BIOTROPICA
THE JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

Space Use by a Neotropical Water Strider (Hemiptera: Gerridae): Sex and Age-Class Difference
Author(s): Nathaniel T. Wheelwright and Gerald S. Wilkinson
Source: *Biotropica*, Vol. 17, No. 2 (Jun., 1985), pp. 165-169
Published by: The Association for Tropical Biology and Conservation
Stable URL: http://www.jstor.org/stable/2388509
Accessed: 03-04-2015 22:09 UTC

NOTES

Space Use by a Neotropical Water Strider (Hemiptera: Gerridae): Sex and Age-class Differences

Differential movement patterns and microhabitat distributions of age classes have recently been reported in several water surface-inhabiting insects (Jamieson and Scudder 1974, Vepsalainen and Jarvinen 1974, Wilson *et al.* 1978, Birch *et al.* 1979). Juvenile age classes may be displaced because of aggression by adults (Wilson *et al.* 1978) or because of selection for different microhabitats (Vepsalainen and Jarvinen 1974). Differential use of space by adult males and females may be the consequence of other behaviors, such as selection of mates or oviposition sites.

This note describes differences in movement patterns and home range size by sex and age classes of a neotropical water strider, *Potamobates tridentatus* Esaki (Hemiptera: Gerridae). Although the intricate locomotory adaptations enabling water striders to skate on the water surface are understood (Milne and Milne 1978), ecological aspects of their movements remain poorly known. As with most insects, we know how water striders move, but not where they go, or how sexes and age classes differ in space use. We present evidence that distinct behavioral patterns are the consequence of differences in body size and ecological requisites, most importantly food and mates.

From 12 to 23 August, 1978, we studied water strider movement patterns in a small stream, the Quebrada Camaronal, at Sirena, Parque Nacional del Corcovado, Osa Peninsula, Costa Rica (8°23′N, 83°20′W), about one kilometer upstream from the Pacific Ocean. The vegetation surrounding the study site is predominantly secondary growth within Tropical Wet Forest (Holdridge 1967), with a discontinuous canopy and no emergent vegetation in the stream. In the mid-rainy season the stream in the study site varied in width from one to four meters and in depth from 5 to 60 cm. Current speed averaged 0.13 $m \cdot sec^{-1}$ and water temperature 25.5°C.

We captured 116 *P. tridentatus* individuals from the first 20 m of the study site and individually marked early instars, fifth instars, adult males, and adult females by painting the mesonota with small spots of enamel paint. We noticed no change in the behavior of water striders after marking. Third and fourth instars were indistinguishable, but fifth instars could be recognized by dorsal pattern, larger size, and the presence of wing buds. The sex of subadults could not be determined. Adult males and females differed in the form of their conspicuous genitalia. We measured middle femur lengths (chosen as a morphological character because of its direct relationship to stride length) on several individual third-fourth instars, fifth instars, and adult females and males; lengths averaged, respectively, 5.7 mm, 6.0 mm, 9.0 mm, and 8.9 mm.

After water striders were marked and left undisturbed for 24 h, we censused the study area in the mornings (0700 h) and/or afternoons (1600 h) on 13 August and from 16 to 23 August. We recorded the location of all individually marked water striders to the nearest 5 meters along a 115 m stream transect during each of 14 censuses. To determine space use on a finer scale, we studied movements while individuals foraged actively during the morning beneath a 2.5 m by 2.5 m frame suspended above the stream 20 m upstream from the lower end of the study site. The frame was divided by a string grid into 100 quadrats, each 625 cm^2. We conducted focal animal sampling for 25 five minute periods, noting at five second intervals the coordinates of the quadrat in which we observed marked individuals. If a focal animal did not remain under the grid for the entire five minute period, that sample was considered an incomplete observation and the data were not included in subsequent analyses.

We quantified four aspects of *P. tridentatus* movement patterns for each age and sex class: home range, activity center, and between-census movement distance, for which we used census data; and local feeding area diversity, for which we used five minute observation sample data. Home range was defined as the maximum distance between all observed locations of an individual; it is therefore a linear measure rather than a traditional measure of area. Activity center was calculated as the mean location (position along transect) of all resightings. We computed home ranges and activity centers only for those animals that were resighted on at least half of the 14 censuses. Between-census movement distances measured the distance moved between consecutive censuses. To determine local feeding area diversity (the tendency to forage widely or remain in a restricted area), we used the Shannon-Wiener information index, $H' = -\Sigma\, p_i \ln p_i$ (Pielou 1974), where p_i was the proportion of time spent in each quadrat during each five minute sampling period.

During the censuses, focal animal sampling, and miscellaneous observations between census periods, we noted feeding behavior and the identities of copulating individuals. Unless otherwise indicated, all statistical tests are two-tailed and are described in Sokal and Rohlf (1969).

