Alternate Modes of Leadership in Collective Behaviour

By

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Abstract

Understanding interactions between individuals is imperative for predicting how groups may react to changing environmental landscapes. Animal populations have displayed variation in behaviour when responding to different environmental cues. Variation in behaviour has been linked to differences in physiology, including metabolic phenotypes and locomotor performance. Understanding how these differences in individuals present themselves in groups provides insight into how physiology affects group behaviour, and how this may change in different contexts. Collective movement in animals is an increasingly prevalent theme in behavioural research, and understanding how and why groups decide to move is critical to our knowledge of animal life. Group movement may emerge from the decisions of one or few individuals, i.e. leadership, or be a shared decision by all individuals. Leadership has been previously linked to individual behavioural traits, which has also been related to physiological differences, however the specific links between physiology and leadership are understudied. Using laboratory experiments, I investigated the role of physiology in leadership of schools of fish, and how different contexts altered leadership in groups in order to examine how groups move and the mechanisms underpinning leadership.

In the first data chapter, I tested whether metabolic composition of groups affected leadership by compiling groups of nine fish according to their standard metabolic rate and recorded their swimming behaviour. We measured behaviour at 15 °C, and again at 18 °C to see how temperature increases affect leadership and group dynamics. We found that metabolic composition had no consistent effect on group behaviour and leadership, but increases in temperature caused fish to be less synchronised and leadership to be disrupted.

The metabolic cost of digestion has been shown to affect individual behaviour. Our second experiment investigated how group behaviour changed with feeding and time since feeding. Before and during feeding showed relationships between behaviour and meal size, where fish that ate the most were found to be followers when a leader was accelerating, however a fish who has eaten more

food is more likely to be a leader when turning. There was no association between meal size and leadership after feeding, however leadership in groups changed before and after feeding events.

Our results from chapter 3 and 4 indicated that different environmental contexts disrupted group behaviour, rather than creating consistent differences in specific individual leadership ability. To see how social context affected these metrics, I tested individual swimming performance testing how cost of transport related to leadership and see how individuals alter their voluntary swim speeds to stay within groups and how this relates to their physiological optimum. We found that higher cumulative costs are found when swimming alone compared to groups. Leadership is also not linked to deviation from optimum swim speed, showing that leaders in groups do not influence groups to swim at their optimum swim speed. This study confirms that leadership is not more costly in terms of transport speed, and overall swimming in groups is less costly than swimming alone.

These results provide evidence that changing contexts affect group behaviour and leadership in schools of fish. Leadership may not be attributed to one or few specific individuals however how leadership is distributed among individuals may still change in different contexts. Chapters 3 and 4 suggest that physiological processes affect leadership behaviour, and chapter 5 shows that social context will affect group behaviour. Our results provide insight into how leadership in groups change in different contexts and how I may expect collective behaviour to change with environmental variation groups may experience in the wild.

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Covid-19 Impact Statement

Due to the global coronavirus pandemic beginning 2020, data collection for an additional chapter was halted mid-experiment and was unable to be completed. Physiological and behavioural measures were intended to be collected in University of Glasgow facilities which were closed to researchers except for essential animal maintenance. While the inclusion of the suggested chapter, which explored leadership in the context of social learning, would have contributed to the findings and conclusions I have made in this thesis, it does not detract from the overall findings presented. Chapter 2 was intended to be submitted as a completed R-package, but due to restrictions in international travel, and therefore liaisons with collaborators, this is now submitted as a methods chapter.

Chapter Status and Contributions

Title	Conception	Methods	Data Collection	Analysis and Interpretation	Manuscript Preparation	Co-authors for publication	Publication Status
2: Development of Code-Based Functions for Extracting High-Resolution Behavioural Metrics From Coordinates	L Cotgrove	L Cotgrove, J Jolles	N/A	L Cotgrove, C. Torney, D. Husmeier, G. Hopcraft	L Cotgrove	Cotgrove, L., Jolles, J. W., Killen, S. S.	R Package to be written, publication aim for mid 2023
3: The effect of temperature and group composition of metabolic phenotypes on leadership and collective behaviours in fish	L Cotgrove	L Cotgrove, T Norin, A Crespel, S Killen, S Marras, P Domenici	A Perrsson, L Pettinau,	L Cotgrove, C. Torney, D. Husmeier, G. Hopcraft , S Killen	L Cotgrove	Cotgrove, L., Perrsson, A., Pettinau, L., Norin, T., Crespel, A., Marras, S., Domenici, P., Killen, S., C. Torney, D. Husmeier, G. Hopcraft	Publication due May 2023
4: Effects of feeding and digestion on leadership and collective behaviour in schooling fish	L Cotgrove	L Cotgrove, SJ Fu, S Killen	L Cotgrove, Y. Wang, L. Wang, L. Hong, Y, Xiao.	L Cotgrove, C. Torney, D. Husmeier, G. Hopcraft, S Killen	L Cotgrove	Cotgrove, L., Ling, H., Wang, Y., Xiao, Y., Wang, L., Fu, S., Killen, S. S., C. Torney, D. Husmeier, G. Hopcraft	Publication due January 2023
5: Determining hidden energetic costs and benefits of sociality in moving animal groups using cost of transport	L Cotgrove, J Jolles, S Killen	L Cotgrove, S Killen, J Jolles	L Cotgrove, A Crespel	L Cotgrove, C. Torney, D. Husmeier, G. Hopcraft, S Killen	L Cotgrove	Cotgrove, L., Jolles, J., Crespel, A., Killen, S, C. Torney, D. Husmeier, G. Hopcraft	Publication due January 2023

Author's declaration

The experiments, analyses, and study questions described in this thesis were conceptualized by L. Cotgrove, with the assistance of S. S. Killen, J.G. Hopcraft, C. Torney and D. Husmeier. L. Cotgrove was responsible of all data analysis, with advice by J. W. Jolles, and managing data collection with the assistance of the following:

Chapter 2: Equations were researched and coded in R by L. Cotgrove, including programming functions and developing reproducible code. Methods were advised by J. W. Jolles, the designing and construction of software package was conducted by L. Cotgrove.

Chapter 3: An original experiment was conceptualised and conducted by A. Perrsson, L. Pettinau, T. Norin, A. Crespel, S. S. Killen, S. Marras and P. Domenici but analysed using rudimentary methods and subsets of data. Using video analysis, data extraction for this chapter was conducted by L. Cotgrove before analysis.

Chapter 4: The experiment was conceptualised by L. Cotgrove with S.S Killen and S. Fu. Data collection was conducted by L. Cotgrove, Y. Wang, L. Wang, L. Hong, Y, Xiao.

Chapter 5: The experiment was conceptualised by L. Cotgrove with S.S. Killen, J. W. Jolles, C. Torney, J. G. Hopcraft and D. Husmeier. Data collection was carried out with the assistance of A. Crespel.

All manuscripts resulting from this thesis were prepared by L. Cotgrove, with assistance and creative input from acknowledged co-authors.

Lucy Cotgrove

1 General Introduction

Group living is ubiquitous among taxa, observed across most environmental contexts and can range from pairs of organisms to large aggregations and communities. Animals in groups may show various degrees of cohesion, and while they may aggregate, they can also be largely independent in their individual actions while maintaining inter-individual distances. Alternatively, they may be synchronous and appear to move as one mass, similar to murmurations in starlings (Major & Dill, 1978) or schools of fish (Katz et al., 2011). Group living may occur at specific life stages (e.g. only in the juvenile stage: Bazazi et al., 2008) or throughout lifespans of individuals (Whitehead et al., 1991; Wittemyer et al., 2005). Group members may experience these social bonds for a lifetime (Dunbar & Shultz, 2007; Buston et al., 2009; Jordan et al., 2010) or these bonds may be ephemeral or unstable (Wilson et al., 2014).

There are many costs and benefits associated with group living including increased mating opportunities (Grueter & Van Schaik, 2010). The competition for successful mating is often greater between individuals, which will increase the risk of injury or death (Croft et al., 2011a; Griffin & Nunn, 2012) while decreasing reproductive opportunities (Kokko & Johnstone, 1999). Another benefit to living in groups is that individuals have access to more resources for example feeding or preferred habitat (Ward & Hart, 2005; Strodl & Schausberger, 2012). As a result, they may be more visible to predators or other competitors which may lead to negative consequences (lack of food; injury/death; loss of territory). Additionally, individuals may get benefits from group living which are more useful independently and in a moment-to-moment basis, such as conserving energy through spatial position and sharing of information that another group member may not be able to perceive (McComb et al., 2001; Swaney et al., 2001; Vital & Martins, 2009).

Group behaviour can also be influenced by environmental conditions, which vary across short and long time scales. Environmental conditions affect migration speeds and locations (barnacle geese: Jonker *et al.*, 2010), where migration

patterns can change due to temperature changes and predation. Long-term environmental effects on sociality are important for predicting group patterns over seasonality or lifespans. Shorter term, moment-to-moment interactions between individuals may be affected by much more subtle shifts in environmental conditions, and study of these effects may give insight into the mechanisms underlying changes that occur over more prolonged timescales (Guttal & Couzin, 2010; Farine et al., 2017). Short term variability in the environment has been shown to affect group behaviour. Cohesion measures how far apart individuals are from each other. Higher temperatures can cause schools of fish to be less cohesive (giant danios: Bartolini et al 2015), however this contrasts with previous studies that zebrafish and guppies are more cohesive at higher temperatures (Weetman et al., 1999; Pritchard et al., 2001). Many schooling fish species only form groups during the day, while at night, the fish tend to increase distances between groupmates, in some cases causing dissolution of the groups (Aoki & Inagaki, 1988; Smith et al., 1993). Locomotion method will change group behaviour, where flocks of birds were closer together when on the ground or water in comparison to flying (Ballerini et al., 2008). In the presence of a predator, groups of stickleback became more synchronised, as individuals perceiving greater threat increase the rate where they receive information from peers (Bode et al., 2010). Polarisation, a measure of whether individuals within a group are facing the same direction, in swarms of crustaceans decreased in the presence of food and in the presence of a predator (O'Brien, 1989). Behaviour may also change with group size, where how information is shared, and the quality of information changes with social scale, in terms of accuracy and amount of information (Jolles et al., 2020a). In great tits (*Parus major*), pairs showed no synchronisation but as group size increased, the time spent to coordinate activity reduced (Aplin et al., 2015). In a study on chacma baboons (*Papio ursinus*), a greater likelihood of synchronous behaviour was found across groups early in the day, when the animals were intent on foraging, and that the animals were more synchronised in woodland as opposed to open habitat, which may relate to the foraging strategies of the animals in woodland, and when the groups were more cohesive (King & Cowlishaw, 2009; King et al., 2009). Group dynamics are important to study as they provide insight into how environmental changes may alter short and long term patterns of social interactions, affecting numerous forms of behaviour and ecological phenomena

including with foraging, predator avoidance, reproduction, disease transfer, and migrations.

1.1.1 Heterogeneity in Group Living

Within animals groups there is among-individual heterogeneity in genotypes and phenotypes (Jolles et al., 2020a). Theoretical work has suggested evolutionary implications of phenotypic variation in groups (Farine et al., 2015), but it is relatively unknown how phenotypic variation affects group behaviour and movement. Individual variation may present itself in terms of physiological state, through metabolic traits, nutritional state or age (Wittemyer et al., 2005; Bazazi et al., 2008; Seebacher & Krause, 2017). Physiological differences are increasingly related to behaviour, where variation may incur differences in sociability, aggression, activity and hunger (Metcalfe et al., 2016). Previous work has explored the relevance of behavioural and physiological phenotypic variation to ecological changes, where individuals may react differently to different stressors, for example individuals may react differently to increasing temperatures (Bartolini et al., 2015; Cooper et al., 2018) or hypoxia (Cook et al., 2011; Killen et al., 2013; Pineda et al., 2020), which may show how these species may react in the face of climate change and increasingly extreme conditions. An increase in research shows that consistent behavioural differences (Ward et al., 2004) can influence group behaviour such as spatial distribution or reactions to environment, but so far the physiological underpinnings in such processes are rarely considered. Studies exploring individual behaviour in the context of groups should consider that individual behaviour may change in response to other group member's behaviour, and this may be governed by the focal individual's motivation and also the physiological capacity to respond (Jolles et al., 2020a).

Collective movement is often related to resource acquisition, and this is suggested to be linked to physiological state (Killen et al., 2017). In this case, resources could be food, suitable habitat, and breeding opportunities. An individual may have autonomy in deciding where to move to and behaviours to express, but group movement requires individuals reach consensuses when

assessing their environment when deciding direction of travel, activities and choices in movement, while remaining cohesive and coordinated (Conradt & Roper, 2005). If collective consensus is not reached then a group may split and benefits of group living are reduced (Krause & Ruxton, 2002; Conradt & Roper, 2007). Organisms that move together must follow quantifiable interaction rules, such as attraction, repulsion, and alignment, which allow them to structure their interactions and maintain group cohesion (Strandburg-Peshkin et al., 2018). Coordination within groups is dependent on how information is transmitted among the individuals (Conradt & Roper, 2005; Conradt & List, 2009). If individuals do not have a complete assessment of their environment, they may rely on interactions with neighbours to guide their movements, which is particularly found in large, synchronous fish schools or bird flocks, where movement is self-organised, and it is unclear if there are leaders but it is ordered movement (Couzin et al., 2002, 2005; Jolles et al., 2020a). When these groups move in a self-organised way, but rely on a degree of social structure or include behavioural differences among individuals, this is referred to as collective behaviour (Jolles et al., 2020a). Ultimately, all group members are able to gain information regardless of "quality" of information from either or both their environment and peers, and understanding how this information influences collective behaviour is critical to understanding the ecology of group movement.

1.1.2 Leadership in Collective Behaviour

Group consensus can stem from egalitarianism where all individuals contribute to a decision, or leadership, where specific individuals or an individual determine or repeatedly influence group behaviour (Reebs, 2001; Conradt & Roper, 2005; Strandburg-Peshkin et al., 2015). Leaders are only successful if followed by other group members which can be instigated voluntarily or via hierarchical dominance. When short term group movements are driven primarily by one or few individuals, then collective behaviour is maintained by leadership. Individuals within a group can be inferred as a leader if it has repeated influence on other members of the group, whether directly or hierarchically (Strandburg-Peshkin et al., 2018), and this influence can be inferred in different ways. It is important to differentiate between influence and leadership, where an

individual may have influence if its actions results in some behavioural change from other individuals in its group (Galton F., 1907), but leadership is a measure of how repeated this influence is. It is important to note that leadership and leaders may be inherent, where leaders are pre-determined according to traits or social status. Alternatively, leadership may be emergent (Couzin et al., 2002; McComb et al., 2001) where leaders are identified from initiating coordinated movements which are linked together, where interaction rules vary according to individual traits, and this affects collective behaviour no matter the mode of leadership (Conradt et al., 2009; Berdahl et al., 2013; Strandburg-Peshkin et al., 2013; Pettit et al., 2015). Previous work has identified small numbers of individuals which have a large influence on groups without any active signalling. Additionally, individuals may try and influence others by using movements and behaviours which are seen as initiations (Morrell et al., 2008), and may change behaviours of potential followers that are obeying more general interaction rules of the group. It is important to note that, regardless of initiation events or influence a leader may have, leading a group is only successful if other individuals are willing or capable of following (Sueur et al., 2009).

It is also important to consider how leadership is spread across a group. It is necessary to consider group interactions in terms of the distribution of influence and the consistency of the influence. The distribution of influence can be distributed or centralized, where each group decision is controlled by a different single individual (distributed, variable leadership), or the same (centralized, unshared leadership). The influence can be consistent, where one individual controls all the group decisions (centralized, unshared leadership) or all individuals contribute equally to all group decisions (shared leadership). Groups with true shared decision-making, in the sense of all individuals contributing to each group decision, can take advantage of the "wisdom of crowds" (Couzin, 2009; Aplin et al., 2015) and other types of collective information processing (Couzin et al., 2002; Conradt & List, 2009), whereas a system in which a different individual controls the decision each time would be more likely to represent "leading according to need" (Berdahl et al., 2013) or leadership by informed individuals (Gavrilets et al., 2016). The tendency to lead in fish is often associated with motivation driven by more information than an individual's peers (Ioannou et al., 2015), or greater need (Bjornson & Anderson, 2018). Reebs

(2001) showed fish (golden shiners, *Notemigonus crysoleucas*) that had been trained to expect food at a particular time and place each day were able to lead the rest of their naive group mates to that location. Within three-spined stickleback (*Gasterosteus aculeatus*) shoals, fish that have found food patches tend to return to them, with uninformed fish locating the food patches by following these individuals (Atton et al., 2012, 2014; Webster et al., 2013). Previous experience of individuals must be considered in leadership analysis as even in emergent systems with no clear social structure, this could affect leadership hierarchies.

Previously, leadership has often been inferred in group experiments using previously conducted behavioural assays in pairs, and the leader is defined as the first individual to leave a refuge (Kurvers et al., 2009) or explore an arena (Herbert-Read et al., 2019). Ultimately, leadership is assessed by measuring influence on the other individuals in the group and subsequent movements to follow those leaders, generating different roles within these groups. Leadership in individuals has been linked to animal behavioural phenotypes, often referred to as personality, when describing latency of reaction in a behavioural assay (Kurvers et al., 2009; Bevan et al., 2018). However, these assays are often conducted in pairs (one leader, one follower) and do not encapsulate group dynamics (Sasaki et al., 2018).

1.1.3 Different Modes of Leadership

There are many studies on leadership in groups which focus on the social interactions between group members, such as dominance or experience (Flack et al., 2012). Studies focus on moving groups and collective behaviour as a precursor to studying larger group dynamics and understanding why leadership occurs, rather than identify which individual is the leader and why this may be. Previously, leadership data has been collected by human observation but this has been on different scales and accuracy in terms of time, space, and numbers or individuals and interactions in comparison to current methods of analysis. Due to recent technological advancement, data can shift from human observation which focused on how individuals influenced whole groups, to using tracking (GPS or

video) exploring individual to individual dynamics. Improved tracking technologically leads to moment-to-moment analysis and individual identification which allows for different modes of leadership to be explored simultaneously and identify the nuances of leadership changes in different environmental contexts.

1.1.4 Spatial position

Leadership in moving groups can be defined by spatial position; animals positioned at the front of a group are assumed to drive direction of travel and are thus may be considered as leaders (spotted hyenas: Smith et al., 2011); roach: Krause et al., 1998). This is an example of individual to group influence, and total influence was assessed by how much time was spent at the front of a group. Moreover, leadership hierarchy is inferred at an individual to individual level by observing which individuals are ahead of others (Altmann, 1974). While using spatial position is one of the most popular ways of defining leadership, this requires the assumption that front positions have the most influence. However, in three-spined sticklebacks, individuals who are further away from their groupmates and on the periphery of groups were more influential in deciding group motion, even when not in anterior positions (Jolles et al., 2017). Other research has shown that animals in the centre of a group can initiate behavioural changes within the group (Leca et al., 2003; Sueur & Petit, 2008b, 2008a; Sueur et al., 2009). Individuals at the front of groups may have greater access to resources (DeBlois & Rose, 1996), and may make decisions which benefit themselves at the cost of the other members of the group (King et al., 2008). Followers benefit from this strategy as they will be led to resources by more informed individuals without having to gather information themselves, which may be costly (Guttal & Couzin, 2010; Björnsson et al., 2018; Palacios-Romo et al., 2019).

1.1.5 Initiating and followship

Identifying individuals that successfully initiate group movements, regardless of their spatial position within the group, is another method of inferring leadership. Initiators are identified by their initial deviation from the current movement vector or centre of the group if stationary, and a number or proportion of the group must then follow within a set time frame. This is regularly carried out by direct observations of individuals using human observation but also from fine scale movement data. This assumes that initiations of group departures are important in determining whole group movement (Strandburg-Peshkin et al., 2015). Identifying leaders in this way can be applied when the group is initially stationary or mid movement, but prior knowledge is required to identify how far away an individual has to move before a successful movement could be initiated, and if distances do not change very much between individuals then this method cannot be used. Initiations may also results from acoustic or visual signals in addition to movement (meerkats: Bousquet & Manser, 2011; white faced capuchins: Boinski, 1993; Campbell & Boinski, 1995). Behaviours such as vocalisations or physical cues can be incorporated into analysis as a measure of initiation success or frequency. This can be in the case of moving from stationary position to moving (Stueckle & Zinner, 2008; King et al., 2011). Initiation of movement may come from previous information obtained by the leader.

Leadership through initiation of movement can be explored using time delays and hierarchical networks, which uses correlations of movements to ascertain which individual, or individuals, have the most influence over group movement (Couzin et al., 2002; Nagy et al., 2010). The time delay between changes in direction of pairs of individuals is used to infer which animal influenced the other. Leadership can be identified by which individual influences others in the group and construct rankings of individuals (Nagy et al., 2010). Time delays are particularly useful when using automated tracking of individuals, as it can use frame by frame moments to measure leadership, but requires individuals to be moving continuously so their directional headings have meaning, and they must be coordinated for their measurements to be distinguished from noise (Nagy et al., 2013; Giuggioli et al., 2015) or initiating group movement using time delays in rummy-nose tetra (Jiang et al., 2017)

1.1.6 Inferring influence from outcomes of decisions

Observing individual preferences of group members and relating them to group behaviour is another way of inferring influence. Additionally, leadership can be assessed by observing decisions and group destination to preference of individuals, as seen in baboons (King & Sueur, 2011) and social learning in fish (Ward et al., 2008) where individual preference or knowledge of specific individuals was able to drive the group. Inferring "destination based" influence requires testing of the preference of group members, which is not always possible with groups of large animals or in the field where you cannot control a population. Even if all preferences are known there may be conflicting factors affecting group decisions such as correlated preferences or physical capability to be a leader or follower (Ward et al., 2018). Individuals whose preferences are tested in a solo setting may alter their preferences in the presence of conspecifics, which will determine leaders and followers, but if two individuals prefer the same location and this is reflected in a group trial, it provides no insight how group behaviour is determined. Preferences could be identified through spending time in abiotic environmental conditions such as temperature (Christensen et al., 2021), or reflect individual status conditions such as hunger (Wilson et al., 2019) but also about innate physiological differences such as optima. Ultimately, individual preferences will be reflected through behaviour, and linking how these preferences affect collective behaviour and what underlies these preferences is critical to understanding the physiological mechanisms behind leadership.

1.1.7 Physiology and Leadership

Differences in behaviour are often attributed to variation in physiology, thus a link between physiology and leadership is likely, specifically in groups which have emergent leadership based on individual state. Leadership can arise from individual differences which then influence collective behaviour. These individual differences can be due to variation in knowledge and experience (Jolles et al., 2014; Webster, 2017; Ward et al., 2018); behavioural phenotypes or personality (Kurvers et al., 2009; Johnstone & Manica, 2011; Nakayama et al., 2012a) or energetic state (Reebs, 2001; Fischhoff et al., 2007), and have all

been linked to physiological phenotypes. Additionally, there is growing evidence that these consistent behavioural differences can present themselves in terms of leaders and followers (Harcourt et al., 2009b; Nagy et al., 2010; Nakayama et al., 2013). By looking at preferences of individuals in an experimental setting, information can be obtained through behavioural assays and physiological measurements to explore the capabilities and relationships between these characteristics and leadership (Ward et al., 2018; Wilson et al., 2019).

Physiological traits related to metabolism and swimming performance are likely to affect individual and group behaviour, and this is likely to be related to leadership and following (Ward et al., 2018). There is variation in minimum metabolic rate (standard metabolic rate (SMR) in ectotherms) within species (Millidine et al., 2006; Rønning et al., 2007; Burton et al., 2011; Killen et al., 2011). Individual standard metabolic rates have rarely been linked to group behaviour, but due to individual assays fish with high SMR are hypothesised to be less cohesive, and fish with low SMR may be more social (Killen et al., 2012b). Maximum metabolic rate (MMR) is also linked to behaviour, specifically position in school (Killen et al., 2012b), which suggests leadership may be related to physiology. Aerobic scope (AS) is the difference between MMR and SMR, and is the capacity for aerobic metabolism above which is required for maintenance. AS constrains the number of aerobic processes (e.g. activity, growth, digestion) that can be performed simultaneously and may affect various aspects of behavioural ecology, for example individuals with lower aerobic scopes may be more sociable and less food motivated (Pörtner & Farrell, 2008; Jørgensen et al., 2012; Marras et al., 2015a; Killen et al., 2017).

Metabolic rate also affects measures of locomotor performance linked to travelling speeds which in turn may affect group behaviour. Locomotor performance can be measured by critical sustained swim speed in fish (Brett, 1964) and has been shown to correlate with both maximum metabolic rate and routine swimming activity (Plaut, 2001; Oufiero & Garland, 2009), suggesting that physiological traits are crucial in understanding behaviour. As metabolic traits are affected by aerobic processes such as digestion and activity, these aerobic processes are have shown to be linked to measures of locomotor performance. Mclean et al. (2018) showed how fish altered their spatial

positions when swimming within a shoal dependent on the interaction between meal size, the energetic cost of digestion, and physiology. Fish that ate the least moved to the front of the school, and fish that ate larger meals moved to the back of the school, however this study was undertaken in a swim tunnel where fish swam at a specific velocity. Individuals may be constrained in their swimming positions by their aerobic scope and swimming capacity while digesting, however testing this in free swimming schools may produce different results (Killen et al., 2012b; Ward et al., 2018), where individuals may be able to maintain their positions and roles within groups despite meal size. Locomotor performance is also linked to spatial position in group, which is a popular measure of leadership, where individuals with higher maximum metabolic rates are suggested to occupy front positions (Killen et al., 2012b).

Additionally, when animals move in their environment, they tend to travel at speeds which are energetically efficient, and leaders may dictate these speeds (Alexander, 2005). Voluntary travel speeds are relatively slow and differences in metabolic phenotype or locomotor performance are unlikely to prevent individuals from maintaining pace with the rest of the group (Ward et al., 2018). Collective movement models predict that variation in locomotor speed means faster animals may adopt front positions (Romey, 1996; Couzin et al., 2002; Herbert-Read et al., 2011; MacGregor et al., 2020). Indeed, there may be animals which are unable to occupy specific spatial positions physically, but group mates may adjust their behaviour to maintain leadership hierarchy. Animal systems with a stable social structure have shown that leaders may be physiologically distinct from their conspecifics, for example the oldest female bison (Ramos et al., 2015) may dictate group movement, or males more likely to copy females in sheep (Gautrais et al., 2007; Michelena et al., 2008). Exploring whether leadership is defined by physiology in more dynamic systems has only been studied a few times. In pigeons, leaders were found to be the older individuals in the group, but this also correlated to the individuals who were the most experienced so hard to disentangle physiology from social effects (Nagy et al., 2010, 2013; Flack et al., 2012). Exploring how leaders may be identified by trackable traits is key to identifying how groups move and how individuals respond to others.

Leadership and followership may interact with environmental factors as physiology changes to cope with environmental stressors. It is known that abiotic environmental factors change behaviour as well as metabolic traits (Killen et al., 2013; Mathot et al., 2015; Cooper et al., 2018) and this must be considered when measuring leadership behaviour. Social environment must be considered as another potential environmental stressor, individuals will act differently when alone, or depending on group size (Jolles et al., 2020a). Rather than fulfil a basic need, i.e eating food after a period of starvation, individuals may elect to maintain social contact than increase short term fitness. Additionally, individuals will compromise physiologically optimum conditions to stay with conspecifics, for example fish will choose to experience higher temperatures than their optimums to stay with their group (Cooper et al., 2018). This may then affect leadership in groups, and understanding how leadership changes under different environmental conditions must be considered.

1.1.8 The Use of Fish in Leadership and Collective Behaviour Studies

In particular, fish are regularly used when exploring heterogeneity within groups (Katz et al., 2011; Jolles et al., 2017, 2020a; Bailey et al., 2022). Additionally, fish are ectotherms, where their external environment affects their internal physiology, which includes their metabolic capacity for activities such as exploration, digestion and swimming capacity. These environmental stressors can be something species may face seasonally, in day to day environmental fluctuations, or in extreme conditions. Environmental stresses will reduce availability in metabolic scope for baseline activities thus causing change in behaviour. These changes in behaviour will be reflected in individuals, but when exploring the intersection with social behaviour, this may change how individuals and groups react. By understanding how this social behaviour changes, and in more detail, leadership, I will be able to predict how groups move in response to the other individuals in the group and the surrounding environment.

The general aim of this thesis is to explore leadership and collective behaviour in different contexts. Within this thesis, different "contexts" in which social dynamics will be tested can be classed as ecological, environmental or physiological, or a mix of these. Ecological contexts include influences such as food availability, group composition and habitat changes. Larger meals or presence of food has been shown to reduce physiological capability for movements, which in turn may decrease leadership ability in individuals. Environmental contexts comprise temperature changes and group size and individual contexts focus on individual physiological measures through metabolic phenotypes. Physiological environmental stressors such as changes in temperature may prevent leadership behaviour being expressed, and affect overall group behaviour. Each project is designed in an attempt to address at least one of these ecological, environmental or individual contexts.

1.4 Aims

Chapter 2: Extracting Behavioural Metrics from Equations

Here, I present the equations used to mathematically describe how the leadership and group metrics used for the rest of this thesis are calculated. These form the methods for the rest of the thesis and are referred to throughout.

Chapter 3: The effect of temperature and group composition of metabolic phenotypes on leadership and collective behaviours in fish

In this laboratory based experiment, I investigated how different compositions of metabolic traits change group behaviour in an open field arena, and how this changed with acute temperature exposure. European minnows (*Phoxinus phoxinus*) were profiled for their SMR, AS and MMR, and sorted into groups of

high, medium or low SMR, or mixed SMR (equal mix of phenotypes). The groups were then placed in an arena to analyse voluntary swimming behaviour at 15 °C and exposed to 18 °C, and their behaviour recorded again. This allowed me to determine the relationship between individual leadership and metabolic phenotype, how leadership in groups may change with temperature, and how group behaviour differs with group composition and temperature change.

Chapter 4: Effects of Feeding and digestion on leadership and collective behaviour in schooling fish.

This experiment investigated how leadership and group behaviour changed during and after a feeding event in qingbo (*Spinibarbus sinensis*). Individuals were able to feed naturally as food items appeared randomly in the arena and this was linked to leadership and group behaviour. Oxygen consumption was measured during feeding in separate fish to investigate if estimated remaining AS after digestion is related to leadership and group behaviour. Data was compared to that of groups that did not experience a feeding event.

Chapter 5: Increased cost of transport as a hidden energetic cost of sociality in moving animal groups

In this study, individual optimum swimming speeds of zebrafish (*Danio rerio*) were compared to voluntary swimming speeds while swimming in groups, pairs and alone. This allowed us to calculate cost of transport in each trial and ascertain if there were unpredicted energetic costs of moving in groups and compromising to maintain social groups than alone. This was then related to individual leadership and group behaviour metrics to see if energetic compromises were taken by individuals with specific leadership roles.

2 Development of Code-Based Functions for Extracting High-Resolution Behavioural Metrics From Coordinates

2.1 Introduction

The increased popularity of automated tracking in behavioural studies and experimental biology has revealed the need for open-source software packages that process positions in orthogonal coordinate systems into individual and group behavioural metrics. A variety of programmes compute the locations of individuals on a frame-by-frame basis, and there are benefits and criticisms of each which need to be considered when conducting a behavioural experiment and analysing the resulting data. These packages also only provide the user with a series of x-y coordinates, which must then be processed to obtain usable measures such as individual speed, directionality, or group-level polarity and cohesion. Some software packages (e.g. Ethovision XT) are able to extract movement metrics directly from videos, but are a black box when outputting behavioural data and may be less suitable for wide usage as are they not open source. There is also difficulty when selecting a programme which allows your individuals to cross over spatially and individual identities to be retained. For example, some programmes allow tracking of multiple individuals but they must be in separate experimental arenas (CTrax; Branson et al., 2009). Other programmes may be more sensitive in terms of the algorithm they use to identify individuals and may fail when backgrounds change slightly, which is especially important to consider when measuring aquatic animals. As well as computational power and suitability, it is necessary to select a tracking programme which is user-friendly and time efficient. Unlike other programmes which are under development, idTracker (2014) has a graphical user interface which allows users to set the parameters for the algorithm to identify individuals. Users can view parameter suitability throughout videos without running the tracking process, which can be time intensive depending on the number of individuals, quality of video and ease of identification. Although generating tracks from videos in idTracker may be time intensive, knowing the correct results are being obtained before starting this process is extremely beneficial, as most other programmes do not have this pre-screening feature (review by Sridhar et al., 2019). Another

benefit to idTracker is that it has a sister programme, idPlayer, which allows users to edit individual locations to correct tracks if the algorithm has mislabelled identities after they have spatially crossed over in the video.

IdTracker provides files with cartesian coordinates for each individual over the video, which then can be used in metric calculation. Using these coordinates, specific types of behaviour can be quantified using mathematical equations to infer social interactions, activity of individuals and group metrics (Couzin et al., 2002; Nagy et al., 2010; Jolles et al., 2017). Here, I describe the calculations I developed and definitions of the metrics I used throughout this thesis, which can be applied to any individual track measured in two dimensions.

2.2 Methods

To investigate collective and individual behaviour, individuals and groups were placed in behavioural arenas and recorded using video cameras with a frame rate of minimum 24 frames per second (fps). Video cameras were positioned directly above arenas to be as close to individuals as possible while still recording the whole arena. Cameras were positioned using tripods or secure structuring (Unistrut or pvc pipes) and did not cast any shadow on the arena. Typically, this was at least 80 cm from the water's surface. Behavioural arenas were illuminated from the top and sides to prevent any shadows, and lighting was arranged to prevent reflection on the water surface. Lights were positioned inside a large tent covered with opaque material to prevent any external disturbance. Arenas had altered features, for example feeding tubes, depending on the research question and were different sizes depending on species used in each investigation.

Videos were collected of each behavioural trial and individual positions in each frame were estimated using idTracker (Pérez-Escudero et al., 2014). After individual tracks were processed, positions were manually inspected for errors and corrected if necessary using idPlayer. If individuals swam extremely close to each other or crossed over each other multiple times in a short time frame, the location for both individuals was unable to be identified by the tracking

software, resulting in missing data. Individual tracks were manually inspected if overall they had more than 15% missing data.

2.2.1 Computation of Behavioural Data

Using the frame-by-frame positions obtained via idTracker, individual and group characteristics were calculated using path geometry and obtained using R v4.0.5 and RStudio v1.4.1103 (R Core Team 2021; RStudio 2022). Equations and descriptions are adapted from Jolles et al. (2018) and Nagy et al (2010). Using ImageJ (Abràmoff et al., 2004), the size of arenas in pixels can be measured from still images from trial videos. From known lengths in cm, I can then calculate a conversion rate as to convert any measurements by pixels to a standard cm scale.

2.2.2 Individual Metrics

The positions of individual *i* at time *t* is indicated by $\boldsymbol{f_i(t)} = (x_i(t), y_i(t))$, where *x* and *y* represent cartesian coordinates in a field of view; Velocities are used in calculations and obtained using positions over time, $\boldsymbol{v_i}(t) = (\boldsymbol{vx_i(t)}, \boldsymbol{vy_i(t)})$. $\Delta t = 1/fps$ is the time interval between position measurements and calculated from the frames per second of recording. Individual distance travelled is calculated by:

$$\boldsymbol{d}_i(t) = \sqrt{(x_i(t) - x_i(t + \Delta t))^2 + (y_i(t) - y_i(t + \Delta t))^2}$$

Individual distance is measured in pixels and is converted to cm or BL in relation to the focal individual. Total individual speed is calculated across whole trials.

Individual velocity at time t is calculated from the forward finite difference:

$$\boldsymbol{v_i(t)} = \frac{\boldsymbol{f_i}(t + \Delta t) - \boldsymbol{f_i}(t)}{\Delta t}$$

Individual speed at time t $\boldsymbol{v_i}(t)$ is calculated from the absolute values of the velocity vector:

$$\boldsymbol{v_i}(\boldsymbol{t}) = |\boldsymbol{v_i}(\boldsymbol{t})| = \sqrt{vx_i^2(t) + vy_i^2(t)}$$

Individual speed is measured in pixels/frame and is converted to cm/s or BL/s in relation to the focal individual. Mean individual speed is calculated across whole trials.

