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이학석사 학위논문

Predator Avoidance and  
Signaling Behavior of Water Striders

소금쟁이의 포식 회피 행동과 신호행동

2013 년 02 월

서울대학교 대학원

생 명 과 학 부

손 재 학

# Predator Avoidance and Signaling Behavior of Water Striders

A Thesis presented by **Jae Hak Son**

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# 소금쟁이의 포식 회피 행동과 신호 행동

## Predator Avoidance and Signaling Behavior of Water Striders

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이 논문을 이학석사 학위논문으로 제출함

2013 년 2 월

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## **Abstract**

# Predator Avoidance and Signaling Behavior of Water Striders

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Ripple communication is used among semi-aquatic insects. Water striders produce ripple signals on the water surface for courtship, copulation, sex-discrimination, territoriality and mate guarding. Not all species of water striders, however, make signals for the same purpose. I investigated in which situation *G. latiabdominis* makes ripple signals. Females, but not males, used the ripple signals more often when they were hungry, suggesting that the signaling is used in securing food resources by hungry females to repel competitors away. The use of signals, however, is not directly related to density, indicating that this signaling is not affected by the density and the correlated frequency of interactions among individuals.

Prey species should avoid areas where predation risk is high. However, if this is impossible, prey should reduce activities that may make them conspicuous and attract predators present in the habitat, such as foraging or mating. Thus, predation risk should change behavioral pattern of prey species. Not all species have same anti-predator behavioral patterns because they have evolved in the presence of different types or number of predators in their habitat. Hence some species, living in high predation risk habitats, probably developed efficient ways to avoid predation, while other species, living in low predation risk habitats, may have not evolved the most efficient ways to avoid predation. I hypothesized that survival rate of three species of water striders, originating from different types of habitats, will be affected by their species specific responses to predators, and that species specific morphology will contribute to the efficiency of predation avoidance. I compared the effect of predator's presence on microhabitat use. I also compared responses to predators (escape initiation distance), and jumping performance of the three species. The survivorship was related to microhabitat use and to the escape initiation distance, rather than on the jumping ability. I predicted that a species with the best survival rate will have superior jumping ability in order to escape from predators at the moment when they were attacked by predators. The jumping ability, however, was probably limited by hydrodynamic and morphological constraints, so jumping appears to contribute little to successfully escaping from predators' attacks.

**Key words:** Signaling behaviors, Food resource acquisition, Anti-predator behaviors, Predator avoidance, Water striders.

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# Table of Contents

Abstract .....	i
Table of Contents .....	iv
List of Tables .....	vii
List of Figures .....	ix
Chapter 1. The effect of hunger and density on the signaling behavior by a water strider, <i>Gerris latiabdominis</i> .....	1
1.1. INTRODUCTION .....	1
1.2. METHODS .....	4
1.2.1. Study subjects and Laboratory conditions.....	4
1.2.2. Experimental design .....	5
1.2.3. Statistical analysis .....	7
1.3. RESULTS .....	11
1.3.1. The effect of treatments on the signaling behavior .....	11
1.3.2. The effect of treatments on the frequency of encounters .....	18
1.4. DISCUSSION .....	24
Chapter 2. Comparison of predator avoidance strategies among three species of water striders from habitats of various predations risks .....	29

2.1. INTRODUCTION .....	29
2.2. METHODS .....	34
2.2.1. Study subjects and Laboratory conditions .....	34
2.2.2. Experimental procedure .....	34
2.2.2.1. Survivorship .....	35
2.2.2.2. Escape initiation distance .....	35
2.2.2.3. Microhabitat use .....	36
2.2.2.4. Jumping ability .....	38
2.2.2.5. Morphological characteristics .....	39
2.2.3. Statistical analysis .....	41
2.2.3.1. Survivorship .....	41
2.2.3.2. Escape initiation distance .....	42
2.2.3.3. Microhabitat use .....	42
2.2.3.4. Jumping ability .....	43
2.2.3.5. Morphological characteristics .....	44
2.3. RESULTS .....	45
2.3.1. Survivorship .....	45
2.3.2. Escape initiation distance .....	47
2.3.3. Microhabitat use .....	49
2.3.4. Jumping ability .....	58
2.3.5. Morphological characteristics .....	61
2.4. DISCUSSION .....	68

REFERENCES .....	78
국문초록 .....	86
Acknowledgements .....	88

## List of Tables

<b>Table 1.1.</b> Signaling analysis in females with <i>control</i> and <i>hunger</i> treatment together ( <i>control + hunger</i> ). .....	13
<b>Table 1.2.</b> Signaling analysis in females with <i>control</i> and <i>density</i> treatment together ( <i>control + density</i> ). .....	14
<b>Table 1.3.</b> Signaling analysis in males with <i>control</i> and <i>hunger</i> treatment together ( <i>control + hunger</i> ). .....	15
<b>Table 1.4.</b> Signaling analysis in males with <i>control</i> and <i>density</i> treatment together ( <i>control + density</i> ). .....	16
<b>Table 1.5.</b> Analysis of encounter rates for stationary female individuals with <i>control</i> and <i>hunger</i> treatment together ( <i>control + hunger</i> ). .....	20
<b>Table 1.6.</b> Analysis of encounter rates for stationary female individuals with <i>control</i> and <i>density</i> treatment together ( <i>control + density</i> ). .....	21
<b>Table 1.7.</b> Analysis of encounter rates for stationary male individuals with <i>control</i> and <i>hunger</i> treatment together ( <i>control + hunger</i> ). .....	22
<b>Table 1.8.</b> Analysis of encounter rates for stationary male individuals with <i>control</i> and <i>density</i> treatment together ( <i>control + density</i> ). .....	23
<b>Table 2.1.</b> Microhabitat use in <i>G. latiabdominis</i> ; proportion of time spent on the water surface during 300-sec trials before and after being attacked by a predator. ....	54

**Table 2.2.** Difference in microhabitat use between females and males of *G. latiabdominis*. ..... 54

**Table 2.3.** Microhabitat use in *G. gracilicornis*; proportion of time spent on the water surface during 300-sec trials before and after being attacked by a predator. .... 55

**Table 2.4.** Difference in microhabitat use between females and males of *G. gracilicornis*. ..... 55

**Table 2.5.** Microhabitat use in *A. paludum*; proportion of time spent on the water surface during 300-sec trials before and after being attacked by a predator. .... 56

**Table 2.6.** Difference in microhabitat use between females and males of *A. paludum*. ..... 56

**Table 2.7.** Inter-specific difference in microhabitat use after experiencing the attack of a predator. .... 57

**Table 2.8.** Tukey’s Honest Significance Difference (Tukey HSD) multiple comparison tests for *species* in two-way ANOVAs of effects of *species* and *sex* on contacted mid leg length (CML) and contacted hind leg length (CHL). .... 65

**Table 2.9.** Tukey’s Honest Significance Difference (Tukey HSD) multiple comparison tests for *interaction* among *species* and *sex* in two-way ANOVAs of effects of *species* and *sex* on contacted mid leg length (CML) and contacted hind leg length (CHL). .... 66

## List of Figures

<b>Figure 1.1.</b> Use of ripple signal in a water strider, <i>Gerris labiabdominis</i> . ...	10
<b>Figure 1.2.</b> Difference between females and males on use of the ripple signal. .....	12
<b>Figure 1.3.</b> In females, interaction effect between <i>size ratio</i> and <i>trial</i> on the frequency in signaling use. ....	17
<b>Figure 2.1.</b> Survival curves for water striders. Curves are the probability of surviving predation as the function of time, accounting for censoring due to survival to the end of the study period. ....	46
<b>Figure 2.2.</b> Reactive (escape) distances of water striders in the approach of a predator, <i>notonectidae</i> . ....	48
<b>Figure 2.3.</b> The time proportion of how long water striders stay on the water against out of the water before and after being attacked by predators. ....	52
<b>Figure 2.4.</b> Body velocity of water striders when they jump up on the water surface. ....	59
<b>Figure 2.5.</b> Time to take mid leg of the insect to reach maximum depth in meniscus. ....	60
<b>Figure 2.6.</b> Morphological condition of contacted mid leg length(CML) and contacted hind leg length(CHL) per sex per species. ....	63

# **Chapter 1. The effect of hunger and density on the signaling behavior by a water strider *Gerris latiabdominis***

## **1.1. INTRODUCTION**

Signals are used by animals in a variety of contexts such like defending territories (Randall 1984, Bee *et al.* 2000), mating (Hagedorn and Heiligenberg 1985), establishing dominance (Zulandt Schneider *et al.* 1999, Fugère *et al.* 2011), and alarming about predators (Manser 2001). Signals are often used to defend resources, such like mates (Wich and Nunn 2002), space (Darden and Dabelsteen 2008), or food (Laidre 2007). Visual and acoustic signals have been extensively studied, but substrate-borne signals have been studied less (Virant-Doberlet and Cokl 2004). Particularly, ripple signals made by water striders on the water surface have been studied relatively little, considering the rich literature on the other aspects of behavior of these insects (Fairbairn and Preziosi 1994, Rowe 1994, Arnqvist and Danielsson 1999, Arnqvist and Rowe 2002).

Ripple signals of water striders have been studied the context of courtship (Wilcox 1972), copulation (Wilcox and Di Stefano 1991, Han and Jablonski 2009a, 2010), sex-discrimination (Wilcox 1979), territoriality (Hayashi 1985) and mate-guarding (Wilcox and Di Stefano 1991). Recently low frequency signals, associated with body bouncing and dominance interactions between individuals competing for food, have been described in one species (Han and Jablonski 2009b). In other species, *Gerris remigis*, water strider males, but not females, used high frequency ripple signals in competition for food resources (Jablonski and Wilcox 1996). The latter two studies indicated that the defense of food resources, or locations with higher food abundance, is one of the main functions of the species-specific and maybe even sex-specific ripple signals in water striders. If this is true, then I may expect the effect of food abundance, or level of hunger, on the use of those signals. I predict an increase in the use of ripple signals when the demand for food increases (e.g., when an individual is hungry). If, however, the function of these signals is to simply keep others away at a specific distance regardless of feeding demands, then one would expect no association with the hunger level. In this situation ripple signals would only be used when another individual approaches within a specific distance. Because this is more likely in higher density of individuals, one would expect an increase in the use of signals in higher density as a simple function of an increase in the

frequency of interactions. These predictions have not been tested. I decided to test these ideas experimentally.

## 1.2. METHODS

### 1.2.1. Study subjects and Laboratory conditions

The water strider *G. latiabdominis* is widely distributed in East Asia and lives in shallow creeks and rice fields. The study subjects were caught early in April 2010 at Mt. Seon-Un Provincial Park near Kwangju in the Southwest part of Korea, and transported to a laboratory at Seoul National University, Seoul.

Female and male sexes were kept separately in two rectangular plastic containers (41×54 cm with a water depth of 5 cm), and fed *ad libitum* with frozen crickets (*Verlarifictorus asperses*). Four floating Styrofoam pieces (2: 40×3 cm, 0.3 cm in thickness, 2: 50×3 cm, 0.3 cm in thickness) were provided as resting sites on the edge of the containers. Every individual was marked on its thorax with a unique combination of color dots using enamel paints. After marking, all individuals were photographed on a plastic board with glued plotting paper using a fixed digital camera, and then body length of each water strider (from the end of the head to the end of the abdomen) was measured from the photo with the image analysis software Image J (<http://imagej.nih.gov/ij/>). The water striders were kept in 13h-light/ 11h-dark cycle.

### 1.2.2. Experimental design

Two days before the experiments, three groups of individually marked females (individuals 20, 21, 21) and three groups of individually marked males (individuals 20, 21, 21) were prepared in 6 rectangular plastic 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. Observations were conducted two days after putting the water striders into the experimental containers. An observer focused for one hour on one container and noted down all encounters between individually marked individuals. An encounter was assumed when one individual (“approaching individual”) moved towards, or passed by, (within 2cm) 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. All signals were low frequency signals associated with shaking the whole body, similar to signals described by Han and Jablonski (2009b). Occasionally, the individuals mounted each other (in the male only basins) indicating the sexual background of the encounter – those encounters were excluded from the analysis.

After the first one-hour-long trial session, each container was assigned randomly to either “control,” “hunger” or “density” 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 four days*. In the *density* treatment, the water striders (one container for males and one for females) were transported to a *container that was twice as large* as the previous container. The remaining two containers (one container with males and one with females) acted as the controls. Four days later the second observation session was carried out in each container in the same manner as above. Hence, the first set of observations for each container was collected before and the second set of observations was collected after the group was subjected to a new treatment for four days. This experimental design does not meet the standards of typical laboratory practices whereas many focal individuals in each treatment would be tested, each individual in a separate container with non-focal individuals, which were not subjected to the treatments, assuring that differences between the treatments could be clearly attributed to the effect of the treatment on only the focal individuals. Our design does not differentiate the effect of hunger or density on the focal individual from the effect of behavior of the non-focal individuals (on the focal individual) that are also subjected to the same treatment (change in hunger or density level). However, this design, where all individuals simultaneously are subject to either hunger or change in density, better

imitates a typical situation in nature where in one pond all interacting individuals are simultaneously affected by the same ecological factor. Therefore, our design more closely represents what actually happens in a natural small pool of water under the effect of decreasing density or decreasing food resources. The design then is more typical of a field study (e.g. ornithological study of a population of birds) whereas one chooses a habitat patch (container) inhabited by a population of individuals (a group of males or females) whose behavior is observed and analyzed during changes in food resource availability or population density (an individual contributes one data point to each analysis). Hence, although the obvious shortcoming of this design is a lack of repetition at the population level (only one container per treatment is used rather than several), I believe that the results are sufficiently informative to study the effect of hunger or density because all other experimental conditions are identical for all containers.

