ความแตกต่างในการหนีผู้ล่าของหอยโข่งพันธุ์พื้นเมือง และหอยเชอรี่ในประเทศไทย

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บทคัดย่อ

การหนีผู้ล่าเป็นลักษณะพฤติกรรมที่สำคัญชนิดหนึ่งที่นำไปสู่การประสบความสำเร็จในการรุกรานของชนิดพันธุ์ต่างถิ่น ในช่วงไม่กี่ทศวรรษที่ผ่านมาหอยเชอรี่ (*Pomacea canaliculata*) ถูกนำเข้ามาในประเทศไทยโดยความตั้งใจ ซึ่งการนำเข้ามาหอยเชอรี่นำไปสู่การลดลงของความหลากหลายทางชีวภาพ โดยเฉพาะหอยโข่งพันธุ์พื้นเมือง (*Pila* spp.) ตลอดจนรบกวนการทำงานของระบบนิเวศ ดังนั้นเพื่อประเมินว่าพฤติกรรมที่แตกต่างในการหนีผู้ล่าอาจเป็นกลไกที่มีผลต่อความสำเร็จในการรุกรานของหอยเชอรี่ซึ่งเป็นชนิดพันธุ์ต่างถิ่น จึงศึกษาพฤติกรรมการหนีผู้ล่าของหอยโข่งพันธุ์พื้นเมือง (*Pila pesmei*) และหอยเชอรี่ (*Po. canaliculata*) ต่อสื่อทางเคมีจากปลาหมอไทย (*Anabas testudineus*) โดยพบว่าหอยทั้ง 2 ชนิดตอบสนองต่อสื่อทางเคมีของปลาหมอไทยโดยหนีไปอยู่ที่ด้านล่างของตู้ทดลอง อย่างไรก็ตามหอยโข่งพันธุ์พื้นเมืองไม่มีการหนีผู้ล่าในช่วงเริ่มต้นการทดลอง แต่มีการหนีผู้ล่าหลังจาก 30 นาทีถึง 60 นาทีของการทดลอง ในขณะที่หอยเชอรี่แสดงการหนีผู้ล่าตั้งแต่ 30 นาทีแรกของการทดลองจนถึง 60 นาทีของการทดลอง ผลการศึกษานี้แสดงให้เห็นว่าชนิดพันธุ์ต่างถิ่นที่รุกรานแสดงพฤติกรรมการหนีผู้ล่าดีกว่าชนิดพันธุ์พื้นเมือง จึงทำให้หอยเชอรี่กลายเป็นชนิดพันธุ์ที่ประสบความสำเร็จในการตั้งถิ่นฐานและส่งผลกระทบต่อประชากรของชนิดพันธุ์พื้นเมือง

คำสำคัญ: ผู้ล่า การหนี ชนิดพันธุ์พื้นเมือง ชนิดพันธุ์ต่างถิ่น ชนิดพันธุ์รุกราน

Differences in Predator Avoidance by Native and Non-native Invasive Apple Snails in Thailand

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Received: 1 August 2016 Accepted: 2 September 2016

Abstract

Predator avoidance is considered to be an important behavioral trait leading to successful invasions of non-native species. In the past few decades, the invasive apple snail (*Pomacea canaliculata*) was intentionally introduced into Thailand. Since its introduction, it has led a decline in biodiversity, especially native apple snails (*Pila* spp.), as well as disturbing the functioning of ecosystems. To evaluate whether behavioral differences in predator avoidance might be an underlying mechanism affecting invasion success of the non-native apple snail, we examined the predator avoidance behavior of the native apple snail (*Pila pesmei*) and the invasive apple snail (*Po. canaliculata*) to chemical cues from the climbing perch (*Anabas testudineus*). We found that both apple snails' species responded to fish chemical cues by going to the bottom. However, *Pi. pesmei* did not begin avoiding predator chemical cues until after 30 min into the treatments while *Po. canaliculata* showed avoidance to predator chemical cues within the first 30 min up to 60 min of the trial. These results suggest that the non-native invasive species exhibited better predator avoidance behavior than native species and this understanding may help explain why invasive apple snails have become successfully established species and impacted native apple snail populations.

Keywords: Predator, Avoidance, Native species, Non-native species, Invasive species

Introduction

Ecologists, conservation biologists, and natural resources managers have widely focused their attention on non-native invasive species because of their rapid spread and their impacts on biodiversity and natural ecosystems (Joshi et al., 2004). Non-native invasive species are accepted as one of the most important threats to biodiversity and ecosystems which they are introduced (Pyšek and Richardson, 2010; Roy et al., 2014) and they also cause economic damage to agriculture, forestry, fisheries and other human activities, as well as have impacts on human health (Wittenberg and Cock, 2001; Fischer et al., 2015). In addition, many of these non-native invasive species can change the functions of native species in their communities, disturb the evolutionary process and have an effect on the abundance and extinction of native organisms (Gurevitch and Padilla, 2004; Jeschke et al., 2014).

