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RESEARCH ARTICLE

The biological control of *Pomacea canaliculata* population by rice-duck mutualism in paddy fields

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Duck has been used as a non-chemical control method against *Pomacea canaliculata* Lamarck, but little is known about its principles that underlie the control of snail populations. An indoor experiment was initially used to observe the predation potential of ducks, followed by replicated field trials. In the indoor studies, ducks effectively preyed on juvenile snails, but had a weak predatory effect on large snails and egg clusters. In the field, application of a rice-duck mutualism system significantly reduced the numbers of snails (especially number of immature individuals), number of snail egg clusters and snail damage to rice plants. The controlling effect was longer and more stable than the chemical application, resulting in a better yield than with the pentachlorophenol sodium and tea seed powder treatment. Our experimental results also suggested that the snail age structure in the rice-duck mutualism plots was shifted towards older snails by ducks preying, indicating a trend towards population decline, and ducks caused snails to oviposit on sites not ideal for hatchling establishment. Throughout the studies, it is suggested that a rice-duck mutualism system could be used for controlling *P. canaliculata* in organic rice production.

Keywords: *Pomacea canaliculata* Lamarck; rice-duck mutualism system; biological control; population dynamics; trait-mediated indirect interactions; density-mediated indirect interactions

1. Introduction

The golden apple snail (*Pomacea canaliculata*, Lamarck) is native to South America but was introduced by Argentina to Taiwan in the 1980s. The snail was intentionally introduced for the purpose of commercial food production without considerations of market demand and ecosystem impact. It was later distributed to most Asian countries by Taiwan (Acosta & Pullin, 1989; Mochida, 1991).

Unfortunately, the market response was poor, and many snail farms were abandoned. In many cases, the escaped snails established, and it is currently recognised as a major pest of rice and other semi-aquatic plants such as algae, azolla

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and duckweed (Hayes, Joshi, Thiengo, & Cowie, 2008; Hirai, 1988; Naylor, 1996). *P. canaliculata* infested approximately 171.4×10^3 ha in Taiwan in 1986, 400×10^3 ha in the Philippines in 1989 and 16.2×10^3 ha in Japan in 1989 (Mochida, 1991). The snail is highly invasive because of its high reproductive rate, voracious appetite, ability to adapt to harsh environmental conditions and absence of native predators or competition from native snails in its new habitats.

In mainland China, *P. canaliculata* was first introduced to Guangdong in 1981, and subsequently spread throughout south China, including Guangxi, Yunnan, Hainan, Fujian, Sichuan, Zhejiang, Jiangxi and Jiangsu provinces. *P. canaliculata* has reduced rice yields from 10 to 90% and water bamboo (*Zizania caduciflora* L.) yields from 10 to 20% (Yu, Wada, Li, & Chen, 2001). In addition to causing substantial economic losses to crops, *P. canaliculata* also damages non-agricultural ecosystems. In some wetland ecosystems, for example, *P. canaliculata* has been associated with a shift from macrophyte-dominated communities to phytoplankton-dominated communities; the decimation of submerged macrophytes and the consequent ecological changes have resulted in the displacement of native aquatic snails and other macroinvertebrates, leading to a loss of biodiversity and ecosystem services (Carlsson, Brönmark, & Hansson, 2004a). In addition, the consumption of *P. canaliculata* (it has become a popular food in some regions) has facilitated the spread of the parasitic nematode *Angiostrongylus cantonensis* (Lv, Zhang, Steinmann, & Zhou, 2008; Tsai et al., 2001), which causes eosinophilic meningoencephalitis in humans (Joshi, 2005). Thus, the Global Invasive Species Program has listed *P. canaliculata* as one of the world's 100 most damaging invasive alien species (Global Invasive Species Database, 2005).

Chemical molluscicides such as methaldehyde, tea seed, pentachlorophenol sodium (PS) and niclosamide are typically applied for control of *P. canaliculata* (Tangkoonboribun, 2009). However, the wide use of these agrochemicals has caused environmental damage and is conflict with the tenets of organic agriculture. Chemical control of *P. canaliculata* has been gradually replaced by integrated approaches combining the utilisation of biopesticides (Suryanto, Jambari, Sajap, & Ahmad, 1999), attractants (Teo, 1999) and natural enemies. These new approaches emphasise measures that are less harmful to the environment than molluscicides (Rondon & Sumangil, 1991). As potential biological control agents in paddy fields, ducks (Gallebu, Jover, & Bongolan, 1992; Pantua, Mercado, Lanting, & Nueva, 1992; Teo 2001), fish (Vromant, Khan, Chau, & Ollevier, 2002; Vromant, Rothuis, Cuc, & Ollevier, 1998) and insects (Barrion, Jackson, & Schoenly, 1997) have been tested. Of these, ducks were found to be practical and highly effective in rice ecosystems (Gallebu et al., 1992; Pantua et al., 1992; Teo, 2001). Previous studies showed that ducks reduced snail numbers by more than 80%, and the suppression in snail numbers was related to duck density and duck breeding season (Teo, 2001; Vega, Villancio, Mendoza, Limosinero, & Mendoza, 1992). In recent years, a form of organic farming associated with species-diversified rice cultivation has been widely practiced in southern China, Japan, North Korea and other countries in Southeast Asia. In this system, ducks are released into the paddy field and coexist with rice plants during the rice cropping season, representing a rice-duck mutualism in which rice provides habitat for the ducks and ducks control pest herbivores (Zhang, Lu, & Zhang, 2002).