### 1.2.3. Statistical Analysis

To determine the effects of hunger and density on *signaling* (binary variable: signaling present or absent) by the *stationary* individual I used, for each sex separately, GLMM (function `glmer` in R) with three fixed factors, the *trial* (*first* and *second*) the *treatment* (*control*, *hunger*, and *density*), and the *size ratio* of the stationary to approaching individual (*continuous*), and the

two-way interactions among them. Additionally, *Individual identities* of the stationary and approaching individuals were used as random factors. I used GLMM to analyze the difference in signaling between males and females within the control treatment only. Finally, to figure out the effect of hunger and density, I analyzed hunger and density treatment with control treatment separately and compared each effect with control (e.g. control + hunger, control + density).

The effect of the treatment and the differences between the sexes in signaling may be mediated by changes in the frequency of encounters. Therefore, I used the Generalized Linear Mixed Model (GLMM; function `glmer` in R) to examine the effect of the fixed factors: *sex* (*female* and *male*), *treatment* (*control*, *hunger*, and *density*), and *trial* (*first* and *second*) as well as the interactions among them, on the number of encounters per hour. This analysis was done separately for stationary and approaching individuals. Although these two analyses (for stationary and approaching individuals) are obviously not independent, they serve to illustrate the effect of hunger or the effect of density on the number of encounters in the population during the experiment. Additionally, to parallel the analysis of signaling, I used GLMM for males and females separately with two fixed factors *treatment* (*control* vs *hunger*, and *control* vs *density*), and *trial* (*first* and *second*), and the ID of an individual (separately approaching and stationary). Finally, I used GLMM to

analyze the difference in signaling between males and females within the control treatment only.

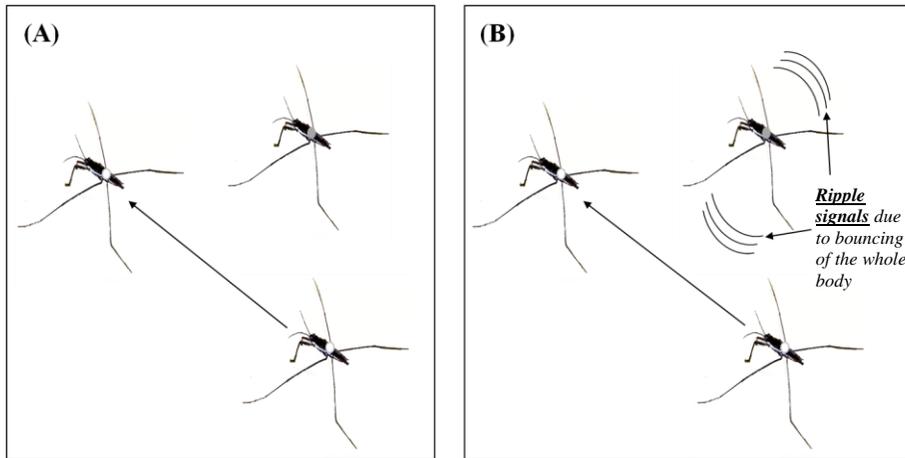


Figure 1.1. Schematic representation of two types of interactions among water striders, *Gerris labiabdominis*. Interaction was assumed when an approaching individual (**white point**) passed by stationary individual (**grey point**) within 2 cm. The ripple signal was produced by a water strider that oscillates its own body and legs. (A) No signaling; stationary individuals did not respond to approaching individuals. (B) Signaling: stationary individuals responded to approaching individuals.

## 1.3. RESULTS

### 1.3.1. The effect of treatments on the signaling behavior

In the control treatment, females produced signals more frequently than the males did ( $\chi^2_1 = 56.78$ ,  $p < 0.001$ ; Figure 1.2). For females, 19 of the 20 individuals sent out signals at least more than once; for males however, 12 of the 20 individuals produced the signals. Because of this difference between females and males in using the signals I analyzed each sex separately.

For females, in the *hunger* treatment, there was an effect of interaction between the trial and size ratio ( $\chi^2_1 = 7.05$ ,  $p < 0.05$ ) on signaling, while no such an interaction effect was observed for females in the *control* treatment ( $\chi^2_1 = 1.51$ ,  $p = 0.219$ ) as well as for females in the *density* treatment ( $\chi^2_1 = 0.10$ ,  $p = 0.753$ ) (Figure 1.3). For males, in the *control*, *hunger*, and *density* treatment, there were no significant effects on signaling.

For females, when I analyzed *control* and *hunger* treatment together using GLMM, there was an effect of interaction between trial and size ratio ( $\chi^2_1 = 3.96$ ,  $p < 0.05$ ; Table 1.1.) on the proportion of signaling. In contrast, the analysis of *control* and *density* treatments together did not reveal an interaction between trial and size ratio ( $\chi^2_1 = 0.71$ ,  $p = 0.40$ ; Table 1.2.). The similar analyses for males revealed no significant effects (Table 1.3.; 1.4.).

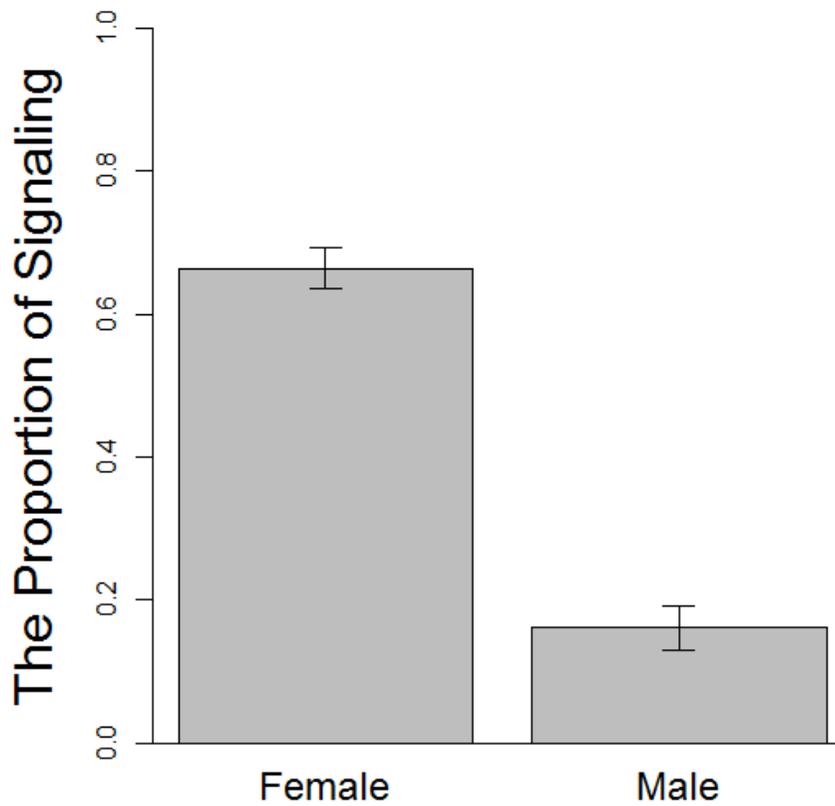


Figure 1.2. Difference between females and males in the frequency of using the signals in the *control* treatment. The frequency of using signals (“proportion of signaling” on vertical axis) is represented by the proportion of interactions with signaling in all interactions of the stationary individual (Figure 1.1).

Table 1.1. Results from the model selection procedure for the comparison of the frequency of signal use by females in the *control* and *hunger* treatments.

(A) Variables remained in a minimal model after model selection approach with stepwise deletion (B) Variables removed during model selection approach with stepwise deletion; p-value is at the moment of stepwise deletion (\*\*\*) :  $p < 0.001$ , \*\* :  $p < 0.01$ , \* :  $p < 0.05$ )

<b>Fixed effect</b>	<b>DF</b>	<b>Chisq</b>	<b>p</b>
<b>(A) Remained in model</b>			
Treatment	1	7.77	< 0.01 **
Size ratio	1	9.53	< 0.01 **
Trial	1	7.95	< 0.01 **
Size ratio × Trial	1	7.99	< 0.01 **
<b>(B) Removed from model</b>			
Treatment × Size ratio	1	2.58	0.112
Treatment × Trial	1	0.31	0.576

Table 1.2. Results from the model selection procedure for the comparison of the frequency of signal use by females in the *control* and *density* treatments.

(A) Variables remained in a minimal model after model selection approach with stepwise deletion (B) Variables removed during model selection approach with stepwise deletion; p-value is at the moment of stepwise deletion (\*\*\*) :  $p < 0.001$ , \*\* :  $p < 0.01$ , \* :  $p < 0.05$ )

<b>Fixed effect</b>	<b>DF</b>	<b>Chisq</b>	<b><i>p</i></b>
<b>(A) Remained in model</b>			
Treatment	1	4.78	< 0.05 *
Size ratio	1	3.57	0.059
Treatment × Size ratio	1	4.55	< 0.05 *
<b>(B) Removed from model</b>			
Trial	1	0.04	0.835
Treatment × Trial	1	0.11	0.738
Size ratio × Trial	1	1.77	0.184

Table 1.3. Results from the model selection procedure for the comparison of the frequency of signal use by males in the *control* and *hunger* treatments.

(A) Variables remained in a minimal model after model selection approach with stepwise deletion (B) Variables removed during model selection approach with stepwise deletion; p-value is at the moment of stepwise deletion (\*\*\*:  $p < 0.001$ , \*\*:  $p < 0.01$ , \*:  $p < 0.05$ )

<b>Fixed effect</b>	<b>DF</b>	<b>Chisq</b>	<b><i>p</i></b>
<b>(A) Remained in model</b>			
<b>(B) Removed from model</b>			
Treatment	1	0.22	0.639
Size ratio	1	0.36	0.548
Trial	1	0.09	0.767
Treatment × Size ratio	1	1.87	0.171
Treatment × Trial	1	0.11	0.132
Size ratio × Trial	1	0.81	0.369

Table 1.4. Results from the model selection procedure for the comparison of the frequency of signal use by males in the *control* and *dentisy* treatments.

(A) Variables remained in a minimal model after model selection approach with stepwise deletion (B) Variables removed during model selection approach with stepwise deletion; p-value is at the moment of stepwise deletion (\*\*\*) :  $p < 0.001$ , \*\* :  $p < 0.01$ , \* :  $p < 0.05$ )

<b>Fixed effect</b>	<b>DF</b>	<b>Chisq</b>	<b><i>p</i></b>
<b>(A) Remained in model</b>			
<b>(B) Removed from model</b>			
Treatment	1	0.22	0.639
Size ratio	1	0.36	0.548
Trial	1	0.09	0.770
Treatment × Size ratio	1	0.35	0.555
Treatment × Trial	1	1.87	0.171
Size ratio × Trial	1	0.84	0.360

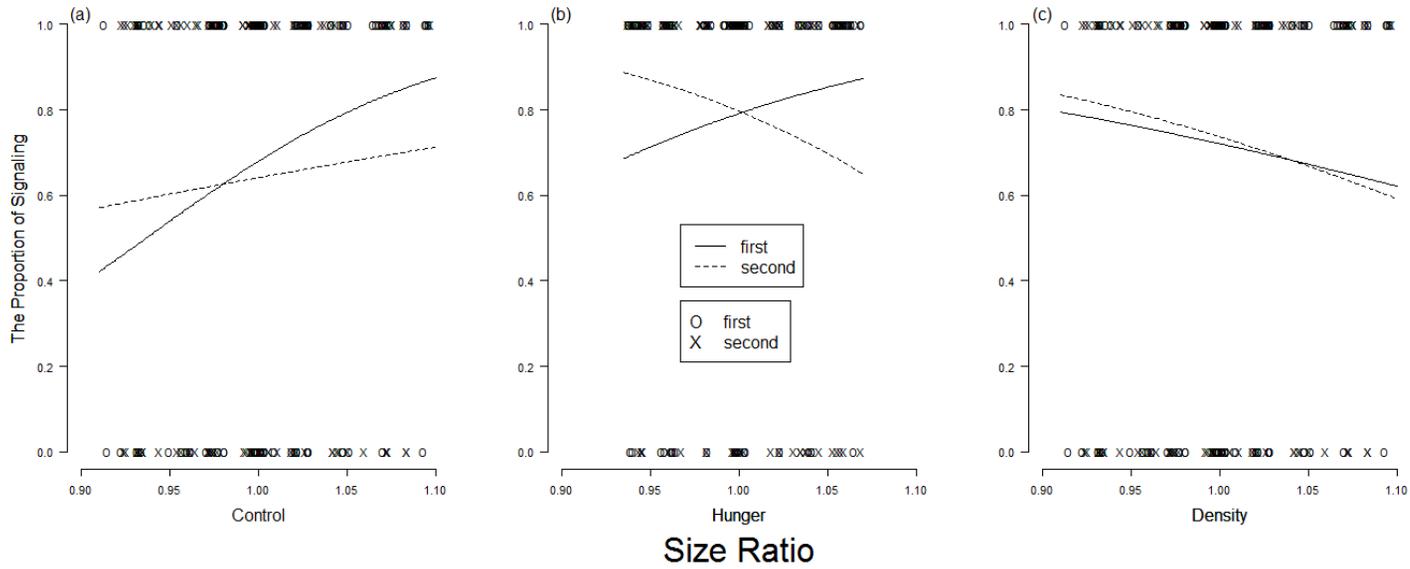


Figure 1.3. In females, interaction effect between *size ratio* and *trial* on the frequency in signaling use. (a) Interaction in control treatment (b) Interaction in hunger treatment (c) Interaction in density treatment

### 1.3.2. The effect of treatments on the frequency of encounters

In the *control* treatment, females (n=20) ( $6.78 \pm 1.96$  encounters/hour/stationary female; [Mean  $\pm$  Standard Error], and  $6.83 \pm 1.20$  encounters/hour/approaching female) participated in the encounters more often than the males did ( $3.73 \pm 0.96$  encounters/hour/stationary male, n = 20, and  $3.73 \pm 0.73$  encounters/hour/approaching male, n = 20) as both stationary and approaching individuals ( $\chi^2_1=4.35, p<0.05$  for encounters as stationary individuals;  $\chi^2_1=10.35, p<0.01$  for encounters as approaching individuals).

