Resource Acquisition and Alternative Mating Strategies in Water Striders[1]

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SYNOPSIS. Behavioral polymorphisms occur among male and female water striders, *Gerris remigis*, when competing for food and mates. Individuals of both sexes vie for positions in the fastest flowing portions of streams. Here prey capture rates are highest, as are those of swimming and aggression. Only the largest females, and males with the largest first appendages, can regularly maintain positions in these areas. The remaining females are arranged along the flow gradient according to their size with the smallest holding positions in pools of slow moving water. For the remaining males neither overall size, nor the size of the first appendages, appears to determine which males swim near the edge of streams, or which males swim as satellites behind those occupying the fast flowing productive areas. Preliminary data show that mating success of edge and satellite males are about equal, but significantly less than that of the centrally positioned males with the largest first appendages. Thus although it appears that morphological phenotype influences male competitive behavior, when the absolute size of the critical trait is small males adopt behavior after assessing the actions of others. For these "subordinate" males, behavioral assessment appears to produce an "ideal free" spatial distribution.

INTRODUCTION

Although natural selection favors individuals who most abundantly transmit their genes to future generations, there is not necessarily any one best means of accomplishing this task. Numerous studies on insects (Cade, 1979; Thornhill, 1979; Parker, 1979; Alcock *et al.*, 1977; Brockman *et al.*, 1979), fish (Warner and Hoffman, 1980), birds (Hogan-Warburg, 1966; van Rhijn, 1973) and mammals (Clutton-Brock *et al.*, 1979; Le Boeuf, 1974; Rubenstein, 1982, and Wirtz, 1980) show that there is much variation among males and females in the ways they mate and acquire resources for provisioning the young. Yet the problem of understanding what factors generate and maintain behavioral polymorphisms still remains.

Ultimately, animals should adopt patterns of behavior that offer the highest reward for the least cost. Since animals differ in size, strength, and experience, it is not surprising to find that even when confronted with the same situation some individuals are better able to acquire resources while reducing, or enduring, costs than are others. Thus while the "best" obtain the most resources the "weak" either do without, or adopt alternative forms of competitive behavior. Such phenotype dependent polymorphisms have been termed "conditional strategies" (Dawkins, 1980) and they usually yield meager rewards.

In some situations the costs and benefits of a behavior are not fixed, but change with its frequency of occurrence. When a behavior increases in frequency, as long as costs associated with it increase or benefits derived from it decrease, alternatives can flourish and will yield equal rewards. These frequency dependent polymorphisms can be maintained in three ways. First, selection can adjust the frequencies of different genetically determined strategies so that the net benefits to be derived from each are equal. Second, selection can favor a genetically determined strategy in which alternative forms of behavior appear stochastically at fixed frequencies. The strategy which fixates is the one in which the alternative behaviors appear with frequencies that produce equal payoffs for each. This type of stochastic polymorphism is termed a "mixed strategy" (Maynard Smith, 1976). Third, individuals can choose among behavior patterns after assessing what others are doing. Each individual, by

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choosing the behavior that yields the highest reward, will produce a frequency distribution of behaviors in which each receives an equal payoff.

It is usually assumed that these two mechanisms for maintaining behavioral alternatives are mutually exclusive since "conditional strategies" depend on individual differences in phenotype, while frequency dependent polymorphisms, especially "mixed strategies," do not. This need not be the case, however, as both mechanisms may operate simultaneously within populations (Parker, 1982). Thus while the largest members of a population behave in one way and control most of the resources, the smallest members of a population may adopt a variety of "mixed strategies" that yield equal but meagre rewards (Rubenstein, 1980a). For water striders it appears that competitive behavior is both conditioned by morphology and the actions of others. Showing how these factors interact and maintain behavioral polymorphisms in a water strider population is the aim of this paper.