Our understanding of the biological control of *P. canaliculata* population by rice-duck mutualism in paddy fields, however, is incomplete. In particular, the effects of ducks on snail population structure and dynamics are unknown. Accordingly, we conducted a field experiment to determine how ducks affect the population dynamics, age composition and reproduction of *P. canaliculata* in rice fields. In addition to ducks as biological control agents, the experiment included two commonly used molluscicides (sodium pentachlorophenol and tea seed powder (TS)) for comparative purposes. The information generated by this research should improve the understanding and efficacy of practical *P. canaliculata* control by rice-duck mutualism in wetland rice ecosystems.

2. Methods

2.1. Experimental materials

Seedlings of the rice cultivar *Oryza sativa* cv. Shengbasimiao, a local variety with a maturity period of 110 days, were provided by the South China Agricultural University. Duck variety *Tadorna tadorna* (L.) was obtained from the local veterinary department. *P. canaliculata* individuals and egg clusters were collected from the rice field around the experimental plots. Prior to the experiments, the collected snails were reared in the laboratory under controlled conditions of 12-hr light–dark regimen, temperature (25 ± 2°C) and pH (6.0–6.5), with fresh cabbage as the main diet. The snails were divided into four ranks according to weight, which was related to stage: I (<0.30 g, hatchlings); II (0.30–1.5 g, juveniles); III (1.5–6.5 g, nearly adult snails); and IV (>6.5 g, adults).

2.2. Predatory potential of ducks on snails and egg clusters

Snail consumption by ducks of different ages (15, 30, 45 and 60 days old) was investigated in the laboratory at the South China Agricultural University, Guangzhou, China. The experimental design was a randomised complete block with four replications for each treatment; each replicate consisted of two ducks of the same age in one holding pen of L 120 cm $\times$ W 80 cm $\times$ H 60 cm. The ducks in each pen were given a total of 10 egg clusters or 50 snails of the following six weight classes: <0.30 g, 0.3–1.5 g, 1.5–4.0 g, 4.0–6.5 g, 6.5–9.0 g and 9.0–20 g. The number of snails or egg clusters remaining in each pen was recorded after 24 h, and the experiment was repeated three times. The ducks were provided with water but were not provided with food other than the snails and eggs. Each pen was tightly covered with a steel mesh to prevent the escape of snails or ducks.

2.3. Field experimental site

The field experiment was conducted between 2006 and 2007 including early and late cropping seasons. The field trial site is located at the Zengcheng Teaching and Research Farm (23°14′N, 113°38′E), about 40 km east of the university campus. The area has a subtropical monsoon climate with an average frost-free period of 346 days. The mean annual air temperature is 20–22°C, the mean annual precipitation is 1800–1900 mm and the mean annual air humidity is 78%. The paddy soil of the experimental site developed from a Latosol. It had pH of 6.0 and contained 33.02 g kg^{-1} organic matter, 18.27 g kg^{-1} total K, 0.54 g kg^{-1} total P, 27.59 mg kg^{-1} available P and 107.98 mg kg^{-1} available N.

2.4. Field experimental design

Field density and sex ratio of *P. canaliculata* were investigated before the experiment, and the wild *P. canaliculata* was removed from the field plots; the density of snails at the field site in early-April was 110 per 100 m^2 and the sex ratio was about 1:1. After the snails were removed, the plots were tilled, and 110 snails were released into each plot; this density of snails matched the average density of snails (from hatchlings to adults) that had been removed. The 110 snails included 30 individuals of ranks I, II and III, and 20 individuals of rank IV; the sex ratio was 1:1 for ranks III and IV.