In the *hunger* treatment, the number of encounters as stationary individuals in the *second* trial was significantly higher than in the *first* trial both in females (from  $4.48 \pm 1.08$  to  $8.81 \pm 1.46$ , n = 21 for encounters as stationary individuals ; effect of trial [*first* and *second*]:  $\chi^2_1 = 28.43, p < 0.001$  for encounters as stationary individuals) and males (from  $3.76 \pm 0.42$  to  $7.95 \pm 2.03$ , n = 21 for encounters as stationary individuals; effect of trial [*first* and *second*]:  $\chi^2_1=29.82, p<0.001$  for encounters as stationary individuals).

In the *density* treatment, there was an effect of the trial [*first* and *second*] only for males (from  $3.76 \pm 0.72$  times to  $5.95 \pm 1.19$ , n = 21 for encounters as stationary individuals;  $\chi^2_1=10.12, p<0.01$  for encounters as stationary

individuals), not for females (from  $8.14 \pm 1.59$  to  $9.29 \pm 1.55$ ,  $n = 21$  for encounters as stationary individuals).

Table 1.5. Results from the model selection procedure for analysis of the encounter rates for stationary female individuals in the *control* and *hunger* treatments (*control + hunger*). . Data in encounter rates follow Poisson distribution. (A) Variables remained in a minimal model after model selection approach with stepwise deletion (B) Variables removed during model selection approach with stepwise deletion; p-value is at the moment of stepwise deletion (\*\*\* :  $p < 0.001$ , \*\* :  $p < 0.01$ , \* :  $p < 0.05$ )

<b>Fixed effect</b>	<b>DF</b>	<b>Chisq</b>	<b><i>p</i></b>
<b>(A) Remained in model</b>			
Trial	1	0.04	0.952
Treatment	1	6.71	< 0.01 **
Treatment × Trial	1	14.49	< 0.001 ***
<b>(B) Removed from model</b>			

Table 1.6. Results from the model selection procedure for analysis of the encounter rates for stationary female individuals in the *control* and *density* treatments (*control + density*). Data in encounter rates follow Poisson distribution. (A) Variables remained in a minimal model after model selection approach with stepwise deletion (B) Variables removed during model selection approach with stepwise deletion; *p*-value is at the moment of stepwise deletion (\*\*\* :  $p < 0.001$ , \*\* :  $p < 0.01$ , \* :  $p < 0.05$ )

<b>Fixed effect</b>	<b>DF</b>	<b>Chisq</b>	<b><i>p</i></b>
<b>(A) Remained in model</b>			
<b>(B) Removed from model</b>			
Trial	1	0.98	0.323
Treatment	1	1.53	0.216
Treatment × Trial	1	0.59	0.440

Table 1.7. Results from the model selection procedure for analysis of the encounter rates for stationary male individuals in the *control* and *hunger* treatments (*control + hunger*). Data in encounter rates follow Poisson distribution. (A) Variables remained in a minimal model after model selection approach with stepwise deletion (B) Variables removed during model selection approach with stepwise deletion; *p*-value is at the moment of stepwise deletion (\*\*\* :  $p < 0.001$ , \*\* :  $p < 0.01$ , \* :  $p < 0.05$ )

<b>Fixed effect</b>	<b>DF</b>	<b>Chisq</b>	<b><i>p</i></b>
<b>(A) Remained in model</b>			
Trial	1	3.48	0.062
Treatment	1	0.07	0.793
Treatment × Trial	1	4.11	< 0.05 *
<b>(B) Removed from model</b>			

Table 1.8. Results from the model selection procedure for analysis of the encounter rates for stationary male individuals in the *control* and *density* treatments (*control + density*). Data in encounter rates follow Poisson distribution. (A) Variables remained in a minimal model after model selection approach with stepwise deletion (B) Variables removed during model selection approach with stepwise deletion; *p*-value is at the moment of stepwise deletion (\*\*\* :  $p < 0.001$ , \*\* :  $p < 0.01$ , \* :  $p < 0.05$ )

<b>Fixed effect</b>	<b>DF</b>	<b>Chisq</b>	<b><i>p</i></b>
<b>(A) Remained in model</b>			
Trial	1	13.21	< 0.001 ***
<b>(B) Removed from model</b>			
Treatment	1	1.47	0.225
Treatment × Trial	1	0.45	0.504

## 1.4. DISCUSSION

This study demonstrated that in a population of hungry individuals the use of signaling during encounters increases and that it is apparently not an effect associated with increase of the frequency of encounters because in a male density treatment I did not observe an increase in the use of signals as the frequency of encounters increased from the first to the second trial (from high to low density). The results are consistent with previous studies showing that water striders become territorial above certain threshold of hunger (Wilcox 1972, Wilcox 1979, Wilcox and Ruckdeschel 1982, Hart 1987, Blanckenhorn 1991), and that they use the signals to defend territories and remain locally dominant (Jablonski and Wilcox 1996). More generally, water striders, *G. remigis*, increased the monopolization of resources valuable for fitness, such as food and mates, when resource availability decreased (Blanckenhorn *et al.* 1998). Signaling by *G. latiabdominis* may be one of several territorial behaviors used to secure resources similarly to *Gerris remigis* with a repertoire of several behaviors for territorial defense: ‘swimming at an intruder’, ‘lunging at an intruder’, ‘jumping on intruder’ (Wilcox and Ruckdeschel 1982). These kinds of behaviors would be more energy consuming and require leaving the local spot with high probability of food arrival (e.g. an insect floating brought by a water current) than signaling,

which allows an individual to remain in the same position. Ripple signals are also used to compete for food and to make competitors retreat (Jablonski and Wilcox 1996).

In *G. latiabdominis*, the high proportion of signaling only in females, but not males, when they are hungry, may imply that the female water striders use the ripple signal to occupy a lot of food resources and energy by keeping competitors away because they are able to secure a space for food resources without competitors. The females, unlike males, have to use extra nutrients and energy to produce eggs and therefore they may be more prudent in expanding the energy for costly behaviors. Thus, selection may favor in females, rather than males, the switch to using a less energetic signaling when their level of food deprivation increases. Although the display behaviors have potential costs to attract predators (Lang 1980, Magnhagen 1991, Han and Jablonski 2010), the females are likely to benefit anyway from securing resources, counterbalancing or surpassing the costs.

The result in females that there was an interaction effect between trial and size ratio in analyzing control and hunger together, while no interaction in analyzing control and density together, suggests that starvation could affect the use of signals by body size difference of signalers (stationary individuals) and intruders (approaching individuals). Water striders compete with one another for mates and food resources and defend territories (Wilcox and Ruckdeschel 1982, Rubenstein 1984, Jablonski 1996), and aggressive

dominance interactions might occur in this situation. Dominant individuals in the dominance interaction could have high fitness consequences because they occupy resources valuable for fitness.

When the female water striders were starved, smaller individuals increased the frequency of signaling compared to larger ones. The increase of signaling frequency in relatively small individuals might be considered as the indicator of dominance interaction, similarly to the research that high-frequency ripple signals used by males of the water strider *Aquarius remigis* increase the dominance of a non-territorial male (Jablonski and Wilcox 1996). Our study presents that the ripple signal in females of the water strider *G. latiablodominis* is probably used in a dominance-setting context and helpful for signalers (stationary individuals) to defend a space likely to contain resources valuable for fitness from intruders (approaching individuals) that try to search for food resources. This signaling will probably make the intruder (approaching individuals) recognize as if a signal sender (stationary individuals) is a strong rival. Resources, such as food, space, and mates, are usually limited in nature, so each individual has to fight and compete with one another in order to possess the resources, which facilitate to increase their fitness.

Water striders tend to establish their own territoriality until they are not at minimum hunger level that the animals can bear but close to a minimum level, then forage elsewhere before becoming dying condition (Wilcox and

Ruckdeschel 1982). The duration of maintaining territories is also affected by competitor density and level of food abundance (Hart 1987). In one species of water striders, *Gerris najas*, reproductive females exhibit territorial behaviors, while males are not (Vepsalainen and Nummelin 1985). Although *G. latiabdominis* can disperse in nature freely to a habitat with low population density and competitor density for resources by flying from a habitat with high population density and high competition, they cannot be freely distributed due to the high level costs of dispersal. Insects held at low competitor density and high food abundance can get greater fitness consequences than those at high density and low food level (Tramontin and Sih 1995), but free distribution does not always guarantee ideal habitats with low density and high food level, and the benefits from obtaining resources are counterbalanced by the increased costs of defense when a large number of competitors exist in the same habitat (Myers *et al.* 1979, 1981). Thus, the competition for resources valuable for fitness between individuals in limited space and high density could take place vigorously.

The decrease in density did not affect signaling and it only affected males with respect to the frequency of encounters: males increased encounter rate after density decreased. The sensitivity of males, but not females, to the density change may be related to crucial role of encounters for male, but not female, fitness. Male fitness, unlike that of females, depends on encounters with females, and therefore it increases approximately proportionately to the

frequency of encounters with females (Parker 1974). I suspect that at higher density (first trial) the individuals were sufficiently close to each other to be able to detect the sex identity of the individuals, but at the lower density they may need to move more in order to increase chances of encountering a female. This might have led to the increase in encounter rate for males in lower density. However, an alternative explanation is that at the higher density the individuals were so close to each other already that there was not sufficient “free space” in which they may move without being harassed by the nearest individuals.

When the water striders were in a hunger state, they moved around and encountered each other frequently compared to a non-hunger state. This condition can be explained as the behavior of organisms searching for food. Even if both females and males increased the number of encounters in a hungry state, only the females increased the frequency of signaling. I could infer that both the females and males of the water strider *G. latiauricularis* forage when they are hungry, but only females actively compete for food resources by producing the ripple signal.

## **Chapter 2. Comparison of predator avoidance strategies among three species of water striders from habitats of various predation risks**

### **2.1. INTRODUCTION**

Predation has long been considered as having a great effect on the behavioral and morphological characteristics of prey species over evolutionary time because prey has to survive by reducing predation risks and then pass on their genes to their posterity. Generally, prey species have evolved two types of survival mechanisms: predator-avoidance and predator-defense mechanisms (Brodie Jr *et al.* 1991). Mating and foraging behaviors increase the predation risk of prey because of attracting predators, so prey species tend to decrease these types of behaviors in order to reduce the predation risk. Prey species have evolved behavioral responses to the presence of predators. The responses will cause a balance between mating and foraging behaviors that increase genetic productivity and predator-avoiding behaviors to maximize their survivorship (Sih 1980, Gilliam and Fraser 1987, Werner

and Anholt 1993). In addition, the morphological traits of prey, which are less flexible than behavioral traits, play a crucial role in reducing predation risk.

The evolution of flexible (induced) responses and fixed (constitutive) defenses may present costs and benefits such as to keep finding resources under threat of predators (Dill 1987, Harvell 1990).

Prey species should be able to evaluate the threat level imposed by predators and fit their behavior into the threat level of the predators (Fraser and Huntingford 1986, Helfman 1989), which induce the flexible behavior of the prey (Harvell 1990). However, if flexible predator avoidance behavior is inappropriate and the cost of collecting and assessing information on predators is expensive due to the low survivorship by frequent attacks of various types of predators, the fixed predator avoidance behavior such as morphological characteristics will be favored in the evolution of prey species (Dill 1987). Animals have not adopted extreme strategies under the risk of predation in such a manner that focuses only on searching for resources regardless of the presence of predators or abandon all opportunities to find resources because of high risk of predation, so that such extreme strategies will drastically reduce fitness of animals (Lima and Dill 1990). Therefore, Prey species may have a combination of two types of anti-predator responses, flexible (induced) responses and fixed (constitutive) defenses, in order to reduce their natural vulnerability to predation. For water striders dwelling on the water surface, the threats of predators lead to a wide range of changes in

the insect's activity. These semi-aquatic insects spend most of their time on the water surface foraging and attempting to mate. In the case of mating activity, males molest very frequently females to mate and females try to resist the males that try to mate. When predators are absent, males appear to win in this struggle since males are able to harass and attempt mating with females incessantly without risks, eventually succeeding in mating. On the other hand, when predators are present, this situation is reversed in favor of females because males are less active to avoid predators and females are less harassed by males attempting to mate. The presence of predators is one of primary factors in changing the behaviors of water striders (Cooper 1984, Haskins *et al.* 1997, Krupa and Sih 1998, 1999).

