Türke, M., **Schmidt, A.**, **Schädler, M.**, Hotes, S., Weisser, W.W. (2018):
Are invasive apple snails important neglected decomposers of rice straw in paddy fields?
Biol. Agric. Hortic. **38** (4), 245 – 257

http://dx.doi.org/10.1080/01448765.2018.1450161

Are invasive apple snails important neglected decomposers of rice straw in paddy fields?

Manfred Türke[a], Anja Schmidt[b], Martin Schädler[b], Stefan Hotes[c] and Wolfgang W. Weisser[a]

[a] Terrestrial Ecology Research Group, Department Of Ecology And Ecosystem Management, Center For Food And Life Sciences Weihenstephan, Technical University Of Munich, Freising-Weihenstephan, Germany;
[b] Department of Community Ecology, Helmholtz-Centre For Environmental Research – UFZ, Halle, Germany;
[c] Department of Ecology, Faculty of Biology, Philipps-Universität, Marburg, Germany

Abstract

Few studies have tested for the potential of invasive species, particularly pests, to contribute to ecosystem services. The apple snail *Pomacea canaliculata* is invasive in many countries around the globe. They are best known as pests of rice and great efforts are made by farmers to control the snails. However, apple snails might also act as decomposers of organic litter, and it was hypothesized that they might enhance the decomposition of rice straw. To test the ability of apple snails to feed on rice straw, choice and no choice feeding experiments were conducted offering rice straw to *P. canaliculata* for 2 weeks. As mature rice plants are not consumed by apple snails, the straw was incubated in water for 5 days and in water with effective microorganisms for 25, 50 and 75 days prior to the feeding experiments. Rice straw of all treatments was consumed by snails without preference (11.6 % more weight loss on average compared to controls in which snails had no access). In another experiment, snails were feed on rice straw for 6 weeks; body mass of snails was measured weekly. In treatments where access to straw was not restricted, all snails survived and body mass remained constant; if access was restricted, snails lost body mass slightly. It was concluded that rice straw served as an alternative food for apple snails. Invasive apple snails spared in times when rice plants are not vulnerable could accelerate nutrient release from rice straw providing a benefit for farmers.

Key words: *Pomacea canaliculate;* golden apple snail; decomposer invertebrates; *Oryza sativa;* effective microorganisms

Introduction

Most studies on the ecology of invasive species are intended to test potential negative impacts of the exotic species on native ecosystems, species or on ecosystem functions and services (Nentwig 2007). Invasive species, particularly pests of horticultural or agricultural plants, however, could also contribute to ecosystem services, if the right management actions are performed. To evaluate the potential of an invasive pest to contribute to the ecosystem function of decomposition associated with the ecosystem service of nutrient cycling in rice fields, we tested whether widespread invasive apple snails feed on rice straw in the laboratory.

Irrigated rice cultivation supplies the staple food for over one third of the world's population, and rice production is one of the most important and successful agricultural activities in Southeast Asia (Kurihara 1989). Farmers apply large amounts of mineral or organic fertilisers to increase their yields. Additionally, crop residues are often applied to the fields either untreated or as ash of burned straw (Hanafi et al. 2012; Samra et al. 2003; Schmidt et al. 2015a; Yadvinder-Singh et al. 2005). The rice straw plowed into the paddy soil is degraded by the decomposer community and nutrients are made available for the next cropping season (Fairhurst et al. 2007). Invertebrate decomposers play a key role in this process (Lekha et al. 1989; Schmidt et al. 2015a, b; Wolters 1991). They break down bigger particles of dead organic material and make them available for micro-decomposers which release nutrients bound in plant tissues into the soil. Invertebrates are particularly important for rice straw decomposition under anaerobic conditions in irrigated rice fields, compensating for reduced microbial decay (Schmidt et al. 2015a b; Schmidt et al. 2016).

Decomposition is essential for enhancing or maintaining soil productivity and therefore crucial for plant growth (Tian et al. 1993). Many studies have been conducted analysing the impact of bacteria (Asari et al. 2007; Weber et al. 2001) and fungi (Abdulla & El-Shatoury 2007) on the decomposition of rice straw, but much less is known about the influence of invertebrates processing the material for microbial decomposition. While experiments proved that earthworms, mites, springtails and millipedes do consume rice straw (Lekha et al. 1989; Tian et al. 1995), no information was found on gastropods, another prominent taxon of macro-decomposers, which are also very common and abundant in rice fields (Roger 1996). In terrestrial ecosystems gastropods break down coarse plant material to smaller fragments making them accessible to digestion by microorganisms (Dallinger et al. 2001). Snails also contribute to the decomposition of leaf litter (e.g. Kuehn & Suberkropp 1998; Tavares et al. 2011) and of grass litter (e.g. Schaller 2013) in aquatic environments. Addition of rice straw to the flood water of rice fields led to increases in snail populations, indicating that straw might serve as a food resource for snails (Roger 1996).

Since the 1980s, the polyphagous apple snails *Pomacea canaliculata* (Lamarck 1822) and *P. maculata* Perry 1810, commonly referred to as golden apple snails, had been introduced to SE-Asian rice fields, where they can build up large populations (Cowie 2002; Horgan et al. 2014; Schneiker et al. 2016). Rice seedlings are particularly vulnerable to the snails during the first weeks of development until about two weeks after transplanting or four weeks after direct-seeding (Litsinger & Estano 1993). As rice plants mature they become unpalatable for the snails, which then mostly consume weeds in rice fields and, thus, can support weed control, reducing the efforts and costs of farmers for weed management (Joshi et al. 2006; Okuma et al. 1994). It was hypothesized that the invasive snails might further switch to a detritivorous feeding mode. However, it seems that nothing is known about the impact of invasive apple snails on decomposition processes of rice straw in paddies, although the role of *P. canaliculata* (López van Oosterom et al. 2013) and of unidentified *Pomacea* species (Tanaka et al. 2006) as detritivores has been highlighted in other ecosystems. Invasive invertebrates can alter decomposition rates by direct consumption, displacement of litter from the soil surface into the soil matrix, facilitation of microbial decomposition or by changing the native decomposer community directly or indirectly (Ehrenfeld 2010). Evans (2012) found that invasive New Zealand mudsnails (*Potamopyrgus antipodarum* (Gray, 1843)) played a more significant role than native invertebrates in the breakdown and decomposition of riparian leaf litter in the invaded areas. This could be the case for *Pomacea* spp. in rice landscapes as well. As demonstrated for macrophyte consumption in natural wetlands in Thailand, apple snails strongly increase the concentrations of the plant growth-limiting nutrients phosphorus and nitrogen in the water (Carlsson et al. 2004), highlighting their potential to support fertilisation of rice fields.

In the studies by Schmidt et al. (2015a, b, 2016) juvenile invasive apple snails were observed regularly in litter bags containing rice straw, motivating the present study. It was hypothesized that the large, voracious invasive apple snail *P. canaliculata* might consume rice straw and consequently contribute to straw decomposition in rice fields. Three experiments were conducted to answer the questions (1) whether *P. canaliculata* contributes to the decomposition of rice straw, (2) whether the feeding activity interacts with the activity of litter-degrading microorganisms, and (3) whether rice straw provides a suitable food source that allows survival and/or growth of the snails.