The first rice-cropping season was planted in mid-April. The following four treatments were used: (1) control treatment (CK), without ducks or molluscicides; (2) PS treatment, in which 60% PS was applied at 8 g m^{-2}; (3) TS treatment, in which TS was applied at 15 g m^{-2}; (4) rice-duck cultivation (DR) treatment, in which ducks but no molluscicides were added. A randomised block design was used, and each treatment consisted of three replicate plots (100 m^2/plot). Plastic barriers and nets were placed around each plot to contain ducks or *P. canaliculata* within the plot. The rice seedlings were planted at a spacing of 25 cm between rows and 20 cm between hills within the same row, four seedlings to a hill. In PS and TS plots, molluscicides were dissolved with water and then applied to the plot using a knapsack sprayer 3 days before transplanting. In DR plots, for control of snails, five adult ducks 6 months old (reared in the last cropping season) were pastured in each plot for 4–5 days before transplantation. As young seedlings are not resistant to trampling disturbance by large ducks in early days after transplantation, the adult ducks were retrieved and transferred to other places before transplanting. At the beginning of the returning-green stage of the rice, five 15-day-old ducklings were introduced into each plot to coexist with rice seedlings. When rice was at the heading stage, which was 60 days after the ducks had been introduced, the ducks were removed from the experimental plots. The water level was maintained at 8–10 cm after the returning-green stage of the rice. The first rice crop was harvested in mid-July. Methods used to evaluate the plots for snail number, snail damage, rice yield and other variables were described in Section 2.5.

The second rice crop was planted on mid-August following the same procedures described for the first rice planting, the snails was removed from the plots before the second planting. As the population increased through the breeding and rapid succession of generations, the snail density in the rice field surrounding the plots was increased to 700 per 100 m^2 in August, and 700 snails were added to each plot after the seedlings were transplanted. The 700 snails included 200 individuals of ranks I, II and III, and 100 individuals of rank IV; the sex ratio was 1:1 for ranks III and IV. The four treatments were applied to the second planting as described for the first planting, and each plot received the same treatment as in the first planting. The water level was once again maintained at 8–10 cm after the returning-green stage of rice. Plots were evaluated in the same manner as for the first planting and as described in Section 2.5. The second crop was harvested in mid-November.

2.5. Plot evaluation

The number and age rank of *P. canaliculata* were determined once every 2 weeks in 10 subplots (1 m $\times$1 m), and the subplots were selected in a zigzag pattern within each plot. The spatial distribution of oviposition sites was determined once each week in each plot, the number of egg clusters in each habitat type (rice plants, weed, ridge, plastic barrier, fence column and fence net) was evaluated.

In the first week after transplanting, the damage percentage and damage scale of seedlings by *P. canaliculata* were evaluated in each of 10 subplots per plot. Damage was assessed on a scale of 1–6 as follows: (1) undamaged; (2) 1–19% of crown area damaged; (3) between 20 and 60% of crown area damaged; (4) $>$60% of crown area damaged; (5) leaves totally absent, only stems remain; and (6) both leaves and stems were absent.

From the time when rice tillers appeared (about 10 days after the seedlings were transplanted), the number of rice tillers was recorded for 60 rice hills per plot; the hills were selected in a zigzag pattern in each plot. At maturity, the total number of spikelet panicles (TNSP), panicle length (PL), spikelet fertility (SF), number of filled grains per panicle (NFGP), thousand grain weight (TGWT) were also determined for 20 hills per plot.

2.6. Data analysis

The SPSS version 11.0 (standard version; SPSS, Chicago, IL, USA) was used for statistical analysis. Before ANOVAs were performed, data were evaluated for normality and homogeneity of variances, and data were $\log_{10}$ or arcsine square-root transformed when they did not satisfy normality assumptions. When ANOVAs were significant, multiple comparison analyses (Least Significance Difference) at 95% confidence level were used to evaluate differences between treatment means.

3. Results

3.1. Predatory potential of ducks on snails and egg clusters

Nearly 100% of small snails (0.3–1.5 g) were consumed regardless of duck age. However, consumption percentage tended to decrease with snail size (Figure 1A). Few of the snails in the two larger weight classes were consumed by 15- or 30 day-old ducks, about 20% were consumed by 45-day-old ducks, and about 40% were consumed by 60-day-old ducks (Figure 1A). The predatory effect on egg clusters was generally low for ducks. Ducks are not apt to devour the whole egg cluster, but to smash the egg cluster and consume parts of it, and the predatory effect was greater for younger ducks than for older ducks (Figure 1B).

3.2. P. canaliculata egg cluster number and location as affected by treatments

In general, the order of egg cluster was greatest in the CK plots followed by PS, TS and DR, respectively. In CK plots, *P. canaliculata* egg clusters were more abundant in the late rice than in the early rice due to the increasing population size (Figure 2). In PS and TS plots, although application of molluscicides maintained egg clusters number at a low level for about 3 weeks, the numbers subsequently increased in

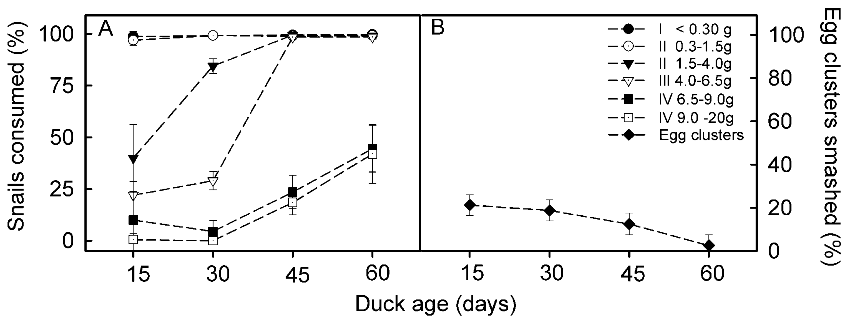

Figure 1. Predatory potential of ducks on snails (A) and egg clusters (B). Values are means ± SD. In the legend, the ranges indicate snail sizes based on weight.

the later period (Figure 2C–F). In DR plots, egg clusters number remained low throughout the cropping cycle.

