

Nonadditive effects of group membership can lead to additive group phenotypes for anti-predator behaviour of guppies, *Poecilia reticulata*

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G × E;
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Abstract

Nonadditive effects of group membership are generated when individuals respond differently to the same social environment and may alter predictions about how behavioural evolution will occur. Despite this importance, the relationship between an individual's behaviour in two different social contexts and how reciprocal interactions among individuals within groups influence group behaviour are poorly understood. Guppy anti-predator behaviour can be used to explore how individuals behaviourally respond to changes in social context. Individuals from two strains were tested for response to a model predator alone and in groups to evaluate how individuals alter their behaviour in response to social context and how group phenotype relates to individual behaviour. Nonadditive effects of group membership were detected for a number of behaviours, revealing that the effect of being in a group differed among individuals. These nonadditive effects, however, yielded an additive group phenotype. That is, the average behaviour of the group was equal to the average of its parts, for all behaviours in both strains. Such an additive group phenotype may have resulted because all individuals within a group respond to the specific social environment provided by the other members of their group.

Introduction

Many animals spend all or significant portions of their lives interacting in groups, with aggregations forming for a variety of reasons including mating, hibernation, sleeping and foraging (reviewed in Allee, 1927) and individuals often alter their expression of traits in response to the specific social context provided by their group (e.g. Moore *et al.*, 1997; Randler, 2005; Ebensperger *et al.*, 2006; Eshel *et al.*, 2006). Studies of schooling in fishes in particular provide a wealth of information on the effect of group size and composition on the average behaviour of individuals within the group. For example,

vigilance behaviour exhibited by individuals in a group increases, often linearly, with group size, reflecting shifts in the balance between selection on predator avoidance and intraspecific competition (e.g. Johnsson, 2003; Kent *et al.*, 2006). The size of the shoal impacts foraging behaviour and efficiency, altering how often on average individuals must approach prey to successfully catch enough food (Foster *et al.*, 2001). Studies of fish schooling behaviour have also explored the impact individuals have on the average behaviour of the group. Decision-making theory explores how interactions among individuals adhering to simple rules generate complex emergent group phenotypes, such as school size, cohesion or shape (reviewed in Sumpter, 2006). Individual preferences for social partners have also been thoroughly explored, with individuals choosing where and with which group to school based on a number of factors including food availability and predation risk (e.g. Hoare *et al.*, 2004), sex ratio (Ruhl & McRobert, 2005),

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phenotypic matching (Hemelrijk & Kunz, 2005), familiarity (Croft *et al.*, 2006), kinship (e.g. Frommen & Bakker, 2004) and previous social learning (Kendal *et al.*, 2004).

The relationship between individual behaviour and group behaviour in such studies has been explored primarily from a group perspective to address how groups behave, how changes in group membership impact the behaviour of the group and how individuals act on average within groups (reviewed in Krause & Ruxton, 2002). Many such studies describe emergent group phenotypes, which are typically behaviours individuals cannot perform alone, such as schooling, and therefore do not provide information about individual behaviour performed in differing social contexts. Additionally, emergent group phenotypes may themselves vary with differences in group size or composition. For example, shoal shape and size may be described by manipulating the members comprising a group and observing how group behaviour changes (reviewed in Sumpter, 2006). Relatively few studies reveal how particular individuals respond to sometimes subtle differences in social context created by different group sizes or composition or whether individuals respond to changes in social context in similar ways (but see Grand & Dill, 1999; Day *et al.*, 2001). Studies that do examine the influence of group size typically explore the relative impacts of risk reduction and intraspecific competition in generating shoal size, individual decisions about with whom to shoal, or the impact of groups on social learning (Magurran & Pitcher, 1987; Grand & Dill, 1999; Day *et al.*, 2001). These approaches are central to understanding the benefits or costs of group living and the evolution of cooperation by providing information about the average behaviour of individuals in groups and the associated fitness consequences.

