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Mechanisms underlying shoal composition in the Trinidadian guppy, *Poecilia reticulata*

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Free-ranging groups are frequently assorted by phenotypic characters. However, very little is known about the underlying processes that determine this structuring. In this study, we investigate the mechanisms underlying the phenotypic composition of shoals of guppies (*Poecilia reticulata*) in a high-predation stream in Trinidad's Northern Mountain Range. We collected 57 entire wild shoals, which were strongly assorted by body length. Shoal encounters staged within an experimental arena showed shoal fission (but not fusion) events to be an important mechanism in generating phenotypic assortment. In the wild, fission and fusion between guppy shoals occurred extremely frequently and thus are unlikely to constrain the opportunities for shoal assortment. However, fission and fusion processes occur under the restrictions imposed by the distribution of individuals within the environment. We observed size specific segregation within the habitat in three dimensions, providing a passive mechanism that contributes to the maintenance of the observed homogeneity of group composition. Furthermore sex differences were found in social behaviour. Individual male guppies switched between shoals more frequently than females and left a shoal more often than females. We argue that shoal composition is determined by habitat segregation on a medium spatial scale and by fission/fusion processes on a small spatial scale (with sex-specific shoal dynamics adding a additional layer of complexity).

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Group living is likely to be based on a continuous decision-making process, with individuals constantly evaluating the profitability of joining, leaving or staying with others, in accordance to an ever changing trade-off between predation pressures and feeding opportunities (Pitcher and Parrish, 1993). Laboratory work on group choice behaviour and theoretical models have contributed to our understanding of the mechanisms underlying the social organisation of open groups (groups where individuals are free to leave and join) (Pitcher and Parrish 1993, Pulliam and Caraco 1984). Despite the attention that group living has received in the literature, few investigations have attempted to establish the mechanisms underlying the formation and maintenance of open groups, of which most fish shoals are a good example. This is partially due to the difficulty of observing and manipulating open groups, which in some instances (e.g. pelagic fish shoals) may comprise of many thousands of individuals (Misund 1993).

Previous investigations have found the composition of free ranging fish shoals to be non random; natural

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shoals are typically size structured and numerically dominated by one species (reviewed by Krause et al. 2000a). These findings support laboratory investigations where individuals have been observed to preferentially associate with groups composed of phenotypically similar individuals (Keenleyside 1955, McCann et al. 1971, Krause and Godin 1994). Homogeneity of group composition has associated benefits. For example, individual anti-predator benefits increase as shoals become more phenotypically assorted (Theodorakis 1989). In addition, phenotypic assortment is thought to have important implications for foraging efficiency with individuals of different phenotypes (e.g. body length) differing in their competitive ability (Krause 1994, Ranta et al. 1994).

Various mechanisms have been proposed to explain phenotypic assortment; in shoaling fish, for example, there are at least three possibilities. First, phenotypic assortment of groups could arise by body length-specific habitat preferences (Bremset and Berg 1999). Second, phenotypic assortment may arise via active and/or passive mechanisms during shoal fission (shoals joining) and fusion (shoals splitting) events. During shoal fission and fusion individuals may actively choose neighbouring fish that are of a similar phenotype, thus providing an individual based mechanism for shoal assortment. Alternatively, it has been proposed that homogeneity in the size composition of groups could be created by passive exclusion of smaller individuals (Krause et al. 2000b). For example, a positive relationship between body length and speed of locomotion (Blaxter and Holliday 1969) has been proposed as a mechanism for creating assortment by size in a number of taxa (krill: Watkins 1992; African ungulates: Gueron et al. 1996). At present it is impossible to distinguish between these mechanisms as information on the outcome of intra-shoal fission and inter-shoal fusion is largely missing.

The aim of this investigation is to link the behaviour of individuals to the structure of groups and in doing so identify the mechanisms underpinning shoaling dynamics in the Trinidadian guppy. The guppy, used extensively as a model in behavioural ecology, has proved invaluable in understanding the evolution of social behaviour in the wild (Magurran et al. 1995). Initially we determine the degree of phenotypic assortment within shoals, since this characteristic of groups has been inferred to have adaptive significance (Theodorakis 1989). We predict that shoals of guppies will be assorted by phenotype (body length), in accordance with the findings of previous investigations (reviewed by Krause et al. 2000a). To test this hypothesis, we collect free-ranging guppy shoals and record the body length and sex of individuals. Second, we predict that both active and passive mechanisms will be fundamental in the generation and maintenance of assortment. Encounters between shoals provide an important opportunity for assortment, since individuals can make decisions based on the composition of available shoals. In addition, shoal fission events may result in assortment by body length through individual choice behaviour. We test this hypothesis by observing encounters between shoals within an experimental arena in the laboratory.