Materials and methods

Snails

The species in this study was *Pomacea canaliculata*. All experiments were conducted in the laboratory at the Technical University of Munich, Freising, Germany between 31 October 2012 and 26 March 2013. Populations of snails were established in the laboratory from eggs of various origins, kept separately to prevent cross-breeding. Snails of different origin had to be used in the experiments as the number of snails from any particular region was limited. Eggs (approximately three egg clusters each) were collected in rice fields in the Philippines at (1) the International Rice Research Institute (IRRI; Los Baños/ Laguna; 14°10′N, 121°15′E; collected 20 January 2012), (2) Batad (Banaue/ Ifugao; 16°56′N, 121°08′E; collected 20 March 2012) and (3) Bangaan (Banaue/ Ifugao; 16°54′N, 121°07′E; collected 21 March 2012). These rice fields were located at study sites of the LEGATO-project on land-use intensity and ecological engineering in irrigated rice (Klotzbücher et al. 2015; Settele et al. 2015; http://www.legato-project.net). In addition, the second generation of a lab population of *P. canaliculata* was used. Individuals of the parental generation were bought from a trader (Thorsten Krüger, Schanzenstr. 40, 90478 Nuremberg, Germany; http://www.krueger-aquaristik.de/). Snails of all populations were bred for several generations in the lab and were identified as *P. canaliculata* rather than the closely related and also invasive species *P. maculata* by taxonomic specialists. Male snails from the Philippine origin were identified based on the morphology of internal organs (Hayes et al. 2012) and two female snails from the aquarium trade population were identified based on mitochondrial COI sequences (Hayes et al. 2012) (both matched accession number EU528593 in GenBank®, www.ncbi.nlm.nih.gov/genbank/). In the Philippines, only *P. canaliculata* has been introduced (Hayes et al. 2008; Horgan et al. 2014). All snails were kept in glass aquaria measuring 29×29×35 cm (L×W×H; 30 l), covered with a glass lid and fitted with a filter (50 -

400 l h^{-1}, 4 W), a heater (20 W; temperature maintained at 22 - 25 °C) and lighting (fluorescent tube, 11 W; 12 hours day^{-1}). Aquaria were provided with aquarium sand and a piece of *Sepia* cuttlebone to provide calcium carbonate for the snails and were filled with approximately 25 l of tap water. About 6 l of the water were changed weekly. Snails were fed with various foods (mostly lettuce, vegetables, shrimp food, fish food, and dried leaf litter) prior to the start of the experiments. Snails used in the experiments had a mean body mass of 2.3 g, which is approximately equivalent to a shell length of 30 mm.

Plant material

The rice straw (*Oryza sativa*, variety NSIC Rc222) used in the experiments originated from IRRI. It was obtained from rice plants harvested in the dry season of 2012 and oven-dried at 60 °C before being transported to Germany.

Pre-experimental incubation of rice straw

It was assumed that consumption of straw by snails might be influenced by the degree to which it has been affected by microorganisms. Therefore, rice straw was incubated for varying periods in water with a mixture of microorganisms (EMB-Aktiv Mikroorganismen, Multikraft Produktions- und HandelsgmbH, 4632 Pichl/Weis, Sulzbach 17, Austria; www.multikraft.com) added to pre-digest rice straw, potentially making it more palatable to the snails; e.g. hemicelluloses and cellulose are decomposed by microorganisms within the first nine weeks (Chen et al. 2010). Four treatments were established, each in a separate aquarium in which straw was incubated with microorganisms at 29 - 30 °C for (1) 75 days, (2) 50 days, (3) 25 days, and without microorganisms for (4) 5 days. This fourth treatment was intended to test whether snails feed on freshly harvested rice straw, not pre-digested by microorganisms. Rice straw was arranged in bundles of 3.04 ± 0.003 g (mean ± SE; N = 50) and tied with plastic cable binders before incubation. Each bundle was placed in a polypropylene bag (35×20 cm L×W) with 1 mm holes. Right after transferring rice straw to an aquarium, 10 ml of microorganisms were added to treatments 1 to 3. EMB-Aktiv consists of 5 % molasses, 90 % water and 5 % eMB concentrate, which is a mixture of photosynthetic and lactic acid bacteria (*Lactobacillus plantarum, L. fermentum, L. casei*), yeasts (*Saccharomyces cervisiae*), and other microorganisms (*Athrobacter* spp., *Cellulomonas* spp.) for digesting hydrocarbons (fat and oil) and cellulose. The dilution that was used was equal to the amount recommended by the manufacturer for compost or waste water processing. Water was not changed during the incubation period. After the respective incubation periods rice straw bundles from all treatments were either used in the feeding experiments (see below) or were transferred to the drying oven at 60 °C for three days (treatment 1-3: 4 bundles each; treatment 4: 5 bundles) and weighed to the nearest 0.01 g.

Choice experiment

One bundle of rice straw from each of the four incubation treatments was transferred to an aquarium (temperature 29-30°C) and fixed to the side of the aquarium, one treatment on each side (Figure 1a). The distribution of treatments was randomized in each of the five replicates. The tops of the bags were kept open with a plastic frame (9×12.5×6.5 L×B×H) to allow access by snails. The rim of the bags was located at 28 cm above the bottom of the aquarium and water was filled to a height of 31 cm so that snails could easily enter the bags without leaving the water by climbing the walls of the aquarium or the bags.

Ten snails from the same source population (Table 1) were added to each of the five aquaria on the next day. They were allowed to feed on the rice straw for 14 days; after this period the experiment was ended and all rice straw samples were dried and weighed. In this experiment, straw was collected together with faeces from snails within bags and weighed together. In addition, snail behavior inside the bags was surveyed as resting, active/moving and active/feeding on rice straw once on each of days 0 to 3, 6 to 10, 13 and 14 (N = 11 days).

No-choice experiment

Snails were also offered rice straw bundles of each of the four incubation treatments without choice (1 replicate each). Two rice bundles of the same treatment were transferred within bags to an aquarium and fixed to two opposite glass walls. One bag was opened to allow access by snails; the other one was closed without access by snails. This experiment was intended to provide information on two aspects. First, it was intended to quantify litter mass loss due to the action of microorganisms during the two week period of the feeding experiment (closed bags), to provide information needed to calculate the litter mass loss due to the activity of snails alone in the choice and in the no-choice experiment. Second, in the choice experiment, certain treatments might completely be avoided by snails if other treatments are more attractive to them; thus, a no-choice experiment is necessary to test whether snails are able to feed on rice straw incubated for a certain time if this is the only food source available.

Ten snails (Table 1) were added to each aquarium and were allowed to feed on the rice straw for 14 days; after this period the experiment was ended and all rice straw bundles were collected. In this experiment, straw was collected together with faeces from snails within bags and weighed together.

