Individual leadership and boldness in shoals of golden shiners (*Notemigonus crysoleucas*)

Caroline Leblond & Stéphan G. Reebs[1]

(Département de Biologie, Université de Moncton, Moncton, NB, E1A 3E9, Canada)

Summary

Shoals of golden shiners (*Notemigonus crysoleucas*) often swim along the perimeter of their large indoor tank at dawn and dusk, and can also be trained to anticipate food arrival by swimming directly towards the food source at midday. In this study all golden shiners in six shoals of 8-12 fish were individually marked with a visible implant elastomer, and shoal movement was video taped in order to determine whether some individuals consistently occupied front positions even when all shoal members were of similar size and experience. There were significant correlations between all three times of day (dawn, midday, dusk) in the mean position (from 1 = first at the front of the shoal to 12 = last at the back) occupied by each fish. In each shoal, 1-3 fish were leaders: all three daily times combined, they had more than twice the occupancy rate of the front two or three positions as expected from chance. In subsequent boldness tests there was a tendency ($p = 0.096$) for these leaders to pass through dark U-shaped tubes more readily than non-leaders. However, after being dipnetted and transferred to a refuge, leaders did not emerge earlier than non-leaders. Individual tendencies to lead may have been underlain by a motivation to feed (which may differ even in fish of similar size and experience) or by intrinsic mobility. On the other hand, a link between leadership and risk-taking remains to be established for captive golden shiners.

Keywords: leadership, boldness, shoaling, position, fish, golden shiner.

Introduction

In animal groups, leadership can be defined as the initiation of a movement, or a changing direction during a movement, made by one or some individual(s) followed by the rest of the group (Krause et al., 2000). Leadership has

been studied mostly in ungulates (e.g., sheep: Arnold, 1977; goats: Escós et al., 1993; pigs: Meese & Ewbank, 1973; cattle: Kilgour & Scott, 1959; Sato, 1982; deer: Carranza & Arias de Reyna, 1987), primates (e.g., Dunbar, 1983; Erhart & Overdorff, 1999; Leca et al., 2003), birds (e.g., Lamprecht, 1992; Beauchamp, 2000) and fish (e.g. *Caranx speciosus*: Yamagishi, 1978; *Gasterosteus aculeatus*: Partridge, 1980; *Rutilus rutilus*: Bumann & Krause, 1993; *Aphyocharax erithrurus*: Levin, 1996; *Notemigonus crysoleucas*: Reebs, 2000, 2001). In fish, leaders usually lead from the front (conceivably, individuals could initiate changes in movement from the back or the side of a group, but this does not seem to be the norm; Krause, 1993a). For this reason, leadership in fish could also be defined as a tendency to occupy front positions. Several factors can influence leadership in that sense. Sub-groups that have been deprived of food (Krause, 1993b; Krause et al., 1998), or that have prior knowledge of where and when food appears (Reebs, 2000, 2001; see also Couzin et al., 2005), or that are bigger (Pitcher et al., 1982; Krause et al., 1998) or smaller (Reebs, 2001) than the rest of the shoal have been shown to occupy front positions more often. However, in part because no study has been conducted with shoals larger than 3 or 4 individually identified fish, there is no information on the leadership tendencies of individuals within homogenous shoals (Krause et al., 2000). With the partial exception of Pitcher et al. (1982), we do not know if some individual fish have an intrinsic tendency to be at the front of a shoal when conditions of feeding, prior knowledge, and body size are held as constant as possible.

One advantage of initiating a shoal movement and being at the head of the shoal is to get to resources first while still having companions that dilute predation risk (Krause et al., 1992; Krause, 1993a, 1994; Deblois & Rose, 1996). Disadvantages are that ambush predators tend to attack individuals at the front (Bumann et al., 1997) and predators in general tend to attack individuals that move more (e.g., Martel & Dill, 1995). These potential costs lead to the hypothesis that leaders might be intrinsically bold. Boldness is considered as a personality trait and is defined as the propensity to take risk (Wilson et al., 1993, 1994). Previous studies have relied on a variety of tests to score boldness (e.g., showing a new object: Verbeek et al., 1994; Wright et al., 2003; showing a new food type: Coleman & Wilson, 1998; showing a threatening stimulus: Magnhagen & Staffan, 2005; or placing in a totally new environment: Brown & Braithwaite, 2004). Some studies found relations between boldness and other variables. For example, Budaev (1997) observed

that solitary wrasses (*Symphodus ocellatus*) were bolder than their schooling counterparts. Fraser et al. (2001) reported that bold Trinidad killifish (*Rivulus hartii*) moved over longer distances after being released back in their native stream. Sneddon (2003) showed that bold rainbow trouts (*Oncorhynchus mykiss*) were able to learn a task more rapidly than shy individuals. Godin & Dugatkin (1996) observed that bolder male guppies (*Poecilia reticulata*) were more attractive to females. Sundström et al. (2004) reported that bold brown trout (*Salmo trutta*) tended to become dominant. Huntingford and Adams (2005) provided a review of work showing that farmed salmonids are bolder than their wild brethen. Brown & Braithwaite (2004) and Brown et al. (2005) found that bold *Brachyraphis episcopi* were the smallest and possibly most metabolically active fish of their group. However, we are aware of only one study having reported a link between boldness and front positions in shoals: Ward et al. (2004) found that bold threespine sticklebacks (*Gasterosteus aculeatus*) (boldness defined as low schooling tendency and quick resumption of foraging after a simulated aerial predator attack) tended to be at the front of a shoal in an indoor flow channel.