A species may become invasive in new areas and impact on native species because of characteristic behavioral traits (Chapple et al., 2012; Phillips and Suarez, 2012; Weis, 2010). Predator avoidance is considered to be important behavioral trait leading to successful invasions of non-native species (Ueshima and Yusa, 2015; Weis, 2010). That is, prey animals often alter their behavioral response in the presence of a predator to increase their chance of survival within invaded areas (Aizaki and Yusa, 2010; Nishiumi and Mori, 2015). Also, Weis (2010) suggested that non-native invasive species may be more successful in avoiding predators than native species. There are a number of different ways in which the non-native invasive species may be successful in terms of predator avoidance. For example, the successful invaders may use a broader range of information about their environment (i.e., chemical cues associated with increased predation risk) than displaced native species, which could protect them from predators (Hazlett et al., 2003). Additionally, the invasive prey species may alter their behavioral responses in the face of predation risk by reduced movement, decreased consumption, reduced activity levels, increased flee distance, and increased use of refuge or predator-free microhabitats (Costa, 2014; Nyström, 2005; Pennuto and Keppler, 2008; Polo-Cavia et al., 2008; Rehage et al., 2005), so they avoid a larger range of predators than the native species.

Many freshwater snails of the family Ampullariidae, known commonly as apple snails, are an important invasive species (Rawlings et al., 2007) that have been introduced outside of their natural ranges throughout the world (Howells et al., 2006). The apple snail (*Pomacea canaliculata*), which is native to South America, has been successful in proliferating to many areas outside its native geographic range (Martin et al., 2012). It has been intentionally introduced from South America into Asia since the 1980s primarily as a human food resource, an aquarium trade, and an agent to control aquatic weed (Cowie, 2002; Li-na et al., 2007; Naylor, 1996). Unfortunately, the practice of using *Po. canaliculata* for human food declined because developed countries have strict health regulations that mostly prohibited its importation and consumers did not like their taste thus, they were intentionally released or escaped aquaculture (Naylor, 1996; Cowie, 2002; Liang et al., 2013). Many became established in the wild and became invasive, leading to a decline in biodiversity, particularly of native apple snails (*Pila* spp.), and impacting the functioning of ecosystems (Cowie, 2002; Naylor, 1996). Its invasion success and negative impacts on native communities have led it to be considered among the 100 worst invasive alien species in the world (Lowe et al., 2004).

Interestingly, individual variation in behavioral traits may have important consequences for species invasion success (González-Bernal et al., 2014; Pennuto and Keppler, 2008). Therefore, the differences in the behavioral response of the native and invasive freshwater snail may elucidate how invasive apple snail becomes a successfully established species and affects native apple snail populations. This understanding further highlights the importance of the management schemes of these species. However, few studies have been conducted on the actual mechanisms (e.g., differential predator avoidance) leading to the displacement of the native species by the non-native invasive species. Moreover, lack of information about responses to predation differs between native and invasive freshwater snails. In the present study, we focused on the predator avoidance of native and non-native invasive species of apple snail. As the apple snails' response is considered a mechanism for escaping from predators (Ichinose et al., 2003), we investigate the predator avoidance behavior of native apple snail (*Pi. pesmei*) and invasive apple snail (*Po. canaliculata*) to chemical cues from the fish predator. We predict that the invasive apple snail will respond in predator avoidance more than the native apple snail.

Research Methodology

Test apple snails

We carried out laboratory experiments with native apple snails (*Pi. pesmei*) and invasive apple snails (*Po. canaliculata*) at Burapha University, Chonburi, Thailand. These apple snails were identified to species with morphological characteristics using the identification key of Brandt (1974), Keawjam (1986) and Hayes et al. (2012). Eighty-seven specimens of *Pi. pesmei* (shell height 26.0 – 30.0 mm) were dug up from mud in an upland rice field (WGS 84: 15°51'50.7"N 103°34'31.1"E) while one hundred and twenty-one *Po. canaliculata* (shell height 26.0 – 29.5 mm) were hand-collected in a lowland rice field from the water in Hua Chang subdistrict, Chaturaphak Phiman district, Roi Et, Thailand (15°51'48.8"N 103°34'32.5"E) in December 2015. The apple snails were brought to the laboratory and transferred into four cement ponds (79 × 79 × 30 cm) that had a mud slope for aestivating and resting. Tap water partially filled in the cement ponds, leaving some of the mud slopes above water. The two apple snails' species were maintained separately in different stock cement ponds and allowed a 5 days acclimation period before testing. These cement ponds were kept under the natural ambient photoperiod and water temperature during experimentation ranged from 26 to 32°C. Each cement pond was covered with nylon net (mesh size 2 mm) and overlaid the edges with bricks to prevent the escape of apple snails. All apple snails were fed *ad libitum* once a day with soft plants (i.e., Chinese cabbage (*Brassica pekinensis*) and lettuce (*Lactuca sativa*)) during the time that they were in the cement ponds. The cement ponds were checked every day, the water was added and plants that were not consumed were removed periodically during the study to avoid fouling.

