

Optimal group positioning after a predator attack: the influence of speed, sex, and satiation within mobile whirlingig swarms

William L. Romey^a and Emily Galbraith^b

^aDepartment of Biology, State University of New York at Potsdam, Potsdam, New York 13676, USA and

^bDepartment of Biological Sciences, University of Cincinnati, Cincinnati, Ohio 45221, USA

The position of animals within fish shoals, bird flocks, and insect swarms is related to individual differences in hunger, body size, and defenses. These differences relate to the way that animals balance multiple selection pressures including food-distribution and predator-attack patterns. However, the role of drafting/slipstreaming (taking advantage of the vortices of those in front of you) and sex on the position of individuals within a polarized group has not been well studied. For example, although hungry fish have been found to prefer positions toward the front of a shoal on average, the mitigating factors of sex, recent predator exposure, and drafting have not been factored into this response. We conducted a controlled laboratory experiment with individually marked whirlingig beetles (Coleoptera: Gyrinidae) where sex and feeding level were controlled and the position of beetles in a polarized group (in a flow tank) was analyzed at 2 different water speeds after exposure to a simulated predator. It was predicted that males and females would balance foraging and predator avoidance needs differently, as suggested by sexual segregation theory and that males might be likely to occupy front positions because of greater energetic needs. We found that in slow water males were more likely to occupy front positions, whereas in fast water females did, suggesting a different trade-off between the sexes in the need to forage versus save energy (draft). Additionally, we found that in slow water it was the hungry males that came to the group's front, whereas hungry females were more likely to move back. These are some of the first observations of the positional complexity with which individuals in congregations display, and several adaptive and nonadaptive explanations for the observed patterns are suggested. *Key words:* congregation, dimorphism, drafting, group, Gyrinidae, positioning trade-offs, sexual segregation, state dependent, swarm. [*Behav Ecol*]

Joining a group can help an individual to avoid predators, travel efficiently (draft), and acquire food (Parrish and Pitcher 1997; Krause and Ruxton 2002). Once in the group, animals may take up a position that balances selection pressures based on state variables. For example, in mobile shoals of fish, where the front represents a compromise between optimal feeding and suboptimal swimming expenditures (drafting), hungry fish move toward the front (Krause et al. 1992). In swarms of whirlingig beetles, where the edge is a compromise between optimal feeding and suboptimal predation risk, hungry beetles move peripherally (Romey 1995). Other factors that might influence an individual's position within the group include size, age, parasite load, boldness, and species (Krause and Ruxton 2002; Rayor and Uetz 1990; Ward et al. 2004). Our general question is does an individual optimize its position within a group in response to multiple environmental selection pressures and multiple individual states? In order to reduce the effects of mating behavior and dominance hierarchies on our results, it was decided to work with relatively simple groups defined as "congregations." Individuals in a congregation are gregarious, have free group entry and exit, have little kinship, and exhibit little dominance patterns (Parrish and Hamner 1997). A polarized congregation is one where their bodies are oriented similarly.

In this study, we consider the effects of 3 selection pressures on the fitness of polarized congregations: feeding, drafting, and predator avoidance (Figure 1). The optimal position for

feeding is at the front of a group (Robinson and Arenas 1991; Krause et al. 1992; Krause 1993b). The optimal position for drafting (= "slipstreaming") is at the back. Individuals at the back save energy by taking advantage of air or water vortices (a Karman vortex street) created by those in front, such as occurs within a peloton of bicycle racers in the Tour de France or swimmers in a triathlon (Delextrat et al. 2003). Drafting is well documented in fish (Herskin and Steffensen 1998; Liao et al. 2003), flying birds (Cutts and Speakman 1994; Weimerskirch et al. 2001), and swimming ducks (Fish 1995). It has also been demonstrated to occur in small invertebrates such as krill (Patria and Wiese 2004). Those at the group's back may reduce their energy output by 10–40% compared with those in front (Herskin and Steffensen 1998). Furthermore, the farther back in a line and the greater the overall speeds, the greater the energy savings (Fish 1995). For organisms swimming at the water's surface, there is also a "bow wave" effect that can help reduce energy expenditures of those in back (Tucker 1969; Fish 1995; Delextrat et al. 2003; Fish and Nicastro 2003). In addition to foraging and drafting differences, there are differences in attack probability relating to group position. In a stationary group, the center of the group is safest (Hamilton 1971; Vine 1971; Romey et al. 2007). In a polarized congregation, the group's back is thought to be the safest when both predator and prey are moving independently in still water (Bumann et al. 1997; Krause et al. 1998). However, when predator and prey are both polarized, the front position in a group might be the safest if a predator is usually oriented upstream.

