INFLUENCE OF BODY SIZE ON LEADERSHIP IN SHOALS OF GOLDEN SHINERS, NOTEMIGONUS CRYSOLEUCAS

by

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Summary

In shoals of uniformly-sized golden shiners (*Notemigonus crysoleucas*), a minority of individuals who know when and where food is available can lead their naïve shoalmates to food. The present study investigated whether such leadership still takes place when leaders and followers are of different body size. Shoals of either 3 small and 9 large shiners, or 3 large and 9 small ones, were trained to expect food around midday in one of the corners of their large tank. The shoals revealed their learning by anticipating food arrival, *i.e.* by spending an increasing amount of time in the food corner up to midday. The 9 similarly-sized shiners were then replaced by 9 others of the same size who had never been in the tank before. When the remaining minority of knowledgeable fish were the large individuals, the new small fish followed them to the food corner the next day. These large leaders occupied front positions, though a few days earlier when the whole shoal had been experienced they had tended to stay at the back of the shoal as it entered the food corner. When the remaining minority of knowledgeable fish were the small individuals, the new large fish refused to follow them on at least half of the six trials. Knowledgeable small fish tended to be at the front of the shoal, either when the whole shoal was experienced or on the few occasions when naïve large fish accepted to follow them. The behaviour of the large fish suggests that they were motivated primarily by wariness, whereas that of the small fish is more compatible with a motivation to find food. Reluctance by large fish to follow small ones may contribute to the body size assortativeness of fish shoals in the wild.

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Introduction

Several aspects of shoaling in fishes are influenced by body size (Hoare *et al.*, 2000a). For example, when given a choice, fishes prefer to form shoals with companions that match their size (Pitcher *et al.*, 1985, 1986; Ranta *et al.*, 1992a, b; Krause, 1994; Krause & Godin, 1994), probably leading to the formation in the wild of shoals that are assorted by body length (Krause *et al.*, 1996a, b; Peuhkuri *et al.*, 1997; Hoare *et al.*, 2000b). In some species, large individuals have also been reported to shoal more often (Paxton, 1996) or to occupy front positions in shoals (Pitcher *et al.*, 1982), though this may not be a general pattern (Hoare *et al.*, 2000a; Krause *et al.*, 2000).

The present study looked at the influence of body size on another aspect of shoaling, namely leadership. Working with a gregarious minnow, the golden shiner (*Notemigonus crysoleucas*), I have recently showed that a small minority of informed individuals can lead the rest of their shoalmates to food in the right place and at the right time of day (Reebs, 2000). I had trained a shoal of 12 fish to expect food at midday in one of the corners of their large tank. The shoal demonstrated that they had learned this spatio-temporal association by visiting the 'food corner' every day, spending an increasing amount of time there up to midday, the normal time of food delivery. After replacing part of the shoal with new individuals that had never been in the tank before, I observed that the remaining experienced individuals (1, 3, or 5, depending on the experiment) kept on visiting the food corner and that the naive individuals followed them. In the present study, I repeated this type of experiment with shoals made up of individuals of different sizes, either small or large, to see if body size could influence the leadership capability of golden shiners. I specifically asked whether large fish would accept to follow small ones, and conversely whether small fish would accept to follow large ones.

There is some basis for expecting that leadership could be affected by body size. In several cases of social learning in vertebrates, it has been shown that young or subordinate individuals copy the actions of older and more dominant companions, but that the reverse does not happen (*e.g.* Japanese macaques washing potatoes or handling stones, Huffman, 1996; female guppies choosing mates, Dugatkin & Godin, 1993). A similar pattern might appear in the present context if we substitute body size for dominance status or age and if we substitute following for copying (though in some birds and mammals, dominance does not always correlate with leadership; see Beauchamp, 2000, and references therein). Moreover, both body size and position within a shoal are related to predation risk: larger fish are less vulnerable to gape-limited predators but are also more visible to others, and fishes at the front of a shoal are more vulnerable to ambush predators (Bumann *et al.*, 1997). Both body size and position within a shoal are also related to foraging: smaller fish often have a stronger motivation to feed (Krause *et al.*, 1998a; Hoare *et al.*, 2000a), perhaps because they process their food or use their reserves more quickly, and hungry fish often occupy front positions in shoals (Krause *et al.*, 1998b). All of this could translate into some size classes expressing a preference for leading or following positions within a fish shoal.