With the above in mind, the present study had two objectives. First, we wanted to test for individual tendencies to lead by describing the frequency with which marked fish occupy various positions in a shoal, larger than just 3 or 4 fish, where all members were of similar size, had similar prior knowledge of the environment, and had equal access to food. Second, we wanted to determine whether leaders scored higher than non-leaders in two tests of boldness. For this we worked with shoals of 8-12 golden shiners (*Notemigonus crysoleucas*) a strongly gregarious species that in nature forms shoals of 8-250 individuals (Krause et al., 1996) which roam widely within lakes (Hall et al., 1979). We used a large indoor tank in which shoals of shiners were already known to display both food-induced and spontaneous movements (Reebs, 2000, 2001).

Material and methods

All manipulations were approved by the Animal Care Committee of the Université de Moncton. Golden shiners were captured with minnow traps in Folly Lake, 12 km south of Moncton, New Brunswick, in June 2004. All fish were brought to the laboratory and placed in 189-L aquaria ($140 \times 30 \times$

45 cm), about 90 individuals per aquarium. Water temperature was 12-15 °C. The photoperiod was natural, indirect sunlight coming from windows in the room. Held fish were fed commercial food flakes at the surface three times a day (mid-morning, mid-day, mid-afternoon).

Six experimental trials were conducted successively between July and December 2004. Each trial started with the selection of 12 fish of similar size from one of the holding aquaria. (Mean total length $\pm$ SD of the fish at the beginning of each of the 6 trials was, respectively, 7.13 ± 0.4, 6.53 ± 0.3, 6.88 ± 0.4, 7.37 ± 0.3, 7.50 ± 0.3, and 6.82 ± 0.3 cm. Mean weight was, respectively, 2.36 ± 0.4, 1.64 ± 0.2, 1.81 ± 0.4, 2.32 ± 0.3, 2.47 ± 0.5, and 1.99 ± 0.4 g.) The fish were anesthetized with tricaine methanesulfonate (125 mg/L) and then individually identified with 1 to 4 sub-cutaneous injections of a visible implant elastomer (Northwest Marine Technology Ltd, Washington State). The four possible mark sites were all on the back: just behind eye level, in front of the dorsal fin, just to the right of the dorsal fin, or near the caudal peduncle. A mark at one site consisted of three thin white lines side by side along the axis of the body, except on the two front sites where the lines could also be perpendicular to the axis of the body. (On the figures, individuals are identified with a four-letter code corresponding to the four mark sites from front to back, with E = longitudinal mark, e = transverse mark, and X = no mark.) Three fish received one mark, three got two marks, three got three, and three got four. Such an equal distribution was done in an attempt to see if the number of marks influenced leadership behaviour.

The 12 marked fish were then placed in a large rectangular opaque tank (1.2 × 1.8 m with water 20 cm deep). The walls and bottom were white, but the position of the tank relative to the windows in the room meant that one-third of the tank at the long end was in the shade, and this is where the fish always stayed when stationary. Water temperature and photoperiod were the same as in the holding aquaria. No food was available on the first and second day in the tank (preliminary experiments had showed that fish did not feed much on those days). Thereafter about 0.3 g of commercial food flakes were delivered at midday (1200 h and 1300 h) by an automatic feeder located in one corner of the tank away from the shade, during a 'training' period of 10 to 14 days designed to teach the fish where and when food became available during the day. The floating food flakes were dropped behind a gate that prevented their dispersal throughout the tank while still remaining available to fish coming up from below. This set-up had been used previously (Reebs,

2000, 2001) to show that fish can learn the time and place of food delivery and that informed golden shiners can lead naïve individuals to food. During those studies the shiners tended to stay in the shade of the tank except during the few hours that preceded food delivery, when together they often left the shade and crossed the tank to quickly inspect the food corner before going back to the shade (an example of food-anticipatory activity after having figured out the spatio-temporal availability of food). They also moved at dawn and dusk, when the shoal circled repeatedly along the perimeter of the tank, perhaps a reflection of the golden shiner's habit of moving from open waters to the littoral of lakes at dawn, and vice-versa at dusk (Hall et al., 1979). Their behaviour was similar in the present study, with the exception that in some trials one or two fish did not accompany the rest of the shoal and almost always stayed in the shade. Such individuals, plus a few cases of mortalities during the course of the trial, were not included in the analysis. (It would have been difficult to predict whether the non-shoalers were bold or shy. Staying in the shade suggests shyness, but being relatively alone suggests boldness.) The final shoal size for analysis in the six trials ended up being, in chronological order (shoals A-F), 11, 9, 12, 12, 8, and 11.

After the training period, shoal movement was recorded for 3-4 days, three times a day: (1) during the first 2 h of daylight (usually starting 15 min before sunrise), coded 'AM', at which time the shoal circled along the perimeter of the tank; (2) during the 2 hours before food delivery, coded 'ANT', when the shoal anticipated food arrival by visiting the food corner directly; and (3) during the last 2 h of daylight, coded 'PM', when the shoal once again circled the tank. We used an overhead camera whose field of view encompassed the corner (40×40 cm) where food was delivered (the shiners visited this corner during food anticipation of course, but also went by it during the circling movements of dawn and dusk). Preliminary observations showed that the order in which golden shiners leave the shady area of the tank is almost identical to the order in which they arrive at the food corner. For each entry of the shoal into the field of view, the identity of the first, second, third, etc. fish to appear was noted. With 1 designating the first front position, 2 the second, etc., it was possible to calculate the mean position of each fish for each of the three daily periods of observation. The sample size (total number of entries into the camera's field of view over the 3-4 days) on which the means were based for AM, ANT, and PM respectively was 34, 87, 34 for

shoal A; 40, 70, 22 for shoal B; 34, 83, 6 for shoal C; 28, 98, 20 for shoal D; 27, 108, 20 for shoal E; and 6, 27, 19 for shoal F.