[place Table 1 near here]

Survival experiment

This experiment was intended to monitor snail survival and weight gain with rice straw as the only food source over a longer period of time. Rice straw (10.04 ± 0.003 g mean ± SE) was incubated for five days in bags in tap water with no microorganisms added, as described above, to allow the straw to soak up water and sink. Two bags were then transferred to each aquarium (similar to the no-choice feeding experiment, but due to the longer duration of the experiment, a mini-filter was added to keep the water clean). One of these bags containing loose rice straw was closed to prevent access by snails and to serve as control and to quantify litter mass loss due to leaching. The second bag either contained loose rice straw with access by snails not restricted (open treatment; 3 replicates), or was a nylon litterbag (15×20 cm, mesh size 0.5×0.5 cm; litterbag treatment; 3 replicates) containing the rice straw. These litterbags are commonly used to assess litter decomposition rates by invertebrates in the field (e.g. Schmidt et al. 2016), and it was expected that they would restrict access by snails. Five snails from IRRI were added to each aquarium. The cumulative weight of snails (individual mass 1.7 - 3.1 g) per replicate was between 11.16 and 12.69 g. Snails were marked individually and weighed before the experiment as well as weekly until the end of the experiment after 6 weeks. After removing the snails from the aquaria, they were blotted dry and water was released from the shells by pushing back the operculum before weighing. Rice straw was taken out after six weeks, and in this case the remaining straw and faeces were separated before being dried and weighed as described above.

Data analysis

All statistical analyses were performed in R 3.1.2 (R Team 2014). For ANOVAs the function *lm* and for Student's t-tests the function *t.test* was used. For general linear mixed models (GLMM) the function *lmer* in the 'lme4' package (Bates et al. 2014) together with the 'lmerTest' package (Kuznetsova et al. 2015) was used, providing an analysis of variance table of type 3 with Satterthwaite approximation for degrees of freedom. In GLMMs it was accounted for nested designs using 'replicate', 'snail individual' and the 'date of observation' as random factors as appropriate. For Tukey's HSD post-hoc tests the function *glht* in the 'multcomp' package (Hothorn et al. 2008) was used. Count data were log-transformed. Mean ± SE are presented throughout the manuscript.

Results

Leaching and microbial decomposition

Leaching and microbial decomposition, i.e. incubation of rice straw in water with or without microorganisms and without access by snails, resulted in litter mass loss of 20.7 % after 5 days and 58.3 % after 75 days (Figure 2). After 75 days of incubation most of the fine, filamentous parts of the straw were decomposed. There were significant differences in dry weight after incubation among treatments (ANOVA; $F_{3,13} = 120.09$; $p < 0.001$). Dry weight was significantly different between all treatments as indicated by Tukey's HSD, except for the 25 day and the 50 day treatments (Figure 2). These pre-digested rice straw treatments were then offered to snails in the feeding experiments.

[place Figure 1 and Figure 2 near here]

Rice straw consumption by snails

Snails were observed feeding on rice straw (Figure 1b and c) in all treatments of all experiments, whether pre-digested by microorganisms or incubated in tap water only, during the entire period of all experiments. Straw remained in all replicates of all treatments at the end of the experiments. Defecated fragments were small (less than 5 mm length) and thin (less than 0.5 mm thickness) sticks. Dried and stuck together they had a texture like rough paper (Figure 1d).

In the no-choice feeding experiment, rice straw had lost significantly more weight after two weeks if snails had access to it (53.4 ± 9.5 %, mean ± SE) than rice straw from which snails had been excluded (43.4 ± 8.2 %), independent of the treatment, i.e. the period of time rice straw was incubated prior to the feeding experiment (paired t-test, df=3, t=4.39, p = 0.0218; Figure 3a). Snail faeces within bags were weighed together with the remaining straw in this experiment. Thus, effective litter mass loss of straw with access by snails can be assumed to be even higher. Therefore, the experiment provided a rather conservative estimate of the contribution of snails to the decomposition process.

Snails had a significant positive effect on rice straw decomposition during the six weeks of the survival experiment, in which no microorganisms had been added to the pre-treatment water (GLMM, $F_{2,5}$=41.93, p < 0.001). In open treatments with access by snails, rice straw lost significantly more weight (73.3 ± 6.2 %, mean ± SE) than straw in controls (closed bags without access to snails) (45.1 ± 1.9 %) (GLMM with Tukey HSD, z = 9.11, p < 0.001) and than straw offered to snails in litterbags (50.1 ± 1.1 %) (z = 5.37, p < 0.001). Litterbags restricted snail access to the straw and consequently reduced straw consumption by snails and there was no significant difference in mass loss between litterbag treatments and controls (z = 1.96, p = 0.117). Faeces from feeding bags were collected separately in this experiment and were considered as litter mass lost due to decomposition. In the open treatments, faeces had a dry weight of 1.37±0.20 g and accounted for 13.6 ± 2.0 % of the initial weight of the rice straw and in the litterbag treatment faeces weighed 0.53 ± 0.13 g accounting for only 5.2 ± 1.3 % of the rice straw. Significance of results of the GLMM and Tukey HSD did not change when faeces were not treated as litter mass being lost as a result of decomposition.

[place Figure 3 near here]

Snail preferences (choice experiment)

There were significant differences in litter mass loss based on the initial amount of straw (3.04 g on average) among incubation treatments at the end of the choice experiment (GLMM; $F_{3,16}$ = 46.69, p < 0.001). Dry weight was significantly different between all treatments as indicated by Tukey's HSD (p < 0.05), except for the 25 day and the 50 day treatment (Figure 3 b). To identify preferences of snails for rice straw of the different incubation treatments, the amount of straw per treatment consumed by snails (calculated as dry weight with access by snails minus dry weight without access by snails) was compared. Snails did not prefer straw from certain treatments over others, but consumed similar amounts of straw from each treatment (GLMM, $F_{3,16}$=3.16, p = 0.053; Figure 4).

On average, 44 ± 0.2 % (mean ± SE, range 32 – 52 %) of all snails were observed within feeding bags per day. There were no significant differences in the number of snails in feeding bags among treatments (GLMM, $F_{3,36}$ = 2.05, p = 0.125) or among the number of days after the start of the experiment on which observations were made ($F_{1,36}$ = 0.62, p = 0.435), but there was a significant interaction between the treatments and the days ($F_{3,36}$ = 4.83, p = 0.00632). Directly after the start of the experiment, more snails were observed in the 50 day and 75 day incubation treatments compared to the other treatments (Figure 5). Already after one day, however, fewer snails were observed in the 50 day treatment and the same was true after two days for the 75 day treatment. The 25 day treatment was attractive on the second day as well, but afterwards most snails were always observed in the 5 day treatment.

[place Figure 4 and Figure 5 near here]

Snail performance (survival experiment)

All snails survived and remained active during the six weeks of the experiment with rice straw as the only food source, except for one individual in the litterbag treatment which died after 24 days. The dead individual was replaced by a new one immediately and was excluded from the analysis. No eggs were deposited, indicating that nutrition provided by straw was probably not sufficient for egg production. The body weight of snails at the start of the experiment was compared with the weekly measurements. In the litterbag treatment, body weight of the snails had slightly but significantly decreased after 29 days and did not increase again until the end of the experiment after 42 days (paired t-tests, df = 13, $p < 0.05$ in the last three weeks, Figure 6a). In the open treatment, there was no difference in body weight of the snails at the start of the experiment and at any of the weekly measurements (paired t-test, df = 14, $p > 0.05$; Figure 6b), except for the measurement after 15 days when body mass had increased by 2.5 ± 1.1 % (mean ± SE; N = 15) (t = 2.53, p =0.0240). When both treatments were analyzed together, the body weight of snails decreased significantly with the duration of the experiment (GLMM; $F_{1,4}$ =23.02, p = 0.00862) with no differences between treatments ($F_{1,63}$ = 2.63, p = 0.109) and no interaction effect of duration and treatment ($F_{1,139}$ = 0.0031, p = 0.956).