Rates of encounters between shoals may act as a constraint on phenotypic assortment, by restricting the opportunities for shoal switching. Accordingly, we predict that in the guppy (as in other small freshwater fish species), small inter-shoal distances will facilitate frequent shoal encounters. To determine the rates of shoal encounters in the guppy population and to provide information on the dynamics of inter-group fusion and intra-group fission, individual fish are tracked in their natural environment. This procedure also provides information on sex differences in social behaviour. Males are predicted to trade off the benefits of shoaling behaviour against searching for mating opportunities, and thus may be expected to move between shoals more frequently and spending less time shoaling than do females (Hughes et al. 1999, Kelly et al. 1999).

Finally, encounters between shoals (creating the opportunity for phenotypic assortment) occur within the constraints imposed by the distribution of individuals within the habitat. Size-specific habitat use may result in the passive assortment of individuals within shoals. To determine whether habitat use is size-specific in the guppy, we conduct visual count transects at different times of the day.

Methods

The study site

A guppy population in the Arima River in the Northern Mountain Range of Trinidad was selected for the investigation. The Arima River is categorised as a high predation site due to the presence of *Crenicichla alta*, one of the major predators of the guppy (Endler 1986). All observations and experiments were conducted between the 1st of April and the 30th of June 2001 during the dry season when the low water level and high water clarity facilitated field observations.

Shoal characteristics

To test our prediction that shoals of guppies will be assorted by phenotype (body length), guppy shoals were captured from the Arima River, using a 2m beach seine. Entire shoals were captured by laying the seine net on the river bottom. When a shoal moved over it the net was raised by two observers enclosing the fish within the seine. Shoals were only selected for analysis when both observers were satisfied that the entire shoal had been captured. The body length (total length) and the sex of individuals within each of the shoals were recorded. To prevent multiple captures of the same individual, sampled shoals were not released into the river until all shoals had been captured.

Data analysis

A randomisation test was used to determine if shoals were significantly more assorted by body length than would be expected by random association. This was achieved by comparing the observed shoal variance in body length to that obtained from simulated data sets. To generate these data sets, individuals from all captured shoals were pooled. Shoals (consisting of the number of individuals in a natural shoal) were then selected at random. One thousand random shoals were generated for each shoal captured. From these we calculated the fraction of generated groups that produced a lower variation in body length than observed. This fraction is then taken to be the probability that we can reject the null hypothesis that assortment by body length is absent in the observed shoals.

Habitat use

Size-specific habitat use may result in non-random encounters between individuals, constraining the opportunities for shoal. Here we test whether small and large fish were found at different positions in the water column, and at different distances from the riverbank as a function of time of day. To determine whether habitat use is size-specific in the guppy visual count transects were carried out by one observer on a section within the Arima River (transect dimensions, length: = 18 m; width: max = 6 m; depth: max = 89 cm). This section was subdivided into 3 sections (each 6m long). The transect consisted of a pool with shallow riffles at either end (connecting it to other pools both up and down stream) and represented a typical habitat within the Arima River. The pool varied in depth and, the bottom substrate was diverse, ranging from vegetation, to sand, to larger rocks. There was partial canopy cover, providing both shaded areas and areas with direct sun light. Transects of this area were repeated 5 times a day at 4 hourly intervals (08:00, 12:00, 16:00, 20:00 and 24:00 hours), over a 5 day period. The observer recorded the number of shoals and individuals and estimated the shoal size and mean body length of shoals. At night observations were made by torch light. Pilot trials indicated that such light had little effect on the behaviour of the fish. Controls showed that the difference between the visual estimates and the real shoal size (determined by subsequent capture of the shoal) was on average $\pm 7.2\%$ for a range of shoal sizes from 1–52 ($n = 20$). Mean shoal body lengths were classified into the three following body length categories: < 15 mm, 16–25 mm and > 25 mm. The difference between the estimated and shoal mean body length was on average ± 1 mm for a range of body sizes 7–36 mm ($n = 50$).