The proportions of adult male, adult female, and fifth instar water striders that were resighted on at least half of the censuses were high—0.71 ($N = 35$), 0.82 ($N = 22$), and 0.78 ($N = 9$), respectively—and not significantly

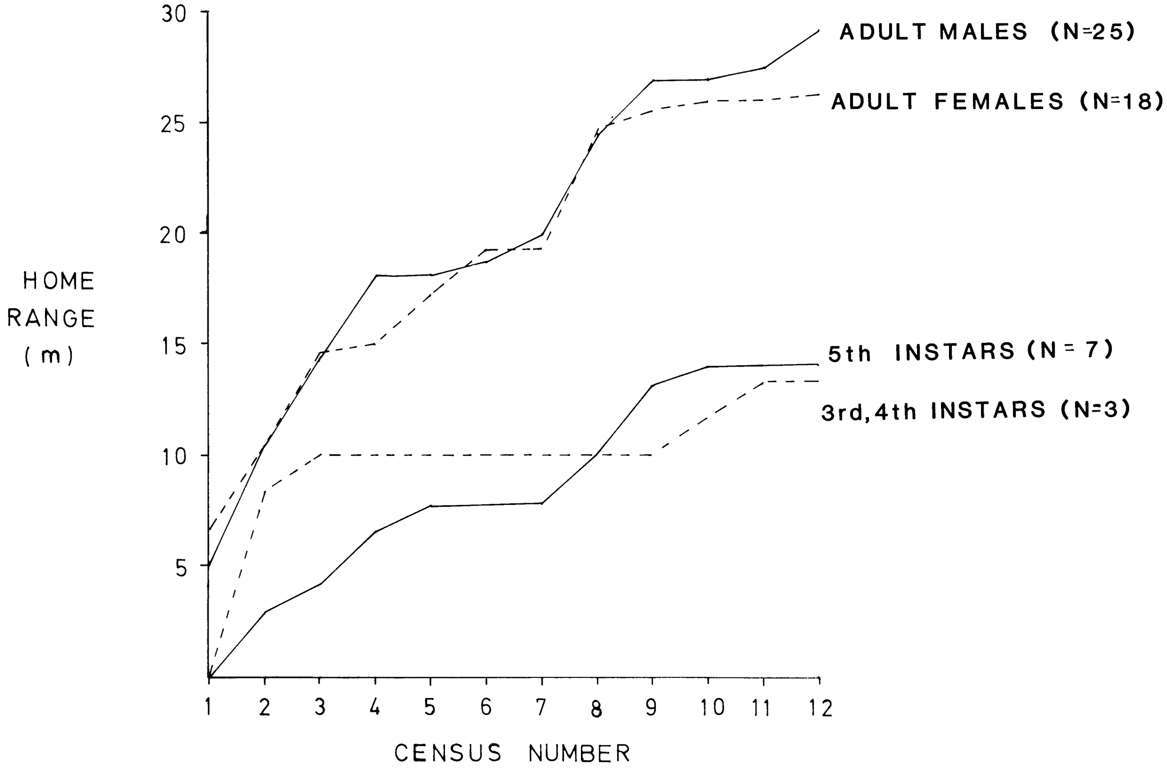

FIGURE 1. Cumulative estimate of home range size versus census number for age and sex classes of marked individual *Potamobates tridentatus* observed during at least half of the censuses.

different ($P > 0.05$, *G*-test; Sokal and Rohlf 1969). Significantly fewer third-fourth instar individuals (3 of 50 marked) were resighted at least half of the time ($P < 0.01$, *G*-test). Because we resighted so few third-fourth instar individuals, they are omitted from the home range, activity center, and between-census movement analyses. Most of the marked third-fourth instar individuals may have molted during the census period, as some gerrids pass through instar stages in 7–11 days (Galbraith and Fernando 1977).

Because the mean home range for adult males ($\bar{x} = 29.3$ m, SD = 19.3, $N = 25$) was not significantly different from the mean home range for adult females ($\bar{x} = 25.8$ m, SD = 13.2, $N = 18$; $P > 0.05$, *Student's t*-test), we pooled home ranges for adults of both sexes. Mean home range for fifth instar striders ($\bar{x} = 12.1$ m, SD = 7.0, $N = 7$) was significantly different from the adults ($\bar{x} = 27.8$, SD = 17.4, $N = 43$; $P < 0.05$, *Student's t*-test). Figure 1 plots mean cumulative estimates of home range size versus census number for animals resighted on at least half of the censuses. For adults and juveniles, the curves appear to approach asymptotes, and therefore probably provide reasonable estimates of actual home range sizes. An alternative, relative estimate of home range size, the standard deviations of the activity centers, averaged for each age-sex class, did not differ among adult males and females ($P > 0.05$, *Student's t*-test), but fifth instar mean standard deviations were significantly smaller than adult means ($P < 0.02$, *Student's t*-test).