After verifying that mean position was similar at all three daily times (see results), data were pooled over those three daily times. We then considered the front two positions in shoals of 8-9 individuals, or the front three positions in shoals of 11-12 fish, and calculated the expected frequency of occupancy of these groups of positions based on a uniform distribution. Any fish whose observed occupancy was at least double the expected frequency was designated a leader.

Immediately after the 3-4 days of the recording period, fish were subjected to two successive boldness tests, the first one being of a novel design, the second being more traditional (see Brown & Braithwaite, 2004). In the first one, three large aquaria (each $140 \times 30 \times 45$ cm) were lined up end to end. The first and second, and second and third, aquaria were connected by a water-filled U-shaped black PVC pipe, 10 cm in diameter, that went up over the edge of one aquarium and down into the other. All fish from the shoal were placed together in the first aquarium. To go from one aquarium to the other, a fish had to swim for about 30 cm through the narrow U-shaped pipe. During the next 14 days, three times a day, the position (aquarium) of each fish was noted. Fish were fed each day, individually where they were. We considered that bolder fish would be the first ones to pass through the pipe and go from one aquarium to the next. Scores (hereafter called 'exploration scores') were attributed to each fish according to the following formula $[(14 - x_1) + (14 - x_2)]/28$, where x_1 is the number of days spent in the first aquarium before moving to the second one and x_2 is the number of days before moving to the third one. Higher scores indicated boldness. Overall, 29 of the 63 tested fish never left the first aquarium; these received a score of 0.

After this first test, all fish were dip-netted and transferred to another large aquarium. This transfer took place in the morning, 24 h after the fish were last fed. The shiners were placed together in a $30 \times 25 \times 10$ cm black Plexiglas box with a 7-cm circular opening on one side. The opening was blocked for 10 minutes, and then opened. For the next 2 h, an observer noted how much time elapsed before each fish came out of the box. Individual scores (hereafter called 'emergence scores') were given based on emergence time relative to the total duration of the test: $(120 - \text{emergence time in minutes})/120$.

Higher scores indicated boldness. Overall, 22 of the 63 fish did not come out of the box within 2 h; these received a score of 0.

Statistical analyses consisted of Pearson's correlation tests and T-tests (SPSS for Windows version 13.0) as well as one binomial test (Conover, 1980). In the correlation tests, each shoal was analyzed separately, and then the 6 p-values were combined with $-2 \sum \ln p$ and tested against a χ^2 distribution (Sokal & Rohlf, 1995). The t-tests compared leaders and non-leaders, and in the case of the boldness scores the data were log-transformed for normality. These 'leaders versus non-leaders' comparisons were done on data pooled over all 6 trials, and we used both the absolute values of each individual and their deviation from the mean of the individual's shoal.

Results

Figures 1-3 show examples (the two shoals of 12 fish, and one of the shoals with 11 fish) of the frequency distribution of positions for each fish during each of the three daily periods of observation. Each of the six shoals had 1-2 fish that appeared to be leaders at all three daily times (e.g., EEEE on Figure 1; XXEX and EEEX on Figure 2; XEXX on Figure 3). An additional 0-2 fish per shoal appeared to be leaders at two of the three daily times (e.g., EEEX on Figure 1; EXEE and EEEE on Figure 3). After the three daily times were pooled, 13 fish (1-3 per shoal, including all 7 examples above) fulfilled our formal criterion for leadership. These leaders averaged 2.59 ± 0.54 (SD) times the expected occupancy rate at the front positions (range: 2.04-3.82).

In contrast to these leaders, some fish were consistently found in the rear half of the shoal (e.g., XEXX on Figure 1; EXEX on Figure 2; EeEE on Figure 3). Figure 1 also shows two odd cases: EEXX tended to be either in the very first position or in the rear half but seldom in between, and EXEE was clearly at the front at time AM but in the rear at times ANT and PM. However, such odd cases were uncommon. Overall, there were significant correlations in mean position occupied between all three daily times (Figure 4; AM versus ANT: $\chi^2 = 60.58$, $p < 0.001$; AM versus PM: $\chi^2 = 31.29$, $p < 0.005$; ANT versus PM: $\chi^2 = 37.19$, $p < 0.001$).