Living organisms, such as fish and aquatic insects, under the water are potential predators of water striders that dwell on the water surface. The type and community of predators are related to the phenotypic traits of the insects. Many studies have revealed the relationship between behavioral characteristics and the presence of predators and compared behavioral responses among species to predators. Among those studies, Haskins *et al.* (1997) found that *A. conformis* moves more actively on the open water than *A. remigis* and spend their time on the water surface even in the presence of predators probably because of its superior moving speed and jumping ability. Only few studies, however, have considered the morphological traits that mediate the water striders' abilities to escape in response to the attacks of

predators. Although rowing locomotion have been analyzed (Hu *et al.* 2003) (Buhler 2007) and imitated with various degrees of biological reality (Suhr *et al.* 2005, Song and Sitti 2007, Suzuki *et al.* 2007), the morphological correlates of the ability to quickly jump away when attacked has not been studied. Therefore, I decided to study three water strider species that differ morphologically and live in habitats of different predation risks.

Three species of water striders, *Gerris latiabdominis*, *Gerris gracilicornis*, and *Aquarius paludum*, have lived in different types of habitats and each species have separately evolved different morphological traits (e.g. body shape and leg length). Streamline-like body shape and long legs will be probably beneficial for water striders to escape from attacks of predators because these characteristics may provide them with excellent escaping ability, such as quick striding or jumping speed on the water surface. Thus, these morphological traits useful for escape may be attributed to predation pressure. *A. paludum* has the most streamline-like body shape and longest legs in the three species of water striders. The morphological traits will greatly affect predator avoidance behaviors of water striders. However, it is not yet known how these three species respond to predators differently, whether the three exhibit different behavior patterns in the presence of predators, and whether the behaviors correlate with morphological traits.

I hypothesized that a species with streamlined body and long legs will have superior escaping ability and so differential predator avoidance behavior

from a species with short legs and less streamlined body.. I tested the predictions that *A. paludum* survives better than the other two species in the pool with predators, based on behaviors in the response to predators and escaping abilities and that the species relies more on the escaping ability caused by morphological states than other two species. In this study, I examined (1) whether the survival rate differs among three species, (2) how sensitive each is to approaching predators, (3) how use in microhabitat are displayed before and after attacked, (4) differences in jumping ability as escaping ability. The responses of the insects to predators could be affected by behavioral traits, such as mating strategies and competition, (Haskins et al. 1997) and by ecological traits, such like habitats, (Krupa and Sih 1999) characteristics. The most efficient anti-predator responses for semi-aquatic insects are fast escape movements (Andersen 1982) or rapid jumping (Jamieson and Scudder 1979) and both (Krupa and Sih 1999) in the moment of being attacked by their own predators. Theses anti-predator responses are closely related to the morphological traits of the insects as well as behavioral and ecological traits. Thus, I also examined (5) the morphological traits that contribute to the escaping ability of water striders.

## 2.2. METHODS

### 2.2.1. Study subjects and Laboratory conditions

*G. latiabdominis* were collected at Mt. Seon-Un Provincial Park near Kwangju in the Southwest part of Korea, and *G. gracilicornis* at Gwanak Mountain near Seoul National University, and *A. paludum* at Yongsan Family Park in Seoul, and then transported to a laboratory at Seoul National University, Seoul. The water striders were then put separately into rectangular plastic containers (41×26 cm, with a water depth of 5 cm) according to the sex of the species, and fed *ad libitum* (till satiation) with frozen crickets (*Verlarifictorus asperses*) each day. Four floating Styrofoam pieces (2: 40×3 cm, 0.3 cm in thickness, 2: 50×3 cm, 0.3 cm in thickness) were provided as resting sites on the edge of the containers. The next day after being transferred to the laboratory, every individual was marked on its thorax with a unique combination of color dots using enamel paints, which confers a singular ID on each individual. After marking, all individuals were photographed on a plastic board that had glued on plotting papers using a fixed digital camera. The water striders were kept in a 13h-light period and 11h-dark period cycle.

### 2.2.2. Experimental Procedure

### **2.2.2.1. Survivorship**

To find out whether each species has a different survival rate, I conducted survival experiments with the three species. After adapting to the experimental environment, six males and females of water striders were transported to one experimental plastic arena box (41×54 cm, with a water depth of 5 cm) per species. There were four replicates for this experiment. Four floating Styrofoam pieces (2: 40×3 cm, 0.3 cm in thickness, 2: 50×3 cm, 0.3 cm in thickness) were provided as resting and sheltering sites on the edge of the containers. Three days before the water striders were put onto the water in the containers, three *notonectidae* predators were placed into one container and then separated from each other so to prevent contact and cannibalistic actions. The predators had not been fed for three days, from when they were put into the boxes to when the water striders were placed into the containers. The experiment began when the six males and six females of water striders were placed into each experimental arena at 9AM. After that, I checked the sex and number of water striders killed by predators till 5PM the next day. During dark periods in light-dark cycle, water striders had not been checked whether they were alive or dead. When the experiment finished, the remaining individuals alive were scored as censored.

### **2.2.2.2. Escape Initiation Distance**

Experiments were conducted in a transparent plastic container (16×23 cm, 5 cm in water depth) to determine how reactive each species of water strider is to approaching predators. Two 1 cm graph papers were glued on the bottom of the container as an indicator of length. Using a high-speed video camera, 1000 frames per second (fps), the interaction between prey and predators was recorded from a vertical view. Twenty male individuals and female 20 ones of each water strider species were attacked by the predator, *notonectidae*, that had not been fed for 48 – 60 h in order to determine the escape initiation distance of each species (distance between the head end of predator and the body center of prey when escape begins) when water striders started moving their legs against the approaching predators (either by skating or jumping up). At this point, the escape initiation distance was measured from the body center of the water striders to the head end of the backswimmers. The measured pixels were converted to units of cm using the length indicators, for the analysis.

### **2.2.2.3. Microhabitat Use**

One experiment was carried out to determine whether predator avoidance induced the insects to disperse and influence their use of microhabitat. A rectangular plastic container (41×26 cm) filled with water (5 cm in depth) was divided into two compartments: one compartment (14×26

cm) with no Styrofoam pieces as resting and refuge sites was provided as a place for prey-predator interactions, and the other with three pieces of Styrofoam (2: 26×3 cm, 0.3 cm in thickness, 1: 20×3 cm, 0.3 cm in thickness) as an experimental place to determine the microhabitat choice of the prey. These two parts were divided with a milky acryl plate under the water and a transparent acryl plate on the water. The transparent one was lifted by hand in order to make it possible for the water striders to move toward the other compartment with no predator after being attacked by a predator in a small compartment. After the prey moved to a large place, the prey and predator were isolated by two acryl plates and contact was never initiated again during the experiment. From that point, the behavior of the water strider in the large compartment was recorded with a digital video camera (SONY Handycam HDR-SR1) from a vertical view for 360 seconds. The behavior filmed for 30 seconds at the beginning and the end was excluded in the measured time in order to remove noise caused by prey-predator interactions and by stabilization on the place. This experiment was performed twice with the same individuals. With one individual, this subject was first recorded with no attack by a predator, and then, the one was filmed for a second time with no attack by a predator two days after. With the other individual, the insect was first recorded with no attack, and then, one was filmed for the second time with an attack by a predator two days afterwards. All these procedures were used for

both sex in each species (*G. latiabdominis* – F: 13, M: 14, *G. gracilicornis* – F: 13, M: 15, *A. paludum* – F: 15, M: 15). Behavior type for microhabitat use was divided into two: staying on the water surface as water time and staying off the water surface (staying on the Styrofoam pieces) as shelter time. The time proportion of the two was used for analysis.

#### **2.2.2.4. Jumping ability**

When predators attack water striders from under the water, the semi-aquatic insects avoid the predators by mainly skating or jumping on the water surface. In an experiment, I compared the three species with regard to their abilities to avoid being captured by a predator and measured their jumping performance and their morphological traits relevant to the jumping performance.

I used two synchronized high-speed cameras (1000fps) to make a film of the jumps of water striders from the water surface at right angle views. The experimental subjects were put into two small perfect square acryl boxes (5×5×5 cm, with a water depth of 2 cm for *G. latiabdominis* and *G. gracilicornis*, 7×7×7 cm, with a water depth of 3 cm for *A. paludum*) since *A. paludum* is too large to be placed into a small one. The 4 side planes of the boxes had 1 cm scale indicators used later to calculate the distances from the video. A bend wire was used to mimic a predator's attack to make the water striders

jump up onto water within the arena (Figure or a photo/ screen shot). After filming, the coordinates of the body center, mid leg joint, and hind leg joint were extracted at five-frame time intervals in order to determine body speed. Near the moment when the water surface meniscus depressed by the leg of a water strider reaches maximum depth I used one frame resolution. I also extracted the latency between the initiation of leg movements and the moment when they reached the maximum depth (i.e. at the maximum depth of the meniscus). The latter measurement indicates how fast the maximum force for the jump is created because they should produce enough force to avoid attacks before predators reach or capture their body. In each species, some individuals were recorded several times and some only once because some jumped up more often on the water surface compared to the others with only one jump when they were stimulated by the wire. Six females and males for *G. latiabdominis*, six females and eight males for *G. gracilicornis*, and six females and eight males for *A. paludum* were used in this experiment.

#### **2.2.2.5. Morphological characteristics**

I measured the morphological characteristics for 24 individuals for each sex in each species, including all individuals that were used in the “jumping” experiment. Each individual was weighed (fresh body mass), and the length of two legs of femur, tibia, tarsus of one of the mid legs and one of the hind legs

ware measured with the Image J program (<http://imagej.nih.gov/ij/>) from digital photos of the individuals. The length of the legs was measured separately for the femur, tibia, and tarsus. The weight of the water striders was measured using a weighing scale (unit: g) with down to four digits of decimals.

When water striders skate and jump up on the water surface, they use their mid legs and hind legs to exploit the surface tension of the water, which gives the insects the driving force for moving on the water surface. For this, water striders build a meniscus below their legs that does not pierce the water surface toward under the water. This force produced by four legs (two mid legs and hind legs) of the water striders should be considered in terms of the weight of each species because the produced force for moving is restricted by the weight. If two individuals with different weights, one heavy and the other light, produce the same force for moving, the lighter individuals will be better at moving quickly than that of the heavier ones.

Small objects can float on a liquid surface because the surface tension of the liquid provides the counteracting force that supports the object's weight on the surface, shaping a meniscus around the face of the object that is in contact with the liquid. Thus, a small thin cylinder is able to float at the interface between gas and liquid until the maximum depth (Vella *et al.* 2006). Semi-aquatic insects, such as water striders, that walk and slide or jump on the water surface have used the force provided by the surface tension of water

to avoid being drowning (Hu *et al.* 2003, Gao and Jiang 2004, Bush and Hu 2006). The flexible cylinder imposes less supporting force per unit length needed for floating than a rigid cylinder when in the same depth, and the long length of the cylinder provides larger contact length to water than short one of that, (Vella 2008). The ideal conditions for semi-aquatic insects to exploit the supporting force for jumping are a long, rigid leg length, which helps the insects to exploit more supporting force on the water.

I assumed that the tibia plus the tarsus length of the leg in water striders (**contacted leg length**) plays critical role in building or shaping the meniscus on the water and obtaining a surface tension force when they jump up. In this case, I considered the mid leg and hind leg of water striders because the meniscus occurs both with the mid leg and hind leg and assumed that the meniscus formed by the two mid legs or two hind legs are equivalent. For inter-specific comparison, I considered the contacted leg length in the relation to the weight.

### **2.2.3. Statistical analysis**

#### **2.2.3.1. Survivorship**

Sixty per cent of the data were censored; 33% by *G. latiabdominis*, 22% by *G. gracilicornis*, 48% by *A. paludum*. The data were analyzed with Cox regression, a non-parametric form of survival analysis (Cox 1972). Species (*G.*

*latiabdominis* [L], *G. gracilicornis* [G], and *A. paludum* [P]) and sex (*female* and *male*) were used as explanatory variables in order to examine the effect on survival under the condition that predators are present. Tukey's test was used for comparisons among species. For simplicity of the interpretation, a six-level factor was made rather than a two-level factor nested within species, *G. latiabdominis female* [LF], *G. latiabdominis male* [LM], *G. gracilicornis female* [GF], *G. gracilicornis male* [GM], *A. paludum female* [PF], and *A. paludum male* [PM]. The factor was also analyzed in way to make intra- and inter-sexual comparisons within and between species.

#### **2.2.3.2. Escape Initiation Distance**

I conducted two-way ANOVAS to analyze the data on escape initiation distance as the response variable with two treatments, species (*G. latiabdominis*, *G. gracilicornis*, and *A. paludum*) and sex (*female* and *male*) as well as the interaction among them. The model selection procedure was performed with the model. After model selection, Tukey's test was also conducted to make a multiple comparisons between the levels of the treatments. These analyses identified if the prey species responded to the approaching predators differently.

#### **2.2.3.3. Microhabitat Use**

I examined the effect of a predator's presence on the proportion of time (within 300sec) during which the water strider stays in the open water calculated as  $(\textit{duration of being exposed}) / (\textit{duration of being exposed} + \textit{duration of being sheltered})$ . Because the data on the proportion of time on the water did not follow a normal distribution, a non-parametric test, the Wilcoxon rank sum test, was used here. The test was done only in same species. Two types of subjects per sex were used in this experiment: one subject is never experienced predators during a series of two trials (1<sup>st</sup> and 2<sup>nd</sup>) as the control [C1 and C2] and the other had no experience with the predator in the 1<sup>st</sup> trial and had experience with the predator only in the 2<sup>nd</sup> trial as a treatment [T1 and T2]. A pair-wise test was used only for comparison within the control and treatment each, but not between the control and treatment. Within species, there was also the test between the two sexes only with the treatment. The data of all three species were analyzed in the same way. To determine whether there was an inter-specific difference in microhabitat use after being attacked, inter-specific comparisons were conducted with the second treatment, T2, for each species within the same sex.

