Territorial Behavior of Both Sexes in the Water Strider *Metrocoris histrio* (Hemiptera: Gerridae) During the Mating Season

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Territorial behavior of overwintered individuals of Metrocoris histrio *was observed in an upstream area. Adults of both sexes held territories, but male territories were larger than those of females. Severe competition occurred among males for territories which give them access to receptive females. The effects of male body length and midleg length on establishment of territories were not significant. The effect of female midleg length on activity of females entering preferred foraging sites was equally not significant. Instead, territorial behavior increased with male age and males stayed longer at prime sites. Females of intermediate age were likely to occupy prime sites. Females had longer territory residence time than males. The sexes were dimorphic with respect to midleg length, and dimorphism in* M. histrio *may be related to a difference in life history, in that sexual selection may be relaxed due to asynchronous adult emergence patterns.*

INTRODUCTION

Animals hold territories when resources are valuable and defendable. Resources are usually mates and/or foods, and both of which increase fitness of territory

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holders. In insects, females sometimes establish feeding territories (Wilcox and Ruckdeschel, 1982; Whitman, 1986; Vepsäläinen and Nummelin, 1985a; Nummelin, 1988), while there are few female mating territories. Since food resource not only influences female survival (Kaitala, 1987; Rowe and Scudder, 1990) but also directly determines the number of eggs that females produce, i.e., reproductive success (Blanckenhorn, 1991b), feeding territories may have been more developed than mating territories in females. In contrast, male insects often establish mating territories (reviewed by Thornhill and Alcock, 1983), because the number of mates directly determines male reproductive success rather than foods in males' adulthood. Thus, mating territories may have been much more developed than feeding territories in males.

Water striders living in fresh water are generally categorized into lentic and lotic. Some males of lentic species establish mating territories associated with ripple signals and limited oviposition sites [Hayashi, 1985 (*Gerris elongatus*); Vepsäläinen and Nummelin, 1985b (*Limnoporus rufoscutellatus*); Wilcox and Spence, 1986 (*L. dissortis* and *L. notabilis*); Nummelin, 1988 (*Rhagadotarsus hutchinsoni*)]. Ripple signals are functional for advertisement in male courtship display and oviposition sites are defendable, thus, male mating territories are considered to have evolved easily. No feeding territories have been reported in either sex there, which may result from unlimited food resources. In a lotic environment, some species of female water striders form feeding territories [Wilcox and Ruckdeschel, 1982 (*G. remigis*); Vepsäläinen and Nummelin, 1985a (*G. najas* and *G. cinereus*); Nummelin, 1988 (*Eurymetra natalensis*)], where food resources may not be rich. Male mating territories have not been reported among these species except in tropical *E. natalensis* (Nummelin, 1988).

Many reports about territoriality in water striders are based on the studies in cold-temperature climates, which cause a high mortality over winter, and simple life histories, where adult stage synchronizes (Wilcox and Ruckdeschel, 1982; Rubenstein, 1984; Vepsäläinen and Nummelin, 1985a,b; Spence and Wilcox, 1986). However, there is a great variation of phenotype in some life-history characters between different habitats, including warmer areas in *G. remigis* dwelling in streams (Fairbairn, 1985). *Metrocoris histrio* populations in different regions also show phenotypic plasticity (Miyamoto, 1961). Kawabata (1955) reported that individuals of both sexes in *M. histrio* tend to defend fixed areas against intruders in artificial ponds at a botanical garden. However, *M. histrio* naturally lives in a small stream in a montaneous area, that is, it is lotic. Suitable areas with a water current slow enough for this small insect are not so abundant in this habitat. We show that both sexes of *M. histrio* establish territories in their natural habitat.

We also compare the factors associated with establishment of territories in water striders. In some cases, body size has been shown to affect territorial behavior (Rubenstein, 1984; Hayashi, 1985; Nummelin, 1988). In others, body

size did not affect territoriality (Vepsäläinen and Nummelin, 1985b; Nummelin, 1988). Using *M. histrio* as a model system, we investigate why these differences may occur and suggest another possible factor that may be associated with the maintenance of territories.

MATERIALS AND METHODS

M. histrio (Hemiptera, Gerridae) is distributed from Hokkaido to the Amami Islands, Japan, and is also found in Korea. It overwinters in both the adult and the egg stages. In Kyushu and along the shore of the Inland Sea of Japan, both of which are warmer than main temperate regions, *M. histrio* also overwinters in the last larval stage (Miyamoto, 1961). Thus in our study area adults, larvae of the last stage and eggs overwinter.

