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13 **Metabolic costs of feeding predictively alter the spatial distribution of individuals in fish schools**
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SUMMARY

Group living is ubiquitous among animals [1, 2] but the exact benefits of group-living experienced by individual groupmates is related to their spatial location within the overall group [3-5]. Individual variation in behavioural traits and nutritional state is known to affect interactions between individuals and their social group [6, 7], but physiological mechanisms underpinning collective animal behaviour remain largely unexplored [8]. Here we show that while fish at the front of moving groups are most successful at capturing food items, these individuals then show a systematic, post-feeding movement toward the rear of groups. Using observations of fish feeding in groups coupled with estimates of metabolic rate in fish consuming different meal sizes, we demonstrate that the magnitude of this shift in spatial position is directly related to the aerobic metabolic scope remaining after accounting for energetic costs of digestion. While previous work has shown that hungry individuals occupy anterior positions in moving groups [9, 10], these results show that the metabolic demand of food processing reduces the aerobic capacity available for locomotion in individuals that eat most, thus preventing them from maintaining leading positions. This basic trade-off between feeding and locomotor capacity could fundamentally dictate the spatial position of individuals within groups, perhaps obviating the role of individual traits in determining spatial preferences over shorter timescales (e.g. hours to days). This may be a general constraint for individuals within animal collectives, representing a key, yet overlooked, mediator of group functioning that could affect leadership, social information transfer, and group decision making.

RESULTS

The spatial positioning of individuals within social groups affects the resources they obtain, the predation risk they experience, and their influence on group decision-making [11, 12]. Individuals with relatively high boldness [11], locomotor capacity [6, 13], or metabolic demand may be found at the front of moving groups more often, where they can maximise food-intake [9, 10, 14]. Receiving less attention in the context of group behaviour is the fact that, at acute timescales, feeding is associated with an increase in metabolic rate due to the energetic costs of the mechanical and biochemical digestion of food and uptake of nutrients [15, 16] – the so-called specific dynamic action (SDA) response. These SDA costs can be substantial and, at their peak, approach an animal's maximum aerobic metabolic rate, thus occupying a significant portion of the aerobic scope available for other physiological functions, including locomotion (AS) [17, 18]. It is therefore possible that, following feeding, individuals that prefer frontal positions within moving groups may be physiologically constrained from occupying these positions.

We examined whether the remaining AS during SDA was related to shifts in spatial positioning by individual common minnows (*Phoxinus phoxinus*) in moving groups following feeding. We observed individual variation in food intake while drift feeding within a swimming flume (Figure 1A; Movie S1). For all fish, we also estimated metabolic rates via rates of oxygen uptake ($\dot{M}_{O_2}$)[19]. Separate fish were measured for changes in oxygen uptake rate after consuming different amounts of food. The metabolic responses of these fish to feeding were used to predict the AS remaining, after accounting for the costs of SDA, for fish in the swimming experiments in relation to food intake and time since feeding.

Each individual was tested for group behaviour twice, across two trials with different groups of conspecifics. The number of food items captured showed strong repeatability across the two trials (Figure 1B; R = 0.667, 95% CI = 0.593–0.722, p < 0.0001). Within trials, the mean position was also repeatable across time periods (R = 0.196, 95% CI = 0.140–0.253, p < 0.0001). Within each time period but between the two trials (Figure 1C), repeatability was maintained but was lowered during and 20 min after feeding (Figure 1D). Mass-standardised standard metabolic rate (SMR; the minimum energy needed to sustain life in an ectotherm) and AS were not related to position within groups before, during, or after feeding (Table S1). Fish at the front of groups and those that were larger at a given position captured the most food items (Figure 2; t = 5.475, p < 0.0001). Absolute SMR, MMR, and AS were all positively correlated with body mass (Figure S1). After standardisation to a common body mass of 2.7 g (the mean mass of all fish at the time of oxygen uptake rate measurements), neither SMR nor AS affected food captured. Fish that consumed the most food had moved to more posterior positions within groups by 40 and 60 min post-feeding (Figure 2B; Table S1).

