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Original Article

Conformity in the collective: differences in hunger affect individual and group behavior in a shoaling fish

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Animal groups are often composed of individuals that vary according to behavioral, morphological, and internal state parameters. Understanding the importance of such individual-level heterogeneity to the establishment and maintenance of coherent group responses is of fundamental interest in collective behavior. We examined the influence of hunger on the individual and collective behavior of groups of shoaling fish, x-ray tetras (*Pristella maxillaris*). Fish were assigned to one of two nutritional states, satiated or hungry, and then allocated to 5 treatments that represented different ratios of satiated to hungry individuals (8 hungry, 8 satiated, 4:4 hungry:satiated, 2:6 hungry:satiated, 6:2 hungry:satiated). Our data show that groups with a greater proportion of hungry fish swam faster and exhibited greater nearest neighbor distances. Within groups, however, there was no difference in the swimming speeds of hungry versus well-fed fish, suggesting that group members conform and adapt their swimming speed according to the overall composition of the group. We also found significant differences in mean group transfer entropy, suggesting stronger patterns of information flow in groups comprising all, or a majority of, hungry individuals. In contrast, we did not observe differences in polarization, a measure of group alignment, within groups across treatments. Taken together these results demonstrate that the nutritional state of animals within social groups impacts both individual and group behavior, and that members of heterogeneous groups can adapt their behavior to facilitate coherent collective motion.

Key words: foraging, group living, hunger, individual state, transfer entropy.

INTRODUCTION

Some of the natural world's most widespread and fascinating phenomena in nature emerge from the actions of, and interactions between, individual members of animal groups. For example, birds, mammals, fishes, and invertebrates regularly form complex and coordinated swarms that provide the bases for the study of collective movement and behavior (reviewed in Ward and Webster 2016). In many cases, our understanding of collective behavior is based on averaging the interactions between the components of the system, the individual group members. In nature, however, groups are often composed of individuals that differ according to their phenotype, their behavior, or according to their immediate needs

and motivations. In this case, the question arises: how do groups comprising a heterogeneous mix of individuals function effectively?

In order for a group of animals to act coherently, individual members must often adapt their behavior to align it with that of the group (Laland 2004; Pike and Laland 2010). This change in behavior can have both quantitative (rate of behavior being performed) and qualitative (type of behavior being performed) implications (Ward and Webster 2016). Further, individuals might also pay a cost (a conformity, or consensus cost) due to differences between their own preferences in regards to the timing or direction of a collective movement, or the speed of such movement, and those of the group (Conradt et al. 2009). The potential for conflict likely increases with differences among group members (Pinkoviezky et al. 2018), particularly in relation to sex (Sundaresan et al. 2007; King et al. 2008), body size (Ward and Krause 2001; Jordan et al. 2010), parasite load (Barber et al. 1998), metabolic

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rate (Biro and Stamps 2010; Ward et al. 2018a), nutritional state (Bazazi et al. 2010), knowledge and experience (Stuenkel and Parrish 2013; Jolles et al. 2014), or behavioral “type” (Jolles et al. 2017). Heterogeneity can also affect group structure and, at times, may result in some individuals having more influence than others over group movement and direction (Dyer et al. 2009b; Pettit et al. 2015).

Collective movement and behavior can therefore be influenced by differences between individual group members and how they respond to both external stimuli from the ambient abiotic/biotic environment as well as internal stimuli such as the level of satiety or hunger (Bazazi et al. 2010). For example, Hansen et al. (2015b) showed that differences in internal state among individuals within fish shoals affected individual spatial position with hungrier individuals moving to the front of the group. Hunger also influences patterns of activity, with deficiency causing animals to increase locomotor behavior associated with searching and exploration (Priyadarshana et al. 2006; Hansen et al. 2015a; but see Riddell and Webster 2017). More specifically, nutritional deprivation can lead to increased inter-individual distances (Robinson and Pitcher 1989a, 1989b) and greater overall swimming and turning speeds as compared with satiated fish (Hansen et al. 2015a; Killen et al. 2016). Thus, differences in internal state can provide an ecologically relevant source of heterogeneity in animal groups.