#### **2.2.3.4. Jumping ability**

Generalized Linear Mixed Model (GLMM) was used to examine the effects of the fixed factors, species (*G. latiabdominis*, *G. gracilicornis*, and

*A. paludum*) and sex (*female* and *male*), as well as the interactions among them, on body speed and time to max depth. The identities of individuals were used as random factors. For an exact estimation, model selection was performed. For the statistical models chosen in the analysis, I conducted Tukey's tests to evaluate significance of pairwise comparisons between the species and sexes.

### **2.2.3.5. Morphological Characteristics**

I examined the effect of the morphological condition on how well water striders exploited the surface tension of water for moving. I performed two-way ANOVA for two separate response variables (morphological condition for the contacted mid leg and hind leg length estimated as residuals from a linear regression of the body mass on the tibia plus tarsus length for each mid leg and hind leg [each hereafter called contacted mid leg length (CML), contacted hind leg length (CHL)]) and used species (*G. latiabdominis*, *G. gracilicornis*, and *A. paludum*) and sex (*female* and *male*) as explanatory variables, as well as the interactions among them. Multiple comparisons (Tukey's 'Honest Significant Difference[HSD]' test) were conducted to examine differences between the levels and then the p-value in the multiple comparisons was adjusted.

## 2.3. RESULTS

### 2.3.1. Survivorship

There were significant species effects (Wald = 14.59, d.f. = 2,  $p < 0.001$ ), and no sex effects (Wald = 1.71, d.f. = 1,  $p = 0.191$ ) on survival. *A. paludum* survived significantly better than *G. gracilicornis* (Wald = 3.73, d.f. = 1,  $p < 0.001$ ), but not *G. latiabdominis* (Wald = 2.11, d.f. = 1,  $p = 0.086$ ) (Fig 2.1.). *G. latiabdominis* and *G. gracilicornis* had similar survival rate (Wald = 1.93, d.f. = 1,  $p = 0.127$ ). In the six-level factor analysis, females of *A. paludum* survived significantly better than males of *G. gracilicornis* (Wald = 3.10, d.f. = 1,  $p = 0.021$ ) and marginally better than females of *G. gracilicornis* (Wald = 2.79, d.f. = 1,  $p = 0.054$ , comparisons with LF and LM, all  $p > 0.1$ ). Females of *A. paludum* had the best survival best, and males of *G. gracilicornis* had the worst survival (Fig 2.1.).

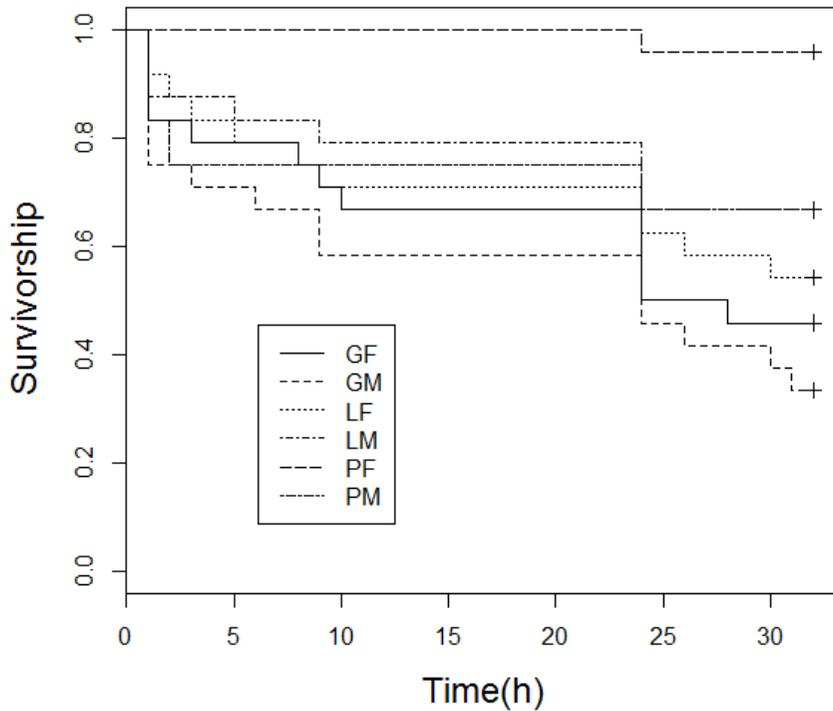


Figure 2.1. Survival curves for water striders. Curves are the probability of surviving predation as the function of time, accounting for censoring due to survival to the end of the study period. Long gap without mortality correspond to overnight period when checking is not done. (PF: *A. paludum* female, PM: *A. paludum* male, GF: *G. gracilicornis* female, GM: *G. gracilicornis* male, LF: *G. latiabdominis* female, LM: *G. latiabdominis* male)

### 2.3.2. Escape Initiation Distance

There was no significant effect of interaction between species and sex ( $F = 0.39$ , d.f. = 2,  $p = 0.679$ ) on the escape initiation distance. After removing the interaction term from the model, there was a significant effect of species ( $F = 10.10$ , d.f. = 2,  $p < 0.001$ ) and sex ( $F = 4.20$ , d.f. = 1,  $p < 0.05$ ) on the escape initiation distance. Females perceived predators at longer distance than males ( $F = 4.21$ , d.f. = 1,  $p < 0.05$ ). In multiple comparisons using Tukey's test, *A. paludum* was more significantly reactive to approaching predators than *G. gracilicornis* ( $p < 0.001$ ) and *G. latiabdominis* ( $p < 0.01$ ). *G. gracilicornis* and *G. latiabdominis* were similarly reactive to approaching predators ( $p = 0.730$ ) (Fig 2.2.)

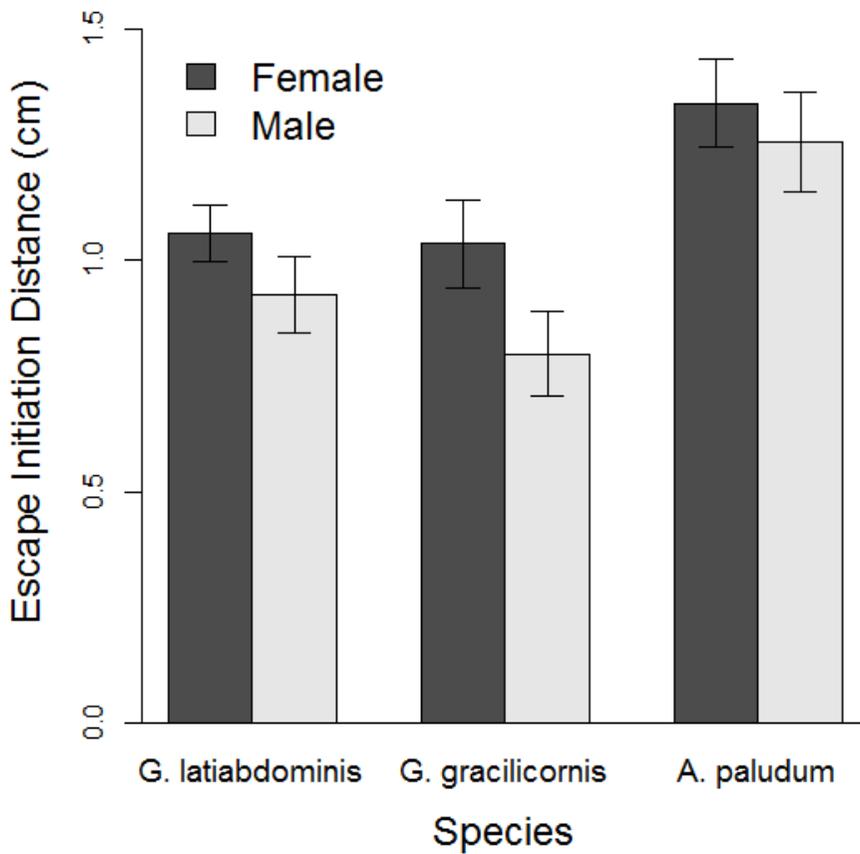


Figure 2.2. Reactive (escape) distances of water striders in the approach of a predator, *notonectidae*. Escape initiation distance means distance between head end of a predator and body center of prey when prey started moving own legs by perceiving the coming predator.

### 2.3.3. Microhabitat use

In *G. latiabdominis*, individuals avoiding attacks from a predator spent more time out of the water than ones that were not attacked. There was significant difference between treatment1 [T1] and treatment2 [T2] (Females; paired test,  $V = 52$ ,  $p < 0.05$ , Males; paired test,  $V = 65$ ,  $p < 0.01$ ; Figure 2.3b), but not between control1 [C1] and control [C2] (Females; paired test,  $V = 4$ ,  $p = 0.789$ , Males; paired test,  $V = 20$ ,  $p = 0.812$ ; Figure 2.3a) (Table 2.1). Individuals in treatment2 [T2], when attacked, stayed significantly longer in the resting sites that provide them with places where they could avoid predators than those in control2 [C2], when not attacked (Females;  $W = 21$ ,  $p < 0.0001$ , Males;  $W = 18.5$ ,  $p < 0.0001$ ) (Figure 2.3; Table 2.1). There was no difference between females and males in microhabitat use before and after attacked by predators (Female treatment1 [T1] and Male treatment1 [T1];  $W = 90$ ,  $p = 0.976$ , Female treatment2 [T2] and Male treatment [T2];  $W = 61$ ,  $p = 0.076$ ) (Figure 2.3; Table 2.2).

In *G. gracilicornis*, both females and males did not change tendency of microhabitat use between before and after attacked : treatment1 [T1]-treatment2 [T2] (Females; paired test,  $V = 3$ ,  $p = 0.583$ , Males; paired test,  $V = 3$ ,  $p = 0.371$ ), control1 [C1]- control2 [C2] (Females; paired test,  $V = 2$ ,  $p = 1$ , Males; paired test,  $V = 2$ ,  $p = 1$ ), and control2 [C2]-treatment2 [T2] (Females;  $W = 85$ ,  $p = 1$ , Males;  $W = 104$ ,  $p = 0.584$ ) (Figure 2.3; Table 2.3).

In addition, there was no difference between females and males in the changes of microhabitat use (Female treatment1 [T1] and Male treatment1 [T1];  $W = 120, p = 0.060$ , Female treatment2 [T2] and Male treatment2 [T2];  $W = 93, p = 0.731$ ) (Figure 2.3; Table 2.4).

In *A. paludum*, both sexes remained longer in the resting sites after avoiding attack from a predator than before attacked (treatment 1 [T1] - treatment2 [T2] comparison; Females: paired test,  $V = 94, p < 0.05$ , Males: paired test,  $V = 101, p < 0.05$ ) (Figure 2.3b; Table 2.5). However, the tendency to change microhabitat uses after experiencing predators was not clear for females (control2 [C2] - treatment2 [T2] comparison; Females:  $W = 61, p = 0.106$ , Males:  $W = 35.5, p < 0.01$ ) (Figure 2.3a; Table 2.5). This species had no intersexual difference in change of microhabitat use due to experiences with predators (Female treatment1 [T1] and Male treatment1 [T1];  $W = 122, p = 0.830$ , Female treatment2 [T2] and Male treatment2 [T2];  $W = 136.5, p = 0.762$ ) (Fig 2.3; Table 2.6).

Individuals in treatment2 [T2] of each species, that is, after attacked, were used for the inter-specific comparison. For females, *G. gracilicornis* spent more time in remaining on the water surface than the other two species, *G. latiabdominis* and *A. paludum* (comparison between *G. gracilicornis* and *G. latiabdominis*;  $W = 18, p < 0.001$ , comparison between *G. gracilicornis* and *A. paludum*;  $W = 178, p < 0.001$ ; Figure 2.3b; Table 2.7). There was no difference between *G. latiabdominis* and *A. paludum*. For males, *G.*

*latiabdominis* remained on the water for the shortest time after attacked, *A. paludum* for an intermediate time, and *G. gracilicornis* for the longest time (comparison between *G. gracilicornis* and *G. latiabdominis*;  $W = 8.5$ ,  $p < 0.001$ , comparison between *G. gracilicornis* and *A. paludum*;  $W = 207$ ,  $p < 0.001$ , and comparison between *A. paludum* and *G. latiabdominis*;  $W = 24$ ,  $p < 0.001$ ; Figure 2.3b; Table 2.7).

*G. latiabdominis* and *A. paludum* shifted staying places in the presence of predators, but *G. gracilicornis* did not change the place where it remained in the presence of predators.

