

Wing dimorphism, territoriality and mating frequency of the waterstrider *Aquarius remigis* (Say)

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Territoriality and mating frequencies were studied in wing dimorphic populations of *Aquarius remigis* (Say), (Heteroptera, Gerridae) in California. Larger females were territorial in populations with winged individuals and in those with individuals of two wing morphs. Winged females were larger than wingless females, and because of their larger body size winged females were more often territorial than wingless ones in dimorphic populations. Males were seldom territorial but were often found either mating or searching for food and mates. Body dimensions were not correlated with mating frequency, but wingless males were found mating more often than winged males. In a laboratory experiment wingless and (smaller) males mated more often than did winged males. Thus, wingless males seem to have a mating advantage over winged. The territorial behaviour that we observed in females, and the association between size and territoriality were similar described on an exclusively wingless population in eastern North America.

1. Introduction

Territoriality is well described among wingless populations of *Aquarius remigis*¹ (Wilcox & Ruckdeschel 1982, Rubenstein 1984, Sih et al. 1990, Blanckenhorn 1991) in eastern North America. According to Rubenstein (1984) largest females held territories, while smaller non-

territorial females were less site specific. Males were either territorial, “edge males” or moved around continuously as satellite males. Territorial males in the middle caught more prey items than did males in the edge areas. Morphological measures were uncorrelated with behaviour among males except that territorial males had wider profemora than did edge males. Prothoracic legs are used by males to grasp females during mating (Rubenstein 1984), and femur width of the prothoracic leg is assumed to be sexually a dimorphic character in *A. remigis*.

¹ This species was formerly known as *Gerris remigis*, but the subgenus *Aquarius* was recently elevated to generic rank on the basis of phylogenetic analysis (Andersen 1990).

In California, many populations of *A. remigis* are wing dimorphic (Kaitala & Dingle 1992). Two behavioural hypotheses are easily studied in dimorphic populations: 1) Winged individuals are larger than wingless as measured by body length (see results). If the behaviour of an individual depends on its body size, the greater the variation in body size among individuals the more they should differ in behaviour. 2) In comparisons between migratory and non-migratory morphs several characters are often associated with high dispersal ability, including large body size and high fecundity (Dingle 1988). Wing dimorphic populations have been successfully used to investigate morphological and life-history characters related to migration (Roff 1986), but non-migrants have rarely been examined for syndromes correlated with adaptations in stable environments or those dominated by density-dependent population dynamics. For example, migratory individuals are often larger than non-migrants, but high competitive ability has been related to large body size (Pianka 1972). It has not been investigated which individuals, migrants or non-migrants, will win in direct competition for resources.

Here we investigate differences in behaviour among individuals of different wing morphs. We ask if the association between territory holding and size observed among wingless individuals (Rubenstein 1984) also occurs in dimorphic and winged populations? We also study possible differences between individuals of different wing morphs with respect to competition for territories and mates.

2. Materials and methods

We studied *A. remigis* at two sites in Cold Creek at the University of California's Stebbins Cold Canyon Reserve (Solano County, California) during 1988–1989. A temporary site contained mainly winged individuals. During the breeding period the population was almost completely winged; we found only six wingless males and no wingless females. This site dried in May and was recolonized after rains during the following December and January. At a permanent site both morphs were present during the breeding season,

and water remained in some small pools throughout the year 1988. Mainly wingless individuals were found on this site over the dry period, when the water area declined dramatically (Kaitala & Dingle 1992).

All waterstriders were individually marked and recaptured about once a week from late February to early April, 1988 and at least once a month during other periods until May 1989 (Kaitala & Dingle 1992). When first captured, individuals were marked and the overall body length as well as the length of the middle femur were measured on site using a caliper with 0.5 mm accuracy. We used body length instead of body weight as a measure of body size, because a female weight was affected by the number of eggs in a female. We also took samples 100 m upstream from the dimorphic site. These individuals were measured by using a microscope with 6–25 × magnification and measurements included body length and middle femur length, as before, and also the width of the first femur as measured from the widest part of the femur. We also checked that females were in a breeding condition. Since all body dimensions measured (except width of the front femur) correlated positively with body length, only body length measures are presented.