In contrast, little attention has been given to understanding how the behaviour of individual members of a group differs across two social contexts or how individuals respond to the specific members of their group. At alternate ends of a spectrum, individuals might all respond similarly to a given group size and composition (additive effects of group membership) or they might respond in quantitatively different ways (nonadditive effects of group membership). These differences in response can impact both group traits and individual traits. When nonadditive effects on individual behaviour occur, the average phenotype of the members of the group does not necessarily represent the phenotype expressed by the group (Agrawal *et al.*, 2001). Exploring the relative influences of additive and nonadditive effects of being in a group on individual phenotype provides information about how individuals, the unit upon which selection acts, respond to changes in social context. Individual level selection might act on individuals in either (or both) individual or group social contexts (Wilson & Dugatkin, 1997) and in either similar or opposing directions (Agrawal *et al.*, 2001). The magni-

tude and direction of evolution of individual phenotypes depends on the relationship among traits expressed in different social contexts (Moore *et al.*, 1997).

The specific social context an individual experiences may vary at both small and large temporal and/or geographical scales (e.g. Kowalczyk *et al.*, 2003; Daura-Lorge *et al.*, 2005; Bhagabati & Horvath, 2006). If all individuals respond to being in a particular social context in similar ways, individual phenotype will reflect additive effects of being in a group, whereas individuals responding differently to the same social context display nonadditive effects of being in a group (Meffert *et al.*, 2002). All individuals decreasing the amount of time spent in vigilance behaviour and increasing time spent foraging in the presence of conspecifics (e.g. Ebensperger *et al.*, 2006) reflects additive effects of being in a group. Nonadditive effects of social context can be conceptualized as a $G \times E$ interaction, where the environment of interest is the social environment (Moore *et al.*, 1997; Wolf *et al.*, 1999). $G \times E$ interactions are known to impact behaviour (reviewed in Meffert *et al.*, 2002). For example, preferences of female house flies constitute the social environment that interacts with male genotype, generating nonadditive effects on male mating behaviour (Meffert *et al.*, 2002; Meffert & Hagenbuch, 2005). However, few other examples of nonadditive effects resulting from interactions between an individual's genotype and its social environment exist. Understanding how being in a group impacts individual behaviour is critical for understanding how behaviour evolves because the existence of nonadditive group effects significantly alters the level of selection that is most important (group vs. individual) in driving phenotypic evolution, even when selection at multiple levels act in similar directions (Agrawal *et al.*, 2001).

The group perspective can provide insight into social effects on individual behaviour. If individuals do not alter their behaviour in response to being in a group, relative to being alone, then the phenotype of the group is additive and described simply by the average (or sum) of all the behaviours of individuals that comprise it – i.e. the group is equal to the sum of its parts (e.g. Parrish & Edelman-Keshet, 1999). When group phenotype is additive, there is a predictable and linear translation between the fitness consequences of an individual's actions in a group and individual fitness. Alternatively, if the effects of group membership on individuals are nonadditive and group phenotype is therefore also nonadditive (the behaviour of a group is not the same as the sum of its parts because individuals respond to being in the group in different ways) then selection acting on individuals in a group context might not have similar results to the same selective pressure acting on the behaviour of individuals alone (*sensu* Brodie, 2000). Put another way, we would predict selection favouring increased levels of a behaviour by individuals behaving in a group context to result in the evolution (assuming

appropriate additive genetic variance) of high levels of the behaviour performed by individuals alone if group effects are additive. If group effects on individuals are nonadditive, we could not predict the evolution of individual behaviours based on selection acting on individuals behaving in a group context.