Material and methods

Golden shiners were captured during the summer in Folly Lake, 12 km south of Moncton, New Brunswick, Canada. Their sex could not be determined. All fish were brought to the laboratory and placed in 190-litre aquaria, 30-90 individuals per aquarium. Water temperature was 16 ± 2°C. Light came from windows in the room and the photoperiod was therefore natural. All experiments were carried out in summer and fall. The longest photoperiod was 15.75 h (sunrise at 0530 h, sunset at 2115 h) whereas the shortest was 12.5 h (sunrise at 0700 h, sunset at 1930 h). All fish were given a minimum of two weeks to habituate to captivity before being used in experiments. During that time they were fed commercial food flakes which were dropped at the surface by automatic feeders five times a day.

Experiments took place in a large rectangular tank (1.2 × 1.8 m with water 18 cm deep). Water temperature and photoperiod were the same as in the holding aquaria. Because of the tank's location close to windows, one end of it was in the shade while the rest was more fully illuminated (Fig. 1). The right and left corners in the light were separated by an opaque partition. The fish could discriminate between these two corners by their position and possibly by using cues from the ceiling and upper walls of the room above the tank (the sides of the tank were opaque).

At the end of the day that preceded the start of a trial, 12 shiners were placed inside the tank. These 12 shiners were 3 small and 9 large ones, or 3 large and 9 small ones. The range of total lengths was 5.5-7.5 cm for the small fish and 9.0-11.5 cm for the large ones. Over all trials, the average difference between large and small individuals within the same shoal was 3.1 cm. While capturing golden shiners in the field, I have observed such differently-sized individuals within the same minnow trap and I assume that they could be found within the same shoal. Some size classes could also form small minorities within shoals in the light of the general assortativeness by body size of shoals observed in natural populations of golden shiners (Krause *et al.*, 1996a, b).

The next day, with a camera hanging from the ceiling and connected to a remote tape recorder, I video-taped the movements of the shoal from 0700 to 1900 h. No food was

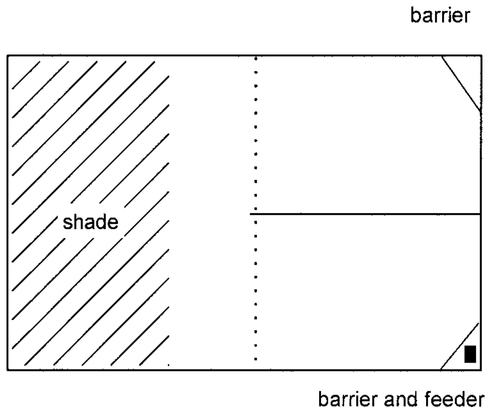

Fig. 1. Overhead view of the experimental tank. The dotted line is imaginary and delineates the entrance to the food corner (bottom) and the non-food corner (top).

delivered on that day. As in Reebs (2000), I expected that this shoal, which I called all-naive, would restrict its activity to the shady area of the tank because of wariness in a new environment (Helfman, 1981; McCartt *et al.*, 1997).

Starting the following day, commercial flakes were delivered twice around midday (1230 and 1330 h) in one of the corners opposite the shady area (Fig. 1). The food was dropped by an automatic feeder which the fish could not see unless they were directly below it. Once on the water, the floating flakes were restricted to a small area in the corner by an opaque Plexiglas barrier at the surface. To get at the food, the fish had to swim to the corner, go beyond the barrier (only 2 cm of which jutted below the surface) and reach for the floating flakes. A few flakes did not stay at the surface and sank to the bottom; originally such sinking flakes may have alerted the fish to the arrival of food.

After 12 days of such regular midday feedings, the food was withheld and the movement of the shoal was video-taped again from 0700 to 1900 h. As in Reebs (2000) I expected that the shoal, which I now called all-experienced, would have learned the spatio-temporal availability of food and that it would anticipate food arrival by paying an increasing number of visits to the food corner, and therefore spend an increasing percentage of time there, up to about midday.

During the next 3 days, the shoal received food around midday again, a renewed reinforcement designed to counter the previous day's negative experience of no food delivery. At the end of the last day, the 9 similarly-sized individuals were removed and replaced by 9 others of the same size but who had never been in the tank before. The next day, no food was given, and the movements of the shoal, which I called the test shoal, were video-taped from 0700 to 1900 h. I chose a ratio of 3 experienced for 9 naive fish because this was the smallest ratio that yielded consistent entrainment in Reebs (2000). Entrainment would be demonstrated if the 9 naive fish, instead of staying in the shade all day as the all-naive shoal had done, followed the remaining 3 experienced fish to the food corner. As in Reebs (2000), it was assumed that the shoal would not split up because of the strongly gregarious nature of golden shiners.