In the water strider *Gerris remigis* individual males and females adopt behaviors that differ from those utilized by other members of their sex when competing for food or mates. Although the data are only preliminary and were obtained towards the end of the 1981 mating season, they suggest that within each sex phenotypic differences determine where animals can forage and mate, and that the effect is stronger among females than among males. This species is particularly interesting because males compete for females and compete with them as well. According to Darwin's (1871) theory of sexual selection, the sexes should compete primarily for different resources. In general females should compete for food to produce many robust young, whereas males should compete for mating access to as many of the best females as is possible. For water striders this principle holds, but males also compete vigorously for food. This additional inter-sexual competition plays an important role in shaping the behavioral alternatives exhibited by members of each sex.

METHODS

Observations were made on individually identifiable water striders inhabiting a section of stream that was bounded at both ends by natural rock piles. Water striders were marked uniquely with dots of colored Liquid Paper correction fluid. In order to characterize phenotype, each individual was sexed, weighed, and scored for overall length as well as the width of the femur on its first pair of legs.

The stream was photographed and maps were made and divided into quadrats. Instanteous scan samples and focal animal samples of behavior were taken throughout the day on consecutive days from early June until mid-September. Samples collected from a two-week period during August were used to construct time budgets, and map coordinates for swimming, fighting, feeding, resting, mating, and ovipositing behavior.

One-way analysis of variance was used throughout to determine if there were any overall effects due to the classification. Then the *a posteriori* Duncan Multiple Range procedure was used to determine if any pair-wise comparisons were significantly different.

GENERAL BIOLOGY

Gerris remigis is a large water strider that lives on the surface-film of moderately flowing, and to a lesser extent, standing water (Riley, 1922). When active, most individuals disperse themselves along the stream, orienting with their heads into the current. Here they row with their middle legs against the current and either "sift" the water for insects that drift by, chase conspecifics, or search for mates. They maintain a relatively constant position in the stream, and they repeatedly drive away intruders with both low intensity approaches and high intensity lunges and "hop-ons." In a sense they are territorial (Wilcox and Ruckdeschel, 1982), but because of the dynamic nature of the substrate, the territoriality is more like Brown's (1964) concept of "Site dependent dominance." In such situations, an animal's likelihood of attacking an intruder and the

probability of its winning the encounter decrease as it goes away from its center of activity. On average water striders defend a circular space about 0.25 m in diameter.

Water striders are active all day but individuals do rest on rocks, leaves, or twigs, especially when handling prey or copulating. Mating is a protracted affair often lasting longer than 6 hr. After the pair separates, the females rest and then oviposit along the stream edge and under rocks.

RESULTS

The behavior animals use while competing for resources can be described in terms of its frquency and location of occurrence. Even if segments of a population exhibit qualitatively similar forms of competitive behavior, as long as they do so at different frequencies and in different places, alternative strategies may exist. Such is the case for both males and females in water strider populations. As shown in Figure 1, the proportion of time that individuals actively search for food or mates varies within each sex. For females the variation is continuous and most animals are actively swimming most of the time. Only about 15% of the population spends more than 50% of each hour resting along the banks on rocks, twigs, or leaves. For males the situation is qualitatively different as males appear to sort out into two distinct groups, those that are extremely active and those that are more quiescent. Approximately 50% of the male population falls into each group. Thus whereas most females are continuously active, only about half the males show such high levels of activity.

Female dispersion

Differences among individuals also occur with respect to where they spend their time actively swimming. As Figure 2 shows, females are not distributed uniformly about the stream. They are concentrated in two major areas near the heads of pools. In order to sample the greatest surface area of water a strider should position itself adjacent to the major currents, preferably immediately downstream from a constriction that narrows the flow of water. Here
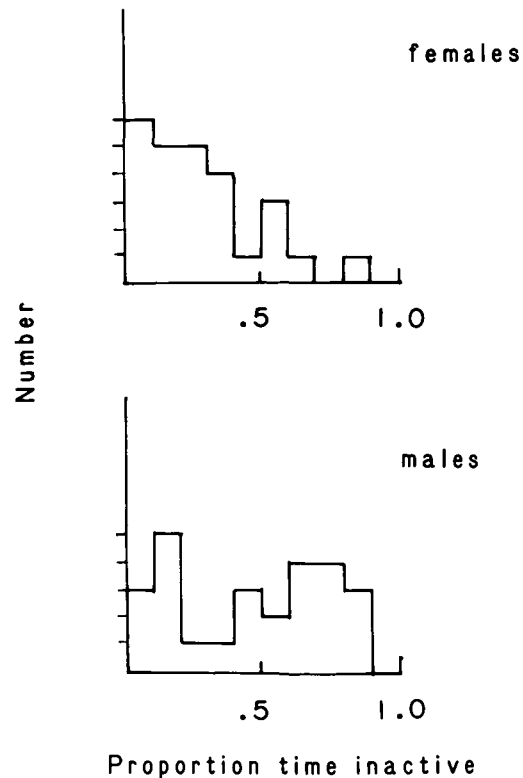

