Effects of common rice field weeds on the survival, feeding rate and feeding behaviour of the crayfish *Procambarus clarkii*

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To check if it is possible for crayfish to reduce the weed biomass in a paddy field, we hypothesised that crayfish can feed on common weeds in a paddy field. The feeding ability of red swamp crayfish, *Procambarus clarkii*, males and females for 4 weeds, *Ludwigia prostrata* Roxb., *Leptochloa chinensis* (L.) Nees, *Echinochloa crusgalli* (L.) Beauv and *Eclipta prostrata* L., commonly found in rice–crayfish fields were evaluated using a quantitative feeding experiment and behaviour observation experiment. The results of the quantitative feeding and behaviour experiments were highly consistent. The *P. clarkii* gender and weed species had no interactive effects on survival rate, the daily feed intake (FI) and percentage of daily feed intake (PFI). The results of the quantitative feeding experiment showed that the FI and PFI values of both *P. clarkii* females and males were significantly higher in the *P. clarkii* feed group than in the weed treatment group. Both FI and PFI were significantly higher in the *L. chinensis* group than in the other treatment groups. The survival rate of *P. clarkii* was significantly lower in the *E. crusgalli* group than in the other treatment groups. The behaviour observation experiment showed that the feeding frequency and duration were in the order of *L. chinensis* > *E. prostrata* > *L. prostrata* > *E. crusgalli*. The results indicate that the *P. clarkii* specimens liked to eat *L. chinensis* (mean PFI was more than 2%), hardly fed on *E. crusgalli*.

The red swamp crayfish, *Procambarus clarkii* (Girard, 1852), is an economically important species in China. In 2018, the output of *P. clarkii* in China was 1.64 million tonnes, so it ranked first in the output of freshwater crustaceans in China; in addition, the output was nearly double the annual output in 20161,2. In 2018, the total area for *P. clarkii* cultivation in China was 1.12 million hectares, and, of this, paddy fields accounted for 0.84 million hectares. Paddy fields accounted for 40% of the total area used for rice cultivation and fisheries in 20183. Rice–crayfish co-culture has a lot of economic benefits, with an increase in net income by 6302.7 USD per hectare4. According to our field survey (data not provided), farmers in some places such as Honghu City in Hubei Province and Yancheng City in Jiangsu Province often widen rice ditches and pay more attention to *P. clarkii* cultivation than rice production, which is against the principles of rice–fish co-culture (Technical specifications for integrated farming of rice and aquaculture animal, SC/T 1135-2017).

Since the twenty-first century, rice–fish co-culture has been widely practiced in paddy fields in Asian countries, especially in China5. The term ‘fish’ refers to a wide range of aquatic animals such as carp, crab and crayfish. Previous studies have suggested that aquaculture animals ushered into paddy fields can provide multiple services to rice ecosystems, i.e. decrease the abundance of insects and weeds, reduce agrochemicals inputs and enhance both soil and rice quality6–8. The aims of rice–fish co-culture are to ensure the stable yield of rice and achieve stable gain and income through the cultivation of aquatic animals. Therefore, it is important to study the ecological services provided by aquatic organisms, such as weed control, in a rice–crayfish co-culture system.

Weed damage has become an important factor that affects rice production, potentially reducing rice yield by 20–80%9. Chemical control is the main method used to control weeds10, however, the wide application of chemical herbicides has caused environmental problems such as pollution, drug resistance and residual toxicity11–13. This has created a demand for sustainable crop management. Previous field studies have shown that rice–crayfish...
In the second week of acclimatization, the *P. clarkii* specimens were fed excessively with pelleted commercial crayfish feed (38% crude protein) every day. In the of Laboratory Animals [Ministry of Science and Technology of China, (2006)398]. accordance with relevant guidelines. evaporation was monitored, and water was supplemented regularly. The plant experiments were performed in a room with a photoperiod of 14 h light: 10 h dark and relative humidity of 60%. During the cultivation, water in the trays till saturation, and the weed seeds were then evenly spread. The trays were placed in a plant culture sinker as shelter. The boxes were filled with approximately 5 L of aerated tap water to a depth of 5 cm. The experi-