Individual state is likely to influence how an individual balances selective forces (McNamara and Houston 1990). Although we know that hungry individuals go to front positions at moderate water speeds when all else is equal (e.g., size

Address correspondence to Dr W.L. Romey. E-mail: romeyw1@potsdam.edu.

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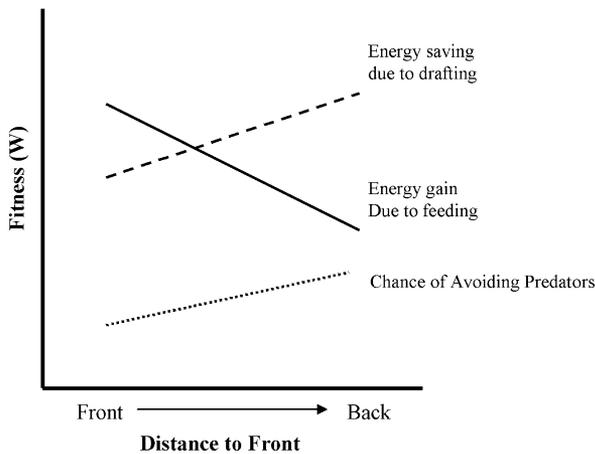


Figure 1
Hypothetical fitness function (W) for an individual within a polarized congregation due to 3 selective forces. Fitness due to energy conservation (drafting) would be highest at the rear of the group (dashed line). Fitness due to energy gain (feeding) would be highest at the front of the group if resources are randomly distributed (solid line). Fitness due to predator avoidance would be greatest at the rear if the prey group is more mobile than the predator. The slope of these 3 lines is likely to depend on water speed and individual differences in hunger and sex, as discussed in the text.

[Krause et al. 1992]), it is not clear how the slopes of these selection pressures (Figure 1) vary as water velocity changes and how the interaction between hunger and sex might influence their relative values. For example, at slow speeds, drafting asymmetries may be negligible compared with feeding asymmetries (Figure 1) and a hungry individual would go to the front to get more food. The predicted slopes of these fitness functions might also vary with water speed. For example, as water speed increases, the slope of the drafting fitness function might increase faster than the feeding fitness function.

The sex of an individual may also influence optimization of group position. Although there is a growing literature on between-group sexual segregation for vertebrates (Ruckstuhl and Neuhaus 2005), few studies of within-group sexual segregation exist (Romey and Wallace 2007) and none, that we know of, for polarized congregations. There are 3 primary hypotheses for explaining sexual segregation between groups: the predation risk hypothesis, the forage selection hypothesis, and the activity budget hypothesis (Ruckstuhl and Neuhaus 2002). These were initially developed for vertebrates with large sexual dimorphism (>20%) but could also apply to systems with less dimorphism. The predation risk hypothesis states that size dimorphism leads to differences in vulnerability and that the larger sex will choose areas that have more food, but are riskier, splitting the group into separate male and female groups. The forage selection hypothesis suggests that dimorphism produces different food requirements that subsequently select for behaviors that lead to separate groups. Third, the activity budget hypothesis states that males and females have inherently different rates of activity that lead to different space use. As well as size differences influencing vulnerability to predators, differences in detectability, escape speed, or physical defenses may also be relevant to sexual segregation (Croft et al. 2004; Krause and Ruxton 2002).