The locations of activity centers differed among age and sex classes, with those of marked adults and juveniles only overlapping in two five meter sections of the study area. Adult males were distributed independently of adult females ($P < 0.05$, *G*-test). Fifth instars were not compared statistically because of the small sample size. The adult female distribution did not differ significantly from a Poisson distribution ($P > 0.2$, *Kolmogorov-Smirnov* test), but the adult male distribution was significantly more aggregated ($P < 0.05$).

In addition to having different dispersion patterns, males moved more widely on a local, short-term scale than females, especially in the afternoons. At such times, male movements were difficult to quantify beneath the grid. Males accounted for 16 of 21 incomplete observation periods due to individuals not remaining beneath the grid for

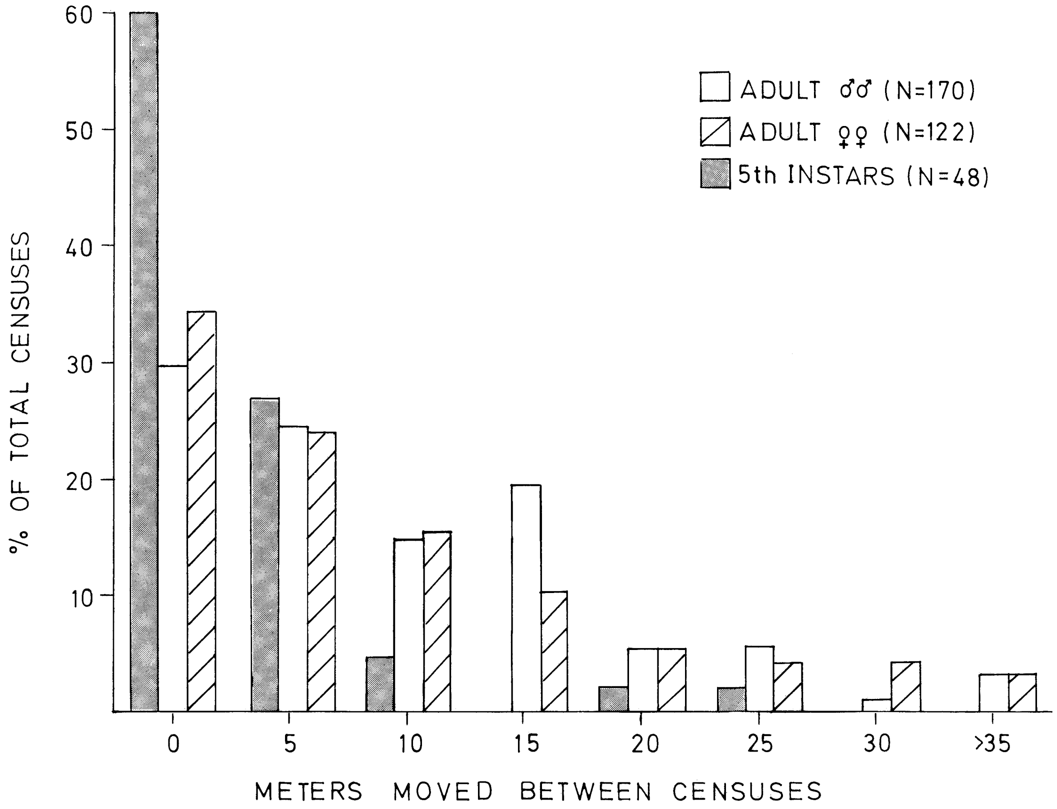

FIGURE 2. Frequencies of the distance moved between consecutive censuses for adult male, adult female, and fifth instar *Potamobates tridentatus.*

the entire five minute period. Differences in movements were correlated with behavior. Foraging individuals typically faced in the direction of the current, maintaining a relatively constant position except for periodic forays to seize floating prey in front or to the side of them (see Jamieson and Scudder 1979). However, adult males commonly strode downstream as well, covering up to 20 $m \cdot min^{-1}$ and attempting to mount any water strider encountered. Adult females moved much less erratically and appeared to forage constantly.

Distances moved between morning and afternoon were compared to those moved between the afternoon and the following morning for each age and sex class. Because there were no significant diurnal differences within each age and sex class ($P > 0.05$, *G*-tests), morning and afternoon censuses were pooled for each age and sex class (Fig. 2). Adult male distributions did not differ significantly from adult females ($P > 0.05$, *G*-test), but fifth instars were significantly more sedentary than adults ($P < 0.01$, *G*-test).