| Treatment group | Initial body length (mm) | Initial body weight (g) | Survival (%) | FI (g/ind.) | PFI (%) |
|-----------------|--------------------------|-------------------------|--------------|-------------|---------|
| Crayfish feed   | Female 63.93 ± 4.55      | 6.43 ± 1.31             | 100%         | 0.20 ± 0.060a | 2.95 ± 0.74a |
|                 | Male 62.57 ± 5.08        | 6.84 ± 2.21             | 100%         | 0.22 ± 0.015a | 3.28 ± 0.85a |
| L. chinensis    | Female 70.04 ± 7.39      | 8.55 ± 1.90             | 91.67 ± 14.43* | 0.17 ± 0.067b | 2.01 ± 0.79b |
|                 | Male 68.03 ± 7.80        | 7.47 ± 2.41             | 83.33 ± 28.87* | 0.18 ± 0.10a  | 2.45 ± 1.36a |
| L. prostrata    | Female 61.62 ± 8.64      | 5.78 ± 2.24             | 83.33 ± 28.87* | 0.085 ± 0.046b | 1.48 ± 0.81b |
|                 | Male 66.20 ± 7.01        | 7.27 ± 2.58             | 91.67 ± 14.43* | 0.13 ± 0.050b | 1.72 ± 0.70b |
| E. prostrata    | Female 67.08 ± 7.35      | 7.52 ± 2.77             | 91.67 ± 14.43* | 0.098 ± 0.041a | 1.30 ± 0.55a |
|                 | Male 65.02 ± 9.29        | 7.39 ± 2.94             | 91.67 ± 14.43* | 0.081 ± 0.035c | 1.09 ± 0.51c |
| E. crusgalli    | Female 61.58 ± 8.15      | 6.18 ± 2.72             | 75.00 ± 0.000  | 0.032 ± 0.015a | 0.51 ± 0.24a |
|                 | Male 66.92 ± 9.09        | 8.24 ± 3.47             | 66.67 ± 14.43b | 0.061 ± 0.034a | 0.75 ± 0.42a |

Table 1. Summary statistics (mean ± SD) of feeding related parameters for *P. clarkii* after different treatments. $FI$ daily feed intake, $PFI$ percentage of the daily feed intake to body weight. Values with different superscripts in each column are significantly different ($P<0.05$). $FI$ (g/ind.) = ($Wd−(Wf/Wc))ni/d$, where $n$ is the total number of *P. clarkii*, and $d$ is days between feedings. PFI (%) = $FI/W$, where $W$ is the mean initial body weight of *P. clarkii* in a weed treatment group.

Quantitative feeding experiment. A total of 30 plastic boxes and 120 *P. clarkii* specimens of the same size (Table 1) were used for the quantitative feeding experiment. On the basis of the density of *P. clarkii* in rice–crayfish fields. *P. clarkii* (about 4 times the field density) were raised in a plastic box (38 × 26 × 12.8 cm, L × W × H). *P. clarkii* males and females were fed the 4 weeds separately; each group was fed with 1 weed, with a pelleted commercial crayfish feed (38% crude protein) as the control. The experiment had 10 treatments, with 3 replicates of each treatment.

At the beginning of the experiment, the healthy *P. clarkii* specimens were weighed and randomly divided into plastic boxes. Each box contained 4 plastic plants (3 cm in diameter and 35 cm in length) separately fixed on a sinker as shelter. The boxes were filled with approximately 5 L of aerated tap water to a depth of 5 cm. The experiment lasted for 2 weeks. No water exchange occurred during the experiment. The pH was 8.02 ± 0.12; dissolved oxygen, 8.82 ± 0.17 mg/L; residual chlorine, < 0.05 mg/L and water temperature, 22.2 ± 0.96 °C. A photoperiod...
of 12 h light (8:30 to 20:30):12 h dark was maintained during the experiment, and light intensity at the water surface was 108–254 lx (light meter LM-332, Japan).

The weeds were fed to *P. clarkii* from 15:00 to 16:00. Before feeding, the weed weight (*W*) was measured using an electronic balance. The weeds were offered to the specimens every 2 days, and the feeding amount was calculated according to the feeding conditions of *P. clarkii*; the feeding amount was 0.77 ± 0.12 g of each weed. Before each feeding, the remaining weeds were removed with a net, placed in a glass culture dish and dried in an oven at 60 °C for 48–72 h. The remaining weeds after drying (*Wd*) were weighed. In addition, 1.0 g (fresh weight) of each weed was weighed and dried in the oven, and the dry weight of 1.0 g weed (*Wc*) was calculated and used to measure the actual weed feed intake of *P. clarkii*. The *P. clarkii* commercial feed was fed to the specimens excessively at 16:00 every day. Before each feeding, the commercial feed was weighed with an electronic balance, and the feed quantity was recorded. At 9:00 every day, the remaining commercial feed was removed with a net, placed in a glass culture dish and dried in an oven at 60 °C for 48–72 h. In addition, 1.0 g of the commercial feed was weighed and placed in a glass culture dish, covered with water and maintained from 16:00 to 9:00, and then dried in an oven, and the dry weight of 1.0 g commercial feed was calculated and used to measure the actual commercial feed intake of *P. clarkii*. During the experiment, the dead *P. clarkii* and moulted shells were removed at 9:00 every day.