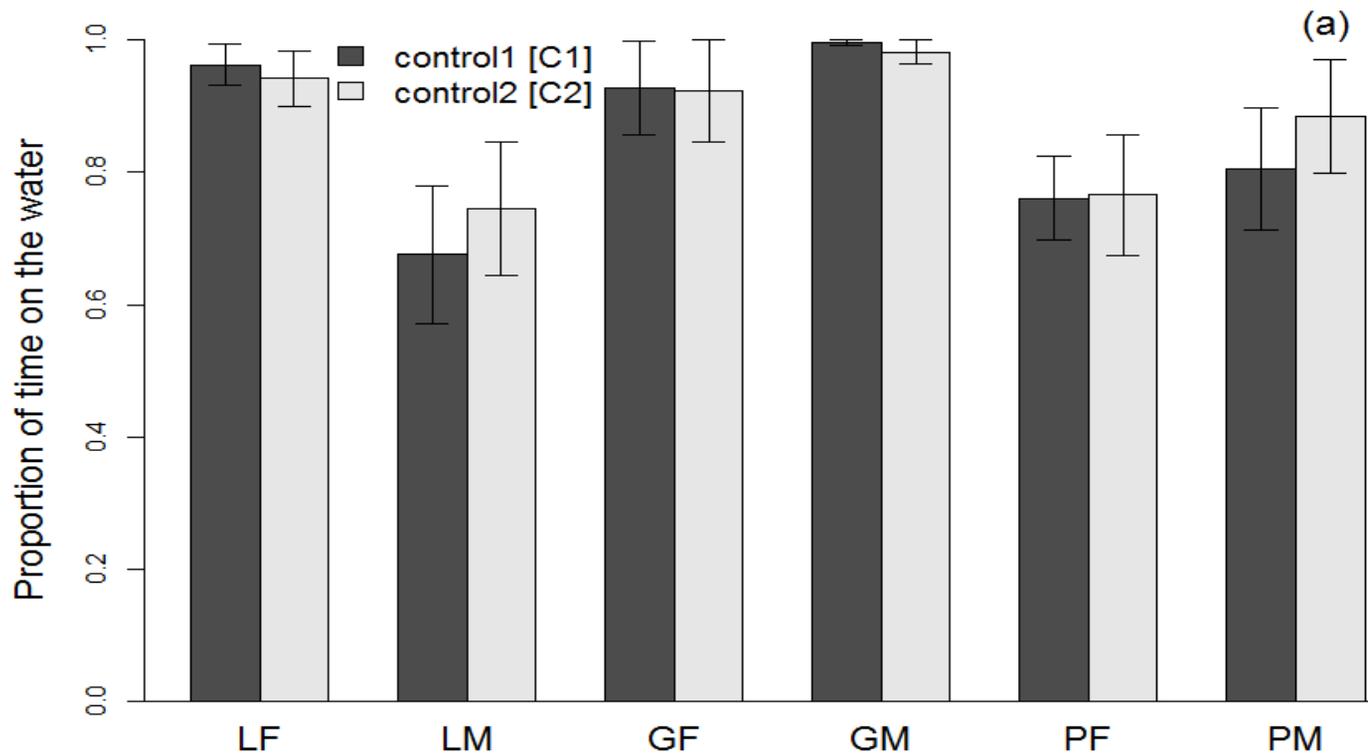


Figure 2.3. The time proportion of how long water striders stay on the water against on the shelter. (a) control (individuals not attacked in both C1 and C2), (b) treatment (individuals attacked only in T2, not T1);

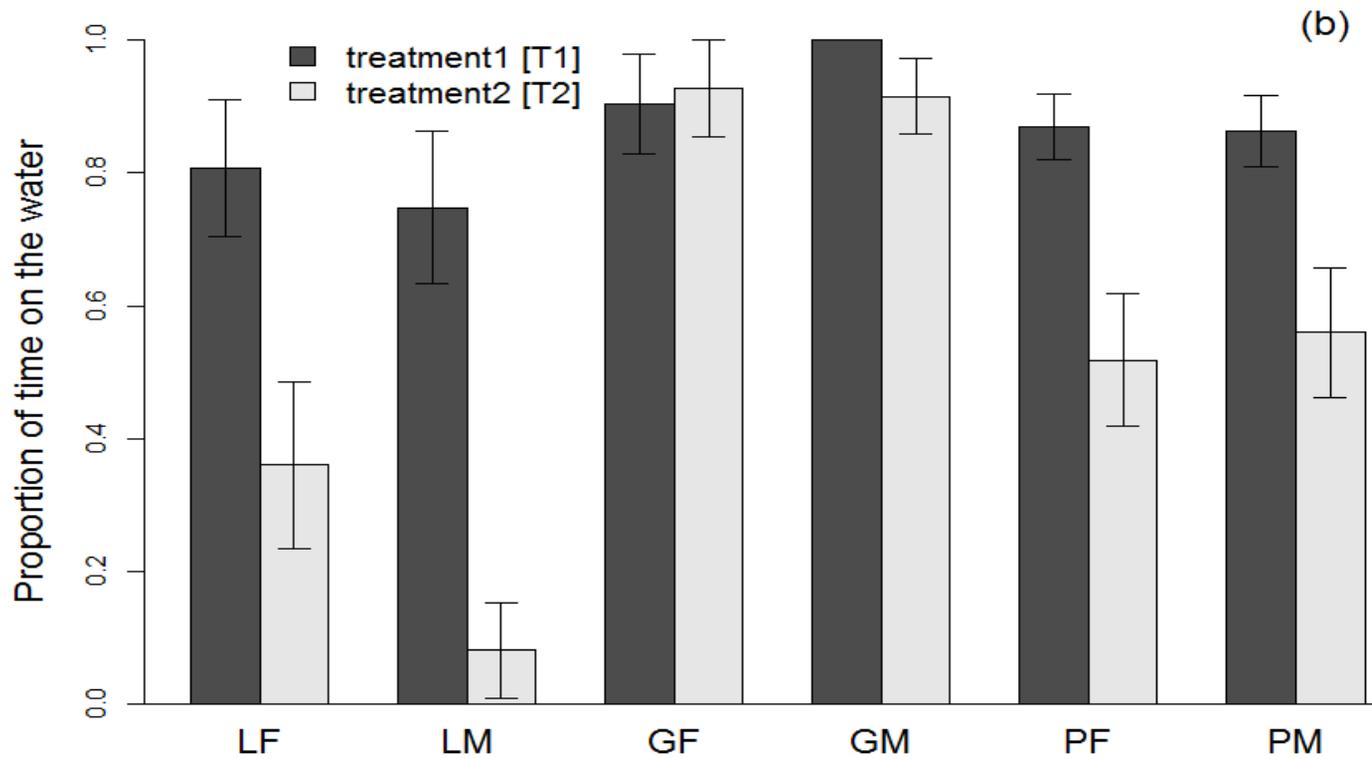


Figure 2.3. (Continued.) Table 2.1 and Table 2.2 for *G. latiabdominis* [L], Table 2.3 and Table 2.4 for *G. gracilicornis* [G], Table 2.5 and Table 2.6 for *A. paludum* [P], and Table 2.7 for inter-specific comparison.

Table 2.1. Microhabitat use in *G. latiabdominis* [L]; proportion of time spent on the water surface during 300-sec trials before and after attacked by a predator (control1 [C1] and control2 [C2]: 1<sup>st</sup> and 2<sup>nd</sup> trial of same individuals in control (Figure 2.3a), treatment [T1] and treatment [T2]: 1<sup>st</sup> and 2<sup>nd</sup> trial of same individuals in treatment (Figure 2.3b); only individuals in treatment2 [T2] experienced the attack of a predator)

Sex	Comparison variables	Statistics	<i>p</i>
Female [F]	T1 – C1	W = 69.5	0.314
	T2 – C2	W = 21	< 0.001 ***
	T1 – T2 (paired)	V = 52	< 0.05 *
	C1 – C2 (paired)	V = 4	0.789
Male [M]	T1 – C1	W = 111	0.514
	T2 – C2	W = 18.5	< 0.001 ***
	T1 – T2 (paired)	V = 65	< 0.01 **
	C1 – C2 (paired)	V = 20	0.813

Table 2.2. Difference in microhabitat use between females and males of *G. latiabdominis* [L]

Comparison variables	Statistics	<i>p</i>
Female T1 - Male T1	W = 90	0.976
Female T2 - Male T2	W = 61	0.076

Table 2.3. Microhabitat use in *G. gracilicornis* [G]; proportion of time spent on the water surface during 300-sec trials before and after attacked by a predator (control1 [C1] and control2 [C2]: 1<sup>st</sup> and 2<sup>nd</sup> trial of same individuals in control (Figure 2.3a), treatment1 [T1] and treatment2 [T2]: 1<sup>st</sup> and 2<sup>nd</sup> trial of same individuals in treatment (Figure 2.3b); only individuals in treatment2 [T2] experienced the attack of a predator)

<b>Sex</b>	<b>Comparison variables</b>	<b>Statistics</b>	<b><i>p</i></b>
Female [F]	T1 – C1	W = 78	0.655
	T2 – C2	W = 85	1
	T1 – T2 (paired)	V = 3	0.584
	C1 – C2 (paired)	V = 2	1
Male [M]	T1 – C1	W = 120	0.351
	T2 – C2	W = 104	0.524
	T1 – T2 (paired)	V = 3	0.371
	C1 – C2 (paired)	V = 2	1

Table 2.4. Difference in microhabitat use between females and males of *G. gracilicornis* [G]

<b>Comparison variables</b>	<b>Statistics</b>	<b><i>p</i></b>
Female T1 - Male T1	W = 120	0.059
Female T2 - Male T2	W = 93	0.732

Table 2.5. Microhabitat use in *A. paludum* [P]; proportion of time spent on the water surface during 300-sec trials before and after attacked by a predator (control1 [C1] and control2 [C2]: 1<sup>st</sup> and 2<sup>nd</sup> trial of same individuals in control (Figure 2.3a), treatment1 [T1] and treatment2 [T2]: 1<sup>st</sup> and 2<sup>nd</sup> trial of same individuals in treatment (Figure 2.3b); only individuals in treatment2 [T2] experienced the attack of a predator)

Sex	Comparison variables	Statistics	<i>p</i>
Female [F]	T1 – C1	W = 126.5	0.154
	T2 – C2	W = 61	0.106
	T1 – T2 (paired)	V = 94	< 0.05 *
	C1 – C2 (paired)	V = 31.5	0.929
Male [M]	T1 – C1	W = 101	0.831
	T2 – C2	W = 35.5	< 0.01 **
	T1 – T2 (paired)	V = 101	< 0.05 *
	C1 – C2 (paired)	V = 7	0.141

Table 2.6. Difference in microhabitat use between females and males of *A. paludum* [P]

Comparison variables	Statistics	<i>p</i>
Female T1 - Male T1	W = 122	P = 0.830
Female T2 - Male T2	W = 136.5	P = 0.762

Table 2.7. Inter-specific difference in microhabitat use after experiencing the attack of a predator (Only treatment2 [T2] of each species was used for the comparison (Figure2.3b))

<b>Sex</b>	<b>Inter-specific comparison</b>	<b>Statistics</b>	<b><i>p</i></b>
	<i>G.latiabdominis</i> [L] – <i>G. gracilicornis</i> [G]	W = 18	< 0.001 ***
Female [F]	<i>G.latiabdominis</i> [L] – <i>A. paludum</i> [P]	W = 77.5	0.243
	<i>G.gracilicornis</i> [G] – <i>A. paludum</i> [P]	W = 178	< 0.001 ***
	<i>G.latiabdominis</i> [L] – <i>G. gracilicornis</i> [G]	W = 8.5	< 0.001 ***
Male [M]	<i>G.latiabdominis</i> [L] – <i>A. paludum</i> [P]	W = 24	< 0.001 ***
	<i>G.gracilicornis</i> [G] – <i>A. paludum</i> [P]	W = 207	< 0.001 ***

### 2.3.4. Jumping ability

There were no effects of sex and of an interaction between species and sex and there was only the effect of species ( $\chi^2_2 = 8.72, p < 0.05$ ) on body speed. Multiple comparisons revealed that only *G. gracilicornis* and *G. latiabdominis* differed significantly in body speed ( $z = 2.69, p < 0.05$ ). There were effects of species ( $\chi^2_2 = 68.37, p < 0.001$ ) and sex ( $\chi^2_1 = 22.30, p < 0.001$ ) and of an interaction between species and sex ( $\chi^2_2 = 7.73, p < 0.05$ ) on the time to max depth. Considering an interaction between species and sex, multiple comparisons were conducted separately for each factor, species and sex. The legs of *G. latiabdominis* reached maximum depth to achieve force for jumping more quickly than the other two species, *G. gracilicornis* ( $z = 7.27, p < 0.001$ ) and *A. paludum* ( $z = 9.10, p < 0.001$ ). *G. gracilicornis* and *A. paludum* did not differ significantly in the time to achieve the maximum force for jumping. Males took less time to reach the maximum depth for jumping than that of the females ( $z = 4.46, p < 0.001$ ).

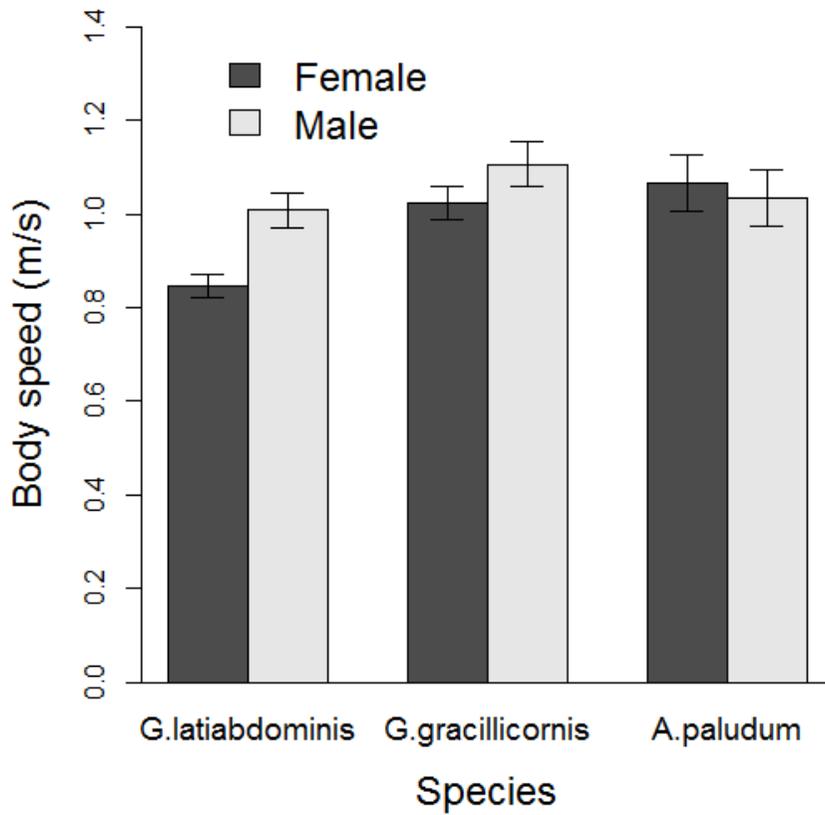


Figure 2.4. Body velocity of water striders when they jump up on the water surface.

