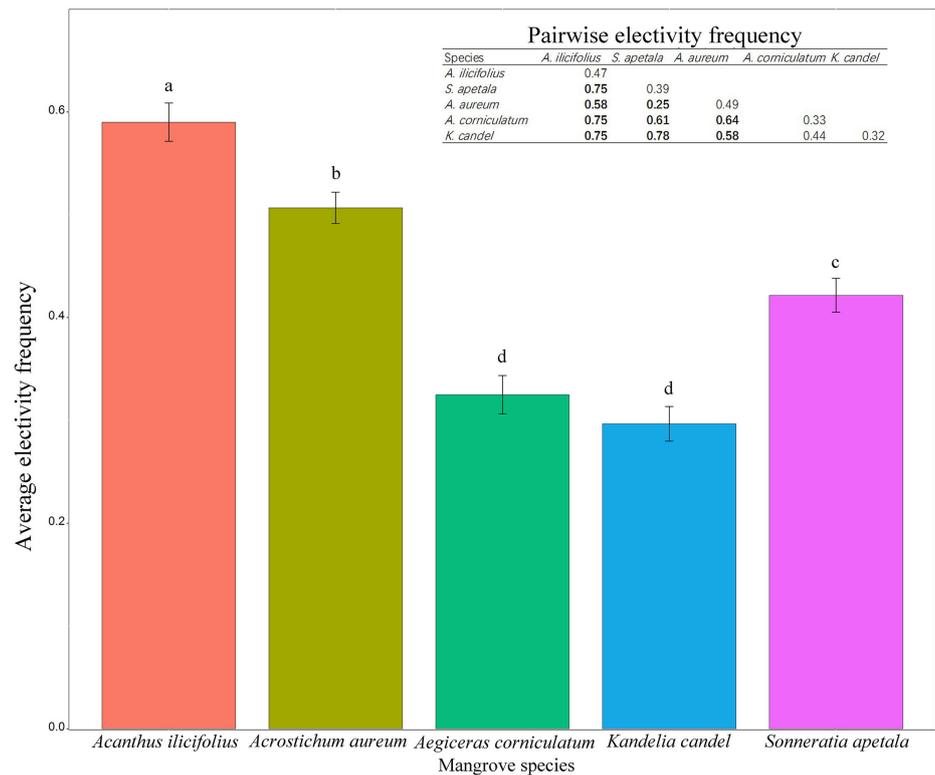


Figure 2. Pairwise and average electivity frequency of *Pomacea canaliculata* in the T-tube test; The electivity frequency (E_f) was the ratio of the number of snails recorded at one end to the total number of snails. The average E_f was used to measure the choices of snails between the same species of mangrove leaves. The value in the table was the frequency of species in the column chosen by snails when compared with species in the row. Significant value was in bold font. T-test was used in comparisons of electivity frequency. ANOVA (Duncan's) was used to compare the average electivity frequency of five species, including *A. ilicifolius* (*Acanthus ilicifolius*), *A. aureum* (*Acrostichum aureum*), *K. candel* (*Kandelia candel*), *A. corniculatum* (*Aegiceras corniculatum*), and *S. apetala* (*Sonneratia apetala*).

were both attractive to the apple snails, with a significant difference from other mangrove leaves.

The feeding test of the apple snail on mangrove leaves

Pomacea canaliculata showed significantly different feeding behaviors on the five species of mangrove in the non-selective and selective feeding tests with respect to absolute feeding ratio (R_a), feeding rate per day (R_t), and feeding amount per snail weight (F_a) (Figure 4) based on ANOVA (Duncan's or Tamhane's T2). In the non-selective feeding test, the F_a and R_t decreased as follows: *A. ilicifolius* > *A. aureum*, *K. candel* > *S. apetala* > *A. corniculatum*. The R_a decreased in the following order: *A. ilicifolius* > *A. aureum* > *K. candel* > *S. apetala* > *A. corniculatum* ($p < 0.05$). The three indicators all showed that the snails fed mainly on *A. ilicifolius* leaves. Regarding *A. ilicifolius*, the R_a reached 0.80 after 120 h. The F_a reached 0.08 g/g, indicating that *A. ilicifolius* accounted for up to 8% of snail individual weight. The R_a was less than 0.05 when snails were fed *A. corniculatum*.

In the selective feeding test, the R_a decreased in the following order: *A. ilicifolius* > *A. aureum* > *K. candel*, *S. apetala* > *A. corniculatum* (Figure 4).