We calculate the acceleration of an individual at time t, where $\boldsymbol{f_i}$ represents individual fish:

$$a_i(t) = \frac{f_i(t + \Delta t) - 2f_i(t) + f_i(t - \Delta t))}{\Delta t^2}$$

The heading at time t is calculated using the angle between the velocity vector and positive y axis given by

$$\psi_i(t) = atan2(vy_i(t), vx_i(t))$$

From heading data at time t, I can calculate turning speed for each individual using change of angle calculated through direction of movement.

$$\gamma_i(t) = \frac{\psi_i(t + \Delta t) - \psi_i(t)}{\Delta t}$$

Angular difference from heading was converted from Cartesian coordinate system with individuals at origin, to radians. The correct angular difference with regard to the periodicity of $\gamma_i(t)$ was calculated, where anti-clockwise from 0 to 180 and clockwise from 0 to 180:

$$\{\gamma_i(t) < -\pi\}: \gamma_i = 2\pi - |\gamma_i(t)| \; or \; \{\gamma_i(t) > \pi\}: -(2\pi - \gamma_i(t))$$

Nearest neighbour distances were calculated from a matrix of distances for all individuals at time *t* and determining the minimum value for each individuals:

$$NND_i(t) = j \in \underset{N}{min}{}_{j \neq i} \left(\sqrt{(x_i(t) - x_j(t))^2 + (y_i(t) - y_j(t))^2} \right)$$

Where N is the set of all individuals. Nearest neighbour distance is measured in pixels and can be converted cm or BL in relation to the focal individual. Mean Neighbour Distance is the mean distance of all individuals across the trial and is measured in pixels and can be converted cm or BL in relation to the focal individual. This is a measure of how close one individual is to the rest of the group over the course of the trial.

2.2.3 Group metrics

Group metrics can be calculated and compared to identify differences between groups and within groups. For each time step the mean coordinates of all individuals were calculated $f_c(t) = (x_c(t), y_c(t))$, where x_c and y_c are the average of the *x* and *y* positions of individuals in groups. These are used to obtain the x-y position for the group centroid f_c which can then be used to calculate group vectors, speed, distance travelled, acceleration and heading at time *t* as in individual metrics, as follows:

Vector of centroid $\boldsymbol{f_c(t)} = (x_c(t), y_c(t))$ denoting position of centroid *c* at time *t*, I approximated the centroid velocity at time t by calculating the forward finite difference:

$$\boldsymbol{v_c(t)} = \frac{f_c(t + \Delta t) - f_c(t)}{\Delta t}$$

Centroid speed at time *t* $v_c(t)$ is calculated from the absolute values of the velocity vector:

$$\boldsymbol{v_c(t)} = |\boldsymbol{v_c(t)}| = \sqrt{vx_c^2(t) + vy_c^2(t)}$$

I calculate the acceleration of the centroid at time t:

$$a_i(t) = \frac{f_i(t + \Delta t) - 2f_i(t) + f_i(t - \Delta t))}{\Delta t^2}$$

Centroid heading at time t is calculated using the angle between the velocity vector and positive y axis given by:

$$\psi_c(t) = atan2(vy_c(t), vx_c(t))$$

Distance from centroid was calculated for all individuals. For each timestep t, the distance from each individual i's location to the centroid can be determined as:

$$DistanceCenter_i(t) = \sqrt{(x_i(t) - x_c(t))^2 + (y_i(t) - y_c(t))^2}$$

Distance from centroid is measured in pixels and can be converted to cm or BL in relation to the focal individual.

To calculate position in group, coordinates of individual positions are required to be transformed dependent on centroid position and heading of group. The coordinate system is first transformed so that the origin is at the group centroid at time t, and the angle between the positive y axis through the centroid and an individual's position is calculated:

$$\delta_i(t) = atan2(x_i(t) - x_c(t),\ y_i(t) - y_c(t))$$

This is then used to calculate the individual's relative direction to the group centroid which is then adapted to fit the Cartesian coordinate system pointing north:

$$\sigma_i(t) = \delta_i(t) - \psi_c(t)$$

$$\{\sigma_i(t) < -\pi\}: \sigma_i = 2\pi - |\sigma_i(t)|\ or\ \{\sigma_i(t) > \pi\}: -(2\pi - \sigma_i(t))$$

From the coordinate transformation, relative position can be calculated for each individuals to the group centre:

$$(x_i', y_i') = DistanceCenter_i(t)(sin(\sigma_i(t)),\ cos(\sigma_i(t)))$$

The transformation means that individuals with greater y coordinates are considered at the front of the group relative to direction of travel at a given time step t. From these values I can calculate proportion of time each individual spends in a position, and look at variation and shuffling of these positions. Position in school is measured from 1 to the maximum number of individuals, where 1 indicates front positions and higher numbers are in the rear. Mean Position in school is a mean position per individual across the whole trial.

Mean interindividual distance can be calculated as a measure of group cohesion, based on the IID_{ij} between all individuals (n) in a group between all fish (n) in the group

$$IID_c(t) = \frac{1}{n(n-1)} \sum_{j=1}^{n} \sum_{\substack{j=1 \\ j \neq i}}^{n} I\,ID_{ij}$$

where

$$IID_{ij}(t) = \sqrt{(x_i(t) - x_j(t))^2 + (y_i(t) - y_j(t))^2}$$

Mean interindividual distance is measured in pixels and is converted to cm.

Alignment of each individual relative to others in the group at each timepoint *t* was calculated and defined as polarisation.

$$\rho(t) = \frac{1}{n} \sqrt{\left(\sum_{i=1}^{n} s\,in(\psi_i(t))\right)^2 + \left(\sum_{i=1}^{n} c\,os(\psi_i(t))\right)^2}$$

Polarity is measured across the group with values ranging from 0 (non-alignment) to 1 (complete polarity).

Swimming vs schooling is the proportion of time (%) spent schooling, defined as when a group is cohesive (within 4 body lengths of a neighbour) and moves with considerable speed and alignment versus shoaling, which is when a group is cohesive but has minimal speed or polarity.

2.2.4 Propagation of Movement

Leadership was measured by quantifying the propagation of movement changes in a group by examining the temporal correlations in acceleration and turning (as listed above) for all pair combinations within groups (Nagy et al., 2010; Katz et al., 2011; Jolles et al., 2017). Speed and direction of two individuals in a dyad were compared up to 150 frames (5 s) before and after a change in movement, in time steps according to the frame rate of the recording. Leading events were identified when an individual's change in motion had the maximum correlation to another individual within 5 s after that time point. The mean time point of events in comparison to other group members was calculated, and will identify whether individuals are leaders (react first) or followers (react after). Leadership networks are able to be constructed from these time delays between all individuals in group following (Nagy et al., 2013). Analysis was restricted to frames where individuals were traveling above 0.25 body lengths per second and within 4 body lengths from other individuals to ensure followers are moving due to interaction rules with the group (Lukeman et al., 2010; Herbert-Read et al., 2011)

Propagation of movement is measured in terms of mean lag after a leadership event (while turning or accelerating) and is measured in frames, where smaller numbers (negative) indicate earlier recorded movement, and therefore leadership. Higher numbers (closer to 0) mean later movement and indicate followership.

Leadership stability quantifies whether leading is performed by the same individual during every change in speed or directionality (0 – disorder, 1 – same individual each event) and leadership consistency quantifies whether leadership is happening at a constant rate through the trial or never, whether or not it is the same individual leading (0 – leadership never occurs, 1 – throughout constantly throughout the trial).

2.3 Discussion

The described equations were coded into R for use and summarised below by individual or group level metric, and the relevant units. I describe metrics which can be calculated from 2 dimensional positions of individuals alone or in a group, in any organism. Tracks can be calculated using any suitable tracking programme and metrics are able to be generated. Previous studies have used such equations in calculating group behaviour of fish (Jolles et al., 2017), birds (Nagy et al., 2010, 2013) or insects (Bazazi et al., 2008). Individual metrics are regular measures of activity in studies outside the collective behaviour discipline (MacGregor & Ioannou, 2021).

Available open source tracking programmes have grown in number over the last 5-10 years as accessibility to programming and resources to build software have increased (review by Sridhar et al., 2019). While this surge in software ability has potential to revolutionise the analysis of behavioural data, a major hurdle to wide-spread usage of these programs is that the data provided by must be transformed into useful metrics. This is not a straightforward endeavour, and there are currently no accompanying open-source tools or R packages available for translating tracked coordinates into behavioural metrics. This is a key reason why black box programmes such as Ethovision XT are so popular, but even these programs require extra user processing to obtain the nuanced leadership metrics and among-individual correlation data I present in this thesis. By creating an open source tool, utilising R freeware which is used globally by data analysts in all fields, I aim to aid projects in behavioural data analysis. However, the code I developed independently could be used by others to facilitate data processing for any software package which exports two-dimensional coordinates.

Table 2.3-1: Table displaying behavioural metrics and units discussed in this thesis.

Individual Metric	Group Metric	Units/Bounding
Mean Individual Speed	Mean Group Speed	px/frame
Total distance travelled	Mean Total Distance Travelled	pixels
Individual Acceleration	Centroid Acceleration	px/second
Individual heading	Group Polarisation	0 (unorganised) – 1 (polarised)
Turning speed	Centroid Direction	-360 – 360°
Mean Lag after Leading Event while Turning		-4 (leading) – 0 (following)
Mean Lag after Leading Event while Accelerating		-4 (leading) – 0 (following)
Average Position in School		1 (front) – number in group (back)
	Leadership Consistency	0 (disorder) – 1 (same individual each event)
	Leadership Stability	0 (leadership never occurs) - 1 (leadership occurs constantly throughout the trial)
Distance from centroid	Area of group	px^2
Interindividual Distance	Average Neighbour Distance	px
	Swimming vs Schooling	% trial 0 (schooling) - 100 (swimming)
Nearest Neighbour Distance		px

3 The effect of temperature and group composition of metabolic phenotypes on leadership and collective behaviours in fish

3.1 Abstract

Group living is ubiquitous among animal taxa and comes with costs and benefits associated with predator avoidance, foraging and reproduction. Collective behaviour is an emergent property of behavioural phenotypes and interactions between groupmates, and differences in traits associated with energy requirements and metabolism may affect emergent group behaviours. Overriding effects of the environment, including differences in temperature, may also modulate the effects of metabolism on group behaviours, especially in ectotherms. Using common minnows (*Phoxinus phoxinus*), the standard metabolic rate (SMR) of individual fish were measured at 15 °C and the shoaling behaviour of free-swimming groups was examined at two temperatures (15 and 18 °C) in an open field (9 fish per group) using groups comprised entirely of fish with either a high SMR (randomly selected from the top 25% of SMR for all fish measured), medium SMR, or low SMR (bottom 25%). A fourth treatment consisted of heterogenous groups with three high, medium, and low SMR fish per group. There were no consistent effects of metabolic composition on leadership or group behaviour. At the higher temperature, groups were less cohesive, in terms of among-individual distances, but were more polarised and moved at a higher speed. While leadership was not related to spatial position within schools for any group composition or temperature, changes in group turning or acceleration was less consistently initiated by specific individuals at 18 °C. These results provide insight into the mechanistic underpinnings of group functioning, and in a wider perspective, how changing environmental temperatures may affect the functioning of fish social groups.

3.2 Introduction

It is increasingly recognised that social groups contain a large degree of among-individual phenotypic heterogeneity and that leadership within groups may be linked to individual behavioural phenotypes (Jolles et al., 2020a). Collective movement requires group members to combine their individual perceptions of the environment and reach a consensus about the speed and direction of travel while remaining some level of cohesiveness (Conradt & Roper, 2005). While collective group decisions can be initiated by an individual, these are only successful if followed by groupmates, either voluntarily or through exerted dominance (Conradt & Roper, 2010). Frontal positions in moving groups are often thought to be occupied by individuals who have more information about the surrounding environment, a greater need for resources, or a higher motivation to locate preferable environments (Couzin et al., 2005; Ioannou et al., 2015). Accordingly, leadership may be a selfish strategy employed to influence collective behaviour in the leader's favour (King et al., 2008). Depending on numerous factors, including within-individual, within-group, and environmental variation, leadership roles within groups be may stable or fluctuate among individuals (Asher & Collins, 2012). If group members fail to reach a consensus in movement or habitat selection, the group may split and the benefits of group living such as protection from predation, increased reproductive opportunities and access to resources may be reduced (Krause & Ruxton, 2002; Conradt & Roper, 2007).

Group splitting could result in among-group phenotypic assortment, particularly for phenotypic traits related to resource demand, locomotion, or habitat preference. For example, the minimum metabolic rate needed to sustain life (standard metabolic rate (SMR) in ectotherms; basal metabolic rate in endotherms) is often correlated with traits known to play a role in leadership within groups, and potentially among-group assortment, including boldness (Metcalfe et al., 2016) and sociality (Cooper et al., 2018), possibly because individuals with a higher SMR have an increased foraging motivation (Killen et al., 2016). Aerobic scope (AS) is defined as the difference between the maximum metabolic rate (MMR) and SMR, where MMR is the maximum amount of

oxygen consumed in aerobic respiration (Norin & Clark, 2016). Furthermore, an animal's aerobic scope is influenced by their SMR, and depending on context, aerobic scope may be related to the spatial position of individuals within moving groups (Killen et al., 2012b; McLean et al., 2018), due to effects on locomotor capacity or feeding motivation. Initially heterogenous groups, which have a mix of individuals with variable metabolic requirements, may fail to reach a consensus leading to group fission and assortment based on individual SMR to reduce conflicting priorities among group members (Seebacher & Krause, 2017). However, any changes in group-level metabolic composition could affect overall group behaviour and functioning. A group composed of all high SMR individuals, for example, may be less cohesive (Killen et al., 2017) if they are all motivated to forage and therefore put less priority on the anti-predation benefits of grouping. Conversely, lower SMR groups may show less goal-orientated behaviour and therefore be more cohesive and coordinated (Careau et al., 2008; Hansen et al., 2020). The analysis of individual physiology when analysing collective behaviour has been understudied, and it is still unknown if individuals naturally group by similar metabolic phenotypes and how these groups may differ in behaviour according to their composition (review by Jolles, King, et al., 2020). As spatial and temporal environmental heterogeneity becomes more common, among group phenotypic assortment may become more likely. The effects of metabolic composition of groups are critical to understanding how groups may move and change their behaviour in variable conditions.

Considering that environmental temperature has direct effects on animal physiology and behaviour, especially for ectotherms, it is surprising how little is known about the influence of temperature on group behaviour. This is a critical knowledge gap given the effects of global climate change on the magnitude and variation in temperatures experienced by social animals. Animals in aquatic environments experience especially pronounced spatial and temporal variation in temperature, with potential effects on a range of processes related to social behaviour including metabolic demand, aerobic scope, aggression, cognition, and locomotor ability (review on performance curves by Killen, Cortese, et al., 2021). As animals encounter acute changes in their environment, an increase in temperature will in general increase metabolic rate and likely movement speed for ectotherms (Bartolini et al., 2015), potentially reducing group cohesion and

coordination as individuals experience increased foraging motivation. The exact effects of temperature change on group behaviour may differ depending on the metabolic composition of the group, particularly because thermal preference can be related to metabolic rate at the individual level (Cooper et al., 2018). More heterogenous groups may therefore show a disproportionately strong reduction cohesion with an increase in temperature, while more homogeneous groups may be better able to maintain cohesion and coordination in the face of an elevation in temperature. Increased knowledge of the effects of temperature on group functioning is important for gaining a fuller understanding of how this crucially important but highly variable environmental factor affects processes such as group foraging and predator avoidance.

Using the common minnow (*Phoxinus phoxinus),* I examined the effect of an acute temperature increase on group movement, and the role of individual metabolic rates and group metabolic composition in collective behaviour. In many ectothermic species metabolic rates are sensitive to shifts in temperature and individual behaviour has been shown to change (Bartolini et al., 2015; McMeans et al., 2020; Morissette et al., 2021). Exploring group behavioural changes in an experimental arena can provide insight into how fish schools respond to seasonal changes and extreme weather events. Minnows are a social species that commonly inhabit areas with high spatiotemporal variation in temperature. At the group level, I examined the effects of group composition on group behaviour by assembling groups of individuals with either relatively high metabolic rates, low metabolic rates, intermediate metabolic rates, or heterogenous groups with equal proportions of each type of individuals. Within groups, leadership was quantified as initiation of changes in the directionality (turning) and speed of movement (acceleration), and via proximity to the front of the group while moving. Specifically, I aimed to address the following questions: 1) How is leadership within groups related to individual metabolic demand, and does this vary with group metabolic composition; 2) How is group movement and cohesion affected by metabolic composition of the group; and 3) how does temperature influence the behaviour of groups with different metabolic compositions and the role of leadership within groups. We hypothesized that schools with high metabolic rates would show a weaker leader-follower dynamic, and when exposed to higher temperatures, groups

would become less cohesive and coordinated, and leadership may decrease in strength.

3.3 Materials and Methods

3.3.1 Experimental Animals

Juvenile common minnows (*Phoxinus phoxinus*) were collected from the River Kelvin, Glasgow, United Kingdom using dip nets. Fish were acclimated in aerated stock tanks (100 x 40 x 30 cm) for 6 months prior to experiments. Throughout the whole experimental process, tanks were supplied with re-circulating, UV treated freshwater on a 12L:12D photoperiod. The water temperature was initially kept between 13 and 14 °C which gradually increased to 14 and 15 °C during the summer months. Fish were fed once a day with bloodworm and commercial fish flakes.

3.3.2 Measurement of Metabolic Traits

After acclimation, a total of 180 fish were subjected to intermittent flow respirometry after a 24 h fasting period to provide estimates of metabolic phenotype (SMR, MMR, AS, for details see Table 8.1-23) (Svendsen et al., 2016; Killen et al., 2021a). Per day, 16 fish were haphazardly caught from holding tanks using dip nets and profiled. Estimates of maximum metabolic rate (MMR) were achieved by manually chasing individual fish in 10 cm water to exhaustion in a circular tank (40 cm diameter). Fish were manually chased to exhaustion for 2 min (Chrétien et al., 2021), exhaustion was determined by the point where fish were no longer receptive to chase stimulus. The manual chase method is assumed to induce maximum oxygen uptake rate as fish recover from anaerobic exercise. Once exhausted, fish were immediately transferred to individual cylindrical glass respirometry chambers (75 mL volume) attached to an intermittent flow respirometry system, containing the glass cylinder and gas impermeable tubing through which water is recirculated using a peristaltic pump. 16 respirometry chambers containing 16 individual fish were submerged in an air saturated, temperature-regulated water bath (15 ± 0.1 °C; 50 L) and shielded from disturbance and light with an opaque plastic cover. Oxygen content of water in the respirometry chambers was recorded every two seconds

using a 4-channel fibre optic oxygen meter with associated oxygen sensors and software (FireStingO2; PyroScience GmBH, Aachen, Germany). Probes were calibrated at the start of the experiment and 100% oxygen saturation was calibrated before every new fish was put in the chamber. Every 8 minutes, an automated flush pump was programmed to flush tubing and chambers for 5 min and fully aerated water would enter the chamber and would return to normoxia. After, the pump would switch off, sealing the respirometry chambers to allow decreases of oxygen due to fish respiration to be measured. Estimates of MMR were obtained by calculating the rates of oxygen uptake for each 8 min interval, disregarding the first and last 30 seconds of the measurement, throughout the first 30 min of recovery immediately following chase protocol; MMR (mg O_2 h^{-1}) was taken as the highest rate of aerobic metabolism during recovery. After MMR measurement, fish remained in their respirometry chambers overnight to allow for measurement of SMR and removed after approximately 20 hrs. Whole animal SMR (mg O_2 h^{-1}) was estimated as the lowest 10^{th} percentile of measurements taken after MMR and the subsequent recovery (Chabot et al., 2016). Absolute aerobic scope (AS) was calculated as the difference between MMR and SMR. Background respiration was measured by measuring oxygen declines in empty chambers for 3 cycles before and after fish were present, and was assumed to be a linear change. Before measuring MMR in the next trial of 16 fish, the system was bleached and rinsed to prevent bacterial build up and water in the trials was continuously exposed to UV lamp.

After respirometry, fish were removed from the chambers, sedated with benzocaine solution (0.1 g L^{-1}) and each individual was measured for length, mass and tagged with a unique Visible Implant Elastomer (VIE) tag combination to allow for identification (Northwest Marine Technology Inc., Shaw Island, USA).

SMR values were adjusted to account for variation in body mass (Cutts et al., 2002; Auer et al., 2015). SMR_{adj} was calculated by adding residuals from the predicted relationship between log-transformed SMR and individual mass to the metabolic rate predicted for a fish with the mean body mass of all fish in the study. Based on adjusted SMR, fish were assigned metabolic phenotypes; high (highest 40 fish) , medium (100 fish) or ; low (lowest 40 fish). Fish were split in

ratios of their adjusted SMR (1 high:2 medium:1 low) between 4 holding tanks (100 x 40 x 30 cm) tanks where they were held throughout the experiment.

3.3.3 Open Field Trial

An open field experimental design using a circular basin with a central column to facilitate swimming (110 x 30cm) was filmed using a Canon EOC 6D camera. Four different group compositions (Table 2) of 9 fish per trial were tested during the experiment. Fish from each SMR bracket were randomly selected from one holding tank at a time for each group to have the same level of familiarity, and were left to acclimate after transfer to the arena for 30 minutes at 15 °C before recording behaviour for 20 minutes. After 15 °C trials were completed, the water temperature of the trial arena was raised to 18 °C over 30 minutes and fish were recorded for a further 20 minutes to look at the effect of acute exposure to higher temperatures on schooling behaviour.

Table 3.3-1: Final numbers of trials with each metabolic composition used in schooling behaviour trials.

	High SMR	Intermediate SMR	Low SMR	Mixed SMR	Total Trials
15 °C	4	4	5	5	18
18 °C	4	4	5	5	18
Total Trials	8	8	10	10	36 trials

3.3.4 Video Analysis

Videos were processed using idTracker (Pérez-Escudero et al., 2014). XY coordinates were identified for individual fish using the programme's algorithm and positions were estimated where possible when individuals crossed over vertically when swimming. Tracks were checked via visual inspection and positions corrected if needed. For all automatically tracked trials, missing and interpolated data for each individual was quantified.

For trials where there was a significant amount of crossing over of individuals, or where the reliability of tracks was under 80%, as calculated by idTracker, manual tracking was used on a subset of frames (imageJ). These subsets were excluded from leadership metrics as the subset results were not found to be representative of these measures. Mean lag after a leadership event while turning and accelerating and position of school had a $R < 0.80$ comparing results from subset and automated tracking of same video ($n = 5$; Pearson's Correlation)). Subset results were used when analysing cohesion and speed metrics as these were found to be representative of a full dataset. Subset videos measured 400 frames total whereas automatic tracking tracked approximately 20,000 frames.

From the coordinates of each individual, movement speed, direction, acceleration and turning speed were calculated for each trial using equations from Jolles et al. 2018 (see Chapter 2 for further details). from individual positions and metrics, group metrics such as polarity and cohesion were calculated. Fish groups were defined as shoaling or schooling depending on cohesion and speed travelled (Pitcher & Parrish, 1993; Delcourt & Poncin, 2012). Propagation of speed and turning changes were calculated as a measure of individual leadership and used to calculate leadership consistency, which was defined by the average correlation of movement, which indicates how consistently followers react to any given leader, and describe whether the group is synchronised or not. If the leader was the same individual throughout the trial, this is described as leadership stability (Nagy et al., 2010; Jolles et al., 2018). Leadership was only quantified for individuals within 4 BLs of another fish, as further than that distance would suggest they are unlikely to be directly interacting with each other.

3.3.5 Statistical Analysis

All statistical analyses were performed in R.4.0.5 (R development Core Team). Linear mixed effect models (lme4, lmertest) estimated using REML were fitted to investigate how metabolic composition of groups and individual differences affected leadership and group behaviour. Model selection was performed by

sequentially dropping non-significant terms starting with lowest t-values but were retained if their removal resulted in higher AIC values (ΔAIC > 2; Arnold, 2010). For each specific model structure see supplementary methods, however for each individual metric of leadership or collective behaviour, group, ID and time of trial were included as random effects and individual size (Total Length), SMR and MMR rank within group, temperature and metabolic composition were included as explanatory variables. For each group metric, group was included as a random effect, and temperature and metabolic composition were included as explanatory variables. Homoscedasticity and normality of residuals were assessed by visual inspection of residual plots and used to determine whether transformation of data was necessary. Metrics associated with propagation of movement (Mean Lag after leadership, Leadership consistency and leadership stability for turns and acceleration) were scaled. Total length of individual, individual speed, average neighbour distance, and group polarity were log transformed for inclusion in statistical models.

3.4 Results

3.4.1 Leadership and group movements are not affected by individual metabolic phenotype

In general, fish that lead their groups while turning tended to also be those that lead while accelerating (Figure 3.4-1; Table 8.1-1). In contrast, position within school was generally not associated with either leadership while turning or leadership while accelerating, except for low SMR groups at 18 °C (leadership while accelerating: $r = 0.38$, $t(41) = 2.62$, $p < .05$; leadership while turning: $r = 0.45$, $t(39) = 3.16$, $p < .01$) and mix SMR groups at 15 °C when accelerating ($r = 0.42$, $t(31) = 2.56$, $p < .05$). Followers in low metabolic composition groups were found at the back of the group in 18 °C when leading while turning and accelerating.

Regardless of temperature, none of SMR rank, MMR rank, or body mass were related to leadership while turning or accelerating, or position in school, and were excluded from the final model (Table 8.1-12; Table 8.1-13; Table 8.1-14; Table 8.1-5). Overall followers had a larger mean lag after leading and so

responded faster to leadership at 18 °C when turning or accelerating . Followers in medium and mixed groups responded slower to leaders than in low groups when turning, where medium groups respond the slowest when turning (Figure 3.4-3; Table 8.1-2). Similarly, while accelerating, followers responded slower in medium, high and mixed groups than in low metabolic composition groups however there was no difference between medium, mix and high groups (Figure 3.4-3; Table 8.1-3).

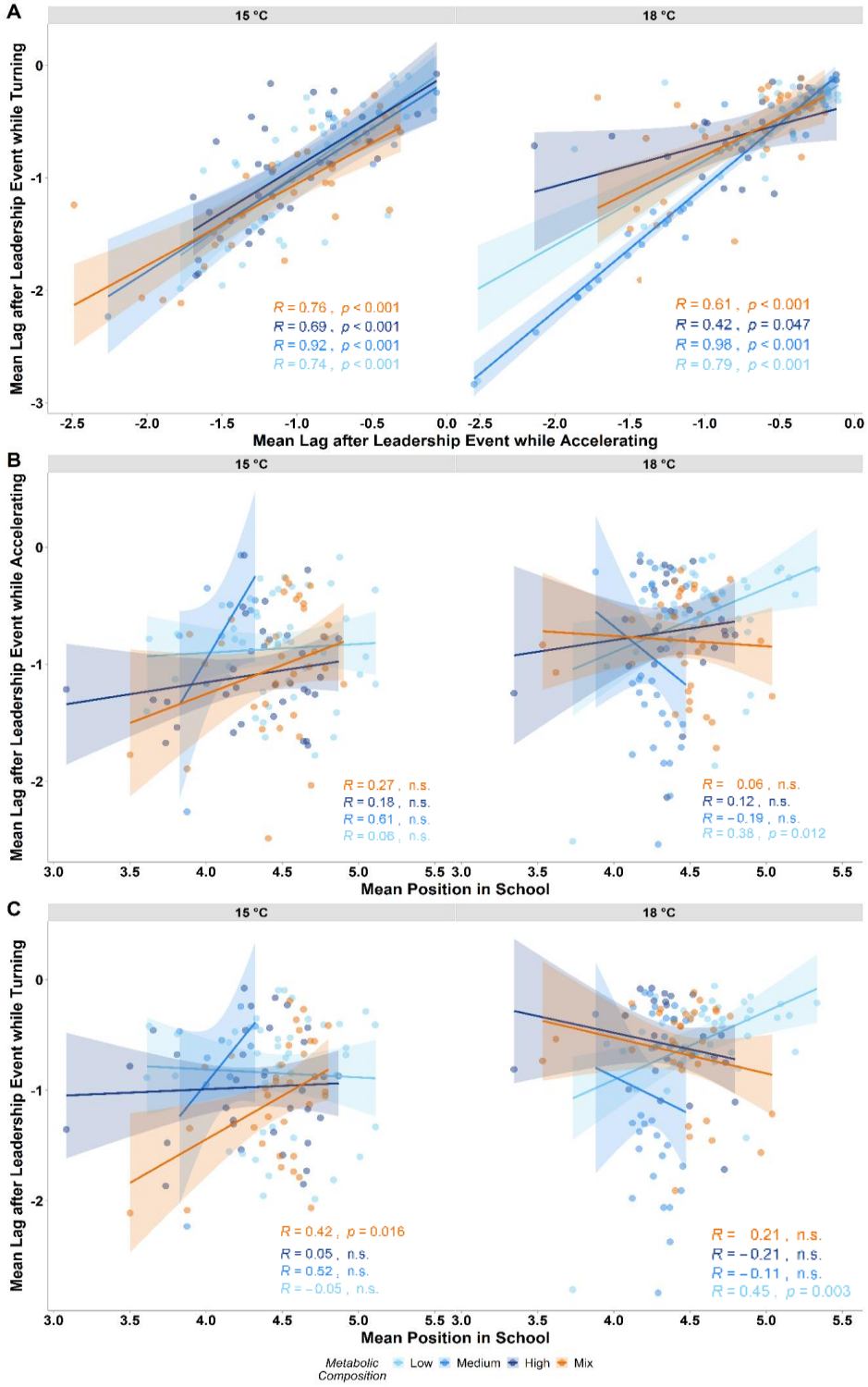

Figure 3.4-1: Comparison of A) Leadership Response while Accelerating and Leadership Response while Turning, B) Mean position in school, where 1 is front of school and 9 is back, and Leadership Response while Accelerating and C) Mean position in school and Leadership while Turning. Points represent individual fish in Low (light blue), Medium (mid blue), High (dark blue), and Mix (orange) metabolic composition. Lines represent linear regression between the behavioural metrics, while the shaded area corresponds to 95% confidence intervals . Both 15 °C and 18 °C temperature treatments are displayed.

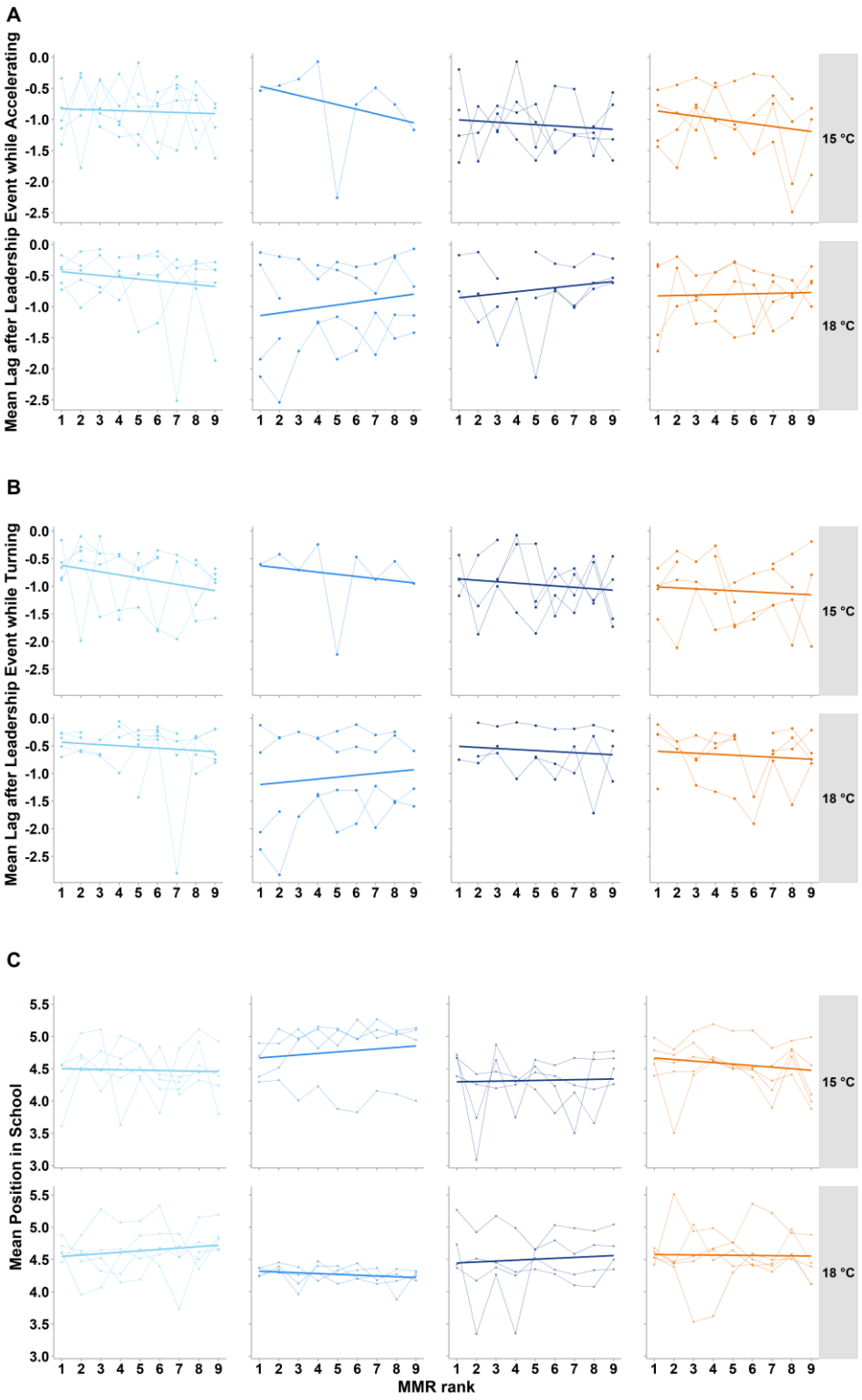

Figure 3.4-2: Relationship between rank of MMR, where 1 is the highest MMR of the group and 9 is the lowest, and mean response to leadership event while accelerating (A), mean lag after leadership event while turning (B), and mean position in school (C). Each line represents a different group within the temperature treatments (15˚C or 18˚C) and group compositions (low: light blue, medium: med blue, high: dark blue and mix: orange) standard metabolic rate represented by the different colours. Thick linear lines represent the linear regression between MMRrank and behavioural metric for each treatment.

3.4.2 Leadership and group movements are affected by the overall phenotypic composition of the group

Leadership while turning is more stable (same individual leading) and consistent (same time interval between followers reacting) at 18 °C compared to 15 °C (Consistency: $t(23) = 4.26$, $p < .001$; Stability: $t(23) = 3.45$, $p < .001$). In leading while accelerating, temperature and metabolic composition did not have an effect on group stability or consistency (Table 8.1-6; Table 8.1-6).

Followers reacted faster to leaders at 18 °C, fish generally swam significantly faster at 18 °C compared to 15 °C for low and mixed metabolic compositions (Low: $t(316) = 11.03$, $p < .001$; Mix: $t(316) = 3.89$, $p < .001$;). In medium metabolic compositions there was a significant decrease in speed at 18 °C ($t(316) = -3.86$, $p < .001$) and there was no difference in high metabolic groups metabolic groups except in comparison to mixed metabolic groups, which swam faster (Table 8.1-7; Table 8.1-8).

Groups were generally more polarised at 18 °C than at 15 °C, but the amount of variation increased at 18 °C. There was an interaction between temperature and metabolic composition, where medium ($t(314) = -10.21$, $p < .001$) and mixed ($t(314) = -2.44$, $p < .05$) groups at 18 °C were less polarised at 15 °C, despite having larger among-group variation. Low and high metabolic groups significantly increased at 18 °C (Table 8.1-7; Table 8.1-10).

In general, groups were less cohesive at 18 °C than at 15 °C. Low and mix groups were the least cohesive at both 15 and 18 °C, followed by high metabolic groups and then medium metabolic groups (Table 8.1-7; Table 8.1-9).

Swimming vs schooling was less varied at among groups at 18 °C, and significantly more time was spent schooling at 18 °C than 15 °C ($t(317) = 17.27$, $p < .001$). There was no difference between metabolic groups for this metric(Table 8.1-7; Table 8.1-11).