[place Figure 6 near here]

Discussion

The invasive agricultural pest snail *Pomacea canaliculata* has been described as a macrophytophagous species in a number of studies, feeding primarily on vegetal material of various plant species (e.g. Estebenet 1995; Lach et al. 2000; Qiu & Kwong 2009). In contrast to most other studies, it was found to mainly feed on detritus in a stream ecosystem in Argentina, where vegetal matter and diatoms were consumed less frequently by the snail (López van Oosterom et al. 2013). Whether they can use senescent plants or leaf litter, however, has rarely been studied experimentally (but see Qiu et al. 2011). The present experiments tested whether *P. canaliculata* will feed on rice straw, which is often incorporated into paddies for fertilisation (Yadvinder-Singh et al. 2005), and could thus act as an important decomposer in rice fields. *Pomacea canaliculata* significantly increased litter mass loss compared to control treatments where snails had no access. It can be concluded that invasive apple snails might be important, as yet neglected, decomposers of rice straw and thus contribute to the nutrient turnover in paddies.

Rice straw consumption by snails

By calculating the difference in litter mass loss with and without snails, snails increased litter mass loss on average by 10 % in the no-choice experiment, by 12 % in the choice experiment (both after two weeks of feeding), and by 28 % in open treatments in the survival experiment (after six weeks). This effect of *P. canaliculata* on rice straw decomposition was at least as large as that of other macro-decomposers tested in the laboratory. Tian et al. (1995) found that earthworms increased the loss in rice straw mass after four weeks by 5.3 %, millipedes by 27.8 % and both together by 36.4 % compared to controls. While synergistic effects with other species were not tested in this study, it is likely that invasive apple snails will also show synergistic effects with other groups of decomposers.

It was expected that the snails would avoid freshly harvested rice straw from mature plants as mature plants are unpalatable to them, probably because silicon has hardened the culms (Litsinger & Estano 1993). This expectation implies that feeding inhibitors are not lost due to leaching after exposure of straw to water. However, Schaller (2013) showed that silicon content in grass litter had no impact on decomposition rates caused by aquatic invertebrates. Silicon in litter is partly leached and is also degraded by microorganisms (Schaller & Struyf 2013; Schaller et al. 2014). However, it was not known whether this applies also to other feeding inhibitors which might be present in freshly harvested rice straw and which might take longer to be degraded by microorganisms (Chen et al. 2010). Therefore, rice straw was incubated for varying periods of up to 75 days in water with microorganisms to pre-digest rice straw. The snails fed on straw independently of incubation time and of the presence/absence of microorganisms. On the other hand, a shift in the attractiveness of straw to snails was found in the choice experiment: straw incubated with microorganisms for a longer time attracted more snails at the beginning of the experiment than straw incubated for a shorter time or straw incubated without microorganisms, which, however, was most attractive a few days after the onset of the experiment. This observed shift in the attractiveness of straw might be related to the preference of snails for fine, filamentous parts of straw rather than thick holms and as soon as these parts are consumed they will move on to the next favored treatment and feed on the fine parts there. As soon as all the fine parts are consumed the straw might become less attractive to or unpalatable for the snails. However, in the 50 day and 75 day pre-treatments most of these fine parts had already been digested by microorganisms prior to the feeding experiments.

Performance of snails feeding on rice straw

All snails except one survived the survival experiment and remained active over a period of six weeks with rice straw as the only food source. However, after six weeks snails did not gain much weight or deposit eggs, but snails with restricted access to rice straw lost more weight. A positive effect of leaf litter on survival of snails has been reported before. Qiu et al. (2011) kept *P. canaliculata* on diets of three macrophytes with either fresh or decaying leaves and measured shell growth and survival for one month. While juveniles of less than 2 cm shell length showed a significant increase in shell size on most of the food types offered, similar to the present results, they found no or only marginal shell increment for snails larger than 2 cm (approximately the same size as most snails in the present experiment). Survival, however, was lower in the experiments by Qiu et al. (2011) ranging from 40 to 90 %, whereas no snails died within the six weeks of the present experiment in the open treatment. Survival of apple snails without food over a period of six weeks is very low. Lach et al. (2000) raised *P. canaliculata* on different macrophytes and also without food. Only about 30 % of the unfed individuals survived until week six (ranging from 0 % to about 70 % depending on the replicate) and the authors assumed that the snails might have had access to some food from surface deposits such as algae. Survival and also growth were generally higher when fed on diets of single plant species. However, when fed with water hyacinth, *Eichhornia crassipes*, snails also showed high mortality rates of almost 70 % in 6 weeks and increased in size only slightly more than unfed individuals. It has to be emphasized that Lach et al. (2000) used hatchlings, which reached a size similar to snails in the present study and with low mortality rates during the course of their experiment only if fed with water lettuce or green-leaf lettuce.

Thus, rice straw can be considered as food that at least allows survival of snails for a longer period of time (at least six weeks).

Application

Pomacea species can contribute to the ecosystem service of weed control in rice fields (Joshi et al. 2006; Okuma et al. 1994). The present results suggested that there is an additional ecosystem service, namely breaking down rice straw in the decomposition process, which could result in an increased or faster release of nutrients. On the other hand, rice plant residue management by farmers will have a direct effect on the performance of the invasive apple snails. Straw incorporated into the soil can serve as a food source for the snails especially in times of food shortage. This is likely to reduce mortality during or after fallow periods and before new rice is planted, particularly in regions where rice fields are permanently flooded, e.g. in some mountainous regions of the Philippines (Klotzbücher et al. 2015), which can result in higher densities of the pest snails at the beginning of the next cropping season when newly transplanted or direct seeded rice plants are especially vulnerable to snail herbivory. This might also be the case in highly productive regions such as the rice production area in the Mekong Delta where dry, fallow periods are exceptionally short (Klotzbücher et al. 2015). Alternatively, if rice straw is burned and ash is applied on paddies, nutrients will be lost and the atmosphere is polluted (Hanafi et al. 2012). Rice straw ash has, however, a lethal effect on *P. canaliculata* (Cuevas et al. 1993). Thus, if farmers suffer from high snail damage, they might prefer to burn rice residues and apply ash on the field instead of plowing the straw into the soil. On the other hand, supporting the snails in times when rice is not growing or not vulnerable, farmers could benefit from a higher nutrient turnover in their fields if they use the method of incorporating the straw. This might be of particular importance in organic rice production, where the application of synthetic fertilisers is limited and nutrient cycling is promoted by the natural features of the crop field. Similarly, the contribution of invasive apple snails to weed control is most important in organic rice fields where herbicide application is avoided (Joshi et al. 2006). In rice production without molluscicide application, invasive apple snails can built up high populations and cause severe economic damage (Schneiker et al. 2016). However, it can be expected that the contribution of snails to nutrient cycling is also high. Finally, it was found that coarse-meshed litterbags (0.5×0.5 cm) commonly used in studies trying to quantify litter decomposition by invertebrates in the field (e.g. Schmidt et al. 2015a) restrict access to litter and will underestimate decomposition by apple snails and probably also other snails. This should be considered in future experiments.

Acknowledgements

We thank Antonio Salamatin and Deomedes Dizon at IRRI for collecting rice straw for the experiments. We are grateful to Heike Reise and Kenneth Hayes for species identification of snails, with additional contributions by Bettina Schlitt, Alfred Lochner, and Rebekka Sontowski. The work was funded by the German Federal Ministry of Education and Research (BMBF funding measure "Sustainable land management") within the LEGATO-project (FKZ 01LL09 17A; 01LL09 17O; 01LL09 17L).