A total of 5 trials, each with new fish from the start, were conducted with a ratio of 3 large and 9 small shiners, while 6 trials used a ratio of 3 small and 9 large shiners. The trials were run in the summer and fall of 1999 and 2000, and they alternated fairly evenly between the two different ratios.

The video-tapes were viewed on fast-forward to measure the percentage of time spent by the shoals in the food corner, in the adjacent (non-food) corner opposite the shady area, and outside of both corners (Fig. 1) for each half-hour of the day. The exact times of entry and departure into and from the corners corresponded to the moment when half of the shoal had passed the line that delimited the entrance to the corners (Fig. 1). The number of entries into a corner was not formally counted because this variable was known to be strongly correlated with the percentage of time spent in that corner (Reebs, 2000).

To compare the all-naive, all-experienced and test shoals within trials in terms of time spent in the food corner, special attention was paid to two particular periods of the day. The first was called the 'food' period and went from 1200 to 1400 h, *i.e.* it encompassed the two normal feeding times (1230 and 1330 h). (Remember however that food was not delivered on any of the days when shoal movement was videotaped.) The second period was called 'anticipatory' and went from 1000 to 1200 h. The difference in behaviour between shoals turned out to be obvious and did not require statistical analysis. All-experienced and test shoals were further compared in terms of the position occupied by the size minority within a shoal as it entered the food corner. For this, 20 entries during the food period were selected haphazardly. For each entry it was noted whether the first, second, etc. fish to enter the food corner was a big or a small one. Relative body size could easily be distinguished on the videotape. For each trial separately, the frequency of position occupancy was compared between the all-experienced and test shoal with a χ^2 test (SPSS 7.5 for Windows).

Results

3 large : 9 small

In all 5 trials, the all-naive shoal spent the daytime in the shady area, as expected. At dawn and dusk, when low light levels extended to the whole tank, the fish sometimes swam around the perimeter of the tank, thereby spending some time within the food corner. In the middle of the day however, no time was spent within the food corner (triangles on Fig. 2).

In all 5 trials, the all-experienced shoal spent an increasing amount of time in the food corner as the day wore on, peaking near the normal time of feeding and decreasing thereafter (squares on Fig. 2). The fish visited only the food corner and not the other one. As before (Reebs, 2000), all-experienced shoals visited the food corner for only 20-30 s at a time, but did this with increasing frequency up to about midday.

In all 5 trials, on test day the 3 large and experienced individuals succeeded in entraining the 9 small and naive fish with them (circles on Fig. 2). The shoal repeatedly entered the food corner and never split up.

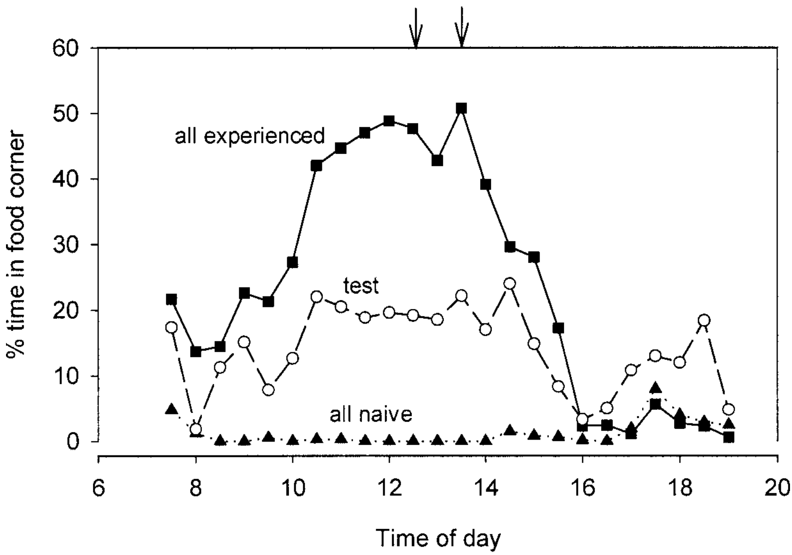

Fig. 2. Average ($N = 5$) percentage of time spent in the food corner of a tank by shoals of 3 large and 9 small golden shiners that had never been in the experimental tank before (all naïve), by the same shoals 12 days later after they had learned that food arrived near midday (all experienced), and by those shoals after the 9 small experienced fish had been replaced by 9 small naïve ones (test). Standard errors have been omitted for clarity; between 1000 h and 1400 h, SEs varied between ±3.3 and ±11.4 for the all experienced and test conditions. Arrows at the top indicate the daily times at which the shoals used to be fed (but food was not delivered on the days when these data were collected).

