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Modeling behavior control of golden apple snails at different temperatures

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ABSTRACT

The golden apple snail (*Pomacea canaliculata*) is a detrimental invasive pest of rice in Asia. Temperature is a critical factor to determine their invasiveness including the behavior and distribution of snails. In this study, the behavioral responses of golden apple snails acclimated to different water temperatures (15 °C, 20 °C, 25 °C, and 30 °C) were examined based on Markov chain analysis, Shannon entropy, and Random forest modeling. Markov chains revealed that most snails maintained their previous behavior at low temperatures, while behavior transition tended to be higher at high temperature. Shannon entropy was also dependent on temperature (low at low temperature and high at high temperature), indicating that snails maintained their previous behavior for a long time at low temperature regardless having motion and motionless behavior, whereas they changed continuously their behavioral types at high temperature. The Random forest model showed that Shannon entropy at low temperature was influenced by crawling at the bottom or at side of the aquarium (motion behavior), while clinging to the side of the aquarium or clinging to the side of the aquarium with stretching out antennae were important behaviors determining Shannon entropy at high temperature. Our results showed that snails controlled their behavior to reduce their thermal stress and maintain a stable internal state in harsh environment. With this mechanism, they are able to overwinter in the open fields with low temperature in Korea, resulting in the increase of potential damage in agricultural ecosystems. Therefore, further study on the development of adequate management system is required to avoid their invasiveness to open water systems and ecological impacts. Finally, Shannon entropy, Markov chain, and Random forest model are useful computation methods to quantify the effects of temperature changes on the behavior of golden apple snails.

1. Introduction

Invasion by exotic species is one of the main causes of the global extinction crisis, causing biodiversity loss and biotic homogenization (Mooney and Hobbs, 2000). Once successfully introduced and established in a new area, invasive species are difficult to be eradicated. Therefore, it is essential to understand the mechanisms and processes of biological invasions. The golden apple snail (*Pomacea canaliculata*) is an exotic species in Asian countries, introduced from South America, which has become a serious agricultural pest, especially to young rice (Halwart, 1994; Wada, 2004; Cowie et al., 2006; Hayes et al., 2008). The golden apple snail was considered a pest in the Philippines in 1986 (Rejesus et al., 1990), and since then there was an annual economic loss of about 1200 million US dollars due to aquatic crop damage (Naylor, 1996). In Japan, the distribution range of this species has increased and, in 1999, ca. 13,000 ha of paddy fields have been damaged (Wada, 2004). In addition to the severe effects of rice paddy, the snail can cause major environmental changes, such as the depletion of macrophytes in natural wetlands (Carlsson et al., 2004). Hence, the golden apple snail is indicated as one of the 100 worst invasive species worldwide by the International Union for the Conservation of Nature (Lowe et al., 2000; Bang and Cho, 2008).

Temperature is a critical factor for successful establishment and colonization of invasive species, including the golden apple snail, in new areas (Baker, 1998; EFSA, 2012), owing to its effects on survival (Seuffert and Martín, 2013), growth rate (Estebenet and Cazzaniga, 1992), reproduction (Seuffert et al., 2010), lung

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ventilation frequency (Seuffert and Martín, 2010), feeding rate (Seuffert et al., 2010), and behavior (Heiler et al., 2008; Seuffert et al., 2010; Seuffert and Martín, 2010). Snails that overwinter in paddy fields are more tolerant to cold conditions than those that do not overwinter (Wada and Matsukura, 2007). They usually remain inactive or bury in muddy bottoms during winter or periods of cold weather conditions (Damborenea, 1996; Seuffert et al., 2010; RDA, 2007). In areas with constant warm temperatures (e.g., 25 °C), females of golden apple snails reproduce only once in their lifetime (i.e., semelparous), whereas in areas with fluctuating temperature conditions (e.g., 7–24 °C), they have multiple reproductive periods (i.e., iteroparous) (Estebenet and Cazzaniga, 1992; Estebenet and Martín, 2002; Seuffert et al., 2010). High movement activity and crawling velocity are observed in areas with high water temperatures (Heiler et al., 2008). However, water temperatures above 30 °C were seen to cause a decrease in activity and an increase in feeding time in laboratory experiments (Seuffert et al., 2010).