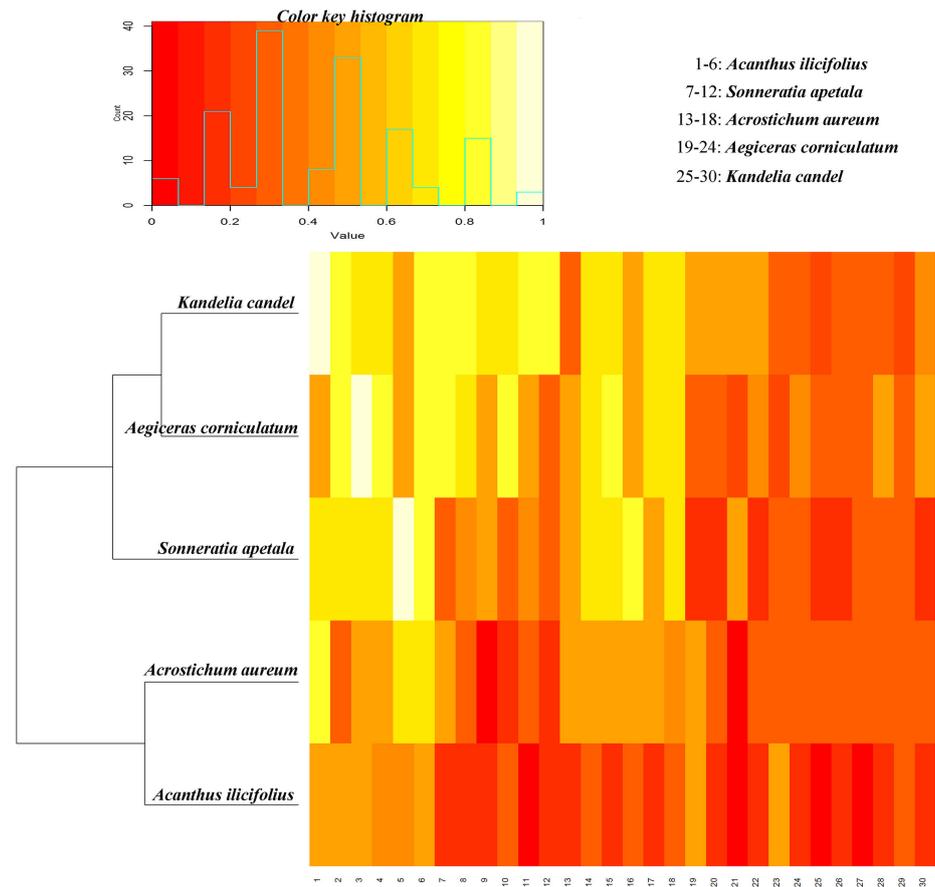


Figure 3. Electivity frequency cluster of *Pomacea canaliculata* in the T-tube test.

The highest R_t and F_a were observed for *A. ilicifolius*, and higher R_t and F_a values were found for *A. aureum* and *S. apetala* than for *A. corniculatum*. The *P. canaliculata* tended to feed on *A. ilicifolius* leaves when leaves from different species were offered simultaneously. The patterns followed by R_t and F_a were similar to those observed in the non-selective test. The *P. canaliculata* still fed on very few *A. corniculatum* leaves.

The growth of P. canaliculata on mangrove leaves

The weight increase ratio, survival ratio, and quantity of egg masses of *P. canaliculata* were significantly different among the five species of mangrove (Figure 5). Based on ANOVA with Tamhane's T2 ($df = 29$, $F = 36.686$, $p < 0.001$), the weight increase ratios of the snails that consumed leaves of *A. aureum* were higher than those of the snails that consumed leaves of *K. candel* ($p = 0.001$), *S. apetala* ($p < 0.001$), and *A. corniculatum* ($p < 0.001$). The weight increase ratios of the snails that consumed leaves of *A. ilicifolius* were also higher than those of the snails that consumed leaves of *K. candel* ($p = 0.003$), *S. apetala* ($p = 0.026$), and *A. corniculatum* ($p = 0.001$). Based on ANOVA with Duncan's ($df = 29$, $F = 10.441$, $p < 0.001$), the survival ratios of the snails that consumed *A. aureum*, *A. ilicifolius*, and *S. apetala* leaves were significantly higher than those of the snails that consumed *K. candel* and *A. corniculatum* leaves. Based on Kruskal-Wallis