However, the test shoal did not spend as much time overall in the food corner as the all-experienced shoal had. During the 'food period', food corner use by the test shoal was on average 43% of that by the corresponding all-experienced shoal (range for the 5 trials: 26-54%). During the 'anticipation period', the same value was 45% (range: 16-82%).

During the tests, the 3 large experienced fish were near the front of the shoal as it entered the food corner, and the first position was always occupied by a large individual (open circles on Fig. 3). Those same big fish had been near the back of the shoal a few days earlier, letting the small individuals take the lead when the whole shoal was experienced (dark circles on Fig. 3). The frequency distributions of position occupancy by the large fish were significantly different between the all-experienced and test conditions in each of the 5 trials (all χ^2 values > 26.42, all $p < 0.0001$; because of small values

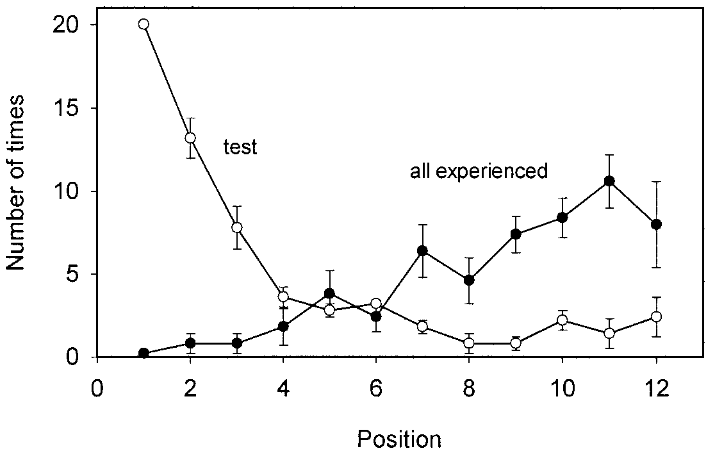

Fig. 3. Average ($N = 5$) number of times, out of 20, that each position in a shoal was occupied by a large fish as the shoal entered the food corner, for the trials when the large fish were in a 3 : 9 minority. Position 1 means the lead position at the front. The accompanying majority of 9 small fish could be as knowledgeable as the 3 large fish (all experienced) or could be ignorant of where and when the food arrived (test).

at numerous positions, the first 6 positions were pooled, as were the last 6 positions, resulting in a 2×2 contingency table in these tests).

3 small : 9 large

In all 6 trials, the all-naive shoal spent the daytime in the shady area, while the all-experienced shoal a few days later showed the typical pattern of increased food corner use up to the normal feeding time (triangles and squares respectively on Fig. 4). The non-food corner was not visited.

The results on test day, when the shoal was made up of the 3 remaining experienced small fish and 9 naive large ones, were variable. In one trial, the whole shoal remained in the shade all day. In three trials, the 3 small fish regularly entered the food corner together but were not followed by the 9 large ones (in these cases, therefore, the shoal splitted, something I had assumed would not happen). Food corner use by this split shoal during the food period was, for the three trials respectively, 49, 57, and 58% of that by the all-experienced shoal a few days earlier. In the remaining two trials, the whole shoal entered the food corner, one at low levels and one at levels comparable to that of the all-experienced shoal (circles and diamonds on Fig. 4).