FIG. 1. Distributions of male and female patterns of inactivity. Each square represents the average proportion of time an individual spent *not* swimming in the stream. Each of 26 females and 26 males were observed for at least 30 hr during 14 consecutive days.

insect abundance is extremely high (Rubenstein, unpublished; also Fig. 3). From Figure 2 it is apparent that some females are positioned closer to the heads of pools than others. Since feeding success ultimately determines a female's reproductive success it is not surprising to find that females aggressively compete for these areas. They do so by establishing territories and excluding intruders. When females at the heads of pools are removed, the ones behind them move into these territories within minutes. The same movements occur naturally whenever females leave the stream to rest along the banks. Given the prevalence of competition it is important to know 1) whether certain females are more likely to obtain these positions, and
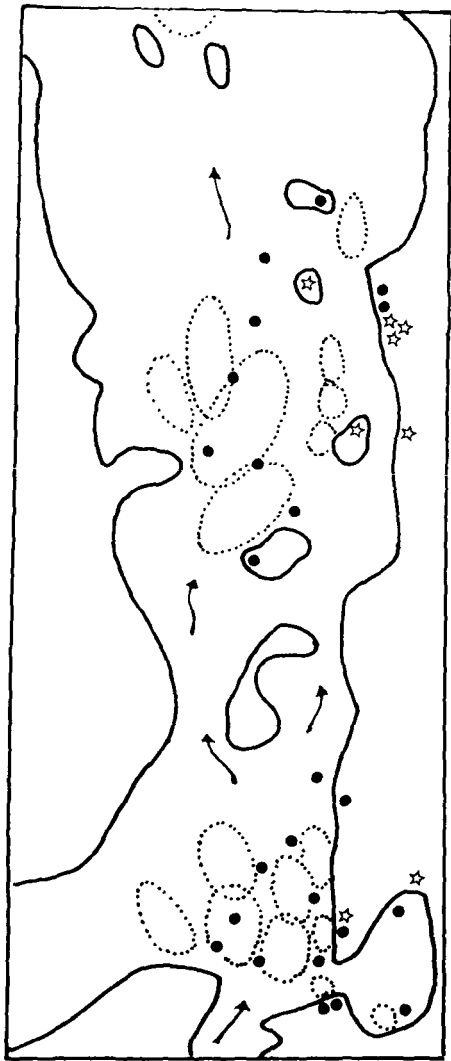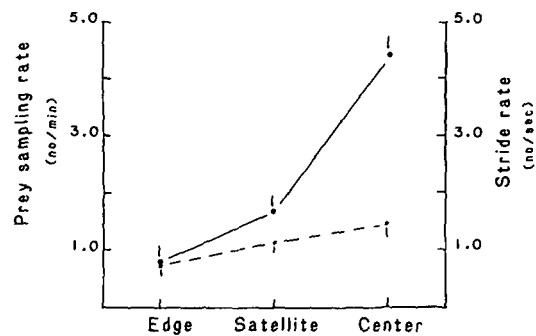
FIG. 3. Costs and benefit associated with different stream positions. Circles (●) indicate the number of drifting objects a male touched per minute; Stars (★) indicate the number of swimming strokes per second a male used to maintain his position in the current. Data represent average rates for 5 central, 4 satellite and 4 edge males. Bars represent standard errors.

FIG. 2. Map of study stream showing the positions of males and females in relation to the major currents. Arrows (→) mark the currents; Closed circles (●) indicate the centers of individual female territories; Dotted lines (·····) designate the boundaries of male territories; Stars (☆) indicate resting males. The map depicts positions during one 3-hr period, but the individuals' positions remained relatively unchanged throughout the two-week period.