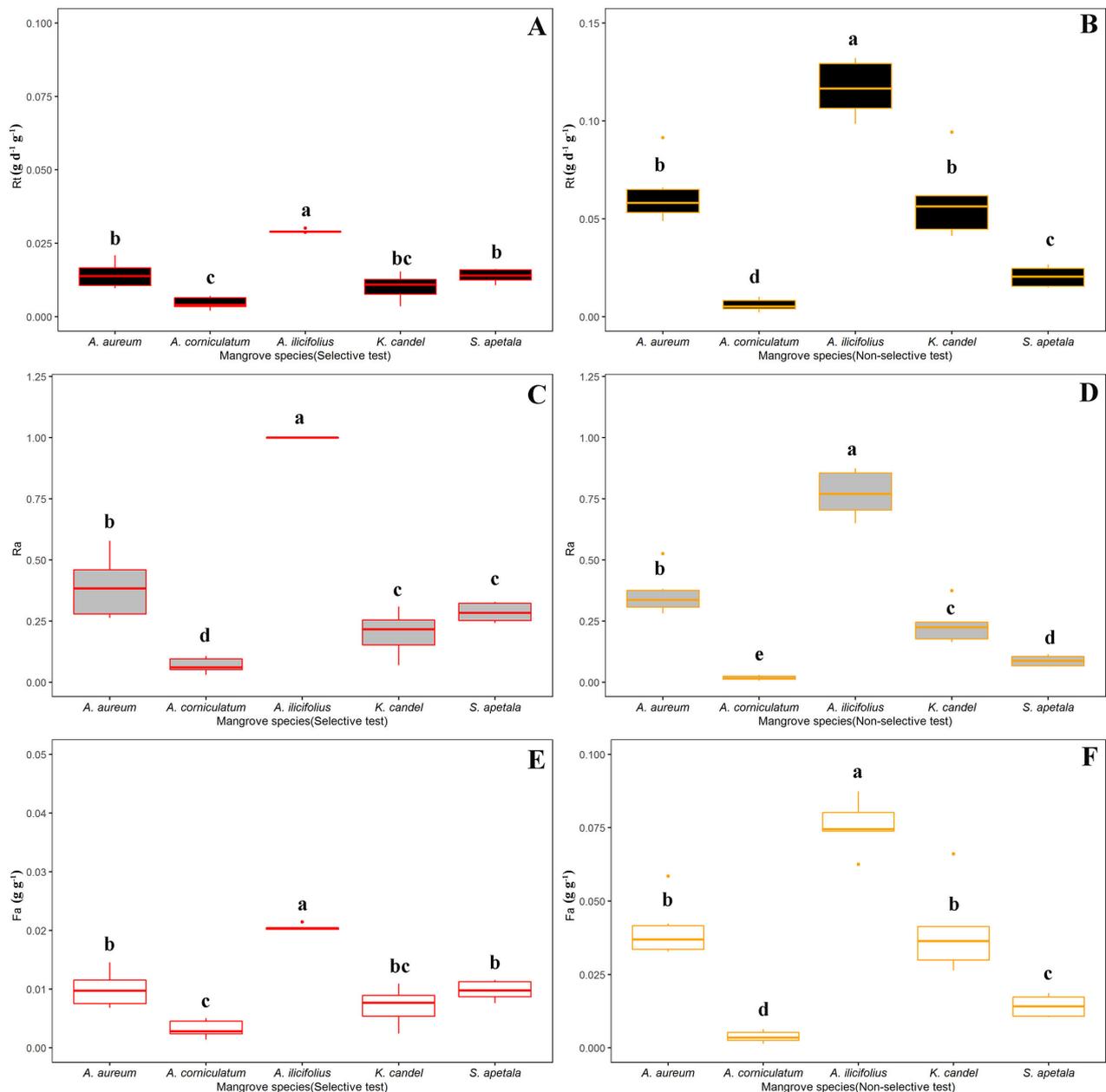


Figure 4. Feeding rate per day (R_t , $g\ d^{-1}\ g^{-1}$), absolute feeding ratio (R_a), feeding amount per snail weight (F_a , $g\ g^{-1}$) of *Pomacea canaliculata* on mangrove leaves under the selective (A, C, E, red box) and the non-selective (B, D, F, yellow box) conditions. ANOVAs (Duncan's or Tamhane's T2) were used to compare the indicators among mangroves, including *A. ilicifolius* (*Acanthus ilicifolius*), *A. aureum* (*Acrostichum aureum*), *K. candel* (*Kandelia candel*), *A. corniculatum* (*Aegiceras corniculatum*), and *S. apetala* (*Sonneratia apetala*).

with Dunn-Bonferroni ($df = 4$, $\chi^2 = 11.727$, $p = 0.019$), a higher quantity of egg masses of the snails fed *A. ilicifolius* was significantly higher than that fed *A. corniculatum* ($p = 0.017$).

Correlation analysis between feeding electivity and chemical, physical characteristics of mangrove leaf

The differences in chemical and physical characteristics of mangrove leaves were analyzed. Based on Duncan's Homogeneous Subsets, among the five species of mangrove, the crude protein ($df = 29$, $F = 8912.746$, $p < 0.001$) and