We found no significant correlations between mean position, at any of the three daily times, and either of exploration score, emergence score, number of marks, body weight, or body length (all $\chi^2 < 13.5$, all $p > 0.3$). We also
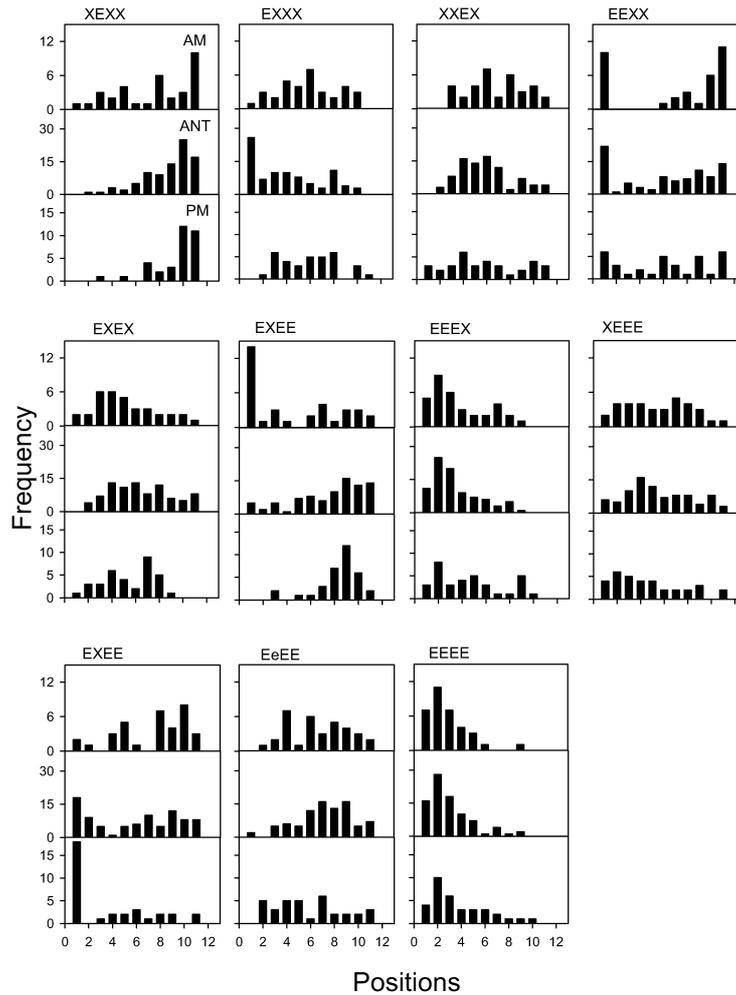
Figure 1. Frequency distribution of positions occupied within shoal A (from 1 = first at the front, to 11 = last at the rear) by each of the 11 golden shiners making up that shoal, at three daily times (AM = dawn, ANT = food anticipation at midday, PM = dusk). Note that the scale of the y-axis varies between times.

did not detect any significant correlation between the two boldness scores themselves ($\chi^2 = 10.24$, $p > 0.5$), or between them and the number of marks, body weight, or body length of the fish (all $p > 0.25$).

However, if the analysis is limited to a comparison of all leaders versus all non-leaders, then leaders tended to score higher in the exploration test
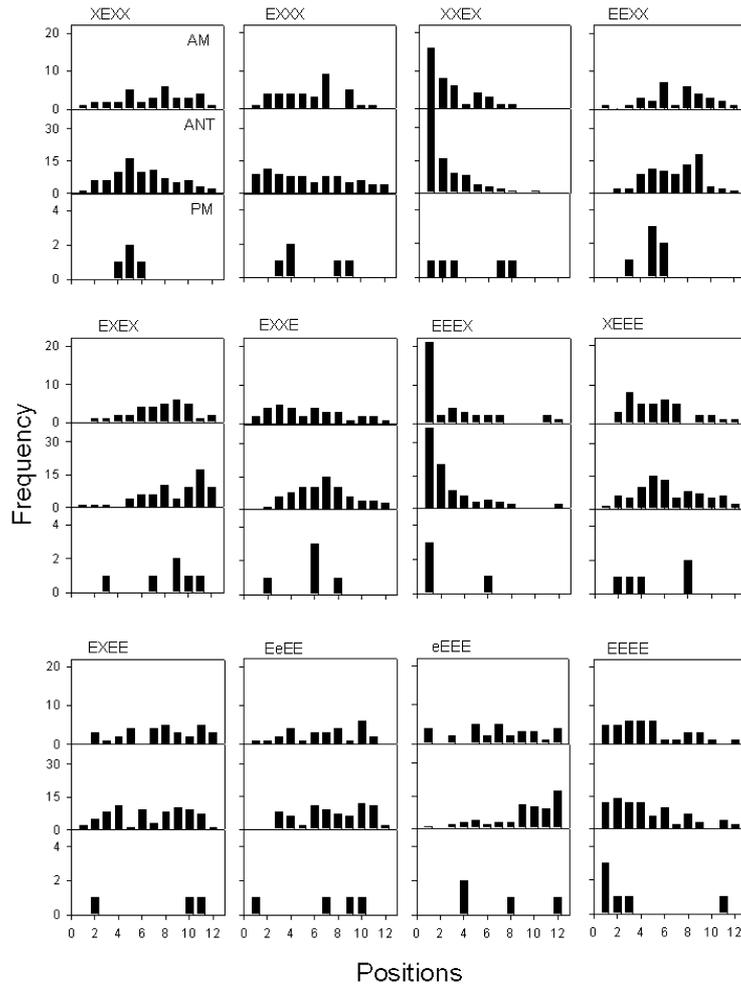
Figure 2. Frequency distribution of positions occupied within shoal C (from 1 = first at the front, to 12 = last at the rear) by each of the 12 golden shiners making up that shoal.