Our study area was a 30-m stretch of an upstream section of the Ino River, near Fukuoka, Kyushu Island, Japan. Areas with a slow water current inhabited by water striders were regarded as "pools," eight of which were included in the study area. Counts of the number of adult male and female water striders were made in each pool from May 15 to July 7, and marked animals were checked for their residence in the study area until August 22, 1985.

From May 15 to July 7, all adults that were seen in the study area were captured, marked individually with paint, and released after measuring the body and midleg length. Most adults marked after June 20 were from overwintered eggs and offspring of overwintered adults or larvae. Only adults marked on May 15 were considered overwintered adults. We judged all individuals marked after May 15 to have eclosed from overwintered larvae. Therefore, the days since marking was a measure of the age of the imagines.

To investigate the residence and movement pattern of adults, marked individuals were identified at 1- to 2-day intervals until August 22. Until June 20 the behavior of focal males and females in the pools was observed for 5 min per individual, and their skating positions were traced on maps. These data were used to determine whether an individual was territorial or nonterritorial. During the observation period all individuals in pools maintained a relatively constant position, even though some active males often left the pools and returned. Individuals which had repelled neighbors approaching were judged "territorial," and those which had not were judged "nonterritorial" even if they had stayed in a fixed area. The area of each pool was measured (Table I) at the beginning of the observations on May 15. The ratio of the number of days a particular male held territories to the total number of days he was observed was calculated to evaluate his potential of territory establishment, i.e., "territoriality index." Similarly, the ratio of the number of days a particular female entered primary pools (Pools 1 and 2) to the total number of days she was observed was an estimate of her potential to enter primary pools, i.e., "pool occupancy index."

Table I. Size of Pools, Average Daily Number of Males and Females, and Residence Times of Individuals in Each Pool from May 15 to June 20 (Pools 1 and 2 are Primary, and Others Are Secondary)

| Pool | Area (m²) | Number (Mean ± SD) | | Residence times (days) | | | |
| | | Male | Female | Range | | Mean ± SD | |
				Male	Female	Male	Female
1	4.0	1.7 ± 0.9	2.5 ± 1.8	1–19	1–33	5.8 ± 5.9	6.1 ± 9.0
2	1.8	1.1 ± 0.9	2.1 ± 1.7	1–17	1–15	3.0 ± 4.7	4.1 ± 4.1
3	1.5	0.9 ± 0.9	1.1 ± 1.4	1–7	1–9	2.0 ± 1.8	2.9 ± 2.5
4	3.7	0.8 ± 0.5	1.2 ± 1.2	1–11	1–18	3.0 ± 3.7	4.3 ± 5.7
5	1.7	0.5 ± 0.6	0.5 ± 0.6	1–4	1–5	1.6 ± 1.1	2.8 ± 1.8
6	1.9	0.9 ± 0.6	1.4 ± 1.6	1–12	1–4	2.1 ± 3.5	1.6 ± 1.1
7	<1	0.7 ± 0.7	0.3 ± 0.6	1–3	1–2	1.5 ± 0.7	1.2 ± 0.5
8	2.3	1.0	0.6 ± 0.7	1–16	1–7	16.0	5.0 ± 2.8

In both sexes, these ratios were repeatedly calculated for each individual day it was observed. Multiple and stepwise regressions were used to analyze the effects of body length, midleg length, and days since marking (adult age) on a male's potential of territory establishment, as well as the effects of midleg length and days since marking on the potential of females to enter primary pools. Because there was little difference in days since marking among individuals in the beginning of the observation period, no data before May 25 were used to calculate either male territoriality or female pool occupancy indices. Body length of females was not analyzed for the tendency of females to enter primary pools because this length changed with time, probably depending on ovary maturity. That is, female body length likely increases until oviposition and decreases after that.

RESULTS

M. histrio shows sexual dimorphism with respect to midleg length (Fig. 1). Whereas the difference in mean body length was not significant between sexes ($t = 0.86$, $P > 0.1$, t test) the mean midleg of males was significantly longer than that of females ($t = 13.2$, $P < 0.005$, t test). Body and midleg lengths of male adults marked after June 24 were 6.0 ± 0.2 and 17.5 ± 0.6 mm ($N = 62$), and those of female adults, 6.0 ± 0.2 and 15.6 ± 0.6 mm ($N = 87$), and the four values were significantly larger than those of overwintered individuals ($P < 0.0001$, t test).