References

Abdulla HM, El-Shatoury SA. 2007. Actinomycetes in rice straw decomposition. Waste Manage. 27:850-853.

Asari N, Ishihara R, Nakajima Y, Kimura M, Asakawa S. 2007. Succession and phylogenetic composition of eubacterial communities in rice straw during decomposition on the surface of paddy field soil. Soil Sci Plant Nutr. 53:56-65.

Bates D, Maechler M, Bolker B, Walker S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. http://CRAN.R-project.org/package=lme4

Carlsson NOL, Brönmark C, Hansson LA. 2004. Invading herbivory: The golden apple snail alters ecosystem functioning in Asian wetlands. Ecology. 85:1575-1580.

Chen H-L, Zhou J-M, Xiao B-H. 2010. Characterization of dissolved organic matter derived from rice straw at different stages of decay. J Soil Sediment. 10:915-922.

Cowie RH. 2002. Apple snails (Ampullariidae) as agricultural pests: their biology, impacts and management. In: Barker GM, editor. Molluscs as crop pests. Wallingford: CAB International; p. 145-193.

Cuevas SC, Banatin ARR, Pua MNG. 1993. Lethal effects of rice straw ash on golden snails. Bato Balani Junior. 13:16-18.

Dallinger R, Berger B, Triebskorn-Köhler R, Köhler H. 2001. Soil biology and ecotoxicology. In: Barker GM, editor. The biology of terrestrial molluscs. Wallingford: CAB International; p. 489–525.

Ehrenfeld JG. 2010. Ecosystem consequences of biological invasions. Annu Rev Ecol Evol S. 41:59-80.

Estebenet AL. 1995. Food and feeding in *Pomacea canaliculata* (Gastropoda, Ampullariidae). Veliger. 38:277-283.

Evans MA. 2012. Impacts of the invasive New Zealand mudsnail (*Potamopyrgus antipodarum*) as leaf litter decomposers [dissertation]. Davis: University of California, Davis.

Fairhurst T, Witt C, Buresh R, Dobermann A. 2007. Rice: A practical guide to nutrient management. Singapore: International Rice Research Institute, International Plant Nutrition Institute, and International Potash Institute.

Hanafi EM, El Khadrawy HH, Ahmed WM, Zabaal MM. 2012. Some observations on rice straw with emphasis on updates of its management. World Appl Sci J. 16:354-361.

Hayes KA, Joshi RC, Thiengo SC, Cowie RH. 2008. Out of South America: multiple origins of non-native apple snails in Asia. Divers Distrib. 14: 701-712

Hayes KA, Cowie RH, Thiengo SC, Strong EE. 2012. Comparing apples with apples: clarifying the identities of two highly invasive Neotropical Ampullariidae (Caenogastropoda). Zool J Linn Soc. 166: 723-753.

Horgan FG, Stuart AM, Kudavidanage EP. 2014. Impact of invasive apple snails on the functioning and services of natural and managed wetlands. Acta Oecol. 54:90-100.

Hothorn T, Bretz F, Westfall P. 2008. Simultaneous inference in general parametric models. Biometrical J. 50:346-363.

Joshi RC, Martin EC, Wada T, Sebastian LS. 2006. Role of golden apple snails in organic rice cultivation and weed management. In: Joshi RC and Sebastian LS, editors. Global advances in ecology and management of golden apple snails. Munoz: Philippine Rice Research Institute; p. 483-488.

Klotzbücher T, Marxen A, Vetterlein D, Schneiker J, Türke M, Nguyen VS, Nguyen MH, Chien HV, Marquez L, Villareal S, Bustamante JV, Jahn R. 2015. Plant-available silicon in paddy soils as a key factor for sustainable rice production in Southeast Asia. Basic Appl Ecol. 16: 665–673.

Kuehn KA, Suberkropp K. 1998. Decomposition of standing litter of the freshwater emergent macrophyte *Juncus effusus*. Freshwater Biol. 40:717-727.

Kurihara Y. 1989. Ecology of some ricefields in Japan as exemplified by some benthic fauna, with notes on management. Int Revue ges Hydrobiol. 74:507-548.

Kuznetsova A, Brockhoff PB, Christensen RHB. 2015. lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-25. http: //cran.r-project.org/web/packages/lmerTest/index.html

Lach L, Britton DK, Rundell RJ, Cowie RH. 2000. Food preference and reproductive plasticity in an invasive freshwater snail. Biol Invasions. 2:279–288.

Lekha A, Chopra G, Gupta SR. 1989. Role of soil fauna in decomposition of rice and sorghum straw. P Indian AS-Anim Sci. 98:275-284.

Litsinger JA, Estano DB. 1993. Management of the golden apple snail *Pomacea canaliculata* (Lamarck) in rice. Crop Prot. 12:363-370.

López van Oosterom MV, Ocón CS, Brancolini F, Maroñas ME, Sendra ED, Rodrigues Capitulo A. 2013. Trophic relationships between macroinvertebrates and fish in a pampean lowland stream (Argentina). Iheringia Sér Zool. 103:57-65.

Nentwig W. 2007. Biological invasions. Berlin: Springer.

Okuma M, Tanaka K, Sudo S. 1994. Weed control method using apple snail (*Pomacea canaliculata*) in paddy fields. Weed Res. 39:114-119.

Qiu J-W, Chan MT, Kwong KL, Sun J. 2011. Consumption, survival and growth in the invasive freshwater snail *Pomacea canaliculata*: does food freshness matter? J of Mollus Stud. 77:189-195.

Qiu J-W, Kwong K-L. 2009. Effects of macrophytes on feeding and life-history traits of the invasive apple snail *Pomacea canaliculata*. Freshwater Biol. 54:1720-1730.

Roger PA. 1996. Biology and management of the floodwater ecosystem in rice fields. Los Baños: International Rice Research Institute

R Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. URL http://www.R-project.org/

Samra JS, Bijay-Singh, Kumar K. 2003. Managing crop residues in the rice-wheat system of the Indo-Gangetic plain. In: Ladha JK, editor. Improving the productivity and sustainability of rice-wheat systems: issues and impacts. Madison, Wisconsin: ASA, CSSA, and SSSA.

Schaller J. 2013. Invertebrate grazers are a crucial factor for grass litter mass loss and nutrient mobilization during aquatic decomposition. Fundam Appl Limnol. 183: 287-295.

Schaller J, Struyf E. 2013. Silicon controls microbial decay and nutrient release of grass litter during aquatic decomposition. Hydrobiologia. 709: 201-212.

Schaller J, Hines J, Brackhage C, Bäucker E, Gessner M. O. 2014. Silica decouples fungal growth and litter decomposition without changing responses to climate warming and N enrichment. Ecology. 95: 3181–3189.

Schmidt A, John K, Arida G, Auge H, Brandl R, Horgan FG, Hotes S, Marquez L, Radermacher N, Settele J, Wolters V, Schädler M. 2015a. Effects of residue management on decomposition in irrigated rice fields are not related to changes in the decomposer community. PloS ONE. 10(7): e0134402.

Schmidt A, Auge H, Brandl R, Heong KL, Hotes S, Settele J, Villareal S, Schädler M. 2015b. Small-scale variability in the contribution of invertebrates to litter decomposition in tropical rice fields. Basic Appl Ecol. 16: 674–680.