Guppies, *Poecilia reticulata*, perform inspections and a suite of other behaviours reflecting boldness in response to predator stimuli, both in the wild (Dugatkin & Godin, 1992) and in inbred ornamental strains (Bleakley *et al.*, 2006). Although inspection behaviour has an underlying genetic basis, and thus evolves in response to predation pressure (Magurran *et al.*, 1992), inspection behaviour is typically modelled using tit-for-tat rules (e.g. Dugatkin & Alfieri, 1991), demonstrating that individuals respond to the behaviour of social partners by altering their own behaviour. Some social partners are more influential than others (Croft *et al.*, 2004), suggesting that nonadditive effects may be important in generating observed behaviour when multiple individuals are present. The social context a guppy experiences is likely to vary widely as well. Guppies prefer to school with varying numbers of conspecifics based on the predation regime they experience (Magurran & Seghers, 1991) and may choose with whom to school based on size (Croft *et al.*, 2003) and familiarity (Croft *et al.*, 2006); however, the degree to which they exhibit these preferences varies within and among populations (Godin *et al.*, 2003). Additionally, although fish are less commonly found alone, populations frequently become highly dispersed following heavy rainfall and when small pools are cut off from main water supplies during dry periods, isolating individuals or extremely small groups (B.H. Bleakley, personal observation).

Guppy anti-predator behaviour and the varied social contexts they may experience thus provide an ideal system to explore both how group phenotype relates to individual behaviour and how individuals respond to being in groups. Inbred strains of guppies have been previously demonstrated to respond appropriately to predatory stimuli (Bleakley *et al.*, 2006) and inbred lines are often an important tool for understanding behavioural evolution (Boake *et al.*, 2002; Higgins *et al.*, 2005; Robison & Rowland, 2005). Use of inbred strains minimizes interactions at the genotypic level, as all individuals within a strain are expected to be highly genetically similar, whereas fish from wildtype (WT) strains are outcrossed and therefore expected to experience both genotypic and phenotypic interactions with conspecifics. The possibility of both genotypic and phenotypic interactions in WT fish is predicted to generate more instances of nonadditive group phenotype and nonadditive effects on individuals of group membership, thereby providing information about the sources of phenotypic variation in social and anti-predator behaviours in guppies (e.g. Moore *et al.*, 1997; Meffert *et al.*, 2002). Combining data from the inbred

and outcrossed strains provides additional information about how conserved these interactions are, even in the absence of selection. This study therefore seeks to determine empirically whether individual behaviour reflects additive and/or nonadditive effects of being in a group and if group phenotype of a guppy shoal is additive, i.e. the sum of its parts.

Materials and methods

Behavioural testing

Two laboratory strains of guppies were utilized: a WT strain originating from a high predation population on the Quare River, Trinidad (e.g. Reznick *et al.*, 2001) and an inbred 1/2Green strain (Bleakley *et al.*, 2006), both maintained in the laboratory for a minimum of five generations. Although the 1/2Green strain has not recently experienced predation, it responds appropriately to visual predatory stimuli (Bleakley *et al.*, 2006). The guppies were kept in two to three strain/population-specific, community tanks comprised entirely of individuals naïve to behavioural experiments. The animals were regularly kept at a constant water temperature of 25 ± 1 °C on a 14 h : 10 h light : dark cycle. All animals were fed Hikari Fancy Guppy Food™ twice daily, 6 days a week, except test animals on test days, which were fed a single time after testing.

Forty individuals from each strain were randomly selected from two or three strain-specific tanks and assigned to groups such that no more than two individuals in any group had any previous social experience with each other. Groups comprised four individuals entirely from one strain or the other, creating 10 WT and 10 inbred groups. Every individual was then tested once alone and once as part of a group, in random order, with 24–48 h between the two trials. Tests were limited to a single trial in each condition as guppies are known to learn quickly (reviewed in Brown & Laland, 2003) and habituate to trial conditions. Trials were completed in a 5-gal tank with an artificial plant for cover on one side, a model of a generalized cichlid predator on the other side, and a 1-inch grid across the back of the tank. The water was changed and the tank thoroughly rinsed before every trial. Individuals or groups were acclimated alone or together, respectively, for 5 min and then introduced into the test tank near the cover plant. Individuals and group trials were recorded for 9 min using a Sony DVD403 digital video recorder (Sony Electronics, Inc., San Diego, CA, USA) and later scored using an event recorder (Ha, 1990) for the behaviour of every individual. Relevant behaviours are described in Bleakley *et al.* (2006). Briefly, all individuals (alone or in groups) were scored for time spent oriented toward the model – a measure of attentiveness; time spent in close proximity to the model and the number of inspections – both measures of boldness; time spent in agitated swimming

and frozen – both responses to perceived threat; and time spent foraging – indicative of a lack of perceived threat.