**Behaviour observation experiment.** To avoid cannibalism among the crayfish, 1 *P. clarkii* (10.03 ± 0.87 g) was placed in a plastic box (38 × 26 × 12.8 cm, L × W × H), and water depth in the box with no shelter was 3 cm. Each group was fed with 1 weed (1.08 ± 0.11 g), with 8 treatments in the experiment and 8 replicates of each treatment. The behaviour of the crayfish in the plastic box was observed and analysed (ViewPoint Zebralab3.3, France). The feeding rhythm of *P. clarkii* occurs mainly at night and in the morning16,17, so the behaviour observation time was from 15:00 to 23:59 and from 00:00 to 10:00.

The behaviour data were analysed using videos (Stomer player, China). The *P. clarkii* specimens caught the weeds with their claws and first appendages: single feeding behaviour. The following parameters were recorded during the experiment: feeding frequency, time of feed intake and duration of *P. clarkii* feeding.

**Statistical analysis.** The daily feed intake (FI) was calculated as follows:

\[
FI \ (\text{g/ind.}) = \frac{[W_i - (W_d/W_c)]}{n/d}
\]

where *n* is the total number of *P. clarkii*, and *d* is days between feedings.

The percentage of daily feed intake (PFI) was calculated as follows:

\[
PFI \ (%) = 100 \times \frac{FI}{W}
\]

where *W* is the mean initial body weight of *P. clarkii* in a weed treatment group.

The statistical analyses were performed using SPSS 23.0, and Origin 2017 (Origin Lab, USA) was used for plotting. FI and PFI were compared between weeds and *P. clarkii* gender by using two-way ANOVA, followed by the LSD multiple comparison test.

**Results**

**Weed consumption.** A summary of the feed intake experiment results is presented in Table 1. The survival rate of both *P. clarkii* females and males in the *P. clarkii* feed group was 100%, whereas *P. clarkii* specimens died in all the other treatment groups. The two-way ANOVA showed that the *P. clarkii* gender and weed species had no interactive effects on FI and PFI (*P* > 0.05; Table 2). No significant differences in FI and PFI were observed between the *P. clarkii* females and males (*P* > 0.05), but the FI and PFI values of different weed species were significantly different (*P* < 0.05; Table 2). The FI and PFI values of both *P. clarkii* females and males were significantly higher in the *P. clarkii* feed group than in the weed treatment groups (*P* < 0.05; Table 1). Both FI and PFI were significantly higher in the *L. chinensis* group than in the other weed treatment groups. No significant differences in FI and PFI values were observed between the *L. prostrata* and *E. prostrata* groups. The FI and PFI of the *P. clarkii* females and males were significantly lower in the *E. crusgalli* group than in the other groups (Table 1).

**Table 2.** Statistical analysis (two-way ANOVA) of the effects of gender and different weeds on the daily feed intake (FI) and proportion of daily feed intake (PFI) of *P. clarkii*. FI daily feed intake, PFI percentage of the daily feed intake to body weight. *Bold characters indicate statistical significance at α = 0.05.*
Feeding characteristics. The commercial feed was basically consumed within 4 h after feeding in the feed intake experiment, so the control group was not used for the behaviour observation experiment. The behavioural analysis results are listed in Table 3. The feeding frequency and duration of *P. clarkii* on the different weed groups are as follows: *L. chinensis* > *E. prostrata* > *L. prostrata* > *E. crusgalli*. No significant differences in feeding frequency and feeding duration were observed between the *P. clarkii* females and males. Both *P. clarkii* females and males were more active from 17:00 to 20:00 (Fig. 1). Both feeding frequency and feeding duration were significantly higher in the *L. chinensis* group than the *L. prostrata* and *E. crusgalli* groups (*P* < 0.05, Table 3). No significant differences in feeding frequency and feeding duration were observed between the *L. prostrata* and *E. crusgalli* groups (*P* > 0.05). The feeding activity of both *P. clarkii* females and males was the least in the *E. crusgalli* group (Table 3).