Here, we present a detailed analysis of how groups of fish adapt their individual and collective behavior in response to differences in hunger state between group members. At the individual level, we calculated mean speed and mean nearest neighbor distance. At the group level, we calculated median polarization as a measure of group coherence or order (Butail et al. 2013, 2014). Polarization within a group is calculated from the angular trajectories of each individual, where a high value (approaching the maximum of 1) indicates that the members of a group are moving along similar trajectories. Furthermore, we examined information flow within each group. The conditions of greater overall group coherence and synchrony are generally predicted to facilitate information flow (Strandburg-Peshkin et al. 2013; Orange and Abaid 2015). To examine this, we calculated mean pairwise transfer entropy for each group. Transfer entropy is an information theoretic measure that models the dynamics of information flow between individuals within a group by measuring the reduction in uncertainty in predicting one time series by knowing the past values of a second time series (Kadota et al. 2011; Butail et al. 2016). Transfer entropy therefore models the directed flow of information from a source to a target (Schreiber 2000; Lizier and Prokopenko 2010; Bossomaier et al. 2016). Transfer entropy has previously been applied to analyze information flow in theoretical models (Wang et al. 2012) and in animal groups (Tomaru et al. 2016; Crosato et al. 2018; Ward et al. 2018b).

In total, we examined 5 different treatments where the ratio of satiated and hungry group members varies to examine how differences in state across shoals of fish affect collective movement. Based on previous work (Hansen et al. 2015a, 2015b), we predicted that groups comprising all, or a majority of, hungry individuals would show greater mean speeds and greater mean nearest neighbor distances. We further predicted that more homogenous groups (with respect to satiety) would demonstrate more coherent collective motion than heterogeneous groups, exemplified by greater polarization and greater mean pairwise transfer entropy.

MATERIAL AND METHODS

The x-ray tetra (*Pristella maxillaris*) is a strongly shoaling species of characin native to South America. The individuals used in this experiment measured 31 ± 3 mm (total body length) and were sourced from a commercial supplier and were the progeny of fish collected from the wild. All fish were initially held in a single 300-L container prior to experimental trials. The day prior to each treatment, the fish to be used in that treatment were placed into two separate holding aquaria to allow the experimental manipulation of hunger levels (the number of fish in each holding tank varied according to which treatment was being conducted). Although separating the fish into separate holding aquaria could be argued to influence the level of familiarity within and between the two separate groups, familiarity based on individual recognition develops slowly, taking between 12 and 21 days (Griffiths and Ward 2007). As the fish were separated for only 1 day, this factor is unlikely to have influenced the outcome of the present study. Fish were marked 2 weeks prior to the experiments using visible elastomer implant tags (Northwest Marine Inc.) to allow for individual identification during trials. We used 8 different tag combinations to allow each individual within an experimental group to be identified and these tag combinations were allocated haphazardly to the hungry or the fed treatment. All holding aquaria and the experimental arenas were maintained at 27 ± 0.5 °C and kept under a 12 h:12 h (light:dark) photoperiod in the animal holding rooms at the University of Sydney. Fish were fed daily with commercial flake food (Nutrafin Max) ad libitum. Fish in the fed treatment were given food at 09:00 AM and 4:00 PM on the day before trials, and at 09:00 AM on the day of trials, whereas the fish in the hungry treatment were not fed the day before or on days of experimental trials. All experiments were conducted between 9:30 AM and 1:00 PM.

The experimental arena consisted of an annulus constructed out of opaque white acrylic. The external and internal diameters of the annulus were 660 and 270 mm, respectively, generating a circular channel 195-mm wide. The arena water depth was 70 mm and contained aged, conditioned water at the same temperature as the holding aquaria.