The results also showed that in CK, PS and TS plots, fewer egg clusters were evident in ridge bank, plastic barrier, fence column and net than on the stems and leaves of rice plants or weeds (Figure 2A–F). In the DR plots, however, more egg clusters were observed at ridge, plastic barrier and fence column than on plants (Figure 2G and H). At the rice heading stage, when ducks were removed, the number of clusters on the rice plants or weeds increased in the DR plots (Figure 2G and H).

3.3. Snail numbers and age structure as affected by treatments

In both early rice and late rice, the number of snails was highest in CK plots (Figure 3A and B) and lowest in DR plots (Figure 3G and H). Although PS and TS suppressed snail numbers early in the cropping cycle, the snail numbers increased later in the season (Figure 3C–F). In late rice, snail numbers increased in the DR plots at the end of the cropping season, after the ducks had been removed.

The percentage of immature snails (hatchlings, juveniles and nearly adult snails) was higher in CK plots than in the other plots (Figure 3). Although PS and TS treatments killed most hatchlings and juveniles early in the crop cycle, the percentages of hatchlings and juveniles increased later in the crop cycle. In DR plots, ducks tended to suppress the percentage of immature snails. In late rice, however, the percentage of juveniles increased at the end of the season, after the ducks had been removed.

3.4. **P. canaliculata** *damage to rice seedlings as affected by treatments*

Figure 4 shows the percentage of seedlings damaged by *P. canaliculata* in the first week after transplanting. At this time in the crop cycle, the seedlings have yet to form any tillers and are therefore more susceptible than older plants to *P. canaliculata*. Snails can easily devour the main stem and even all parts of young seedling before the seedling produces a tiller. In the CK plots, a substantial percentage of the seedlings were damaged (the snails removed all aboveground biomass in some cases), and the percentage was greater in the late rice than in the early rice owing to the