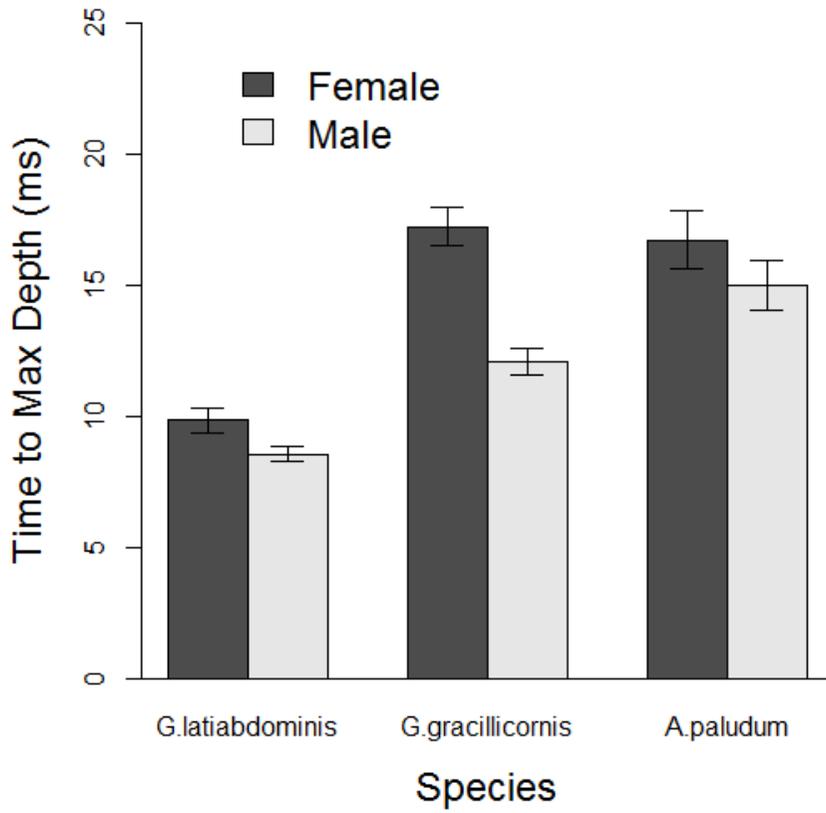


Figure 2.5. Time to take mid leg of the insect to reach maximum depth in meniscus.

### 2.3.5. Morphological characteristics

For the contacted mid leg length (CML), there were significant effects of species ( $F = 74.74$ ,  $df = 2,138$ ,  $p < 0.001$ ) and sex ( $F = 89.86$ ,  $df = 1,138$ ,  $p < 0.001$ ) as well as interaction ( $F = 11.78$ ,  $df = 2,138$ ,  $p < 0.001$ ). In addition, for the contacted hind leg length (CHL), there were significant effects of species ( $F = 84.07$ ,  $df = 2,138$ ,  $p < 0.001$ ) and sex ( $F = 71.69$ ,  $df = 1,138$ ,  $p < 0.001$ ) as well as interaction ( $F = 8.91$ ,  $df = 2,138$ ,  $p < 0.001$ ) (Fig 2.6.).

For contacted mid leg length (CML), *A. paludum*(P) had the highest value, and the other two species, *G. latiabdominis*(L) and *G. gracilicornis*(G), did not differ significantly from each other (Table 2.8.). For the other response variable, contacted hind leg length (CHL), *A. paludum*(P) had a significant higher value than the other two species, but there was no difference between *G. latiabdominis*(L) and *G. gracilicornis*(G) (Table 2.8.). *G. gracilicornis* males and *A. paludum* males did differ significantly in weight ( $t = 12.95$ ,  $df = 46$ ,  $p < 0.001$ ), but the females of *G. gracilicornis*(G) and of *A. paludum*(P) did not differ significantly in weight ( $t = 0.10$ ,  $df = 37.96$ ,  $p = 0.92$ ). Although females of *G. gracilicornis*(G) and *A. paludum*(P) had similar weight, comparison of the morphological characteristics between the females in these two species would be a good indicator to infer how the morphological traits of water striders have an effect on jumping and moving ability. Females of *A. paludum* were significantly longer in contacted mid leg length (CML) and

contacted hind leg length (CHL) than the females of *G. gracilicornis* (Table 2.9).

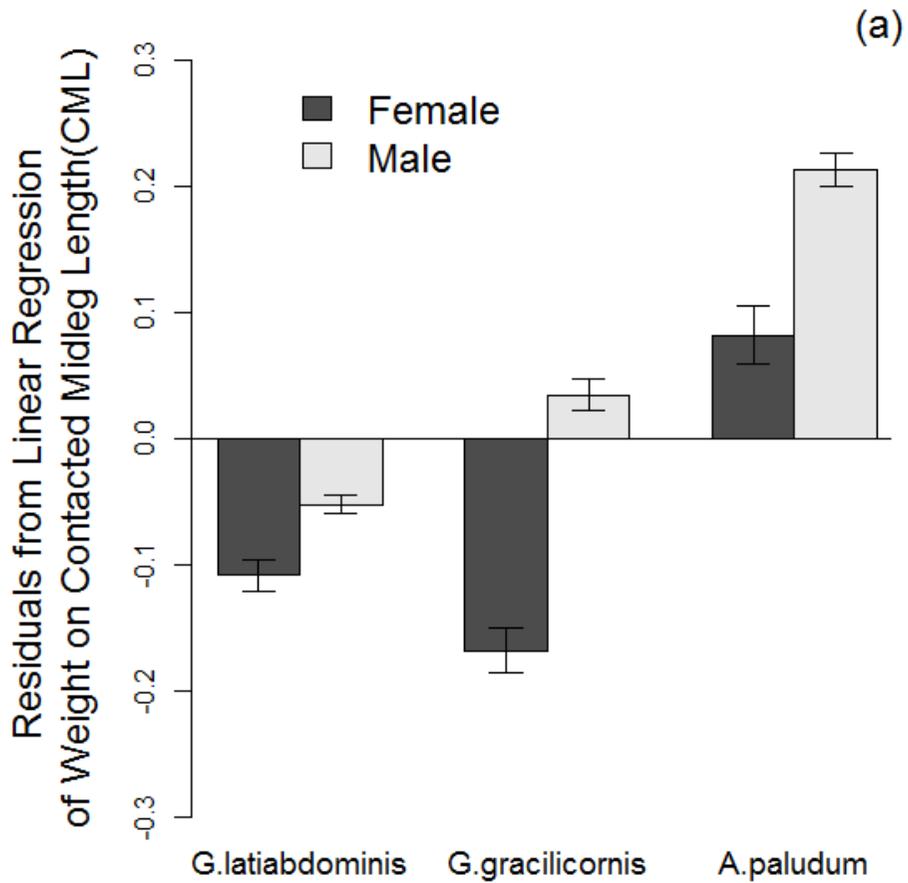


Figure 2.6. Residuals from linear regression of weight (a) contacted mid leg length (CML) and (b) contacted hind leg length (CHL) per sex per species. (Water striders support their own weight on the water surface by using a surface tension of water. The portion of tarsus and tibia in water strider's legs make a contact with water surface.)

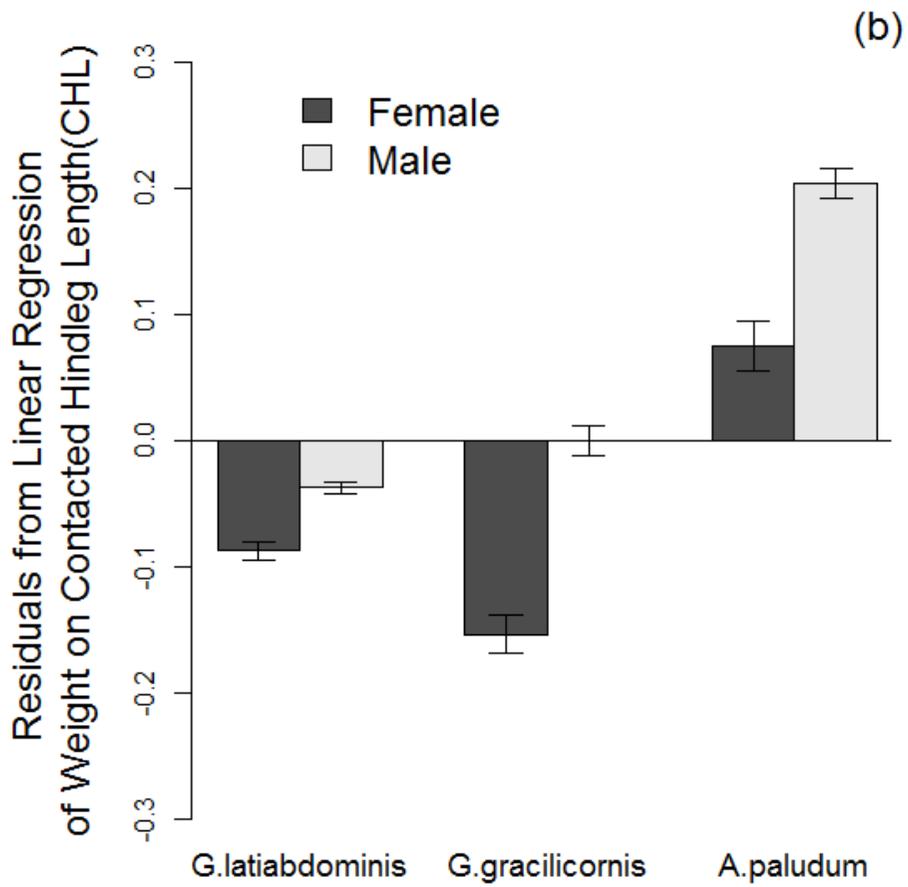


Figure 2.6. Continued.

Table 2.8. Tukey's Honest Significance Difference (Tukey HSD) multiple comparison tests for *species* in two-way ANOVAs of effects of *species* and *sex* on contacted mid leg length (CML) and contacted hind leg length (CHL). Comparison Source (L: *G. latiabdominis*, G: *G. gracilicornis*, P: *A. paludum*).

<b>Response variable</b>	<b>Comparison source</b>	<b>Difference</b>	<b>Adjusted <i>p</i></b>
contacted mid leg	L - G	-0.014	0.634
length (CML)	P - G	0.214	< 0.001 ***
	P - L	0.228	< 0.001 ***
contacted hind leg	L - G	0.014	0.498
length (CHL)	P - G	0.216	< 0.001 ***
	P - L	0.171	0.095

Table 2.9. Tukey's Honest Significance Difference (Tukey HSD) multiple comparison tests for *interaction* among *species* and *sex* in two-way ANOVAs of effects of *species* and *sex* on contacted mid leg length (CML) and contacted hind leg length (CHL). Comparison Source (F: Female, M: Male).

<b>Response variable</b>	<b>Comparison source</b>	<b>Difference</b>	<b>Adjusted <i>p</i></b>
contacted mid leg length (CML)	LF-GF	0.060	0.065
	PF-GF	0.250	< 0.001 ***
	GM-GF	0.202	< 0.001 ***
	LM-GF	0.115	< 0.001 ***
	PM-GF	0.381	< 0.001 ***
	PF-LF	0.190	< 0.001 ***
	GM-LF	0.143	< 0.001 ***
	LM-LF	0.056	0.100
	PM-LF	0.321	< 0.001 ***
	GM-PF	-0.047	0.234
	LM-PF	-0.134	< 0.001 ***
	PM-PF	0.131	< 0.001 ***
	LM-GM	-0.087	< 0.001 ***
	PM-GM	0.178	< 0.01 **
	PM-LM	0.265	< 0.001 ***

contacted hind leg length (CHL)	LF-GF	0.066	< 0.01 **
	PF-GF	0.229	< 0.001 ***
	GM-GF	0.154	< 0.001 ***
	LM-GF	0.116	< 0.001 ***
	PM-GF	0.357	< 0.001 ***
	PF-LF	0.162	< 0.001 ***
	GM-LF	0.087	< 0.001 ***
	LM-LF	0.050	0.072
	PM-LF	0.291	< 0.001 ***
	GM-PF	-0.075	< 0.001 ***
	LM-PF	-0.112	< 0.001 ***
	PM-PF	0.129	< 0.001 ***
	LM-GM	-0.037	0.314
	PM-GM	0.204	< 0.001 ***
PM-LM	0.241	< 0.001 ***	

Table 2.9. continued

## 2.4. DISCUSSION

My study revealed that three species of water striders, *G. latiabdominis*, *G. gracilicornis*, and *A. paludum*, behaved differently from each other when they were exposed to predators. These different responses to predators may cause different survival rate among the three species. It is well known that distribution of predation risk in the habitat affects the distribution of water strider individuals in the habitat (Cooper 1984, Haskins *et al.* 1997, Krupa and Sih 1999). Predation risk leads to reduction in mating (Sih and Krupa 1992, 1995, Krupa and Sih 1998, 1999), and foraging (Sih *et al.* 1990). The semi-aquatic insects avoid their predators at the edge of streams or out of the waters where predators under the water do not approach the insects. The inter-sexual struggles that occur during mating have high risks and costs for female water striders since the struggles attract predators and cause energetic expenditure. As well as reducing the chance of being attacked, escaping from predators in the moment of being attacked is one of important ways for survival. Andersen (1982) implied that fast escaping movements are probably efficient anti-predator response for semi-aquatic insects and Jamieson & Scudder (1979) reported vertical jumping as an anti-predator behavior.

