laboratory conditions (Gaffney & Webster, 2018)'.

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In a paper this year (Gaffney and Webster 2018) we presented a series of experiments in which we investigated the effects of arena size and inter-observation duration upon basic social network structure metrics and related measures for shoals of threespine sticklebacks *Gasterosteus aculeatus* L. 1758. We were motivated to perform this experiment by the question of whether such measurements can meaningfully be compared between experiments run by different researchers and under different conditions. An unanticipated finding arising from this work was that many of the measured network metrics tended to remain consistent within groups across observations. In his recent commentary, Jolles (2018) highlights the concordance between our finding of consistency of social network metrics and of his measures of collective motion (Jolles *et al*. 2017), with both studies dealing with functional and mechanistic aspects of grouping behaviour that probably influence one another. Jolles (2018) goes on to suggest how these approaches might be used to further explore fish shoal

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social organisation. We thank Jolles (2018) for his comments and endorse his suggestions, adding a few of our own in this response.

As Jolles (2018) identifies, we were unable to account for any effects of individual characteristics in shaping the social interactions recorded in our study, since these were not measured (or else were controlled for). Local assortment within shoals can arise through active shoaling preferences, such as preferences for familiar or similarly-sized individuals, as well as passively due to differences in factors including swimming speed and sociability, as shown by Jolles *et al*. (2017). Existing studies provide insight into how active preferences can affect the local shoal structure. Atton *et al*. (2014) showed that familiarity based upon prolonged interaction and shared diet type had a significant effect, albeit quite small, upon shoal social network structure, with dyadic interactions occurring more frequently between familiar than unfamiliar pairs of fish. Interestingly, Atton *et al*.'s (2014) study found that familiarity played a much stronger role in determining social foraging dynamics than it did in shaping dyadic interactions, suggesting that association network approaches alone may be insufficient to capture the full effects of familiarity upon some of the functional consequences of shoal organisation. Ward *et al*. (2017) found that within naturally occurring shoals observed in the wild, neighbouring fish tended to be more closely matched in body size compared with more separated shoal members, though it was not clear whether this was due to active or passive assortment. To date, active and passive factors have largely been explored separately. In reality, multiple factors and their interactions probably play a role in shaping shoal structure, including familiarity, personality, size, condition and variation in metabolic and physiological characteristics. It would be fascinating to account for these together, in truly comprehensive investigation of how fish shoals form and function.

Finally, we suggest that we are at a stage where we can take what we have learned in the laboratory and apply it to fish shoals in the wild, as many researchers are already

beginning to do. Laboratory experiments are extremely valuable for quantifying behavioural interactions in animal groups, allowing potentially confounding factors to be controlled for while manipulating variables of interest and allowing methods for making fine measurements to be tweaked in the absence of the noise inherent to the natural environment. Ultimately, however, one aim of such laboratory experiments is to generate hypotheses about how animals behave under natural conditions (Ward *et al*. 2017). Accordingly, findings from the laboratory can be used to formulate expectations about how the same animals might behave in the wild, which should be used to develop experiments and studies in natural settings.

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