Next, to quantify the increase in metabolic rate during the SDA response, fish separate to those used during the swimming trials were fed known quantities of food, then measured for $\dot{M}_{O_2}$ using intermittent-closed respirometry. The SDA response of each individual was modelled be applying a polynomial function to the $\dot{M}_{O_2}$ data for 40 h after feeding (Figure 3A). Fish that ate larger meals during feeding trials showed higher peak levels of $\dot{M}_{O_2}$ after feeding associated with the digestion and assimilation of the food, and larger fish had a higher peak $\dot{M}_{O_2}$ (Table S2). Fish that ate more also took longer for $\dot{M}_{O_2}$ to return to baseline (Table S2). Neither meal size nor body mass affected the time post-feeding at which peak $\dot{M}_{O_2}$ occurred, with peak $\dot{M}_{O_2}$ occurring on average 93.90 ± 11.39 min post-feeding. There was individual variation in this response, however, and when time was broken into the 12 min intervals during which $\dot{M}_{O_2}$ was recorded, the median time at peak $\dot{M}_{O_2}$ post-feeding was 60 min (Figure 3A).

152   Based on measurements of $\dot{M}_{O_2}$ during these feeding trials, a multiple regression was constructed to
153   estimate the $\dot{M}_{O_2}$ of fish during the swimming trials, according to the following equation (r^2 = 0.385, p
154   < 0.0001):

156   $Log_{10} \dot{M}_{O_{2,increase}}$ = -1.859 + (0.00727t) + (0.814B)+ (1.643log_{10} mass)   eq. 1,

158   where $\dot{M}_{O_{2,increase}}$ = the increase in $\dot{M}_{O_2}$ above SMR; t = time post-feeding (min); B = meal size (% of
159   body mass); and mass = fish body mass (g).

161   Applying this equation to fish observed in swimming trials, the predicted percentage of AS
162   remaining, after accounting for the predicted rise in $\dot{M}_{O_2}$ post-feeding, decreased with meal size and
163   time (Figure 3B and C; Table S3). Fish that ate larger meals showed greater posterior movement
164   within groups, and this effect strengthened over time (Figure 4A and B; Table S4). Individuals with a
165   lower AS remaining after feeding (standardised to a common body mass) moved toward the back of
166   groups (Figure 4C, Table S4), an effect that did not interact with time post-feeding. This backward
167   movement was not due to those fish spending more time at the front of the group and becoming
168   fatigued, or having nowhere to move besides back: during control trials in which fish were not fed,
169   repeatability of positioning across observation times was high (R = 0.595, 95% CI = 0.459–0.707; p =
170   0.001; Figure S2, Table S5).

172   **DISCUSSION**

173   The magnitude of the shift in spatial position by individuals within schools after feeding was
174   systematic and related to meal size during feeding and the AS remaining after accounting for SDA.
175   Previous work has shown that individual boldness [11, 12], movement speed [6], and AS [13, 20] can
176   all influence individual position within groups. However, our results suggest that, at least over short
177   timeframes on the scale of hours, the physiological costs of feeding could negate effects of intrinsic
178   traits on spatial positioning and leadership within groups, with individuals moving toward the rear of
179   groups after they feed. In the wild, it is possible that individuals at the front of groups may eat the
180   most, or highest quality, food items [21], but then be forced to move back within the group with
181   others that have fed less taking over anterior positions. After feeding, individuals that might
182   otherwise act as leaders might be physiologically unable to occupy the spatial positions that would
183   allow them to influence the group.

184   The position occupied by individuals within groups after feeding was related to: (1) the amount of
185   food consumed during feeding; (2) the time since feeding; and (3) the proportion of AS remaining
186   during meal processing. Feeding motivation may have influenced spatial positioning, as individuals
187   consuming little or no food during feeding consistently obtained positions at or near the front of
188   schools within the hour after feeding. This is consistent with previous observations in which food-
189   deprived individuals occupied frontal positions more frequently than satiated conspecifics [10, 22].
190   Although positions at the front of fish schools are associated with the highest degrees of food intake,
191   the available evidence suggests that, in many systems, they also have the highest risk of predation
192   [23, 24, but see 25]. It therefore stands to reason that, once an individual has fed to satiation or
193   exhausted the food resource, it should move to a less-risky position within the group. Indeed, in the
194   current study, individuals consuming larger meals had moved towards the back of the school by 60
195   min after feeding. However, the persistent effect of remaining AS on the positioning of fish after
196   feeding within groups strongly suggests that metabolic constraints imposed by meal processing had
197   a direct role in dictating positions occupied by individuals. Notably, the effect of meal size increased
198   with time since feeding, while the effect of available AS was consistent across observation periods.
199   This suggests that fish moved back within groups as they reached thresholds for available AS during
200   meal digestion and assimilation, regardless of the time since feeding. If motivation was the primary