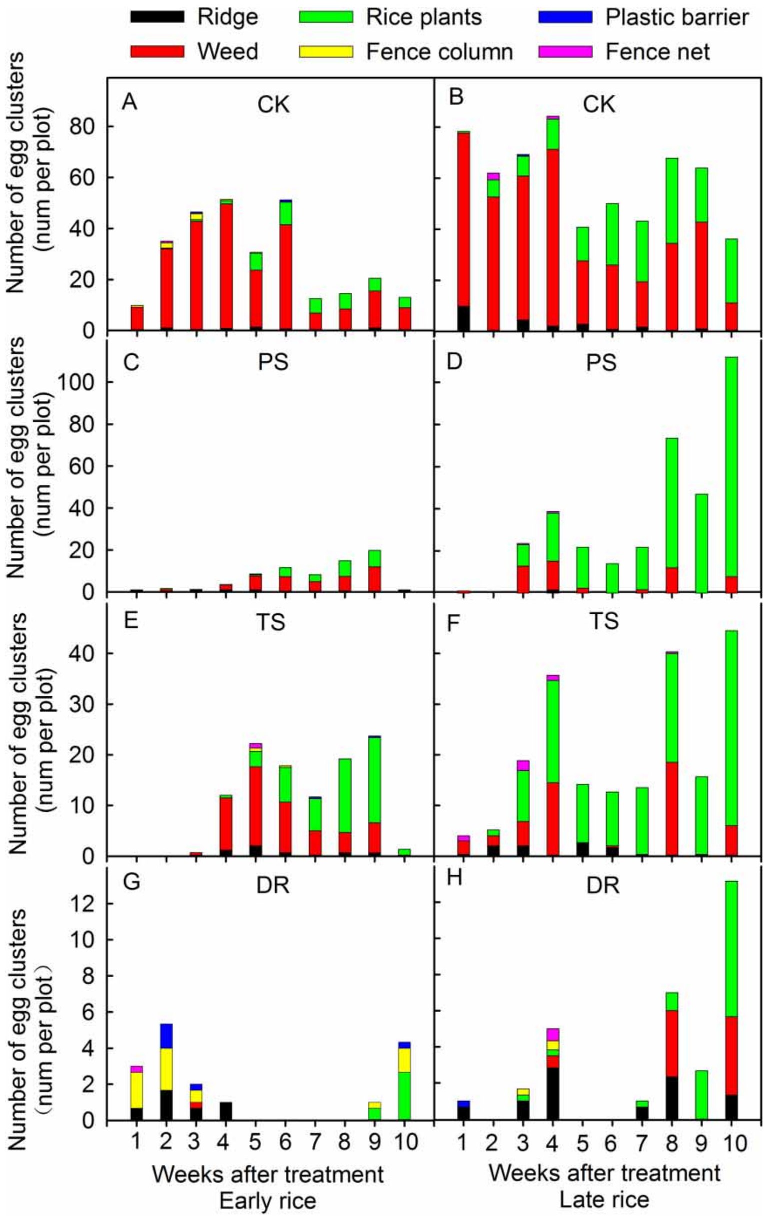

Figure 2. Number of *P. canaliculata* egg clusters and location of clusters in rice plots as affected by treatments and time in early rice and late rice. CK: control without ducks or molluscicides. PS: pentachlorophenol sodium treatment. TS: tea seed powder treatment. DR: duck treatment.

higher population density. The percentage of seedlings damaged was greatly reduced by molluscicides and ducks.

Figure 5 shows the damage ratings for seedlings in the first week after transplanting (before tillering). The damage ratings were significantly higher in the

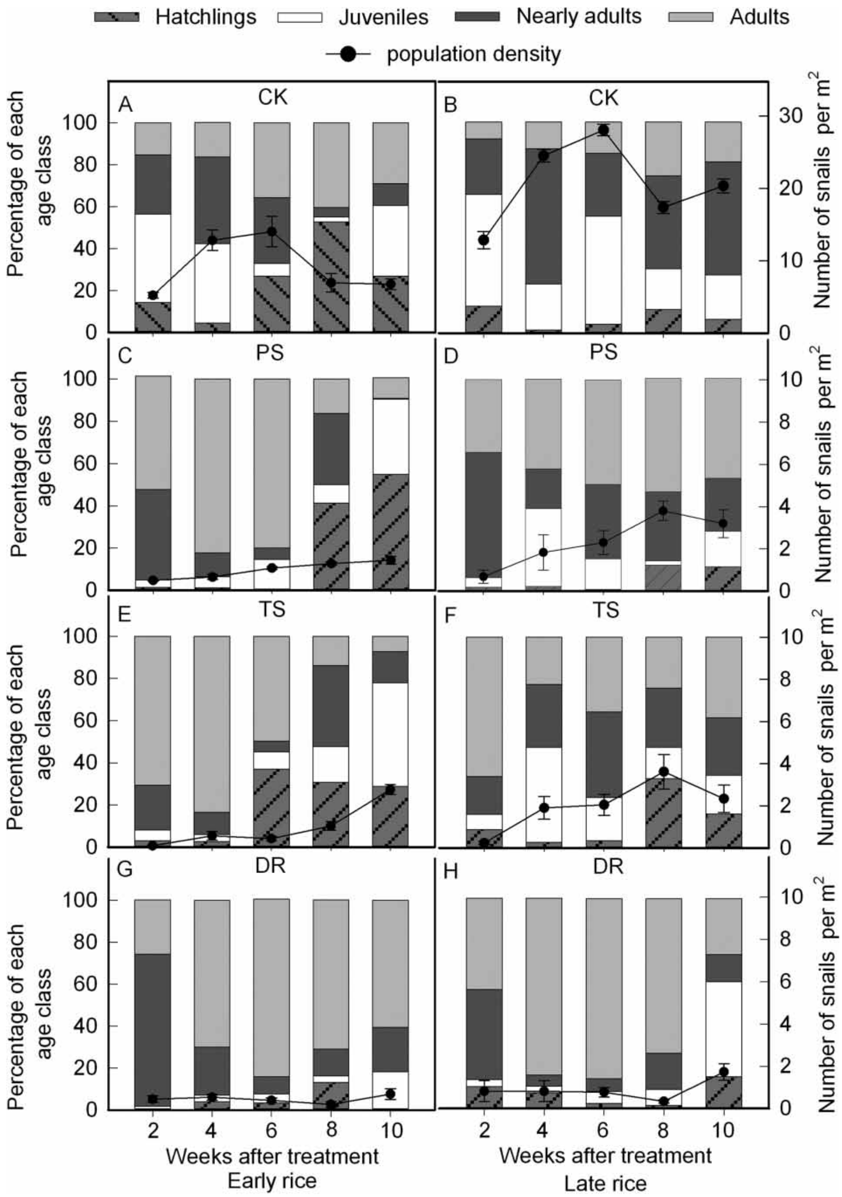

Figure 3. Age structure of *P. canaliculata* and number of snails per m^2 as affected by treatment and time. Note the change in scale for snail numbers among the panels. CK: control without ducks or molluscicides. PS: pentachlorophenol sodium treatment. TS: tea seed powder treatment. DR: duck treatment. For snail number, values are means ± SD.