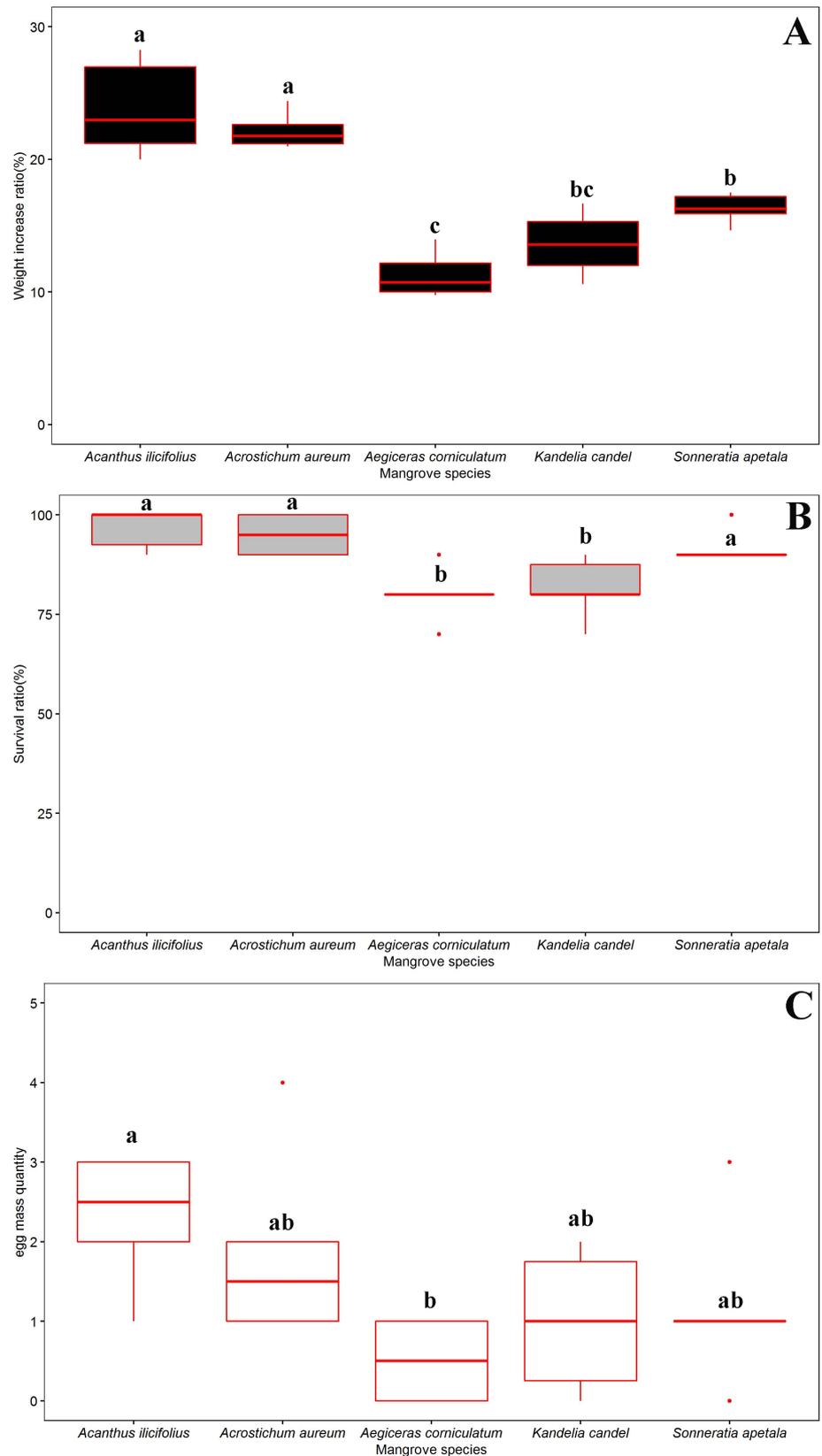


Figure 5. Weight increase ratio (A, black), survival ratio (B, grey) and egg masses quantity (C, white) of *Pomacea canaliculata* on mangrove leaves. ANOVA with Tamhane's T2 ($df = 29$, $F = 36.686$, $p < 0.001$) was used to compare the weight increase ratio. ANOVA with Duncan's ($df = 29$, $F = 10.441$, $p < 0.001$) was used to compare the survival ratio. The Kruskal-Wallis with Dunn-Bonferroni ($df = 4$, $\chi^2 = 11.727$, $p = 0.019$) was used to compare the quantity of egg masses.

total nitrogen contents ($df = 29$, $F = 9465.516$, $p < 0.001$) were both in the order *A. ilicifolius* > *A. aureum* > *S. apetala* > *K. candel* > *A. corniculatum* (Table S3). Based on Tamhane's T2, the total phenolic contents ($df = 29$, $F = 382.231$, $p < 0.001$) of *A. corniculatum*, *S. apetala*, and *K. candel* leaves were higher than those of *A. ilicifolius* ($p < 0.001$) and *A. aureum* ($p < 0.001$). The tannin contents ($df = 29$, $F = 910.136$, $p < 0.001$) of *A. corniculatum*, *S. apetala*, and *K. candel* leaves were also higher than those of *A. ilicifolius* ($p < 0.001$) and *A. aureum* ($p < 0.001$). The crude fiber contents ($df = 29$, $F = 450.328$, $p < 0.001$) of *A. aureum* and *A. corniculatum* were significantly higher than those of other mangrove species, supported by p -value less than 0.001 for each comparison. The wax content ($df = 29$, $F = 266.266$, $p < 0.001$) in *A. ilicifolius* leaves was significantly lower than that of *A. aureum* ($p = 0.013$), *S. apetala* ($p < 0.001$), and *K. candel* ($p < 0.001$). The total chlorophyll content ($df = 29$, $F = 14.089$, $p < 0.001$) of *A. aureum* was significantly lower than that of *A. ilicifolius* ($p < 0.001$) and *K. candel* ($p = 0.014$), whereas the chlorophyll a/b content ($df = 29$, $F = 9.166$, $p < 0.001$) of *S. apetala* was higher than that of *K. candel* ($p = 0.015$), *A. aureum* ($p = 0.017$), and *A. ilicifolius* ($p < 0.001$). Based on Duncan's Homogeneous Subsets, the lignin contents were in the order *A. corniculatum* > *A. aureum* > *K. candel* > *S. apetala* > *A. ilicifolius* ($df = 29$, $F = 513.837$, $p < 0.001$).