(Figure 5), though the difference was marginally non-significant ($p = 0.096$ for the absolute scores and $p = 0.111$ for the scores relative to the shoal's mean). Another way to analyze the data is as follows: of the 13 leaders, 9 had an exploration score higher than the median score of their shoal, while 4 had a lower score than the median. Though suggestive, the difference is not significant on a binomial test ($p = 0.133$).
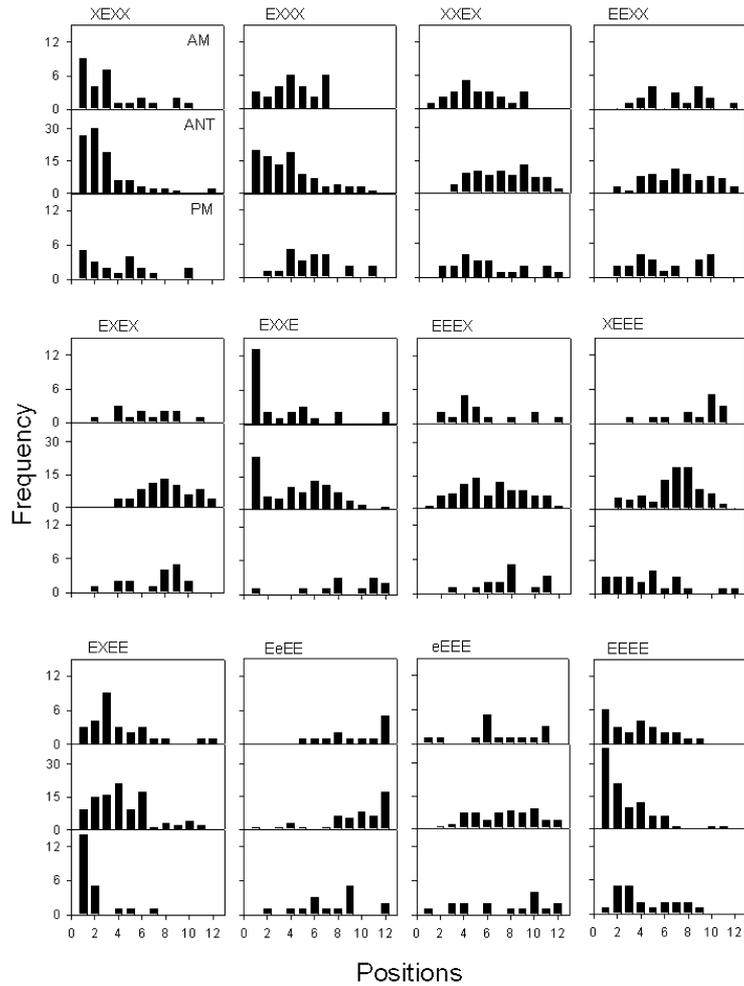
Figure 3. Frequency distribution of positions occupied within shoal D (from 1 = first at the front, to 12 = last at the rear) by each of the 12 golden shiners making up that shoal.

No significant difference was detected (all $p > 0.3$) between leaders and non-leaders in emergence score (Figure 5), number of marks, body weight and body length, be it in terms of absolute values or values relative to the shoal mean. We tried the same analyses with leaders defined for each separate daily times rather than for all times combined, but again no significant differences with non-leaders were found.
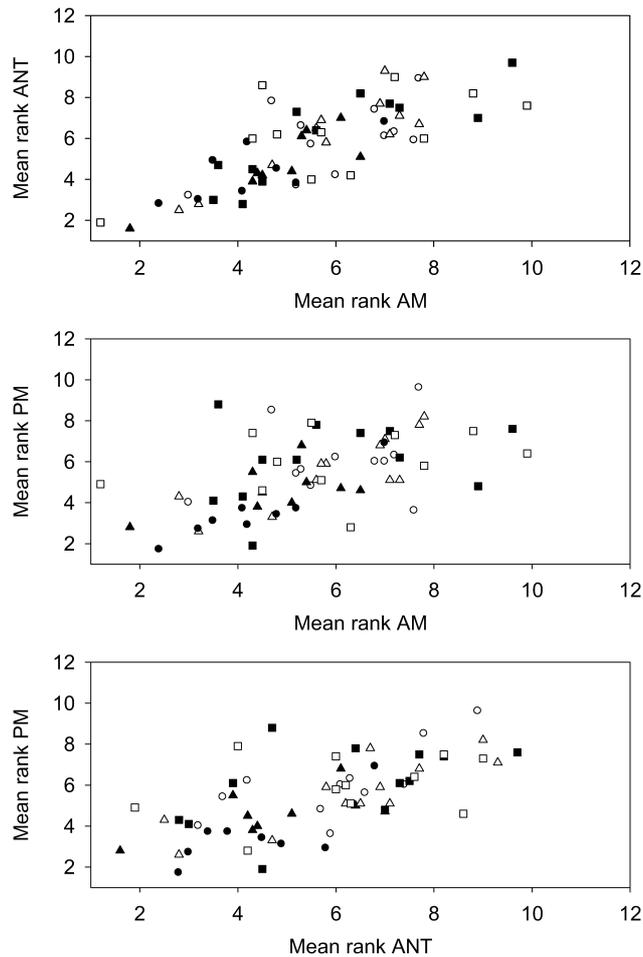
Figure 4. Correlations between individual mean position occupied by golden shiners at three different daily times (AM = dawn, ANT = food anticipation at midday, PM = dusk). The six shoals studied are represented by different symbols.

Discussion

This is the first study to provide a description of the frequency distribution of positions for all members of shoals larger than 3-4 individuals, where all fish are of similar size and experience. Pitcher et al. (1982) had provided similar data but for only four individuals in one shoal of 10 differently-sized mackerel. As in Pitcher et al. (1982), we found intra-individual variation in position occupancy, but leaders could nevertheless be identified. In our study,
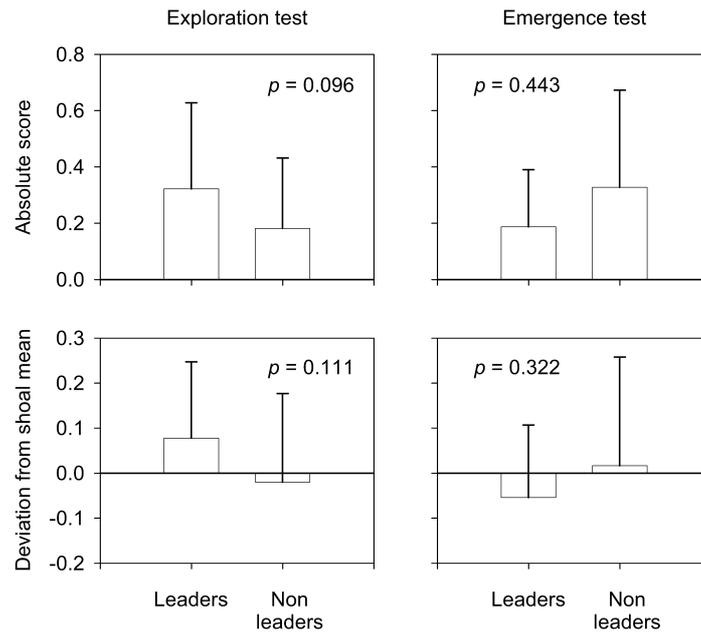
Figure 5. Boldness scores (overall mean $\pm$ SD), expressed as absolute values and as deviations from the respective shoal's mean, of golden shiners categorized as leaders ($N = 13$) or non-leaders ($N = 50$). The *p*-value refers to the result of a *T*-test on log-transformed data.

the same leaders tended to occupy front positions in two different movement contexts: during direct visits to a food corner and during circling of the tank at dawn (especially) and dusk.