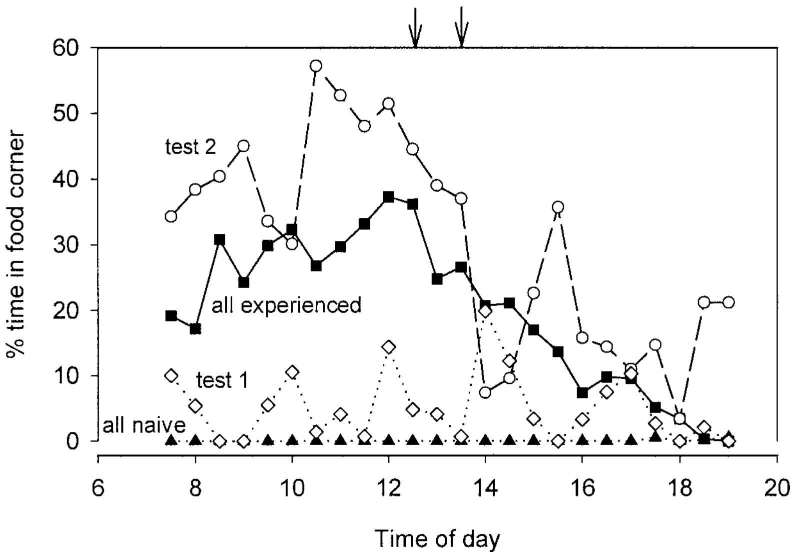

Fig. 4. Average ($N = 5$) percentage of time spent in the food corner by shoals of 3 small and 9 large golden shiners that had never been in the experimental tank before (all naïve), and by the same shoals 12 days later after they had learned that food arrived near midday (all experienced). Standard errors have been omitted for clarity; between 1000 h and 1400 h, SEs were always 0 (all-naive) or varied between ±7.3 and ±10.9 (all experienced). Also shown are the results of the only two test shoals, in which the 9 large experienced fish were replaced by 9 large naïve ones, that entered the food corner intact. Arrows at the top indicate the daily times at which the shoals used to be fed (but food was not delivered on the days when these data were collected).

When all-experienced shoals entered the food corner, the 3 small individuals tended to occupy the first few positions or the very last one (dark circles on Fig. 5). In the two trials when the whole test shoal entered the food corner, the three small and experienced fish tended to be in the first three lead positions of the test shoal (open circles and squares on Fig. 5). In the two corresponding all-experienced shoals, those three fish had also been near the front, but not so much in the very first position. χ^2 tests (in which the last 7 positions were pooled because of small values at some of those positions, resulting in a 2 × 6 contingency table) revealed a significant difference in the position of small fish between the test shoal that visited the food corner often and its corresponding all-experienced shoal ($\chi^2 = 19.58$, $p = 0.0015$) and an almost significant difference between the test shoal that visited the food corner a little and its corresponding all-experienced shoal ($\chi^2 = 10.15$, $p = 0.07$).

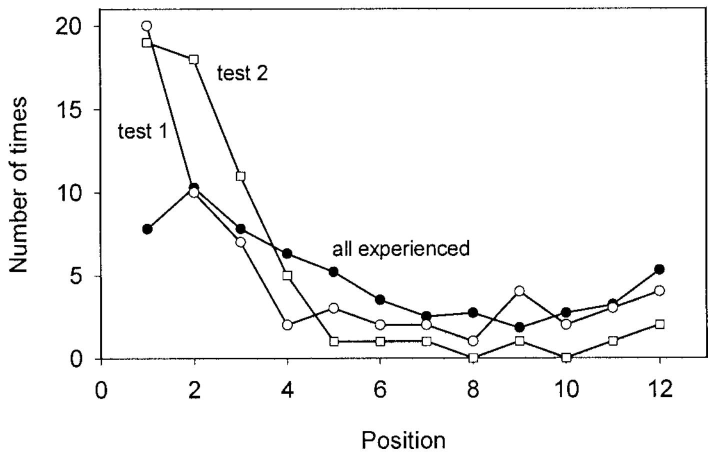

Fig. 5. Average ($N = 5$) number of times, out of 20, that each position in a shoal was occupied by a small fish as the shoal entered the food corner, for the trials when the small fish were in a 3 : 9 minority and for when the accompanying majority of large fish was knowledgeable about the food (all experienced). Standard errors have been omitted for clarity; they varied between ±0.7 and ±2.4. Also shown are the results for the only two trials where the test shoal entered the food corner intact.

Discussion

The present study confirms Reebs' (2000) findings that a minority of informed fish can lead a whole shoal to food (for other examples of leading and following, this time in birds, see de Groot, 1980; Brown, 1986; Greene, 1987; Rabenold, 1987; Waltz, 1987). Such entrainment can benefit leaders as well as followers (for a similar situation in birds, see Heinrich, 1994; Marzluff *et al.*, 1996). Leading shiners can leave the safety of a shady area and still benefit from the well-known anti-predation features of a big shoal. Followers benefit through the discovery of a new food site and in sharing the food there if it is abundant enough (which it was in this study). The present study also confirms directly that informed fish lead their shoal from the front. Reebs (2000) had only provided indirect evidence of this.