At the onset of an experimental trial, groups of 8 fish were selected haphazardly from their respective holding tank(s) and transferred to the experimental annulus via dip-net and bucket. Trials were 15 min in length with the initial 13 min allocated for acclimation to the experimental environment and the final 2 min allocated to behavioral observations/recording. This period of acclimation was based on observations during our previous studies of this species (Schaerf et al. 2017). Trials were recorded using a Canon G1X camera positioned 1.5 m over the arena filming at 25 fps at a resolution of 1080p. Our experimental protocol consisted of 5 treatments representing different ratios of hungry versus satiated individuals in each group, as follows: 8 hungry, 8 satiated, 4:4 hungry:satiated, 2:6 hungry:satiated, 6:2 hungry:satiated. Based on an a priori power analysis, we performed 11 replicates for each of the 5 treatments. After the completion of each trial, fish were added to a different 300-L container. No fish were reused in the experiment.

Data analyses

To quantify the behavior of the fish, we analyzed the 2 min sections of footage from our recordings (i.e., minutes 13–15 of each trial). This period was selected on the basis of a pilot study which indicated that the behavior of fish added to an arena takes between

10 and 12 min to stabilize after their introduction. Video file sections were converted to .avi files using VIRTUALDUB (virtualdub.org) and then tracked using Ctrax (Branson et al. 2009), providing a time series of (x,y) coordinates for each fish. From these data, we calculated the mean speed of the group, the mean speed for each individual, the mean distance between fish for each group, and the mean nearest neighbor distance for each individual. We calculated group polarization (as per Schaefer et al. 2017), opting for the median as a measure of central tendency as this better reflects the distribution of the data in this case.

Transfer entropy was calculated on time series of heading differences (as detailed in Crosato et al. 2018) for each pair of individuals within each group, across all samples. Specifically, we used the Kraskov, Stögbauer and Grassberger estimator (Kraskov et al. 2004) from the Java Information Dynamics Toolkit open-source software (Lizier 2014) with 4 nearest samples used in the search space and an embedding history length for target of $k = 3$ with embedding delay $\tau = 1$ selected to maximally remove (bias-corrected) stored information in the target being misattributed as transfer (Garland et al. 2016) as averaged across all fish and a source-target time delay of $u = 5$ (20 ms) selected to optimize the transfer detected (Wibral 2013). This then allowed us to determine mean pairwise transfer entropy for each group. For each individual trial, we calculated the surrogate distribution of the mean transfer entropy under the null hypothesis that there was no (directed) relationship between source and target (see Lizier 2014; describing techniques in Lizier et al. 2011; Vicente et al. 2011). For an average transfer entropy estimated from N samples, each surrogate transfer entropy is estimated by resampling the source value for each of the N samples, then computing the new average transfer entropy over the new surrogate samples. The transfer entropy estimate can then be compared with the surrogate distribution to test whether there is a statistically significant directed relationship. Specifically, if the observed value for transfer entropy is greater than at least 50 of 1000 resamples, we can conclude that the observed transfer entropy is greater than the null expectation at an alpha value of 0.05.

All data were analyzed in R version 3.3.2 (R Development Core Team 2011). Data were inspected using $Q-Q$ plots and examined for departures from normality using Shapiro–Wilks tests and the equality of variances using Levene’s test. The mean speed of the group, the mean distance between fish, median polarization, and mean pairwise transfer entropy were analyzed using general linear models, with treatment as our effect. Individual speed and nearest neighbor distance were analyzed using the lme4 package (Bates et al. 2015), fitting generalized linear mixed-effects models and specifying gamma distributions to account for skew in the data, with treatment (as a numeric factor, describing the proportion of hungry individuals in a group) and the satiety of each individual (hungry or fed) as fixed effects. Group ID was added as a random effect to control for the nonindependence of individuals within each shoal.

RESULTS

Data used in the following analyses are accessible in the electronic supplementary information.

Speed

The mean speed of the group differed across treatments ($F_{1,33} = 12.235$, $P < 0.001$; see Figure 1a). Mean individual speed differed across group composition treatments ($\chi^2 = 71.13$, degrees