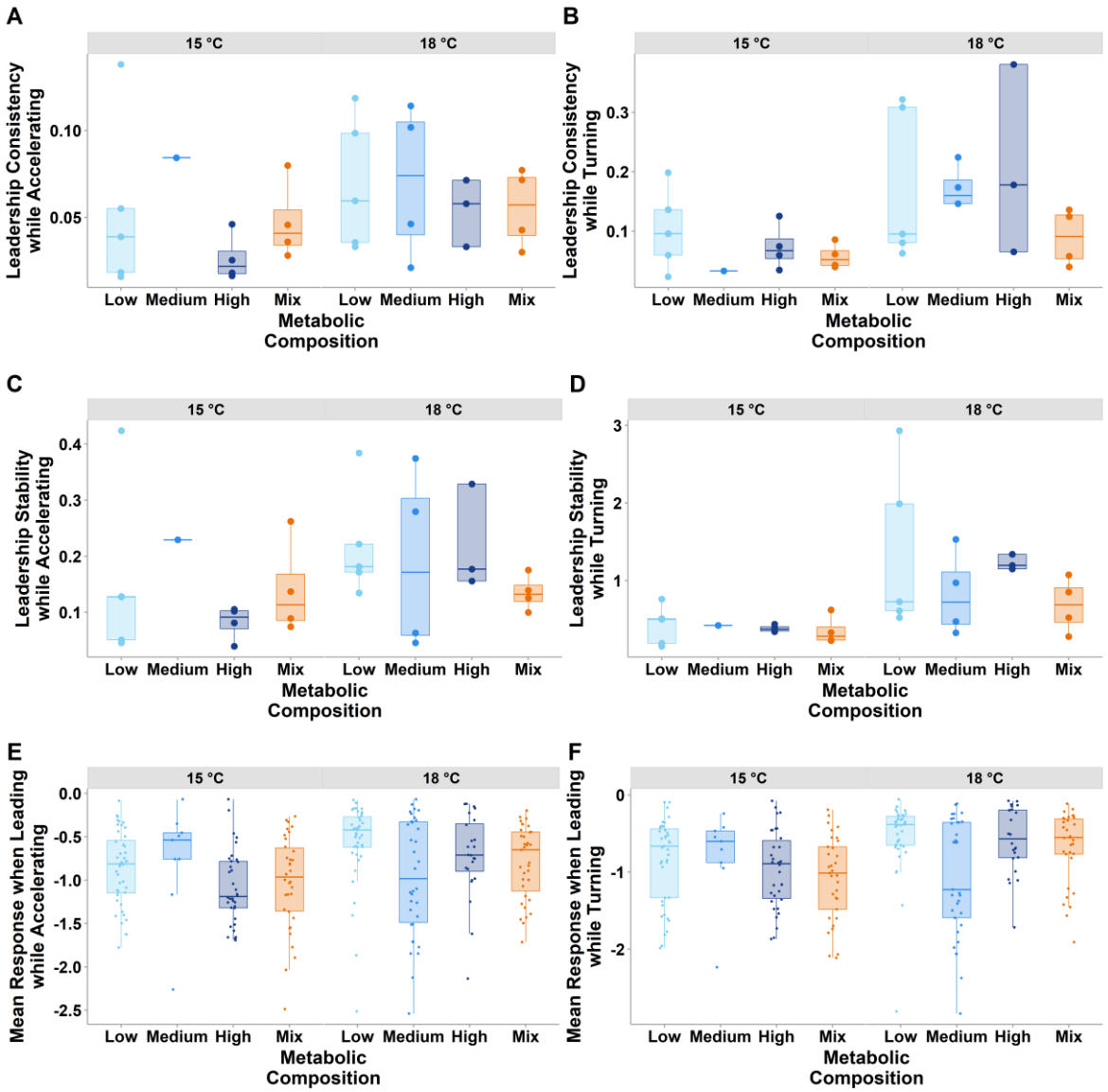

Figure 3.4-3: Boxplots of group leadership metrics for Low, Medium, High and Mix metabolic compositions at 15 °C and 18 °C temperature treatments. Boxplot upper and lower hingers represent the 25th and 75th percentiles respectively and the horizontal line within the box represent the median. Length of the whiskers represents the range of datapoints between each hinge.

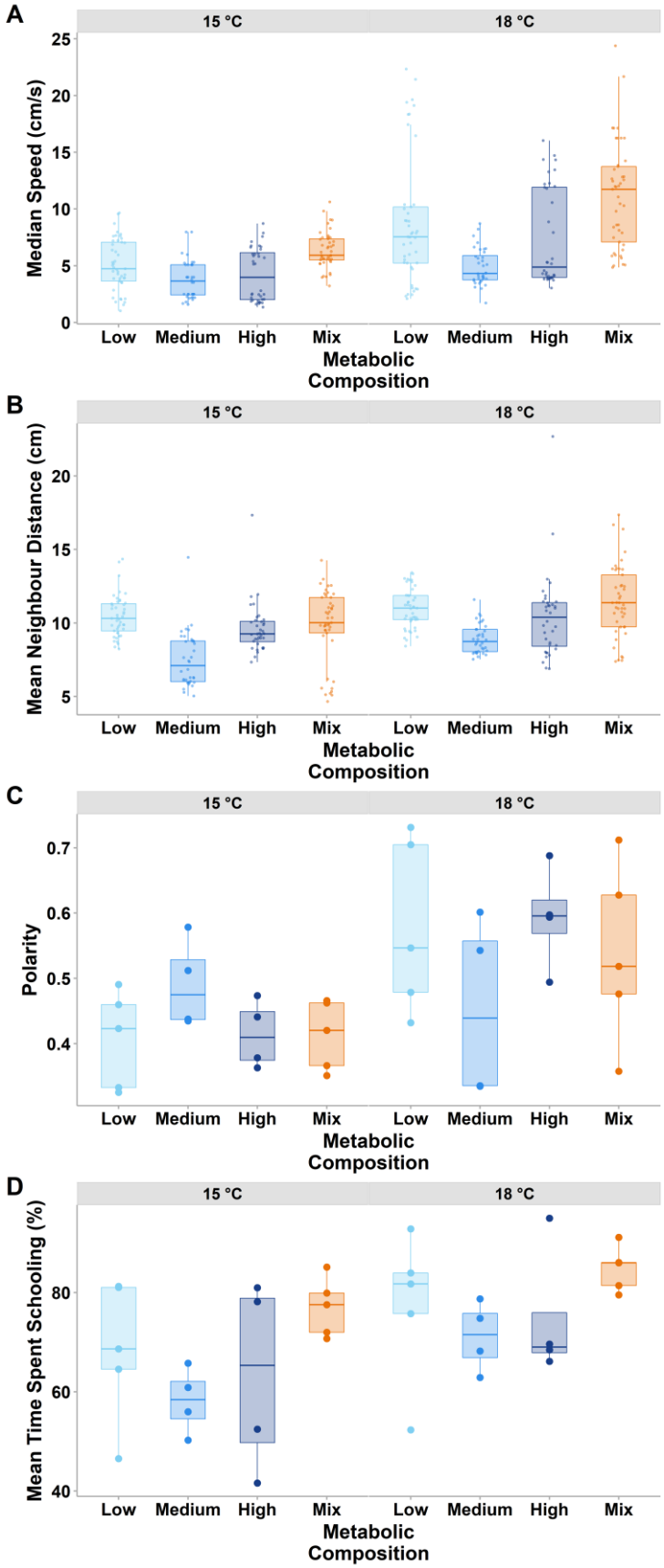

Figure 3.4-4: Boxplots of group behavioural metrics for Low, Medium, High and Mix metabolic compositions at 15 °C and 18 °C temperature treatments. Boxplot upper and box represent the median. Length of the whiskers represents the range of datapoints between each hinge.

3.5 Discussion

There was no consistent effect of metabolic composition of groups on individual behaviour of leaders and followers, but an acute temperature shift caused different metabolic compositions to change their group behaviour to differing extents. For example, depending on the temperature and exact metabolic composition, different groups showed varying degrees of leadership consistency, leadership stability, and group movement speed. Within groups, there was no effect of metabolic rank on metrics of individual behaviour. Interestingly, position within school when moving was not correlated with either leadership when turning or leading when accelerating. However, in low metabolic rate groups, leaders when both turning and accelerating were found at the back of the group, indicating that propagation of movement does not necessarily come from the front of a group, contrasting with previous work (Leblond & Reebs, 2006; Nagy et al., 2010). Overall, these results indicate that while temperature is an important factor affecting both individual and group behaviours, the exact magnitude of these effects may depend on the traits present within social groups and the degree of within group heterogeneity in metabolic rates.

The effects of metabolic composition on group behaviour were complex and dependent on the prevailing ambient temperature. For example, group movement speed only increased with temperature for the low and mixed composition groups. Previous work has shown increased temperature can cause increased swimming speed and decreased group cohesion (Davis et al., 2019) but the result here suggests that the magnitude of this effect is dependent on the metabolic composition of the group. Additionally, while previous work has found that group cohesion can decrease with temperature in fish (Bartolini et al., 2015), the results here show no effect of temperature on cohesion but instead indicate that low and mixed groups are generally the least cohesive. Fish have been found to be less cohesive at higher testing temperatures and more polarized at lower testing temperatures, with higher tail beat frequency at maximum testing temperatures. Weetman et al. (1999) and Pritchard et al. (2001) found that fish swam closer together at higher temperatures, but (Bartolini et al., 2015) found opposite, however this is in water flow therefore high energy expenditure while swimming is required (Johansen & Esbaugh, 2017). Fish at higher temperatures could have greater energetic demands and

have decreased cohesion to increase foraging opportunities (Pitcher & Parrish, 1993; Hoare et al., 2004). However, fish activity and speed increased at higher temperatures, which could also decrease cohesion (Robinson & Pitcher, 1989), contrasting with evidence that individual nearest neighbour decreases as fish swim faster (Partridge et al., 1983; Gimeno et al., 2018). Reduced cohesiveness of groups caused by increasing temperatures can lead to alterations in ecological interactions such as dilution of information transfer, changes in competition for resources and predation response (Ioannou, Couzin, James, Croft, & Krause, 2011; Malavasi et al., 2013; Weetman, Atkinson, & Chubb, 1998). On a wider scale, the thermal environment may enhance or hinder the benefits of group living through resource availability, which could lead to disrupting established relationships or affecting opportunities to form new bonds, such as increased temperatures increased roost decay and thus roost switching, facilitating and increase in information transfer (Willis & Brigham, 2004; Wilkinson et al., 2019; Patriquin et al., 2016; Wildeet al., 2018). In social weavers, individuals spent more time thermoregulating and less time associating with conspecifics (Rat et al., 2020).

Group metabolic composition did not affect leadership stability or consistency, but an increase in temperature causes leadership to be less stable and less consistent between individuals, with leadership changing among individuals more frequently and groups becoming less synchronised. In heterogenous groups of individuals past work has shown there may be divergence in behaviour for individuals with different thermal optima, for example three spined stickleback may forego associations with conspecifics as the difference between environmental and individual's preferred temperature increases (Cooper et al., 2018). Individual heterogeneity in metabolism may result in unequal distribution of behaviours which generate and maintain structure in social groups (Cowlishaw & Dunbar, 1991). In the present study, heterogenous groups show no difference in leadership consistency or stability at higher temperatures in comparison to homogenous groups, however temperature has a significant effect on both leadership stability and consistency when turning, where groups at 18 °C have more consistent leadership where the leading fish maintains their role throughout the trial. Some individuals, regardless of physiology, may maintain their role within groups despite environmental stressors. The disruption of

leadership at 18 °C suggests that even though there may not be clear leadership in groups by one or few individuals, the cues used in coordination of groups are disrupted.

Metabolic composition of group did not affect individual rates of leadership while turning or accelerating. Leadership was not driven by one consistent individual, and there is not consistent leadership at 18 °C. Previous work has suggested spatial positioning, leadership and foraging performance of individuals was conditional on behavioural phenotypic composition of their group (Jolles et al., 2018), which may be translated to physiological composition. Previously, leadership has been found to be a repeatable trait in individual stickleback (Georgopoulou et al., 2022), and other work looking at sticklebacks have also shown consistent leader-follower interactions (e.g. Bevan et al., 2018a; Jolles, Mazué, et al., 2020) which have shown that temperature disrupts group dynamics.

While previous work has suggested that metabolic traits can be linked to spatial positioning or leadership within groups under specific contexts (Killen et al., 2017; Ward et al., 2018). The results here show that initiation of group changes in directionality or speed are not related to rank SMR or MMR within moving groups. Harcourt et al. (2009) and Nakayama et al. (2016; 2012) showed individuals that leave cover and explore environments ("bold" behavioural phenotype) also displayed stronger leadership tendencies. Additionally, boldness has been correlated to high metabolic rates (Metcalfe et al., 2016), which suggested that leaders may have higher metabolic phenotypes than followers. We also hypothesised that individuals with a higher SMR may have a higher feeding motivation, and therefore be more goal-oriented in their movement and be more likely to initiate group movement. The current study suggests that leadership when turning or accelerating is not strongly influenced by metabolic phenotypes only, and may be influenced by other physiological or behavioural metrics. It is notable that, while the lack of a link between leadership and metabolic traits was consistent across temperatures, it is possible that differing results could be obtained depending on the prevailing environmental conditions. For example, when in a fast flow, fish with higher maximum metabolic rate and aerobic scope have been found to be near front of schools (Killen et al., 2012b).

In contrast, individuals with a lower aerobic capacity have been observed to be near the back of schools while moving in still, benign conditions (Ward et al., 2018), possibly because higher performing leaders would decrease group cohesion. I also theorised that groups with more heterogeneity in metabolic traits may show stronger links between leadership and either SMR or MMR. On the contrary, I observed no effect of metabolic composition on correlations between leadership and metabolic traits. It is possible that, under relatively benign conditions, variation in metabolic phenotypes within groups is unlikely to be sufficient to prevent lower performing individuals from maintaining pace with the group, as voluntary swimming speeds in fish tend to be efficient and relatively slow compared to their theoretical maximum (Bale et al., 2014). Under faster moving conditions or when swimming against a stronger flow, it may become difficult for fish with low AS and MMR to maintain their positions at the front of the group. Front positions are the most energetically expensive to maintain and as hypothesised by Killen et al. (2012), lower performing individuals may be forced to adopt positions at the back of the group where they can save energy, should the speed of the group increase. Regardless, the results here suggest that group structuring or splitting based on metabolic phenotypes are unlikely for European minnows, at least under the conditions tested here. The spatial position of an individual within the group did not affect leadership while either turning or accelerating at either test temperature, indicating that propagation of movement does not necessarily come from the front of a school of fish. This contrasts with previous evidence that leadership of motion and frontal positions in moving groups are positively correlated (Nagy et al., 2010; Herbert-Read et al., 2011; Katz et al., 2011; Gimeno et al., 2018). The relationship between leadership and spatial positioning could be species specific, where propagation of movement and position in group also depends on how animals aggregate and school, the number of animals, and the location of the study (field or experiment). Interestingly, in low metabolic groups, initiators of group turns or changes in speed were found at the rear of groups, suggesting that leadership cues may be generated through some other means, rather than visual or movement cues from more anteriorly located groupmates.

The effects of temperature on social behaviour are unlikely to be the same across all group members. Indeed, dominance status can affect how individuals

respond to temperature, and thereby, the extent to which groups shift to more- or less-ordered states (Kochhann et al., 2015). While temperature shifts could influence cohesiveness, synchronicity of members could also be affected. If a group is homogenous in terms of their metabolic composition and therefore food and energy requirements, members may have similar activity budgets and temperature shifts may enhance cohesiveness by inducing group movement (Michelena et al., 2008; Conradt & Roper, 2010). Our study found that mixed metabolic groups had more variation in cohesion than homogenous groups, but in general were not different from high, medium, or low metabolic groups. However, higher activity levels could disrupt cohesion by making it more difficult for individuals to maintain physical proximity (Hurst, 2007; Bartolini et al., 2015; Colchen et al., 2017). While the results here show that groups with mixed metabolic composition were generally less cohesive, this trend was not statistically significant, possibly owing to the relatively low number of groups that were tested. This trend is in line with suggestions that groups with high phenotypic variation may have decreased cohesion and a higher propensity for group fission (Delgado et al., 2018), as well as a reduced capacity information transfer, foraging efficiency, and predator avoidance (reviewed by Killen et al., 2017)

Differences between collective behaviour patterns from other studies may be due to species specific differences, where black neon tetra of similar sizes and group number were more polarized and cohesive than studies of zebrafish (Soria et al., 2007; Gimeno et al., 2016). Moreover, these species-specific differences may be exacerbated depending on the experimental arena, where species may react differently to height of the water column, and orientate themselves to enhance information transfer which may be different to how they aggregate in the wild (Magurran, 1990; Couzin, 2007). Similarly, when quantifying leadership in terms of position in school, Partridge (1980) found that in minnow dyads there are clear leader-follower interactions (i.e. one fish at the front). Leadership then dissolves in larger groups and so while leader-follower dynamics may be present in some groups of species, they may not be seen in minnows. Our study adds to the growing evidence that integrating physiological measures into studies of individual variation in collective behaviour is imperative when determining group functioning and how this changes with environmental

stressors. Increasing temperatures has been shown to disrupt group behaviour while in experimental settings, however traditionally experiments only utilise one or two stressors which may not reflect the variability in field environments leading to confounding affects. Additionally, these temperature affects are analysed over acute change. While our study is not aimed at replicating the environmental fluctuations of real-world systems, the next steps would be to assess whether different stressors have independent effects on collective behaviour and whether the trends we see in controlled environments are reflected in the field. Linking these works to seasonal or long-term temperature changes is imperative to understanding how fish schooling behaviour and leadership will be affected as animals experience more extreme weather events due to shifts in climate change. Understanding how these roles emerge and change over time will be imperative to understanding individual- and group-level behavioural evolution (Bengston & Jandt, 2014).

4 Effects of feeding and digestion on leadership and collective behaviour in schooling fish.

4.1 Abstract

Position within a group can be related to aerobic metabolic scope and hungry fish have been shown to occupy anterior positions within a moving school. After feeding, the metabolic cost of digestion reduces swimming capacity, and fed fish are unable to maintain front positions within groups. Notably, however, this previous work has been performed with fish swimming against a current. Here we investigated schooling behaviour during and after feeding in a free-swimming environment to study how group dynamics change to accommodate the cost of digestion for individuals after feeding. Using qingbo carp (*Spinibarbus sinensis*), we examined the routine shoaling behaviour of free-swimming schools in an open field arena (9 fish per group) before and after a feeding event. Specific Dynamic Action was measured to understand metabolic rate post feeding, and these results were applied to behavioural data to determine the relationship between metabolism, meal size and behaviour. I provide evidence that while meal size is not necessarily associated with leadership across short (2 hour) timescales, feeding within a group does affect behaviour after feeding. Fed groups reacted slower when a leader was turning compared to control groups that were not fed, but reacted faster to leaders that were accelerating. Meal size didn't affect who was the leader after feeding, but whether any fish in the group ate or not had more influence on group behaviour. Overall, my results show how overall group behaviour, but not leadership changes and spatial positioning, is constrained by feeding and provide insight as to how food availability affects group dynamics, providing important information how moving groups traverse a changing world.

4.2 Introduction

Group living has been observed in all animal taxa, and the costs and benefits of sociality have been explored in a variety of contexts (Krause & Ruxton, 2002; Ward & Webster, 2016). While collective behaviour has been comparatively well studied, the importance of the individual physiological and behavioural differences within these groups is not as well understood (Metcalfe et al., 2016; Seebacher & Krause, 2017). Individual benefits from grouping may include reduced predation risk, reduced energetic cost of locomotion, and increased access to mates and social information. Individuals must trade-off these benefits against costs of group living, which may include increased competition for food, increased visibility to predators, and greater transmission rates of parasites and disease (Ward & Webster, 2016). The extent of compromises are likely to be unequal among individuals within a group, depending on their specific phenotype. In turn, the phenotypes of individuals within groups will be affected by a range of intrinsic and extrinsic factors, and potentially show plastic changes over short or longer timescales. While individual phenotypes and the degree of heterogeneity within groups appears fundamental to how groups function, the overall effects of phenotypic changes on groups functioning remaining almost entirely unknown.

Group living has been observed in all animal taxa, and the costs and benefits of sociality have been explored in a variety of contexts (Krause & Ruxton, 2002; Ward & Webster, 2016). While collective behaviour has been comparatively well studied, the importance of the individual physiological and behavioural differences within these groups is not as well understood (Metcalfe et al., 2016; Seebacher & Krause, 2017). Individual benefits from grouping may include reduced predation risk, reduced energetic cost of locomotion, and increased access to mates and social information. Individuals must trade-off these benefits against costs of group living, which may include increased competition for food, increased visibility to predators, and greater transmission rates of parasites and disease (Ward & Webster, 2016). The extent of compromises are likely to be unequal among individuals within a group, depending on their specific

phenotype. In turn, the phenotypes of individuals within groups will be affected by a range of intrinsic and extrinsic factors, and potentially show plastic changes over short or longer timescales. While individual phenotypes and the degree of heterogeneity within groups appears fundamental to how groups function, the overall effects of phenotypic changes on groups functioning remaining almost entirely unknown.

Factors such as food availability and metabolic cost of digestion can greatly influence individual physiology and possibly their behaviour within a social group. Differences in hunger state among individuals generates variability in behaviour (Reichard et al., 2008; Björnsson et al., 2018), where hungrier individuals will take more risks while foraging (Balaban-Feld et al., 2019), occupy the frontal positions of moving groups (Krause, 1993, 1994; McLean et al., 2018), or show increased movement speeds (Spiegel et al., 2013; Hansen et al., 2015, 2020). Moreover, the effect of nutritional state will vary over time as animals feed and move through their environment. Another important consequence of feeding, besides changes in hunger state, is the metabolic cost of digestion, termed specific dynamic action (SDA; Axelsson et al., 2000; Axelsson & Fritsche, 1991). After feeding, the energy required for the mechanical and chemical breakdown of food and its subsequent assimilation, can constrain the capacity for other oxygen-demanding physiological processes within an animal's aerobic scope (e.g. locomotion). For ectotherms in particular, the rise in metabolism can be substantial, possibly occupying the majority of an animal's aerobic capacity, depending on meal size (Spiegel et al., 2013; Hansen et al., 2015). Depending on the environmental context, aerobic scope can affect the spatial positioning of individuals within moving groups (Killen et al., 2012b; Ward et al., 2018). For example, a reduction in available aerobic scope after feeding, combined with lowered feeding motivated, may cause individuals within moving groups to move to more posterior positions within groups (McLean et al 2018). Despite this, however, it remains unknown how these changes in spatial following feeding may affect leader-follower dynamics within groups and overall group activity, coordination, and cohesion.

Leadership requires an individual to initiate behaviours or movements in conspecifics while maintaining group cohesion and coordination (Couzin et al.,

2002, 2005). Leader-follower dynamics can be affected by individual differences within the group such as movement speed (Pettit et al., 2015), experience (Flack et al., 2012), behavioural phenotype (Sasaki et al., 2018) or physiology (Ward et al., 2018). Leadership is often defined by position within group, where individuals at the front of groups may have greater access to resources (DeBlois & Rose, 1996). Although leaders may make decisions which benefit themselves (King et al., 2008), followers can benefit as they will be led to resources by more informed individuals without having to gather information themselves (Guttal & Couzin, 2010; Björnsson et al., 2018; Palacios-Romo et al., 2019). While leaders can clearly have a strong influence on group behaviour, including group foraging (Atton et al., 2012, 2014; Webster et al., 2013)), risk-taking, and migration route choice, change in leadership due to environmental factors could alter group functioning. For example, changes in foraging motivation or activity level due to locomotor constraints after feeding could render leaders less able to direct group movements or indeed remain leaders at all. The extent to which this may occur in free-ranging groups remains unknown but could fundamentally alter the way that social groups function.

In this study I used qingbo (*Spinibarbus sinensis*), a highly gregarious cyprinid fish species as a model of fish behaviour. Qingbo are one of the most common fish in the Yangtze River system, with an omnivorous diet. Previous work has examined the effects of food availability on locomotor capacity (Zhao et al., 2012; Pang et al., 2014) and sociability (Killen et al., 2016) but the effects of food availability on leadership is unknown. We tested the following questions: (i) Does size of meal affect leadership within groups; (ii) How does leadership change with time after feeding in relation to changes in the metabolic costs of digestion; and(iii) How does group behaviour change after feeding and is this linked to individual meal size and digestive costs.

4.3 Methods

4.3.1 Experimental Animals

Approximately 270 juvenile Qingbo (*Spinibarbus sinensis*) were obtained from a local supplier and housed at Chongqing Normal University, China for at least 30 days before experiments began. Fish were maintained in a large laboratory stock tank in recirculating, aerated freshwater at 20°C and fed to satiation daily (commercial bloodworm), the photoperiod was 14L:10D. Fish were fasted for 24 hours prior to tagging, and 12 hours before behavioural trials, with 30 groups of 9 fish were randomly selected to take part in trials from the stock population. They were measured for length and mass, then tagged for identification with Visible Implant Elastomer tags (Northwest Marine Technology Inc., Shaw Island, USA). Groups of fish were contained in tanks separate from the main population to acclimatise as a group and encourage schooling behaviour and familiarisation with group mates.

4.3.2 Behavioural trials and measurements

After social acclimation, the individuals from a group were simultaneously placed into an oval arena (120 x 60 cm) and left to acclimatise for 1 hour before the recording began. 10 minutes after the beginning of the trial, fish were exposed to a feeding event, which lasted approximately 10 minutes. The arena was permanently fitted with 6 flexi tubes which were attached to the walls of the arena at different points and using syringes, one blood worm was inserted into the arena using alternating tubes haphazardly to encourage swimming around the arena. 50 worms in total were inserted approximately every 5 – 10 seconds and the number of worms consumed by each fish was noted. Each trial was recorded from above using a Go Pro Hero 4 (30 fps) for a total of 3 hr 20 min, to later examine behaviour before, during, and after a feeding event. Behaviour was recorded for 27 groups in total, including 10 control groups which were not fed but were recorded for the same time duration.

Behaviour was compared for individual fish and between the control and testing groups throughout the trials. The testing group videos were spilt into time periods, 10 minutes before feeding, during feeding (10 minutes) and behaviour was compared after feeding for 5 minutes (9000 frames) every 20 minutes. For the control groups, tracks were split into ten minutes, ten minutes and 5 minutes (9000 frames) every 20 minutes for 3 hours, to mimic the same splits as in the feeding trials. For each video segment, individual fish were tracked using idTracker (2014) and then positions were manually corrected if needed. From these tracks and positions, leadership metrics were calculated via temporal correlations (Nagy et al 2010; Jolles et al 2018) and position in school (Krause, 1993). Behavioural metrics such as polarity, cohesion and acceleration were calculated and compared between control and treatment groups and during each time period of trial (see Chapter 2 for calculations and descriptions).

4.3.3 Estimation of metabolic cost of feeding

The increase in oxygen consumption following feeding, or Specific Dynamic Action (SDA), of qingbo was measured to compliment the behavioural measurements from the open field trials. SDA was measured using continuous-flow respirometry (Fu et al., 2011; Auer et al., 2015), consisting of 4 respirometry systems, each consisting of 50 L experimental water bath (20°C) holding 10 glass respirometry chambers. The respirometry set ups were covered with an opaque plastic cover to minimise disturbance. A large reservoir was kept under each respirometry set up, where water oxygen content kept to saturation using air stones, and temperature maintained to 20°C using aquarium heaters. An additional heater was placed in the water bath containing respirometry chambers in order to maintain temperature when water circulated through system. A submerged pump moved water from the reservoir to a small water tower above each respirometry set up to generate a constant flow through the respirometry set up. Flow of water was controlled using a switch between the water tower and the distributing pipe to each chamber and was measured for each respirometer immediately after each oxygen measurement was taken by observing the time taken for 100 ml of water to flow through the respirometer.

Water from the outlet of each chamber was filtered and returned to the reservoir tank.

Fish were placed in individual glass respirometers and individual flow rates were measured after individual oxygen consumption recorded, however this was set to allow for oxygen consumption levels to be detected without letting the oxygen content drop below 80% saturation. Chambers had a maximum internal diameter of 45 mm, and the size of the chamber was chosen such that the fish could not swim, but was able to turn around if needed. The size of chamber was accounted for in oxygen uptake calculations, as flow rate is used in continuous flow respirometry. Dissolved oxygen content of water at outlet of the respirometers for individual fish was manually recorded using a water oxygen meter (HQ20; Hach Company, Loveland, CO, USA) once per hour for 10 hours. An additional fish-free chamber served as a control measure of background respiration rates measure for any background oxygen uptake by bacteria, which was subtracted from each individual fish in that respirometer.

Each set up measured 9 individual fish and one chamber in each set up was left empty as a control and measured at the same time as individual fish, allowing for 36 fish to be measured in total per day, fish were fed set numbers of bloodworms before immediately being placed within the respirometry chambers (one fish per chamber). Naïve qingbo (n = 36) were starved for 48 hours before being measured for oxygen uptake for 40 hours following feeding different amounts of food items (0, 5, 10, 15, 20 or 25 bloodworms). Fish that were fed 0 worms were used as a control to account for the oxygen consumed during handling. Fish were immediately placed into respirometers and measured using the same protocol as SMR to quantify the oxygen consumption of individuals while digesting increasing food amounts, which is used to form part of a predictive equation to quantify specific dynamic action. This data was then used to calculate the oxygen uptake (MO_2: mg O_2 h^{-1}) of individual fish using equation 1, where ΔO_2 is the difference in oxygen concentration (mg O_2 L^{-1}) between an experimental and control respirometer, and v is the water flow rate in an experimental chamber (L h^{-1}).

Equation 1: $MO_2 = \Delta O_2 \times v$

When removed after 10 hours, fish were measured for length and weight To account for any effects of handling during feeding or transfer to the respirometry chambers during the period over which specific dynamic action was measured, the mean oxygen consumption for the control fish was subtracted from all fed individuals.

Individual SDA responses were modelled by applying a polynomial function to the oxygen uptake data for 24 hours after feeding. The function for each individual was then used to estimate the time until peak oxygen uptake, time taken to reach this peak, and return to baseline oxygen uptake. Based on measures of oxygen uptake during respirometry-based feeding trials, a multiple regression was constructed including number of worms eaten, time since feeding and fish body mass to estimate oxygen consumption of fish during behaviour trials according to the SDA response.

Predicted change in oxygen consumption over the course of the behavioural trials was predicted using this equation, accounting for the predicted rise in oxygen consumption post feeding, decreasing with meal size and time.

4.3.4 Statistical Analysis

All statistical analyses were performed in R.4.0.5 (R development Core Team). Linear mixed effect models or Generalised Linear Mixed Effect Models (lme4, lmertest) estimated using REML were fitted to investigate how meal size, time since feeding, and treatment affected leadership and group behaviour. Model selection was performed by sequentially dropping non-significant variables starting with lowest t-values, but were retained if their removal resulted in higher AIC values ($\Delta AIC > 2$ Arnold 2010). For each specific model structure and model selection see supplementary methods (Table 8.2-10 – Table 8.2-15), however for each metric of leadership or collective behaviour, group and ID were included as random effects and meal size, time since feeding, mean mass fish in each group and treatment were included as explanatory variables. Homoscedasticity and normality of residuals were assessed by visual inspection of residual plots, and used to determine whether transformation of data was

necessary. Mean Lag after leadership for both turns and acceleration were scaled and plotted on the negative axis, where lower numbers indicate earlier leadership. Mass, individual speed, average neighbour distance, and group polarity were log transformed.

4.4 Results

4.4.1 Measures of Leadership and Food Availability

Fish that ate the most food items during the feeding trial were those that, both before and during feeding, had the greatest lag response in terms of acceleration but the lowest lag response for turning (acceleration: ($t(1633) = 3.10$, $p = 0.002$; turning: $t(1633) = -2.22$, $p = 0.027$; Figure 4.4-1A-B; Figure 4.4-2). In other words, fish that fed most were those that were leaders for the direction of group movement but followers in terms changes in group speed (accel: Table 8.2-2; turns: Table 8.2-3).

Post-feeding, the number of food items consumed was not related to leadership in terms of either group turning or accelerating (Figure 4.4-1A-B and 2). Also post-feeding, fish responded faster to a leader's change in speed compared to pre-feeding, but responded slower to changes in directionality($t(1631) = -2.18$, $p = 0.029$). Before, during, and post-feeding, larger fish were more likely to initiate or respond quicker to changes in group speed but there was no effects of body size on leadership or response to changes in group turning.

As time progressed after feeding, individuals that ate less during the feeding trial moved toward the front of the group while schooling ($t(1631) = 3.14$, $p = 0.002$; Figure 4.4-2C). Larger fish also moved to the front of the group as time since feeding increased ($t(1631) = 1.97$, $p = 0.049$), but there was no direct relationship between fish body mass and number of food items they consumed during the feeding trial (Table 8.2-4).

In fed groups post feeding, mean lag after a leadership event while accelerating decreased compared to in controls but increased after turning, meaning that individuals reacted quicker to leader's change after feeding but slower to

changes in directionality (t(201) = -2.18; Table 8.2-2 (t(762) = 3.10, p = 0.002; Table 8.2-3).

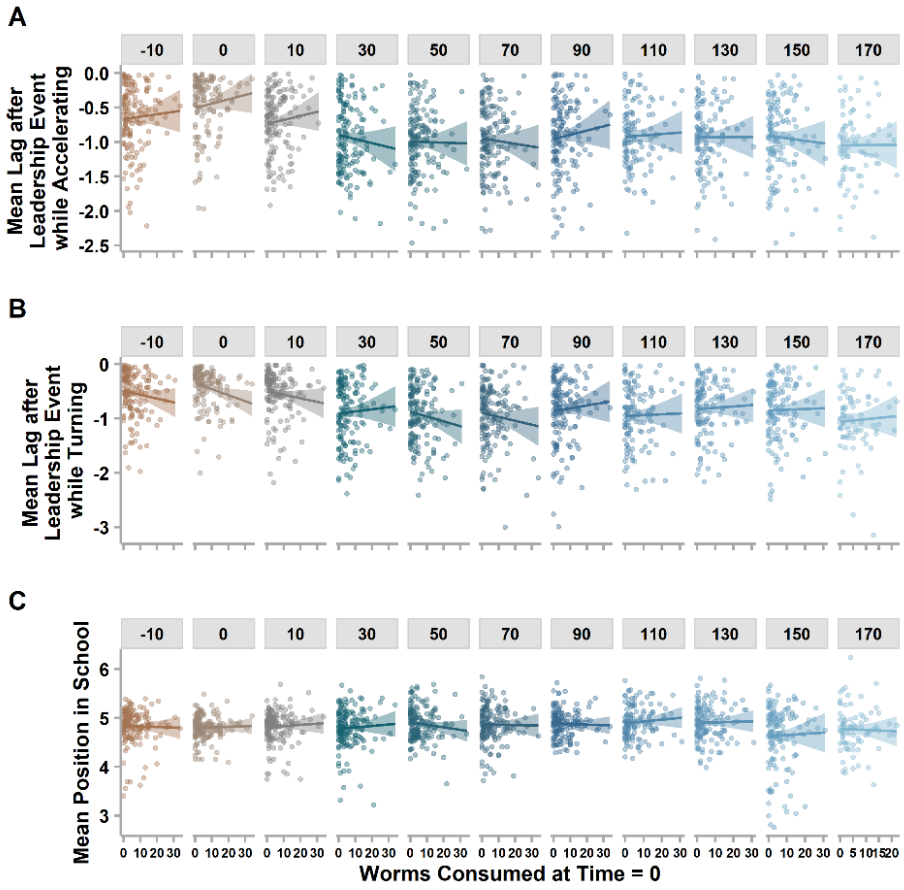

Figure 4.4-1: (A) Relationship between Mean Lag after Leadership Event while Accelerating and number of food items eaten during a period of feeding. (B) Relationship between Mean Lag after Leadership Event while turning and number of food items eaten during a period of feeding. (C) Relationship between mean position in school and number of food items eaten during a period of feeding. Panels show time in minutes after feeding, where -10 indicates the 10 minutes before feeding (time 0). Points represent data for individual qingbo. Trendline calculated with glm and shaded areas represent the 95% confidence intervals.

