Effect of sex, hunger and relative body size on the use of ripple signals in the interactions among water striders *Gerris latiabdominis*

Jae Hak Son [a], Chang Seok Han [b], Sang-im Lee [a,c], Piotr G. Jablonski [a,d,*]

[a] *Laboratory of Behavioral Ecology and Evolution, Department of Biological Sciences, Seoul National University, Seoul 151-742, Republic of Korea*
[b] *Evolution & Ecology Research Centre, The University of New South Wales, Sydney, Australia*
[c] *Institute of Advanced Machinery and Design, Seoul National University, Seoul 151-742, Republic of Korea*
[d] *Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland*

A B S T R A C T

Water striders use ripple signals in aggressive interactions between individuals for access to food. We asked whether water striders produce ripple signals more frequently when they are hungrier and when the value of food resources is higher. We also asked if and how the use of signals depends on the size difference between interacting individuals. We found that females used ripple signals more often than males did. The experiment suggested that use of aggressive ripple signals is affected by hunger in females – the sex with high demands for food resources. Among females, but not males, we found out that the probability of using signals in response to the approaching intruder depended both on the degree of hunger and on the size of the focal animal relative to the size of the intruder. Before starvation, the probability of a female using a signal in an interaction with an intruder was higher when the individual's size was larger relative to the intruder. After starvation, the focal individuals were more likely to signal when their size was smaller relative to the intruder. The results are consistent with the idea that these signals may reveal information about the signalers weight or hunger level, and specific hypotheses are suggested for the future studies.

© 2014 Korean Society of Applied Entomology, Taiwan Entomological Society and Malaysian Plant Protection Society. Published by Elsevier B.V. All rights reserved.

Introduction

Substate-vibrational signals are frequently used by many insects (Cocroft and Rodríguez, 2005). However, these signals have been less investigated compared to visual and acoustic signals in animals (Virant-Doberlet and Cokl, 2004). Particularly, the ripple signals on the water surface made by water striders have not been well studied, compared to the rich literature on other behaviors of these insects (Fairbairn and Preziosi, 1994; Rowe, 1994; Arnqvist and Danielsson, 1999; Arnqvist and Rowe, 2002). Several existing papers about ripple signals of water striders have focused on the context of courtship (Wilcox, 1972), copulation (Wilcox and Di Stefano, 1991; Han and Jablonski, 2009a, 2010), sex discrimination (Wilcox, 1979), mate guarding (Wilcox and Di Stefano, 1991), territoriality (Hayashi, 1985; Nummelin, 1987), and direct competition for food resources (Wilcox and Ruckdeschel, 1982; Jablonski and Wilcox, 1996; Han and Jablonski, 2009b). We focused on the last two contexts with the idea of exploring some general issues in the evolution of aggressive and signaling behaviors in animals.

In the context of food-based territories and aggressive interactions water striders are known to use either high frequency ripples produced with their front legs (Jablonski and Wilcox, 1996) or low frequency ripples produced by the bouncing of the whole body up and down on the water surface (Han and Jablonski, 2009b). It has been shown in two species that as a satiated water strider becomes hungry, and as food items became more valuable in terms of fitness-enhancing resources (Riechert, 1979; Parker and Rubenstein, 1981), an individual switches to territorial defense behaviors (Wilcox and Ruckdeschel, 1982; Jablonski, 1996) at sites with perceived higher probability of encountering prey (Jablonski, 1996; Jablonski and Ściński, 1999), despite the costs of aggressiveness due to enhanced predation risk (Krupa and Sih, 1998). Similarly, reproductive-phase females, for whom a food item has especially high value (V) due to an immediate effect on the number of eggs laid (Blanckenhorn, 1991), are more likely to defend food-based territories than nonreproductives (Jablonski, 1996). Therefore, we hypothesized that in a similar manner hunger and sex (or reproductive phase) should affect the use of aggressive ripple signals in other water strider species. This hypothesis is consistent with theoretical expectation that signals carry information about the motivation to defend the resources, which is positively correlated with the current value of

* Corresponding author at: Laboratory of Behavioral Ecology and Evolution, School of Biological Sciences, Seoul National University, Seoul 151-742, Republic of Korea. Tel.: +82 2 880 8158; fax: +82 2 878 8158.
E-mail address: SNULBEE@behecolpiotrsangim.org (P.G. Jablonski).

resources (Parker, 1974; Parker and Knowlton, 1980; Parker and Rubenstein, 1981; Sigurjónsdóttir and Parker, 1981).

We focused on the recently described low frequency signals (Han and Jablonski, 2009b). Because these signals are produced by bouncing the whole body up and down on the water surface, the resulting water ripples may contain information about the body size of the signaling individual (Han and Jablonski, 2010), hence in general about the Resource Holding Power of an individual (Parker, 1974). If the signals reveal information about the individual's size or strength then the use of those signals may also be affected by the body size of a signaler relative to the body size of the intruder (Enquist and Leimar, 1983, 1987, 1990; Leimar and Enquist, 1984). Therefore we expected that the use of low frequency signals by water striders may depend on the relative size between the two contestants. Body size may additionally affect the use of signals because larger organisms may tolerate starvation longer than smaller ones (due to the difference in the size of reserves and metabolic rate during food deprivation; (Kirk et al., 1999; Stelzer, 2006)).