201 factor causing individuals to change their position, then fish that ate the most should have moved
202 back within the group almost immediately after feeding.
203
204 The increase in $\dot{M}_{O_2}$ following feeding can be considerable, and depending on meal size, can occupy
205 a large proportion of an individual's total AS at its peak [17, 18, 26, 27]. Several fish in the current
206 study were estimated to have substantial decreases in AS after feeding, which would be expected to
207 constrain locomotor ability [27, 28]. Individuals consuming the largest meals, and thus exhibiting the
208 highest peak rise in metabolic costs during digestion, adjusted spatial positions to the back of groups
209 where the costs of locomotion are generally reduced due to vortices produced by anterior
210 groupmates [29, 30]. There may also be interactions among intrinsic physiological traits, feeding
211 motivation or ability, and the magnitude of the SDA response. Fish with a larger AS feed more when
212 given the opportunity [31], and SDA is positively linked to meal size [26]. It is therefore plausible
213 that, in scenarios where food is abundant, individuals with a higher AS may eat more and,
214 paradoxically, be more constrained than fish with a lower AS but that eat less. Furthermore, fish that
215 ate more in the current study were found to have $\dot{M}_{O_2}$ elevated for longer periods (up to 11 h post-
216 feeding), suggesting that fish that eat more will also be constrained by SDA for a longer duration.
217 Notably, there was variation in the digestive "strategy" employed by individuals. Some fish had a
218 high peak $\dot{M}_{O_2}$ but return to baseline more quickly, while other take longer to digest but with a lower
219 peak $\dot{M}_{O_2}$. The cause of this variation is unknown but undoubtedly contributed to uncertainty in
220 predictions of remaining aerobic scope after feeding. Our estimates of the energetic costs of
221 foraging may have also been under-estimated for some individuals because we could not account for
222 the physical acceleration and turning to capture food (Movie S1).
223
224 Despite changes in spatial positioning among individuals after feeding, there remained a degree of
225 repeatability in positions occupied by individuals. Repeatability of positioning between trials before
226 feeding suggests that individuals prefer specific positions within groups in the absence of food. This
227 is corroborated by trials in which fish were not fed, where repeatability of positioning was
228 maintained throughout trials (Figure S3). Repeatability decreased during feeding, probably because
229 fish were shuffling positions during competition for food items, but then re-stabilised as time after
230 feeding increased. Future work is needed to understand the consequences of these changes in
231 repeatability caused by feeding constraints for the costs and benefits of group membership
232 experienced by individuals, and for the potential selection on phenotypic traits that are normally
233 assumed to correlate with spatial positioning within groups (e.g. boldness) [32, 33]. For example, re-
234 shuffling of individuals within moving groups, or changes in repeatability due to SDA, could disrupt
235 social niche formation [34, 35] or influence group cohesion.
236
237 In conclusion, data from the present study demonstrate a series of complex interactions between
238 feeding and intrinsic physiological mechanisms that determine the spatial positions that individuals
239 will occupy within moving animal groups. Individuals that obtained more food during foraging
240 showed a predictable pattern of movement to more posterior positions within the group that was
241 tied directly to available AS during meal digestion. Changes in position will alter the costs and
242 benefits experienced by individuals in different locations within the group. This information is critical
243 for understanding how our current knowledge of collective behaviour may extend to ecologically
244 relevant scenarios [36, 37]. Additional work is required to understand how these processes interact
245 with factors such as boldness on determining spatial positioning within groups. Over prolonged
246 timescales, intrinsic behavioural or physiological traits may influence positional preference, but
247 these effects may be overridden over shorter timescales due to locomotor constraints after feeding.
248 More research is also needed to understand the consequences of locomotor constraints for group
249 leadership, group learning, and group decision-making, particularly if group leaders or
250 demonstrators are physiologically incapable of occupying specific positions within groups.
251