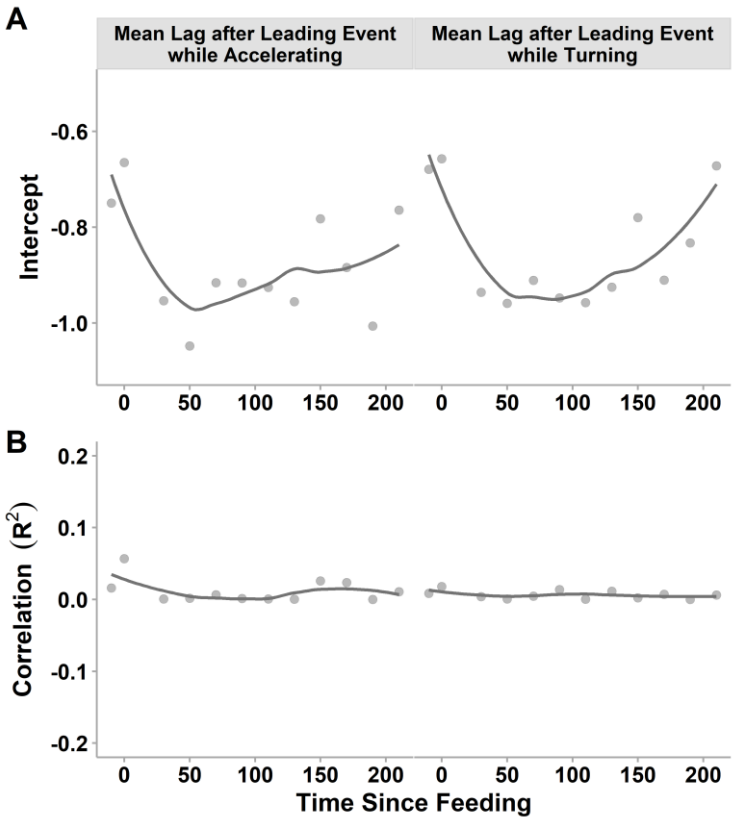

Figure 4.4-2: Plots of values in linear regression (Pearson's correlation) between for leadership metrics over time, using data from each regression line in figure 4.6-1, showing intercept of regression line (A) and R^2 (B). Intercept represents the magnitude of difference in value, and R^2 represents relation to number of food items consumed at time 0 and how they change over time in the trial (Time Since Feeding).

4.4.2 Group Behaviour and Food Consumption

During feeding, fish that ate the most food items were those that moved faster and had a larger mean distance from the group centroid (Figure 4.4-3; Figure 4.4-4). Post-feeding, however, the number of food items eaten showed no relation to either individual movement speed or distance from centroid. As time progressed since feeding, fish swim speeds gradually declined before beginning to increase at around 110 minutes post-feeding ($t(1632) = -8.35$, $p < .001$; Table 8.2-6). Group cohesion, measured as mean fish distance from the group centroid, was lowest when feeding occurred (i.e. fish were more spread apart), but similar to group speed, groups gradually became more cohesive post-feeding, stabilizing around 110 min post-feeding. Overall, larger fish had a higher mean distance from centroid compared to smaller fish ($t(1631) = 3.24$, $p = 0.001$; Table 8.2-5). Individuals in groups became more polarised after feeding, peaking at around 70 min post-feeding ($t(1635) = -3.21$, $p = 0.001$;

Table 8.2-7).

For mean speed (t(1632) = -2.41, p = 0.016; Table 8.2-6) and mean distance from centroid (t(1631) = -3.45, p < .001; Table 8.2-5) there were differences between the feeding trials and controls, where fish that fed swam slower and were more cohesive after feeding than in control groups with no feeding. There was no difference in polarity between feeding trials control groups (Table 8.2-15).

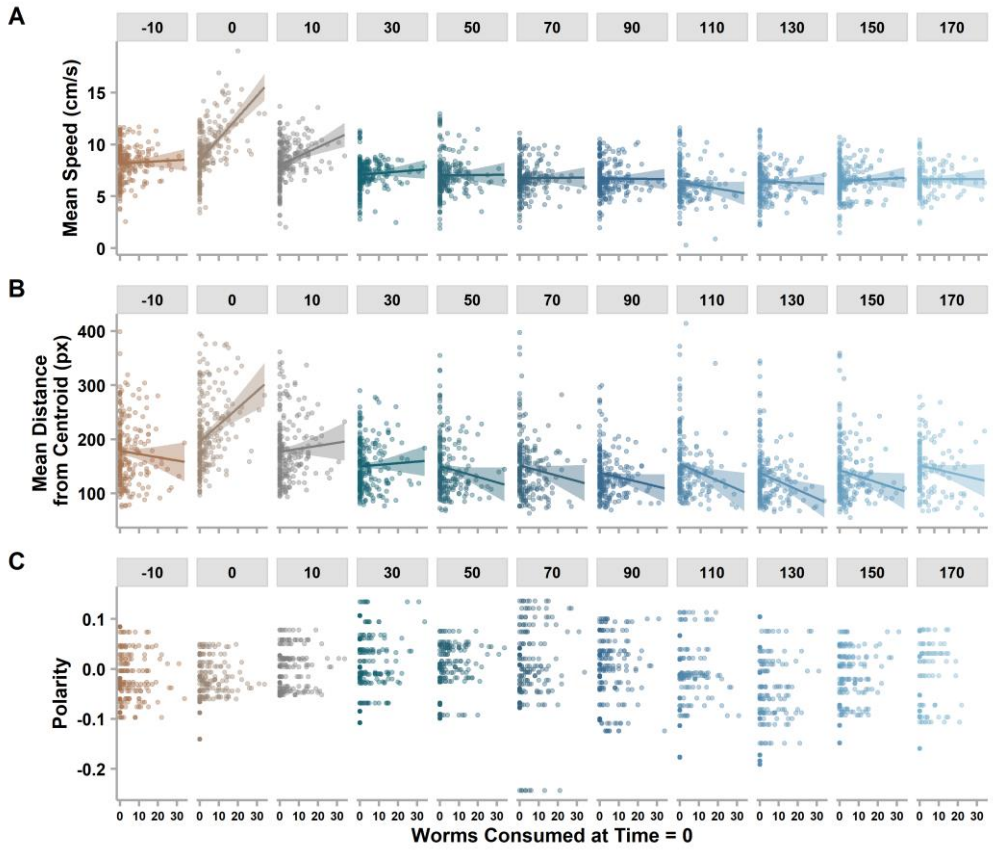

Figure 4.4-3: (A) Relationship between individual mean speed and number of food items eaten during a period of feeding. (B) Relationship between group cohesion and number of food items eaten during a period of feeding. (C) Relationship between polarity and number of food items eaten during a period of feeding. Panels show time in minutes after feeding, where -10 indicates the 10 minutes before feeding (time 0). Points represent data for individual qingbo. Trendline calculated with glm and shaded areas represent the 95% confidence intervals.

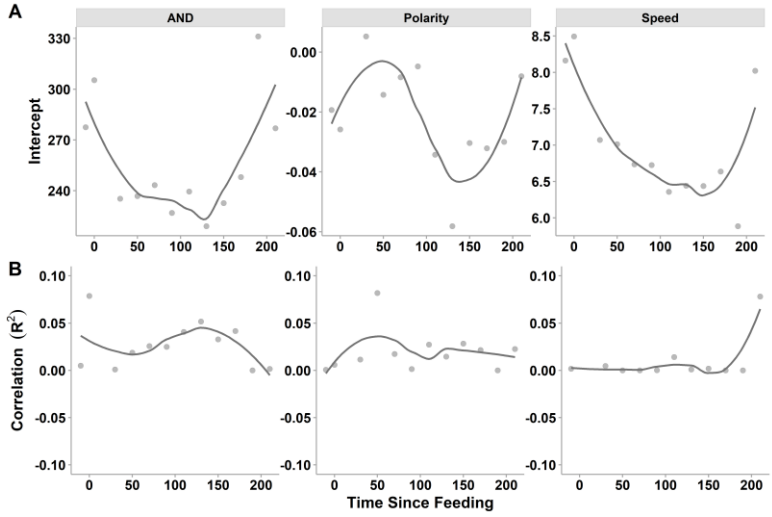

Figure 4.4-4: Plots of values in linear regression (Pearson's correlation) between for leadership metrics over time, using data from each regression line in figure 4.6-3, showing intercept of regression line (A) and R^2 (B). Intercept represents the magnitude of difference in value, and R^2 represents relation to number of food items consumed at time 0 and how they change over time in the trial (Time Since Feeding).

4.4.3 Specific Dynamic Action

There was no effect of food items consumed on the time taken to reach peak oxygen consumption after feeding, larger meals resulted in a higher peak in oxygen uptake as compared to smaller meals (Table 8.2-9). Fish that ate the smallest meals did not show an identifiable peak in oxygen uptake, but displayed a shallow, gradual rise in oxygen uptake throughout the measurement period. The median time to reach peak oxygen uptake post-feeding was 160 minutes (Figure 4.4-5).

The effects of meal size and time since feeding from the SDA measurements were subsequently applied to individuals in the behavioural trials, to estimate to predicted rise in oxygen uptake post-feeding and any associated effects on individual behaviour. In general, fish that ate more food items were predicted to show the greatest increase in oxygen uptake, and the variation in oxygen uptake among individuals increased as time progressed post-feeding (Figure 4.4-6; Table 8.2-8; Table 8.2-9).

There was no consistent relationship between predicted increase in oxygen uptake post feeding with mean lag after a leadership event while accelerating or turning, or mean position in school (Figure 4.4-7). Before feeding, during feeding and 30 minutes post feeding, if predicted oxygen uptake increased, mean lag after leadership while accelerating was smaller ($t(2110) = 2.06$, $p = 0.039$; Table 8.2-8). In later times post feeding, there was no relationship between mean lag after leadership event while accelerating and predicted increase in oxygen uptake.

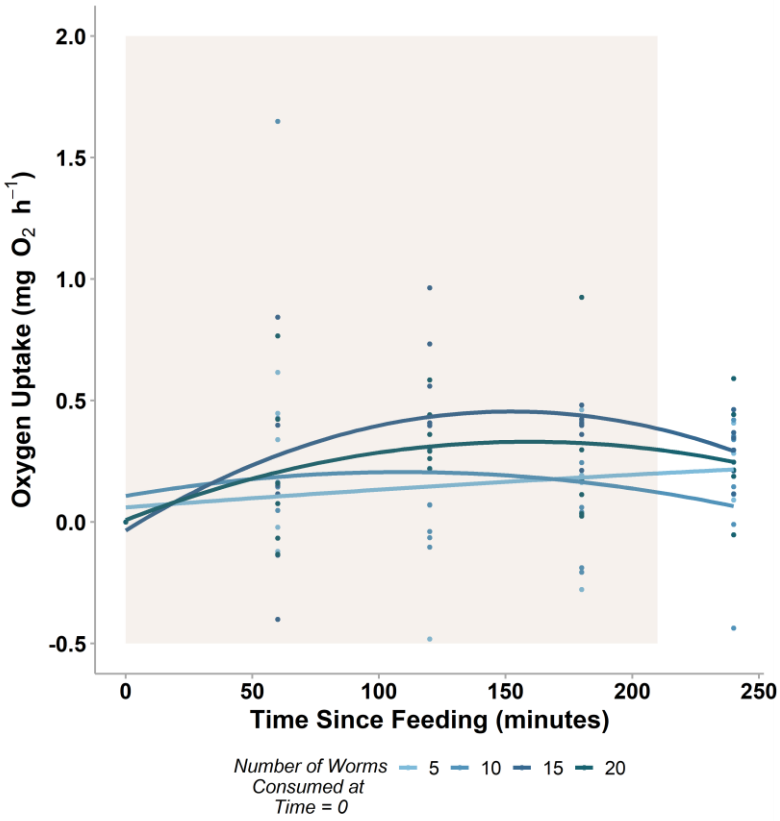

Figure 4.4-5: Changes in oxygen consumption with time in individual qingbo after consuming various amounts of food. Each curve represents data for one individual and is a polynomial function (detailed in the main text). The vertical shaded area is the time period corresponding to feeding and the subsequent 3 hours in the group swimming trials.

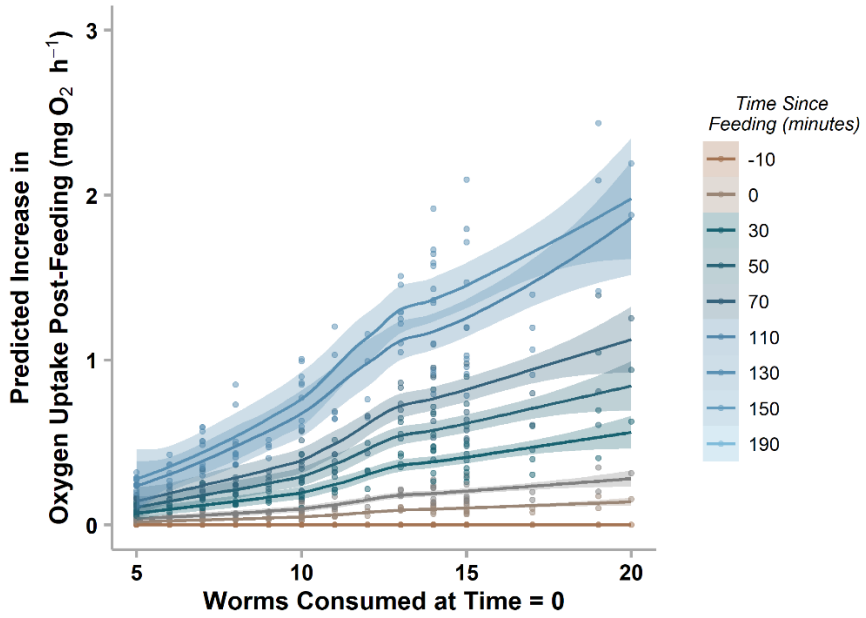

Figure 4.4-6: The relationship between change in predicted available oxygen after feeding and number of food items consumed at time 0. Different lines and colours represent different time periods in minutes after feeding. Predictive line calculated via loess and shaded area around each line represents 95% CI.

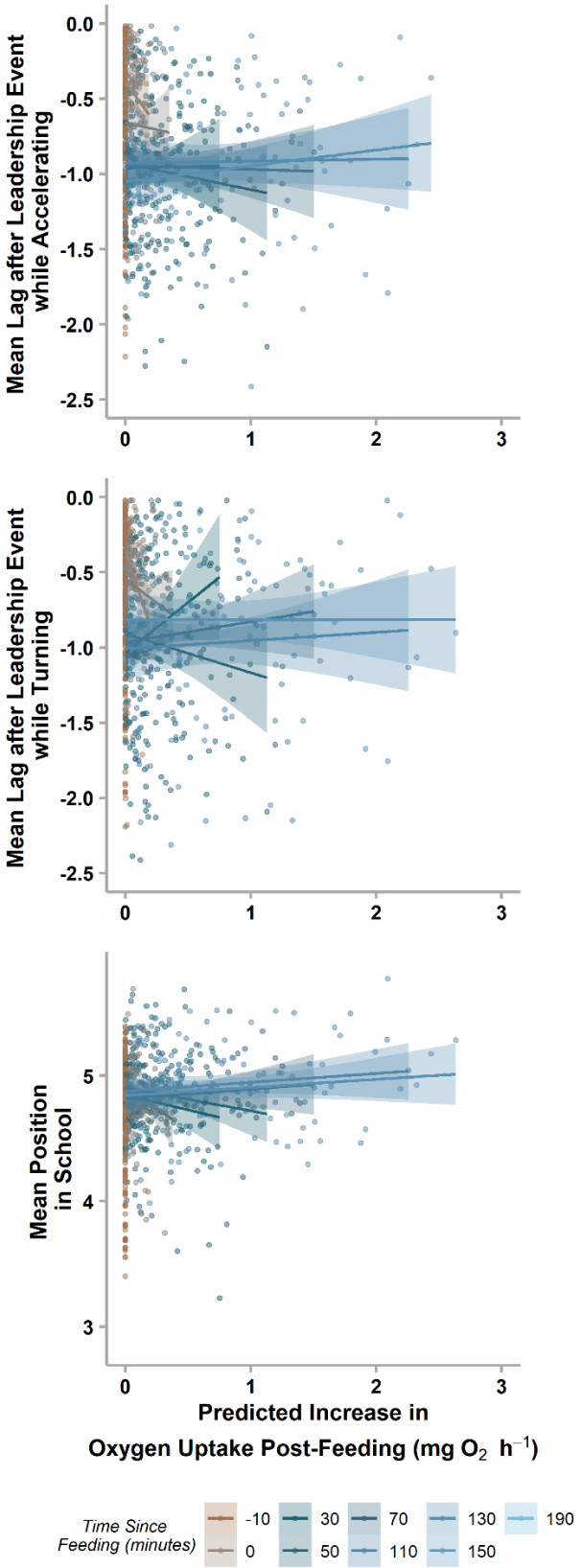

Figure 4.4-7 Scatterplots to show the relationship between the predicted increase in oxygen uptake post feeding and leadership metrics. Different lines and colours represent different time periods in minutes after feeding. Predictive line calculated via general linear model and shaded area around each line represents 95% CI.

4.4.4 Leadership Correlations

There was a strong positive correlation between mean lags after leadership event while accelerating and turning across all experimental time periods (feeding trials: r = 0.62, p < .001; control: r = 0.53, p < .001; Table 8.2-1). There was no correlation between either mean lag after leadership event while accelerating or turning and mean position in school for feeding trials (Figure 4.4-8). For control groups, however, there was a weak negative correlation between mean position and school and mean lag after leadership event while turning (r = -0.22, p < .001).

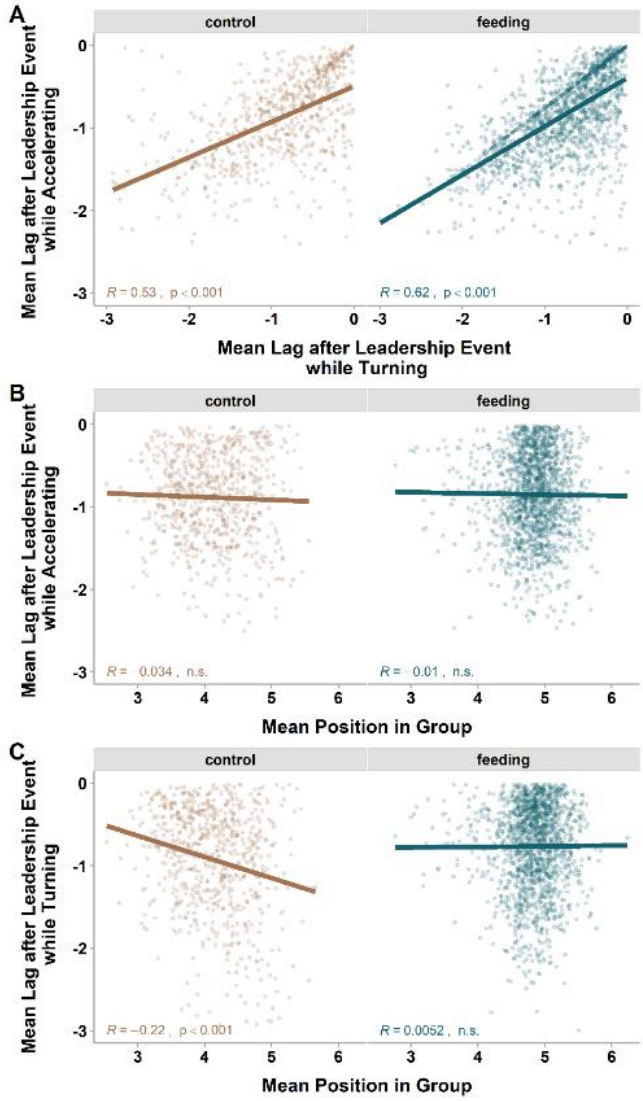

Figure 4.4-8: Scatter plots showing the correlation between leadership metrics: Mean Lag after Leadership Event while Turning and Mean Lag after Leadership Event while Accelerating (A), Mean Lag after Leadership Event while Accelerating and Mean Position in Group (B), Mean Lag after Leadership Event while Turning and Mean Position in Group (C). Extreme grouping of points in panel A attributed to very small

differences between mean lags while turning and accelerating, where points represent individual fish at every time point in every trial.

4.5 Discussion

While previous work has shown that the spatial positioning of individuals within moving social groups can change due to the metabolic costs of feeding and digestion (McLean et al., 2018), my data show much more direct effects on leader-follower dynamics, including how changes of speed and directionality propagate across free-ranging groups, and can manifest from the common act of food consumption. Before and during feeding, fish that ate the most were found to be followers when the group was changing speed, but those same fish were most likely to lead group changes in directionality while turning. After feeding, however, there was no association between the amount of food consumed by individuals and their status as a leader or follower in terms of group speed or directionality. At the group level, however, individuals in feeding trials responded slower to changes in direction by leaders in comparison to unfed control groups, and faster to changes in group speed. In contrast to previous work, there was little or no effect of spatial positioning on the amount of food that fish were able to consume, and conversely, the amount of food eaten had no effect on the spatial position within groups that individuals occupied during the digestive period after feeding. Polarity, cohesion and speed of groups changed with time since feeding, unlike control groups which were not fed. Finally, unlike previous work examining schools swimming against a flow (McLean et al. 2018), I observed no consistent effect of the metabolic costs of digestion on individual behaviour within groups post-feeding. Together, these results suggest that, in free-ranging groups, the behavioural conformity required to maintain group cohesion may alter relationships between bioenergetics and behaviour at the individual level.

Before and during feeding, fish that ate more lead the directional movements of the group but were followers in terms of changes in group speed. In general, leadership while turning and accelerating are strongly correlated, and so this result suggests that, at least under the conditions of my study, initiation of group turning was important for being able to obtain food items. In my assay, food was introduced at various points throughout the arena, and accordingly, the fish would need to turn from one location to the next to obtain the food items.

Individuals that turned first may have therefore been most likely to find and obtain the food; while others would then speed up while attempting to reach the feeding location, possibly explaining why apparent initiators of changes in group speed where actually the least successful at finding food. Interestingly, leadership of group turning, even before food was introduced to the arena, was a predictor of which individuals would obtain the most food once it was available. This again highlights that those individuals that are predisposed for exploration or initiators of group changes in directionality may be most capable of finding food sources that are unpredictably scattered throughout an area.

Followers reacted slower to leaders immediately after feeding, but gradually resumed pre-feeding reaction times as time since feeding progressed. This pattern of change in leader-follower dynamics was not present in the control groups that did not feed, indicating that this trend was most likely due to the effects of feeding and digestion and not baseline changes in information transfer or re-enforcement of leader-follower roles over time (Nie & Fu, 2017; Tóth et al., 2017). This rise in oxygen consumption post-feeding may occupy a large portion of an individual's total aerobic scope, which can then constrain locomotor ability (Soofiani & Priede, 1985; Norin & Clark, 2016), or reduce the motivation to move and react to others. Indeed, overall movement speed decreased post-feeding, providing additional evidence of a locomotor constraint causing a decrease in movement and likely reaction speeds. While increased swim speed is known to use most energy per unit time in fish, theoretical (Hughes & Kelly, 1996) and empirical work (Wilson et al., 2013) also suggests that turning can be more energetically costly than straight forward movement, possibly explaining why even responses to group changes in directionality may be reduced post-feeding. In any case, the results here demonstrate nuanced effects of digestion on leader-follower dynamics post-feeding, linking physiological processes at the individual level to behaviour at the group level.

In contrast to some previous work (Krause, 1993; Hirsch, 2007a), there was no consistent relationship between spatial position relative to the forward movement of a school, either during or after feeding, and the number of food items that an individual consumed. Firstly, during feeding, fish in frontal positions were no more likely to obtain food items compared to individuals

located in other positions within the group. This contrasts with previous work, where individuals near the front of moving groups were most able to obtain food items within their movement path (DeBlois & Rose, 1996). In the current study, however, food items were presented in an unpredictable pattern throughout the arena, seemingly reducing the importance of spatial positioning on food acquisition and instead highlighting the importance of initiation of movement after food detection. Perhaps more strikingly, there was no effect of the amount of food consumed on the spatial position occupied by individual post-feeding, during the digestive phase. It has previously been shown that, in constantly moving groups, metabolic constraints imposed by digestion can limit the locomotor capacity of individuals that have fed the most, causing them to subsequently occupy more posterior positions within the group (McLean et al., 2018). In the current study, the overall group response to feeding was to reduce movement, obviating the need for individuals which have eaten the most to "keep pace" at the rear of a moving group. The results here show that the interplay between spatial positioning and food consumption is likely highly context dependent and influenced by the pattern of prey availability during feeding and subsequent demands on group movement post-feeding.

While overall group speed decreased immediately post-feeding and group cohesion increased (before both gradually returned to pre-feeding levels), the amount for food consumed did not influence post-feeding swim speed or average neighbour distances at the individual level. This also suggests that, despite heterogeneity in amount of food consumed, individuals still conform to the rest of the group, altering their behaviour to match those that did eat more. Our results also suggest that factors that directly affect some group members may influence others by proxy. Previous work has shown that fish in groups with a higher proportion of hungry fish swim 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 (Wilson et al 2016). Although I did not examine the proportion of fish that ate no food within a group, I observed that groups with a mix of nutritional states (feeding trials) swam faster than control groups. Although individuals may have independent preferences for expressing behaviour, the lack of differences within groups show that regardless of physiological state or prior feed intake, the social environment modulates how

behaviours are expressed and individuals may conform to the movement speed of their group mates. Although animals increase speed when seeking food, they often increase their turning rate, which may contribute to the difference in speeds and polarisation of the control group compared to the fed groups (Bennison et al., 2018).

The number of food items consumed had no relationship with position in school, movement speed, or cohesion pre-feeding. During feeding, fish that ate more swam faster and were further away from the group, although these were not the fish initiating changes in group speed. Previous studies have explored the role of behaviour in food intake rate, finding that increased activity and low sociability can be positively related to feeding or growth rate in a social context (Wilson et al., 2013). Additionally, high foraging tendency and front positions have been linked to fish with lower social proximity (Jolles et al 2017). Interestingly, increased cohesion and swimming speed is often associated with an increased metabolic rate and a sign of stress (Svendsen et al., 2021). After acclimation and over time in the trial we would expect groups to become more coordinated, have less activity and to see polarisation and speed to be positively related. We show that after feeding, groups initially swam slower over time and more cohesive, which could be because individuals were no longer restricted in speed and aerobic scope by their digestion, and so their preferred speed while searching for more resources may be faster, and also explain why these speeds are different to control groups. After feeding, fish are more satiated and so the motivation to move in order to increase feeding opportunities may be less, and so they will prioritise increasing cohesion and safety in groups. Other studies have found that nutritional stress had little effect on voluntary speeds and inter individual distances of fish (Hansen et al., 2020, 2021), which suggests cohesiveness is easier to maintain when not having to compromise between feeding and group cohesion, and so this may be reflected in our results over time (Tunstrøm et al., 2013).

Throughout the post-feeding phase in fed groups, individuals gradually resumed their pre-feeding swimming speeds and levels of group-level cohesion. As digestion processed and time increased, it is possible individuals became less metabolically constrained. When we predicted SDA response with different food

item amounts, eventually metabolic rate should decrease again to baseline levels of oxygen consumption, which is within the behavioural trial length. Individuals may also have been more motivated to resume their normal levels of activity and cohesion, and this was not altered by the amount of food eaten. Group cohesion, information transfer and group decision making in fish are believed to be mediated mainly through movement, and adaptable inter-individual interaction rules can buffer the effects of variability in internal and external stimuli (Katz et al., 2011). After feeding, fish may be motivated to resume regular patterns of movement to share information within the group. Individuals in groups who may not be metabolically constrained, i.e ate no food items, still maintained group behaviour and matched their behaviour to those in the group who did feed. Despite unequal food distribution, those who did not eat were motivated to conform to other's behaviour in the group, likely in order to maintain group cohesion and information transfer.

Predicted increase in oxygen uptake after feeding was not linked to mean lag after leadership events while turning or accelerating, or position in school, which suggests that the SDA response may not constrain leadership after feeding in a group context. Unlike previous observations groups that were swimming against a flow, and therefore required to constantly maintain forward movement, my results indicate that in free-ranging groups, overall reduction in group activity post-feeding erode potential links between post-feeding increases in individual oxygen uptake and behaviour within a group. There are at least two scenarios that could explain the observed trends: (1) any amount of food intake will cause a general reduction in movement and leadership capacity (or motivation) for individuals within groups; or (2) fish that consumed the most food become constrained in their locomotor ability, reduced their movement frequency and speed, and other individuals also reduce their own movement to maintain group cohesion. Further studies could explore how individual predicted remaining aerobic scope after feeding could alter individual behaviour in a group (Mclean et al 2018). There are likely to be interactions between physiological traits, feeding motivation or ability and magnitude of specific dynamic action response. Fish with larger aerobic scopes consume more when given the opportunity (Auer et al., 2015), and I have confirmed that specific dynamic action is positively linked to meal size (also Secor, 2009). It is therefore

important to examine how individuals with varying specific dynamic action responses may respond to different meal sizes, and how this relates to individual behaviour as well as group. Additionally, further studies could focus solely on the feeding period, where moment-to-moment changes in behaviour and leadership likely occur, and link to how vision and olfactory cues play a role in group behaviour during feeding.

The current study adds to the growing evidence that collective behaviour is driven by various internal and external factors, and that ecological context is key for the expression of social behaviour. Here I show that leadership is distributed among individuals, but it changes in feeding contexts. Previous work has shown that age, position and behavioural phenotype may influence leadership (Jolles et al., 2018; Sueur et al., 2018), and while these phenotypes may be linked to physiology in previous studies, there is no relationship in the current work. I show that leadership through temporal correlation is not necessarily linked to position in school, and leadership may be altered by energetic state. Leadership may change on a moment-to-moment basis, and while consistent differences over time may enhance emergence of leader or follower roles, these may be overruled by immediate reactions stemming from motivation and the capacity to lead after feeding. Research is needed to understand the consequences of locomotor constraints for group leadership, group learning, and group decision making in other ecological situations, particularly if leaders are physiologically incapable of occupying specific roles within groups. Teasing apart the relationships between leadership and bioenergetics will lead to better understanding of group behaviour in self-organised and hierarchical systems, and improve further experimental design or inform theoretical models of animal movement.

5 Determining hidden energetic costs and benefits of sociality in moving animal groups using cost of transport

5.1 Abstract

Group living is widespread among animal taxa and comes with costs and benefits associated with predator avoidance, foraging and reproduction. While individuals in moving groups move at a similar speed to maintain group cohesion, the extent to which group members deviate from their own optimal locomotor speed and accumulate disparate energetic costs of transport per unit distance moved has not been investigated. For example, leaders may move at their own optimal movement speed, with groupmates changing their own speed to match the leaders, and therefore accumulating higher costs of transport due to moving at a non-optimal speed. Here, I observed swimming behaviour in single zebrafish (*Danio rerio*), as well as fish in pairs and in groups of four, to examine variation in movement speed among individuals in moving groups. Each individual was also measured for optimal swimming speed and minimum cost of transport using swim-tunnel respirometry. Fish in groups accumulated lower costs of transport per unit distance compared to fish swimming alone or in pairs. Within each pair and group, leadership was not related to individual optimal swimming speed, and there was no evidence that pairs or groups were moving closer to the leader's individual optimum speed. Despite these findings, however, individuals with a lower optimal speed within each pair or group had a higher cumulative cost of transport during group movements. These results suggest that while convergence on a common group movement speed may facilitate group cohesion, the cumulative energetic deficit acquired while moving at a non-optimal speed may constitute an important but to date unrecognised cost of group living. This work explores the energetic costs of social behaviour and how individuality can alter collective movement, while confirming that it is energetically more efficient to move in a group rather than alone.

5.2 Introduction

Group living is common among animals and confers benefits associated with resource acquisition (Ward & Hart, 2005), information transfer (Swaney et al., 2001), predator avoidance (Santos et al., 2014) and efficiency of movement (Killen et al., 2012a). To gain the advantages of group living and prevent group splitting (Krause & Ruxton, 2002; Conradt & Roper, 2007), group members must engage in some degree of behavioural synchronisation through emulating movements of their neighbours. Although the internal state of animals can motivate them to move from one location to another (Sergio & Newton, 2018) the environment the animal experiences is also expected to influence variation in these movements, and this includes their social environment. It is thought that animal movement is ultimately defined by the trade-offs between the environment that determines the energetic cost of movement and the benefits associated with achieving these movement-driven goals (Halsey, 2016).

Individual locomotor performance influences dispersal, foraging and predation, and behavioural interactions (Hillman et al., 2014; Husak et al., 2006; Irschick and Garland, 2001). Locomotor performance is related to muscle power output and the energetic cost to achieve that power output, which is in turn determined by metabolic rate. Within social groups, there can be variation in locomotor costs experienced by individuals, due to individual differences in physiology, activity level, or their spatial position within the group, and these differences may influence interactions among groupmates (Curtin and Woledge, 1991; Lichtwark and Wilson, 2005; Woledge et al., 2009). Activity of individuals and the associated energetic costs are often explored in terms of movement costs per unit time, but how this is related to voluntary swim speeds and how this changes as groups conform to the movement patterns of their social group is largely unknown. While the energetic cost per unit time can provide a useful metric of movement costs over a given timeframe, it is the cost of transport *per unit distance* that defines movement efficiency. For an individual animal, their optimal movement speed in that which minimises their costs of movement per unit time, and in animals that run, swim, or fly, this usually occurs at some intermediate speed where there is a trade-off between inertial and frictional

forces. While the minimum cost of transport and optimal movement speed are often used to compare locomotor performance among species or transport methods (Tucker 1970) and can influence interindividual differences in behaviour, the relevance of optimal movement speeds in social behaviour has not been examined.

Theory predicts that voluntary speed reflects minimisation of the cost of transport (i.e. the energy used for a given distance travelled), which occurs at a locomotor speed that is a fraction of maximal speed (Weihs, 1973; Pettersson and Hedenstrom, 2000; Wickler et al., 2000; Claireaux et al., 2006; Palstra et al., 2010). In reality, however, voluntary movement speed will likely differ from optimal speeds due to various trade-offs associated with foraging, predator avoidance, or dispersal (Weihs, 1973; Irschick and Losos, 1998; Husak and Fox, 2006; Humphries et al., 2010; Wilson et al., 2013). In addition, due to among-individual differences in optimal speeds, some individuals in moving social groups are likely to deviate from their own optimum speeds, to a greater extent than others, to maintain group cohesion and continue to derive the benefits of group membership. The extent to which such a compromise occurs, has not been studied, but the accumulation of excess and uneven movement costs among group members could constitute an unrecognised cost of social group membership. In addition, inequality in the locomotor costs among group mates may influence leader-follower dynamics within groups, especially if leaders are more likely to move near their own optimal speed while others are forced to conform but swim at speeds that, for them, are non-optimal.

Coordination of group behaviour is achieved via consensus reaching, which involves a compromise for some group members that deviate from their own optimal patterns of behaviour (Plaut, 2001). Consensus can either be driven by influential individuals, causing a hierarchal leadership influence (Nagy et al 2010; King et al 2008), or decision-making can be distributed among multiple individuals (Strandburg-Peshkin et al., 2015; Gall et al., 2017). Regardless of leadership via one or multiple individuals, the other members must copy these movements or risk losing spatial cohesion and the benefits of group membership (Conradt & Roper, 2005; Couzin et al., 2005; Ioannou et al., 2015). Leadership can be defined as a disproportionate influence on collective movement, through

spatial position (Pettit et al., 2013b), behavioural similarity (Harcourt et al., 2009a) or directional correlation delay (Nagy et al., 2010). Further, the manner in which leaders exert influence and followers respond can be affected by individual differences within the group related to movement speed (Petit et al 2015), experience (Flack et al 2012), behavioural phenotype (Sasaki et al., 2018) or physiology (Ward et al., 2018). In addition to increasing the locomotor costs for specific group members, heterogeneity in optimal movement speed or minimal costs of transport within groups could alter the influence that leaders are able to have within their social groups or the capacity of others to follow, therefore possibly disrupting overall group cohesion, coordination, and the emergent benefits of grouping.

Using zebrafish (*Danio rerio*) as a model, I explored how indidivual cost of transport per unit distance varies with group size, and how variation from optimum swim speed is related to overall group behaviour and individual behaviour within groups. Zebrafish are a shoaling species that will swim individually in swim tunnel respirometers, thus allowing their cost of transport per unit distance to be accurately estimated on an individual basis. By measuring optimum swim speed in individuals and voluntary swimming behaviour when alone, in pairs, and in groups, I investigated whether individual optimum swim speed affects leadership, whether cumulative cost of transport while moving is affected by individual optimum swim speed and leadership, and whether group size alters the cumulative cost of transport during routine swimming. I predicted that: (1) Individual optimum speeds are linked to leadership in groups, (2) individuals who lead group movements will display the least compromise, in terms of deviating from their own optimal swim speed; and (3) individuals will compromise their optimum swim speed to a larger degree while in a group compared to in pairs and alone.