The observer recorded the position of each shoal, or of individual fish within the transect by recording both the x and y co-ordinates (distance from the bank and distance along the transect). The location, species and body size of all predators observed were also noted. The vertical position of fish of different body lengths within the water column was quantified by selecting fish or shoals at random and placing a meter rule vertically in the water. The total depth of the water and the distance that the individual/shoal was from the surface was recorded. Guppy body length was also estimated (as above). Pilot trials showed this procedure to have little effect on behaviour, with individuals not altering their depths in the presence of the ruler.

Individual behavioural observations

Individual rates of shoal exchange

To asses the potential for individuals to exchange between shoals, individual guppies were selected without regard to sex from within a 6m long stretch of the Arima River. Although our sample was not truly random, we endeavoured to select individuals without prejudice. The observer selected a new individual for each successive observation (a method used previously by Magurran and Seghers (1994) to recorded behavioural characteristics in guppy populations). Fish were in such high density that it was highly unlikely that the same individual was selected twice. The fish were then visually followed for periods of up to 10 min, by an observer standing motionless in the water. During that time all social interactions involving the focal individual were recorded, including the number of encounters with conspecifics and the occurrence of join, stay and leave decisions. An encounter was defined as occurring when the focal fish came within four body lengths of a shoal or another individual, a criterion that has been used successfully in previous investigations (Krause et al. 2000b). In addition, the time at which these events occurred was recorded. A total of 24 fish were observed. A visual count transect (see section (d) on habitat use) was conducted during the observations within the study area to determine the density of groups/individuals in the area.

Sex differences in shoal exchange

We predict that the rates of shoal exchange will differ between the sexes. Males are predicted to trade off the benefits of shoaling behaviour against searching for mating opportunities, and thus may be expected to move between shoals more frequently and spend less time shoaling than do females (Hughes et al. 1999, Kelly et al. 1999). To test this prediction guppies were captured from a pool in the Arima River using a 2m beach seine and transferred to the laboratory. The fish were given an identification mark on the dorsal surface by injecting a small amount of Alcian blue, using the method described by Hoare et al. (2000). All guppies were anaesthetised with tricaine methanesulfonate (MS-222 Sigma Chemical, St Louis) prior to marking. This procedure allowed the test fish to be clearly identified upon release. After marking, the fish were kept under laboratory conditions for a minimum of 1 day and a maximum of 4 days, fed ad-libitum on tropical aquarium fish flakes and kept at a constant water temperature of 27°C. Individual marked fish (15 male and 15 females) were released singly into the pool from which they had been collected. The sex and the body length of fish were recorded prior to release. The release of test fish into the pool was standardised by placing the focal fish into a release cylinder located within the pool. The focal fish remained in the cylinder for 10 minutes prior to release. For each trial the cylinder was placed in the same location. The test fish were then released into the pool by raising the cylinder using a remote pulley mechanism.

After release, the observer was able to visually track the marked fish for periods of up to 10 min and for a minimum time of 2 min. The number of shoal and individual encounters (as defined above) made by the marked fish (or by the shoal within which the marked fish was present) and the frequency of fission and fusion events involving the marked fish were recorded. In addition, the times at which these events occurred were also recorded. A control experiment was conducted to examine the effect of marking on shoal choice behaviour. Following the method of Krause and Godin (1994), test fish were given a two-way choice between stimulus shoals (one marked with the above method and one sham injected) within a experimental aquarium (tank dimensions: 60 × 30 cm, water depth: 10 cm). All fish were size matched (± 1.5 mm). The time that the test fish spent within the response zone (within four body lengths) of each shoal was recorded. The proportion of time a test fish spends in one zone partially determines the time spent in the other response zone, thus paired t-tests cannot be used as the data are not independent (Svensson et al. 2000). Instead, one-sample t-tests were used, comparing the percentage (of the total time spent shoaling) with the sham injected shoal, with the null hypothesis of no preference (i.e. 50% of the total shoaling time will be spent in either response zone). All percentages were arcsine transformed prior to statistical analysis.

Shoal fission and fusion as a mechanism for shoal assortment

We predict that both active and passive and mechanisms during shoal fission and fusion will be fundamental in the generation and maintenance of assortment. To test this prediction we used a 2 m beach seine to collect a total of 500 guppies (approximately 250 males and 250 females) from the Arima River. The fish were kept under laboratory conditions prior to the experiment, fed ad-libitum on tropical aquarium fish flakes and kept at a constant water temperature of 27°C. After 7 days a total of 40 shoals were created, each containing 5 males and 5 females (for fish over 15 mm) and 10 randomly selected individuals for fish under 15 mm (where sex was visually difficult to determine). Small (un-sexed) fish were used to ensure encounters could be staged between shoals that differed substantially in body length. Fish were assigned to shoals so that they were assorted by body length within but not between shoals (for fish less than 20 mm ± 2.2 mm; greater than 20 mm ± 6.2 mm, because of sexual dimorphism).