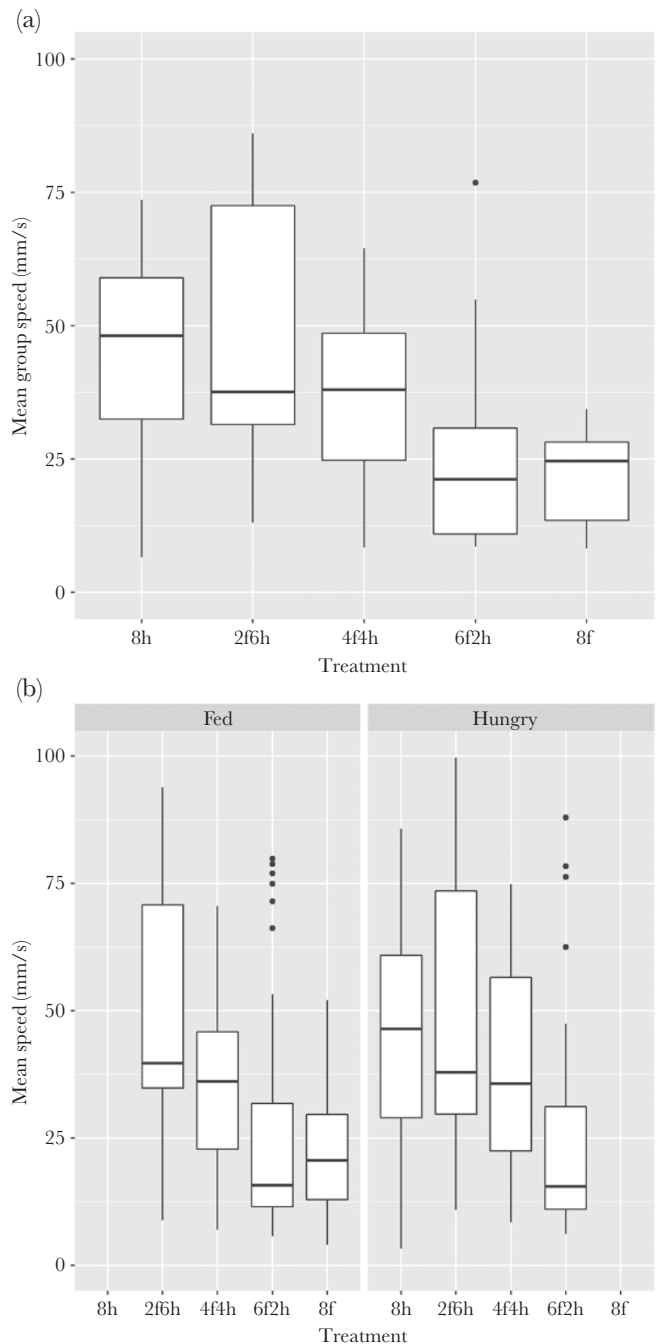


Figure 1

Group speed (mm/s) across treatments shown by (a) mean speed of the group and (b) mean speed of individuals, showing fed (left panel) and hungry (right panel) fish. Experimental treatments differed in composition of test groups based on individual differences in hunger state. Groups of 8 individuals comprised differing numbers of hungry (h) or fed (f) to satiation.

of freedom [df] = 1, $P < 0.001$); however, there was no significant difference between hungry and well-fed fish ($\chi^2 = 0.178$, df = 1, $P = 0.675$), and there was no significant interaction between the two factors ($\chi^2 = 2.113$, df = 1, $P = 0.146$). Fish in treatments that had more hungry fish swam faster compared with treatments with fewer hungry fish (see Figure 1b). Based on the Akaike Information Criterion, including group as a random effect improved the fit of the model.

Group cohesion

The mean distance between individuals within groups differed across treatments ($F_{1,53} = 16.974$, $P < 0.001$), with generally greater distances between fish in groups comprising a majority of hungry fish (Figure 2a). Mean nearest neighbor distance differed across group composition treatments ($\chi^2 = 49.789$, $df = 4$,