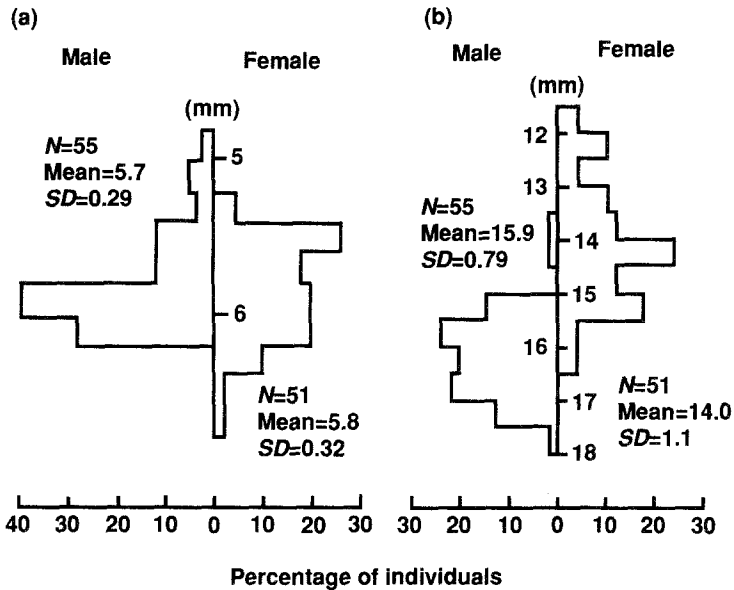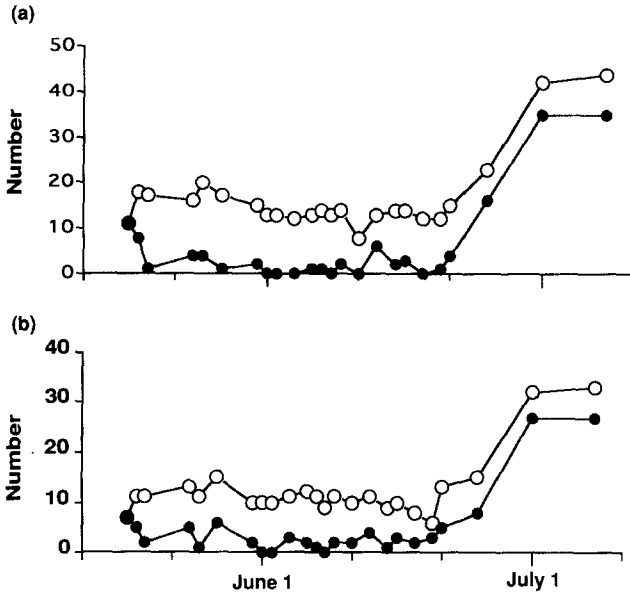Numbers of overwintered individuals slightly decreased over time (Fig. 2).

Fig. 1. Frequency distribution of (a) body and (b) midleg length for adult males and females marked between May 15 and June 20.

Large numbers of unmarked adults were found on and after June 24, which were the first summer generation (i.e., offspring of overwintered striders), and the total population size increased drastically.

Females remained within the study area longer than males (Fig. 3), which means that females lived longer than males. Residence time was not correlated with either body or midleg length in either sex (male—$N = 117$, $r = 0.08$, $P > 0.1$, for body and $r = 0.003$, $P > 0.1$, for midleg; female—$N = 138$, $r = 0.03$, $P > 0.1$, for midleg).

Figure 4 shows one particular section of the study area to illustrate the variability in male territorial behaviors. One male (No. 3) held territory broadly in a central part of Pool 2, with four female territories adjacent to the male territory. Although usually territorial males covered only small areas, similarly to the females, the males sometimes patroled the entire pool and persistently attacked intruding males and intensively expelled them all from the pools (eight cases). However, there was no attack observed by territorial males on females entering the pool. Aggression between resident females was observed whenever females came into contact but was milder than between males. Two territorial females which had combated other females disappeared the next day, of 10 cases. We could find only one case in which a resident female attacked and
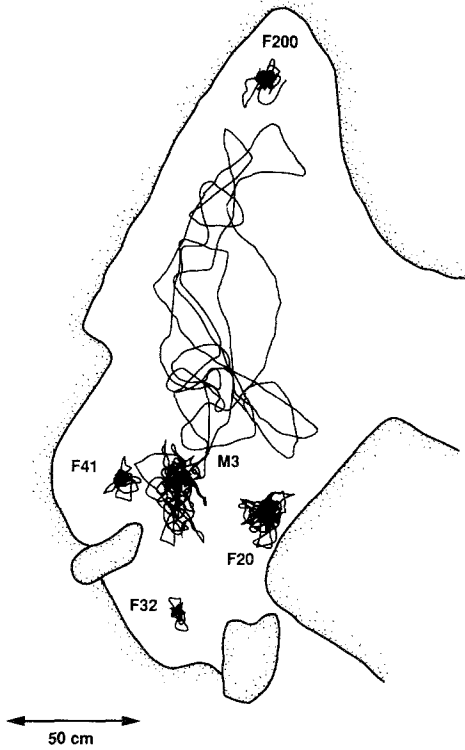
(a)