Fish predator

We selected the fish species native to Thailand to assess predator avoidance behavior of apple snails in this study. The climbing perch (*Anabas testudineus*) is a freshwater fish that is available in almost all freshwater systems such as ponds, swamps, canals, lakes, rivers, streams and estuaries (Mustafa et al., 2010; Hossain et al., 2012). Also, it was found in shallow wetlands and rice fields with apple snails (Carlsson et al., 2004). Larvae and young fry tend to be plankton feeders while older perch are omnivorous that feed on insects, worms, crustaceans, molluscs, small fish, algae, soft plants and organic debris (Mustafa et al., 2010; Hossain et al., 2012). In previous studies, the climbing perch also reduced numbers of the apple snail, especially the neonates with shell height 2 – 10 mm (Carlsson et al., 2004). Thus, we considered climbing perch potentially effective predator of both species of apple snails.

Anabas testudineus were collected from a pond in Bang Samak subdistrict, Bang Pakong district, Chachoengsao, Thailand (WGS 84: 13°33'21.7"N, 100°56'05.7"E). All fish were allowed to acclimatize for 3 days in an aquarium (45 × 30 × 30 cm) containing 12 L dechlorinated tap water and maintained at the temperature of the non-aerated water was approximately 27°C. The aquarium was covered with opaque paper to minimize disturbing stimuli from outside. We also covered the top of an aquarium with nylon net (mesh size 2 mm) and overlaid with corrugated plastic sheet and rocks to prevent the escape of fish. The fish were fed twice daily with commercial fish pellets that do not contain the extracts from mollusks and they were not fed for 24 h prior to use in experiments.

Experimental design

Predator avoidance behavior of the two apple snail species to chemical cues released from fish was examined in separate test tank (30 × 30 × 30 cm with 3 L of dechlorinated tap water). In each observation, we selected a designated apple snail of 26–30 mm shell height randomly and tested competitors in the same size range. All observations were conducted between 17:30 and 00:30 in a room that was quiet and darkened, with no outside disturbances, simulating the natural conditions under which apple snails are most active (Heiler et al., 2008; Kwong et al., 2009; Watanabe et al., 2015).

We imposed one of two treatments on each test tank: predator treatment (fish odor) and control (no predator odor). One individual of each species was placed in an aquarium for 10 min preceding a trial. After 10 min of acclimation, a volume of 0.2 L of water from an aquarium that had been stocked with *A. testudineus* (total length 178–202 mm, $n = 3$) was gently poured on the surface water in each test tank. In controls, the same volume of tap water was added. We ran 30 trials per apple snails species tested both in predator treatment and control treatment. From previous observation (Ichinose et al., 2003) had shown that the response of apple snails is strongest between 30 min and 1 h after being exposed to the treatment, we recorded the position of each apple snail using a digital camera at the start, 30 min and 60 min later. The apple snail was at or above the water surface was classified as using the surface habitat while an individual had any contact with the bottom of the test tank was classified as using the bottom habitat (Carlsson et al., 2004). We regarded bottom habitat use as the predator avoidance response in this study. After each trial, apple snails were removed and kept separately by species in cement ponds. To avoid any confounding effects associated with olfactory cues from conspecific and/or heterospecific, the used test tanks were drained, cleaned and refilled the water for use on the following trial.

Statistical analyses

The relative difference in predator avoidance behavior between the native apple snail (*Pi. pesmei*) and the invasive apple snail (*Po. canaliculata*) was analyzed with the Fisher's exact test modified for data arranged in a 2 × 2 table. The Fisher's exact test can be used to assess the significance of a difference between the proportions of the two groups as it is categorical variables with small sample size (Routledge, 2005). We tested the proportions of the total number of apple snails that were found at the surface habitat and the bottom habitat between *Pi. pesmei* and *Po. canaliculata*. Additional analyses were conducted for each trial time (30 min and 60 min) and each predator treatments (fish odor and control) separately. The significance level of $p < 0.05$ was considered to indicate statistical differences. Statistical analyses were conducted using SPSS 21.0.