2) what factors determine which females succeed in this competition.

To answer these questions we first must define the boundaries surrounding these most productive areas, and then categorize individuals based on how frequently they use these areas. Since the average diameter

of a female's territory is 0.25 m, a conservative diameter of 0.5 m was used to delineate the boundary of an area centered about each stream constriction. Females were classed as frequent or "central" users if they spent more than 50% of their active swimming time within the boundary, whereas an infrequent or "peripheral" user was defined as one who spent less than 50%, but more than 25%, of its time in these areas. Individual females showed consistent tendencies to swim in certain areas, and no females spent less than 25% of their time in these productive areas.

There is a significant size difference among females occupying central or peripheral areas ($F(1,32) = 21.3$; $P < 0.001$). On average central females ($\bar{x} = 53.9$ mg) were heavier than peripheral females ($\bar{x} = 45.2$ mg). Thus it appears that a weight dependent female hierarchy determines where a female can forage. As will be shown below, each position confers different benefits, but also involves different costs.

Male dispersion

Differences in swimming location also occur among males. As Figure 2 shows, males are also distributed non-randomly, and like females their territories are generally situated near the most "productive" areas. According to sexual selection the-

ory, this is where males should position themselves since this is where they will maximize their mating prospects. However, at these sites they too can survey the greatest surface area of water in search of prey, and as a result come into competition with potential mates. Removing males swimming in the productive sites almost always resulted in a nearby male filling the vacancy. And as in the case of females, males show consistent tendencies to forage near or far from these productive sites. For males, however, a sizeable fraction of the population spent less than 25% of their active swimming time in the productive areas. As a result, males must be separated into three categories: central, satellite, and edge males.

As Figure 3 shows, swimming in different areas results in significant differences in energetic costs $(F(2,11) = 11.6; P < 0.005)$, and benefits $(F(2,11) = 41.2; P < 0.001)$. Clearly, central males contact floating objects significantly more often than either edge or satellite males. And although most of the prey from the best current areas have been removed before they get to the satellites, the amount satellites obtain is still significantly greater than that obtained by edge males (Duncan Multiple range procedure). Such gains entail increased costs, however. The stride rate of central males exceeds that of satellite males, which in turn significantly exceeds that of edge males. But although stride rates increase with proximity to the productive areas, they do so at a slower rate than do the foraging gains. Thus satellite males derive a small net gain over edge males, but that of central males is much greater still.

Although it appears that satellites might be fairing better energetically than edge males, this difference might be erased if the costs of aggression could also be included in the cost-benefit equation. Table 1 shows that the rates of aggression differ significantly for males swimming in different locations $(F(2,32) = 7.83; P < 0.005)$. Edge males are involved in about one third the fights of either central or satellite males. According to the Duncan procedure, the small increase in fighting rate that central males display over satellites is not statisti-

TABLE 1. *Rates of aggression.*

Type male	No males	No fights/hr	SE
Central	11	27.8	3.6
Satellite	13	22.5	3.8
Edge	8	7.3	1.6

cally significant. Although equating swimming and fighting costs is difficult, the increase in fighting that central males engage in is probably not enough to negate its disproportionate foraging gains. But the net energetic gain that satellites register over edge males is small, especially when compared with the large increase in costs of aggression. Thus it appears that at least with respect to proximate payoffs satellite males are performing about as well as edge males, but substantially worse than central ones.