Encounters between shoals were staged by simultaneously releasing two shoals into an experimental arena (outdoor concrete pool: 196 × 265 cm at a water depth of 8 cm and temperature of 27°C). The shoals were placed within release cylinders (one at either end of the arena), for a ten minute acclimation period prior to release. Subsequently the two cylinders were raised simultaneously (using a remote pulley mechanism), allowing the two shoals to move freely within the experimental arena. The outcome of the encounter between the two shoals was recorded (e.g. fusion, no fusion or partial fusion). If the encountering shoals did not merge during the first encounter, the two shoals were removed from the experimental arena and the body lengths of individuals within the shoals recorded. If on encounter the shoals merged, the resulting shoal was followed until a fission event occurred.

Shoal fission events were divided into two categories (Fig. 1). Rear fission events, were defined as when the

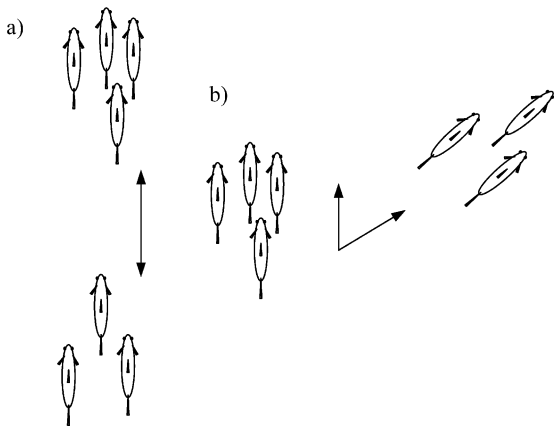

Fig. 1. Diagram showing the two forms of fission events that were recorded a) a rear fission event, b) a lateral fission event.

two resulting shoals maintained the same direction of travel and fission occurred due to differential swimming speeds. We defined lateral fission events as those in which the two resulting shoals were separated due to different directions of travel. Shoal fission was defined as the point at which two shoals were separated by four body lengths or more. After a fission event occurred, the two shoals were removed from the arena and all individuals within a shoal were measured and sexed. If shoal capture was not successful (i.e. individuals evaded the net with the possibility of exchanging individuals), the trial was abandoned. Each shoal was tested a maximum of 3 times under different encounter combinations (any given shoal combination/pair was tested only once) over a 3 day period.

Data analysis

As in the analysis of wild shoals (see Shoal characteristics in the Methods section) a randomisation test was used to determine if the shoals were more assorted by body length after a fission event than would be expected by chance. One of the two shoals resulting from the first fission event was selected at random. The within-shoal variance in body length in the selected shoal was compared to that of a generated data set. The simulated data set was made by entering the body lengths of the pre-fission shoal into the model and then generating a single shoal at random, its size being determined as that of one of the observed post fission groups. This process was repeated 1000 times for each randomly selected shoal from a given fission event. We calculated the fraction of the data set that produced a lower variation in body length than observed. This fraction is then taken to be the probability that we can reject the null hypothesis that no assortment by body length had generated the observed shoals.

Results

Shoal and population characteristics

A total of 57 shoals were captured ranging in size from 2 to 47 (median = 5). In 56 cases the shoals consisted entirely of guppies with the exception of one group where a juvenile Aequidens pulcher was found within the shoal. The shoal size distribution of the observed shoals followed a power law distribution, with shoals of a smaller size being more frequent the population ($n = 57$, $r^2 = 0.54$, $p < 0.001$, Fig. 2). The variance of body length within shoals ($n = 57$) was significantly less than that expected by random assortment (randomisation test: 1000 simulations, Fisher's omnibus test $f_{57} = 427.46$, $p < 0.001$). Furthermore, shoals were significantly female biased (i.e. greater than 50% females, Chi^2 test, $n = 54$, $\chi^2 = 50.1$, $p < 0.01$, percentage of females per shoal: mean ± SD = 76 ± 12.6%).