Results

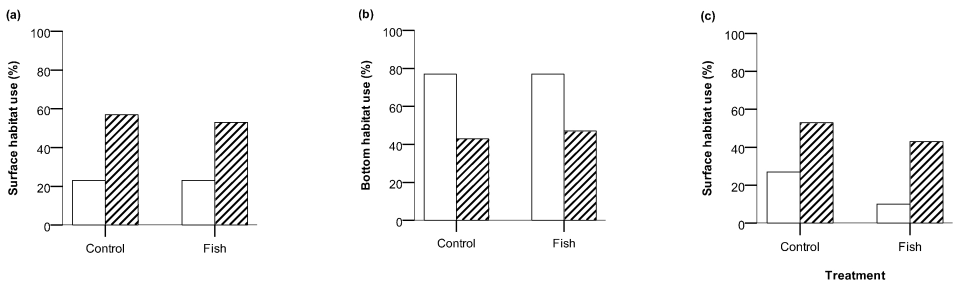
There were significant differences in the proportions of habitat use of *Pi. pesmei* and *Po. canaliculata* both in 30 min and 60 min after being exposed to control treatment or predator treatment (Fisher's exact test, 2 × 2 table, $p < 0.05$; Table 1). We observed at 30 min after the addition of treatment cues, *Pi. pesmei* occupying the bottom habitat (76.67%) higher than in the surface habitat (23.33%), however, they did not change their response to fish chemical cues in comparison to the control in any habitat use (Figure 1a, b). On the other hand, *Po. canaliculata* in the control treatment used the bottom habitat (43.33%) less than in the surface habitat (56.67%). Also, *Po. canaliculata* in the fish treatment used the bottom habitat (46.67%) less than in the surface habitat (53.33%). Nevertheless, *Po. canaliculata* increased their bottom habitat use when exposed to fish cues (1.1-fold compared to the controls; Figure 1b). At 60 min after the treatment both in the control treatment and the fish treatment, *Pi. pesmei* used the bottom habitat (73.33% and 90.00%, respectively) higher than in the surface habitat (26.67% and 10.00%, respectively). While, *Po. Canaliculata* both in the control treatment and the fish treatment used the bottom habitat (46.67% and 56.67%, respectively) less than in the surface habitat (53.33% and 43.33%, respectively). Thus, *Pi. pesmei* used the surface habitat less often than *Po. canaliculata* both in the control treatment and the fish treatment (Figure 1c) but the two apple snails species increased their use of the bottom habitat by 1.2-fold compared to the controls (Figure 1d).

Discussion

This study shows the behavioral differences in predator avoidance of non-native invasive and native apple snail species. Indeed some evidence suggests that several aquatic species exhibit predator avoidance behavior upon their detection of the predator's signature odor, i.e., a kairomone which is chemical cues released by one species (predator) and received by a second species (prey) (Ferrari et al., 2010). Likewise, the apple snails in our study detect predators through the odor of climbing perch (*A. testudineus*). Our observations corroborated the pattern seen in the earlier study of apple snail response to predation cues in the absence of refuge structure (Carlsson et al., 2004), the addition of chemical cues from predator to the tank resulted in an increase in the proportions of apple snails at the bottom habitat. As apple snails detected the climbing perch's odor on the water surface, they may reduce predation risk by going to the bottom that would be easier and safer than going to the surface (Ichinose et al., 2003). Moreover, we found that both apple snail species responded to predator odor but their pattern of response was different. The native apple snail (*Pi. pesmei*)

Table 1 The result from Fisher's exact test testing the proportion of apple snails (*Pi. pesmei* or *Po. canaliculata*) found at the surface habitat and the bottom habitat in different treatments (control or predator treatment) in 30 min and 60 min after being exposed to treatments. (N represent number and percentage of apple snails found at surface or bottom of the test tank)

Habitat use	**N**		**Fisher's exact**	***p* value**
	Pi. pesmei	***Po. canaliculata***		
Control treatment				
Trial time: 30 min				
Surface habitat	7 (23.33%)	17 (56.67%)	7.111	0.008
Bottom habitat	23 (76.67%)	13 (43.33%)		
Trial time: 60 min				
Surface habitat	8 (26.67%)	16 (53.33%)	4.511	0.032
Bottom habitat	22 (73.33%)	14 (46.67%)		
Predator treatment				
Trial time: 30 min				
Surface habitat	7 (23.33%)	16 (53.33%)	5.829	0.016
Bottom habitat	23 (76.67%)	14 (46.67%)		
Trial time: 60 min				
Surface habitat	3 (10.00%)	13 (43.33%)	9.031	0.004
Bottom habitat	27 (90.00%)	17 (56.67%)		