There were differences in behaviour between large and small fish. When in a minority, large fish tended to stay at the back of the all-experienced shoal as it entered the food corner, though they accepted to occupy lead positions when they were the only ones knowledgeable about food. They were then readily followed by the small naive fish. The 55-57% reduction in food corner use by the test shoal relative to the all-experienced shoal in the 3 large : 9 small condition is slightly more than the 45% (anticipation period) or 30% (food period) reduction observed by Reebs (2000) with shoals of uniformly-sized fish, but food corner use was still substantial. For their part the small fish, when in a minority, did not necessarily stay at the back even in the all-experienced shoals. Often they were at the front. They were still at the front when they were the only ones knowledgeable, but in that case the large fish did not often follow them. Inertia on the part of the large shoalmates may have prevented the small fish from going to the food corner (1 trial) or may have forced them to split from the group and forego the anti-predation benefits of a large group while in the food corner (3 trials). In my previous work with this experimental paradigm, I had not seen splitting in similarly-sized shoals; I had only seen it with very large shoals of 33 individuals (Reebs, 2000).

The behaviour of the large fish seems to reflect greater wariness than motivation to feed (see Peuhkuri, 1997, 1998, for a similar finding in sticklebacks). Staying at the back of the shoal can be advantageous because ambush predators, which are not uncommon in freshwater systems, tend to attack prey at the front of a shoal (Bumann *et al.*, 1997). Loss of feeding opportunities from being a little late at the food corner may have been partly compensated by the large individuals' greater gape and better capacity to ingest large flakes. (Golden shiners practice scramble competition rather than interference competition but greater size is still an asset in that case.) Reluctance to follow unfamiliar small leaders, electing instead to stay in the shade in the company of other similarly-sized shiners when ignorant of the food situation and wary because of a new environment, is also compatible with anti-predation response. It is true that large fish also accepted to lead when they were the only ones knowledgeable, and that they were then in the front (vulnerable to ambush) and in a visible size minority (vulnerable to the oddity effect, Landeau & Terborgh, 1986; Theodorakis, 1989) but perhaps their experience of successfull foraging in a known place without any previous signs of predator activity, combined with the impossibility of letting other individuals take the lead, overcame their wariness.

In contrast, the behaviour of the small fish seems to reflect a strong motivation to feed at the expense of predation risk. When naive, small shiners readily followed unfamiliar leaders that may have appeared knowledgeable about food (as in Reebs & Gallant, 1997; Lachlan *et al.*, 1998). When knowledgeable, and irrespective of the experience status of their larger shoalmates, small fish were most commonly at the front, a characteristic of hungry individuals (Krause *et al.*, 1998b) as in an effort to be the first ones to get to the food. Some of the small fish even accepted to leave the safety of the shade and go to the food corner even though the rest of the shoal did not follow. This behaviour suggests a mechanism, in addition to active shoal choice, that might explain why in nature shoals are often made up of members of uniform size. Small fish accept to follow small leaders (Reebs, 2000) but if large fish refuse to follow small leaders, then in their search for food all small fish may split from a mixed shoal, leaving only the static large individuals behind.

Is there a parallel between the reluctance of large wary fish to follow small ones and the apparent refusal of older macaques and guppies, for example (Huffman, 1996; Dugatkin & Godin, 1993), to copy the actions of younger conspecifics? Perhaps there is. In Reebs (2000), large wary shiners accepted to follow large knowledgeable leaders. Why were they reluctant to follow small knowledgeable ones here? On the other hand, the answer to the above question may reside in the tendency for some fish to prefer the company of similarly-sized individuals because of anti-predation benefits. This tendency could make it more difficult to follow differently-sized fish rather than similarly-sized ones, at least in fish that are motivated primarily by wariness.

In conclusion, although there are probably benefits for both leading and following shiners in the present experimental paradigm, body size can influence the willingness of these fish to act as leaders or followers. Small fish appear to be willing leaders and followers. Large fish on the other hand may lead only if they are the only ones knowledgeable, and they do not follow so readily when the leaders are much smaller than they are. This is compatible with a priority for predation avoidance by large individuals and a priority for foraging on the part of the small ones. There may be alternative explanations however. Perhaps leadership is favored instead (or in addition to foraging and predation considerations) by intrinsically high levels of swimming activity or exploratory behaviour on the part of some individuals (Wilson *et al.*, 1993; Budaev, 1997a, b; Beauchamp, 2000) and this tendency could be found most often in young (small) fish. Controlled manipulations of hunger levels and predation risk are necessary to confirm the part that these variables play in the differences observed between the leadership behaviour of various size classes.

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