Statistical analyses: effects of group membership on individual behaviour

Statistical analysis was performed in JMP (SAS, 1989–2002). Data were normalized using log or square root transformations, such that pairs were always similarly transformed (i.e. values for numbers of inspections while alone were transformed in the same manner as numbers of inspections while in groups). Correlations between the behaviour of an individual alone and behaviour in group were then calculated for both strains to assess how behaviour in the group is related to individual behaviour. Correlations between the behaviour of an individual alone and in a group were extremely low, in all cases less than 0.2, suggesting that individuals alter their behaviour while in their social group. As a result, we utilized a mixed linear model with a single fixed effect: social context (alone or group) and random effects: individual identity, treatment order, group identity (the specific group to which an individual belonged), and group \times context interaction to evaluate the effect of interacting in a group on individual behaviour. Nonadditive effects of being in a group were identified by significant group \times context interactions, indicating that not all groups of individuals respond to their social context in the same way. Individual identity was not a significant source of variance for any behaviour for either the inbred or outcrossed WT strains (Table 1) and was therefore removed from the final model. No differences associated with treatment order were detected and this effect was also removed from the final model. Step-up false discovery rate (FDR) was applied to the entire data set after the linear mixed model to reduce type I error associated with multiple tests (reviewed in Garcia, 2004).

Statistical analyses: group phenotype

The average for each behaviour was calculated for each group, both as the average of a group of interacting individuals (group_G) and as the average for the four members of the group behaving alone (group_A). Both averages, group_{Ak} and group_{Gk} , were calculated as $(\sum_{i=1}^4 Z_i)/4$ where Z is the behaviour of the i th individual in the k th group. Averages are mathematically equivalent to sums and we therefore use them interchangeably. The change in behaviour for each group was then calculated as $\text{group}_{Ak} - \text{group}_{Gk}$ and averaged across all groups for the inbred and WT strains independently, estimating the change in mean behaviour between individuals alone and in groups for each behaviour for each strain of fish. Zero change indicates no difference in the average behaviour of individuals behaving alone vs. in groups and thus additivity of group phenotype. The mean

change was then evaluated for difference from zero using both a Wilcoxon signed rank test and a mixed model (described above).

This research adhered to the Association for the Study of Animal Behaviour/Animal Behaviour Society Guidelines for the Use of Animals in Research and the guidelines provided by the Institutional Animal Care and Usage Committee (locally, BIACUC protocol no. 05-075).

Results

Effects of group membership on individual behaviour

Additive effects of being in a group (i.e. all individuals respond to being in a particular group in the same way) were found for time spent in agitated swimming and time spent oriented toward model in the inbred strain. In both cases, individuals spent significantly less time engaged in the behaviour when in the presence of social partners than when alone (Table 1, Group Identity Effect). Nonadditive effects of group membership were observable as significant group \times social context interactions. Such effects were identified in the inbred strain for time spent in close proximity and time spent oriented toward the model (Fig. 1, Table 1, Interaction Effect) and for the WT strain in time spent in close proximity and oriented toward the model and the number of inspections (Fig. 1, Table 1, Interaction Effect).

Group phenotype

Group phenotype for all behaviours in both strains were determined to be additive, i.e. the average behaviour of individuals behaving alone did not differ from the average behaviour of individuals behaving in groups, except for a marginally significant difference between individual and group averages for time spent in agitated swimming in the inbred strain. When corrected for multiple tests using a step-up FDR procedure, this difference is no longer significant (Fig. 2, Table 1, Social Context Effect). The Wilcoxon signed rank test found no significant difference from zero between the average of individuals behaving alone and in groups for any behaviour. For the inbred strain, the difference between average behaviour alone and in a group was less than 25% of the average behaviour displayed across all individuals in the alone treatment, and thus represents a relatively small change in behaviour. The average change between groups of individuals behaving alone and together was much higher in the WT strain, such that the average change was roughly equal to the average behaviour across all individuals behaving alone. Despite the magnitude of the change, the agreement between the Wilcoxon signed ranks test and the mixed model suggest that individual differences truly are averaged out across groups, such that group phenotype is largely additive.