5.3 Methods

5.3.1 Animals

25 zebrafish (*Danio rerio*) total were selected randomly from five different families (5 fish from each family) and kept in aquariums in University of Glasgow in accordance to UK Home Office regulations. Fish were housed in the same tank (30 cm×40 cm×30 cm) and maintained at 28 °C (± 0.5 °C) throughout the trial period. The tank was supplied with UV treated recirculating water. Fish were fed daily with a combination of commercial fish flakes and live *Artemia* nauplii, except when fasted prior to experiments, and maintained on a 13:11 hour light:dark photoperiod. Fish were approximately 8 months old at the start of the trial (reared at University of Glasgow from May 2018) and 10 months at the end of the trial. Fish were tagged with visual implant elastomer (VIE) (Northwest Marine Technology, WA, USA) one month before trials began (Rácz et al., 2021) and measured at the beginning and end of the investigation period for standard length, total length, and wet mass. Sex was also noted. Sex and family were identified before selection to ensure fish of different families were tested in pair and group behavioural trials fish to control for potential familial effects. Both males and females were tested In trials fish of the same sex were used to avoid aggression between the fish. Pairs and groups were selected to ensure fish were not tested with the same fish more than once.

5.3.2 Swimming Performance

Measurements of individual swimming performance and cost of transport were conducted in a Blazka-type swim-tunnel respirometer (Loligo Systems, Denmark) measuring (ID 26.4 x L 100 mm, Volume: 170 mL). Water flow through the working section was made laminar by a honeycomb lattice. Flow speed within the tunnel was controlled with motor and external control box, calibrated using a laser digital particle tracking velocimetry and associated software(Loligo Systems, Denmark). Temperature of the swim tunnel and surrounding water bath was maintained at 28 C (+- 0.1 C) to match fish holding temperature and an air stone was placed in the water bath to maintain oxygen content of water entering the chamber. A camera was placed above the swim tunnel respirometer and the top and sides of the swim tunnel were covered in black plastic to

prevent disturbance except window for camera to record fish behaviour and identify the speed threshold where burst swimming, and thus anaerobic movement, occurred. Water oxygen content was measured every 2 s using a Firesting oxygen meter and associated sensors (PyroScience GmbH, Aachen, Germany). Oxygen content in the swimming tunnel was kept above 80% air saturation at all times via intermittent flushing of the chamber using a pump system (6 minute measurement period: 2 minute flush).

Prior to swim tunnel trials, individual fish were fasted for 24 hours to account for the metabolic cost of digestion before being transferred in water using a funnel to the respirometer to prevent air exposure and additional stress. Fish were acclimated in the swim tunnel for approximately 12 hours overnight while swimming gently at 2 body lengths (BL)/s (Plaut, 2000). During the trial, flow speed was increased by 1 BL/s per speed increment, and three flush/measurement cycles were measured per speed increment. The trial ended when fatigue occurred, defined as the point when the fish could no longer maintain swimming position and made contact with the downstream grid of the respirometer for 2 seconds. When fatigue occurred, swim speed was recorded, then flow speed was immediately lowered to 2 BL/s and fish were left to recover for at least 30 minutes before being returned to their holding tank (Hammill et al., 2004; Seebacher et al., 2015).

Fish were fed as soon as they exited the respirometer and returned to their tank. Fish were tested twice to measure the repeatability of the U_{opt} protocol, with at least 24 hours between tests to allow for recovery. Fish were not tested more than twice to prevent training effects. Before and after each swimming trial, three measurements of oxygen consumption were taken to account for bacterial respiration.

To calculate cost of transport (Tucker, 1970), speeds at which burst swimming occurred were not included for each trial calculation. Using individual oxygen consumption (MO_2), a polynomial curve (k = 2) was fitted to the data and the parabola of this curve was identified to estimate minimum cost of transport (COTmin), and the speed at which this occurred (optimum swim speed; U_{opt}), where:

$$COTmin = min\left\{\frac{MO_2}{swim\ speed}\right\}$$

For two fish, one trial each was excluded due to disturbance and stress which caused the oxygen consumption during these trials to be unusually high. Mean COTmin was taken of the two trials where possible and, from this value, optimum swim speed (BL/s) was calculated by locating the lowest point or parabola in these curves (Figure 8.3-1)

5.3.3 Behaviour

After optimum swim speed trials for each individual, fish were allowed to recover for at least 48 hours. Individual fish were placed in isolation and fasted for 24 hours before trials, then placed in an oval arena measuring 65 x 45 x 6 cm. Water was replaced every trial to control for any olfactory effects and water was aerated using an air stone. Water temperature was controlled to 28 ± 0.1 °C using a heating coil and the in-flow and air stone were located outside of the trial arena to encourage consistent water temperature and aeration across the arena. Fish acclimated for 20 min before recording started. Fish were tested alone twice, and once as part of a pair and once as part of a group of 4 individuals. Fish were tested under the same conditions as individual trials as in pair and group trials.

Fish swimming behaviour was recorded using a Sony Handycam FDR-AX53 4K for 20 minutes and subsequently tracked using idTracker (2014) to ascertain behavioural metrics for speed, position in school, and propagation of movement through acceleration and turning (see Chapter 2 for details). Additionally, cumulative cost of transport was calculated by using each individual's cost of transport at each swimming speed, estimated from swim tunnel respirometry data from that individual. The cost of transport was then summed over the whole trial. For each individual in each trial, the difference (U_{diff}) between their average speed throughout the trial (BL/s) and their mean U_{opt}, where:

$$U_{diff} = \overline{Speed} - U_{opt}$$

5.3.4 Statistical Analysis

The consistency of an individual fish's U_{opt} (adjusted repeatability, R_{adj}) was calculated using the rptR package (Stoffel et al 2017). The overall R_{adj} using a LME structure, including total length to account for any variation in body size.

All statistical analyses were performed in R.4.0.5 (R development Core Team). Linear mixed effect models (lme4, lmertest) estimated using REML were fitted to predict mean cumulative cost of transport with either leadership rank while turning or accelerating in pairs and groups, and included Optimum swim speed rank (within each pair or group) and group size as fixed effects in both models and group_id as a random effect (Table 8.3-7; Table 8.3-8). Leadership rank while turning and leadership rank while accelerating were highly correlated (Pearson's: R(121) = 0.82, p <0.001) and therefore separate models were used to determine whether each of these indices of leadershp were related to indiviual Optimum swim speed. For all analysis, mean position was dropped from models due to non significance during model selection. Model selection was performed by sequentially dropping non-significant variables starting with lowest t-values, but were retained if their removal resulted in higher AIC values (ΔAIC > 2 Arnold 2010). A separate model was constructed ignoring leadership metrics and including all group sizes (alone, pair, group). For this (Table 8.3-10), cumulative cost of transport as the response variable including Optimum swim speed rank, mean swim speed, and all group sizes (alone, pair, group) as explanatory variables, and group ID as a random effect. Homoscedasticity and normality of residuals were assessed by visual inspection of residual plots, and used to determine transformation of data, where leadership metrics were scaled and transformed to positive axis.

5.4 Results

5.4.1 Does optimum swim speed affect leadership?

Optimum swim speed was highly repeatable (R_{adj} = 0.726, p < 0.001; Table 8.3-12; Figure 5.4-1). In both pairs and groups, U_{opt} had a no effect on leadership, with no link between U_{opt} and leading while either turning (R^2 = 0.13, p = 0.352) or accelerating (R^2 = 0.23, p = 0.109; Figure 5.4-2). Similarly, there

was no correlation between U_{opt} and mean swim speed (BL/s) in the open field trials (R^2 = 0.02, p = 0.794).

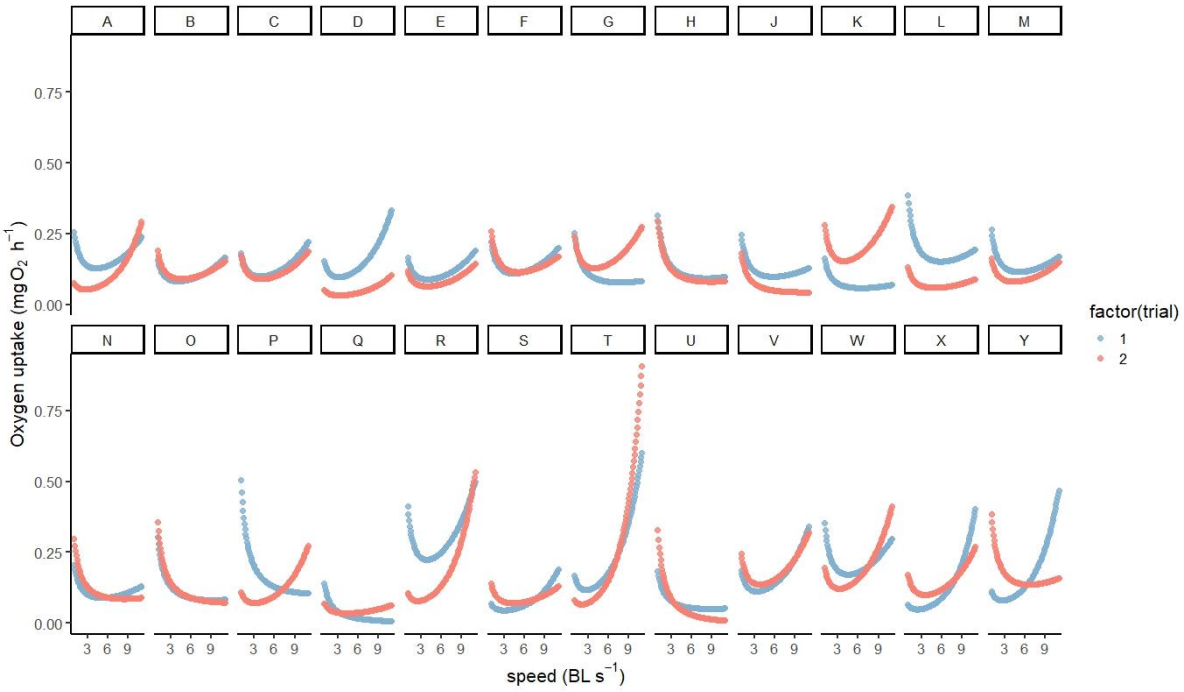

Figure 5.4-1: Results from swim tunnel respirometry for each individual. Different colour lines represent the oxygen uptake for two trials for each individual (separated by panel). U_{opt} calculated from mean parabola of curves.

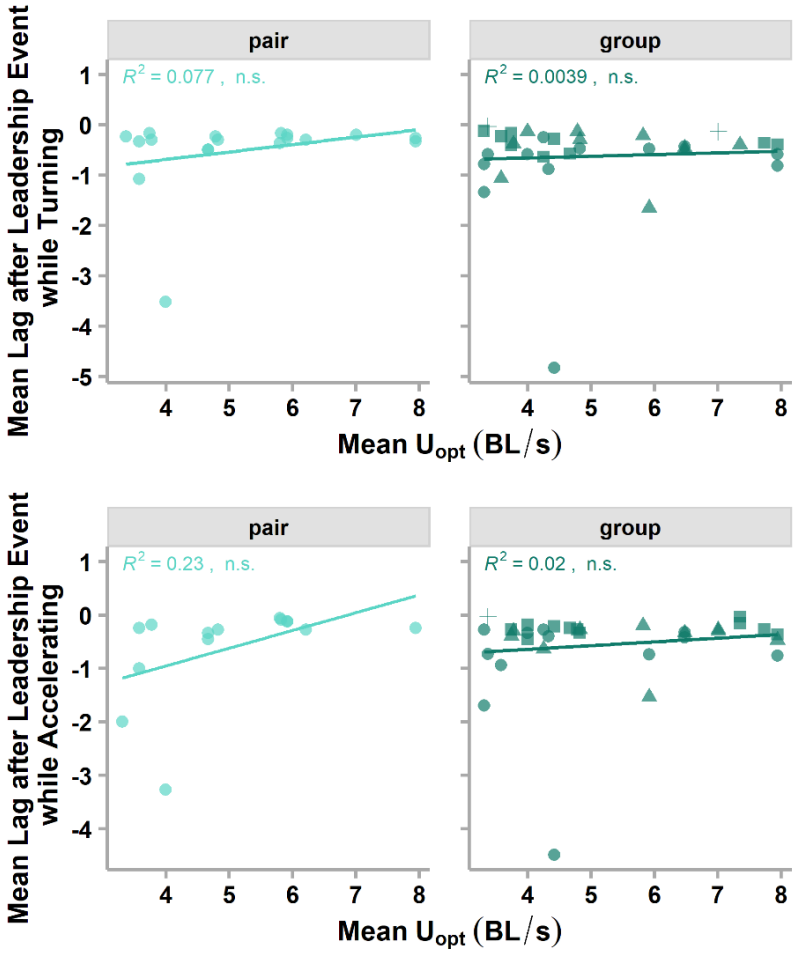

Figure 5.4-2: Scatter plots to show optimum swim speed (Uopt; BL/s) for each individual fish and leading response while turning (A) and accelerating (B) in pairs and groups. For both leadership when accelerating and leadership when turning, a general linear model has been fitted.

As with the previous chapters in this thesis, correlations were conducted between the measures of leadership, separated by group size. Leadership while turning and leadership while accelerating was not correlated with spatial relative positioning while moving in either pairs or groups (Table 5.4-1; Figure 5.4-3), however leadership while turning and accelerating were positively correlated (pair: ($r = 0.996$, $p < .001$; group: $r = 0.96$, $p < .001$). Data for one individual was highly influential on this relationship, but leadership during turning and accelerating remained correlated even after removal of this individual (pair: $r = 0.95$, $p < .001$; group: $r = 0.78$, , $p < .001$).

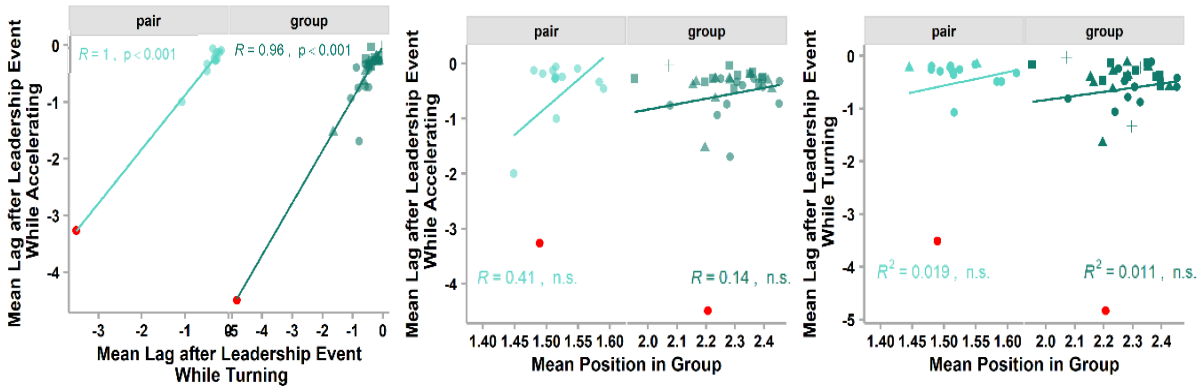

Figure 5.4-3: Scatterplots showing correlations among Leading while turning, leading while accelerating and mean position in group. Red dot indicates an influential point and outlier which was removed to check whether the two measures of leadership are still correlated. Trendlines here are to show the visual relationship between the two leadership variables.

Table 5.4-1: Correlations between leadership metrics for pairs and group trials.

Group Size	Variable 1	Variable 2	r	n	p - value
Pair	LeadTurnResp	LeadAccelResp	0.99	13	p <.001
	LeadTurnResp	AvePosSchool	0.14	18	n.s.
	LeadAccelResp	LeadTurnResp	0.99	13	p <.001
	LeadAccelResp	AvePosSchool	0.41	14	n.s.
	AvePosSchool	LeadTurnResp	0.14	18	n.s.
	AvePosSchool	LeadAccelResp	0.41	14	n.s.
Group	LeadTurnResp	LeadAccelResp	0.96	31	p <.001
	LeadTurnResp	AvePosSchool	0.1	33	n.s.
	LeadAccelResp	LeadTurnResp	0.96	31	p <.001
	LeadAccelResp	AvePosSchool	0.14	34	n.s.
	AvePosSchool	LeadTurnResp	0.1	33	n.s.
	AvePosSchool	LeadAccelResp	0.14	34	n.s.

5.4.2 Cumulative cost of transport in group sizes

When comparing cumulative cost of transport across individuals in the different group-size treaments, there were weaker correlations between individuals moving alone and individuals in a pair (Pearson correlation: r = 0.42, t(120) = 5.03, p < .001), and those alone and in a group (r = -0.08, t(120) = -0.88, n.s), as compared to the correlation observed between those in a pair and those in a

group (r = -0.30, t(120) = -3.43, p < .001). There was a smaller change in cumulative cost of transport in a pair and in a group compared to when alone, and it was more costly to be alone than in any group size. Additionally, a higher cumulative cost of transport was incurred in the trials with fewer fish per group (Figure 5.4-4).

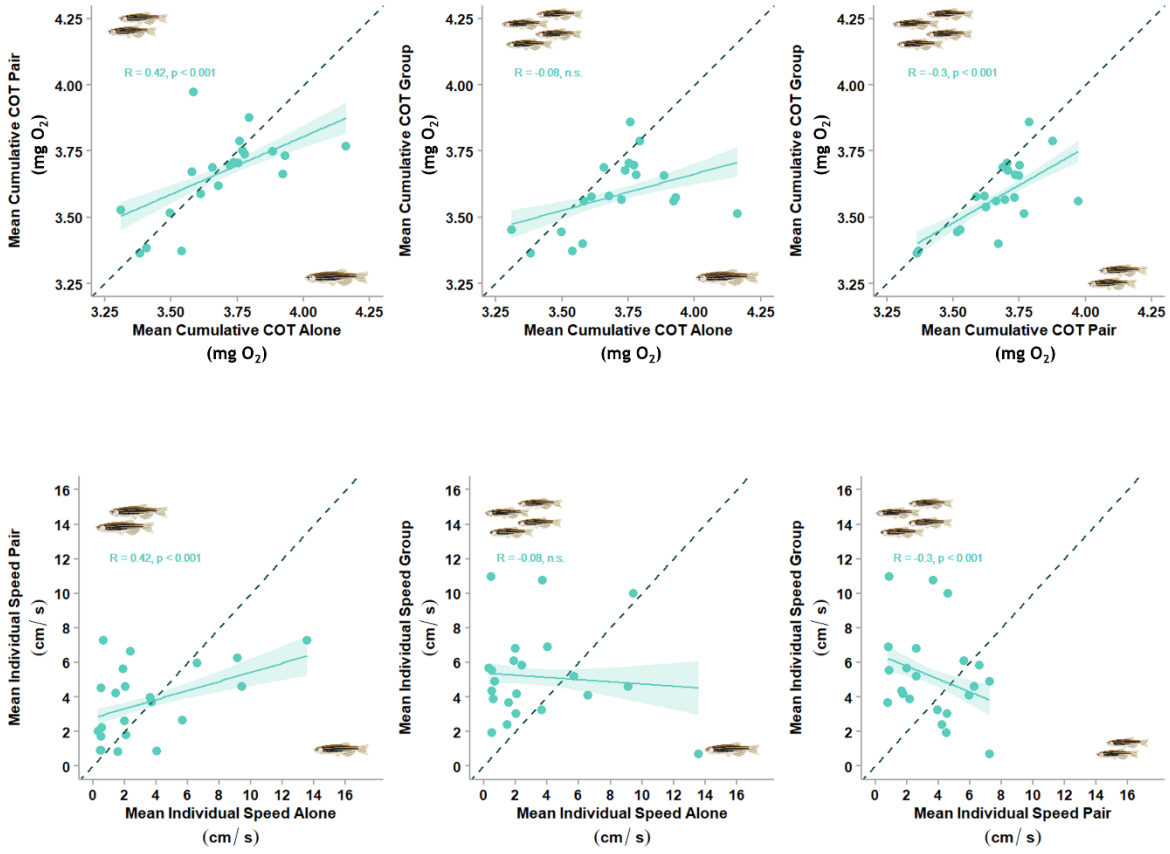

Figure 5.4-4: Scatterplots showing correlations between cumulative cost of transport between individuals in different group sizes (top row) and correlations between mean speed at different group sizes of individuals in different group sizes (bottom row): Alone vs Pair; Alone vs Group; Pair vs Group. Dashed line shows 1:1 line for comparison

5.4.3 Is cumulative cost of transport affected by leadership?

For all group sizes, there was no effect of mean swim speed on cumulative COT. Individuals in groups had a lower cumulative COT than single fish (t(117) = -2.66, p < .01; Table 8.3-2), and there was no difference in cumulative COT between

swimming in a pair and alone or in a group and a pair (Table 8.3-13; Figure 5.4-5). However, a more direct comparison of pairs versus groups, incorporating individuals within-group ranks for leadership when accelerating, leadership when turning, and U_{opt}, showed that individuals swimming within groups had a lower cumulative COT as compared to those swimming in pairs (Accel: $t(76) = -2.62$, $p < .01$; Turns: $t(76) = -2.78$, $p < .01$). .

For pairs and groups, within-group leadership rank while accelerating (Table 8.3-5) was not related to cumulative COT among individuals, but leaders while turning had a higher cumulative COT ($t(76) = 2.67$, $p < .01$; Table 8.3-4). However, individuals with a higher U_{opt} relative to others in their group had a higher cumulative cost of transport ($t(76) = 2.30$, $p < .05$). For both leadership while accelerating and turning, followers swam slower than leaders (Accel: $t(76) = -2.47$, $p < .05$; Turns: $t(76) = -2.96$, $p < .01$). There was no difference in mean speed between groups and pairs of fish. Within group rank for U_{opt} was not related to cumulative COT.

5.4.4 Is individual speed affected by the U_{opt} of leaders?

Mean speed for individuals was greater in groups than when swimming alone, but there was no difference between swimming speed in pairs and groups or pairs and alone ($t(115) = 3.54$; Table 8.3-6). Larger fish in groups swam slower than smaller fish ($t(115) = -3.41$, $p < .001$), but this was not the case in pairs or when swimming alone.

Individuals in groups with lower U_{opt} deviated more from their U_{opt} (U_{diff}) while swimming than individuals with higher U_{opt} ($t(117) = -9.80$, $p < .001$); Fish deviated more from their optimum swim speed when swimming alone compared to groups, and those swimming in pairs deviated more from their optimums compared to groups (Table 8.3-1).

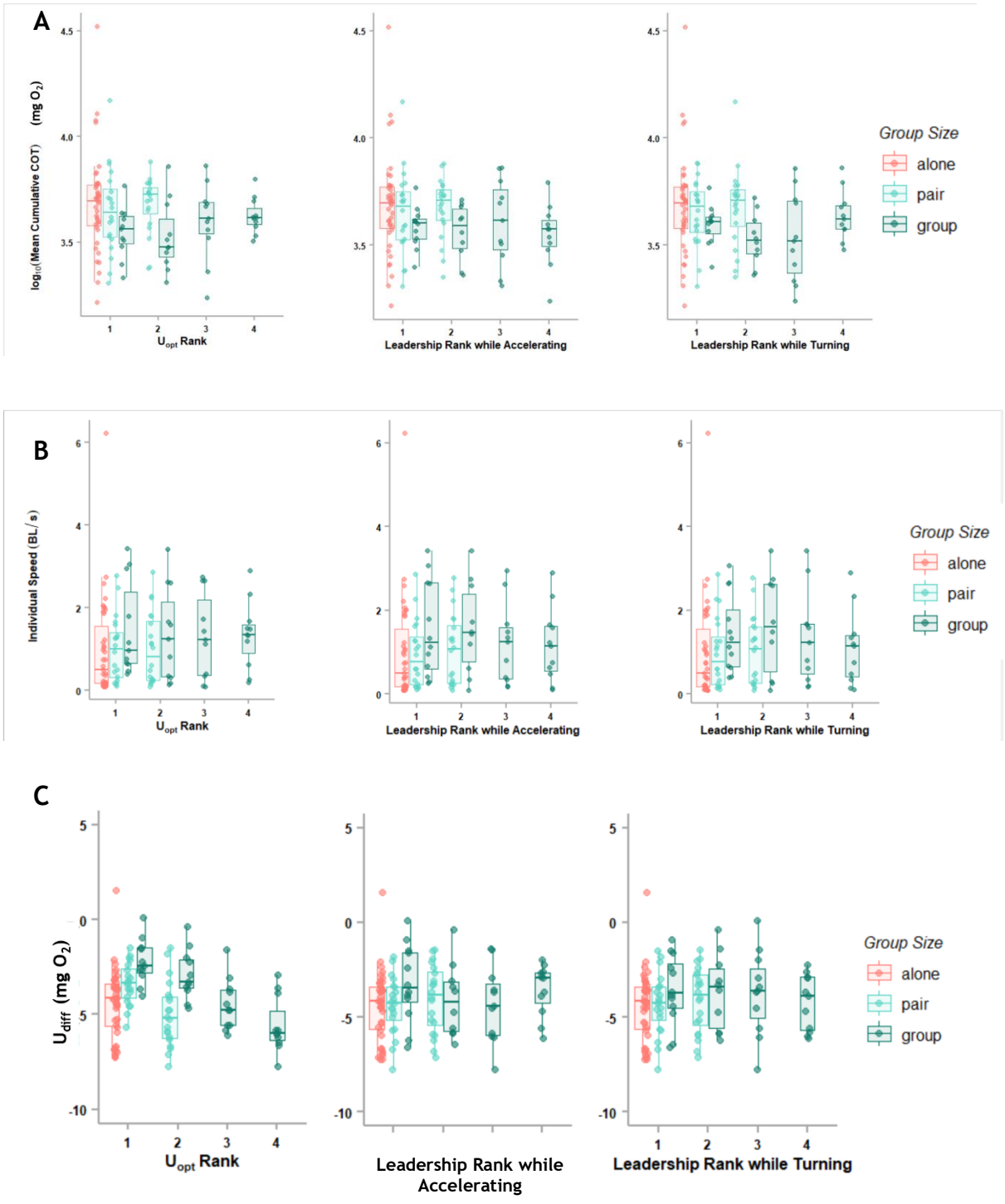

Figure 5.4-5: Boxplots to show the relationship for A) Individual mean cumulative cost of transport, (b) Individual Speed and (c) difference between optimum swim speed and mean voluntary speed of group compared to rank of optimum swim speed (left), leadership while accelerating (centre) and leadership while turning (right) where 1 is the lowest optimum swim speed and indicates leadership while accelerating or turning, and 4 indicates higher optimum swim speeds and followship after a leadership event.

5.5 Discussion

My results show that higher cumulative locomotor costs are incurred in groups with fewer individudals, where swimming alone is the most costly, followed by swimming in a pair, while swimming in a four was the least costly. It is notable that this difference in locomotor costs is due to inherent differences in swimming efficiency while moving at different speeds, and not due the to hydrodynamic benefits of swimming in formation that is normally the focus of studies examining the energetic costs of swimming in groups. Optimum swim speed was not a predictor of individual speed in the open field arena, suggesting that fish do not voluntarily swim at their theoretical optimum for minimising the costs per unit distance travelled. Optimum swim speed was also not linked to leadership through propagation of movement or position in school in pairs or groups of fish. There was no evidence that followers within groups are influenced to swim at speed closer to the U_{opt} of the groups' leaders as compared to their own, with no consistent effects of leadership on the cumulative COT experienced by individuals. This study confirms that while leadership is not any more or less costly than following, in terms of transport cost per unit distance travelled, swimming in groups appears to shift the balance of the trade-offs associated with engaging in activity, such that all group members can increase their efficiency of movement by swimming at speeds closer to their U_{opt} relative to if they are swimming alone. Still, however, those individuals with the lowest U_{opt} within groups accumulated the greatest locomotor costs, suggesting there remains some imbalance among individuals in the energetic costs and benefits living and moving in groups.

Individual optimum swim speed was not related to voluntary swim speed in any group size. While theoretical work suggests that voluntary swim speed may align with that which provides the minimum cost of transport (Pettersson & Hedenström, 2000; Claireaux et al., 2006; Palstra et al., 2010), empirical work suggests that individuals will often move at speeds slower than their predicted minimum cost of transport. This is because other factors, such as predation risk or the physiological constraints of foraging may also shift behaviours away from predictions based on efficiency (Higham et al., 2015). Functional demands of prey capture (Han et al., 2017), or conservation of aerobic scope (Killen et al., 2007), may all cause individuals to deviate from their predicted optimal speed.

In the current study, I observed that although fish in pairs and groups did not display a statistically significant increase in mean movement speed, the trend toward increased speed that was observed was biologically significant in that it decreased the predicted cumulative COT of group members. While swimming alone, individuals may have swam moderately slower or in a more saltatory manner, causing them to incur a greater cumulative COT per unit distance travelled. Fish in groups swim marginally faster, probably due to a reduction in perceived risk, but are also more likely to swim continuously with reduced need for constant costly bouts of acceleration or deceleration. Increased energetic costs typically arise when stabilising swimming posture and maintaining direction at lower speeds, and swimming against disturbing frictional forces at higher speeds. While there is likely to be a small energetic cost to pigeons that compromise on speed to fly in a flock (Sankey et al., 2019), this does not appear to occur for zebrafish swimming in schools. Previous work has shown fish swimming alone do not receive the energetic benefit of swimming with a group (Marras et al., 2015b) due to not being able to take advantage of the vortices produced by groupmates to help propel their own forward movement. Additionally, there may be increased energy use while swimming alone, due to the stress of social isolation, which can not be measured by examining movement patterns (Nadler et al., 2016; Rupia et al., 2016). Deviation from this optimum when swimming voluntarily demonstrates how an individual's energy is partitioned into locomotion and estimate remaining capacity for expressing behaviours and other physiological processes. My results show that individuals in groups may be able to conserve additional energy while swimming due to a reduction in the cost of transport per unit distance, and may allow energy to be used on other physiological processes such as growth or reproduction.

While fish in groups displayed an overall decrease in cumulative COT compared to those swimming alone, there was a large degree of within-group individual variation in locomotor costs per unit distance. This indicates that the costs and benefits of group membership are not equal among groupmates, regardless of the overall locomotor benefits of moving in a group. The cost of compromising energetically optimum swim speeds could possibly be offset through behavioural adjustments. For example, fish that incur an increased COT due to strong deviations from their own U_{opt} could choose spatial positions within group that

allow them to further reduce their locomotor costs by taking advantage of vortices produced by groupmates (Usherwood et al., 2011). In any case, differences in the total energy devoted to movement among groupmates due to inequalities in the COT would represent a costs of group living that has so far been overlooked, but could greatly affect the residual energy that individuals can allocate to other physiological processes (Sumich, 1983). While I found no evidence to suggest that leaders were directly influencing the cumulative locomotor costs incurred by groupmates, it is still possible that heterogeneity in factors such as U_{opt} and minimum COT could encourage group splitting or assortment to reduce the compromises being made by specific individuals within groups (Couzin, 2006).

Cumulative cost of transport was not linked to leadership or relative U_{opt} within groups , indicating that leadership may not cause groupmates to incur more energetic cost in the form of speed or movement by following. Group behaviour is likely to be governed by local interaction rules in response to external environments, and individuals are hypothesised to modulate their behaviour in terms of their cohesion and speed to maintain group structure (Couzin et al., 2002). Slower individuals will be able to maintain their position at the rear of the group due to social forces, unless they are physically unable to keep up, despite the increased energetic cost (Herbert-Read et al., 2011; Katz et al., 2011; Jolles et al., 2017). Similarly, faster individuals may slow down as their distance increases from the front of the group to stay with the group (Jolles et al., 2017). It was assumed that leadership would cause some individuals to vary from their optimum more than others in a group, by swimming faster or slower than their optimum. However, differences in cost of transport are not linked to leadership, and there is no difference in leadership between pairs and groups, suggesting that members of the group must be reaching a consensus in locomotion speed. This corroborates (Sankey et al., 2019) with the goldilocks principle, where birds deviate from their preferred individual speed to fly at as part of a group, which may not be the physiological optimum. In this case, while fish reached a consensus of speed to stay within group, this was faster than their optimums. Given that relative within-group optimum swim does not affect which individual is the leader, and individuals that lead do not differ from their U_{opt} in mean swim speed more or less than followers, it is apparent that while there are

imbalances in the cumulative costs that individuals occur while moving in groups, this inequality is not directly related to leader-follower dynamics and is more due to the physiolgoical, behavioural, and morphological characteristics of individual fish.

Leadership metrics while turning and accelerating are correlated with each other but not position in school, suggesting that leadership does not always come from the front of a group. Previous work in pairs of fish (Ward et al., 2004; Nakayama et al., 2013; Jolles et al., 2014) have only used position in school as a proxy of leadership, especially in pairs. Leadership is often linked to position in school and the frontal positions in school are more energetically expensive, while fish at back of school do not have as much hydrodynamic expense. When investigasting leadership in groups in behavioural assays, position in school is not the only important metric of behaviour to consider when analysing collective behaviour, and propagation of movement must be considered. As leadership through propagation of movement is not related to position in school, it suggests that if there are other energetic costs of leadership rather than cost of transport, the cost of leadership does not change. Additionally, social animal groups including mammals such as horses, primates and marine mammals have displayed social hierarchy and dominance behaviour which indicates which animal is leading, and not necessarily from the front (King & Sueur, 2011; Lewis et al., 2011; Krueger et al., 2014; Tokuyama & Furuichi, 2017). In synchronous groups where individual identification is more difficult and hierarchies are less obvious, leadership may be more nuanced. In pairs of pigeons, Petit et al. (2013) found interaction rules were mediated by turning responses, not acceleration and deceleration. This suggests that individuals could fly at their preferred speeds and faster individuals could turn more while allowing the group to remain cohesive. Indeed, it was observed that individuals who led via turning propagation of movement also led via acceleration. However, relating this to physiological capacity for movement has yet to be confirmed, as propagation of movement and initiation of turns and acceleration may also incur cost in a moment-to-moment basis, and therefore warrant analysis on a smaller time scale.

In conclusion, I show that leadership is not necessarily linked to locomotor capacity as expressed in optimum swim speed or cost of transport, confirming that fish tend towards consensus. Deviation from optimum swim speed and cost of transport is one proxy which can provide vital information for individual state space movement models which can integrate social aspects into movement predictions. Models are available which use water depth, velocity and turbidity to look at bioenergetics in specific modes of activity i.e. foraging (Jowett et al., 2021), but it is important to consider inter-individual interactions when predicting schooling behaviour using inference models. Individuals may alter their movement in relation to their physiology and social scale, and may contribute to models of bioenergetics in specific modes of activty. The present study forms the foundation for the investigation of how physiological capacity affects individual and group level mechanisms influencing collective movement. Previously, deviation from individual optimum locomotion speed and incurring cost of transport has rarely been considered in social behaviour, and linking this to leadership is novel. Leadership is not linked to optimum swim speeds or cumulative cost of transport which adds to increasing knowledge of what makes a leader, and how groups react to behavioural and physiological heterogeneity. Cost of transport is just one measure of bioenergetics of leadership and it is imperative for future work to identify other hidden energetic costs and benefits to group living.

6 General Discussion

6.1 Summary

Environmental variability affects group movement and this is integral to understanding collective behaviour. By using fish of different species as models, and integrating behavioural analysis with physiological data, I have shown that leadership in schools of fish changes under different environmental or social conditions. While specific metabolic traits may not be directly related to individual leadership, both metabolism and swimming performance can play important roles in driving group behaviour. By quantifying the movement of individuals in groups, across different environmental contexts, I have gained novel insights into how physiology interacts with behaviour and how this may be applied to larger groups in the wild.

The studies presented are among the first to thoroughly link different forms of leadership in groups to physiology and variation in environmental context. Previous studies have explored how group behaviour changes in different contexts, or how leadership is displayed in groups, but not at how leadership changes with the environment. In the last decade the ability to track animals in the lab has progressed enough to make strong conclusions, and there has been an increased need to understand how changing environments affect physiological and behaviour ecology. Prior to this, research on leadership in animal groups was relatively scarce. Measuring group behaviour and leadership in the field is near-impossible in groups of fish where animals are difficult to observe, and individuals may be recruited to (or leave)the group at any moment. It is also complex to gather individual physiological measures in the wild and tag individuals in a short amount of time without altering their behaviour. Finally, the environmental conditions are shaped by many abiotic and biotic factors which will change with time and space, therefore it is difficult to measure behaviour consistently and accurately while attributing behavioural changes to the correct environmental factor.