CK plots than in the other plots for scale 5 ($F = 78.71$, $P < 0.05$, for early rice; $F = 11.68$, $P < 0.05$, for late rice) and scale 6 ($F = 93.38$, $P < 0.05$, for early rice; $F = 229.28$, $P < 0.05$, for late rice). There were no significant differences between DR, PS and TS treatments for scale 1 ($F = 13.21$, $P > 0.05$, for early rice; $F = 36.46$, $P > 0.05$, for late rice).

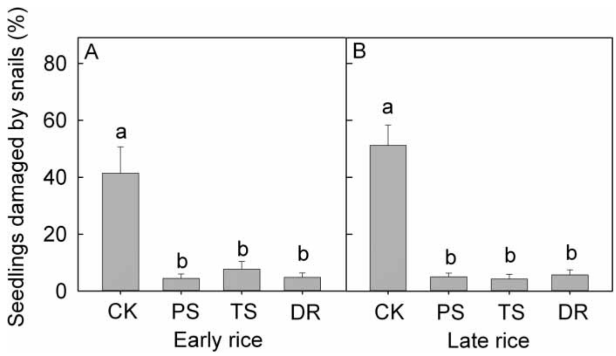

Figure 4. The percentage of seedlings damaged by *P. canaliculata* 1 week after transplanting as affected by treatments in early rice (A) and late rice (B). CK: control without ducks or molluscicides. PS: pentachlorophenol sodium treatment. TS: tea seed powder treatment. DR: duck treatment. Values are means + SD. Bars with different letters are significantly different at $P < 0.05$ (LSD).

3.5. Rice tillering as affected by treatments

In early rice, there were significantly fewer tillers in CK plots than in the other plots at weeks 2 and 3 ($F = 13.88$, $P < 0.05$, for week 2; $F = 22.14$, $P < 0.05$, for week 3; Figure 6A), while no significant differences were found between DR, PS and TS treatments ($P > 0.05$). In late rice, tiller number was greatly suppressed in the CK plots relative to the other plots at weeks 2 and 3 ($F = 79.48$; $P < 0.05$, for week 2; $F = 57.06$; $P < 0.05$, for week 3; Figure 6B), and there were significantly fewer tillers in CK, TS and DR plots than in the PS plots at week 3 ($P < 0.05$).

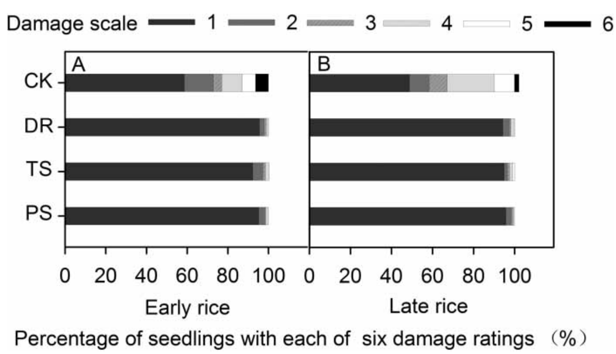

Figure 5. The rating of damage caused by *P. canaliculata* to rice seedlings 1 week after transplanting as affected by treatments in early rice (A) and late rice (B). Damage was rated on a scale of 1–6 as follows: 1, undamaged; 2, 1–19% of crown area damaged; 3, between 20 and 60% of crown area damaged; 4, >60% of crown area damaged; 5, leaves totally absent, only stems remain; and 6, both leaves and stems absent. CK: control without ducks or molluscicides. PS: pentachlorophenol sodium treatment. TS: tea seed powder treatment. DR: duck treatment.

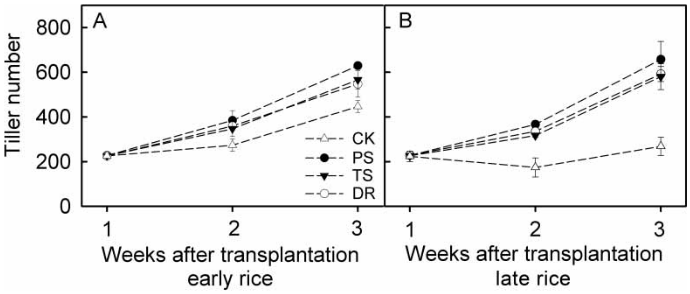

Figure 6. Tiller number (per 60 hills) in the first 3 weeks after transplanting as affected by treatments in early rice (A) and later rice (B). Values are means ± SD CK: control without ducks or molluscicides. PS: pentachlorophenol sodium treatment. TS: tea seed powder treatment. DR: duck treatment.

3.6. Yield parameters as affected by treatments

For all yield parameters except panicle length (PL), parameter means were generally greater ($P < 0.05$) in plots with ducks or molluscicides than in control plots (Table 1). In addition, TNSP and yield were greater in plots with ducks than in plots with molluscicides ($F = 4.13$; $P < 0.05$, for TNSP; $F = 6.43$; $P < 0.05$, for yield).