Schmidt A, John K, Auge H, Brandl R, Horgan FG, Settele J, Zaitsev AS, Wolters V, Schädler M. 2016. Compensatory mechanisms of litter decomposition under alternating moisture regimes in tropical rice fields. Appl Soil Ecol. 107:79-90.

Schneiker J, Weisser WW, Settele J, Nguyen VS, Bustamante JV, Marquez L, Villareal S, Arida G, Chien HV, Heong KL, Türke M. 2016. Is there hope for sustainable management of golden apple snails, a major invasive pest in irrigated rice? NJAS - Wagen J Life Sc. 79: 11-21.

Settele J, Spangenberg JH, Heong KL, Burkhard B, Bustamante JV, Cabbigat J, Chien HV, Escalada M, Grescho V, Hai LH, et al. 2015. Agricultural landscapes and ecosystem services in South-East Asia-the LEGATO-Project. Basic Appl Ecol. 16:661-664.

Tanaka MO, Ribas ACA, de Souza ALT. 2006. Macroinvertebrate succession during leaf litter breakdown in a perennial karstic river in Western Brazil. Hydrobiologia. 568:493-498.

Tavares DS, Maia RC, Rocha-Barreira CA. 2011. Contribution of *Melampus coffeus* (Gastropoda, Ellobiidae) to leaf litter decomposition in the middle estuary of the Pacoti river, Ceara, Brazil. Iheringia Sér Zool. 101:56-60.

Tian G, Brussaard L, Kang BT. 1993. Biological effects of plant residues with contrasting chemical compositions under humid tropical conditions: effects on soil fauna. Soil Biol Biochem. 25:731-737.

Tian G, Brussaard L, Kang BT. 1995. Breakdown of plant residues with contrasting chemical-compositions under humid tropical conditions - effects of earthworms and millipedes. Soil Biol Biochem. 27:277-280.

Weber S, Stubner S, Conrad R. 2001. Bacterial populations colonizing and degrading rice straw in anoxic paddy soil. Appl Environ Microb. 67:1318-1327.

Wolters V. 1991. Soil invertebrates - effects on nutrient turnover and soil structure - a review. Z Pflanzenernähr Bodenkd. 154:389-402.

Yadvinder-Singh, Bijay-Singh, Timsina J. 2005. Crop residue management for nutrient cycling and improving soil productivity in rice-based cropping systems in the tropics. Adv Agron. 85:269-407.

Table 1. Body mass distribution of snails used in the feeding experiments. Ten snails were used in each experiment. The days in the replicate column refer to the pre-incubation time of rice straw. Sum is the cumulative body mass of all snails in an aquarium.

			Body mass (g)				
Experiment	Replicate	Origin	Min	Max	Mean	SD	Sum
Choice	1	IRRI	1.2	2.8	2.1	0.5	19.2
Choice	2	IRRI	1.7	2.8	2.2	0.3	19.5
Choice	3	IRRI	0.9	2.8	2.0	0.5	18.9
Choice	4	Batad	2.2	8.7	4.6	2.5	42.8
Choice	5	Bangaan	1.7	2.9	1.9	0.4	17.6
No-choice	5 days	Trader	0.6	6.2	2.2	1.9	21.3
No-choice	25 days	Trader	0.6	8.1	2.4	2.5	23.8
No-choice	50 days	Trader	0.5	7.1	2.5	2.6	24.1
No-choice	75 days	Trader	0.4	7.9	2.7	2.5	26.2

Figure 1. (a) Setup of the choice feeding experiment, (b) *Pomacea canaliculata* feeding on rice straw, (c) rice straw and snail faeces in a feeding bag, (d) dried rice straw together with faeces after being offered in the feeding experiment.

Figure 2. Litter mass loss of rice straw (mean ± SE) caused by leaching and microbial decomposition. Rice straw (3 g) was incubated in tap water without microorganisms for 5 days (N = 5 samples) or in tap water with microorganisms added for 25, 50 and 75 days (N = 4 samples per treatment). Different letters above bars indicate significant differences between treatments (GLMM followed by Tukey's HSD, $p < 0.01$).

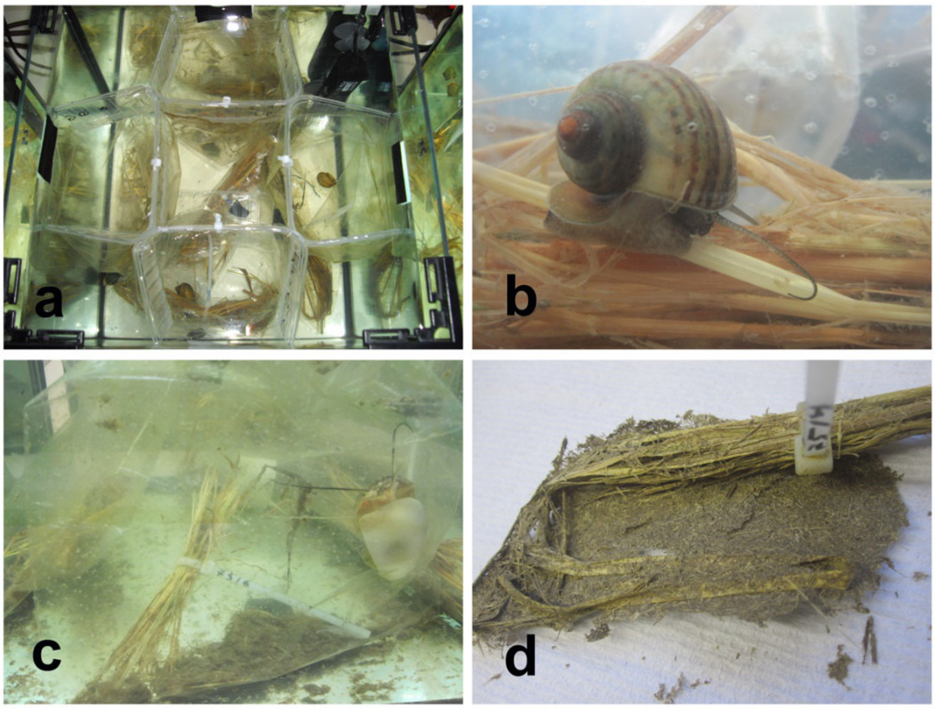
Figure 3. Litter mass loss of rice straw (mean ± SE) caused by the interaction of microbes and straw consumption by snails. Prior to feeding experiments rice straw was incubated in tap water without microorganisms for 5 days (5d) or in tap water with microorganisms added for 25 (25d), 50 (50d) and 75 days (75d). (a) No-choice feeding experiment: in each replicate there was straw of only one incubation treatment, one sample of rice straw with access to snails (= snails, N = 1 replicate treatment^{-1}) and one sample without access by snails (= control (no snails), N = 1 replicate treatment^{-1}). (b) Choice feeding experiment: in each replicate snails were allowed to feed on straw of all incubation treatments (N=5 replicates treatment^{-1}). In (a) results of a paired t-test are shown. Different letters above bars in (b) indicate significant differences between treatments (GLMM followed by Tukey's HSD, $p < 0.01$).

Figure 4. Dry weight of rice straw consumed by snails of the four different incubation treatments in the choice feeding experiment. Results are given as mean ± SE. There were no significant differences between treatments (GLMM, $p > 0.05$).