Animals' behavior and physiological responses are influenced by environmental factors. Therefore, understanding the behavior of invasive species is the first step in developing an effective control and management method. However, it is difficult to analyze behavioral data of organisms as they exhibit nonlinear and complex behaviors (Bae and Park, 2014). Therefore, the analysis of such data requires the use of appropriate analytical and modeling methods, including statistical and computational approaches (Chon et al., 2004). The Shannon information theory can be used to quantify variation in behavior, duration of behavior, and behavior complexity of organisms, using different sequences of behavioral types (Fig. 1). In fact, the Shannon entropy (Shannon and Weaver, 1949) has been widely applied in animal behavior analysis, e.g., in hermit crabs (Hazlett and Bossert, 1965), dolphins (McCowan et al., 1999), the rufous-bellied thrush (Da Silva et al., 2000), and the Japanese medaka (Fukuda et al., 2010). However, only a few studies focus on behavioral sequences (Gherardi and Pieraccini, 2004). A behavioral sequence can be modeled through the Markov chain, a discrete random process in which the probability of a system in the next time step depends only on the current state of the system and is independent of the previous step (Guan et al., 2008). The Markov chain has been used to analyze landscape changes (e.g., Baker, 1989), population ecology (e.g., Seneta, 1966; Fujiwara and Caswell, 2002), and behavioral ecology (Lusseau, 2003). Since it quantifies the dependency between the present state and the state in the next time step, it can be used to compare the probability of behavioral transitions in response to different environmental conditions (Lusseau, 2003).

Most studies dealing with behavior have either used short time observations (e.g., for 2 h) or only studied a certain type of behavior at a time, such as ventilation frequency or activity. To our knowledge, there are little quantitative researches on short time interval responses in behavior. Therefore, in this study, the behavioral response of golden apple snails to different water temperatures was examined based on short time interval data (i.e., every minute). Specifically, three steps of analyses were conducted: (1) the degree of behavior complexity at different water temperatures was compared based on Shannon entropy; (2) the duration of behavior as well as behavior transitions were compared through Markov chain analysis; and (3) the factors determining behavior complexity were evaluated based on Random forest model.

2. Materials and methods

2.1. Test organisms and behavioral observations

Test organisms were obtained from a farm of golden apple snails (*P. canaliculata*) in Korea (http://www.gpwoolunge.co.kr/). A stock population was maintained in an aquarium with dechlorinated tap water (water temperature: 25 °C ± 1 °C; L16: D8) and a 3-cm layer of sand at the bottom, for at least 2 months before starting the experiments. In order to rule out irregular behavior (e.g., spawning and mating), only males were used. These were identified based on the presence of testis, observed through the translucent shell (Takeda, 1999), or by a humped operculum (Estebenet et al., 2006) and a body size (>25 mm) (Seuffert et al., 2010).

The behavior of test organisms was observed in aquaria (30 cm × 30 cm) filled with water to a depth of 15 cm and with a

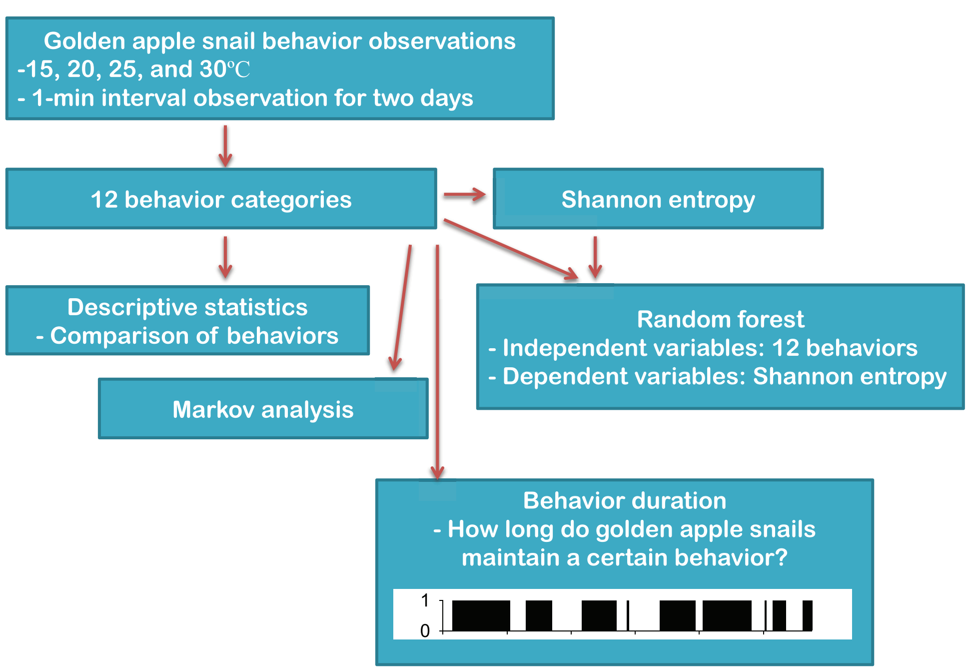

Fig. 1. Flow chart of behavior data analyses of golden apple snails.