Body weight and length never featured as significant variables in our results. This is a verification that, as we intended, fish were sufficiently similar in size within each shoal. There was not enough variance in body size for this factor to exert an effect on leadership. At a larger scale (about 6 versus 10 cm in body length), smaller golden shiners tend to lead more than larger ones (Reebs, 2001). However, even at a similar body size there might still be inter-individual differences in growth rate, metabolic activity, and therefore tendency to feed. Such differences may explain leadership tendency.

It is likely that hunger was the motivation behind the direct visits that shoals made to the food corner at midday. In this context, leaders might have been the hungrier individuals. The strong correlation between mean position at dawn (AM) and midday (ANT) suggests that hunger may also

have underlain leadership early in the morning. Food-anticipatory activity in golden shiners that are fed once a day start on average 4.5 h before food delivery (Reebs & Lague, 2000), and fish in the morning had not been fed for at least 18 h. Days are 15 h long in July but only 9 h long in December at our latitude. For the last two shoals that we tested (in November and December), the end of the AM observation period and the beginning of the ANT observation period were separated by only 1-2 h. For these shoals at least, the AM movements might have been partly motivated by food-anticipatory activity or by foraging, even though they were not direct visits to the food corner. A possible experiment to elucidate this question would be to temporarily isolate the leaders and over-feed them, and/or to food-deprive fish that tend to stay in the back half of the shoal, and see if their mean position is affected at both dawn and midday. Another possibility is to directly measure the number of feeding acts by leaders and non-leaders at different times of day (something that unfortunately was not possible with the food delivery system we used, as the shoal fed as a compact mass and individuals could no longer be distinguished).

The motivation behind leadership at dusk is harder to define, inasmuch as the motivation behind the dusk movements in general is uncertain (we have already alluded to diel patterns of habitat choice, but only comparisons with non-migrating populations or long-term captives could throw light on this question). There were overall correlations between mean position at PM and mean position at AM and ANT, so perhaps hunger also motivated dusk movements. However, the correlations involving PM were not as strong as the one between AM and ANT, which suggests that other motivations come into play during the dusk movements.

One possible motivation, at all times of day, is general activity level (intrinsic rather than hunger-motivated), the most mobile fish tending to be leaders more often. In preliminary experiments we have compared the movement frequency of two shoals made up of old leaders from all six shoals with that of two shoals made up of old followers, and found some evidence (albeit statistically nonsignificant) that the shoals of old leaders moved more often (unpubl. data).

We found some weak evidence (p-values around 0.1) that leading shiners were more exploratory than non-leaders based on the boldness test that involved swimming through tubes. A tendency for exploration is consistent both with a motivation to find food and with high mobility. However, leaders

did not score significantly higher than non-leaders in the test that involved emerging from a refuge after being dip-netted. Perhaps this was caused by a shortcoming in our experimental protocol, which entailed that the emergence test always be administered immediately after the exploration test. Maybe the boldest fish in the exploration test found themselves alone or in relatively small groups for extended periods of time in the second or third aquarium, possibly an 'unnerving' experience that made them more circumspect in the ensuing emergence test and reduced their risk-taking tendency to the level of the non-leaders. Using multiple tests of boldness is a valuable approach, but care must be taken to either randomize the order of the boldness tests or separate them sufficiently in time so that any after-effects can dissipate.

Given the general lack of correlation between mean position and boldness scores, and between the two boldness scores themselves, it is worthwhile discussing whether shiners perceived movements within our tank and our two boldness tests as entailing risk. Predatory fish seem to be absent in the shiners' lake of origin, but there are kingfishers and herons, and the latter could be defined as ambush predators. In the tank, the shoals invariably kept to the shade, a behaviour typical of wary fish (Helfman, 1981; McCartt et al., 1997). Therefore it seems reasonable to assume that movements across or around the tank were perceived as somewhat risky by the fish. Exploring a new environment (a dark tube) is risky mostly because the fish tended to do it alone (the fish usually appeared one by one in the second and third tank of our experimental set-up) and shoaling is one of the main anti-predator strategies of minnows in general and golden shiners in particular. Coming out of a refuge after being dipnetted could be viewed as risky, inasmuch as fish may conceive of environments with dipnets as dangerous (exposure to a real predator, or a realistic predator model, or alarm substance – which golden shiners have; Godard et al., 1998 – would have been a better test). However, assessing the degree to which risk is perceived is a difficult task.

The main problem is that risky behaviour is usually the result of a trade-off between risk aversion (or the lack thereof) and other motivations, such as hunger, curiosity, or the need to maintain some inter-individual distance. So when an individual adopts a more risky behaviour than another, it is not easy to determine if this is because its intrinsic risk aversion is lower or because the motivation behind the behaviour (hunger when traveling to a food corner, curiosity when exploring a tube, desire to avoid crowding when leaving a refuge) is higher. It is difficult to measure risk aversion in a context

completely devoid of other motivations, or in situations where these other motivations can be safely assumed to be at similar levels for all individuals. In our experiment for example, we tried to standardize past experience and body size but in the absence of feeding tests or metabolic measurements we cannot exclude possible differences in hunger.