We studied the relative influence of 3 external selection pressures (drafting, foraging, and predator avoidance) and how individual differences (satiation and sex) mediate the decision of where individuals position themselves within a con-

gregation. To do this, we carried out a laboratory study with 2 levels each of feeding, water speed, sex, and time since a predator attack. We then measured the distance of marked individuals to the front and center of a group. Some of our predictions included a shift in the position of food-deprived beetles from the front of a group in slow water to the back in fast water as the need to obtain food is overshadowed by the need to save energy due to drafting. Also, based on the hypothesis that males have greater energy needs than females in this system, we predict that males, in particular, will occupy forward positions in slow water. In addition, if positioning is related to predator avoidance and the sexes have differences in the ability to avoid predators, then we predict that the group should be sexually segregated soon after a predator attack but not later. We believed that most of the selection pressures in a mobile group such as ours would relate to front-back differences and that any observed segregation within the group would have to do with front-back orientation rather than the “center-peripheral” differences found in stationary groups.

STUDY SPECIES

Whirligig beetle (Gyrinidae) groups/swarms are one of the few congregation-forming species of insects; they form groups of unrelated individuals (Nürnberg, 1996), outside of mating season (Heinrich and Vogt 1980), that are unrelated to dominance hierarchies (Romey, in preparation). They make a useful study organism because they exist in 2-dimensional groups at the water's surface that can be easily maintained in the laboratory, marked, and filmed. Also, there is a wide literature on their grouping and predator avoidance behaviors (Newhouse and Aiken 1985; Fitzgerald 1987; Vulinec and Miller 1989). Whirligig beetles feed on randomly dispersed food particles (usually dead insects) at the water's surface and exist in both pond and stream environments (Kolmes 1983). They mate in early summer, then form large groups in late summer and autumn (Heinrich and Vogt 1980). Beetles group in the day and then may disperse at night by swimming and/or flying (Thorp and Covich 2001). Some species, such as that used here, form polarized groups in rivers in which the group maintains a position near a visual landmark such as a tree. Life on the water's surface exposes them to a variety of aerial and aquatic predators. Fish eat them (Eisner and Aneshansley 2000) and prefer to attack the periphery of stationary groups (Romey et al. 2007). Aquatic birds also prey on them regularly (Bendell and McNicol 1995; Alvo and Campbell 2000). Grouping helps deter risk of predation in whirligig beetles by means of the many-eyes effect (Vulinec and Miller 1989), confusion effect, and dilution effect (Watt and Chapman 1998). Although these beetles are well known for their erratic protean display, they maintain relatively fixed positions within a group when undisturbed. The following sex differences have been reported in the literature for disparate gyrid species: 1) females have more stored fat than males in autumn (Svensson 2005); 2) males weigh 4% more than females in late summer (Romey and Wallace 2007); and 3) females have a higher mortality rate than males (Eijk 1986).

METHODS

Whirligig beetles (*Dineutes discolor*) were collected from the Raquette River in Potsdam, NY, USA, using dip nets on June 30 and July 8, 2004, and were transported to the laboratory at the State University of New York at Potsdam. They were separated by sex, according to tarsal hair density (Ferkinhoff and Gundersen 1983) and then randomly into 2 different feeding treatment groups. The resulting 4 populations were marked

with a unique color pattern by trapping them between soft packing foam and wire mesh and applying a 1-mm diameter paint dot using oil-based Faber-Castell Paint Pens on the elytra (wing cover). Past studies have indicated that there is no observable change in behavior in beetles due to this marking procedure or the particular color used (Romey 1995).