4. Discussion

In indoor experiments, ducks effectively preyed on small snails, but had weak predatory effect on large snails and egg clusters. However, the field experiments demonstrated that although *P. canaliculata* cannot be eradicated by the biological control of rice-duck mutualism, duck preying can still remarkably bring down the pest population in both the early and late rice seasons, and the controlling effect was longer and more stable as compared with the PS and TS application.

Information concerning a population's age structure can provide insight into the processes that determine how the population increases or decreases over time (Andrzejczyk & Brzeziecki, 1995; Svensson & Jeglum, 2001). Moreover, estimation of age structure is necessary for predicting future trends in population structure (McCartney, Armstrong, Gwynne, Kelly, & Barker, 2006). Our experimental results

Table 1. Yield parameters of rice as affected by treatments.

Treatment	TNSP	PL (cm)	SF (%)	NFGP	TGWT (g)	Yield (kg per plot)
CK	11.3 ± 2.6c	23.4 ± 1.9a	74.9 ± 6.1b	123.2 ± 19.6b	13.1 ± 1.1b	24.8 ± 4.1bb
PS	12.1 ± 4.6bc	22.7 ± 2.1a	79.4 ± 2.1a	133.4 ± 13.1a	14.4 ± 2.3a	31.8 ± 9.8ab
TS	13.1 ± 3.2b	22.8 ± 4.8a	79.5 ± 2.9a	133.5 ± 19.3a	14.0 ± 2.4a	34.2 ± 9.3ab
DR	15.7 ± 1.1a	23.2 ± 1.1a	80.6 ± 2.7a	138.2 ± 11.6a	14.0 ± 1.9a	38.7 ± 7.2aa

TNSP, total number of spikelets per panicle; PL, panicle length; SR, spikelet fertility; NFGP, number of filled grains per panicle; TGWT, thousand-grain weight; CK, control without ducks or molluscicides; PS, pentachlorophenol sodium treatment; TS, tea seed powder treatment; DR, duck treatment.
Values are means ± SD. Means in a column followed by a different letter are significantly different at $P < 0.05$ (LSD).

suggested that the snail age structure in the rice-duck mutualism plots was shifted towards older snails by ducks preying, indicating a trend towards population decline. Although the application of molluscicides delayed the development of new generations of *P. canaliculata*, as indicated by the reduced number of immature snails, however, this effect did not last; about 6 weeks after the molluscicides were applied, *P. canaliculata* numbers and the proportion of immatures began to increase. That the effect of ducks was greater and more consistent than the effect of the molluscicides can be explained in two ways. First, although ducks had less effect than the molluscicides on larger snails, the consumption of smaller snails by ducks not only directly reduces the overall population size but also limits the number of *P. canaliculata* that attain the reproductive stage. Second, the development of successive generations of *P. canaliculata* was reduced, as ducks preyed upon the snails, the oviposition frequency and the number of egg clusters oviposited reduced. Although ducks preferentially consumed small rather than large snails, duck consumption of smaller snails was substantial in both the laboratory and field. Because small *P. canaliculata* snails have higher density and foraging abilitiy than large ones, they may pose a greater threat to aquatic vegetation than adults (Boland et al. 2008; Carlsson & Brönmark, 2006). From an ecological perspective, biological control typically results from density-mediated indirect interactions (DMIIS) in which the presence of a predator reduces the density of a prey and thereby indirectly affects other organisms (Schmitz, Krivan, & Ovadia, 2004; Trussell, Ewanchuk, & Bertness, 2002; Werner & Peacor, 2003). Under general circumstances, predator consumption of prey results in the release of the prey's food (Abrams, 1995; Werner & Peacor, 2003). The results presented above indicate that, by greatly reducing the population size of *P. canaliculata*, ducks reduced *P. canaliculata* damage to rice and increase rice yield for both early and late rice.