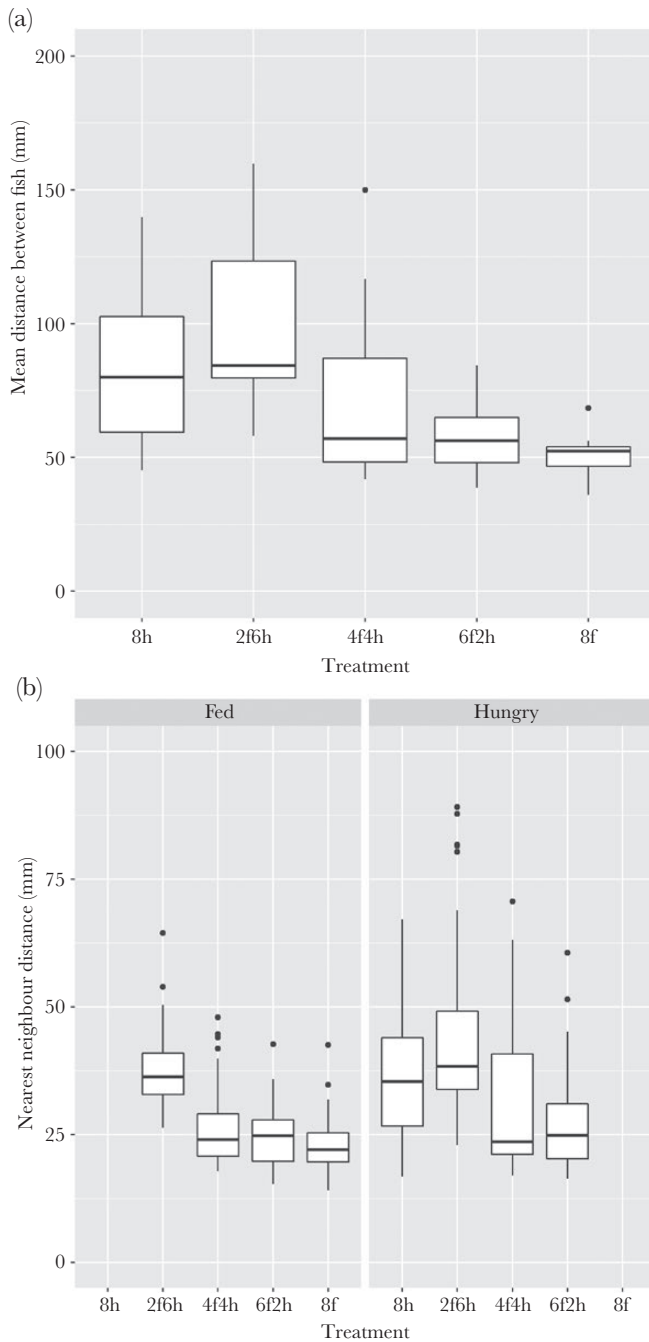


Figure 2 Group cohesion measured by interindividual distances (mm) across treatments shown by (a) mean distance between fish within groups and (b) mean nearest neighbor distances of individuals, showing fed (left panel) and hungry (right panel) fish. Experimental treatments differed in composition of test groups based on individual differences in hunger state. Groups of 8 individuals comprised differing numbers of hungry (h) or fed (f) to satiation.

$P < 0.001$) and between hungry and well-fed fish ($\chi^2 = 24.288$, $df = 1$, $P < 0.001$). There was a significant interaction between the 2 factors ($\chi^2 = 5.075$, $df = 1$, $P = 0.024$). Fish in treatments that had more hungry fish had greater nearest neighbor distances compared with treatments with fewer hungry fish, whereas hungry fish generally had larger nearest neighbor distances than well-fed fish (Figure 2b).

Transfer entropy

There was a significant difference between treatments in mean pairwise transfer entropy ($\chi^2 = 9.83$, $df = 4$, $P = 0.002$; see Figure 3). Groups that had a high proportion of hungry fish tended to have a higher mean pairwise transfer entropy, which indicates the potential for greater information flow in such groups.

Figure 4

Polarization

We did not observe any significant differences in median polarization across treatments ($F_{1,53} = 2.218$, $P = 0.142$; see Figure 4).