To standardize hunger levels, all beetles were fed freeze-dried bloodworms at a rate of 0.2 g per 50 beetles twice per day during their first 3 days of captivity. Whirligig beetles maintain their weight at this feeding level (Romey 1995). After this period, half the beetles were designated as “food deprived” (=hungry) and subsequently received half this amount for 3 days (0.1 g bloodworms per 50 beetles twice per day) whereas the other half (designated as “satiated”) were maintained at the original feeding level. During the initial 3 days, beetles were held in multiple 300 L, 2.5 m diameter, stock pools filled with aged tap water to a depth of 4 cm. After marking, beetles were moved to polyethylene treatment tanks (50-cm diameter) filled with aged tap water to a depth of 15 cm. In the laboratory, a constant temperature of 20 °C was kept, and a timer maintained a 13:11 light:dark cycle with overhead 32-W fluorescent bulbs.

A variable-speed airlift flow tank (a larger version of that pictured in Soluk and Collins [1988]) was constructed where beetles swam against a current to maintain a fixed position. The outer tank (Rubbermaid: 152 cm wide × 168 cm long × 62 cm deep) was filled with aged tap water to a depth of 43 cm. Inside this, a bottomless steel frame (91.7 × 63.3 × 50.5 cm) was placed with 5 cm sticking above the surface. To generate water flow, bubblers were placed on one side of the tank. Increasing or decreasing air flow controlled water speed. To minimize turbulence, a 4-mL thick plastic sheet was secured at the water’s surface. Lighting for the experimental tank was provided by two 120-W halogen bulbs and two 75-W tungsten lamps suspended 100 cm above the water surface.

For a given trial, 6 beetles from each of the 4 treatment groups (satiated/food-deprived male/female) were assembled into a group of 24 and placed into the flow tank. The group was given a 30-min acclimation period and then exposed to a fright stimulus consisting of a 1 × 3 cm stick passed rapidly from the front to the back of the group. Beetles respond rapidly to such a disturbance by a short-lived protean display of rapid circling for 15–20 seconds before settling back to a fixed and stable position within a group. Two instantaneous scan samples (Altmann 1974) were then taken of each group 1 and 6 min after the disturbance with an Olympus Camedia C-5060 digital camera with remote trigger mounted 140 cm above the water surface. The 5.1-megapixel camera was set at f2.8, 1/60ths shutter speed. All pictures were taken by a hidden observer using a remote-control shutter.

Twenty replicate groups of beetles were assembled and filmed over a 2-week period. The first week, 200+ beetles were gathered, marked, and treated as above. Each day multiple groups (mode = 5) of 24 individuals were sampled at random by sweeping a net through the rapidly whirling beetles. On a given day, each beetle was used only once. At the end of the day, beetles were returned to stock tanks to feed and mix overnight. The next day random sets of beetles were re-sampled from the 200. Although beetles were reused, they were not with the same set of individuals as before and the group was the unit of replication (Romey and Wallace 2007). Thirteen replicate groups were filmed during the first week (over 4 days). The second week, a new set of 200 beetles were obtained from the field, marked, and filmed (7 groups). Ten groups were run at a slow speed (1 cm/s), and 10 groups were exposed to the faster speed (10 cm/s) at random. These velocities were in the range that beetles would naturally experience, and they were easily able to swim to maintain positions

in the flow tank. The time of day and time of week were added to the statistical model to determine if there were unintended differences between our replicates. The hour of the day was added as one of 3 categories (7:00–9:50, 10:00–13:50, 2:00–5:00), and the time of the week was the number of days since the first day of filming of a particular set of beetles (1–4).

Analysis of digital images

Scaled coordinates of the beetles were obtained using ImageJ software (Rasband 2004). Beetles more than 10 body lengths away from the group or clinging to the sides or bottom of the tank were not considered in the analysis. On average, 73% of beetles joined groups for the first scan sample. There was no difference in the identity of the number of grouping (vs. non-grouping) beetles with respect to sex or hunger levels ($\chi^2 = 0.022$, $P = 0.882$). From the beetle’s individual coordinates, 2 measures of group position were calculated for each beetle: distance to the front (DTF) of the group and distance to the center (DTC) of the group. To calculate DTF, the distance back from the frontmost beetle was calculated from the *xy* coordinates. The DTC was calculated by determining the distance of each beetle away from the geometric center of the group (Romey and Wallace 2007).