Based on ANOVA with Tamhane's T2, the hardness ($df = 29$, $F = 20.365$, $p < 0.001$) of *A. aureum* leaves was lower than that of the leaves of *A. ilicifolius* ($p = 0.001$) and *A. corniculatum* ($df = 29$, $F = 513.837$, $p < 0.001$) (Table S4). Based on Duncan's Homogeneous Subsets, the thickness of *A. corniculatum* leaves was significantly lower than that of leaves of *A. ilicifolius* and *S. apetala* ($df = 29$, $F = 18.871$, $p < 0.001$). The highest moisture was observed for *A. ilicifolius* leaves ($df = 29$, $F = 143.166$, $p < 0.001$). The leaf areas of *A. ilicifolius* and *A. aureum* were significantly higher than those of the other mangrove leaves ($df = 29$, $F = 80.720$, $p < 0.001$). Based on Tamhane's T2, *A. aureum* leaves had the highest aspect ratio ($df = 29$, $F = 94.261$, $p < 0.001$) compared to *A. corniculatum* ($p < 0.001$), *K. candel* ($p = 0.001$), *S. apetala* ($p = 0.001$), and *A. ilicifolius* ($p = 0.004$).

A significant relationship was observed between the leaf characteristics and feeding electivity indicators. There was a significant linear relationship between the chemical characteristics of the mangrove leaves, including the lignin, nitrogen, phenolic, protein, and tannin contents, and the feeding electivity indicators (Table S1). The lignin, tannin, and total phenol contents were negatively correlated with the electivity indicators, and higher r^2 values were observed for the electivity indicators in the selective test than in the non-selective test. The nitrogen and protein contents were positively correlated with all the electivity indicators. High r^2 values were observed in the two tests. The total chlorophyll content was also positively related to absolute feeding ratio and feeding rate per day in the non-selective test. The leaf area and moisture characteristics both showed a significant

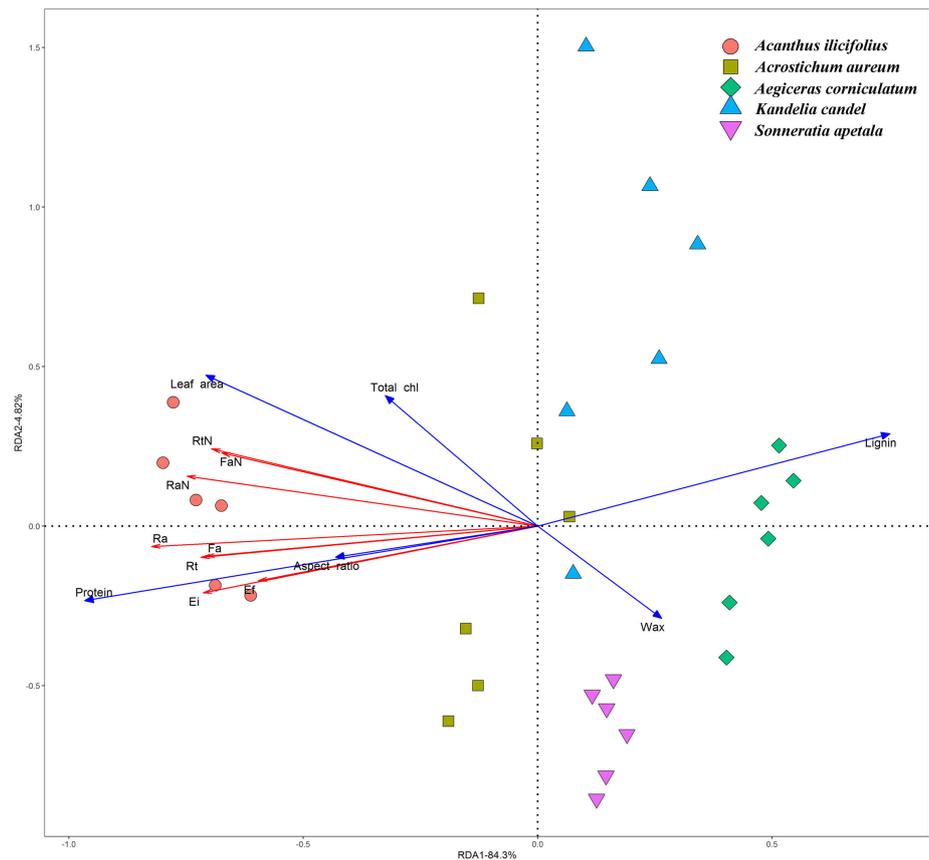


Figure 6. Redundancy analyses (RDA) on the correlations between feeding electivity indicators and plant characteristics. *Fa* and *FaN* (Feeding amount per snail weight in the selective and non-selective test, g g^{-1}); *Ra* and *RaN* (absolute feeding ratio in the selective and non-selective test, g g^{-1}); *Rt* and *RtN* (feeding rate per day in the selective and non-selective test, $\text{g d}^{-1} \text{g}^{-1}$); *Ef* (Electivity frequency); *Ei* (Ivlev's Electivity indicator).

linear relationship with the feeding electivity indicators (Table S2). The aspect ratio of the mangrove leaves was significantly correlated with *E*, *Ef*, and *Ra*, *Rt*, and *Fa* in the non-selective test. The liner regression resulted in higher r^2 values for the moisture content than for the other characteristics.