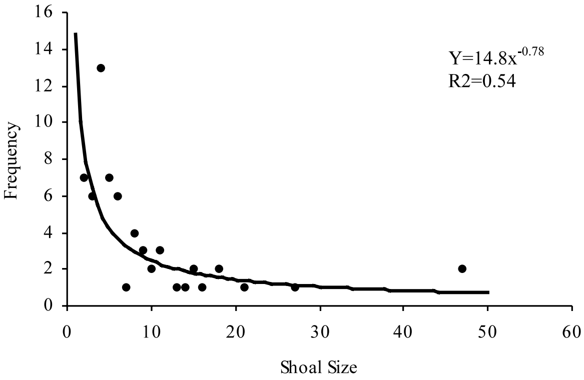

Fig. 2. Shoal-size distribution for wild guppy shoals from the Arima river $n = 55$ with a power trend line fitted ($p < 0.001$).

Habitat use

A significant relationship was found between the fish body length and depth below the surface at 12:00 h. Larger fish were closer to the bottom and smaller fish closer to the surface of the river (linear regression on log-transform data, $n = 48$, $r^2 = 0.59$, $F = 69.2$, $p < 0.001$, Fig. 3a). However, no trend was found between body length and the distance from surface at 24:00 hours (Fig. 3b) with the majority of fish of all sizes distributed either on the substrate or at the water surface (linear regression on log-transform data, $n = 60$, $r^2 = 0.02$, $F = 0.137$, $p > 0.05$).

There was also a significant relationship between the time of day and the distance from the bank for small (< 15 mm) medium (16 to 25 mm) and large (> 26 mm) fish. Fish of all size classes moved closer to the bank at midnight (Friedman test: chi^2 values, small = 10.2, medium = 10.64, large = 11.72, $p < 0.05$, in all three cases, Fig. 4a). At midday a strong trend was observed between the distance from the bank and body length, with larger individuals being observed to be further from the bank than smaller individuals (Fig. 4a).

The shoal size distribution changed on a diurnal cycle, with the proportion of single individuals increasing towards the evening and being at their maximum at 24:00 hours (Friedman test: chi^2 value = 10.4, $p < 0.05$ Fig. 4b).

Individual behavioural observations

Randomly selected individuals

A mean density of 12 fish per m^2 (SD = 7.7) and a mean density of 3 groups per m^2 (SD = 0.6) were

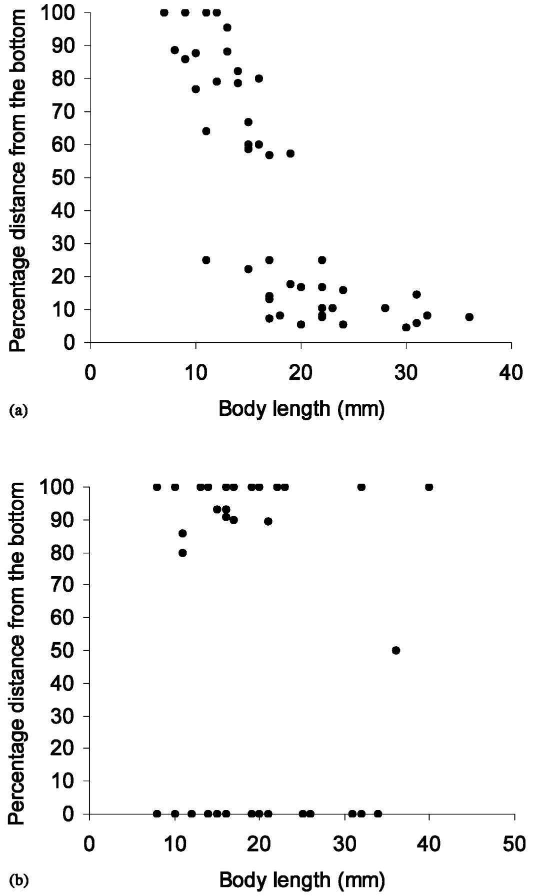

Fig. 3. Relationship between body length and position of fish in the water column (percentage distance from the bottom (100% = fish at river surface)) at 12:00 hrs (linear regression on log-transform data, n = 48, $r^2 = 0.59$, F = 69.2, $p < 0.001$, Fig. 3a), and b) 24 hrs (linear regression on log-transform data, n = 60, $r^2 = 0.02$, F = 0.137, $p > 0.05$).