Statistical analysis

Both DTF and DTC data were normally distributed within most groups (as determined by a Kolmogorov–Smirnov normality test). Mixed-model analysis of variance (SPSS v 11.5) was used to test the fixed effects of speed, sex, and satiation on DTC and DTF while controlling for the random effect of group. A full model was calculated first, and then separate models were calculated for the 2 water velocities. The time since the predator attack is not compared directly because individual beetles were not tracked individually between photographs. The hour, day, and week of the replicate were included in the full model, but the week was omitted for the split model because all replicates were run on one day. Marginal means and error bars are reported in the figures.

RESULTS

Water speed, sex, and satiation all had significant influences on whether individual beetles occupied the front or back (DTF) of a group soon after a simulated attack but not later. In fast water, beetles grouped more tightly than in slow water (Figure 2a and Romey WL, personal observation). There was a significant interaction effect between sex and speed on DTF (Table 1) so that in slow water the males occupied more forward positions than females, whereas the females occupied more forward positions in fast water (Figure 2a). In both slow and fast waters, hungry individuals were significantly more likely to be at the front of a group than satiated individuals (Table 1, Figure 2b).

When considering the water speeds independently (Table 2), there was a significant interaction effect between sex and satiation on DTF in the slow water but not the fast. Specifically, in slow water, hungry males were more likely than hungry females to be positioned toward the front (Figure 3a) whereas the satiated males and females did not occupy different positions. At the higher speed, sex did not influence front/back positioning, only satiation; hungry males and females were both more likely to be toward the front of a group than satiated individuals (Table 2, Figure 3b).

Satiation also influenced center/edge positioning of beetles (DTC). Regardless of water speed, satiated individuals were more likely to be at the center of a group than hungry

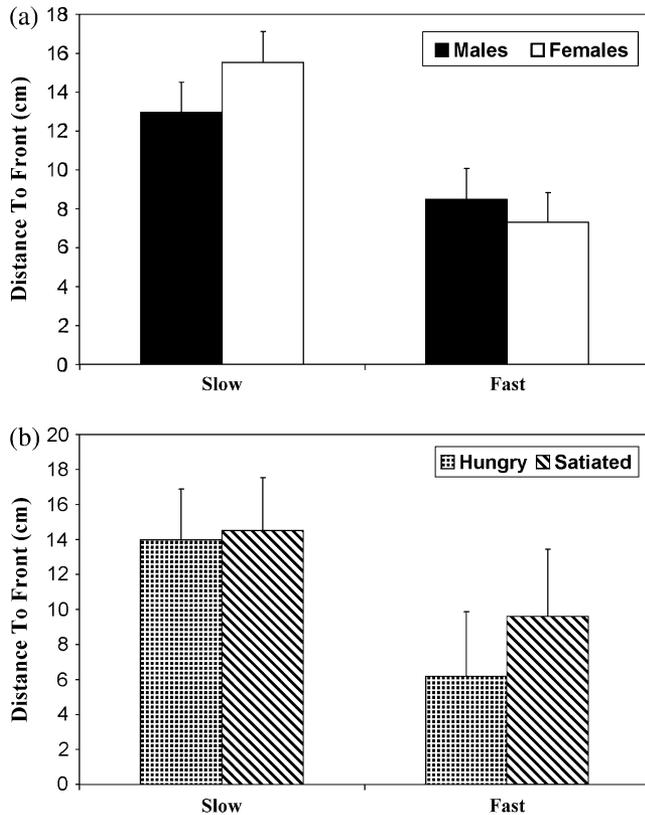


Figure 2

Marginal mean and standard error of a beetle's DTF with respect to (a) sex and water speed and (b) satiation and water speed 1-min after attack. The smaller the DTF the closer a beetle to the front of the group. There was a significant interaction effect between sex and water speed (Table 1). There was a marginal interaction effect between satiation and water speed (Table 1, $P = 0.059$).

individuals (Table 1). However, there was a marginal interaction effect between satiation and speed on DTC (Table 1) because in fast water (but not slow) hungry individuals were significantly more likely to be on the periphery of a group (have a higher DTC) than satiated individuals whereas at the low velocity neither hunger nor sex influenced DTC (Table 2).