The *P. clarkii* females and males of the *L. chinensis* group ate every hour during the observation period, and the feeding duration was longer from 19:00 to 20:00 and 4:00 to 5:00 for the females and from 18:00 to 19:00 and 2:00 to 4:00 for the females (Fig. 1). The *P. clarkii* males in the *L. prostrata* group fed frequently from 17:00 to 19:00, whereas the *P. clarkii* females fed frequently from 16:00 to 17:00. The *P. clarkii* males in the *E. prostrata* group fed frequently from 17:00 to 23:00, whereas the *P. clarkii* females fed frequently around 5:00. Both *P. clarkii* females and males in the *E. crusgalli* group showed the lowest feeding frequency and duration, but both *P. clarkii* females and males exhibited a relatively long feeding time from 21:00 to 22:00.

*P. clarkii* exhibited 2 living states: active and static. When it started to move, it may have been looking for food. When it fed on the weeds, it used 2 positions: lying on its side for feeding (Fig. 2a) and feeding on its front (Fig. 2b). When *P. clarkii* fed on the weeds, it first used its cheliped to catch the weeds and then used its mouthparts to complete feeding (Fig. 2a, b). *P. clarkii* would lie on its side when it was still, for example, for sleeping (Fig. 2c).

### Discussion

*P. clarkii* is one of the most important invasive species found worldwide, and its ecological plasticity allows it to live in different types of environments. The great ecological plasticity of *P. clarkii* is also expressed in its feeding habits attributable to its polytrophic feeding behaviour. Previous studies have established a food chain suitable for its growth needs on the basis of the food sources in its living environment. Therefore, is the fact that crayfish can reduce weed biomass in paddy fields related to this ecological characteristic? In this study, *P. clarkii* showed a strong appetite for some weeds, such as *L. chinensis*, and the PFI of *L. chinensis* was more than 2%. The results of the quantitative feeding and behaviour observation experiments were highly consistent. The *P. clarkii* specimens mostly preferred to eat *L. chinensis*, but hardly ate *E. crusgalli*. No significant differences were observed in the feeding amount with respect to *L. prostrata* and *E. prostrata*, however, according to the behaviour experiment results, the *P. clarkii* specimens preferred *E. prostrata*.

Previous studies on the diversity of weed communities in rice fields have shown that the density of *L. prostrata* and *E. prostrata* in the rice–crayfish co-culture system has significantly reduced when compared with rice monoculture, and the biomass of these 2 weeds continues to decrease with the increase in the duration of rice–crayfish co-culture. In this study, the results showed that the feeding ability of *L. prostrata* and *E. prostrata* by *P. clarkii* was better and probably achieved by direct ingestion. However, the results obtained for *L. chinensis* and *E. crusgalli* were inconsistent with those of previous field studies. The biomass of *L. chinensis* and *E. crusgalli* decreased first (< 4 years) and then increased (7–8 years) with an increase in the duration of rice–crayfish co-culture, and both weed densities have been found to be lower in the rice–crayfish co-culture system than in the rice monoculture system. This showed that *P. clarkii* can also control *L. chinensis* and *E. crusgalli*. However, in the present study, almost no *P. clarkii* specimen fed on *E. crusgalli*. In our study, increased feeding on *L. chinensis* was observed, relative to all the other weeds examined. Previous field investigations have reported that the biomass of *L. chinensis* was still significantly higher than that of *L. prostrata* and *E. prostrata*, suggesting decreased consumption of *L. chinensis*. Therefore, it is unclear how *P. clarkii* controls weeds, especially *L. chinensis* and *E. crusgalli*, as it seems that the weeds were not controlled by direct feeding. *P. clarkii* can directly feed on agricultural seeds such as rice seeds, which contain high protein and/or energy. Therefore, another possibility is that *P. clarkii* inhibits weed growth by ingesting weed seeds or suppressing weed seed germination through burrowing.

*P. clarkii* is an opportunistic, omnivorous feeder, and its diet includes submersed macrophytes, algae, invertebrates and detritus. Generally, *P. clarkii* likes to feed on aquatic plants, but there as a few studies on *P. clarkii* feeding on terrestrial plants. During *P. clarkii* cultivation, fishermen generally grow aquatic plants such as *Hydrilla*. The great ecological plasticity of *P. clarkii* live in different types of environments. The great ecological plasticity of *P. clarkii* is also expressed in its feeding habits attributable to its polytrophic feeding behaviour. Previous studies have established a food chain suitable for its growth needs on the basis of the food sources in its living environment. Therefore, is the fact that crayfish can reduce weed biomass in paddy fields related to this ecological characteristic? In this study, *P. clarkii* showed a strong appetite for some weeds, such as *L. chinensis*, and the PFI of *L. chinensis* was more than 2%. The results of the quantitative feeding and behaviour observation experiments were highly consistent. The *P. clarkii* specimens mostly preferred to eat *L. chinensis*, but hardly ate *E. crusgalli*. No significant differences were observed in the feeding amount with respect to *L. prostrata* and *E. prostrata*, however, according to the behaviour experiment results, the *P. clarkii* specimens preferred *E. prostrata*.