DISCUSSION

Shoals comprising predominantly hungry fish showed significant differences in their patterns of individual and collective behavior in comparison to shoals with predominantly satiated fish. Fish in groups with a higher proportion of hungry fish swam faster than those with a lower proportion of hungry fish, although there was no difference between the speeds of hungry and well-fed fish within groups. This suggests that although hungry and fed fish have different swimming speed preferences, the social environment mediates the expression of these preferences such that fish adapt and conform to the speeds of their group mates. Furthermore, our

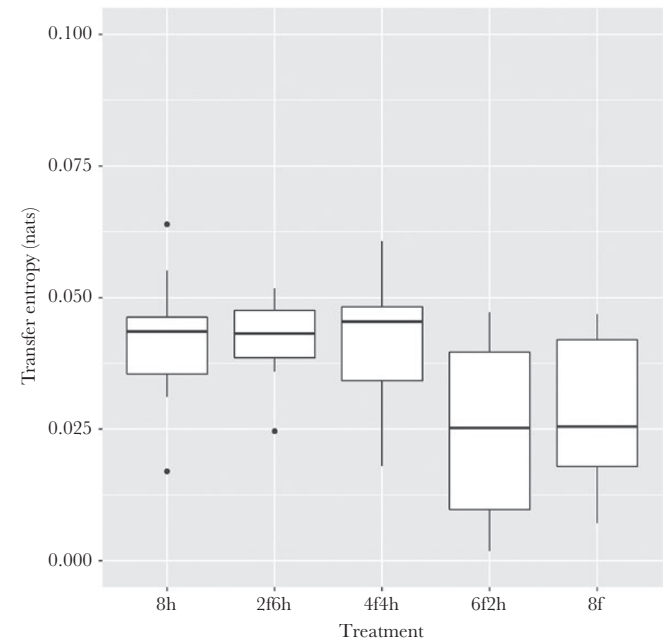


Figure 3

Mean pairwise transfer entropy (measured in nats, the natural log of bits) across 5 treatments. Experimental treatments differed in composition of test groups based on individual differences in hunger state. Groups of 8 individuals comprised differing numbers of hungry (h) or fed (f) to satiation.

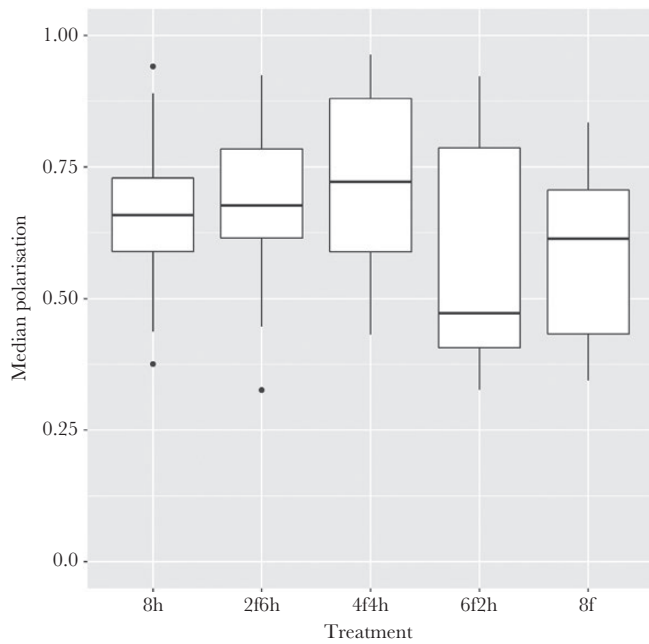


Figure 4

Median polarization across treatments. Experimental treatments differed in composition of test groups based on individual differences in hunger state. Groups of 8 individuals comprised differing numbers of hungry (h) or fed (f) to satiation.

finding that groups (the random effect in our models) had different intercepts in terms of individual speeds implies that although groups differed in speed, the individuals within each group tended to conform to one another in this regard. Collective behavior is characterized by a high degree of responsiveness of group members to near neighbors, which in turn shapes the emergent behavior of the group as a whole. Ultimately, as seen in the present study, this favors conformity among group members and increases the coordination and coherence of group-level behaviors. This was exemplified in a study on three-spine sticklebacks (*Gasterosteus aculeatus*), where despite considerable variation among groups in behaviors including swimming speed, alignment, and cohesion, each group expressed predictable and repeatable patterns of behavior consistent with the idea of group-level personality (Jolles et al. 2018; see also Burns et al. 2017).