Chapter 2 explains how behavioural metrics were calculated using individual identity tracking and geometry. Temporal correlations and position in group relative to direction was used to identify leadership rank. Coordinate data was used in the calculation of polarity, cohesion, speed and distance. This work underpinned the

remainder of the thesis and was itself a major contribution to the field. Although there are various software packages available for the tracking of animal movements in experimental settings, most of these simply output a series of x-y coordinates, leaving it up to the user to turn these into useful data. While many of the subsequent calculations are relatively straight-forward (e.g. for calculating speed or distance moved), many are complex, including those required for group cohesion, polarity, and the spatial positioning of individuals within groups. My work in coding these calculations allow the relevant metrics to be quickly calculated from any dataset with x-y coordinates from individual animals, and I anticipate these functions will be of great use to researchers in this field going forward.

Chapter 3 explored the relationship between metabolic composition of groups, group behaviour, and acute temperature exposure in *P. phoxinus*. Here I asked whether group composition of high, medium, and low or a mix of metabolic rates affected group swimming behaviour, and whether an acute rise in temperature changes this behaviour. Individual leadership while turning or accelerating and position in school was not affected by metabolic phenotype. While metabolic composition in groups did not have a consistent effect on group behaviour, groups with different compositions reacted differently to temperature increase. In medium and mixed groups at 18 °C followers did not respond as quickly to leaders while turning and accelerating as compared to when tested at 15oC. In high groups, followers did not respond as quickly in leadership when accelerating at 18C, in comparison to low groups. Leadership while turning is more stable and consistent at 18 °C compared to 15 °C but this is not the case while accelerating. At 18 °C, fish generally swam faster, were more polarised but were less cohesive.

In Chapter 4, I looked at how feeding behaviour and subsequent energetic costs of digestion affects group behaviour, where individuals in groups were allowed to feed and then behaviour measured for the next three hours. Their behaviour was then examined in relation to specific dynamic action, and whether individual capacity for digestion was linked individuals behaviour in groups and well as the behaviour of the group as a whole. Feeding altered the behaviour of leaders, where individuals that ate more were likely to be leaders while turning, and those that ate less were more likely to be leaders while accelerating. Individuals that ate more moved to the front of the group over the course of the trial. In feeding trials, fish reacted slower when a leader was turning compared to control groups, and reacted faster to

leaders that were accelerating. After feeding, polarity, cohesion and speed of groups changed with time since feeding.

Finally, in Chapter 5 I examined the interplay among leader-follower dynamics, optimal movement speed, and cumulative locomotor costs of individuals in moving groups. Higher cumulative swimming costs are incurred in groups with fewer indiviudals, where swimming alone is the most costly group size, interms of cost of transport per unit distance. Fish did not voluntarily swim at their optimum swim speed, and optimum swim speeds were not related to leadership through propagation of movement or position in school. Leadership was also not related to degree to which fish deviated from their U_{opt} while swimming, in pairs or in groups. Accordingly, leaders did seem to directly influence the swimming speed of the rest of the group, suggesting that individuals reach a concensus swimming speed.

6.2 Metabolism, Temperature, and Leadership

Metabolic traits are often been correlated with behaviours that can in turn be associated with leadership (Nakayama et al., 2016). In specific contexts, for example, metabolic rate is positively correlated with boldness, activity, and associability, all of which have been observed to be linked with spatial positioning within groups (Killen et al., 2012b; Metcalfe et al., 2016). An animal's aerobic scope is influenced by their standard metabolic rate, and aerobic scope may be related to the spatial position of individuals within moving groups, due to effects on locomotor capacity or motivation (Killen et al., 2012b; McLean et al., 2018). I show here that neither position in group nor temporal correlations of leadership were related to metabolic traits, suggesting that metabolic rate is not a driver of leadership in groups. If leadership was highly dependent on metabolic rate, I would expect to see differences groups with different metabolic compositions, and differences among individuals exaggerated in mixed metabolic composition groups (review by Jolles, King, et al., 2020). However, my results suggest that leadership may still be related to internal state and be changed with environmental stress. Although there is no link between standard metabolic rate and leadership, increasing temperature alters leadership in groups depending on

metabolic composition, indicating that low metabolic rate individuals reacted more than other groups to leaders at 18 °C. In general, all groups swam faster at 18 °C, so for low metabolic rate fish to be reacting to an even greater extent to this temperature increase suggests that they may be experiencing higher stress than individuals in the other groups (Svendsen et al., 2021). In general, fish at higher temperatures reacted slower to leaders and were less synchronised in their movements, indicating that even though higher temperatures may not directly affect individual leadership, physiological disruption affects group behaviour. Our findings suggest that while individual capacity for leadership within a group may not always have a strong bioenergetic basis, acute temperature change can disrupt leader-follower relationships and group functioning, which compliments studies showing that decision making and routine behaviour are affected by temperature increase (Prosser & Nelson, 1981; Reilly & Thompson, 2007).

6.3 Food availability and Leadership

More consistent feeding is one of the most important benefits of living as part of a group, and understanding how leadership and group behaviour intersect with feeding behaviour is critical to our understanding of populations (Hirsch, 2007b; Ioannou et al., 2019). My work shows that where individuals that ate more were likely to be leaders while turning, and those that ate less were more likely to be leaders while accelerating, suggesting that leadership may be linked to energetic state, but more influential than individual feeding success is whether any fish in the group fed, i.e before and after feeding. More information is needed about individual trade-offs of group living, namely, if schooling fish could have an unlimited number of food items before group motivation changes, would we expect to see equal distribution of food items, informing us as to how feed availability affects group behaviour in the wild. Before and during feeding, fish that ate the most were followers when a leader was accelerating, but fish that ate more during feeding were more likely to lead group changes in directionality via turning. After feeding, during digestion, there was no association between meal size and leadership while turning or accelerating, or position in school. After feeding, however, individuals reacted quicker to leaders, which could be

related to information transfer in the group, rather than leadership specifically (Sueur et al., 2009; Ioannou et al., 2015). If there is more potential food in an arena, it would make sense that groups would react faster to acquire more food. My work showed that behaviour while feeding may be very different to post feeding. This could be because individuals within groups modulate their behaviour to maintain positions, however individuals did not have repeatable positions in school.

My work highlights the need to understand consequences of locomotor constraints for group leadership and understanding if there is physiological constraint on occupying leadership roles. In chapter 3, I also observed behavioural changes with environmental change, with increases in temperature, leadership stability and consistency decreases, likely due to physiological response to stress. In chapter 5 I observed that followers do not compromise their optimum swim speeds differently than leaders, showing that while leadership may be linked to aspects of physiology, the traits I focused on may not be directly related to swimming performance under the conditions studied.

6.4 Locomotor performance and Leadership

In chapter 4, I show that leadership through propagation of movement or position in school is not linked to an individual's optimum swim speed. Similarly, leadership is also not linked to deviation from optimum swim speed, showing that leaders in groups do not influence groups to swim at their own optimum swim speed. I also show that leadership may not incurr more energetic cost in movement than following. Chapter 4 results are interesting to compare to chapters 3 and 5, where physiological capacity does not consistenly affect individual leadership, but does affect group behaviour and coordination. This study confirms that leadership is not more costly in terms of transport speed, and overall swimming in groups is less costly than swimming alone. Leadership when acceleratying tended to be less costly than leadership while turning. Linking chapter 5 trends to results of chapter 4, where those that ate more were likely to be leaders while turning, suggests that there may be unidentified physiolgoical consequences of different modes of leadership. Past work in birds has shown that individuals reach a concensus on travelling speed, which is an

average of all indidivuals preferred swim speed (Sankey et al., 2019). Here, I saw that leadership metrics are not related to influence on group speed, and yet a concensus movement speed is also reached. While I measured cumulative cost of transport over the trial duration, it would be interesting to investigate the exact cost of leading while accelerating or turning in comparison to position in school, or as a measure of efficiency (Faustino et al., 2017). Interestingly, pairs and individudal fish may be experiencing a level of stress which may not be reflected in our cumulative cost of transport data. Ionly examined female fish, to decrease chances of chasing in pairs, through aggression or mating behaviour, but there may have been interactions we did not catch in our video analysis (Bass & McKibben, 2003). Also, when alone, fish may have not exhibited normal volitional swimming behaviour as part of a stress response to not being part of a group in a new environment. While cost of transport and optimum swim speed are not correlated with position in school or leadership, only pairs or groups of four were tested, so this work provides initial data to ascertain whether this non-correlation is seen in larger groups and in more complex environments.

6.5 Future Work

It is clear that there is still much to be done to understand leadership in moving groups. One of the prevailing themes of this thesis is that temporal correlations of movement, i.e. leadership when turning and accelerating are not necessarily linked to spatial positioning within moving groups . Many previous studies discuss how leadership is correlated to behavioural phenotypes, or how leadership emerges in different environmental contexts (Leblond & Reebs, 2006; Kurvers et al., 2009; Bevan et al., 2018). Future work might give more consideration to the suitability of the form of leadership being examined in relation to the study question. Past work has had much success defining leadership by social rank, movement and dominance cues, however these social groups often have complex and pre-determined social structure, such as baboons (Strandburg-Peshkin et al., 2015) or orca (Croft et al., 2011b), where the leader can be identified through more than one mode of movement or signal. It is important to consider that while these individuals may have experienced similar situations to those depicted in these experiments (e.g. feeding events and groupmates) before experimental trials, looking at emerging leadership in these novel set ups is critical to determining whether leadership is

purely based on physiology. By testing individuals with no prior knowledge of the experiment, we show that leadership is not reliant on physiology and that context over longer time scales or learning is imperative to consider in future work.

Realistically, including individual tracking in every behaviour study of fish groups may not be possible due to time and computing constraints of frame by frame individual identity tracking and extracting leadership metrics. For example, in experiments looking at pairs of animals, leaders are usually quantified as the individual at the front of the pair. However, I show mean lag after a leadership event while turning and accelerating is not correlated to position in group. This lack of relationship highlights that some other method of quantifying leadership is required to understand the initiations of moment-to-moment movements of groups. It would be interesting to be able to mathematically quantify if leadership occurred from the edges or periphery of groups in larger school. Those on the edge of the group may have access to the same information that a fish in the front has, but may be benefiting energetically from less hydrodynamically expensive spatial positions (Abraham & Colgar, 1988; Deng & Shao, 2006). More recent tracking software such as Trex (Walter & Couzin, 2021) can identify individuals and also their field of vision, which would be interesting to see how leadership propagates through a group in relation to vision.

It is human nature to attribute patterns we recognise in ourselves in other organisms. Biologists commonly anthropomorphise animals, explaining movements and behaviours with principles that we have identified in our conspecifics. Despite the relatively small group sizes we have used in this work, where leadership is not identifiable in any one individual we could be seeing how self-organised groups start to operate (Ioannou, 2017). Swarm behaviour is the collective motion of self-propelled entities and is emergent from a group of animals and do not follow any central coordination (Hemelrijk & Hildenbrandt, 2012). There is a possibility that this is the case in this work, and generally in the study of leadership in fish, where overall order occurs through local interactions between parts of an initially disordered system (Ioannou, 2017). We must consider that some characteristics are unable to be quantified by our own characteristics, and use mathematical principles to be able to predict these movements. More likely, is that there are ways of communicating between fish and interaction rules we are yet to identify which dictate these leader-follower relationships.

Understanding the mechanisms how individuals perceive their social environment and decide leadership rather than focusing on which individual is the leader is the natural next stage to this research (Strandburg-Peshkin et al., 2018). Future research could focus on how sensory capacity and sensory cues can drive leadership in groups. Olfaction, hearing, gustation and vision are all critical in mediating physiological and behavioural responses to the environment, and understanding how these are used in group behaviour is currently unknown. Work has shown that olfactory cues are used in movement and orientation, but how differences in sensory cues relate to groupmates is an unknown area (Tavolga & Wodinsky, 1965; Kasumyan, 2000; Hubbard et al., 2002).

Future work will ideally explore different forms of leadership in groups in varying environments and experimental settings. This will allow us to understand the moment-by-moment changing dynamics in groups, and how groups react to different stimuli. Future work is likely to use telemetry tracking of whole populations with high resolution data to analyse leadership in groups on a large scale (Nathan et al., 2022). While this data nearly exists in lake ecosystems, not every organism in a population has been tagged, and the error margins for estimating exact individual positions to the degree in which you can predict leadership are still too large (Lennox et al., 2021). As accessibility of software and technological power to track individuals accurately in 3D space improves, our knowledge of how groups of fish interact with their group mates and environment will increase. This thesis looks at schooling behaviour in a two-dimensional plane, however, in their natural habitat, schools of fish are likely to occupy three dimensional space, and so leadership could also propagate through the z-axis, as opposed to what I have measured in my studies. The data presented in this thesis could inform agent based models, predicting how leadership or preferences effect individual decision making, social behaviour and aggregations in habitats (Alós et al., 2012). Knowledge will also inform further research when building theoretical models of group movement, allowing us to predict larger scale movements such as migrations or habitat shifts in reaction to changing climates.

Past work has explored leadership in terms of position in school in groups in a flow system, or in volitional swimming studies in still water, however it would be interesting to analyse how leadership and group behaviour presents itself in a stream system where groups are required to decide between volitional swimming

and exploration or maintaining positions within the water column. Differences in leadership in flow systems and volitional swim speed may allude to physiological differences in leaders from followers which we were unable to identify in this work. Analysis of individuals through genotyping via molecular genetics could highlight whether leadership is a heritable trait, and the extent to which leaders are born, not made (Árnason et al., 2009). Further physiological traits could be included such as measuring respiratory frequency via accelerometery and profiling of swimming performance (e.g. Stehfest*, 2003) to characterise leaders. Additionally, raising juveniles and incorporating some level of social learning into their upbringing compared to naïve fish could inform us how leadership develops in groups over time. Alternatively, this could highlight how information transfers through a group to maintain egalitarianism.

6.6 Conclusions

To conclude, what we understand about leadership and collective behaviour has vastly improved since technology is able to calculate metrics over more extreme time and spatial scales than we ever could before (Oudman et al., 2020; Lennox et al., 2021). Understanding how animal groups decide to move is critical to ecosystem health, conservation management or any species vulnerable to human exploit, whether by sustainable measures or not (Kölzsch et al., 2015; Biro et al., 2016; Sasaki & Biro, 2017). Research on leadership in fish is increasing in complexity, and the nuances surrounding behavioural and physiological phenotypes, and heterogeneity in groups is only just being understood (Jolles et al., 2020a). Unlocking the physiological principles underlying leadership in groups can provide us with insight to how populations may react in changing environments, which is becoming more crucial as planet earth experiences more extreme weather events and changing climates.

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8 Appendix

8.1 Chapter 3 Supplementary Materials

Table 8.1-1: Pearson's product-moment correlation between Mean Lag after Leadership Event while Accelerating and Mean Lag after Leadership Event while Turning. The correlation coefficient is indicated by r. 95% Confidence Intervals are represented by 95% CI, t shows the t statistic associated with the correlation and df indicates the degrees of freedom. P value indicates the significance of the result.

Group	r	95% CI	t	df	p- value
Low SMR:15 °C	0.74	0.56-0.85	6.90	39	<0.001
Medium SMR: 15 °C	0.92	0.67-0.98	6.37	7	<0.001
High SMR: 15 °C	0.69	0.45-0.84	5.30	31	<0.001
Mix SMR: 15 °C	0.76	0.55-0.8	6.24	29	<0.001
Low SMR:18 °C	0.79	0.63-0.88	7.88	38	<0.001
Medium SMR: 18 °C	0.98	0.95-0.99	24.98	31	<0.01
High SMR: 18 °C	0.42	0.008-0.71	2.11	21	<0.05
Mix SMR: 18 °C	0.61	0.33-0.79	4.17	30	<0.001

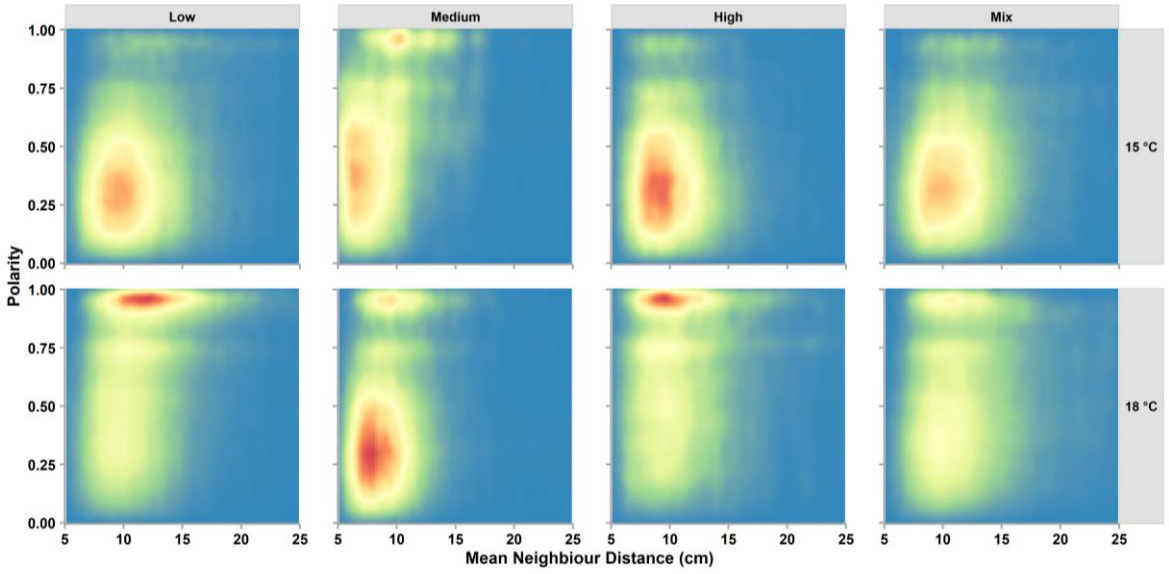

Figure 8.1-1: Density plot of Polarity (1 = aligned, 0, unorganised) and Minimum Neighbour Distance (cm). Plots show data for every available frame and individual and the majority (XX) of the data. Red indicates more time spent within those intersections of data and blue indicates no time spent within those parameters.

Table 8.1-2: Results of the best-fit model for Mean Lag after Leadership Event While Turning (LeadTurnResp). Results of the best-fit model from Table 8.2-11. Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors. Standard error in brackets in estimate column; statistic shows the t statistic associated with the variable and df indicates the degrees of freedom. P value indicates the significance of the result.

Coeffcient	Estimates	Statistic	df	p value
Intercept	-0.71 (0.07)	-10.21	144.12	<0.001
MMRrank	-0.02 (0.01)	-2.43	101.00	0.017
18 °C	0.01 (0.05)	0.13	137.94	0.897
Medium Metabolic Composition	-0.05 (0.08)	-0.69	171.88	0.494
High Metabolic Composition	-0.03 (0.07)	-0.42	122.05	0.676
Mixed Metabolic Composition	-0.04 (0.07)	-0.58	105.88	0.560
Random Effects				
σ^2	0.15			
$\tau_{00\ group:ID}$	0.00			
$\tau_{00\ ID}$	0.00			
N_{group}	18			
N_{ID}	122			
Observations	249			
Marginal R^2 / Conditional R^2	0.026 / NA			

Table 8.1-3: Results of the best-fit model for Mean Lag after Leadership Event While Accelerating (LeadAccelResp). Results of the best-fit model from Table 8.2-10. Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors. Standard error in brackets in estimate column; statistic shows the t statistic associated with the variable and df indicates the degrees of freedom. P value indicates the significance of the result.

Coeffcient	Estimates	Statistic	df	p value
Intercept	-0.84 (0.05)	-16.91	187.58	<0.001
18 °C	0.02 (0.05)	0.32	140.29	0.752
Medium Metabolic Composition	-0.03 (0.08)	-0.35	179.69	0.724
High Metabolic Composition	-0.04 (0.07)	-0.60	126.24	0.549
Mixed Metabolic Composition	-0.05 (0.06)	-0.82	105.16	0.416
Random Effects				
σ^2	0.15			
$\tau_{00\ group:ID}$	0.00			
$\tau_{00\ ID}$	0.00			
N_{group}	18			
N_{ID}	124			
Observations	257			
Marginal R^2 / Conditional R^2	0.003 / NA			

Table 8.1-4: Results of the best-fit model for Mean Position in School.

Table 8.2-12 Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors. Standard error in brackets in estimate column; statistic shows the t statistic associated with the variable and df indicates the degrees of freedom. P value indicates the significance of the result.

Coeffcient	Estimates	Statistic	df	p value
Intercept	4.48(0.05)	83.61	316.00	<0.001
18 °C	0.16(0.08)	2.07	158.00	0.040
Medium Metabolic Composition	0.28(0.08)	3.51	316.00	0.001
High Metabolic Composition	-0.16(0.08)	-1.98	316.00	0.049
Mixed Metabolic Composition	0.09(0.08)	1.23	280.37	0.219
18 °C: Medium Metabolic Composition	-0.65(0.11)	-5.71	158.00	<0.001
18 °C: High Metabolic Composition	0.03(0.11)	0.25	158.00	0.799
18 °C: Mixed Metabolic Composition	-0.16(0.11)	-1.52	158.00	0.130
Random Effects				
σ^2	0.13			
$\tau_{00\ group:ID}$	0.00			
$\tau_{00\ ID}$	0.00			
N_{group}	18			
N_{ID}	126			
Observations	324			
Marginal R^2 / Conditional R^2	0.139 / NA			

Table 8.1-5: Tukey Post-hoc test examining between group differences of Mean Position in School in different Metabolic Compositions (MRcomp) and temperatures. SE represent standard error; df represents degrees of freedom; Lower and Upper CI show 95% confidence intervals; t-ratio shows t-ratio associated with statistic; p value shows significance.

MR Comp Comparison	Temp	Estimate	SE	df	Lower CI	Upper CI	t - ratio	p - value
Low - High	15	0.16	0.08	245.98	-0.00	0.32	1.92	0.06
Low - Mix	15	-0.09	0.08	216.86	-0.25	0.06	-1.20	0.23
High - Mix	15	-0.25	0.08	222.38	-0.42	-0.09	-3.06	<0.01
Low - High	18	0.13	0.08	245.98	-0.03	0.29	1.58	0.12
Low - Mix	18	0.07	0.08	216.86	-0.08	0.22	0.88	0.38
High - Mix	18	-0.06	0.08	222.38	-0.22	0.10	-0.74	0.46

Table 8.1-6: Results of the best-fit model for group Leadership metrics;Lead turn con; leadturnstab; leadaccelcon;p leadaccelstab.

Table 8.2-13Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors. Standard error in brackets in estimate (est) column; statistic (stat) shows the t statistic associated with the variable and df indicates the degrees of freedom. P value indicates the significance of the result.

	LeadTurnCon				LeadAccelCon				LeadTurnStab				LeadAccelStab			
Coeffcient	**Est**	**Stat**	**df**	**p value**	**Est**	**Stat**	**df**	**p value**	**Est**	**Stat**	**df**	**p value**	**Est**	**Stat**	**df**	**p value**
Intercept	-0.41 (0.09)	-4.49	16.88	<0.001	-0.92 (0.11)	-8.61	16.88	<0.001	-1.13 (0.11)	-10.14	15.28	<0.001	-1.39 (0.10)	-13.45	15.76	<0.001
18 °C	0.40 (0.09)	4.17	14.62	0.001	0.18 (0.11)	1.65	14.62	0.120	0.31 (0.09)	3.38	13.35	0.005	0.15 (0.09)	1.65	13.81	0.122
Medium Metabolic Composition	-0.11 (0.14)	-0.79	15.92	0.443	-0.06 (0.16)	-0.38	15.92	0.708	-0.02 (0.17)	-0.12	15.57	0.904	0.07 (0.16)	0.47	15.76	0.645
High Metabolic Composition	0.04 (0.12)	0.30	10.82	0.771	-0.09 (0.14)	-0.65	10.82	0.532	-0.01 (0.16)	-0.07	11.91	0.947	-0.14 (0.14)	-1.00	11.51	0.340
Mixed Metabolic Composition	-0.14 (0.12)	-1.22	11.51	0.247	-0.07 (0.14)	-0.50	11.51	0.629	-0.22 (0.15)	-1.47	12.43	0.167	-0.02 (0.14)	-0.11	12.10	0.913
Random Effects																
σ2	0.06				0.08				0.05				0.06			
τ00	0.00 group				0.00 group				0.03 group				0.01 group			
ICC									0.33				0.21			
N	18 group				18 group				18 group				18 group			
Observations	30				30				30				30			
Marginal R2 / Conditional R2	0.411 / NA				0.108 / NA				0.305 / 0.531				0.161 / 0.333			

Table 8.1-7: Results of the best-fit model from group metrics for tables 8.1-12-15. Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors. Standard error in brackets in estimate (est) column; statistic (stat) shows the t statistic associated with the variable and df indicates the degrees of freedom. P value indicates the significance of the result.

	logSpeed				Mean sw.vs sh				logAND				LogPol			
Coefficient	**Est.**	**Stat**	**df**	**p**	**Est.**	**Stat**	**df**	**P**	**Est.**	**Stat**	**df**	**P**	**Est.**	**Stat**	**df**	**P**
Intercept	0.65 (0.03)	20.27	269.38	<0.001	67.84 (4.66)	14.55	14.11	<0.001	0.98 (0.02)	62.40	218.01	<0.001	-0.40 (0.03)	-14.96	15.80	<0.001
18 °C	0.21 (0.03)	5.99	158.00	<0.001	10.07 (0.58)	17.27	305.00	<0.001	0.03 (0.01)	2.43	158.00	0.016	0.15 (0.01)	11.68	302.00	<0.001
Medium Metabolic Composition	-0.12 (0.05)	-2.44	269.37	0.015	-8.17 (6.98)	-1.17	14.00	0.261	-0.16 (0.02)	-6.73	213.95	<0.001	0.08 (0.04)	2.13	15.80	0.049
High Metabolic Composition	-0.10 (0.05)	-2.03	269.32	0.044	-3.81 (6.98)	-0.55	14.00	0.594	-0.05 (0.02)	-2.02	208.91	0.044	0.01 (0.04)	0.29	15.80	0.776
Mixed Metabolic Composition	0.14 (0.05)	3.12	216.58	0.002	8.08 (6.58)	1.23	14.00	0.240	-0.04 (0.02)	-1.91	136.34	0.059	0.01 (0.04)	0.28	15.80	0.786
18 °C:Medium Metabolic Composition	-0.08 (0.05)	-1.46	158.00	0.145					0.06 (0.02)	3.09	158.00	0.002	-0.20 (0.02)	-10.21	302.00	<0.001
18 °C:High Metabolic Composition	0.04 (0.05)	0.81	158.00	0.420					-0.00 (0.02)	-0.01	158.00	0.988	0.01 (0.02)	0.30	302.00	0.767
18 °C:Mixed Metabolic Composition	0.01 (0.05)	0.21	158.00	0.834					0.05 (0.02)	2.78	158.00	0.006	-0.04 (0.02)	-2.44	302.00	0.015
Random Effects																
σ^2	0.03				27.51				0.00				0.00			
τ_{00}	0.02 $_{group:ID}$				106.67 $_{group}$				0.00 $_{group:ID}$				0.00 $_{group}$			
ICC	0.42				0.79				0.68				0.46			
N	18 $_{group}$				18 $_{group}$				18 $_{group}$				18 $_{group}$			
	126 $_{ID}$								126 $_{ID}$							
Observations	324				324				324				324			
Marginal R^2 / Conditional R^2	0.336 / 0.612				0.314 / 0.859				0.229 / 0.757				0.366 / 0.655			

Table 8.1-8: Tukey Post-hoc test examining between group differences of average speed in cm/s for different Metabolic Compositions (MRcomp) and temperatures. SE represent standard error; df represents degrees of freedom; Lower and Upper CI show 95% confidence intervals; t-ratio shows t-ratio associated with statistic; p value shows significance.

MRcomp Comparison	Temp	estimate	SE	df	Lower CI	Upper CI	t - ratio	p - value
Low - Medium	15	0.12	0.05	269.37	0.02	0.21	2.44	0.02
Low - High	15	0.10	0.05	269.32	0.00	0.19	2.03	0.04
Low - Mix	15	-0.14	0.05	216.58	-0.23	-0.05	-3.12	<0.01
Medium - High	15	-0.02	0.05	269.36	-0.12	0.08	-0.39	0.69
Medium - Mix	15	-0.26	0.05	242.92	-0.35	-0.16	-5.39	<0.001
High - Mix	15	-0.24	0.05	225.74	-0.33	-0.14	-4.98	<0.001
Low - Medium	18	0.19	0.05	269.37	0.10	0.29	4.02	<0.001
Low - High	18	0.06	0.05	269.32	-0.04	0.15	1.16	0.25
Low - Mix	18	-0.15	0.05	216.58	-0.24	-0.06	-3.35	<0.001
Medium - High	18	-0.14	0.05	269.36	-0.24	-0.04	-2.71	<0.01
Medium - Mix	18	-0.35	0.05	242.92	-0.44	-0.25	-7.18	<0.001
High - Mix	18	-0.21	0.05	225.74	-0.30	-0.11	-4.32	<0.001

Table 8.1-9: Tukey Post-hoc test examining between group differences of average neighbour distance in different Metabolic Compositions (MRcomp) and temperatures. SE represent standard error; df represents degrees of freedom; Lower and Upper CI show 95% confidence intervals; t-ratio shows t-ratio associated with statistic; p value shows significance.

MRcomp Comparison	Temp	estimate	SE	df	Lower CI	Upper CI	t ratio	P value
Low - Medium	15	0.16	0.02	213.95	0.11	0.20	6.73	<0.001
Low - High	15	0.05	0.02	208.91	0.00	0.09	2.02	0.04
Low - Mix	15	0.04	0.02	136.34	-0.00	0.08	1.91	0.06
Medium - High	15	-0.11	0.02	213.54	-0.16	-0.06	-4.48	<0.001
Medium - Mix	15	-0.12	0.02	168.70	-0.16	-0.08	-5.39	<0.001
High - Mix	15	-0.01	0.02	146.38	-0.05	0.03	-0.40	0.69
Low - Medium	18	0.10	0.02	213.95	0.05	0.15	4.22	<0.001
Low - High	18	0.05	0.02	208.91	0.00	0.09	2.04	0.04
Low - Mix	18	-0.01	0.02	136.34	-0.05	0.03	-0.56	0.58
Medium - High	18	-0.05	0.02	213.54	-0.10	-0.00	-2.09	0.04
Medium - Mix	18	-0.11	0.02	168.70	-0.15	-0.07	-4.99	<0.001
High - Mix	18	-0.06	0.02	146.38	-0.10	-0.02	-2.71	<0.01

Table 8.1-10: Tukey Post-hoc test examining between group differences of mean polarity in different Metabolic Compositions (MRcomp) and temperatures. SE represent standard error; df represents degrees of freedom; Lower and Upper CI show 95% confidence intervals; t-ratio shows t-ratio associated with statistic; p value shows significance.

MRcomp Comparison	Temp	estimate	SE	df	Lower CI	Upper CI	t - ratio	p - value
Low - Medium	15	-0.08	0.04	15.80	-0.17	-0.00	-2.13	0.05
Low - High	15	-0.01	0.04	15.80	-0.10	0.07	-0.29	0.78
Low - Mix	15	-0.01	0.04	15.80	-0.09	0.07	-0.28	0.79
Medium - High	15	0.07	0.04	15.80	-0.02	0.16	1.75	0.10
Medium - Mix	15	0.07	0.04	15.80	-0.01	0.16	1.87	0.08
High - Mix	15	0.00	0.04	15.80	-0.08	0.09	0.03	0.98
Low - Medium	18	0.11	0.04	15.80	0.03	0.20	2.81	0.01
Low - High	18	-0.02	0.04	15.80	-0.10	0.07	-0.43	0.67
Low - Mix	18	0.03	0.04	15.80	-0.05	0.11	0.90	0.38
Medium - High	18	-0.13	0.04	15.80	-0.22	-0.04	-3.08	<0.01
Medium - Mix	18	-0.08	0.04	15.80	-0.16	0.01	-1.96	0.07
High - Mix	18	0.05	0.04	15.80	-0.03	0.14	1.28	0.22

Table 8.1-11: Tukey Post-hoc test examining between group differences of swimming vs schooling in different Metabolic Compositions (MRcomp) and temperatures. SE represent standard error; df represents degrees of freedom; Lower and Upper CI show 95% confidence intervals; t-ratio shows t-ratio associated with statistic; p value shows significance.

MRcomp Comparison	Temp	estimate	SE	df	Lower CI	Upper CI	t - ratio	p - value
Low - Med	15	8.17	6.98	14.00	-6.79	23.14	1.17	0.26
Low - High	15	3.81	6.98	14.00	-11.15	18.78	0.55	0.59
Low - Mix	15	-8.08	6.58	14.00	-22.19	6.03	-1.23	0.24
Med - High	15	-4.36	7.36	14.00	-20.14	11.41	-0.59	0.56
Med - Mix	15	-16.25	6.98	14.00	-31.22	-1.29	-2.33	0.04
High - Mix	15	-11.89	6.98	14.00	-26.86	3.07	-1.70	0.11
Low - Med	18	8.17	6.98	14.00	-6.79	23.14	1.17	0.26
Low - High	18	3.81	6.98	14.00	-11.15	18.78	0.55	0.59
Low - Mix	18	-8.08	6.58	14.00	-22.19	6.03	-1.23	0.24
Med - High	18	-4.36	7.36	14.00	-20.14	11.41	-0.59	0.56
Med - Mix	18	-16.25	6.98	14.00	-31.22	-1.29	-2.33	0.04
High - Mix	18	-11.89	6.98	14.00	-26.86	3.07	-1.70	0.11

Table 8.1-12: List of all linear mixed effect models (LMEs) in model selection performed for LeadTurnResp (Mean lag after a leadership event while turning). SMRrank is the rank of individual SMR in group. MMRrank is the rank of individual MMR in group. AvePosSchool is the mean position in school throughout the trial. Temp is the temperature treatment; logTL is the log-transformed total length of the fish; MRComp is the metabolic composition of the group; ID indicates individual fish ID and group is group ID. df represents degrees of freedom and AIC shows the Akaike Information Criterial for the model. Chi-squared and p value represents the difference between the previous model.