(b)

Fig. 2. Seasonal change in number of adults of male (a) and female (b) observed in the study area. Filled circles, total number of adults; open circles, number of unmarked adults caught and released after marking.

Fig. 3. Residence time of individually marked adults from May 15 to June 20 in the study area. Filled circles, males; open circles, females.

Fig. 4. Comparison of territory structures in Pool 2 with one male and four females on June 3. The line tracings were derived from continuous records on the map in direct observation.

expelled an intruding female. Female contacts were generally not so severe because of their restricted movements.

Foraging was observed in only six cases, five of which were by females. Four dipterans, one isopteran, and one third-instar larva of *M. histrio* were fed. One female captured a tiny twig and another one captured a small leaf mistaken for their food.

Because of the scarcity of foraging behavior, food was likely the main indicator of the quality of pools for females and mates for males. Since female territories were always much smaller than the pool size, the number of females in each pool could reflect the quality of the pool. Pools with many females were considered valuable for males. Therefore, pools were categorized as either primary or secondary sites based on whether they contained a daily average of two

or more females or fewer than two females between May 15 and June 20 (Table I). Pools 1 and 2 were primary sites, and others were secondary.

Only a single male was territorial in each pool, even when the pool was inhabited by other males. In contrast, multiple females were simultaneously territorial (e.g., Fig. 4). Especially in primary pools, there were usually more females than males (Table I).

Mating was observed 10 times. Courtship behavior occurred when a territorial male approached and repeatedly touched a swimming female, but in most cases females rejected and attacked the male. When the male was not attacked by the female, he mounted her and remained on her back for several minutes in copulation. During the last period of copulation, for about 30 s, the female repeatedly wrenched and, finally, terminated the mating by forcing males to dismount.

The number of females in a pool had a weak correlation with the area of the pool ($r = 0.458$, $N = 7$, $P > 0.1$; Table I). In a multiple linear regression analysis, the pool occupancy index (Y_1) was predicted by two independent variables, female adult age (X_1) and midleg length (X_2), as $Y_1 = -0.02 + 0.01X_1 + 0.01X_2$ ($r = 0.27$, $N = 211$, $P = 0.0003$). In a stepwise regression, variation in X_1 accounted for 7% of the variance in Y_1, and variation in X_2 accounted for 1%. In a subsequent single polynomial regression, the equation $Y_1 = -0.02 + 0.06X_1 - 0.00157X_1^2$ highly significantly fit the data on age (X_1) (Fig. 5a; $r = 0.43$, $N = 211$, $P = 0.0001$) but not the data midleg length ($Y_1 = 5.78 - 0.76X_2 + 0.03X_2^2$; $r = 0.05$, $N = 211$, $P = 0.78$). These results show that not midleg length but age influenced the potential of females to enter primary pools and females of intermediate age were likely to occupy the primary sites.

Males held territories longer in pools with more females (Fig. 6; $r = 0.66$, $P < 0.01$). Consequently, territories lasted a little longer in primary pools (mean $\pm$ SD $= 5.7 \pm 6.8$ days, $N = 12$) than in secondary pools (3.5 ± 3.6 days, $N = 17$, $P = 0.27$, t test). According to multiple regression, the male territorial index (Y_2) was well described with three independent variables as $Y_2 = -0.13 + 0.02X_3 + 0.37X_4 - 0.01X_5$ ($r = 0.52$, $N = 156$, $P = 0.0001$), where X_3 is male adult age, X_4 is male body length, and X_5 is male midleg length. In a stepwise regression, variation in X_3 explained 24% of the variance in Y_2, variation in X_4 explained 1%, and variation in X_5 explained 2%. Older males appeared more likely to establish territories (Fig. 5b), a tendency which was consistent with the individual histories of five of the territorial males given in Table II. These individuals came to establish territories late during their adult life, whereas they were all nonterritorial early on.