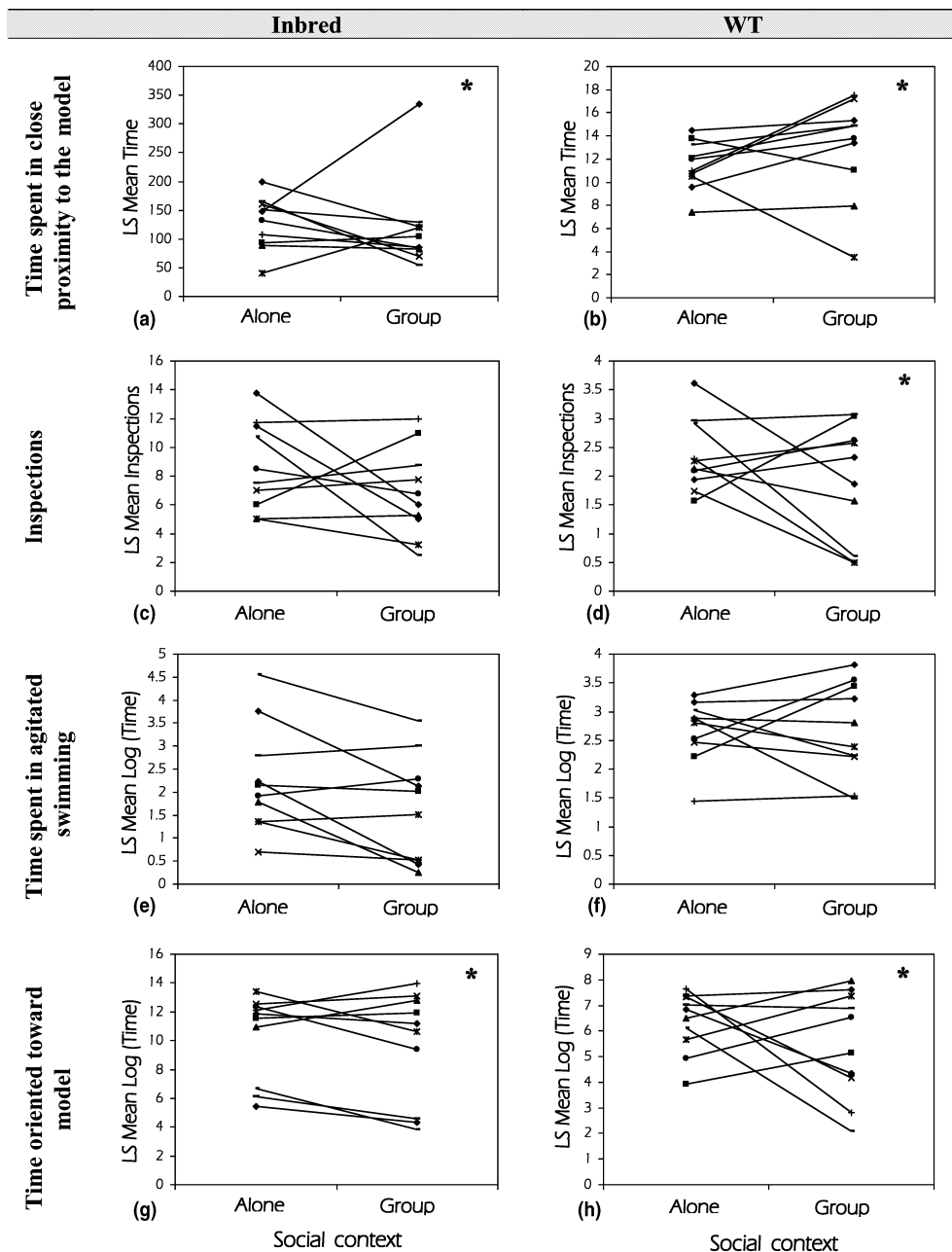


Fig. 1 Interaction between groups and social environment for time spent in close proximity (a,b), inspections (c,d), time spent oriented toward the model (e,f) and time spent in agitated swimming (g,h) for both the inbred and WT strains. Each point represents the average behaviour within a group for that treatment. Asterisks indicate significant interactions between groups and social context after step-up false discovery rate correction.