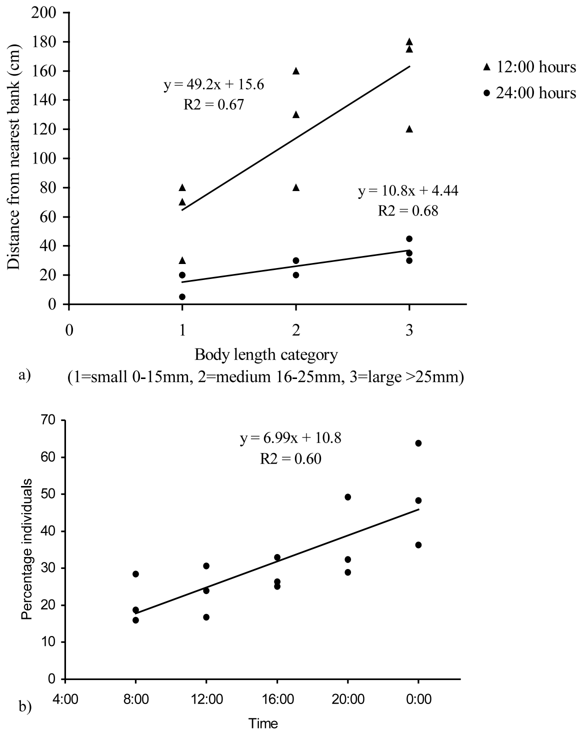

Fig. 4. a) The relationship between body length and distance from the nearest bank at two time intervals (midnight and midday), and b) the relationship between time of the day and the percentage of single fish.

found. Twenty-nine individual fish were followed for an average time of 65s (SD = 107, max = 559 s, min = 10 s) through a total of 116 shoal encounters. Individuals spent a mean of 66.5% (SD = 29) of their time alone. Encounters between tracked individuals and shoals or other individuals occurred on average every 14 s (SD = 11). On average 62% (SD = 38) of encounters by the focal individuals (n = 24) resulted in fusion of the shoals involved. Association between the focal fish and its new shoal lasted on average only 10 s (SD = 9.6) before the focal individual left the shoal or the shoal dispersed.

Comparison of males and females

Control experiments showed that the presence of an identification mark did not alter the shoal choice behaviour of individuals, with no difference between the time that the test fish spent with the marked shoal or the sham injected shoal, for both males (one-sample t-test $t_{15} = -1.29$, $p > 0.05$) and females (one-sample t-test, $t_{15} = -0.63$, $p > 0.05$).

Male fish were involved in shoal encounters significantly more frequently than females (t-test, $t = -3.81$ n = 15, $p < 0.01$, males: mean ± SD = 16 ± 5 s; females mean ± SD = 31 ± 16 s). During fission events male fish were significantly more likely to leave a shoal as an individual than female fish (t-test, t = 3.98 n = 15, $p < 0.001$, males: mean ± SD = 86.7 ± 16.9%; females: mean ± SD = 50.8 ± 30.3%). No significant difference was found between males and females in the percentage of encounters resulting in fusion (t-test, t = 1.5, n = 15, $p > 0.05$, males: mean ± SD = 47 ± 16.9%; females: mean ± SD = 56 ± 22%). There was also no significant difference in the percentage of time that males and females spent as individuals (t-test, $t = -0.15$, n = 15, $p > 0.05$, males: mean ± SD = 66.5 ± 14%; females: mean ± SD = 56.5 ± 23.5%).

Fission and fusion

A total of 33 encounters were observed between shoals that differed in mean body length by more than 5 mm. Of the 33 encounters, 29 resulted in fusion. The mean difference in body length between the fusing shoals was 10 mm (SD = 3.9), while for the encounters not resulting in fusion it was 12 mm (SD = 4.2). The small sample size for encounters not resulting in fusion (4) prevents statistical comparisons being made between these values.

Of the 29 shoal encounters that resulted in fusion, the first fission event was observed and the resulting shoals successfully captured in 28 instances. Lateral fission events occurred significantly more frequently than rear fission events (chi^2 test, $n = 28$, $\chi^2 = 11.6$, $p = 0.001$, lateral $n = 23$, rear $n = 5$). In three instances, the first fission event resulted in one fish leaving the main group. A minimum of two fish per shoal was required to investigate whether assortment by body length after a fission event differed significantly from that expected by random associations. Therefore the three fission events consisting of one fish were eliminated from the subsequent analysis. Following the first fission event, the within-shoal variation (for one of the two resulting shoals selected at random, $n = 25$) was overall significantly lower than that of the simulated shoals assuming random assortment (randomisation test: 1000 simulations, Fisher's omnibus test $f_{25} = 97.4$ $p = 0.01$).