This pattern of site dependent benefits can be modelled by modifying slightly the Verner-Orians polygyny threshold model (Verner, 1964; Orians, 1968). As depicted in Figure 4, fitness will decline as territory quality deteriorates, whether an individual is the sole, or central, user of the territory, or whether it is a satellite user. As a result, whenever there are differences in territory quality, it may pay some males to cease foraging as sole users of poor current areas and become satellites in superior current areas, even though access to food and mates is restricted. Since the model is constructed in terms of fitness, it is important to ascertain whether the differences in proximate rewards described above translate into differences in reproductive success. As a first approximation mating success will be used to compare the success of the various strategies. But sperm competition and fecundity differences among females inhabiting different portions of the stream may somewhat alter the quantitative relationships. As Figure 5 shows, central males achieve significantly more matings per day than either satellite or edge males $(F(2,15) = 4.3; P < 0.05)$. The Duncan procedure shows that the difference among satellites and edge males is insignificant. Thus at least towards the end of the breeding season a
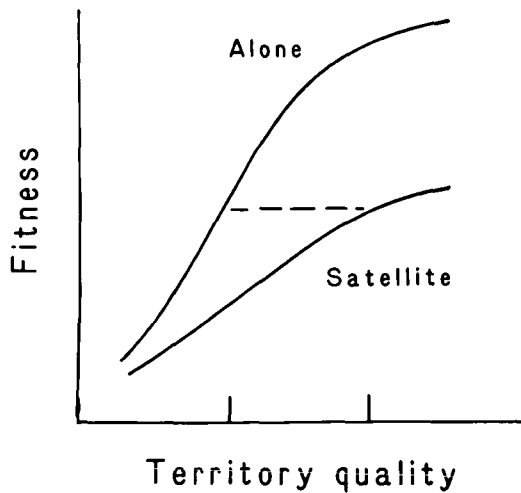
Fig. 4. Model of satellite threshold. Solid lines show that fitness always declines as territory quality deteriorates. But for any given territory quality, sole occupancy, or occupying the central positions, always yields a higher fitness than can be obtained by occupying a peripheral, or satellite, position. Dotted line indicates the territory qualities where central and satellite positions yield equal fitnesses.
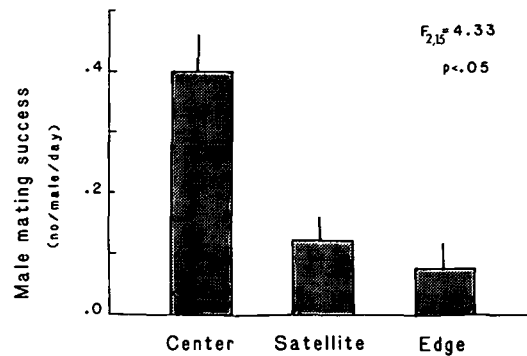

Fig. 5. Mating success of males in different locations. Daily averages based on the number of copulations recorded for 5 central males, 5 satellite males and 7 edge males during five consecutive days. Bars represent standard errors.

few males are mating significantly more often than the majority of males.

The fundamental question that remains is what aspects of the environment or male behavior or morphology are responsible for causing males to adopt differing behavior patterns. For females overall body length and weight determined whether or not females occupied the best foraging areas. For males, however, neither phenotypic attribute seemed to be involved (Table 2). There were no significant differences among the weights ($F(2,31) = 0.2$; $P < 0.7$) or the lengths ($F(2,30) = 0.1$; $P < 0.9$) of males foraging in central, satellite, or edge sites.

The absence of a correlation with male behavior and overall male size does not eliminate the role of some other aspect of phenotype. Despite the fact that males are smaller than females they are more aggressive and often displace them from feeding areas. This superior fighting ability may be correlated with the fact that among males and females of equivalent size males have significantly wider femurs on their first legs than females. It is these appendages that

males use in fighting and sending surface signals (Wilcox, 1979). They are also used to secure and clasp females during copulation. Their role in aggression and copulations, however, need not be mutually exclusive. When males attempt to mount females, females usually jump into the air and roll over. By behaving in this manner females may be exercising a form of mate choice; only the strongest or most adroit males can hang on. What benefits a female derives from having such a male on her back for many hours is not clear. But in general for females, foraging in a highly contentious area may not be without its costs since attacks are frequent. But as Table 3 shows, during copulation females suffer significantly fewer attacks than when they forage in the same area unpaired (paired $t_{11} = 6.4$; $P < 0.01$). With reduced harassment a female can go about the business of feeding more efficiently. By testing all males, females can clearly identify the secure clasping males, but perhaps they can also identify the best fighters and dominant males, those who will be attacked less often.