We also studied *A. remigis* at two sites on Santa Cruz Island off the coast of Southern California near Santa Barbara. One site was a permanent pool in Cascada Stream that debouches into the second site, the Ranch Stream that runs through the island's central valley and becomes partly dry during the summer (Kaitala & Dingle 1992). For these individuals we also measured body length, mid-femur length, and fore-femur width.

Mating success of males was estimated by whether they were paired (mating or post copulatory guarding) or single when captured. Differences in mating success among morphs were also investigated experimentally in the laboratory. Ten winged females were each kept in separate aquaria with two wingless males and two winged males. Prior to experiment all individuals were allowed to mate at least once to check that they were in breeding condition. All wingless males were smaller than winged males. Aquaria were checked for matings once a day during a ten day

period. It should be noted that if a female was kept only with two males they were rarely paired, hence four males were used.

We defined individuals as territorial if they kept their positions in the middle of the stream for at least 15–25 minutes before we caught them for marking or identification, and if they had been noted to defend the area against other individuals. This should be a sufficient measure because territorial females have been observed to keep their positions for weeks (Blanckenhorn 1991). At Cold Creek we combine the data from all reproductively active individuals marked in February and early March of 1988 when the adult populations consisted only of breeding individuals. The data for behaviour of each individual are used only from the time of the first capture.

3. Results

3.1. Body size

Since many behavioural processes are dependent of body dimensions we first compare the differences in body sizes between sexes and the two wing morphs. An ANOVA ($n = 127$) shows significant effect on both wing morph ($F_{1,125} = 110$, $P < 0.001$) and sex ($F_{1,125} = 17.7$, $P < 0.001$; interaction morph \times sex $F_{2,122} = 0.177$, $P = 0.68$) on body length, females being larger than males and winged individuals being larger than wingless. We also measured the width of the first femur because this is thought to be a sexually dimorphic character (Rubenstein 1984). Despite their smaller body size, males had wider femurs in their prothoracic legs than females ($F_{1,125} = 247$, $P < 0.001$), but there were no significant differences between wing morphs within sex ($F_{1,125} = 1.971$, $P = 0.16$). This supports the hypothesis that a wide prothoracic femur is a male linked character.

3.2. Territoriality

Over six observation periods during February–March 30–65% of females were territorial, whereas at most only 6% of males were territorial. Number of territorial females was fairly

constant over time (range 10–13) at the temporary site but varied more (range 6–12) at the permanent site. Territorial females were larger than non-territorial females (Table 1). In the dimorphic site winged females were also more often territorial (59%, $n = 29$) than wingless (32%, $n = 28$; G -test, $G^2 = 5.4$, $P < 0.05$, $df = 1$). The difference in territoriality between individuals of the two wing morphs may be due to differences in body size or in wing morph. Covariance analysis, using size as a covariate and wing morph as the independent variable revealed no additional effect of wing morph on behaviour ($F_{1,56} = 0.23$, $P = 0.64$).

Pairing frequency was highly dependent on territoriality, since females in the middle of the stream were paired more often (permanent 80%, $n = 25$, temporary 53%, $n = 36$) than females in the edge areas (28%, $n = 32$, 0%, $n = 7$; $G^2 = 16.0$, $P < 0.001$ for the permanent site and $G^2 = 12.4$, $P < 0.001$ for the temporary site). Unpaired females stayed quiescent most of the time on the edges of the stream.

3.3. Male mating success

Most males were either coupled or searching for mates and were seldom territorial. At the winged site in Cold Canyon an average of 56 % of males censused were paired (range 48–60 %, based on six captures) and in the wing dimorphic site a mean of 65 % of males (range 55–86 %) were paired. We did not find single males resting at the stream edge which could be categorized as

Table 1. Female length (mm) in relation to territoriality. n = sample size, CI = 95% confidence interval. $t_{34} = 3.1$, $P = 0.004$ at the temporary site and $t_{55} = 6.1$, $P < 0.001$ at the permanent site.