DISCUSSION

M. histrio inhabits small pools with a low current speed in mountain streams. Since it is difficult for small species like *M. histrio* to maintain positions in faster currents, the individuals are restricted to areas with slow-moving water.
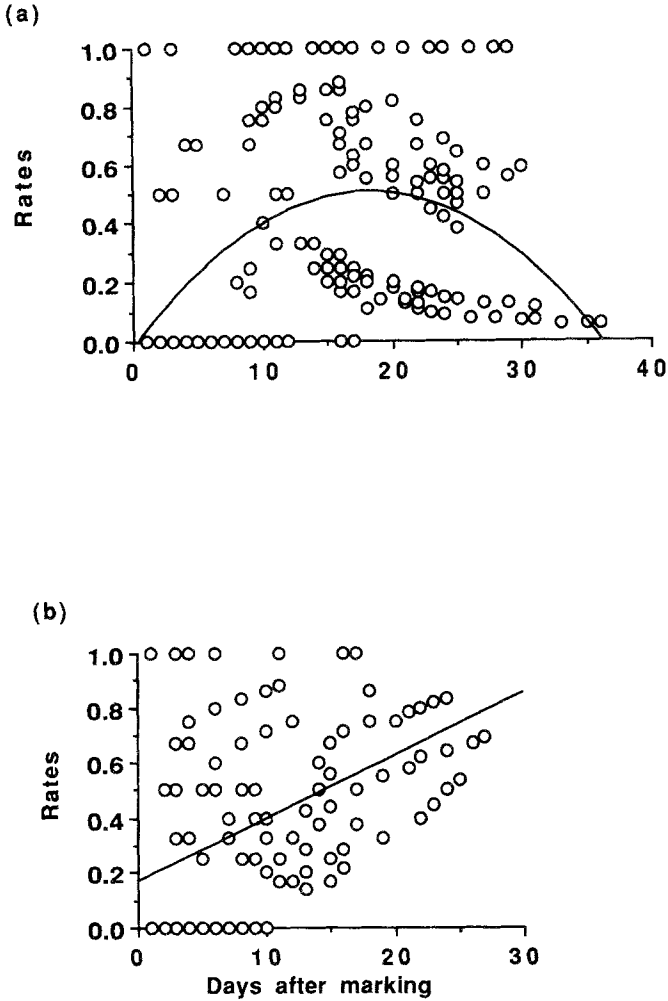
(a)

(b)

Fig. 5. Days since marking (adult age) in relation to (a) the "female pool occupancy index" and (b) the "male territoriality index."

Places where food is obtainable should also be limited. We considered that the foraging success of *M. histrio* was low, i.e., food resource was limited, because we could not observe foraging behavior of *M. histrio* so often. We judge that their territories were at least for foraging as observed in nonreproductive *G. remigis* (Wilcox and Ruckdeschel, 1982; Blanckenhorn, 1991a). Territories of male *M. histrio* were also for mating because territorial males expelled intruders of only the same sex. Male water striders possess mating territories when some
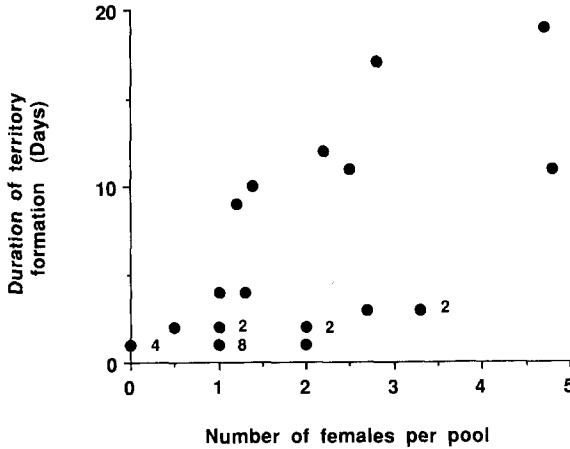
Fig. 6. The relationship between the duration of male territory ownership in pools and their mean daily number of females ($Y = 0.007 + 2.64X$, $r = 0.64$, $P < 0.01$).

resources are limited. The resources were oviposition sites in lentic environments (Hayashi, 1985; Vepsäläinen and Nummelin, 1985b; Spence and Wilcox, 1986; Nummelin, 1988). In contrast, the resources were foraging sites in lotic areas where females hold foraging territories (Rubenstein, 1984; Vepsäläinen and Nummelin, 1985a; Nummelin, 1988), and to acquire mates male *M. histrio* defend the foraging sites where females aggregate.