Despite the tendency of group members to adapt and conform their swimming speeds within groups, there were differences in overall group cohesion and in nearest neighbor distances between hungry and well-fed fish at the individual level. Groups with a majority of hungry fish were less cohesive while hungry fish were positioned on average at a greater distance from their nearest neighbors than satiated fish (Hoare et al. 2004). This may be an adaptive response to the need to forage as greater interindividual distances reduce competition while still permitting access to social information (Brown and Laland 2003). The lack of any significant difference in polarization among treatments suggests that despite being less cohesive, groups with a higher proportion of hungry fish were not less aligned and thus maintained their ability to perform effective and coherent collective movements. In addition, we found significant differences in transfer entropy across treatments. Information theoretic measures, such as transfer entropy, are being increasingly recognized as important in collective processes as they provide a framework for more rigorous testing of information flow

in biological systems (Schreiber 2000; Bossomaier et al. 2016). As such, the fact that transfer entropy differs across our treatments suggests that there are differences in the dynamics of information flow within groups in relation to individual hunger state (Butail et al. 2016). In particular, shoals with greater numbers of hungry individuals had greater mean pairwise transfer entropy, implying greater potential information transfer among group members than occurred in shoals with more satiated individuals. This result is somewhat surprising, given our other results showing that hungry individuals had greater nearest neighbor distances. Although these results might seem counterintuitive, possible explanations for this include producer–scrounger foraging dynamics (Vickery et al. 1991), where hungry individuals are actively searching for food patches while simultaneously being responsive to neighbors’ movements to best exploit potential foraging opportunities that arise. In addition, the pattern may be explained by the faster swimming speeds of groups with a higher proportion of hungry individuals. There was, however, no significant difference in polarization (group alignment) across treatments, despite the strong established link between speed and polarization (Viscido et al. 2004; Ward et al. 2017; Kent et al. 2019). A potential explanation for this surprising result is that although animals increase speed when seeking food, they often increase their turning rate (Bennison et al. 2018), which might cancel out the effect of greater speed on polarization. In line with this, O’Brien (1989) reported a decrease in alignment in groups of foraging crustaceans. Group-level differences in transfer entropy were particularly sharp at a point between 4f4h and 6f2h, which may be indicative of a phase transition, but an accurate characterization of such critical regime would require a more refined parameterisation in larger groups (Spinney and Lizier 2018). Although we focused on pairwise information transfer, multivariate extensions to the transfer entropy, including conditioning on other information sources, can also be used in order to capture higher-order relationships (Vakorin et al. 2009; Lizier and Prokopenko 2010; Williams and Beer 2011; James et al. 2016). This may also help to discriminate among information flows in hungry–sated, hungry–hungry, and sated–sated pairs and precisely determine leader–follower relationships (Sun et al. 2014).

Our results show that differences in hunger state result in strong and obvious patterns of behavioral variability in otherwise similar animal groups and provide novel insights into the ways in which heterogeneous groups are able to function. The composition of groups has a strong effect on the expression of group behavior. Heterogeneity among group members requires that they integrate their behavior in order to function effectively together, and indeed this has been demonstrated in relation to the personalities of individual group members and the behavior of groups (Sih and Watters 2005; Magnhagen and Bunnfeld 2009; Webster and Ward 2011; Aplin et al. 2013; Keiser and Pruitt 2014; Pruitt and Keiser 2014; Hunt et al. 2018). In this context, a heterogeneous mix of different personalities can combine to form the most effective group (Dyer et al. 2009a; Pruitt and Riechert 2011; Wray et al. 2011). In specific relation to collective behavior, heterogeneity requires that individuals adapt their own behavior in order to achieve coordination and consensus (Conradt and Roper 2000; Stienessen and Parrish 2013). The present study demonstrates that individuals can and do adapt their behavior; however, given the many ways that animals in social groups differ from one another, understanding how animals deal with heterogeneity in their social groups represents a fundamental aspect of collective behavior that can be used to examine behavioral or ecological outcomes.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Wilson et al. (2019).

Ethics: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed were in accordance with the ethical standards of the University of Sydney and were approved by the Animal Ethics Committee of the University of Sydney (ref no. 2015/807).

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