Model	df	AIC	x^2	p value
LeadTurnResp ~ SMRrank + MMRrank + AvePosSchool + temp + logTL + MRcomp + SMRrank*temp + SMRrank*AvePosSchool + SMRrank*logTL + SMRrank*MRcomp + MMRrank*SMRrank + MMRrank*temp + MMRrank*AvePosSchool + MMRrank* logTL + MMRrank*MRcomp + AvePosSchool*logTL + AvePosSchool*temp + AvePosSchool*MRcomp + temp*logTL + temp*MRcomp + logTL*MRcomp + (1|ID/group)	37	442.58		
LeadTurnResp ~ SMRrank + MMRrank + AvePosSchool + temp + logTL + MRcomp + SMRrank*temp + SMRrank*logTL + SMRrank*MRcomp + MMRrank*SMRrank + MMRrank*temp + MMRrank*AvePosSchool + MMRrank*logTL + MMRrank* MRcomp + AvePosSchool*logTL + AvePosSchool* temp + AvePosSchool*MRcomp + temp*logTL + temp* MRcomp + logTL*MRcomp + (1|ID/group)	36	440.59	0.01	0.921
LeadTurnResp ~ SMRrank + MMRrank + AvePosSchool + temp + logTL + MRcomp + SMRrank*temp + SMRrank*logTL + SMRrank*MRcomp + MMRrank*SMRrank + MMRrank*AvePosSchool + MMRrank*temp + MMRrank*logTL + MMRrank*MRcomp + AvePosSchool* logTL + AvePosSchool*temp + AvePosSchool* MRcomp + temp*logTL + temp*MRcomp + logTL*MRcomp + (1 | ID/group)	35	439.34	0.75	0.387
LeadTurnResp ~ SMRrank + MMRrank + AvePosSchool + temp + logTL + MRcomp + SMRrank*temp + SMRrank*logTL + SMRrank*MRcomp + MMRrank*SMRrank + MMRrank*AvePosSchool + MMRrank*logTL + MMRrank*MRcomp + AvePosSchool* logTL + AvePosSchool*MRcomp + temp*logTL + temp* MRcomp + logTL*MRcomp + (1|ID/group)	34	438.05	0.71	0.398
LeadTurnResp ~ SMRrank + MMRrank + AvePosSchool + temp + logTL + MRcomp + SMRrank*temp + SMRrank*logTL + SMRrank*MRcomp + MMRrank*SMRrank + MMRrank*AvePosSchool + MMRrank*logTL + MMRrank*MRcomp + AvePosSchool* logTL + AvePosSchool*MRcomp + temp*logTL + logTL* MRcomp + (1|ID/group)	31	441.03	8.98	0.030
LeadTurnResp ~ SMRrank + MMRrank + AvePosSchool + temp + logTL + MRcomp + SMRrank*temp + SMRrank*logTL + SMRrank*MRcomp + MMRrank*SMRrank + MMRrank*AvePosSchool + MMRrank*logTL + MMRrank*MRcomp + AvePosSchool* logTL + AvePosSchool*MRcomp + temp*logTL + logTL*MRcomp + (1|ID/group)	28	439.07	4.04	0.257
LeadTurnResp ~ SMRrank + MMRrank + AvePosSchool + temp + logTL + MRcomp + SMRrank*temp + SMRrank*logTL + SMRrank*MRcomp + MMRrank*SMRrank + MMRrank*AvePosSchool + MMRrank*logTL + MMRrank*MRcomp + AvePosSchool* logTL + temp*logTL + (1|ID/group)	25	436.45	3.37	0.338
LeadTurnResp ~ SMRrank + MMRrank + AvePosSchool + temp + logTL + MRcomp + SMRrank*temp + SMRrank*logTL + SMRrank*MRcomp + MMRrank*SMRrank + MMRrank*AvePosSchool + MMRrank*logTL + MMRrank*MRcomp + AvePosSchool* logTL +	24	434.45	0.00	0.945

(1|ID/group)				
LeadTurnResp ~ SMRrank + MMRrank + AvePosSchool + temp + logTL + MRcomp + SMRrank*temp + SMRrank*logTL + SMRrank*MRcomp + MMRrank*AvePosSchool + MMRrank* logTL + MMRrank*MRcomp + AvePosSchool*logTL + (1 | ID/group)	23	432.47	0.02	0.889
LeadTurnResp ~ SMRrank + MMRrank + AvePosSchool + temp + logTL + MRcomp + SMRrank*logTL + SMRrank*MRcomp + MMRrank*AvePosSchool + MMRrank*logTL + MMRrank* MRcomp + AvePosSchool*logTL + (1|ID/group)	22	430.53	0.06	0.805
LeadTurnResp ~ SMRrank + MMRrank + AvePosSchool + temp + logTL + MRcomp + SMRrank*logTL + SMRrank*MRcomp + MMRrank*logTL + MMRrank*MRcomp + AvePosSchool* logTL + (1|ID/group)	21	428.75	0.22	0.638
LeadTurnResp ~ SMRrank + MMRrank + AvePosSchool + temp + logTL + MRcomp + SMRrank*logTL + SMRrank*MRcomp + MMRrank*MRcomp + AvePosSchool*logTL + (1|ID/group)	20	428.89	2.14	0.144
LeadTurnResp ~ SMRrank + MMRrank + AvePosSchool + temp + logTL + MRcomp + SMRrank*logTL + MMRrank*MRcomp + AvePosSchool*logTL + (1|ID/group)	17	425.75	2.86	0.414
LeadTurnResp ~ SMRrank + MMRrank + AvePosSchool + temp + logTL + MRcomp + SMRrank*logTL + AvePosSchool* logTL + (1|ID/group)	14	421.82	2.07	0.558
LeadTurnResp ~ SMRrank + MMRrank + AvePosSchool + temp + logTL + MRcomp + SMRrank*logTL + (1|ID/group)	13	421.13	1.31	0.252
LeadTurnResp ~ SMRrank + MMRrank + AvePosSchool + temp + logTL + MRcomp + (1|ID/group)	12	420.42	1.29	0.256
LeadTurnResp ~ MMRrank + AvePosSchool + temp + logTL + MRcomp + (1|ID/group)	11	418.64	0.22	0.639
LeadTurnResp ~ MMRrank + temp + logTL + MRcomp + (1 | ID/group)	10	417.84	1.20	0.273
LeadTurnResp ~ MMRrank + temp + MRcomp + (1 |ID/group)	**9**	**415.99**	**0.15**	**0.696**

Table 8.1-13: List of all linear mixed effect models (LMEs) in model selection performed for LeadAccelResp (Mean lag after a leadership event while accelerating). SMRrank is the rank of individual SMR in group. MMRrank is the rank of individual MMR in group. AvePosSchool is the mean position in school throughout the trial. Temp is the temperature treatment; logTL is the log-transformed total length of the fish; MRComp is the metabolic composition of the group; ID indicates individual fish ID and group is group ID. df represents degrees of freedom and AIC shows the Akaike Information Criterial for the model. Chi-squared and p value represents the difference between the previous model.

Model	df	AIC	χ^2	p value
LeadAccelResp ~ SMRrank + AvePosSchool + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + MMRrank* temp + MMRrank*AvePosSchool + MMRrank*logTL + MMRrank* MRcomp + SMRrank*temp + SMRrank*AvePosSchool + SMRrank*logTL + SMRrank*MRcomp + AvePosSchool* logTL + AvePosSchool*temp + AvePosSchool* MRcomp + temp*logTL + temp*MRcomp + logTL*MRcomp + (1 | ID/group)	37	422.38		
LeadAccelResp ~ SMRrank + AvePosSchool + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + MMRrank* temp + MMRrank*AvePosSchool + MMRrank*logTL + MMRrank* MRcomp + SMRrank*temp + SMRrank*AvePosSchool + SMRrank*logTL + SMRrank*MRcomp + AvePosSchool* temp + AvePosSchool*MRcomp + temp*logTL + temp* MRcomp + logTL*MRcomp + (1|ID/group)	36	420.53	0.16	0.692
LeadAccelResp ~ SMRrank + AvePosSchool + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + MMRrank* temp + MMRrank*AvePosSchool + MMRrank*logTL + MMRrank* MRcomp + SMRrank*AvePosSchool + SMRrank*logTL + SMRrank*MRcomp + AvePosSchool*temp + AvePosSchool* MRcomp + temp*logTL + temp*MRcomp + logTL*MRcomp + (1 | ID/group)	35	418.54	0.00	0.951
LeadAccelResp ~ SMRrank + AvePosSchool + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + MMRrank* temp + MMRrank*AvePosSchool + MMRrank*logTL + MMRrank* MRcomp + SMRrank*AvePosSchool + SMRrank*logTL + SMRrank*MRcomp + AvePosSchool*temp + AvePosSchool* MRcomp + temp*logTL + logTL*MRcomp + (1|ID/group)	32	417.89	5.36	0.148
LeadAccelResp ~ SMRrank + AvePosSchool + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + MMRrank* AvePosSchool + MMRrank*logTL + MMRrank*MRcomp + SMRrank*AvePosSchool + SMRrank*logTL + SMRrank* MRcomp + AvePosSchool*temp + AvePosSchool* MRcomp + temp*logTL + logTL*MRcomp + (1|ID/group)	31	417.06	1.17	0.279
LeadAccelResp ~ SMRrank + AvePosSchool + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + MMRrank* logTL + MMRrank*MRcomp + SMRrank*AvePosSchool + SMRrank*logTL + SMRrank*MRcomp + AvePosSchool* temp + AvePosSchool*MRcomp + temp*logTL + logTL* MRcomp + (1|ID/group)	30	415.06	0.00	0.987
LeadAccelResp ~ SMRrank + AvePosSchool + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + MMRrank* MRcomp + SMRrank*AvePosSchool + SMRrank*logTL + SMRrank*MRcomp + AvePosSchool*MRcomp + temp*logTL + logTL*MRcomp + (1|ID/group)	29	415.75	2.68	0.101
LeadAccelResp ~ SMRrank + AvePosSchool + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + SMRrank* AvePosSchool	26	410.94	1.19	0.755

+ SMRrank*logTL + SMRrank*MRcomp + AvePosSchool*temp + AvePosSchool*MRcomp + temp*logTL + logTL*MRcomp + (1|ID/group)				
LeadAccelResp ~ SMRrank + AvePosSchool + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + SMRrank* AvePosSchool + SMRrank*logTL + SMRrank*MRcomp + AvePosSchool*MRcomp + temp*logTL + logTL*MRcomp + (1 | ID/group)	25	409.03	0.09	0.769
LeadAccelResp ~ SMRrank + AvePosSchool + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + SMRrank* AvePosSchool + SMRrank*logTL + SMRrank*MRcomp + temp*logTL + logTL*MRcomp + (1|ID/group)	22	406.11	3.08	0.379
LeadAccelResp ~ SMRrank + AvePosSchool + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + SMRrank* logTL + SMRrank*MRcomp + temp*logTL + logTL*MRcomp + (1 | ID/group)	21	404.43	0.32	0.570
LeadAccelResp ~ SMRrank + AvePosSchool + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + SMRrank* logTL + temp*logTL + logTL*MRcomp + (1|ID/group)	18	399.99	1.56	0.670
LeadAccelResp ~ SMRrank + AvePosSchool + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + SMRrank* logTL + temp*logTL + (1|ID/group)	15	396.21	2.22	0.528
LeadAccelResp ~ SMRrank + temp + logTL + MRcomp + MMRrank + (1|ID/group)	11	394.31	6.11	0.191
LeadAccelResp ~ SMRrank + temp + logTL + MRcomp + (1 | ID/group)	10	392.70	0.39	0.535
LeadAccelResp ~ temp + logTL + MRcomp + (1|ID/group)	9	390.99	0.29	0.591
LeadAccelResp ~ temp + MRcomp + (1|ID/group)	**8**	**389.00**	**0.01**	**0.934**

Table 8.1-14: List of all linear mixed effect models (LMEs) in model selection performed for AvePosSchool. AvePosSchool is the mean position in school throughout the trial. SMRrank is the rank of individual SMR in group. MMRrank is the rank of individual MMR in group. Temp is the temperature treatment; logTL is the log-transformed total length of the fish; MRComp is the metabolic composition of the group; ID indicates individual fish ID and group is group ID. df represents degrees of freedom and AIC shows the Akaike Information Criterial for the model. Chi-squared and p value represents the difference between the previous model.

Model	df	AIC	χ^2	p value
AvePosSchool ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + MMRrank*temp + MMRrank*logTL + MMRrank* MRcomp + SMRrank*temp + SMRrank*logTL + SMRrank*MRcomp + temp*logTL + temp*MRcomp + logTL*MRcomp + (1|ID/group)	29	293.11		
AvePosSchool ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + MMRrank*temp + MMRrank*logTL + MMRrank* MRcomp + SMRrank*temp + SMRrank*logTL + SMRrank*MRcomp + temp*MRcomp + logTL*MRcomp + (1|ID/group)	28	291.11	0.00	0.953
AvePosSchool ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + MMRrank*temp + MMRrank*logTL + MMRrank* MRcomp + SMRrank*temp + SMRrank*logTL + temp*MRcomp + logTL*MRcomp + (1|ID/group)	25	285.83	0.71	0.870
AvePosSchool ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + MMRrank*temp + MMRrank*logTL + MMRrank* MRcomp + SMRrank*temp + temp*MRcomp + logTL*MRcomp + (1 | ID/group)	24	283.99	0.16	0.687
AvePosSchool ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + MMRrank*temp + MMRrank*logTL + SMRrank* temp + temp*MRcomp + logTL*MRcomp + (1|ID/group)	21	279.70	1.71	0.635
AvePosSchool ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + MMRrank*logTL + SMRrank*temp + temp* MRcomp + logTL*MRcomp + (1|ID/group)	20	277.91	0.22	0.642
AvePosSchool ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank*SMRrank + SMRrank*temp + temp*MRcomp + logTL* MRcomp + (1|ID/group)	19	276.45	0.54	0.463
AvePosSchool ~ SMRrank + temp + logTL + MRcomp + MMRrank + SMRrank*temp + temp*MRcomp + logTL*MRcomp + (1 | ID/group)	18	275.77	1.32	0.250
AvePosSchool ~ SMRrank + temp + logTL + MRcomp + SMRrank* temp + temp*MRcomp + logTL*MRcomp + (1|ID/group)	17	273.82	0.04	0.836
AvePosSchool ~ SMRrank + temp + logTL + MRcomp + temp* MRcomp + logTL*MRcomp + (1|ID/group)	16	272.38	0.56	0.453
AvePosSchool ~ temp + logTL + MRcomp + temp*MRcomp + logTL*MRcomp + (1|ID/group)	15	270.42	0.04	0.849
AvePosSchool ~ temp + logTL + MRcomp + temp*MRcomp + (1 | ID/group)	12	268.56	4.14	0.247
AvePosSchool ~ temp + MRcomp + temp*MRcomp + (1|ID/group)	**11**	**267.97**	**1.41**	**0.235**

Table 8.1-15: List of all linear mixed effect models (LMEs) in model selection performed for logSpeed. logSpeed is the log transformed mean speed of individuals in cm/s. SMRrank is the rank of individual SMR in group. MMRrank is the rank of individual MMR in group. Temp is the temperature treatment; logTL is the log-transformed total length of the fish; MRComp is the metabolic composition of the group; ID indicates individual fish ID and group is group ID. df represents degrees of freedom and AIC shows the Akaike Information Criterial for the model. Chi-squared and p value represents the difference between the previous model.

Model	df	AIC	χ^2	p value
logSpeed ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + MMRrank*temp + MMRrank*logTL + MMRrank*MRcomp + SMRrank*temp + SMRrank*logTL + SMRrank*MRcomp + temp* logTL + temp*MRcomp + logTL*MRcomp + (1|ID/group)	29	-66.85		
logSpeed ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + MMRrank*temp + MMRrank*logTL + SMRrank*temp + SMRrank*logTL + SMRrank*MRcomp + temp*logTL + temp* MRcomp + logTL*MRcomp + (1|ID/group)	26	-72.82	0.03	0.999
logSpeed ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + MMRrank*temp + MMRrank*logTL + SMRrank*temp + SMRrank*logTL + temp*logTL + temp*MRcomp + logTL* MRcomp + (1|ID/group)	23	-78.29	0.53	0.913
logSpeed ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + MMRrank*temp + MMRrank*logTL + SMRrank*temp + SMRrank*logTL + temp*logTL + temp*MRcomp + (1|ID/group)	20	-83.28	1.01	0.799
logSpeed ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + MMRrank*temp + MMRrank*logTL + SMRrank*logTL + temp*logTL + temp*MRcomp + (1|ID/group)	19	-85.21	0.08	0.782
logSpeed ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + MMRrank*temp + MMRrank*logTL + SMRrank*logTL + temp*MRcomp + (1|ID/group)	18	-87.03	0.18	0.672
logSpeed ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + MMRrank*logTL + SMRrank*logTL + temp*MRcomp + (1 | ID/group)	17	-88.86	0.17	0.684
logSpeed ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + MMRrank*logTL + temp*MRcomp + (1|ID/group)	16	-88.92	1.94	0.164
logSpeed ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + temp*MRcomp + (1|ID/group)	15	-90.11	0.81	0.367
logSpeed ~ SMRrank + temp + MRcomp + MMRrank + MMRrank*SMRrank + temp*MRcomp + (1|ID/group)	14	-91.71	0.40	0.526
logSpeed ~ SMRrank + temp + MRcomp + MMRrank + MMRrank*SMRrank + (1 | ID/group)	11	-92.60	5.10	0.164
logSpeed ~ temp + MRcomp + temp*MRcomp + (1|ID/group)	11	-94.10	3.48	0.062
logSpeed ~ SMRrank + temp + MRcomp + MMRrank + (1|ID/group)	**10**	**-91.12**	**4.98**	**0.026**

Table 8.1-16: List of all linear mixed effect models (LMEs) in model selection performed for logPol. logPol is the log transformed polarity of a group over a trial. SMRrank is the rank of individual SMR in group. MMRrank is the rank of individual MMR in group. Temp is the temperature treatment; logTL is the log-transformed total length of the fish; MRComp is the metabolic composition of the group; ID indicates individual fish ID and group is group ID. df represents degrees of freedom and AIC shows the Akaike Information Criterial for the model. Chi-squared and p value represents the difference between the previous model.

Model	df	AIC	χ^2	p value
logPol ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + MMRrank*temp + MMRrank*logTL + MMRrank*MRcomp + SMRrank*temp + SMRrank*logTL + SMRrank*MRcomp + temp* logTL + temp*MRcomp + logTL*MRcomp + (1 | group)	28	-796.70		
logPol ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + MMRrank*temp + MMRrank*logTL + MMRrank*MRcomp + SMRrank*temp + SMRrank*logTL + temp*logTL + temp* MRcomp + logTL*MRcomp + (1 | group)	25	-802.70	0.00	1.000
logPol ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + MMRrank*temp + MMRrank*logTL + MMRrank*MRcomp + SMRrank*logTL + temp*logTL + temp*MRcomp + logTL* MRcomp + (1 | group)	24	-804.69	0.00	0.966
logPol ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + MMRrank*temp + MMRrank*logTL + SMRrank*logTL + temp*logTL + temp*MRcomp + logTL*MRcomp + (1 | group)	21	-810.69	0.01	1.000
logPol ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + MMRrank*logTL + SMRrank*logTL + temp*logTL + temp*MRcomp + logTL*MRcomp + (1 | group)	20	-812.64	0.05	0.823
logPol ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + MMRrank*logTL + SMRrank*logTL + temp*logTL + temp*MRcomp + (1 | group)	17	-818.61	0.03	0.999
logPol ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + MMRrank*logTL + temp*logTL + temp*MRcomp + (1 | group)	16	-820.61	0.00	0.968
logPol ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* SMRrank + MMRrank*logTL + temp*MRcomp + (1 | group)	15	-821.76	0.84	0.358
logPol ~ SMRrank + temp + logTL + MRcomp + MMRrank + MMRrank* logTL + temp*MRcomp + (1 | group)	14	-823.73	0.03	0.865
logPol ~ temp + logTL + MRcomp + MMRrank + MMRrank*logTL + temp*MRcomp + (1 | group)	13	-825.73	0.00	0.997
logPol ~ temp + logTL + MRcomp + MMRrank + temp*MRcomp + (1 | group)	12	-827.70	0.04	0.848
logPol ~ temp + logTL + MRcomp + temp*MRcomp + (1 | group)	11	-829.70	0.00	0.980
logPol ~ temp + MRcomp + temp*MRcomp + (1 | group)	**10**	**-831.69**	**0.01**	**0.923**

Table 8.1-17: List of all linear mixed effect models (LMEs) performed for logAND. LogAND is the log transformed mean neighbour distance for each individual. SMRrank is the rank of individual SMR in group. MMRrank is the rank of individual MMR in group. Temp is the temperature treatment; logTL is the log-transformed total length of the fish; MRComp is the metabolic composition of the group; ID indicates individual fish ID and group is group ID. df represents degrees of freedom and AIC shows the Akaike Information Criterial for the model. Chi-squared and p value represents the difference between the previous model.

Model	df	AIC	χ^2	p value
logAND ~ SMRrank + temp + MRcomp + MMRrank + MMRrank*SMRrank + MMRrank*temp + MMRrank*MRcomp + SMRrank*temp + SMRrank* MRcomp + temp*MRcomp + (1|ID/group)	22	-607.00		
logAND ~ SMRrank + temp + MRcomp + MMRrank + MMRrank*SMRrank + MMRrank*temp + MMRrank*MRcomp + SMRrank*MRcomp + temp*MRcomp + (1|ID/group)	21	-609.00	0.00	0.978
logAND ~ SMRrank + temp + MRcomp + MMRrank + MMRrank*SMRrank + MMRrank*temp + MMRrank*MRcomp + temp*MRcomp + (1 | ID/group)	18	-614.85	0.15	0.986
logAND ~ SMRrank + temp + MRcomp + MMRrank + MMRrank*temp + MMRrank*MRcomp + temp*MRcomp + (1|ID/group)	17	-616.72	0.13	0.717
logAND ~ SMRrank + temp + MRcomp + MMRrank + MMRrank*temp + temp*MRcomp + (1|ID/group)	14	-620.61	2.10	0.551
logAND ~ temp + MRcomp + MMRrank + MMRrank*temp + temp*MRcomp + (1 | ID/group)	13	-622.33	0.29	0.593
logAND ~ temp + MRcomp + MMRrank + temp*MRcomp + (1|ID/group)	12	-623.94	0.39	0.533
logAND ~ temp + MRcomp + temp*MRcomp + (1|ID/group)	**11**	**-624.10**	**1.84**	**0.175**

Table 8.1-18 List of all linear mixed effect models (LMEs) performed for mean.sw.sh. Mean.sw.sh is the mean time a group spent swimming rather than shoaling. Temp is the temperature treatment; MRComp is the metabolic composition of the group; group is group ID. df represents degrees of freedom and AIC shows the Akaike Information Criterial for the model. Chi-squared and p value represents the difference between the previous model.

Model	df	AIC	χ^2	p value
mean.sw.sh ~ temp + MRcomp + temp*MRcomp + (1 | group)	10	2072.03		
mean.sw.sh ~ temp + MRcomp + (1 | group)	**7**	**2078.49**	**12.46**	**0.006**

Table 8.1-19: List of all linear mixed effect models (LMEs) performed for LeadAcccelCon. LeadAccelCon is the leadership consistency while accelerating. Temp is the temperature treatment; MRComp is the metabolic composition of the group; group is group ID. df represents degrees of freedom and AIC shows the Akaike Information Criterial for the model. Chi-squared and p value represents the difference between the previous model.

Model	df	AIC	χ^2	p value
LeadAccelCon ~ temp + MRcomp + temp*MRcomp + (1 | group)	10	19.38		
LeadAccelCon ~ temp + MRcomp + (1 | group)	**7**	**18.77**	**5.39**	**0.146**

Table 8.1-20: List of all linear mixed effect models (LMEs) performed for LeadTurnCon. LeadTurnCon is the leadership consistency while Turning. Temp is the temperature treatment; MRComp is the metabolic composition of the group; group is group ID. df represents degrees of freedom and AIC shows the Akaike Information Criterial for the model. Chi-squared and p value represents the difference between the previous model.

Model	df	AIC	χ^2	p value
LeadTurnCon ~ temp + MRcomp + temp*MRcomp + (1 | roup)	10	13.64		
LeadTurnCon ~ temp + MRcomp + (1 | group)	**7**	**9.58**	**1.94**	**0.585**

Table 8.1-21: List of all linear mixed effect models (LMEs) performed for LeadAccelStab. LeadAccelStab is the leadership stability while accelerating. Temp is the temperature treatment; MRComp is the metabolic composition of the group; group is group ID. df represents degrees of freedom and AIC shows the Akaike Information Criterial for the model. Chi-squared and p value represents the difference between the previous model.

Model	df	AIC	χ^2	p value
LeadAccelStab ~ temp + MRcomp + temp*MRcomp +(1 | group)	10	13.53		
LeadAccelStab ~ temp + MRcomp + (1 | group)	**7**	**13.69**	**6.16**	**0.104**

Table 8.1-22: List of all linear mixed effect models (LMEs) performed for LeadTurnStab. LeadTurnStab is the leadership stability while turning. Temp is the temperature treatment; MRComp is the metabolic composition of the group; group is group ID. df represents degrees of freedom and AIC shows the Akaike Information Criterial for the model. Chi-squared and p value represents the difference between the previous model.

Model	df	AIC	χ^2	p value
LeadTurnStab ~ temp + MRcomp + temp*MRcomp + (1 | group)	10	17.10		
LeadTurnStab ~ temp + MRcomp + (1 | group)	**7**	**15.82**	**4.72**	**0.193**

Table 8.1-23: Checklist of 53 essential criteria for the reporting of methods for aquatic intermittent-flow respirometry (Killen et al 2021).

Number	Criterion and Category	Response	Value (where required)	Units
	EQUIPMENT, MATERIALS, AND SETUP			
1	Body mass of animals at time of respirometry	Mean	2.7	g
2	Volume of empty respirometers	Y	96	mL
3	How chamber mixing was achieved	Peristaltic pump		
4	Ratio of net respirometer volume (plus any associated tubing in mixing circuit) to animal body mass	Na		
5	Material of tubing used in any mixing circuit	Na		
6	Volume of tubing in any mixing circuit	Na		
7	Confirm volume of tubing in any mixing circuit was included in calculations of oxygen uptake	Na		
8	Material of respirometer (e.g. glass, acrylic, etc.)	glass		
9	Type of oxygen probe and data recording	FireStingO2 4-channel optical oxygen meter and asso- ciated sensors and software (Pyro Science GmbH, Aachen, Germany)		
10	Sampling frequency of water dissolved oxygen	2 seconds	2	sec
11	Describe placement of oxygen probe (in mixing circuit or directly in chamber)	In mixing circuit		
12	Flow rate during flushing and recirculation, or confirm that chamber returned to normoxia during flushing	Chamber returned to normoxia		
13	Timing of flush/closed cycles	3 min open, 8 min close		
14	Wait (delay) time excluded from closed measurement cycles	Na		
15	Frequency and method of probe calibration (for both 0 and 100% calibrations)	Na		
16	State whether software temperature compensation was used during recording of water oxygen concentration	NA		
	MEASUREMENT CONDITIONS			
17	Temperature during respirometry	13 C	13	C
18	How temperature was controlled	Temperature regulator and water bath with heating coil		

19	Photoperiod during respirometry	Na		
20	If (and how) ambient water bath was cleaned and aerated during measurement of oxygen uptake (e.g. filtration, periodic or continuous water changes)	Aerated with air stone and pumped through UV filter		
21	Total volume of ambient water bath and any associated reservoirs	50 L	50	L
22	Minimum water oxygen dissolved oxygen reached during closed phases	Na		
23	State whether chambers were visually shielded from external disturbance	Opaque plastic blind		
24	How many animals were measured during a given respirometry trial (i.e. how many animals were in the same water bath)	Maximum of 16 per respirometry trial		
25	If multiple animals were measured simultaneously, state whether they were able to see each other during measurements	NA		
26	Duration of animal fasting before placement in respirometer	24 hours	24	h
27	Duration of all trials combined (number of days to measure all animals in the study)	Na		
28	Acclimation time to the laboratory (or time since capture for field studies) before respirometry measurements	3 weeks	3	weeks
	BACKGROUND RESPIRATION			
29	State whether background microbial respiration was measured and accounted for, and if so, method used (e.g. parallel measures with empty respirometry chamber, measurements before and after for all chambers while empty, both)	Empty respirometer measurement before and after trial		
30	State if background respiration was measured at beginning and/or end, state how many slopes and for what duration	3 slopes		
31	State how changes in background respiration were modelled over time (e.g. linear, exponential, parallel measures)	Linear		
32	Level of background respiration (e.g. as a percentage of SMR)	Na		
33	Method and frequency of system cleaning (e.g. system bleached between each trial, UV lamp)	System bleached between each trial		
	STANDARD OR ROUTINE METABOLIC RATE			
34	Acclimation time after transfer to chamber, or alternatively, time to reach beginning of metabolic rate measurements after introduction to chamber	First 5 hours excluded		
35	Time period, within a trial, over which oxygen uptake was measured (e.g. number of hours)	15 h total	15	h
36	Value taken as SMR/RMR (e.g. quantile, mean of lowest 10 percent, mean of all values)	Lowest 10^{th} percentile		
37	Total number of slopes measured and used to derive metabolic rate (e.g. how much data were	NA		

	used to calculate quantiles)			
38	Whether any time periods were removed from calculations of SMR/RMR (e.g. data during acclimation, periods of high activity [e.g. daytime])	Data during acclimation		
39	r^2 threshold for slopes used for SMR/RMR (or mean)	Na		
40	Proportion of data removed due to being outliers below r-squared threshold	Na		
	MAXIMUM METABOLIC RATE			
41	When MMR was measured in relation to SMR (i.e. before or after)	Before		
42	Method used (e.g. critical swimming speed respirometry, swim to exhaustion in swim tunnel, or chase to exhaustion)	Chase to exhaustion		
43	Value taken as MMR (e.g. the highest rate of oxygen uptake value after transfer, average of highest values)	Highest MO2 value after transfer		
44	If MMR measured post-exhaustion, length of activity challenge or chase (e.g. 2 min, until exhaustion, etc.)	2 min	2	min
45	If MMR measured post-exhaustion, state whether further air-exposure was added after exercise	No further air exposure		
46	If MMR measured post-exhaustion, time until transfer to chamber after exhaustion or time to start of oxygen uptake recording	Less than 10 s	<10	sec
47	Duration of slopes used to calculate MMR (e.g. 1 min, 5 min, etc.)	2 min slopes	2	min
48	Slope estimation method for MMR (e.g. rolling regression, sequential discrete time frames)	NA		
49	How absolute aerobic scope and/or factorial aerobic scope is calculated (i.e. using raw SMR and MMR, allometrically mass-adjusted SMR and MMR, or allometrically mass-adjusting aerobic scope itself)	Mass adjusted SMR and MMR		
	DATA HANDLING AND STATISTICS			
50	Sample size	180	180	
51	How oxygen uptake rates were calculated (software or script, equation, units, etc.)	Slopes extracted from Labchart		
52	Confirm that volume (mass) of animal was subtracted from respirometer volume when calculating oxygen uptake rates	Na		
53	State whether analyses accounted for variation in body mass and describe any allometric mass-corrections or adjustments	Standardized to mean body mass using residuals		

8.2 Chapter 4 Supplementary Materials

Table 8.2-1: Pearson's Correlation Table for leadership metrics for feeding and control treatments. Variables 1 and 2 show leadership metrics where LeadTurnResp, LeadAccelResp and AvePos School represent mean lag after leadership event while turning, mean lag after leadership event while accelerating and mean position in school respectively. R shows correlation coefficient, n shows number of datapoints and p value displays significance, where "n.s." means non-significant.

Treatment	Variable 1	Variable 2	r	n	p - value
feeding	LeadTurnResp	LeadAccelResp	0.62	1534	p <.001
	LeadTurnResp	AvePosSchool	0.0019	1575	n.s.
	LeadAccelResp	AvePosSchool	-0.01	1576	n.s.
control	LeadTurnResp	LeadAccelResp	0.53	641	p <.001
	LeadTurnResp	AvePosSchool	-0.22	677	p <.001
	LeadAccelResp	AvePosSchool	-0.034	674	n.s.

Table 8.2-2: Results of the best-fit model from Table 8.2-10 for Mean Lag after Leadership Event While Accelerating. Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors. Standard error in brackets in estimate column; statistic shows the t statistic associated with the variable and df indicates the degrees of freedom. P value indicates the significance of the result.

Coefficient	*Estimates*	*Statistic*	*df*	*p value*
Intercept	-0.44 (0.17)	-2.53	192.63	0.012
TimeSinceFeed	0.00 (0.00)	1.70	1533.86	0.089
FeedingTrial	-0.41 (0.19)	-2.18	201.13	0.030
Mass	-0.12 (0.04)	-2.84	185.76	0.005
TimeSinceFeed: FeedingTrial	0.00 (0.00)	-2.39	1533.38	0.017
FeedingTrial: mass	0.12 (0.05)	2.56	193.39	0.011
Random Effects				
σ^2	0.22			
$\tau_{00\ FishID:GroupID}$	0.00			
ICC	0.01			
N_{FishID}	206			
$N_{GroupID}$	25			
Observations	1639			
Marginal R^2 / Conditional R^2	0.008 / 0.018			

Table 8.2-3: Results of the best-fit model from Table 8.2-11 for Mean Lag after Leadership Event While Turning. Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors. Standard error in brackets in estimate column; statistic shows the t statistic associated with the variable and df indicates the degrees of freedom. P value indicates the significance of the result.

Coeffcient	*Estimates*	*Statistic*	*df*	*p value*
Intercept	-0.96 (0.04)	-22.40	768.79	<0.001
TimeSinceFeed	0.00 (0.00)	1.73	1518.77	0.083
FeedingTrial	0.16 (0.05)	3.10	762.36	0.002
TimeSinceFeed: FeedingTrial	-0.00 (0.00)	-2.22	1515.04	0.027
Random Effects				
σ^2	0.27			
$\tau_{00\ FishID:GroupID}$	0.02			
ICC	0.06			
N_{FishID}	206			
$N_{GroupID}$	25			
Observations	1639			
Marginal R^2 / Conditional R^2	0.007 / 0.070			

Table 8.2-4: Results of the best-fit model from

Table 8.2-12 for MeanPositionSchool. Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors. Standard error in brackets in estimate column; statistic shows the t statistic associated with the variable and df indicates the degrees of freedom. P value indicates the significance of the result.

Coeffcient	*Estimates*	*Statistic*	*df*	*p value*
Intercept	4.91 (0.27)	17.93	232.53	<0.001
TimeSinceFeed	-0.00 (0.00)	-4.75	1480.37	<0.001
FeedingTrial	-0.00 (0.30)	-0.01	229.42	0.991
Mass	-0.17 (0.07)	-2.56	227.55	0.011
TimeSinceFeed: FeedingTrial	0.00 (0.00)	3.14	1474.96	0.002
FeedingTrial:mass	0.15 (0.07)	1.97	223.31	0.050
Random Effects				
σ^2	0.13			
$\tau_{00\ FishID:GroupID}$	0.06			
ICC	0.31			
N_{FishID}	206			
$N_{GroupID}$	25			
Observations	1639			
Marginal R^2 / Conditional R^2	0.379 / 0.574			

Table 8.2-5: Results of the best-fit model from

Table 8.2-14 for log10(DistCent). Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors. Standard error in brackets in estimate column; statistic shows the t statistic associated with the variable and df indicates the degrees of freedom. P value indicates the significance of the result.

Coeffcient	*Estimates*	*Statistic*	*df*	*p value*
Intercept	2.50 (0.10)	25.39	255.10	<0.001
Mass	-0.07 (0.02)	-3.07	255.18	0.002
TimeSinceFeed	-0.00 (0.00)	-7.44	1461.17	<0.001
FeedingTrial	-0.37 (0.11)	-3.45	230.29	0.001
mass:TimeSinceFeed	0.00 (0.00)	6.47	1460.02	<0.001
FeedingTrial:mass	0.08 (0.03)	3.24	224.48	0.001
Random Effects				
σ^2	0.01			
$\tau_{00\ FishID:GroupID}$	0.01			
ICC	0.39			
N_{FishID}	206			
$N_{GroupID}$	25			
Observations	1639			
Marginal R^2 / Conditional R^2	0.080 / 0.437			

Table 8.2-6: Results of the best-fit model from

Table 8.2-13 for logSpeed. Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors. Standard error in brackets in estimate column; statistic shows the t statistic associated with the variable and df indicates the degrees of freedom. P value indicates the significance of the result.

Coeffcient	*Estimates*	*Statistic*	*df*	*p value*
Intercept	0.97 (0.08)	11.47	226.48	<0.001
TimeSinceFeed	-0.00 (0.00)	-8.35	1455.30	<0.001
Mass	-0.03 (0.02)	-1.31	220.81	0.193
FeedingTrial	-0.22 (0.09)	-2.41	221.80	0.017
FeedingTrial:mass	0.06 (0.02)	2.79	216.04	0.006
Random Effects				
σ^2	0.01			
$\tau_{00\ FishID:GroupID}$	0.01			
ICC	0.40			
N_{FishID}	206			
$N_{GroupID}$	25			

Coeffcient	*Estimates*	*Statistic*	*df*	*p value*
Observations	1639			
Marginal R^2 / Conditional R^2	0.062 / 0.437			

Table 8.2-7: Results of the best-fit model from

Table 8.2-15 for polarity. Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors. Standard error in brackets in estimate column; statistic shows the t statistic associated with the variable and df indicates the degrees of freedom. P value indicates the significance of the result.

Coeffcient	*Estimates*	*Statistic*	*df*	*p value*
Intercept	-0.01 (0.01)	-1.01	27.62	0.320
TimeSinceFeed	-0.00 (0.00)	-3.21	1621.03	0.001
Random Effects				
σ^2	0.00			
$\tau_{00\ GroupID}$	0.00			
ICC	0.36			
$N_{GroupID}$	25			
Observations	1639			
Marginal R^2 / Conditional R^2	0.004 / 0.359			

Table 8.2-8: Results of the best-fit model from Table 8.2-16 for change in SDA. Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors. Standard error in brackets in estimate column; statistic shows the t statistic associated with the variable and df indicates the degrees of freedom. P value indicates the significance of the result.