Discussion

This is the first study to demonstrate the importance of both passive (e.g. size specific habitat use) and active (active decisions made during shoal encounters) mechanisms leading to phenotypic assortment of groups. As expected, shoals of Trinidadian guppies were phenotypically assorted by body length. The results of fission and fusion experiments and observations on the natural distribution of individuals and shoals in the field suggest that both active and passive mechanisms are important in creating the observed homogeneity of body length within groups.

Composition of free-ranging shoals

In accordance with previous investigations (reviewed by Krause et al. 2000a) the composition of free ranging guppy shoals were found to be non-random, with shoals being clearly assorted by body length. The observed homogeneity of group composition is likely to have adaptive significance for individuals, for example by reducing predation risk (Theodorakis 1989).

Shoals of guppies were strongly female biased, but further work is necessary to establish whether this simply reflects a female biased sex ratio in the Arima river. Alternatively, differences in male and female social behaviour could generate the biased shoal sex ratio. For example, it has been reported that female guppies invest greater effort in anti-predator behaviour than males (Magurran and Seghers 1994) and spend more time shoaling (Magurran et al. 1992). However, our behavioural observations of individuals of a known sex found no significant difference between the time that males and females spent in social groups.

Potential mechanisms for the observed homogeneity of group size composition fall into two categories: shoal mate choices during shoal fission and fusion events and habitat choices based on body length.

Shoal fission and fusion as a mechanism for body length assortment

Shoal fission and fusion provides individuals with opportunities to exchange (or leave) shoals with others of a similar phenotype, thus shoal fission and fusion events may be an important mechanism in maintaining phenotypic assortment. Our investigation suggests that intra-shoal fission and not fusion is important in generating body length assortment within groups.

Shoal fission events were subdivided into two categories, lateral and rear. We define lateral events as active, since individuals make an active decision to alter their swimming direction in relation to the main shoal. However, rear fission events may represent a combination of both active (individuals actively choosing to alter their swimming speeds) and passive (physiological constraints on swimming speeds) mechanisms. Although both active and passive mechanisms may be involved in fission events active (lateral) events occur with greater frequency. The findings of the current investigation provide strong support for active mechanisms being important in maintaining the homogeneity of group size composition during shoal fission events. Further evidence that group fission is an important mechanism in generating phenotypic assortment comes from studies on the red deer (*Cervus elaphus*). In this species activity synchronisation (e.g. the time at which individuals forage) is important in determining the outcome of fission and fusion events leading to social segregation (Conradt and Roper 2000). Support for the importance of shoal fusion as a mechanism leading to the homogeneity of group size composition has been previously demonstrated in the banded killifish, *Fundulus diaphanus* (Krause et al. 2000b). In this species the outcome of shoal encounters (join or no join) was dependent on the body length differences between the shoals, with shoals of equal body lengths more likely to join.

Rates of shoal encounters in the field

Encounters between shoals give individuals the opportunity to switch shoals, making decisions based on their own phenotype and the phenotypic composition of the available groups. The rate of shoal encounters is dependent (in part) on the shoal size distribution. Within this guppy population randomly selected individuals spend 66.5% of time away from social groups. This is reflected in the frequency of single individuals and small groups relative to the number of large shoals. The rates of shoal encounters, which occurred on average every 14 s, were the highest recorded for any species to date. In contrast shoal encounters in the banded killifish and golden shiners, *Notemigonus crysoleucas*, occur every 1.1 min (Krause et al. 2000b), while in the marine environment herring (*Clupea harenus*) shoals in coastal Norwegian waters meet on average every 13.7 min (Pitcher et al. 1996). The rapid rates of shoal encounters observed in the current investigation are unlikely to constrain the opportunities for phenotypic assortment within the species.

During a shoal encounter the benefits of inter-shoal exchange are expected to depend on the sex of an individual. Male guppies benefit by encountering novel females (Hughes et al. 1999), but may have to trade off the antipredator benefits of shoaling for increased mating opportunities. Females, in contrast, prefer to associate with familiar individuals and are therefore proposed to form the core of a shoal (Griffiths and Magurran 1998). Our behavioural observations showed that male guppies were involved in shoal encounters twice as frequently as females, and also moved between shoals more rapidly than females. However, no significant difference was found between the time that males and females spent away from social groups, with both sexes spending over 50% of their time alone.