RDA analysis was performed on significantly related traits and electivity indicators (Figure 6). The results showed that the protein content, aspect ratio, and leaf area were positively related to the indicators of *Ef*, *E*, *Ra*, *Rt*, and *Fa*. The leaf area and total chlorophyll content were both positively associated with indicators *RtN* (feeding rate per day in the non-selective test) *FaN* (Feeding amount per snail weight in the non-selective test), and *RaN* (absolute feeding ratio in non-selective test). The lignin and wax contents were significantly negatively related to all the electivity indicators. RDA confirmed that *A. ilicifolius* leaves were the preferred food for *P. canaliculata*. A significant positive association was observed between *A. ilicifolius* leaves and protein content, aspect ratio, leaf area, total chlorophyll content, and the electivity indicators. *A. corniculatum* leaves were closely related to lignin and wax contents, making them a non-preferred food for the *P. canaliculata*.

PCA was performed for the significantly correlated chemical and physical characteristics of the five species of mangroves and feeding electivity indicators

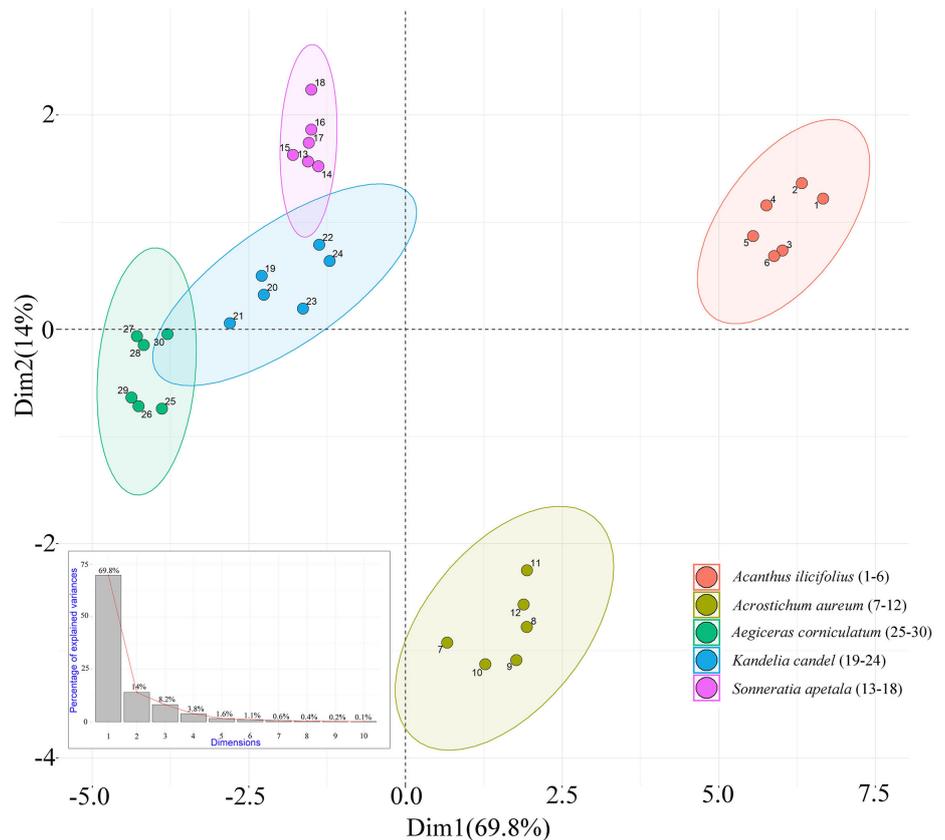


Figure 7. Principal component analysis (PCA) analysis between characteristics of mangroves and feeding electivity indicators of the apple snail (*Pomacea canaliculata*); Embedded panel represented the contribution ratio of each component.

(Figure 7). The two observed principal components (PCs), PC1 and PC2, explained 70% and 14% variations of the variation, and their eigenvalues both exceeded 1. PCA showed that mangrove leaves were significantly clustered into five groups, indicating that *P. canaliculata* can discriminate the mangrove leaves through chemical and physical characteristics.

Discussion

Survival and feeding on mangrove leaves under salt stress

Although *P. canaliculata* is a freshwater species, a recent study confirmed that *P. canaliculata* can tolerate salinity stress of 4‰ with the alligator weed (*Alternanthera philoxeroides*) as a food source (Yang et al. 2018). Given that other *Pomacea* snail egg masses can survive and produce hatchlings after being periodically submerged by tides (Martin and Valentine 2014), the use of various macrophytes as a food source could alter food webs and compromise mangrove conservation efforts. The removal of dead individuals in the chamber led to a change in snail density. However, such change did not affect the feeding of remaining snails as we provided enough leaves and maintained the water quality. As a result, our study demonstrated that *P. canaliculata* can survive by feeding on mangrove leaves, although mangrove leaves are not as rich in nutrients as duckweed,

as the latter is a common food source (Liu et al. 2012). This phenomenon was related not only to the presence of necessary nutrients in the mangrove leaves, which supported the normal metabolism of the snails, but also to the starvation tolerance of the snails, as they feed very little when only *A. corniculatum* leaves were provided. *Pomacea canaliculata* can survive for 11 months under dry conditions and 29 months under moist conditions without feeding (Yusa et al. 2006). Mangrove litter is an essential component in the carbon cycle of mangroves, and the production of litter reached 11.8 Mg·ha⁻¹·yr⁻¹ (Kamruzzaman et al. 2017). As a result, the mangrove litter is a potential food source of *P. canaliculata* in low-salinity mangrove habitats, consistent with field observations of *P. canaliculata* in brackish wetlands near the shore (Letelier et al. 2016).