The time since the simulated predator attack influenced the positioning of the beetles, the effects noted above were for 1 min after the attack. However, 5 min later, many of these effects were no longer observed. There were no significant effects on DTF or DTC due to the main experimental factors (sex, satiation, and speed) in the full model (Table 1) and only a sex \times satiation effect on DTF in the slow water in the separated model (Table 2). The timing of the replicate did not influence the DTF in either model (Tables 1 and 2), although the hour and day influenced DTC (Table 1), especially in the fast water trials (Table 2). As the hour and day progressed, the mean DTC decreased (the beetles grouped more tightly overall).

DISCUSSION

At fast speeds, groups were structured by satiation levels alone, but at slow speeds there was an interaction between sex and satiation. In fast water, hungry beetles were found in the front and satiated beetles were in the back (Table 2, Figure 3b). The explanation for this fits into our optimality framework (Figure 1); in fast waters we predicted a strong asymmetry

Table 1

Mixed-model analyses of variance testing the effects of sex, satiation (hunger), and speed on whether a beetle moves to the front of a group (DTF) or toward the center (DTC)

	1 min after attack			6 min after attack		
	df	F	P	df	F	P
DTF						
Sex	1, 346	0.83	0.362	1, 355	1.05	0.306
Satiation	1, 346	6.78	0.010*	1, 354	1.37	0.242
Speed	1, 12	3.73	0.078	1, 12	0.34	0.573
Sex \times satiation	1, 345	2.54	0.112	1, 354	1.81	0.179
Sex \times speed	1, 346	6.13	0.014*	1, 355	0.66	0.418
Satiation \times speed	1, 346	3.59	0.059	1, 353	0.06	0.803
Sex \times satiation \times speed	1, 345	2.26	0.134	1, 353	3.28	0.071
Hour	2, 12	0.92	0.424	2, 13	1.17	0.341
Day	3, 12	0.72	0.557	3, 13	0.37	0.776
Week	1, 12	3.42	0.090	1, 13	0.38	0.549
DTC						
Sex	1, 346	0.62	0.434	1, 352	0.00	0.999
Satiation	1, 346	5.46	0.020*	1, 352	0.14	0.705
Speed	1, 12	0.21	0.655	1, 12	2.19	0.165
Sex \times satiation	1, 345	1.10	0.296	1, 352	0.34	0.559
Sex \times speed	1, 346	0.21	0.645	1, 352	2.16	0.143
Satiation \times speed	1, 346	3.52	0.062	1, 352	0.46	0.496
Sex \times satiation \times speed	1, 345	0.06	0.814	1, 352	2.48	0.116
Hour	2, 12	0.12	0.892	1, 12	5.21	0.024*
Day	3, 12	0.21	0.886	1, 12	8.87	0.002*
Week	1, 12	1.27	0.283	1, 12	3.49	0.087

Group was included as a random effect ($N = 10$ groups of 24 beetles for each speed). Hour, day, and week were included to determine if there was any effect of time on the 20 replicate groups. (*Significant P value).

(large slope) due to drafting, a medium asymmetry due to foraging (food particles would have a greater chance of getting into the middle), and a medium effect of the predator-attack fitness function. So, hungry individuals would want to go to the front to obtain food, whereas satiated individuals would want to go to the back to draft and avoid predators. This has been previously observed for polarized shoals of fish; hungry individuals go to the front of groups (Krause 1993a). Hunger state also significantly influenced the distance of a beetle to the group's center in our study (Table 1); in fast water, hungry males and females were peripheral (large DTF). This would help them to find more food as supported by previous studies of nonpolarized whirling groups (Romey 1995; Romey and Wallace 2007).