Size specific habitat use

If individuals are distributed within the habitat in a non-random manner (e.g. size specific habitat use), it will limit the opportunities for interactions to occur, and may lead to the passive phenotypic assortment of groups. In this study we document body length segregation within the habitat on three dimensions. At mid-day individuals of smaller body lengths were found nearer to the riverbank and closer to the top of the water column. This provides a potential passive mechanism that is likely to contribute to the observed homogeneity of individual body lengths within groups.

Habitat use results from a trade off between foraging gains and predation risk (Gilliam and Fraser 1987), and size-specific habitat use has been reported previously in other fish species (Greenberg et al. 1996, Lightfoot and Jones 1996, Bremset and Berg 1999, Heggenes et al. 1999). Size-specific habitat segregation may be explained by body length differences in competitive ability (Bremset and Berg 1999), and predation risk (Post and Evans 1989, Fuiman and Magurran 1994), restricting the distribution of small individuals within the habitat (Werner and Hall 1988). Size-specific habitat use showed a clear diurnal pattern, with the body length differences between habitats being dramatically reduced during the night when all fish moved closer to the river bank and segregation by positioning within the water column reduced. These observations support previous anecdotal observations by Seghers (1973), who reported that guppies use shallow refuges at night remaining close to the river banks in high predation rivers.

Previous experiments have shown fish to respond to a change in predation risk by moving to protected habitats (Cerri and Fraser 1983, Werner et al. 1983). When dark, predation risk to the guppies potentially changes as a result of two factors. Firstly the occurrence of a nocturnal predator Hoplias (*Hoplias malabaricus*). Secondly, there may be a reduction in the efficiency of shoaling behaviour as an anti-predator response at lower light intensities, due to the importance of vision in co-ordinating anti-predator behaviour (Pavlov and Kasumyan 2000). Our findings illustrate how both passive and active mechanisms are important in creating the observed homogeneity of body length within groups. On a coarse scale the size-specific distribution of individuals within the habitat will result in the passive assortment of shoals based on body length. On a finer scale, shoal fission (largely through active mechanisms) is important in maintaining the homogeneity of group size composition.

Ecological implications

An understanding of the mechanisms underlying the social organisation of the guppy helps to elucidate the ecological implications of group living. For example, co-operative behaviour has previously been proposed to occur within group living fish species (e.g. tit-for-tat predator inspection, Milinski 1987). The rate at which social groups break apart and form, and individual exchange during shoal encounters may act as a constraint on the evolution of co-operative behaviour (Michod and Sanderson 1985, Toro and Silio 1986, Mesterton-Gibbons 1992). Group stability has been previously proposed to favour the evolution of reciprocal altruism allowing partnerships to develop between individuals. Stable associations between familiar individuals, may also confer other benefits; for example individuals might gain information on their companions previous behaviour during competitive interactions, and familiarity may reduce the risk of predation (Chivers et al. 1995) and facilitate feeding benefits (Metcalfe and Thomson 1995).

In the current investigation the behavioural observations of individuals illustrate that shoal “decay rate” is rapid within the guppy. Shoals of guppies represent temporary associations between individuals, with individuals spending a mean time of only 10 seconds as a member of any one shoal, and over 50% of their time as individuals. Both males and females remain within a shoal for less than 20 seconds on average before leaving as an individual. Consequently most associations between individuals within shoals will persist on a time scale of seconds. This is far short of the time required for familiarity to develop within the guppy (approximately 12 d, Griffiths and Magurran 1997). Thus the findings of the current investigation suggest that if familiar recognition occurs in the guppy it is unlikely to be a the result of shoal fidelity, as individuals exchange shoals rapidly, and spend a significant proportion of time on their own. Similarly, previous investigations studying shoal structure have largely failed to find fidelity by individuals to a particular group (Helfman 1984, Hoare et al. 2000, see Barber and Ruxton 2000 for an exception).

Knowledge of group dynamics, for example rates of inter-group exchange and phenotype distributions within the population and habitat, is essential for predicting the rates at which pathogens (Loehle 1995, Mollison and Levin 1995) and information will spread through a population. The social transmission of information has been demonstrated in shoaling fish in the form of predator recognition (Magurran and Higham 1988) and in the guppy as the learning of foraging routes (Laland and Williams 1997). In the current investigation, individual guppies were found to encounter a limited subset of the population due to size-specific habitat use and active shoal mate choice. Population sub-structuring of this kind will result in information spreading through the population in a non-random manner, a finding that may have important implications for models predicting information transfer in animal populations.

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