The feeding electivity of P. canaliculata on mangrove leaves

Little research has discussed the feeding electivity of *P. canaliculata* on mangrove leaves, and reports have mainly focused on freshwater macrophytes (Fang et al. 2010; Wong et al. 2010; Horgan et al. 2014). *Pomacea canaliculata* can compete with native benthic snails by monopolizing food resources in freshwater habitats (Fang et al. 2010). We found that *P. canaliculata* could feed on various mangrove leaves, indicating they have a competitive advantage over native mangrove animals, as they also selectively feed on mangrove leaves by discerning differences by smell (Fratini et al. 2001). Based on the water temperature in winter (2002–2011) (Liu 2013), the mean winter water temperature in this region where we sampled was over 25 °C. By contrast we found that water temperature ranged from 15.5 to 25.5 °C at the sampling location in 2018. A previous study found that food consumption of *P. canaliculata* lowered when the water temperature decreased from 25 °C to 15 °C (Bae et al. 2021). We speculated that *P. canaliculata* could feed on mangrove leaves in Guangzhou wetlands but grazing may be reduced from slight low-temperature stress in winter. Considering the cold tolerance of *P. canaliculata* after acclimation (Yoshida et al. 2014), the *P. canaliculata* could outcompete native benthic animals by utilizing mangrove leaves. Benthic snails play an important role in litter decomposition in mangrove ecosystems. Adult *Terebralia palustris* was shown to consume 10.5 mangrove leaves at a density of 10.5 individual m⁻² in a *Rhizophora mucronata* forest (Fratini et al. 2004). Similarly, *P. canaliculata* could function in litter decomposition, altering the benthic food web and accelerating the nutrient cycle. The *P. canaliculata* possibly showed a comprehensive impact on mangrove wetland.

The coexistence of leaves from multiple mangrove species in the selective test changed the feeding behavior of *P. canaliculata*. The increase in *Ra* (absolute feeding ratio) showed that *P. canaliculata* tended to feed more on the preferred food under competitive conditions. The decrease in

R_t (feeding rate per day per snail) and F_a (feeding amount per snail weight) indicated that the intraspecific competition adversely affected the food consumption and digestion of each individual. A different feeding phenomenon was observed for the leaves of the least preferred species (*A. corniculatum*). *Pomacea canaliculata* had no choice but to feed on *A. corniculatum* leaves when leaves from other species were not provided; this finding was supported by the increased R_a value and the unchanged R_t and F_a values.

Slight differences occurred in the electivity of *P. canaliculata* among the three kinds of feeding tests. *Pomacea canaliculata* showed a higher E_f (electivity frequency) for *A. aureum* than for *S. apetala* and *K. candel*. There was no significant difference in the value of the indicator E (electivity indicator) of *S. apetala*, *A. aureum*, and *K. candel*. The *P. canaliculata* did not consume all the *A. ilicifolius* leaves in the non-selective test, whereas the feeding ratio of *A. ilicifolius* in the selective test reached 100.00%. This phenomenon indicated that *P. canaliculata* adjusted their electivity by feeding on a substitute species according to food availability. A possible reason for this pattern was that competitive intensity varied between the feeding tests, and strong intraspecific competition existed when the leaves of the mangrove species were mixed in the selective test. Native snails or crabs commonly have distinct feeding electivity on the mangrove leaves. The mangrove snail *Terebralia palustris* can consume seven species of mangrove leaves; they prefer *Rhizophoraceae* leaves and do not consume leaves of *Xilocarpus granatum* (Fratini et al. 2008). The intertidal crabs *Neosarmatium smithi*, *N. asiaticum*, *N. malabaricum*, and *Muradium tetragonum* tended to collect more leaves from *Bruguiera* spp. and *Rhizophora apiculata* than from *Excoecaria agallocha* (Cannicci et al. 2018). We speculated that *P. canaliculata* may adjust its feeding electivity and conflict with benthic animals in local habitats when food sources are limited. Invasion by *P. canaliculata* may have led to nutritional niche differentiation among native benthic animals.

Relationship between feeding patterns and the characteristics of the mangrove leaves

There was no significant correlation between the crude fiber contents of the mangrove leaves and the electivity indicators. The strong digestive capacity of *P. canaliculata* was related to endogenous cellulose (Imjongjirak et al. 2008). The cellulase activity of the mangrove snail (*Cerithidea cingulate*) was approximately $0.1 \mu\text{mol}\cdot\text{min}^{-1}\cdot\text{mg}^{-1}$, which was far lower than the average cellulase activity of the apple snail (approximately $2.0 \mu\text{mol}\cdot\text{min}^{-1}\cdot\text{mg}^{-1}$) (Chen et al. 2013; Liu et al. 2014; Luo et al. 2015; Imjongjirak et al. 2008). Moreover, the cellulase activities ($0.2\text{--}0.7 \mu\text{mol}\cdot\text{min}^{-1}\cdot\text{mg}^{-1}$) of the mangrove benthic snails *Cerithidea rhizophorarum*, *C. cingulata*, *Batillaria multiformis*,

and *B. attramentaria* were also significantly lower than those of *P. canaliculata* (Chen et al. 2013; Liu et al. 2014; Luo et al. 2015). Mangrove leaves are often rich in cellulose, and cellulose reached 10.6% in *Ceriops tagal* leaves (Neilson and Richards 1989). Compared to the native benthic snail, *P. canaliculata* had an advantage in terms of their ability to digest the cellulose in mangrove leaves, which may have led to a competitive feeding pressure against the native benthic snails.