Coeffcient	*Estimates*	*Statistic*	*df*	*p value*
Intercept	0.00 (0.00)	-168.94	850.00	<0.001
NoWorms	1.19 (0.00)	148.77	850.00	<0.001
log(mass)	1.13 (0.04)	3.66	850.00	<0.001
log(TimeSinceFeed + 1)	1.77 (0.01)	133.57	850.00	<0.001
Random Effects				
σ^2	0.03			
$\tau_{00\ FishID:GroupID}$	0.00			
N_{FishID}	117			
$N_{GroupID}$	17			
Observations	856			
Marginal R^2 / Conditional R^2	0.977 / NA			

Table 8.2-9: Results of the general linear model to describe Specific Dynamic Action curves, where log.mass indicates log transformed mass in grams and NoWorms indicates number of worms fed, with a suffix of how many worms in that group. 5 worms is the baseline. Standard error in brackets in estimate column; statistic shows the t statistic associated with the variable and df indicates the degrees of freedom. P value indicates the significance of the result.

	Peak Oxygen Consumption				**Time to Peak Oxygen Consumption**				**Time to Return to SMR**			
Coefficient	*Estimate*	*Statistic*	*df*	*p value*	*Estimate*	*Statistic*	*df*	*p value*	*Estimate*	*Statistic*	*df*	*p value*
Intercept	-0.46 (0.49)	-0.93	19.00	0.363	-209.74 (574.30)	-0.37	19.00	0.719	1488.64 (489.79)	3.04	16.00	0.008
log.mass	0.35 (0.25)	1.40	19.00	0.177	281.63 (294.92)	0.95	19.00	0.352	-624.31 (252.17)	-2.48	16.00	0.025
NoWorms10	0.15 (0.16)	0.91	19.00	0.375	50.38 (191.05)	0.26	19.00	0.795	133.27 (164.51)	0.81	16.00	0.430
NoWorms15	0.54 (0.19)	2.88	19.00	0.010	34.54 (217.63)	0.16	19.00	0.876	-214.33 (192.86)	-1.11	16.00	0.283
NoWorms20	0.43 (0.20)	2.22	19.00	0.039	116.91 (227.27)	0.51	19.00	0.613	-190.22 (191.72)	-0.99	16.00	0.336
Observations	24				24				21			

Table 8.2-10: List of all linear mixed effect models (LMEs) performed for LeadAccelResp. LeadAccelResp is the lag of response to a leadership event while acclerating, where higher values indicate higher propensity to lead and lower values mean higher propensity to follow while accelerating.No Worms indicates number of worms eaten at time 0, TimeSinceFeed indicates time since feeding at time 0 in minutes and Treatement is whether the fish were feeding or control group. Individual fish was nested within group for random factors. Bold indicates selected model.

Model	df	AIC	χ^2	p value
LeadAccelResp ~ NoWorms*TimeSinceFeed + NoWorms* Treatment + TimeSinceFeed*Treatment + Mass*NoWorms + Mass*TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	12	2169.73		
LeadAccelResp ~ NoWorms*TimeSinceFeed + NoWorms* Treatment + TimeSinceFeed*Treatment + Mass*TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	11	2168.01	0.28	0.599
LeadAccelResp ~ NoWorms*Treatment + TimeSinceFeed* Treatment + Mass*TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	10	2166.16	0.15	0.695
LeadAccelResp ~ NoWorms + NoWorms*Treatment + TimeSinceFeed*Treatment + Mass*Treatment + (1 | FishID:GroupID)	9	2167.29	3.12	0.077
LeadAccelResp ~ NoWorms + TimeSinceFeed*Treatment + Mass*Treatment + (1 | FishID:GroupID)	9	2167.29	0.00	
LeadAccelResp ~ TimeSinceFeed*Treatment + Mass* Treatment + (1 | FishID:GroupID)	8	2169.03	3.75	0.053

Table 8.2-11: List of all linear mixed effect models (LMEs) performed for LeadTurnResp. LeadTurnResp is the lag of response to a leadership event while acclerating, where higher values indicate higher propensity to lead and lower values mean higher propensity to follow while turning. No Worms indicates number of worms eaten at time 0, TimeSinceFeed indicates time since feeding at time 0 in minutes and Treatement is whether the fish were feeding or control group. Individual fish was nested within group for random factors. Bold indicates selected model.

Model	df	AIC	χ^2	p value
LeadTurnResp ~ NoWorms*TimeSinceFeed + NoWorms* Treatment + TimeSinceFeed*Treatment + Mass*NoWorms + Mass*TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	12	2605.22		
LeadTurnResp ~ NoWorms*TimeSinceFeed + NoWorms* Treatment + TimeSinceFeed*Treatment + Mass*TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	11	2603.23	0.01	0.927
LeadTurnResp ~ NoWorms*Treatment + TimeSinceFeed* Treatment + Mass*TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	10	2601.23	0.00	0.985
LeadTurnResp ~ NoWorms*Treatment + TimeSinceFeed* Treatment + Mass*TimeSinceFeed + (1 | FishID:GroupID)	9	2600.07	0.84	0.360
LeadTurnResp ~ NoWorms*Treatment + TimeSinceFeed* Treatment + (1 | FishID:GroupID)	7	2598.03	1.97	0.374
LeadTurnResp ~ NoWorms + TimeSinceFeed*Treatment + (1 | FishID:GroupID)	7	2598.03	0.00	
LeadTurnResp ~ TimeSinceFeed*Treatment + (1 | FishID:GroupID)	6	2596.09	0.06	0.807

Table 8.2-12: List of all linear mixed effect models (LMEs) performed for AvePosSchool. AvePosSchool is the mean position in school for each individual relative to the group's direction of travel in every frame for individual fish in each group. No Worms indicates number of worms eaten at time 0, TimeSinceFeed indicates time since feeding at time 0 in minutes and Treatement is whether the fish were feeding or control group. Individual fish was nested within group for random factors. Bold indicates selected model.

Model	df	AIC	χ^2	p value
MeanPositionSchool ~ NoWorms + TimeSinceFeed + Treatment + NoWorms* TimeSinceFeed + TimeSinceFeed*Treatment + Mass*NoWorms + Mass*TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	12	1640.70		
MeanPositionSchool ~ NoWorms + TimeSinceFeed + Treatment + TimeSinceFeed* Treatment + Mass*NoWorms + Mass*TimeSinceFeed + Mass* Treatment + (1 | FishID:GroupID)	11	1638.74	0.04	0.841
MeanPositionSchool ~ NoWorms + TimeSinceFeed + Treatment + TimeSinceFeed* Treatment + Mass*TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	10	1636.91	0.17	0.679
MeanPositionSchool ~ TimeSinceFeed + Treatment + TimeSinceFeed* Treatment + Mass*TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	9	1635.28	0.37	0.540
MeanPositionSchool ~ TimeSinceFeed*Treatment + Mass*Treatment + (1 | FishID:GroupID)	8	1633.39	0.11	0.744

Table 8.2-13: List of all linear mixed effect models (LMEs) performed for logSpeed. logSpeed is the median speed of individual fish in each group over each trial duration. No Worms indicates number of worms eaten at time 0, TimeSinceFeed indicates time since feeding at time 0 in minutes and Treatement is whether the fish were feeding or control group. Individual fish was nested within group for random factors. Bold indicates selected model.

Model	df	AIC	χ^2	p value
log10(MeanSpeed) ~ NoWorms*TimeSinceFeed + TimeSinceFeed* Treatment + Mass*NoWorms + Mass*TimeSinceFeed + Mass* Treatment + (1 | FishID:GroupID)	12	-2626.33		
log10(MeanSpeed) ~ NoWorms*TimeSinceFeed + TimeSinceFeed* Treatment + Mass*TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	11	-2628.31	0.02	0.891
log10(MeanSpeed) ~ NoWorms + TimeSinceFeed*Treatment + Mass*TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	10	-2629.84	0.48	0.489
log10(MeanSpeed) ~ TimeSinceFeed*Treatment + Mass*TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	9	-2630.25	1.59	0.207
log10(MeanSpeed) ~ Mass*TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	8	-2628.65	3.59	0.058
log10(MeanSpeed) ~ TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	7	-2627.31	3.34	0.067

Table 8.2-14: List of all linear mixed effect models (LMEs) performed for logDistCent. logDistCent is the mean distance from centroid of individual fish in each group over each trial duration. No Worms indicates number of worms eaten at time 0, TimeSinceFeed indicates time since feeding at time 0 in minutes and Treatement is whether the fish were feeding or control group. Individual fish was nested within group for random factors. Bold indicates selected model.

Model	df	AIC	χ^2	p value
log10(DistCent) ~ NoWorms*TimeSinceFeed + TimeSinceFeed* Treatment + Mass*NoWorms + Mass*TimeSinceFeed + Mass* Treatment + (1 | FishID:GroupID)	12	-2139.11		
log10(DistCent) ~ NoWorms*TimeSinceFeed + TimeSinceFeed* Treatment + Mass*TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	11	-2141.08	0.03	0.853
log10(DistCent) ~ NoWorms*TimeSinceFeed + Mass*TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	10	-2142.43	0.65	0.422
log10(DistCent) ~ NoWorms + Mass*TimeSinceFeed + Mass* Treatment + (1 | FishID:GroupID)	9	-2140.84	3.59	0.058
log10(DistCent) ~ Mass*TimeSinceFeed + Mass*Treatment + (1 | FishID:GroupID)	8	-2141.53	1.31	0.253

Table 8.2-15: List of all linear mixed effect models (LMEs) performed for Polarity. Polarity is a value indicating how polarised individuals are, where 1 = all facing the same direction and 0 = disorganised. No Worms indicates number of worms eaten at time 0, TimeSinceFeed indicates time since feeding at time 0 in minutes and Treatement is whether the fish were feeding or control group. Individual fish was nested within group for random factors. Bold indicates selected model.

Model	df	AIC	χ^2	p value
Pol ~ TimeSinceFeed + Treatment + TimeSinceFeed*Treatment + Mass*TimeSinceFeed + Mass*Treatment + (1|GroupID)	9	-5019.31		
Pol ~ TimeSinceFeed + Treatment + TimeSinceFeed*Treatment + Mass*Treatment + (1|GroupID)	8	-5020.35	0.96	0.327
Pol ~ TimeSinceFeed + Treatment + Mass*Treatment + (1 | GroupID)	7	-5021.62	0.72	0.395
Pol ~ TimeSinceFeed + Treatment + (1|GroupID)	5	-5023.81	1.81	0.404
Pol ~ TimeSinceFeed + (1|GroupID)	4	-5022.59	3.22	0.073

Table 8.2-16: List of all generalised linear mixed effect models (GLMEs) performed for ChangeSDA. ChangeSDA is the percentage change in predicted oxygen consumption after feeding in behavioural trials. No Worms indicates number of worms eaten at time 0, TimeSinceFeed indicates time since feeding at time 0 in minutes and Treatement is whether the fish were feeding or control group. Individual fish was nested within group for random factors. Bold indicates selected model.

Model	df	AIC	χ^2	p value
ChangeSDA ~ NoWorms*TimeSinceFeed + Mass* NoWorms + Mass*TimeSinceFeed + (1 | FishID:GroupID)	9	-7417.55		
ChangeSDA ~ NoWorms*TimeSinceFeed + Mass* TimeSinceFeed + (1 | FishID:GroupID)	8	-7419.54	0.00	0.948
ChangeSDA~ NoWorms + Mass + TimeSinceFeed + Mass*TimeSinceFeed + (1 | FishID:GroupID)	7	-7418.63	2.91	0.088
ChangeSDA~ NoWorms + Mass + TimeSinceFeed + (1 | FishID:GroupID)	6	-7420.50	0.14	0.711

8.3 Chapter 6: Supplementary Materials

Table 8.3-1: Results of the best-fit model for all data from Table 8.3-11 for Udiff. Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors.

Coeffcient	*Estimates*	*Statistic*	*df*	*p value*
Intercept	-3.35(1.42)	-2.35	115.00	0.020
U_{opt}Rank	-3.08(0.91)	-3.37	59.72	0.001
trialpair	2.39(1.49)	1.60	114.59	0.112
trialgroup	8.31(2.15)	3.87	93.93	<0.001
Mass	0.17(3.22)	0.05	114.66	0.957
U_{opt}Rank:mass	4.40(2.15)	2.05	60.03	0.045
trialpair:mass	-3.62(3.24)	-1.12	114.98	0.266
trialgroup:mass	-13.64 (4.87)	-2.80	85.93	0.006
Random Effects				
σ^2	0.96			
$\tau_{00\ group\_id}$	1.43			
ICC	0.60			
$N_{\ group\_id}$	70			
Observations	123			
Marginal R^2 / Conditional R^2	0.302 / 0.719			

Table 8.3-2: Results of the best-fit model for all data Table 8.3-10 for mean cumulative cost of transport. Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors.

Coeffcient	*Estimates*	*Statistic*	*df*	*p value*
Intercept	3.30(0.12)	28.25	114.93	<0.001
trialpair	0.06(0.06)	0.92	41.33	0.361
trialgroup	-0.01(0.07)	-0.14	15.91	0.893
MeanSpeed	0.06(0.02)	2.72	109.96	0.008
Mass	0.72(0.23)	3.06	113.85	0.003
trialpair:ave.speed.cms	-0.02(0.01)	-1.89	46.11	0.064
trialgroup:ave.speed.cms	-0.03(0.01)	-2.40	30.03	0.023
ave.speed.cms:mass	-0.09(0.04)	-2.50	111.64	0.014
Random Effects				
σ^2	0.03			
$\tau_{00\ group\_id}$	0.00			
ICC	0.15			
$N_{\ group\_id}$	70			
Observations	123			
Marginal R^2 / Conditional R^2	0.158 / 0.281			

Table 8.3-3: Results of the best-fit model for all data from Table 8.3-9 for mean speed in BL/s. Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors.

Coefficient	*Estimates*	*Statistic*	*df*	*p value*
Intercept	-2.97(2.04)	-1.46	71.39	0.149
TL	1.11(0.57)	1.95	71.39	0.055
trialpair	2.61(2.34)	1.11	102.01	0.269
trialgroup	7.97(2.25)	3.54	94.92	0.001
TL:trialpair	-0.72(0.65)	-1.11	102.64	0.271
TL:trialgroup	-2.13(0.63)	-3.41	96.25	0.001
Random Effects				
σ^2	0.20			
$\tau_{00\ group\_id}$	0.88			
ICC	0.82			
N_{group_id}	70			
Observations	123			
Marginal R^2 / Conditional R^2	0.085 / 0.834			

Table 8.3-4: Results of the best-fit model for pairs and group data from Table 8.3-8 for mean cumulative cost including leadership rank while turning. Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors.

Coefficient	*Estimates*	*Statistic*	*df*	*p value*
Intercept	3.56(0.06)	59.88	78.82	<0.001
LeadRankTurns	0.07(0.03)	2.69	61.28	0.009
MeanSpeed	0.02(0.01)	1.86	78.35	0.067
trialgroup	-0.10(0.04)	-2.31	29.80	0.028
leadrank.turns:ave.speed.cms	-0.01(0.00)	-2.79	70.14	0.007
Random Effects				
σ^2	0.02			
$\tau_{00\ group\_id}$	0.01			
ICC	0.23			
N_{group_id}	31			
Observations	84			
Marginal R^2 / Conditional R^2	0.166 / 0.362			

Table 8.3-5: Results of the best-fit model for pair and group data from Table 8.3-7 looking at mean cumulative cost of transport including leadership rank while accelerating. Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors.

Coeffcient	*Estimates*	*Statistic*	*df*	*p value*
Intercept	3.54 (0.07)	52.99	75.62	<0.001

Coeffcient	*Estimates*	*Statistic*	*df*	*p value*
U_{opt}Rank	0.04 (0.02)	2.30	46.98	0.026
MeanSpeed	0.02 (0.01)	1.48	75.53	0.143
trialgroup	-0.13 (0.05)	-2.62	38.32	0.013
LeadRankAccel	0.05 (0.03)	1.79	56.75	0.079
ave.speed.cms:leadrank.accel	-0.01 (0.00)	-2.47	62.58	0.016
Random Effects				
σ^2	0.02			
$\tau_{00\ group\_id}$	0.01			
ICC	0.24			
N $_{group\_id}$	31			
Observations	84			
Marginal R^2 / Conditional R^2	0.170 / 0.369			

Table 8.3-6: Results of the best-fit model for all data from Table 8.3-9 for speed in BL/s. Marginal R2 describes the proportion of variance explained by the fixed factors alone. Conditional R2 describes the proportion of variance explained by both fixed and random factors.

Coeffcient	*Estimates*	*Statistic*	*df*	*p value*
Intercept	-2.97 (2.04)	-1.46	71.39	0.149
TL	1.11 (0.57)	1.95	71.39	0.055
trialpair	2.61 (2.34)	1.11	102.01	0.269
trialgroup	7.97 (2.25)	3.54	94.92	0.001
TL:trialpair	-0.72 (0.65)	-1.11	102.64	0.271
TL:trialgroup	-2.13 (0.63)	-3.41	96.25	0.001
Random Effects				
σ^2	0.20			
$\tau_{00\ group\_id}$	0.88			
ICC	0.82			
N $_{group\_id}$	70			
Observations	123			
Marginal R^2 / Conditional R^2	0.085 / 0.834			

Table 8.3-7: List of all linear mixed effect models (LMEs) performed for MeanCumulativeCost for pairs and groups. MeanCumulativeCost is the mean cumulative cost of transport for each group. Group Size indicates Size of Group, TL is Total Length of fish in cm, U_{opt}Rank, LeadRankAccel and LeadRankTurns indicate rank of optimum swim speed and leader rank while accelerating and turning, where 1 has the lowest optimum and is the leader, and 4 shows following or high optimum swim speed. Mean Position in School indicates position in school where high values are the rear of group and low values the front. GroupID indicates group was included as a random effect. Bold indicates selected model.

Model	df	AIC	χ^2	p value
MeanCumulativeCost ~ LeadRankAccel*U_{opt}Rank + U_{opt}Rank*MeanSpeed + LeadRankAccel*GroupSize + LeadRankAccel*MeanSpeed + GroupSize*MeanSpeed + U_{opt}Rank*GroupSize + Mass*LeadRankAccel + Mass*U_{opt}Rank + Mass*MeanSpeed + Mass*GroupSize + (1 | group_id)	18	-58.35		
MeanCumulativeCost ~ LeadRankAccel*U_{opt}Rank + U_{opt}Rank*MeanSpeed + LeadRankAccel*GroupSize + LeadRankAccel*MeanSpeed + GroupSize*MeanSpeed + U_{opt}Rank*GroupSize + Mass + LeadRankAccel + Mass*U_{opt}Rank + Mass*MeanSpeed + Mass*GroupSize + (1 | group_id)	17	-60.34	0.01	0.941
MeanCumulativeCost ~ LeadRankAccel*U_{opt}Rank + U_{opt}Rank + MeanSpeed + LeadRankAccel*GroupSize + LeadRankAccel*MeanSpeed + GroupSize*MeanSpeed + U_{opt}Rank*GroupSize + Mass + LeadRankAccel + Mass*U_{opt}Rank + Mass*MeanSpeed + Mass*GroupSize + (1 | group_id)	16	-62.31	0.03	0.866
MeanCumulativeCost ~ LeadRankAccel*U_{opt}Rank + U_{opt}Rank + MeanSpeed + GroupSize + LeadRankAccel*GroupSize + LeadRankAccel*MeanSpeed + GroupSize*MeanSpeed + Mass + LeadRankAccel + Mass*U_{opt}Rank + Mass*MeanSpeed + Mass*GroupSize + (1|GroupID)	15	-64.22	0.09	0.763
MeanCumulativeCost ~ LeadRankAccel*U_{opt}Rank + U_{opt}Rank + MeanSpeed + GroupSize + LeadRankAccel*GroupSize + LeadRankAccel*MeanSpeed + GroupSize*MeanSpeed + Mass + LeadRankAccel + Mass*U_{opt}Rank + Mass*GroupSize + (1|GroupID)	14	-66.11	0.12	0.733
MeanCumulativeCost ~ LeadRankAccel*U_{opt}Rank + U_{opt}Rank + MeanSpeed + GroupSize + LeadRankAccel*GroupSize + LeadRankAccel*MeanSpeed + Mass + LeadRankAccel + Mass*U_{opt}Rank + (1|GroupID)	13	-67.80	0.31	0.578
MeanCumulativeCost ~ LeadRankAccel*U_{opt}Rank + U_{opt}Rank + MeanSpeed + GroupSize + LeadRankAccel*GroupSize + LeadRankAccel*MeanSpeed + Mass + LeadRankAccel + Mass*U_{opt}Rank + (1 | group_id)	12	-69.40	0.40	0.527
MeanCumulativeCost ~ LeadRankAccel*U_{opt}Rank + U_{opt}Rank + MeanSpeed + GroupSize + LeadRankAccel*GroupSize + LeadRankAccel*MeanSpeed + Mass + LeadRankAccel + (1|GroupID)	11	-70.69	0.71	0.400
MeanCumulativeCost ~ LeadRankAccel*U_{opt}Rank + U_{opt}Rank + MeanSpeed + GroupSize + LeadRankAccel*MeanSpeed + Mass + LeadRankAccel + (1 | group_id)	10	-71.81	0.88	0.349
MeanCumulativeCost ~ U_{opt}Rank + MeanSpeed + GroupSize + LeadRankAccel* MeanSpeed + LeadRankAccel + (1|GroupID)	**8**	**-71.09**	**4.72**	**0.094**

Table 8.3-8: List of all linear mixed effect models (LMEs) performed for MeanCumulativeCost for pairs and groups. MeanCumulativeCost is the mean cumulative cost of transport for each group. Group Size indicates Size of Group, TL is Total Length of fish in cm, U_{opt}Rank, LeadRankAccel and LeadRankTurns indicate rank of optimum swim speed and leader rank while accelerating and turning, where 1 has the lowest optimum and is the leader, and 4 shows following or high optimum swim speed.Mean Position in School indicates position in school where high values are the rear of group and low values the front. GroupID indicates group was included as a random effect. Bold indicates selected model.

Model	df	AIC	χ^2	p value
MeanCumulativeCost ~ LeadRankTurns*U_{opt}Rank + LeadRankTurns* GroupSize + LeadRankTurns*MeanSpeed + GroupSize*MeanSpeed + U_{opt}Rank*GroupSize + U_{opt}Rank*MeanSpeed + Mass*LeadRankTurns + Mass*U_{opt}Rank + Mass*MeanSpeed + Mass*GroupSize + (1 | group_id)	18	-62.99		
MeanCumulativeCost ~ LeadRankTurns*U_{opt}Rank + LeadRankTurns* GroupSize + LeadRankTurns*MeanSpeed + GroupSize*MeanSpeed + U_{opt}Rank*GroupSize + U_{opt}Rank*MeanSpeed + Mass*LeadRankTurns + Mass*U_{opt}Rank + Mass*GroupSize + (1|GroupID)	17	-64.90	0.08	0.771
MeanCumulativeCost ~ LeadRankTurns*U_{opt}Rank + LeadRankTurns* GroupSize + LeadRankTurns*MeanSpeed + GroupSize*MeanSpeed + U_{opt}Rank*GroupSize + Mass*LeadRankTurns + Mass*U_{opt}Rank + Mass*GroupSize + (1|GroupID)	16	-66.81	0.09	0.760
MeanCumulativeCost ~ LeadRankTurns*U_{opt}Rank + LeadRankTurns* GroupSize + LeadRankTurns*MeanSpeed + GroupSize*MeanSpeed + U_{opt}Rank*GroupSize + Mass*U_{opt}Rank + Mass*GroupSize + (1 | group_id)	15	-68.80	0.01	0.912
MeanCumulativeCost ~ LeadRankTurns*U_{opt}Rank + LeadRankTurns* GroupSize + LeadRankTurns*MeanSpeed + GroupSize*MeanSpeed + Mass*U_{opt}Rank + Mass*GroupSize + (1|GroupID)	14	-70.59	0.21	0.648
MeanCumulativeCost ~ LeadRankTurns*U_{opt}Rank + LeadRankTurns* GroupSize + LeadRankTurns*MeanSpeed + GroupSize*MeanSpeed + Mass*U_{opt}Rank + (1|GroupID)	13	-71.74	0.84	0.358
MeanCumulativeCost ~ LeadRankTurns*U_{opt}Rank + LeadRankTurns* MeanSpeed + GroupSize*MeanSpeed + Mass*U_{opt}Rank + (1 | group_id)	12	-72.72	1.03	0.311
MeanCumulativeCost ~ LeadRankTurns*U_{opt}Rank + LeadRankTurns* MeanSpeed + GroupSize*MeanSpeed + Mass + (1|GroupID)	11	-73.88	0.84	0.359
MeanCumulativeCost ~ LeadRankTurns + U_{opt}Rank + LeadRankTurns* MeanSpeed + GroupSize*MeanSpeed + Mass + (1|GroupID)	10	-74.55	1.33	0.249
MeanCumulativeCost ~ LeadRankTurns + U_{opt}Rank + LeadRankTurns* MeanSpeed + GroupSize + MeanSpeed + Mass + (1|GroupID)	9	-75.38	1.17	0.279
MeanCumulativeCost ~ LeadRankTurns + U_{opt}Rank + LeadRankTurns* MeanSpeed + GroupSize + MeanSpeed + (1|GroupID)	8	-73.76	3.61	0.057
MeanCumulativeCost ~ LeadRankTurns*MeanSpeed + GroupSize + (1 | group_id)	**7**	**-72.01**	**3.75**	**0.053**

Table 8.3-9: List of all linear mixed effect models (LMEs) performed for MeanSpeedBL. MeanSpeedBL is the mean speed for individuals in bodylengths per second. Group Size indicates Size of Group, TL is Total Length of fish in cm, U_{opt}Rank, LeadRankAccel and LeadRankTurns indicate rank of optimum swim speed and leader rank while accelerating and turning, where 1 has the lowest optimum and is the leader, and 4 shows following or high optimum swim speed. Mean Position in School indicates position in school where high values are the rear of group and low values the front. GroupID indicates group was included as a random effect. Bold indicates selected model.

Model	df	AIC	χ^2	p value
MeanSpeedBL ~ U_{opt}Rank*GroupSize + LeadRankTurns*U_{opt}Rank + LeadRankTurns*GroupSize + TL*U_{opt}Rank + TL*GroupSize + TL* LeadRankTurns + (1|GroupID)	15	313.23		
MeanSpeedBL ~ U_{opt}Rank*GroupSize + LeadRankTurns*GroupSize + TL* U_{opt}Rank + TL*GroupSize + TL*LeadRankTurns + (1|GroupID)	14	311.25	0.01	0.905
MeanSpeedBL ~ LeadRankTurns*GroupSize + TL*U_{opt}Rank + TL* GroupSize + TL*LeadRankTurns + (1|GroupID)	13	309.26	0.01	0.924
MeanSpeedBL ~ LeadRankTurns*GroupSize + TL*U_{opt}Rank + TL* GroupSize + (1|GroupID)	12	307.36	0.10	0.752
MeanSpeedBL ~ LeadRankTurns*GroupSize + TL*GroupSize + (1|GroupID)	10	303.68	0.32	0.852
MeanSpeedBL ~ TL*GroupSize + (1|GroupID)	**8**	**302.88**	**3.20**	**0.202**

Table 8.3-10: List of all linear mixed effect models (LMEs) performed for MeanCumulativeCost for all groups. MeanCumulativeCost is the mean cumulative cost of transport for each group. Group Size indicates Size of Group, TL is Total Length of fish in cm, U_{opt}Rank, LeadRankAccel and LeadRankTurns indicate rank of optimum swim speed and leader rank while accelerating and turning, where 1 has the lowest optimum and is the leader, and 4 shows following or high optimum swim speed.Mean Position in School indicates position in school where high values are the rear of group and low values the front. GroupID indicates group was included as a random effect. Bold indicates selected model.

Model	df	AIC	χ^2	p value
MeanCumulativeCost ~ U_{opt}Rank + GroupSize + MeanSpeed + GroupSize* MeanSpeed + U_{opt}Rank*GroupSize + U_{opt}Rank*MeanSpeed + U_{opt}Rank*Mass + GroupSize*Mass + MeanSpeed*Mass + (1 | group_id)	16	-55.61		
MeanCumulativeCost ~ U_{opt}Rank + GroupSize + MeanSpeed + GroupSize* MeanSpeed + U_{opt}Rank*GroupSize + U_{opt}Rank*MeanSpeed + U_{opt}Rank*Mass + MeanSpeed*Mass + (1|GroupID)	14	-59.27	0.34	0.845
MeanCumulativeCost ~ U_{opt}Rank + GroupSize + MeanSpeed + GroupSize* MeanSpeed + U_{opt}Rank*MeanSpeed + U_{opt}Rank*Mass + MeanSpeed*Mass + (1|GroupID)	13	-61.27	0.01	0.929
MeanCumulativeCost ~ U_{opt}Rank + GroupSize + MeanSpeed + GroupSize* MeanSpeed + U_{opt}Rank*Mass + MeanSpeed*Mass + (1 | group_id)	12	-63.16	0.10	0.749
MeanCumulativeCost ~ U_{opt}Rank + GroupSize + MeanSpeed + GroupSize* MeanSpeed + MeanSpeed*Mass + Mass + (1|GroupID)	11	-65.06	0.11	0.746
MeanCumulativeCost ~ GroupSize*MeanSpeed + MeanSpeed* Mass + (1|GroupID)	**10**	**-64.51**	**2.55**	**0.110**

Table 8.3-11: List of all linear mixed effect models (LMEs) performed for Udiff for all groups. Udiff is the difference between optimum swim speed and mean swim speed in behavioural trials. Group Size indicates Size of Group, TL is Total Length of fish in cm, U_{opt}Rank, LeadRankAccel and LeadRankTurns indicate rank of optimum swim speed and leader rank while accelerating and turning, where 1 has the lowest optimum and is the leader, and 4 shows following or high optimum swim speed. Mean Position in School indicates position in school where high values are the rear of group and low values the front. GroupID indicates group was included as a random effect. Bold indicates selected model.

Model	df	AIC	χ^2	p value
Udiff ~ U_{opt}Rank + GroupSize + Mass + U_{opt}Rank*GroupSize + U_{opt}Rank* Mass + GroupSize*Mass + (1|GroupID)	11	439.94		
Udiff ~ U_{opt}Rank + GroupSize + Mass + U_{opt}Rank*Mass + GroupSize*Mass + (1 | group_id)	10	440.46	2.52	0.113

Table 8.3-12: Adjusted repeatability (Radj) of Optimum swim speed was calculated using rptR package (Stoffel et al., 2017). TL is the total length of the individual and fish is the fish ID which was included in the model as a random effect. 23 fish were measured twice to get 46 observations.

Model Structure		Radj	95% CI	p value
1:	U_{opt} ~ TL + (1| fish)	0.726	0.509 – 0.852	<0.001

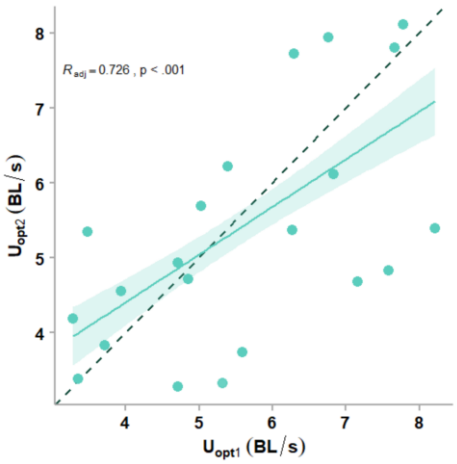

Figure 8.3-1: Scatter graph showing Optimum swim speed for each individual fish at the first and second swimming trial in bodylengths per second showing the linear regression line and 95% confidence interval. Dashed line shows 1:1 line which indicates exact repeatability. Radj displays adjusted-R for repeatbility and significance.

Table 8.3-13: Table showing the results of the Tukey's posthoc model comparisons of the effect of group size on cumulative cost of transport using the emmeans package.

Group Size Comparison	estimate	SE	df	t - ratio	p - value
alone - pair	0.0398	0.0424	78.9	0.939	0.62
alone - group	0.1363	0.0459	43.7	2.971	0.01
pair - group	0.0965	0.0458	30.1	2.107	0.11

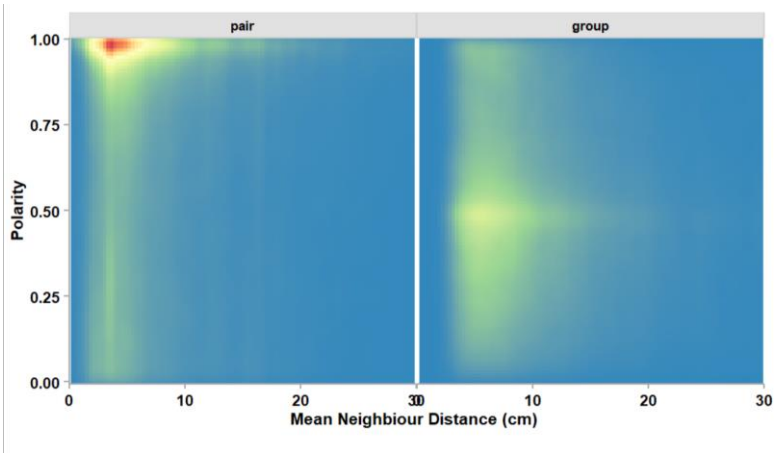

Figure 8.3-2: Heatmap to show polarity vs cohesion in mean neighbour distance (cm). Different panels represent the different group sizes.

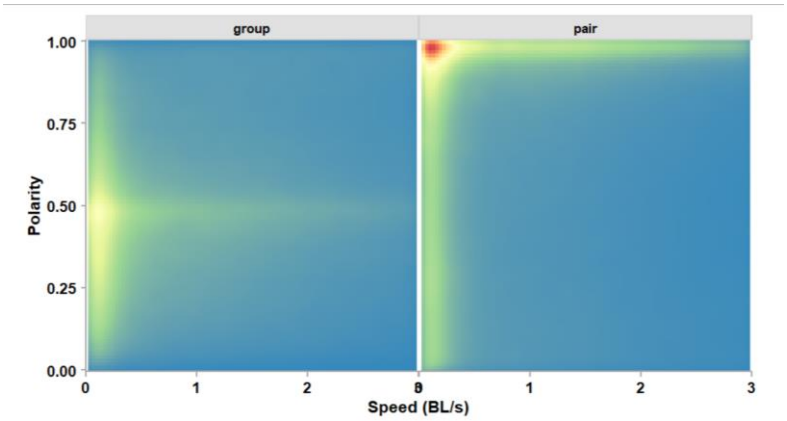

Figure 8.3-3: Heatmap to show polarity vs speed in bodylengths/s. Different panels represent the different group sizes.

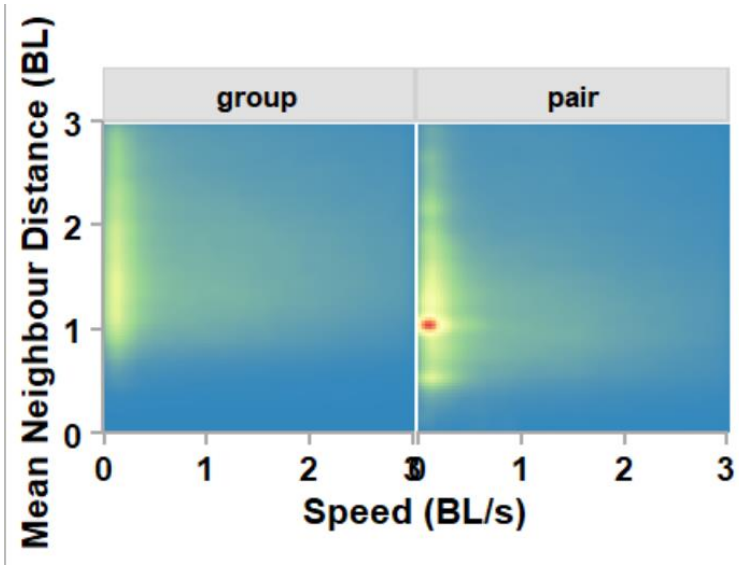

Figure 8.3-4: Heatmap to show cohesion in bodylegnths vs speed in bodylengths/s. Different panels represent the different group sizes.