In addition to affecting prey food via DMIIS, predators can also affect prey food by changing prey behaviour (McIntosh & Townsend, 1996). Ducks had a weak predatory effect on egg clusters in the indoor experiment; however, they maintained the number of *P. canaliculata* egg clusters at a low level in the field plots. Previous studies have shown that the risk of predation can increase during prey copulation (Ronkainen & Ylönen, 1994; Sih, Krupa, & Travers, 1990; Ward, 1986). Predation risk around the time of copulation can increase for many reasons. For example, searching for a partner can increase the chance of encountering a predator (Magnhagen, 1991), and copulating pairs may be more conspicuous than non-copulating individuals and may have a reduced ability to escape (Ward, 1986). In the rice-duck system, snails that are copulating or depositing egg clusters may be more susceptible to capture by ducks because of limited mobility and increased conspicuousness. It is also possible that the mere presence of ducks may induce an alarm response (as discussed in the previous paragraph) that reduces *P. canaliculata* mating frequency and mating duration in paddy fields.For many organisms, selecting a suitable oviposition habitat is crucial for larval survival (Jaenike, 1978; El Keroumi et al., 2010; Lloyd & Martin, 2004; Martin, 1998), and ducks evidently affected the locations selected by *P. canaliculata* for oviposition. In paddy fields, females usually oviposit on a stem of the rice plants and weeds. These sites represent ideal locations for establishment of *P. canaliculata* hatchlings, as they are not directly exposed to the sun, high temperature and rain, and with shallow water below to ensure their young will survive after hatching. In plots with ducks, however, a relatively small percentage of clusters was present on weeds and rice plants and a relatively high percentage were present fence columns, nets and plastic barriers; the latter locations are not ideal for larval establishment. If we assume that the distribution of egg clusters reflects the distribution of oviposition sites (we recognise that the distribution of egg clusters also reflects removal clusters by predation), the results indicate that duck predation reduces *P. canaliculata* numbers by causing snails to select sub-optimum oviposition sites.

Previous studies in paddy fields showed that *P. canaliculata* bury themselves in response to the injured conspecifics or presence of predators (Carlsson, Kestrup, Mårtensson, & Nyström, 2004b; Ichinose, Yusa, & Yoshida, 2003). In the field experiment of this study, we observed that snails in plots with ducks often seemed to exhibit an alarm response (they withdrew into the shell or moved into the soil) even when not being attacked by ducks. The importance of trait-mediated indirect interactions (TMIIs), in which changes in the traits of the prey (behaviour, morphology and life history) in the presence of a predator mediate the interaction between other organisms, is increasingly being recognised (Preisser, Bolnick, & Benard, 2005; Schmitz et al., 2004; Turner, Bernot, & Boes, 2000; Yoshie & Yusa, 2011). Studies with various animals have proven that predation risk affects prey foraging and mating behaviours (Forsgren, 1992; Magnhagen, 1991; Rowe, 1994; Sih, 1988; Sih et al., 1990), and if a behaviour increases predation risk, individuals are expected to behave in a way to minimise or avoid these risks. In many cases, foraging decreases if predators are present (Chase, Wilson, & Richards, 2001; Peacor & Werner, 2000; Sih & Krupa, 1992). Therefore, this study suggests that ducks reduce the damage to rice not only by consuming *P. canaliculata* but also by changing their foraging and mating behaviours. However, the alarm response in *P. canaliculata* requires more research in nature condition, as *P. canaliculata* may bury themselves in the substrate in response to other factors, including shallow water (Yusa, Wada, & Takahashi, 2006) or extreme temperatures (Wada & Yoshida, 2000).

Molluscivorous fish such as the common carp (*Cyprinus carpio*) and cat fish (*Clarias gariepinus*) prey on and effectively control small snails in rice fields (Halwart, Viray, & Kaule, 1998; Su Sin, 2006). The earlier reports indicate that ducks can also control snail pests in rice fields, and the utilisation of duck is more practical than the fish culture which requires keeping deep water in fields. The use of ducks has a long history among rice farmers in Asia and has been a focus of research concerning *P. canaliculata* management (Cowie, 2002; Carlsson et al., 2004b; Teo, 2001). The results of the current study indicate that, although rice-duck mutualism did not eliminate the *P. canaliculata*, and even if the snails can be temporarily eradicated in the plot, they would re-infest the field through irrigation or other sources of water. The ducks, however, did maintain snail numbers at low levels and provided more stable control than two molluscicides.

In addition to reducing the snail damage, rice-duck mutualism increased the rice yield, confirming inferences from previous surveys (Choi et al., 1996; Esmaili, Mobaser, Heydari Sharifabad, Akbarpour Roushan, & Eftekhari, 2007; Hossain, Sugimoto, Ahmed, & Islam, 2005; Kang et al., 1995). Earlier research reported that rice-duck mutualism increased rice yield by reducing insect pests (Men, Ogle, & Lindberg, 2002; Zhang, Zhao, Chen, & Luo, 2009b), diseases (Huang et al., 2005; Yang et al., 2004), and weeds (Hossain, Ahmed, Islam, Mahabub, & Bangladesh, 2000; Li, Wei, Zuo, Wei, & Qiang, 2012; Zhang, Xu, Chen, & Quan, 2009a), and this mode is being combined with organic rice production in China (Li et al., 2012; Zhang et al. 2009b). In addition, duck manure improves the nutrient content and physical structure of the paddy soil (Zhang, 2012). Ducks also benefit from the interaction in that the rice field provides both food and shelter. The farmer benefits because in addition to achieving increased rice yield without using chemicals, he or she can eventually harvest the ducks in the form of eggs and meat (Zhang et al., 2002).

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