Given that different motivations can counteract risk aversion, perhaps it is not surprising that several studies, including the present one, have found some aspects of risk-taking to be context specific (Coleman & Wilson, 1998; Réale et al., 2000). However, some studies have also found that boldness or personality traits can be generalized from one context to another (e.g., Beauchamp, 2000; Ward et al., 2004; Svartberg et al., 2005), suggesting the existence of behavioural syndromes (Sih et al., 2004).

Finally, a technical consideration: we note that our use of visible implant elastomer allowed good identification of each individual, though the camera had to be relatively close (we tried, for example, to hang the camera on the ceiling to view the full tank from above, but the marks then could not be reliably detected). We note also that the number of marks never correlated with any behavioural variables, giving us confidence that the marking technique did not unduly affect behaviour. Malone et al. (1999) similarly found no effect of the use of visible implant elastomer on the growth, survival, and vulnerability to predation in reef fishes. Croft et al. (2004, 2005) also found no effect of visible implant elastomer tags on the shoaling behaviour of guppies.

Acknowledgements

References

Arnold, G.W. (1977). An analysis of spatial leadership in a small field in a small flock of sheep. — Appl. Anim. Ethol. 3: 263-270.
Beauchamp, G. (2000). Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches. — Behaviour 137: 301-314.
Brown, C. & Braithwaite, V.A. (2004). Size matters: a test of boldness in eight populations of the poeciliid *Brachyraphis episcopi*. — Anim. Behav. 68: 1325-1329.

Brown, C., Jones, F. & Braithwaite, V. (2005). In situ examination of boldness-shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. — Anim. Behav. 70: 1003-1009.

Budaev, S.V. (1997). Alternative styles in the European wrasse, *Symphodus ocellatus*: boldness-related schooling tendency. — Env. Biol. Fish. 49: 71-78.

Bumann, D. & Krause, J. (1993). Front individuals lead in shoals of three-spined sticklebacks (*Gasterosteus aculeatus*) and juvenile roach (*Rutilus rutilus*). — Behaviour 125: 189-198.

Bumann, D., Krause, J. & Rubenstein, D. (1997). Mortality risk of spatial positions in animal groups: the danger of being in the front. — Behaviour 134: 1063-1076.

Carranza, J. & Arias de Reyna, L. (1987). Spatial organization of female groups in red deer (*Cervus elaphus* L.). — Behav. Proces. 14: 125-135.

Coleman, K. & Wilson, D.S. (1998). Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. — Anim. Behav. 56: 927-936.

Conover, W.J. (1980). Practical nonparametric statistics, 2nd edn. — John Wiley & Sons, New York.

Couzin, I.D., Krause, J., Franks, N.R. & Levin, S.A. (2005). Effective leadership and decision-making in animal groups on the move. — Nature 433: 513-516.

Croft, D.P., James, R., Ward, A.J.W., Botham, M.S., Mawdsley, D. & Krause, J. (2005). Assortative interactions and social networks in fish. — Oecologia 143: 211-219.

Croft, D.P., Krause, J. & James, R. (2004). Social networks in the guppy (*Poecilia reticulata*). — Proc. R. Soc. Lond B, 271 (Biol Lett Suppl 6): S516-S519.

Deblois, E.M. & Rose, G.A. (1996). Cross-shoal variability in the feeding habits of migrating Atlantic cod (*Gadus morhua*). — Oecologia 108: 192-196.

Dunbar, R.I.M. (1983). Structure of gelada baboon reproductive units IV. Integration at group level. — Z. Tierpsychol. 63: 265-282.

Erhart, E.M. & Overdorff, D.J. (1999). Female coordination of group travel in wild *Propithecus* and *Eulemur*. Int. J. Primatol. 20: 927-940.

Escós, J., Alados, C.L. & Boza, J. (1993). Leadership in a domestic goat herd. — Appl. Anim. Behav. 38: 41-47.

Fraser, D.F., Gilliam, J.F., Daley, M.J., Le, A.N. & Skalski, G.T. (2001). Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. — Am. Nat. 158: 124-135.

Godard, R.D., Bowers, B.B. & Wannamaker, C. (1998). Responses of golden shiner minnows to chemical cues from snake predators. — Behaviour 135: 1213-1228.

Godin, J.-G. & Dugatkin, L.A. (1996). Female mating preference for bold males in the guppy, *Poecilia reticulata*. — Proc. Natl. Acad. Sci. 93: 10262-10267.

Hall, D.J., Werner, E.E., Gilliam, J.F., Mittelbach, G.G., Howard, D., Doner, C.G., Dickerman, J.A. & Stewart, A.J. (1979). Diel foraging behavior and prey selection in the golden shiners (*Notemigonus crysoleucas*). — J. Fish Res. Bd. Canada 36: 1029-1039.

Helfman, G.S. (1981). The advantage to fishes of hovering in shade. — Copeia 1981: 392-400.

Huntingford, F. & Adams, C. (2005). Behavioural syndromes in farmed fish: implications for production and welfare. — Behaviour 142: 1207-1221.

Kilgour, R. & Scott, T.H. (1959). Leadership in a herd of dairy cows. — Proc. New Zeal. Anim. Product. 19: 36-43.

Krause, J. (1993a). Positioning behaviour in fish shoals: a cost-benefit analysis. — J. Fish Biol. 43 (Suppl. A): 309-314.