Figure 5. Number of snails observed in bags containing rice straw incubated for 5, 25, 50 and 75 days, counted on 11 days during the 14 days of the choice feeding experiment. Only snails within bags were considered. There is a shift in the preference of different incubation treatments by snails over time as also indicated by a significant interaction term of days and treatment (GLMM, $p < 0.01$).

Figure 6. Weight change of snails feeding on rice straw in the survival experiment. (a) Snails had restricted access to rice straw (litterbag treatment; N = 14 snails); (b) access to rice straw was not restricted (open treatment; N = 15 snails). The dashed line indicates the initial weight of snails. Significant differences at $p < 0.05$ between the initial and the respective weight are indicated by asterisks (paired t-tests). Results are given as mean ± SE.

Figure 1. (a) Setup of the choice feeding experiment, (b) *Pomacea canaliculata* feeding on rice straw, (c) rice straw and snail faeces in a feeding bag, (d) dried rice straw together with faeces after being offered in the feeding experiment.



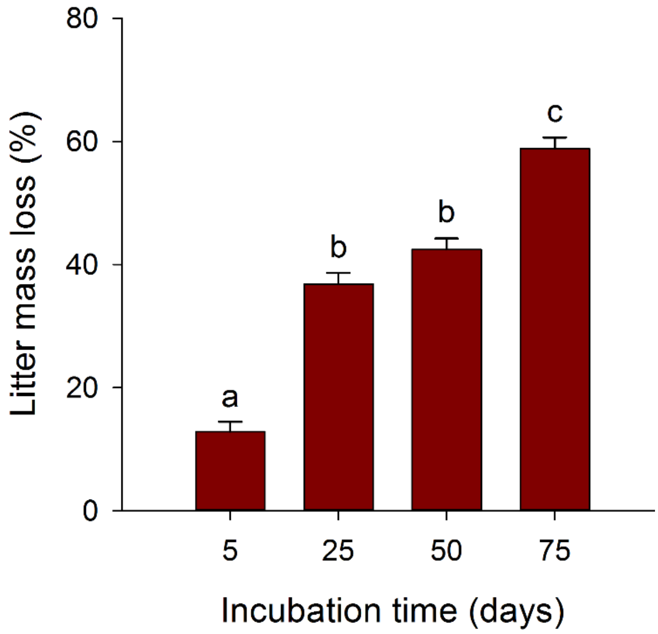


Figure 2. Litter mass loss of rice straw (mean ± SE) caused by leaching and microbial decomposition. Rice straw (3 g) was incubated in tap water without microorganisms for 5 days (N = 5 samples) or in tap water with microorganisms added for 25, 50 and 75 days (N = 4 samples per treatment). Different letters above bars indicate significant differences between treatments (GLMM followed by Tukey's HSD, $p < 0.01$).

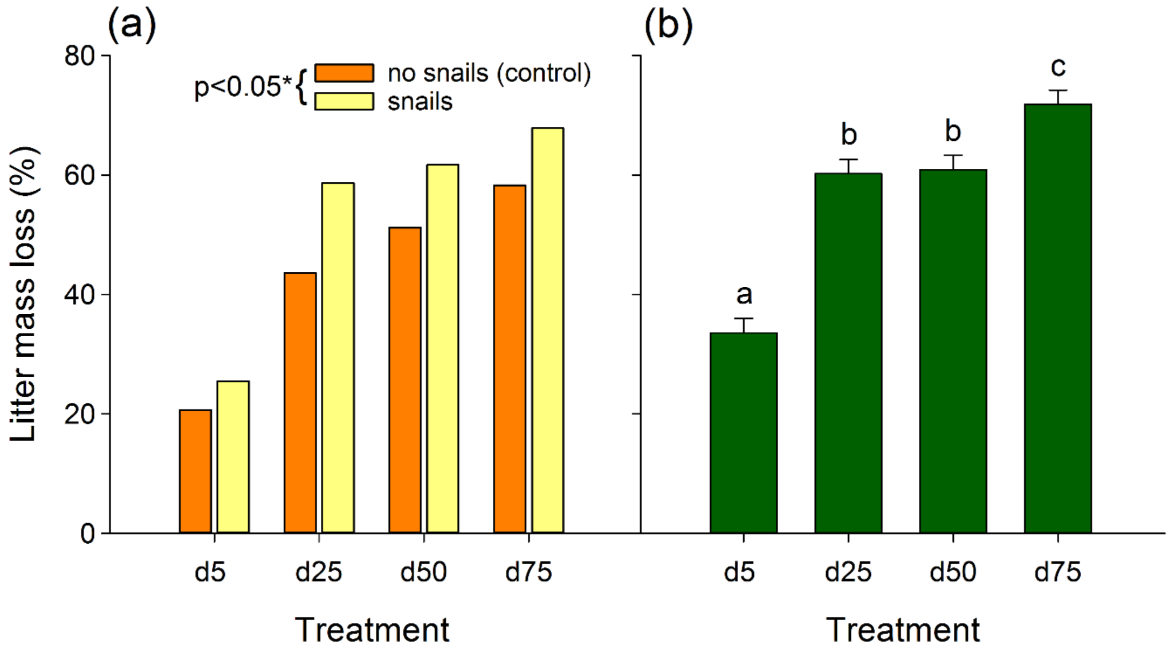


Figure 3. Litter mass loss of rice straw (mean ± SE) caused by the interaction of microbes and straw consumption by snails. Prior to feeding experiments rice straw was incubated in tap water without microorganisms for 5 days (5d) or in tap water with microorganisms added for 25 (25d), 50 (50d) and 75 days (75d). (a) No-choice feeding experiment: in each replicate there was straw of only one incubation treatment, one sample of rice straw with access to snails (= snails, N = 1 replicate treatment^{-1}) and one sample without access by snails (= control (no snails), N = 1 replicate treatment^{-1}). (b) Choice feeding experiment: in each replicate snails were allowed to feed on straw of all incubation treatments (N = 5 replicates treatment^{-1}). In (a) results of a paired t-test are shown. Different letters above bars in (b) indicate significant differences between treatments (GLMM followed by Tukey's HSD, p < 0.01).

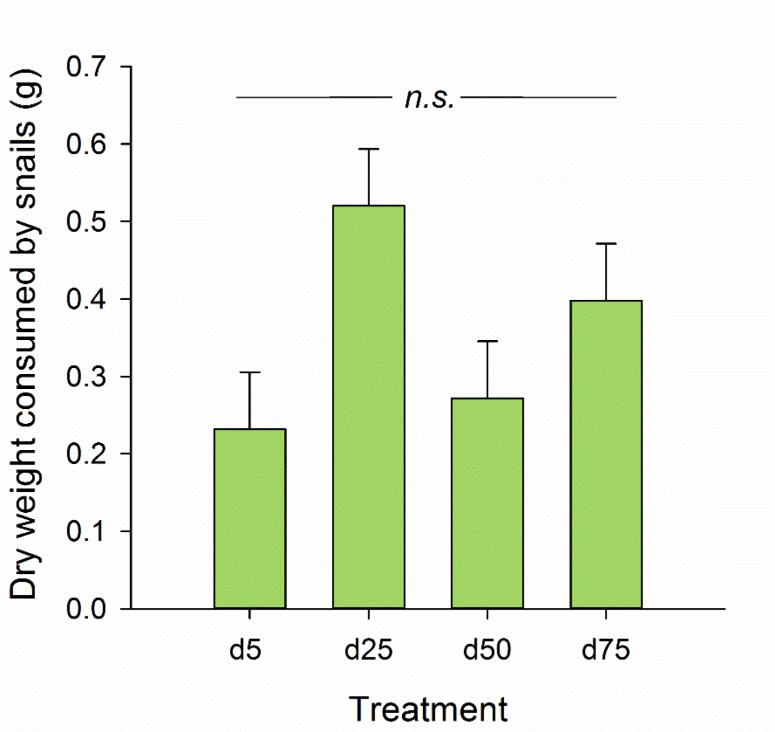


Figure 4. Dry weight of rice straw consumed by snails of the four different incubation treatments in the choice feeding experiment. Results are given as mean ± SE. There were no significant differences between treatments (GLMM, $p > 0.05$).