Tannins and phenols are chemical defense substances in mangrove leaves, which have antioxidant and bacteriostatic activities (Nabeelah Bibi et al. 2019). Tannin negatively affected the feeding electivity of *Sesarma plicata* for mangrove leaves of *K. candel*, *Bruguiera gymnorrhiza*, and *A. corniculatum* (Chen and Ye 2008). We also found that the preferred leaves (*A. ilicifolius*) had the lowest total phenol and tannin contents, suggesting that the vulnerability of mangrove forests to *P. canaliculata* was closely related to mangrove species. The snails avoided or fed less on *A. corniculatum* leaves due to their high contents of tannin and total phenolic. However, a previous study of *P. canaliculata* reported no significant correlation between feeding rate and phenol content in wetland plants, in that study, the total phenol contents of the tested plants (over 75%) were 0.6–7.5% (Wong et al. 2010). Here, the total phenol content of the mangrove leaves was 60–140 mg·g⁻¹, which was higher than that in previously recorded for freshwater plants. We concluded that there was a negative correlation between the feeding electivity of *P. canaliculata* and the phenol contents of the mangrove leaves.

We found that *P. canaliculata* preferred the mangrove leaves rich in nitrogen, similar to the feeding electivity of the mangrove crabs. The feeding patterns of eight species of crabs were closely related to the nitrogen compounds in mangrove leaves (Nordhaus et al. 2011). *Pomacea canaliculata* preferred freshwater plants with high nitrogen contents (Wong et al. 2010). Our result indicated that salinity stress did not change the demand of *P. canaliculata* for plant nitrogen.

There was a significantly positive correlation between the moisture of the mangrove leaves and the electivity indicators. In freshwater habitats, the feeding of *P. canaliculata* was negatively related to the dry matter of 21 wetland plants, indicating a positive correlation between the leaf moisture and feeding electivity (Wong et al. 2010). A mangrove crab (*Perisesarma eumolpe*) showed a preference to the high-moisture leaves of *Ceriops decandra*, partly due to the ability of the low-salinity fluid in these leaves to alleviate stress (Aminuddin and Arai 2017). We found that the leaf area and leaf aspect ratio both influenced the feeding of snails. Leaves with a larger area and a longer length could provide a convenient location for feeding and were conducive to adhering behavior, which indirectly promoted the feeding of *P. canaliculata* on the mangrove leaves.

RDA showed the feeding of *P. canaliculata* was strongly affected by the mangrove leaf characteristics. The five species of mangrove were clearly differentiated in the feeding test, as confirmed by PCA. The snails could distinguish among the species of leaves in the invaded habitat. These five mangroves of *A. ilicifolius*, *A. aureum* (Wang et al. 2003), *Kandelia candel* (Sun et al. 1998), *Aegiceras corniculatum* (Wei et al. 2008), *Sonneratia apetala* (Ren et al. 2008) are widely distributed in South China coast. We speculated that mangroves composed of *A. ilicifolius* and *A. aureum* might be vulnerable to *P. canaliculata*. Meanwhile, the mangrove composed of the other three species, if coexisting with *A. ilicifolius* or *A. aureum*, may also become the new invaded habitats due to the available leaf litter for the snails. The feeding electivity of *P. canaliculata* was both influenced by the physical and chemical characteristics of the mangrove leaves. The complex natural environment, fluctuations in water quality, and the presence of nonspecific natural enemies may cause changes in the feeding behaviors of *P. canaliculata* in a mangrove forest. As an omnivorous animal, *Pomacea canaliculata* can survive by feeding algae, phytoplankton, and plant materials (Horgan et al. 2014). Mangrove wetlands are rich in organic residues and algae, which possibly become food sources for *P. canaliculata*. *Pomacea canaliculata* could become a crucial primary consumer in the food chain of mangrove ecosystems. The spread of *P. canaliculata* in mangroves may pose a risk to native benthic animals by competing for food. However, the feeding behaviors of *P. canaliculata* could adversely improve the nutrients release of plant litter to the environment. Further studies including gut contents analysis and stable isotopes method can improve the understanding of the role of *P. canaliculata* in mangrove ecosystems.

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Data availability statement

The data presented in this study are available at <https://figshare.com/s/eb821470ab57e89495fb>.

Authors' contribution

Jinling Liu: conceptualization, formal analysis, investigation, writing – original draft; Benliang Zhao: conceptualization, review and editing, supervision; Yunhui Li: formal analysis, investigation; Xiaoyu Deng: resources, investigation; Yue Qiao: resources, investigation; Jingting Xu: resources; Siqi Xu: resources.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. The sampling location and the apple snails.

Figure S2. T-shaped tube device used in the feeding electivity test.

Table S1. Linear regression parameters of chemical traits of mangrove leaf and electivity indicators.

Table S2. Linear regression parameters of physical traits of mangrove leaves and electivity indicators.

Table S3. Chemical characteristics of mangrove leaf in the feeding electivity test.

Table S4. Physical characteristics of mangrove leaf in the feeding electivity test.

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