Krause, J. (1993b). The relationship between foraging and shoal position in a mixed shoal of roach (*Rutilus rutilus*) and chub (*Leuciscus cephalus*): A field study. — Oecologia 93: 356-359.

Krause, J. (1994). Differential fitness returns in relation to spatial position in groups. — Biol. Rev. 69: 187-206.

Krause, J., Bumann, D. & Todt, D. (1992). Relationship between the position preference and nutritional state of individuals in schools of juvenile roach (*Rutilus rutilus*). — Behav. Ecol. Sociobiol. 30: 177-180.

Krause, J., Godin, J.-G. & Brown, D. (1996). Size-assortativeness in multi-species fish shoals. — J. Fish Biol. 49: 221-225.

Krause, J., Hoare, D., Krause, S., Hemelrijk, C.K. & Rubenstein, D.I. (2000). Leadership in fish shoals. — Fish Fish. 1: 82-89.

Krause, J., Reeves, P. & Hoare, D. (1998). Positioning behaviour in roach shoals: the role of body length and nutritional state. — Behaviour 135: 1031-1039.

Lamprecht, J. (1992). Variable leadership in bar-headed geese (*Anser indicus*): an analysis of pair and family departures. — Behaviour 122: 105-119.

Leca, J.-B., Gunst, N., Thierry, B. & Petit, O. (2003). Distributed leadership in semifree-ranging white-faced capuchin monkeys. — Anim. Behav. 66: 1045-1052.

Levin, L.E. (1996). Passage order through different pathways in groups of schooling fish, and the diversified leadership hypothesis. — Behav. Proces. 37: 1-8.

Magnhagen, C. & Staffan, F. (2005). Is boldness affected by group composition in youg-of-the-year perch (*Perca fluviatilis*)? — Behav. Ecol. Sociobiol. 57: 295-303.

Malone, J.C., Forrester, G.E. & Steele, M.A. (1999). Effects of subcutaneous microtags on the growth, survival, and vulnerability to predation of small reef fishes. — J. Exp. Marine Biol. Ecol. 237: 243-253.

Martel, G. & Dill, L.M. (1995). Influence of movement by Coho salmon (*Oncorhynchus kisutch*) parr on their detection by common mergansers (*Mergus merganser*). — Ethology 99: 139-149.

McCartt, A.L., Lynch, W.E. Jr. & Johnson, D.L. (1997). How light, a predator, and experience influence bluegill use of shade and schooling. — Env. Biol. Fish. 49: 79-87.

Meese, G.B. & Ewbank, R. (1973). Exploratory behaviour and leadership in the domesticated pig. — Brit. Vet. J. 129: 251-259.

Partridge, B.L. (1980). The effect of school size on the structure and dynamics of minnow schools. — Anim. Behav. 28: 68-77.

Pitcher, T.J., Wyche, C.J. & Magurran, A.E. (1982). Evidence for position preferences in schooling mackerel. — Anim. Behav. 30: 932-934.

Réale, D., Gallant, B.Y., Leblanc, M. & Festa-Bianchet, M. (2000). Consistency of temperament in bighorn ewes and correlates with behaviour and life history. — Anim. Behav. 60: 589-597.

Reebs, S.G. (2000). Can a minority of informed leaders determine the foraging movements of a fish shoal? — Anim. Behav. 59: 403-409.

Reebs, S.G. (2001). Influence of body size on leadership in shoals of golden shiners, *Notemigonus crysoleucas*. — Behaviour 138: 797-809.

Reebs, S.G. & Laguë, M. (2000). Daily food-anticipatory activity in golden shiners: A test of endogenous timing mechanisms. — Physiol. Behav. 70: 35-43.

Sato, S. (1982). Leadership during actual grazing in a small herd of cattle. — Appl. Anim. Ethol. 8: 53-65.

Sih, A., Bell, A.M., Johnson, J.C. & Ziemba, R.E. (2004). Behavioral syndromes: an integrative overview. — Quart. Rev. Biol. 79: 242-277.

Sneddon, L.U. (2003). The bold and the shy : individual differences in rainbow trout. — J. Fish Biol. 62: 971-975.

Sokal, R.R. & Rohlf, F.J. (1995). Biometry, 3rd edn. — W.H. Freeman and Co., New York.

Sundström, L.F., Petersson, E., Höjesjö, J., Johnsson, J.I. & Järvi, T. (2004). Hatchery selection promotes boldness in newly hatched brown trout (*Salmo trutta*): implications for dominance. — Behav. Ecol. 15: 192-198.

Svartberg, K., Tapper, I., Temrin, H., Radesäter, T. & Thorman, S. (2005). Consistency of personality traits in dogs. — Anim. Behav. 69: 283-291.

Verbeek, M.E.M., Drent, P.J. & Wiepkema, P.R. (1994). Consistent individual differences in early exploratory behaviour of male great tits. — Anim. Behav. 48: 1113-1121.

Ward, A.J.W., Thomas, P., Hart, P.J.B. & Krause, J. (2004). Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). — Behav. Ecol. Sociobiol. 55: 561-568.

Wilson, D.S., Clark, A.B., Coleman, K. & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. — Trends Ecol. Evol. 9: 442-446.

Wilson, D.S., Coleman, K., Clark, A.B. & Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. — J. Comp. Psychol. 107: 250-260.

Wright, D., Rimmer, L.B., Pritchard, V.L., Krause, J. & Butlin, R.K. (2003). Inter and intra-population variation in shoaling and boldness in the zebrafish (*Danio rerio*). — Naturwiss. 90: 374-377.

Yamagishi, H. (1978). Behavioural studies on schooling of fishes I. Leading-following relationship of the young golden trevally, *Caranx speciosus* (Forsskål) in captivity. — Zool. Mag. 87: 12-18.