Discussion

Additive effects of being in a group were found for inspections and time spent oriented toward the model in the inbred strain. In both cases, the mean incidence of the behaviour decreased in the group compared with individual behaviour. Both inspections and time spent

oriented toward the model reflect vigilance to predator threat. Many studies, across taxa, document decreases in vigilance with increases in group size related to safety in numbers and/or the benefits of ‘many eyes’ scanning for threats (e.g. Magurran *et al.*, 1985; Elgar, 1989). However, increases in group size may also increase competition among group members (Grand & Dill, 1999;

Strain/behaviour	Model effects	F	P	
Inbred	Agitated swimming	Individual	0.9805 _{30,80}	NS
		Group Identity	7.019 _{9,80}	$P = 0.0039^*$
		Social Context (Treatment)	5.902 _{1,80}	$P = 0.0379$
		Group × Context Interaction	1.196 _{9,80}	NS
	Proximity	Individual	1.0927 _{30,80}	NS
		Group Identity	0.119 _{9,80}	NS
		Social Context (Treatment)	1.171 _{1,80}	NS
		Group × Context Interaction	3.083 _{9,80}	$P = 0.0043^*$
	Orientation on model	Individual	1.1581 _{30,80}	NS
		Group Identity	13.24 _{9,80}	$P = 0.0003^*$
		Social Context (Treatment)	1.592 _{1,80}	NS
		Group × Context Interaction	3.834 _{9,80}	$P = 0.0007^*$
Inspections	Individual	0.6978 _{30,80}	NS	
	Group Identity	1.863 _{9,80}	NS	
	Social Context (Treatment)	1.078 _{1,80}	NS	
	Group × Context Interaction	1.569 _{9,80}	NS	
Outcrossed	Agitated swimming	Individual	1.144 _{30,80}	NS
		Group Identity	2.105 _{9,80}	NS
		Social Context (Treatment)	0.0002 _{1,80}	NS
		Group × Context Interaction	1.244 _{9,80}	NS
	Proximity	Individual	1.150 _{30,80}	NS
		Group Identity	1.852 _{9,80}	NS
		Social Context (Treatment)	1.281 _{1,80}	NS
		Group × Context Interaction	3.834 _{9,80}	$P = 0.0007^*$
	Orientation on model	Individual	0.9045 _{30,80}	NS
		Group Identity	0.794 _{9,80}	NS
		Social Context (Treatment)	1.107 _{1,80}	NS
		Group × Context Interaction	3.245 _{9,80}	$P = 0.0028^*$
Inspections	Individual	1.6113 _{30,80}	NS	
	Group Identity	0.8956 _{9,80}	NS	
	Social Context (Treatment)	1.517 _{1,80}	NS	
	Group × Context Interaction	4.019 _{9,80}	$P = 0.0005^*$	

Asterisks indicate effects that are significant after step-up false discovery rate (Garcia, 2004).

Johnsson, 2003). Both competition and stronger or more frequent tit-for-tat interactions among WT individuals may limit the possibility of additive effects of being in a group on individual phenotype.

Nonadditive effects of being in a group were found for time spent in close proximity and time spent oriented toward the model in the inbred strain and for both those behaviours and the number of inspections in the WT strain, with some individuals increasing the time spent engaged in or incidence of a behaviour while in a group and some decreasing. Such nonadditive effects can be generated in at least two ways. First, although all four individuals in the shoal are in the same group, they are not experiencing identical social environments: individual A's social environment comprises individuals B, C and D but individual B's social environment comprises A, C and D. If individual A produces many inspections while individual B produces few inspections, then A's social group produces on average many fewer inspections than B's social group. Thus the two individuals are responding

to quantitatively different social environments. Second, individuals may vary in how responsive they are to a given social environment, both in the likelihood of altering their behaviour in the presence of a social group and in the direction and magnitude of the change they produce in response to their social group.