	<i>n</i>	mean	CI
Temporary site			
territorial	22	15.86	15.66–16.06
non-territorial	14	15.40	15.19–15.62
Permanent site			
territorial	25	15.42	15.20–15.64
non-territorial	32	14.52	14.32–14.73

edge individuals according to Rubenstein (1984). The distribution of individuals among territorial, mating, and single male categories for the two sites is given in Table 2. We observed size differences among behavioural categories at the temporary site (Kruskal-Wallis, $H_2 = 9.303$, $P < 0.01$) but not at the permanent site (One-way ANOVA, $F_{2,43} = 0.28$, $P = 0.75$). But in the winged population between non-territorial mating and single males there were no differences in size (Mann-Whitney, $z = 1.79$, $P = 0.07$). In the dimorphic population the analysis of covariance for differences in size using wing morph as a covariate showed no differences in size among behavioural categories ($F_{2,43} = 1.04$, $P = 0.36$).

Winged males were larger than wingless at both the Cold Canyon (mean \pm SE: 15.4 ± 0.61 , 14.26 ± 0.53 ; $t_{63} = 8.03$, $P < 0.0001$) and Santa Cruz Island (15.59 ± 0.55 , 14.50 ± 0.67 , $t_{115} = 12.41$, $P < 0.001$) sites, but did not appear to have a mating advantage because of larger size.

In view of the observation that there was a size difference between wing morphs yet no size difference between mated and unmated males, we investigated whether females mated more often with winged or wingless males. In all three instances studied females mated more frequently with wingless males (Table 3). Probably because of small sample sizes no single case was statistically significant; for the pooled results, however, there was a significant difference between morphs.

In the laboratory experiment females mated more often with one of the wingless males than with winged (mean mating frequency \pm SE, 3.6 ± 0.56 for wingless males and 1.6 ± 0.45 for

winged; $t = 2.635$, $P < 0.025$, Wilcoxon two-sample t -test). Thus females do mate more often with wingless (and smaller) males, at least under conditions of male-biased sex ratio where one would expect considerable competition among males for matings.

Because of the generally smaller size of apterous males, we were prompted to ask if there was some other aspect of their morphology which compensated for the size difference. The most obvious choice is the femur of the prothoracic leg, which is enlarged in males and presumably enhances their ability to clasp females while mating (males may ride on the female's backs for several hours while paired). Measurements were made on striders captured on two samples from Santa Cruz Island (Table 4). Although there was a tendency for mated males to have broader prothoracic femora, differences were not statistically significant. The results are thus inconclusive, and the question of compensation for small body size remains for the present unresolved.

4. Discussion

One could argue that the two wing morphs of *A. remigis* represent different life history strategies and therefore a direct comparison of competitive

Table 2. Differences in body length (mm) among males of different behavioural categories. CI = 95% confidence interval.

	<i>n</i>	mean	CI
Temporary site			
territorial	3	15.75	15.26–16.23
mating	24	15.00	14.78–15.22
single	18	14.51	14.12–14.91
Permanent site			
territorial	3	14.73	14.01–15.42
mating	28	14.49	14.21–14.77
single	13	14.38	13.85–14.91

Table 3. Mating frequencies among males of the two wing morphs winged and wingless (G -test statistics with corresponding significance levels P , and degrees of freedom df , ns = not significant).

	mating	alone	df	G ²	P
Cold Creek					
winged	15	11	1	0.986	ns
wingless	13	5			
Ranch Stream					
winged	4	15	1	2.031	ns
wingless	11	16			
Cascada Stream					
winged	7	3	1	1.386	ns
wingless	21	3			
Total			3	4.4027	ns
Pooled			1	4.0354	<0.05
Heterogeneity			2	0.3673	ns

ability is meaningless. Winged individuals colonize temporary regions of streams (Kaitala & Dingle 1992) and in these habitats wingless individuals are seldom found. However, there are many habitats where both morphs regularly co-exist and are likely to compete. These dimorphic populations are found during the breeding season in permanent pools of small creeks and during the dry period in permanent rivers in the Central Valley of California as well as on mountain streams of Sierra Nevada (Kaitala & Dingle 1992).