In *M. histrio* female-biased sex ratios within pools resulted from sexual differences in territorial behavior, since only territorial males excluded intruders of the same sex from holding territories in the same pool. As a consequence, male territories were much larger than those of females.

The difference in territorial behavior between males and females indicates that competition for space (or mates) is more severe in males than in females. This sexual difference may be reflected in the greater midleg length of males. Males of *G. elongatus* had longer midlegs than females, and among males midleg length correlated positively with territory ownership (Hayashi, 1985). However, in spite of the conspicuous sexual dimorphism in *M. histrio* with respect to midleg length, there was no relation between midleg length and territorial ownership. Territory formation, rather, was associated with age, estimated as days after marking, than with body size. Variance of the midleg length in male *M. histrio* was significantly smaller than that in *G. elongatus* (Hayashi, 1985). The difference between these two species may result from the difference in their life histories. Male *G. elongatus* have discrete generations owing to simultaneous adult emergence (Hayashi, 1985). Among competing males of similar age, those with longer midlegs likely have great access to receptive

Table II. The Influence of Days Elapsed After Marking on Male Territoriality: +, Territorial; −, nonterritorial

Days elapsed after marking	Male number				
	1	3	4	30	203
1	−	−	−	−	−
2	−				
3					−
4					−
5					
6		−	−	−	−
7	−	+	+	+	
8	−			+	+
9		+	+		+
10	−			−	+
11					
12				+	+
13				+	+
14		+	+	+	
15	+	+	+	+	
16	+	+	+		
17	+			+	
18		+	+		
19	−			+	
20		+	+		+
21	+	+	+	+	+
22	+	+	+	+	
23	+	+	+		
24	+			+	
25					
26				+	+
27				+	

females. In contrast, male *M. histrio* have, to some extent, overlapping generations (Miyamoto, 1961), and older males therefore dominate matings because of their high territory holding potential. As in other gerrids, it likely takes some time for newly emerged adults of both sexes to reach sexual maturity. This may explain why young males did not form territories but had better chances to establish territories later in life. Furthermore, older males should compete more strongly for females because of their shorter life expectancy.

Male water striders often exhibit multiple mating tactics. There are two patterns of association of male territoriality with male size. First, body or midleg length of males has been shown to affect establishment of territories in *G. remigis* (Rubenstein, 1984), *G. elongatus* (Hayashi, 1985), *L. dissortis* and *L. notabilis* [(Spence and Wilcox, 1986); not intraspecific but interspecific], and *T. albovittatus* (Nummelin, 1988). In these species there was a clear relationship between male territoriality and male size. Second, male size did not affect male

territoriality in *L. rufoscutellatus* (Vepsäläinen and Nummelin, 1985b), *G. swak-opensis* (Nummelin, 1988), and *M. histrio* (this study). In the first group, intra-specific variance in male size was large, whereas it was small in the second group. Females are typically larger then males in the Gerrinae (Fairbairn, 1990). However, in species with male mating territoriality, sexual selection is expected to favor large males (Fairbairn, 1990), resulting in increased variation in male size parameters.

In species where size does not influence male territoriality, other factors can be expected to be relevant. As shown in *M. histrio*, age is one such variable. [In most species of the Halobatinae, the body length of the male is almost equal to or longer than that of the female (see Miyamoto, 1961).] However, although sexual selection does not appear to result in a body size dimorphism in *M. histrio*, such a sexual dimorphism exists with respect to midleg length. Males display greater mobility than females, as was apparent in this study. Males were more active at and about their territories (Fig. 4) and had lower residence times at territories (Fig. 3). The data in Fig. 3 could also mean that they die sooner than females, i.e., that males have a lower life expectancy. (According to personal observation, very few individuals which had disappeared in our study area were found outside of the area. Thus, most disappearing individuals were considered dead.) The lower residence time at territories in males may equally reflect a higher physiological cost of mobility, which in turn may affect selection on midleg length. However, selection on midleg length may be related to foraging capacity in both females and males, and this itself may not have anything to do with mating.

ACKNOWLEDGMENTS

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