### Table 3. Behavioural statistics of *P. clarkii* in different weed treatment groups (mean ± SD). Values with different superscripts in each column are significantly different (*P* < 0.05).

| Weed treatment group | Repetition | Feeding frequency | Feeding duration (s) |
|----------------------|-----------|-------------------|---------------------|
|                      |           | Female            | Male                |
| *L. prostrata*       | 8         | 34.00 ± 24.40a    | 32.13 ± 20.86a      |
|                      |           | 1228.75 ± 113.94a | 935.88 ± 595.12a    |
| *L. prostrata*       | 8         | 8.88 ± 4.30a      | 20.25 ± 20.70a      |
|                      |           | 175.00 ± 90.93a   | 349.13 ± 442.06a    |
| *E. prostrata*       | 8         | 17.25 ± 10.31ab   | 25.88 ± 17.46ab     |
|                      |           | 535.00 ± 523.25ab | 443.88 ± 224.83ab   |
| *E. crusgalli*       | 8         | 6.38 ± 4.93b      | 3.88 ± 2.59b        |
|                      |           | 151.88 ± 108.76b  | 82.8 ± 55.40b       |

### Table 3. Behavioural statistics of *P. clarkii* in different weed treatment groups (mean ± SD). Values with different superscripts in each column are significantly different (*P* < 0.05).
Figure 1. Feeding activity of *P. clarkii* during the observation period.
verticillata and Elodea nuttallii. The large amount of L. chinensis consumed by P. clarkii in the present study shows the unlimited potential of P. clarkii to control weeds in rice fields. Both L. chinensis and E. crusgalli are graminaceous plants, but the feeding selectivity of these 2 weeds with respect to P. clarkii was very different. L. chinensis seedlings are tender, which may make its taste closer to that of aquatic plants. In addition, olfaction plays an important role in the feeding process of P. clarkii, and it is possible that the odour of L. chinensis attracts P. clarkii to a greater extent than that of E. crusgalli. The results of the quantitative feeding experiment showed no significant differences in the feeding amount of the P. clarkii males and females in the L. prostrata and E. prostrata groups, however, the results of the behaviour observation experiment showed that the feeding frequency of the P. clarkii males was higher than that of the females in the L. prostrata and E. prostrata groups. P. clarkii males are more aggressive than the females, so it is possible that the differences in their behaviour are because the P. clarkii males frequently move, search for food and eat.

All the weeds used in this study were newly grown seedlings. The appearance of weeds changes greatly in different growth stages. Therefore, the conclusions drawn on the basis of the P. clarkii specimens feeding on the weed seedlings in this study are not necessarily applicable to weeds in other growth stages. Freshwater crayfish have a dietary protein requirement of at least 30–35% for optimal growth. The percentage of crude protein content in dry L. chinensis and E. crusgalli is 8.44% and 11.84%, respectively. Although moulting of P. clarkii was observed in the weed groups in the present study, the P. clarkii specimens in the weed groups died with the extension of culture time, whereas the P. clarkii specimens in the feed group continued to grow well. Obviously, it is impossible for P. clarkii to feed on only weeds in a rice field, as the nutrition in weeds cannot completely meet the requirements for important life history events of P. clarkii, such as moulting and reproduction. However, the high ecological plasticity of P. clarkii makes its use in controlling weeds in rice fields possible. In a rice field, which has high amounts of plant material and low macroinvertebrate diversity, animal food is less important. Therefore, the use of P. clarkii in controlling weeds in a rice field needs to be studied further.

Conclusions
This study provides direct evidence that crayfish feed on common weeds in paddy fields, suggesting that crayfish may be used to reduce the weed biomass in paddy fields. P. clarkii preferred to eat L. chinensis and hardly fed on E. crusgalli. The mean percentage of daily feed intake to body weight per P. clarkii for L. chinensis was more than 2%.

Figure 2. Feeding behaviour of P. clarkii (using L. chinensis as an example). (a) Feeding in the side direction, (b) Feeding in the front direction, (c) no motion.
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Author contributions
Q.Y., Z.T., W.Z. and G.S. conceived and designed the study; Q.Y., W.L. and X.S. conducted the experiments; Q.Y. and W.H. drafted the initial manuscript and performed the subsequent revisions; Y.B. and W.L. provided guidance for data analysis and W.Z. agreed to be accountable for all aspects of the study and solve any problems involved in the accuracy and integrity of any part of the study.

Competing interests
The authors declare no competing interests.

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