Although we predicted that the outcrossed WT strain should exhibit more nonadditive effects of being in a group, both the inbred and outcrossed strains exhibit nonadditivity in at least half of the measured behaviours, suggesting that social environment may be an extremely important influence on individual guppy behaviour. Such nonadditive effects of group membership on an individual's phenotype will impact the way that an individual experiences selection. For example, male guppies that inspect more frequently have shorter life expectancies (Dugatkin, 1992) but may have better access to mates (Godin & Dugatkin, 1996). If an individual responds to its group by increasing its inspection frequency, the balance between natural

Table 1 Linear mixed model showing additive effects of being in a group (Group Identity), nonadditive effects of being in a group (Group × Social Context) and additivity of group phenotype (Social Context).

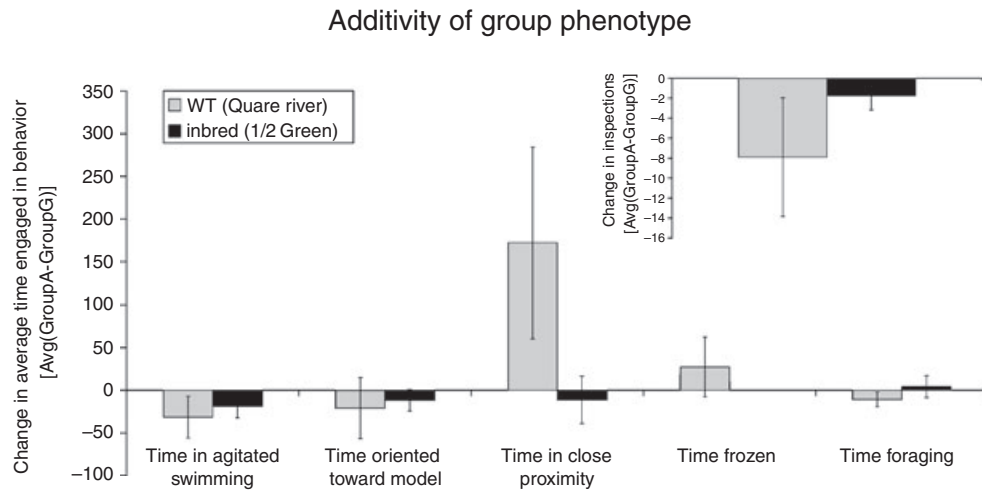


Fig. 2 The average of groups of individuals behaving alone is compared with the average of those same individuals behaving in a group. The zero line indicates no net change between the two conditions and therefore additive group phenotype. Error bars reflect standard error. Additive group phenotype was found for all behaviours in both strains.

selection and sexual selection will be shifted, altering how behavioural traits respond to selection. Additionally, nonadditive effects are expected to play a large role in the evolution of subdivided natural populations because particular combinations of genotypes or genotypes and environments are differentially prevalent in different subpopulations (Agrawal *et al.*, 2001). The background in which an allele is expressed (in this case social background) varies among populations, and therefore how an individual experiences selection, as well as the outcome of selection, will vary among populations (Brodie, 2000). In the wild, guppy populations are potentially subdivided (Russell & Magurran, 2006). Understanding how nonadditive interactions between individuals and their social groups impact social and anti-predator behaviour therefore becomes important for understanding how such behaviours are likely to evolve.