Furthermore, dispersal by flight occurs prior to breeding after which most individuals histolyze flight muscles (Kaitala & Dingle 1992) so that during the breeding period, winged individuals are functionally wingless.

Winged females were territorial more often than wingless; territoriality depends on body size (or body parts highly correlated with body size) with larger females being more often territorial (Rubenstein 1984, this study). The larger body size of winged females is an advantage in direct resource competition, since prey capture rates are higher among territorial individuals than others (Rubenstein 1984).

Table 4. Differences in body length (mm) and width of the first femur (mm) between mating and single males in two streams of Santa Cruz Island. Differences were not significant ($t_{44} = 1.72$, $P = 0.09$ for Ranch Stream, $t_{32} = 0.80$, $P = 0.43$ for Cascada) and in femur width ($t_{44} = 0.14$, $P = 0.89$ for Ranch Stream and $t_{32} = 1.31$, $P = 0.20$ for Cascada). CI = 95% confidence interval.

	<i>n</i>	mean	CI
Body length			
Ranch stream			
mating	31	14.72	14.35–15.09
single	15	15.07	14.83–15.31
Cascada			
mating	27	14.74	14.18–15.78
single	7	14.98	14.48–15.00
Femur width			
Ranch stream			
mating	31	0.776	0.758–0.793
single	15	0.773	0.746–0.800
Cascada			
mating	27	0.783	0.723–0.843
single	7	0.756	0.738–0.773

However, even if wingless females were poorer competitors in direct food competition, they may have the advantage of breeding earlier than winged females. The building of flight muscles takes about a week in waterstriders (Andersen 1973), so that prereproductive period is longer among winged individuals, and also colonization by flight may delay reproduction. For example, in our dimorphic site some wingless females contained fully developed eggs and were mating already in December, three weeks prior to colonization by winged individuals (Kaitala & Dingle 1992).

Only the largest females were territorial; the rest of the females were met on the edge areas. Most territorial females were coupled with males whereas most females in the edges were alone. Wilcox (1984) also found that 97% of the single females were found at the edges of streams. Staying in an edge area may be a tactic for avoiding costs caused by male sexual harassment (Krupa et al. 1990, Kaitala & Dingle unpublished). Thus for reproductive females there are two options; they can either be territorial and get more food but be a target for male attacks, or they can adopt a less effective sit-and wait foraging tactic (Rubenstein 1984) and avoid costs of harassment by males (Krupa et al. 1990, Kaitala & Dingle unpublished).

Our results differ from those of Rubenstein (1984) who described a situation where males were main territory holders. In our populations most of the males stayed coupled with females during the day and “edge males” could not be identified. The differences between the two studies may reflect differences in densities of the populations or the fact that our study was made early in the breeding season in order to be sure that all individuals were in breeding condition, whereas Rubenstein (1984) conducted his studies in August when at least some individuals are likely to belong to a new generation and thus be non-breeding.

Rubenstein (1984) showed that territorial males mated more often than did non-territorial males. We could not directly test this since we found only a few territorial males and we did not follow their behaviour continuously. All 6 territorial males were winged and of large size which may indicate that territoriality in males also de-

depends on overall body size. On the contrary wingless, and smaller males were mating more often than winged. The only body dimension larger among wingless males was the width of first femurs. However, these measurements were not significantly different between mating and single males in our samples. Larger sample sizes are needed to test the effect of femur widths on male behaviour since, as noted by Rubenstein (1984), there seems to be only a weak advantage associated with wider femurs.

In conclusion: individuals of the two wing morphs often coexist and compete for resources. The comparison between morphs has shown that in competition for territories, because of their larger size, winged individuals have an advantage especially among females, whereas wingless males were mating more often than winged.

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