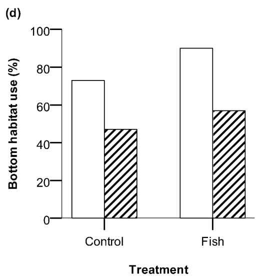


Figure 1 The effects of chemical cues (control and fish) on habitat use (surface or bottom of the tank) of *Pi. pesmei* (open bars) and *Po. canaliculata* (hatched bars) in 30 min (a, b) and 60 min (c, d) after the treatment.

did not show avoiding predator odor until 30 min after being exposed to treatments. However, the invasive apple snail (*Po. canaliculata*) responded to fish chemical cues by increasing their use of the bottom habitat which showed avoidance to predator odor within the first 30 min until as long as these trials were conducted (60 min). Hence, it is possible that *Po. canaliculata* was more sensitive to predators and would exhibit stronger avoidance response to predator odor than *Pi. pesmei*. Interestingly, *Po. canaliculata* shows predator avoidance behavior to fish chemical cues although this apple snail has no co-evolutionary history with this fish species, suggesting that it could be quite general in the response of the apple snail to fish cues (Carlsson et al., 2004). This finding also provides evidence to support the hypothesis that the invasive apple snail respond in predator avoidance more than the native apple snail and probably contributes to the displacement of native species by non-native invasive species (i.e., invasion success). Our study is consistent with the previous study (Hazlett et al., 2003) that the non-native invasive species use a broader range of chemical cues concerning predation risk than native species which increases the likelihood of avoiding predation and this behavioral response may contribute to invasion success in new environments.

In addition to its greater ability to detect and respond to the odor of predator, the non-native invasive species had more effective avoidance behavior against predator than the native species (Weis, 2010). For example, Pennuto and Keppler (2008) found that the invasive amphipods (*Echinogammarus ischnus*) reduced the distance moved to more fish predators than the native amphipod (*Gammarus fasciatus*). This implies that the distance moved in the presence of predators (attack distance) may be important in attracting the attention of potential predators which the reduction in attack distance is able to decide the level of risk and alter its behavior accordingly (Dill and Fraser, 1984). In other words, the greater movement of the species may be more attractive, leading to a higher possibility of being detected by predators (Pennuto and Keppler, 2008). Additionally, some evidence suggests that the non-native invasive species seemed to respond more strongly to the presence of predators than did the native species. For example, Nyström (2005) found that the non-native signal crayfish (*Pacifastacus leniusculus*) responded to the presence of predators by increasing their use of refuges compared to the native species. Consequently, it is suggested that the species that spent more time outside refuges in the presence of predators may cause an increased risk of predation and is likely to be a key component of the displacement of native species by non-native invasive species (Bubb et al., 2006).

Conclusion

The results of this experimental study indicate that the non-native invasive apple snail (*Po. canaliculata*) was more sensitive to predation risk and would increase the use of safer habitat than the native apple snail (*Pi. pesmei*). This finding supports the idea that the non-native invasive species exhibited more predator avoidance behavior than native species which may contribute to becoming successfully established species and affect native apple snail populations (i.e., invasion success). These results provided an interesting opportunity for further studies that examine the behavioral differences in predator avoidance which might be a causal mechanism increasing the success of the non-native invasive species. Also, this study might help in emphasize the risks for freshwater biodiversity created by the uncontrolled translocation of *Po. canaliculata* and other similar non-native invasive species.

Acknowledgments

This study was funded by a PhD scholarship to Piyaruk Pradabphetrat from the Office of the Higher Education Commission (OHEC), Thailand and by a research grant to Chantima Piyapong from Burapha University through the National Research Council of Thailand (Grant number 62/2559). We are grateful to the Erasmus Mundus Action 2 Project Swap and Transfer of the European Union (Grant agreement number 2013-2537/001-001-EMA2) and academic coordination of Burapha University, Thailand and University of Innsbruck, Austria. A special thanks to Bungorn Thaewnonngiw, Mahasarakam University, Thailand, for her help collecting specimens. We also thankful to Pongrat Dumrongrojwattana, Burapha University, Thailand, for his aid in identifying apple snail species based on external morphology and Phimpawee Suwanno who provides statistical advice. Many thanks Jirapat Banmak and Krongthong Thangsitthi for assisting in the laboratory.

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