Despite individual variation both within and across trials, group phenotype was additive for all behaviours except for a trend toward nonadditive group phenotype for time spent in agitated swimming in the WT strain. Although this result is not significant after step-up FDR correction, it is nevertheless intuitive that all individuals might be less agitated when in a group context compared with behaving alone, therefore exhibiting a nonadditive group phenotype. Reduced genetic variation in the inbred strain may have sufficiently diminished variation in individual behaviour to produce additive group phenotype for agitated swimming, irrespective of group context. Both strains of guppies exhibited additive group phenotype for all other measured behaviours. This is somewhat surprising, given the wealth of the literature on the emergent phenotypes associated with shoaling in fishes (e.g. Holker & Breckling, 2005). However, emer-

gent phenotypes frequently represent behaviours that individuals cannot perform alone, such as producing a distinctively shaped shoal (Parrish *et al.*, 2002), and thus emergent group phenotypes may be qualitatively different from behaviours performed by individuals in a group context. As with agitated swimming, inbreeding may generate additive group phenotype for all the other observed behaviours in the 1/2Green strain. Populations of wild guppies from different predation regimes vary in how they participate in group interactions, with fish from high predation regimes displaying tit-for-tat strategy much more frequently than those from low predation regimes (Dugatkin & Alfieri, 1992). The WT strain used in this experiment originated from a 'high predation' and thus relatively more cooperative, population (Dugatkin & Alfieri, 1992), potentially generating more consistent interactions and greater additivity of group phenotype.

Additivity of group phenotype suggests that in guppies, understanding the behaviour of individuals adequately predicts how the group as a whole will behave. On average, sets of individuals behave the same alone and in social groups; however, individual phenotypes respond nonadditively to being in a group. The results of this study therefore illustrate that additivity of group phenotype and nonadditivity of group effects on individual phenotype are not mutually exclusive, even for a single behavioural trait. One explanation for this apparent contradiction lies in the fact that individuals in a given group experience different social environments. In the hypothetical group described above, individuals A and B produce high and low levels of behaviour respectively and respond to quantitatively different social environments, despite being in the same social group. If, as a result of their interactions, A decreases its behaviour

while B increases its behaviour, we observe nonadditive effects of the group on the individual, whereas the mean behaviour of the group may not have changed [i.e. $(2+10)/2 = 6$ and $(4+8)/2 = 6$] between social settings, generating additive group phenotype. Guppies have previously been found to respond to larger groups with increases in 'conformity' positive frequency-dependent social learning (Day *et al.*, 2001). These results suggest a mechanism by which reciprocal interactions among individuals can lead to all individuals behaving more similarly to their shoaling partners.

Traits that reflect interactions among individuals are termed 'interacting phenotypes' (Moore *et al.*, 1997). Interacting traits can evolve in response to direct selection and in response to both linear and nonlinear social effects alone or in combination, even when there is no genetic correlation between the interacting and effector traits. The rate of evolution in such situations is not linear, however, and the direction of evolution can be opposite that of direct selection when nonlinear social effects are present, in part because selection operating at one level of organization may interfere with selection at another level (i.e. group vs. individual; Agrawal *et al.*, 2001). The presence of nonadditive group effects on individual guppy behaviour therefore alters our predictions regarding the process and trajectory of behavioural evolution. If there is an additive relationship between what an individual does alone and in a group, then selection acting on behaviour performed in one social context leads to a correlated response in the behaviour performed in the other social context. The strength of the correlation between behaviours performed in the two contexts determines the magnitude and direction of the correlated response, with the context under which selection is strongest (group vs. individual) dragging the behaviour in the other context along (Lande & Arnold, 1983). Additivity of the group phenotype suggests that group phenotype could evolve in a correlated fashion to individual behaviour if selection acts most strongly on individuals alone. However, the presence of nonadditive effects of group membership on individual behaviour means the reciprocal may not hold – that is, we cannot predict a correlated response in behaviour performed alone if selection acts most strongly on individuals behaving in groups. Additionally, nonadditive effects provide a mechanism for maintaining additive genetic and phenotypic variation, even in the presence of strong directional selection, such as selection generated by strong predation pressure (reviewed in Brodie, 2000). Guppies from high predation regimes school more readily and inspect potential predators in groups (Magurran & Seghers, 1994), providing individuals ample opportunity to experience nonadditive effects of being in a group and thus a mechanism for maintaining behavioural variation even in the presence of strong directional selection on behaviour. Understanding behavioural

evolution in animals that routinely behave in different social contexts therefore requires understanding how individuals may be impacted by nonadditive effects of being in a group, such as those found in anti-predator behaviour in guppies.

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