Here we examined how starvation influences signaling behaviors in *Gerris latiabdominis* in unisexual experimental groups where signaling for sexual reproduction does not occur, and individuals attempt to keep intruders away from specific locations. We predicted an increase in the use of signals when demand for food resources increases (e.g. when individuals are hungry). We also predicted that females may be more susceptible to this effect due to higher energy demands (required for egg production and extended periods of carrying guarding males). We also asked whether the use of signaling depends on the relative body size between the two competitors

Materials and methods

Study subjects

The water strider *G. latiabdominis* was previously regarded as a subspecies of *G.lacustris*, (*G. lacustris latiabdominis* Myamoto; e.g. in Tetsuo (1991)) but current molecular evidence elevates it to the species level (e.g. Damgaard (2008)). The species is broadly distributed in East Asia. Its typical habitats comprise rice fields and associated canals and irrigation ponds (Kanyukova, 1982, 2002; Harada, 1998; Hayashi, 2006; Kawano et al., 2006). Its diet consists of small invertebrates that fall on the water surface (Olejniczak et al, 2007). The study subjects were caught in early April at Mt. Seon-Un Provincial Park in southwestern part of Korea (35.498N, 126.588E) and were immediately transported to the laboratory.

Laboratory conditions

Sexes were kept separately in two rectangular plastic containers (41 × 54 cm, 5 cm in water depth), and fed ad libitum with frozen crickets (*Verlarifictorus asperses*). Four floating pieces of Styrofoam (2: 40 × 3 .cm, 0.3 cm in thickness, 2: 50 × 3.cm, 0.3 cm in thickness) were provided on the edge of the containers as resting sites. The water striders were kept in 13 h-light/11 h-dark cycle. Every individual was marked on the upper surface of thorax with a unique combination of color dots using enamel paints. After marking, all individuals were photographed against a paper printout of a grid (1 × 1 cm), and body length of each water strider (from the tip of the head to the tip of the abdomen) was measured from the digital photo using Image J (http://imagej.nih.gov/ij/).

Experimental design

The experiments were designed to closely imitate a normal field situation of a small water pond. Two days before the experiments, two groups of individually marked females (20 and 21 individuals) and two groups of individually marked males (20 and 21 individuals) were separately prepared in 4 rectangular experimental containers (41 × .26 cm) filled with water (5 cm in depth). In each of these

containers, three Styrofoam pieces (1: 40 × .0.5 cm, 0.3 cm in thickness, 2: 24 × .0.5 cm, 0.3 cm in thickness) were provided on the edge. Two days later, the behavior of water striders during encounters in each container was observed and noted down by an observer for 1 h. An encounter was assumed when one individual ("*approaching individual*") moved toward or passed by (within 2 cm) another individual, who remained stationary at this moment ("*stationary individual*"). If the stationary individual signaled, the encounter was scored as "*signaling*", otherwise it was scored as "*non-signaling*" (because the approaching individuals did not signal). It was apparent that the signals by the stationary individuals were produced in response to sensing the ripples produced by the movements of the approaching individuals. Tarsal vibration receptors might have been used in this situation (Perez Goodwyn et al., 2009). We have not observed the signals from the "approaching individuals".

After the first, 1-h-long trial session, each container was assigned randomly to either "control" or "hunger" treatment for each sex separately. In the hunger treatment (one container for males and one for females), the water striders were deprived of food for 4 days. The remaining two groups (one container with males and one with females) acted as the controls where food was continuously delivered. Four days later, the second observation session was carried out for each group in the same manner as above. Hence, the first set of observation in each container was done before and the second set of observations was done after the group was subjected to a new treatment for 4 days.

Although the records of the ripple signals were conducted by visual observation, this method is sufficient to record the presence or absence of signals during interactions between experimental subjects because most interactions were single events that occurred at the time when no other interaction occurred in a group. Only rarely two interactions occurred simultaneously, in most of these cases the presence or absence of a signal could have been reliably established as well. This experimental design does not meet the classical standards of typical laboratory practices where many focal individuals in each treatment are tested and each individual is put in a separate container with non-focal individuals (which are not subject to the treatments) assuring that differences between treatments could be clearly attributed to the effect of treatment on focal individuals only. In our study, both focal and nonfocal individuals were put into the same container and went through the same treatment. Hence, our design does not differentiate the effect of hunger on the focal individual from the effect of behavior of nonfocal individuals that are also subject to the same treatment (change in hunger level). However, this design, where all individuals simultaneously are subject to change in hunger, better imitates a typical situation in nature where in one small pond all interacting individuals are simultaneously affected by the same ecological factor (hunger in our case). The design is more typical of a field study where one chooses a habitat patch (similar to our experimental container) inhabited by a population of individuals (a group of males or females) whose behavior is observed and analyzed during changes in food recourse availability (an individual contributes one data point to each analysis). Hence, although the obvious shortcoming of this design is lack of repetition at the population level (only one container per treatment is used rather than several), we believe that the results are sufficiently informative to indicate the effect of starvation in groups of water strider individuals in a natural situation.

Statistical analysis

Analysis within control

First, we used the Generalized Linear Mixed Model (GLMM) (function glmer in R) to analyze the difference in signaling between males and females within the control groups. We used *signaling* of the *stationary* individual as a response variable (binary variable: signaling present or absent), and three explanatory variables: the individual *sex* (binary: *male* or *female*), the *trial* (*first* or *second*), and the *size ratio* of the