Within-group sexual segregation occurred at slow water speeds. This is previously undocumented for polarized congregations in general. We found that hungry males occupied forward positions in the congregation, whereas hungry females occupied the back (Table 2, Figure 2a). Sexual segregation theory (Ruckstuhl and Neuhaus 2002) helps to explain some of these differences based on dimorphism. Although the dimorphism in whirling beetles is small (4%: Romey and Wallace 2007) it would explain the trade-off between foraging and predator avoidance. Because males are slightly heavier than females, there could be differences in energy needs and attack susceptibilities. Based on our predicted differences in food acquisition (males may need more food than females because of a higher metabolic rate and less time to forage during the early summer mating period) and chance of

Table 2
Mixed-model analyses of variance testing the effects of sex and satiation (hunger) on whether a beetle moves to the front of a group (DTF) or toward the center (DTC) at 2 different water speeds

	1 min after attack			6 min after attack		
	df	F	P	df	F	P
DTF						
Slow water						
Sex	1, 182	4.85	0.029*	1, 177	1.26	0.263
Satiation	1, 182	0.22	0.640	1, 176	0.30	0.582
Sex × satiation	1, 181	4.02	0.046*	1, 176	3.94	0.049*
Hour	2, 5	1.58	0.297	2, 5	1.77	0.269
Day	2, 5	0.56	0.604	2, 5	0.08	0.929
Fast water						
Sex	1, 165	1.49	0.224	1, 178	0.03	0.859
Satiation	1, 164	13.55	0.001*	1, 177	1.39	0.240
Sex × satiation	1, 164	0.01	0.942	1, 177	0.17	0.679
Hour	1, 7	0.20	0.667	1, 7	0.13	0.731
Day	1, 6	0.53	0.493	1, 6	0.20	0.670
DTC						
Slow water						
Sex	1, 183	0.75	0.387	1, 178	1.28	0.259
Satiation	1, 182	0.18	0.675	1, 176	0.02	0.884
Sex × satiation	1, 181	0.93	0.336	1, 176	0.57	0.450
Hour	2, 4	1.79	0.272	2, 5	0.71	0.540
Day	2, 5	2.87	0.151	2, 6	0.25	0.787
Fast water						
Sex	1, 164	0.03	0.855	1, 179	0.81	0.369
Satiation	1, 164	7.80	0.006*	1, 178	0.49	0.486
Sex × satiation	1, 164	0.30	0.585	1, 178	1.83	0.178
Hour	1, 6	0.03	0.876	1, 7	120.63	0.000*
Day	1, 6	0.05	0.839	1, 6	229.91	0.000*

Group was included as a random effect ($N = 10$ groups of 24 beetles for each speed). (*Significant P value).

avoiding predators (Figure 1), males should go to the front. Similar to a previous study in a nonpolarized group of whirligigs (Romey and Wallace 2007), sexual segregation was more pronounced soon after a predator disturbance than several minutes later, suggesting that differences in predator avoidance abilities between the sexes is more important than feeding differences, at least in slow waters. However, further studies should be carried out to test if whirligig predators (such as fish and aquatic birds) attack the front or back of polarized whirligig swarms. Furthermore, sexual segregation theory does not incorporate drafting.

The optimality framework that we developed (Figure 1) may be a more flexible tool for the prediction of individual positions within a congregation. For example, if the energy gain and predator avoidance curves are in opposition, as we predict here, then food deprivation of an individual should cause a change in position. Whereas, if there is a strong effect of 2 complementary curves, such as drafting and predator avoidance (Figure 1), then the effects of feeding may not structure the group. Evidence from other species of whirligig beetle (Eijk 1986) suggests that females may generally have a higher mortality rate than males. Therefore, they may take up safer locations at the back of the group.