As a short term measure of space use, we recorded "foraging area" (the number of quadrats in which focal individuals were recorded during each five minute observation period) and the corresponding information index (H′) for that sample (Table 1). Although mean number of quadrats and H′ were less for the smaller third-fourth and fifth instars than adult females and males, these differences were not significantly different because of small sample sizes and high variance ($P > 0.1$, for both quadrat number and diversity, *Kruskal-Wallis* test).

During nine days of observations, we observed 16 copulations involving six marked females and 12 marked males (copulations were distinguished from simple mountings by the longevity of coupling and joining of genitalia). Three marked females copulated with more than one male during this period, and one of these females copulated with five different males in as many days. In contrast, no marked male was observed to copulate more than once during the study. One male remained clasped to a female for at least five hours, until sunset. In our sample, the sex ratio of adults was skewed, 37 males to 24 females. However, this is not significantly different from a 1:1 sex ratio ($P > 0.1$, *G*-test).

TABLE 1. *Short-term foraging area expressed as the number of unique 625 cm^2 quadrats occupied during five minute samples and the diversity (H′) of quadrat use.*

	Number of quadrats			H′	
	N	$\bar{x}$	SD	$\bar{x}$	SD
Adult males	9	11.0	5.2	1.80	0.53
Adult females	6	8.8	7.0	1.44	0.90
Fifth instars	5	7.6	3.4	1.46	0.75
Third–fourth instars	5	7.0	2.6	1.27	0.27

Adult *P. tridentatus* differ from juveniles in having larger home ranges and possibly larger local feeding areas. These differences could most simply be explained as a consequence of different body sizes. If two water striders take equal numbers of strides per unit time, the larger-limbed individual will travel farther (Vepsalainen and Jarvinen 1974). Counts of strides per minute suggest that adults actually strode faster than the smaller juveniles (98.6 strides/min for adults, $N = 15$, SD = 21.7; 80.8 strides/min for juveniles, $N = 8$, SD = 11.3 in the same current), which would augment the size differences. Adult males and females, with similar femur and body lengths, did not have significantly different home range sizes, local feeding areas, or distances moved between censuses. Yet, body size differences cannot explain the dispersion differences between the sexes, and they are unlikely to account for longer-term or more fine-scale space use by water striders.

Microhabitat separation did not appear to occur between any age or sex class of this species during the course of the study (*cf.* Wilson *et al.* 1978). We did observe occasional agonistic interactions between males searching for mates or stealing another water strider's prey. However, adult female *P. tridentatus* activity centers were distributed randomly in the study area, whereas adult male water striders appeared to be aggregated. The random distribution of adult females would be expected if their movements were determined solely by foraging and if prey drop randomly into the stream from overhanging vegetation. Although occasional dense food patches certainly occur, such as when aggregated lepidopteran larvae fall from trees overhanging the stream, these may be unpredictable or short-lived. Water striders appeared to capture randomly encountered floating insects; they were never seen in foraging aggregations. Assuming that males and females take similar prey, sexual differences in space use are unlikely to be due to exploitation of food. Instead, they are probably due to differences in mating behavior.

If receptive females are scarce or difficult to defend, males would be expected to attempt to maximize encounter rates with females by searching widely. The rapid, erratic long-distance movements typical of adult males in the afternoon could be attempts to locate receptive females. Juveniles, like adult females, spent most of their time foraging in one area, although they covered less space than females.

Adult females mated promiscuously over the observation period whereas adult males either did not, or did so less frequently. Copulation usually lasted for many hours. While neither prolonged copulation nor mate guarding is unusual among insects (Parker 1974), the apparent lack of promiscuity among male water striders suggests that there are physiological constraints on mating frequency in males, such as time for replacement of the spermatophore. The number of receptive females may also be limiting at any one time, even though males appeared to be more common than females.

Mate choise appears likely in *P. tridentatus* mating behavior. Although some copulating pairs strode passively for hours, we observed other pairs in which the female, when grasped by the male, increased stride and turning rates, often flipping onto the male's back, in an apparent attempt to dislodge the male. Because of the limited duration of this study, however, we know little about individual, seasonal, or annual differences in mating behavior or space use patterns.

Discussions with members of the Organization for Tropical Studies' course 78.3 helped shape this study. J. Godinez Guzman and the rest of the staff at Parque Nacional del Corcovado were generous with their time and knowledge of the area. David Hart, Kent Redford, Steve Rissing, and Jean Stout made useful comments on the manuscript, which Grace Russell helped prepare. G. Stonedahl kindly identified the water striders. GSW received financial support from the Department of Biology, University of California at San Diego and NTW from the Graduate School Research Fund, University of Washington and a Carr Postdoctoral Fellowship from the University of Florida.

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Nathaniel T. Wheelwright

Section of Ecology and Systematics
Cornell University
Ithaca, New York 14853, U.S.A.

Gerald S. Wilkinson

Department of Biology
University of California at San Diego
La Jolla, California 92093, U.S.A.