Table 2 shows, however, that the effect of this phenotypic feature on accounting for the spacing of males throughout the stream is somewhat equivocal. Although ANOVA shows no overall difference in femur size among males of the different strategies ($F(2,19) = 3.04$; $P < 0.07$), the Duncan procedure reveals that central

TABLE 2. *Phenotypes of males adopting differing strategies.*

Phenotypic attribute	Type of male		
	Central	Satellite	Edge
Weight (mg)	47.90 ± 1.20	46.0 ± 0.09	46.6 ± 1.93
Length (mm)	1.41 ± 0.08	1.43 ± 0.08	1.41 ± 0.09
Femur width (mm)	0.65 ± 0.01	0.62 ± 0.02	0.59 ± 0.01

males have wider femurs than edge males. Femurs of satellite males are intermediate in size and do not differ significantly from either of the other alternatives. The data suggest that this phenotypic feature does correlate with the adoption of the two most extreme strategies. But it is too early to conclude that femur width is solely responsible for determining which role a particular male will adopt. If future research demonstrates that satellite males show claspers that are significantly smaller than those of central males, but larger than those of edge males, then it seems likely that phenotypic differences associated with fighting and sexual ability would be constraining both a female's and a male's options. But even if additional data show that the differences among satellite and edge males are not significant, phenotype would still account for some behavioral structuring of the population; only males with the largest femurs are able to dominate the most productive sites. As for the satellite and edge males, the fact that their reproductive successes are equal suggests that males with small femurs might be switching among these options after assessing the actions of other similarly proportioned males.

DISCUSSION

For the giant water strider both males and females require swimming space on streams in order to acquire food and mates. And as in other surface dwelling insects, competition determines who gains access to the most productive sites which are located in swift current areas (Wilson *et al.*, 1978). Competitive success for individuals of each sex is governed in part by morphology. For females overall body size determines whether or not a female can forage in the best areas. For males it appears

that size of the femur on the first pair of legs partially determines where an individual can position itself. Since success at mating requires that males hang on during formidable rejection attempts by females, it may be that males with small femurs, by not being able to cope with large females, abandon the areas where large females reside and forage in locations where contact with females is restricted to smaller ones. Occasionally, however, large females rest along banks, and when they are quiescent, I have twice seen edge males succeed in mounting them.

As for satellite males, they appear to be caught in the middle. With claspers not differing significantly in size from those of males falling into the other two categories, it is not surprising to find that satellites occasionally mate with females occupying the best stream locations. They do so only when central males are absent from their territories, or are already engaged in copulations. Since copulations last for many hours the prospects of a satellite mating in central areas should be greater when the number of simultaneously sexually active females is large (Rubenstein, 1980*b*). This was not the case during this study, but should occur earlier in the summer.

During this study satellite males mated as frequently as edge males. If female rejection selects for males with large femurs then a weak pattern of assortative mating should occur. Males with large femurs should be able to mate with all females, but males with smaller ones should be limited to mating with smaller females. If more data indicates that satellites have on average larger femurs than edge males, then satellites might derive higher reproductive success. This would come about because larger females carry more eggs (Rubenstein,

TABLE 3.   *No. attacks sustained per hour while swimming before or during copulation.*

Female	Attacks sustained:	
	Alone	Copulating
P2BP	24	11
PGB	28	17
PBPB	30	19
PBPB	24	19
YPY	37	22
RY	42	37
PB2Y	25	15
PBP	32	28

unpublished data). Whether or not the differences in male mating success described in this study translate into differences in fitness will depend on the prevalence of sperm competition. Presently experiments are underway to measure this effect.

That females should attempt to reject males and then copulate for prolonged periods is intriguing. Generally the adaptive value of long copulations is interpreted from the male perspective as enhancing chances of paternity, or from the female's perspective as a means of acquiring resources for her offspring (Boggs, 1981). The findings of this study suggest that females may also benefit by using male dominance within his territory as a "shield" to reduce harassment by other males and females. Such reductions have played important roles in shaping the behavior of females in other species (Rubenstein, unpublished). Whether or not this is the case in water striders is as yet unclear.

ACKNOWLEDGMENTS

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