As well as the aforementioned adaptive explanations for our results, several proximate explanations should be considered. These provide a nonadaptive alternative hypothesis (“rule of thumb”) that would lead the beetles to the observed positions (Parrish et al. 2002). Difference in preferred nearest neighbor distance (NND) is one rule of thumb that could lead an individual to a position indirectly, without having complete knowledge of the group (Romey 1996; Kunz and Hemelrijk

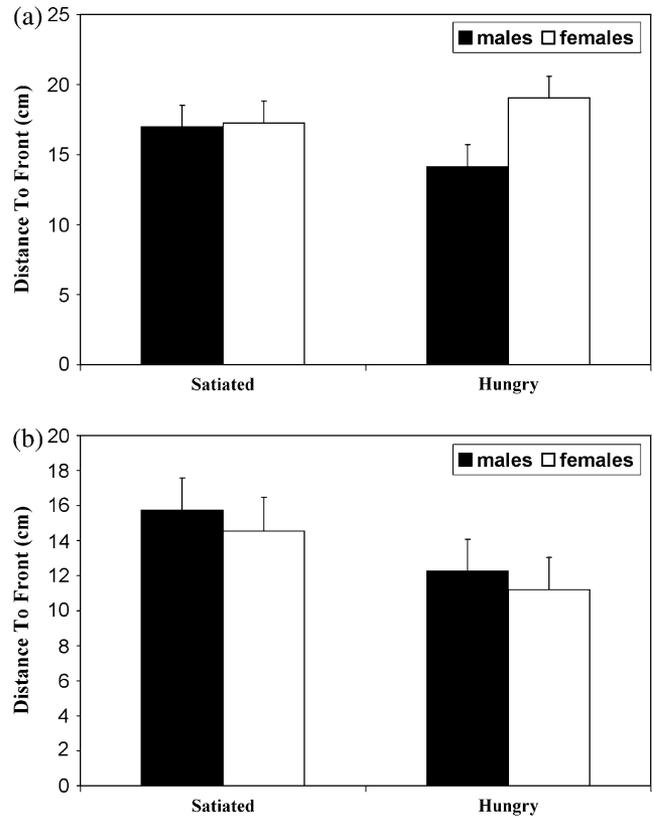


Figure 3
 Marginal mean and standard error of a beetle's DTF with respect to feeding treatment and sex 1-min after attack in slow (a) and fast water (b). The smaller the DTF the closer a beetle to the front of the group. At the slow speed, there was a significant interaction effect between sex and satiation (Table 2). At the fast water speed, there was a significant effect of satiation on DTF (Table 2).

2003). Previous findings have shown that hungry individuals on the outside sometimes have a larger NND (Romey 1996). However, the effects of sex and satiation might reinforce each other. For example, our results could be explained by hungry males having the largest preferred NND and satiated females having the smallest NND. A spatially explicit simulation model by Kunz and Hemelrijk (2003) predicts that larger individuals (or those with a larger preferred NND) would occupy positions at the front and edges of a moving group.

In conclusion, we demonstrated that individuals choosing positions within groups make complex trade-offs while attempting to simultaneously optimize foraging, predator avoidance, and drafting and that the decisions they make are influenced by individual differences in sex and hunger. Our primary findings were that in slow water males are more likely to occupy the front positions, especially hungry males, whereas females were more likely to go toward the back, with hungry females the furthest back. The back of the group is likely to be the best place for saving energy and avoiding predators, whereas the front of the group is likely the best place to obtain food, such as in the proposed fitness functions (Figure 1). Future studies that quantify the relative shapes of these functions at different water speeds would be helpful in understanding grouping behavior generally. For the predator avoidance function in a stream environment, such as we studied here in which predator and prey are both polarized, there is little data as to whether the relationship would be positive (as we propose in Figure 1) or negative. Additionally,

experiments should be devised which could differentiate between foraging and predator avoidance; they both predict that a prey should move forward in the group. Other questions to be addressed include the influence of differences in size, parasite load, and defensive abilities on how individuals balance these fitness functions. Simulation models, which parameterize different selection levels and the influences that individual differences have on them, would be especially useful.

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