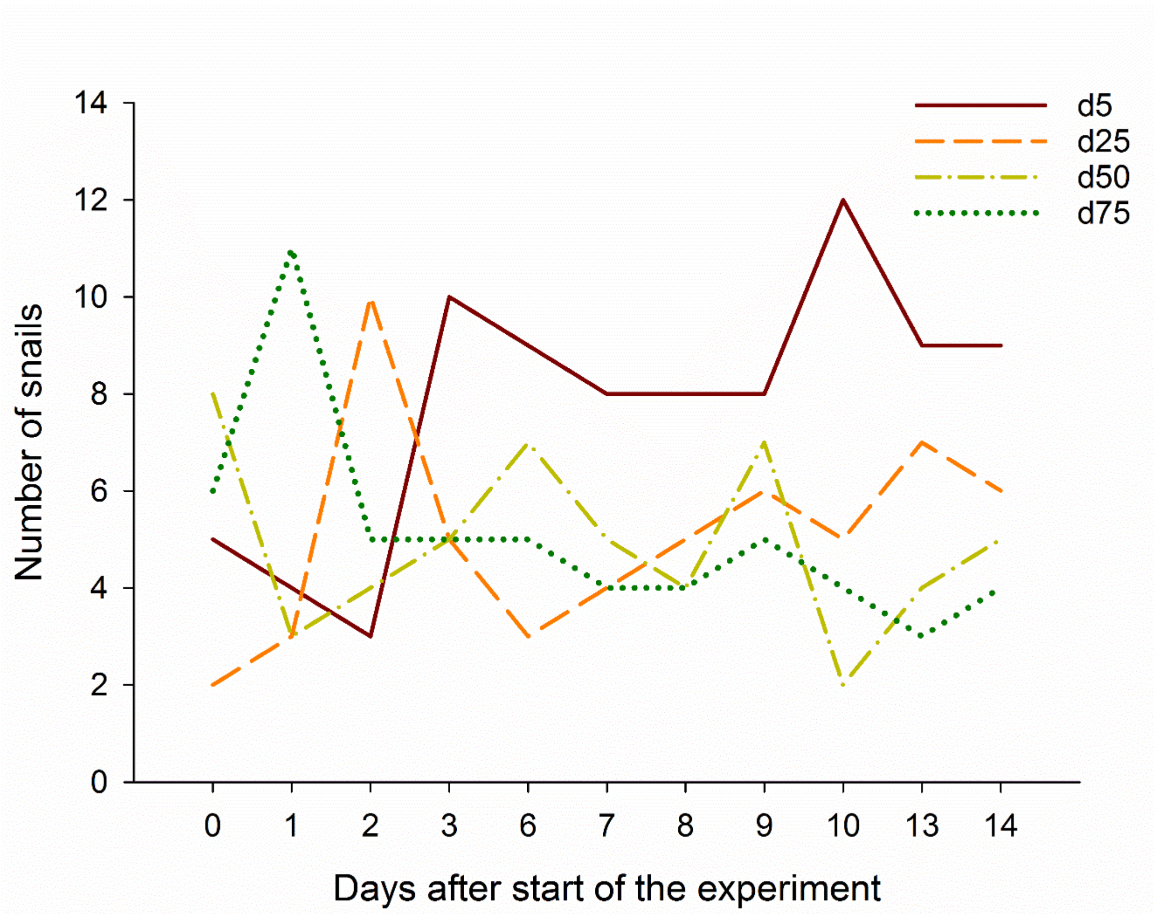


Figure 5. Number of snails observed in bags containing rice straw incubated for 5, 25, 50 and 75 days, counted on 11 days during the 14 days of the choice feeding experiment. Only snails within bags were considered. There is a shift in the preference of different incubation treatments by snails over time as also indicated by a significant interaction term of days and treatment (GLMM, $p < 0.01$).

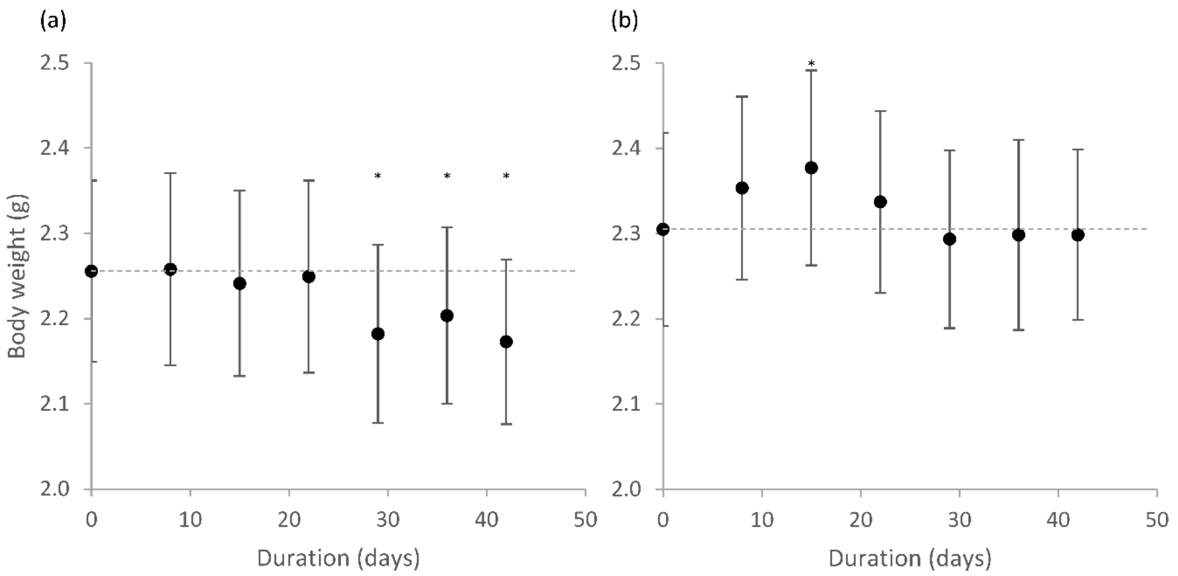


Figure 6. Weight change of snails feeding on rice straw in the survival experiment. (a) Snails had restricted access to rice straw (litterbag treatment; N = 14 snails); (b) access to rice straw was not restricted (open treatment; N = 15 snails). The dashed line indicates the initial weight of snails. Significant differences at $p < 0.05$ between the initial and the respective weight are indicated by asterisks (paired t-tests). Results are given as mean ± SE.