Since these escaping and vertical jumping abilities are determined by the driving force made by the morphological characteristics of water striders, I

should take the morphological traits into account to evaluate the escaping ability from predators. However, few studies have suggested that morphological characteristics may affect escape movement, such like skating and jumping (Krupa and Sih 1999). From here on, I will first discuss how the morphology has an effect on escape movement from an engineering point of view. Next, I will discuss how survival in water striders is affected by escape movements, by the distance that they perceive between them and approaching predators and by the habitat distribution through a comparison of three species of water striders in our study.

In a model representing a water strider's jumping, it was assumed that semi-aquatic insects employ the force provided by surface tension in order for the insects to jump up on the water surface; thus, the velocity of the water strider's body during jumping was elicited from the surface tension force by the law of momentum conservation (EunJin unpublished). For simplification of the calculations, only values of change in the height of the body and legs were applied to the model. Vella *et al.* (2006) suggested that, in a static state, a thin and long cylinder could be floating at the interface between gas and liquid until the maximum depth (for water, 3.84mm) without piercing the water surface or breaking off the meniscus. The model of EunJin (unpublished) explains that water striders could have the maximum jumping speed of the body when the depth of the meniscus produced by the legs of water striders is about half of the insects' legs. For speedy jumping, while

water striders with long legs (*A. paludum* in our study) make a meniscus under each leg for jumping, the depth of which would be the maximum depth at the moment that the meniscus breaks off, the insects with short legs (*G. latiabdominis* in our study) would produce a meniscus with the depth of half their leg length. For water striders with long legs, it is beneficial that the meniscus is maintained for a long time because the insects could exploit the large surface tension for jumping, which increases the body speed in jumping. However, water striders with short legs do not need to reach the maximum depth of meniscus for maximum speed, which means that the insects could jump up with maximum speed in a short time.

As well as the exploited supporting force, mass should be taken into account when water striders make a movement since the weight of water striders affect the velocity of the body. Except for females in *G. gracilicornis* and *A. paludum*, all males and females in the three species differed in weight. Our results show that the females of *A. paludum* had significantly long legs compared to the females of *G. gracilicornis* even if the females of the two species had a similar weight. The fact that the females of the two species had a different leg length and similar weight may imply that the two species have different abilities in exploiting the surface tension on the water surface when they jump up or skate on the water. According to the model mentioned above, the females of *A. paludum* should have better jumping ability than the females of *G. gracilicornis*. In this study, there was no significant difference in body

speed for jumping between the females of the two species. The lack of difference may be attributed to three hydrodynamic factors.

First, in the model, the maximum depth to achieve the maximum force for jumping is approximately half of the leg length for semi-aquatic insects, but the legs in the females of *A. paludum* are too long to reach the optimal depth for jumping before the meniscus break down, preventing the insect from obtaining the maximum force provided by the surface tension for jumping and for the maximum body speed during jumping. Second, Vella (2008) described that the flexible cylinder beyond a certain length does not increase the usable total maximum force any further because the portion of the lengthened cylinder cannot make contact with the water surface and it does not provide even little force. This may mean that the females of *A. paludum* cannot get enough force to jump up better than the females of *G. gracilicornis* despite the fact that *A. paludum* has relatively long legs that enable the species to get more surface tension if the relatively long legs of the species make contact with water surface in menisci. Finally, increase in the length of a cylinder means increase in the flexibility of the cylinder, and the flexible cylinder supports less force per unit length than the rigid cylinder (Vella 2008). Thus, although *A. paludum* with relatively long legs make menisci of the same depth as *G. gracilicornis*, *A. paludum* is not probably able to achieve the enough force and momentum for jumping.

Hu (2003) illustrated the relation between leg length and body size in the *Gerridae* family of water striders showing that as the size of the insects increases, the legs become longer in proportion. Because the weight of the insect proportionally increases depending on its body size, the water striders with a large body size may evolve long legs, which enable them to distribute their weight on the water surface for floating on the water. Morphological differences, such as streamline body shape and leg length, in water striders may be able to explain different responses to predators between congener species since species with morphological modifications, such as long limbs, probably exhibit better speed and jumping ability than species with short limbs (Haskins *et al.* 1997, Krupa and Sih 1999). The superior jumping ability of a species with long limbs could be explained by the research of Vella (2008) that as the length of the cylinder increases, the maximum total force exploited by the cylinder increases, but the maximum total force does not increase if the length of the cylinder goes beyond some point.

Our result for “Time to Max Depth” is consistent with the idea of the model because short-limbed species with a relatively small weight (*G. latiabdominis* in our study) need relatively short time to achieve enough force for jumping, but *G. gracilicornis* and *A. paludum* did not differ in the time to achieve maximum force. This may be because of a limitation in the maximum depth of the meniscus produced by water striders (Vella *et al.* 2006). Water striders with heavy weight should get larger force and momentum for jumping

than those with light one. The large force and momentum could be achieved when the menisci are maintained for long, which means that legs of water striders stay within the menisci for long time. The surface tension force used for jumping depends on the meniscus shape; a horizontal meniscus gives more force provided by the surface tension than tiled and pointed menisci, and the shape of the meniscus depends on the length of the cylinder at the interface and the depth of the meniscus (Vella 2008). This means that maintaining the meniscus for a relatively longer time would provide a relatively larger momentum, and our result shows that the weighty species kept their meniscus longer to gain a momentum suitable for jumping. I assumed that the tibia plus the tarsus length of the legs is an important determinant of the meniscus shape made by water striders because parts of the tibia and tarsus in the legs of the insects are usually in touch with the water. In the contacted length of the legs in relation to weight, *A. paludum* had a significantly larger value than *G. gracilicornis*, but in jumping speed, the females in the two species did not differ significantly, which may mean that the shape of meniscus does not make a significant difference in the surface tension force for jumping between the two species.

Even if some species are related, they all do not have the same predator avoidance behaviors; few studies have presented the mechanisms describing why prey species have different responses to predators (Lima and Dill 1990, Werner 1991, Abrahams and Healey 1993, Peckarsky 1996).

Peckarsky (1996) showed that related prey species have different reactive distance when approached by predators and the species also differ in the species-specific predation risk. This difference may be attributed to a difference in morphological defenses and behavioral responses to common predators (Harvell 1990). Water striders with long limbs could be less likely to be killed by predators thanks to superior jumping ability provided by their own morphology (Haskins *et al.* 1997, Krupa and Sih 1999). For long-limbed species to jump up on the water surface, they have to maintain a meniscus for a relatively long time. This may imply that long-limbed species are very sensitive to approaching predators. Here, I found that *A. paludum* responded most quickly to the approach of a predator, which illustrate that the species has enough time to escape from a predator by skating or jumping. In addition, the reactive distance of prey species to predators may be determined by the complexity in predator communities or by the frequency of being attacked.

Predators can affect prey species in terms of distribution within a habitat and foraging success (Stein and Magnuson 1976, Peckarsky and Dodson 1980, Cooper 1984, Peckarsky 1996). There is conflict between searching for resources and staying safe when predators are abundant in the habitat. Haskins *et al.* (1997) suggested that species with morphological benefits that make speedy movement possible stay in the open water where predators attempt to attack the prey, and Krupa and Sih (1999) suggested that two species with a similar morphology exhibit the similar predator avoidance

responses. Our study revealed that *G. gracilicornis* with superior jumping ability stayed longer in the open water right after being attacked than that of the other two species. Although *A. paludum* had a similar jumping ability to *G. gracilicornis*, it had a relatively short time of staying on the water. This may mean that *A. paludum* is highly reactive and sensitive to attacks or approaches of predators. In addition, the high risk of being eaten by predators may induce prey species to stay in a safe place despite the costs from reduced foraging.

The predation risk of prey should be understood in terms of mating, competition, morphology, and ecology as well as prey-predator interaction because those factors could affect anti-predator responses (Krupa and Sih 1999). From the threat of predation, water striders actively make changes in mating dynamics (Sih 1988, Sih *et al.* 1990, Sih and Krupa 1992) because mating could greatly increase the chance of being attacked and decrease the survival rate. In our study, although *G. gracilicornis* had superior jumping ability, it had lower survival than that of *G. latiabdominis* when predators were present. Han and Jablonski (2010) demonstrated that *G. gracilicornis* males use a tapping signal to induce females to participate in copulation, along with attracting predators to come and attack the females. A long mating duration also increases predation risk; *G. gracilicornis* females postpone response to males mounted on them, called intromission, which puts females in danger of predation (Han and Jablonski 2010). Copulation in *G.*

*gracilicornis* is not coercive by males since females have hidden genitalia, so males have signaling behavior that allow females to copulate (Han and Jablonski 2009a). This behavior probably makes the males of the species invest more energy in copulation than other species with coercive mating behavior, so the males may exhibit post-copulation mounting for a relatively long time to ensure that their sperm are fertilized. Staying on the water in the presence of predators also keeps the species at high risk of predations.

The mating dynamics of *A. conformis* could be affected by inter-specific interference because social interaction of *A. conformis* with a related species, *A. remigis*, reduces mating activity of *A. conformis* and induces the species to choose a habitat with predators instead of the closely related species for mating (Haskins *et al.* 1997). This may imply that *A. conformis* have excellent escaping ability to avoid being eaten and do activities in the pool with predators given the choice between two pools, one including *A. remigis* and the other including predators. *A. conformis* and *A. nebularis* are sister species (Andersen 1990) with ecological and morphological similarities, and both species are very wary of predators (Krupa and Sih 1999). In our study, although *G. gracilicornis* and *A. paludum* had similar jumping ability, *A. paludum* was more cautious and reactive to predators than *G. gracilicornis*. This may indicate that jumping at the moment of a predator's attack is probably not an important determinant of survival. Long thin legs could enable semi-aquatics insect to float on the water with only the surface tension

force and provide them with speedy sliding on the water surface (Hu *et al.* 2003). I may not mention that the morphology of water striders plays a critical role in anti-predator behaviors or strategies even if the benefits of morphological modification help the insect to deal with predation risk.

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## 국 문 초 록

잔물결 의사소통은 반 수생곤충들 사이에서 이용된다. 소금쟁이는 구애, 교미, 성별 구분, 영토, 그리고 배우자 방어를 위해 잔물결 신호를 만들어낸다. 하지만, 모든 소금쟁이 종들이 같은 목적을 위해 잔물결 신호를 보내지 않는다. 나는 비교적 큰 무리에서 생활하는 경향을 가진 한 종의 소금쟁이 (*Gerris latiaabdominis*) 가 어떠한 상황에서 이러한 잔물결 신호를 만들어내는지 조사했다. 이 종의 암컷들은 배고픈 상태에서 더 자주 이러한 신호를 만들어 내었지만, 이러한 경향은 수컷에서는 발견되지 않았다. 이것은 신호를 만드는 것이 배고픈 암컷들이 경쟁자를 쫓아내고 음식 자원을 확보하는데 이용한다는 것을 암시한다. 하지만, 이러한 신호의 이용은 개체수의 밀도에 직접적인 관련성이 없고, 이 소금쟁이의 신호가 개체간 상호작용의 상관빈도와 밀도에 의해 영향을 받지 않는다는 것을 나타내주고 있다.

동물 종들은 생존을 위해 포식자가 많은 장소를 피해야 한다. 하지만, 이것이 불가능하다면, 피식자들은 그들 서식지에 있는 포식자로 하여금 피식자를 인지하도록 만들 수도 있는 교미행동과 섭식행동을 줄여야 한다. 그래서, 포식의 위험은 피식자 행동 패턴을 변

화시킨다. 서식지 마다 포식자의 유형과 수가 다르기 때문에, 모든 소금쟁이 종들이 같은 반 포식 행동 패턴을 가지고 있지 않다. 나는 세 종의 소금쟁이의 형태학적인 특징들에 근거하여 포식자에 대한 피식자의 특이적 반응들이 이 종들의 생존에 영향을 줄 것이라 가설을 세웠다. 따라서, 나는 반 포식행동으로서 미세서식지 사용, 포식자에 대한 반응도, 그리고 점프 능력을 측정하였다. 소금쟁이의 생존은 점프 능력 보다는 미세서식지 사용과 포식자에 대한 반응 정도가 관련이 있었다. 소금쟁이들이 포식자들로부터 공격받는 순간에 포식자로부터 도망가기 위해서, 뛰어난 점프능력을 가진 소금쟁이 종이 최고의 생존율을 나타낼 것이라 예측을 하였지만, 점프 능력에 대한 차이를 발견하지 못하였다. 이것은 유체 역학적이고 소금쟁이의 형태학적인 한계 때문일지도 모른다.

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