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403 **FIGURE 1.** Repeatability of behaviour during group feeding and swimming trials. (A) Top view of
404 swim tunnel during tests of schooling behaviour in common minnows (*P. phoxinus*). Fish were
405 ranked according to the position of the tip of the snout in relation to the front of the school.
406 Positions in this theoretical example are indicated by numbers to the bottom left of fish. (B)
407 Repeatability of food items captured. (C) Repeatability of mean spatial position occupied within a
408 school of six *P. phoxinus* across two group trials. Each data point represents one individual fish. For
409 illustrative purposes, solid lines in panels B and C represent linear regressions. To make overlapping
410 points visible, points in panel B are slightly offset (horizontally) from their true value. Shaded area in
411 panel B represents the 95% confidence intervals (not shown on panel C for visual clarity). (D)
412 Changes in repeatability within each time interval before, during, and after feeding, using data
413 collected during the two trials. The grey shaded area in panel D represents the 95% confidence
414 interval on repeatability estimates. The green horizontal line represents repeatability of mean
415 position across time periods (see Results for details). Numbers beneath data points equal p-values
416 for repeatability estimates. Sample size is n = 123 individuals tested in two replicate trials. See also
417 Movie S1.
418
419 **FIGURE 2.** The relationship between mean spatial position of individual minnows within a school of
420 six fish and the amount of food items eaten during a period of feeding. The feeding period is
421 designated as time 0. For positions, 1 = at the front of the school and 6 = at the back of the school.
422 There are two points per individual (each fish was tested twice). For illustrative purposes, solid lines
423 represent linear regressions. Shaded areas around lines represent the 95% confidence intervals.
424 From left to right, each plot shows data during feeding (0), and at 20, 40, and 60 min post-feeding.
425 Sample size is n = 123 individuals tested in two replicate trials. See also Table S1.
426
427 **FIGURE 3.** The effects of feeding on oxygen uptake rate ($\dot{M}_{O_2}$) and remaining aerobic scope. (A)
428 Changes in $\dot{M}_{O_2}$ with time since feeding various amounts of food in individual *P. phoxinus*. Each
429 curve represents data for one individual and is a polynomial function (detailed in the main text).
430 Green horizontal line represents the mean MMR of fish used in the schooling trials; the green
431 shaded area represents the upper and lower standard deviations. The orange shaded area is the
432 time period corresponding to feeding and the subsequent 60 min in the group swimming trials. (B
433 and C) Predicted percentage of aerobic scope remaining for individual fish in group swimming trials
434 after feeding, based on the amount of food consumed by each individual (B: food items eaten; C:
435 meal size in terms of % body mass) and time since feeding. Each data point represents data for one
436 individual; there are two points per individual (each fish was tested twice). For illustrative purposes,
437 solid lines represent linear regressions. Shaded areas around lines represent the 95% confidence
438 intervals. Sample size is n = 123 individuals tested in two replicate trials. See also Table S2 and Table
439 S3.
440
441 **FIGURE 4.** The effect of food intake and remaining aerobic scope on changes in position at various
442 times since feeding. (A) Effect of food items consumed; (B) Effect of relative meal size (% body
443 mass); (C) Effect of the % of aerobic scope remaining. Positive values indicate the number of
444 positions moved towards the front of the school while negative values indicate the number of
445 positions moved towards the back of the school. Each data point represents data for one individual;
446 there are two points per individual (each fish was tested twice). For illustrative purposes, solid lines
447 represent linear regressions. Shaded areas around lines represent the 95% confidence intervals.
448 Sample size is n = 123 individuals tested in two replicate trials. See also Figure S2, Table S4, and
449 Table S5.
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453

454 **STAR METHODS**
455 **Contact for reagent and resource sharing**
456 Further information and requests for resources and reagents should be directed to and will be
457 fulfilled by the Lead Contact, Shaun Killen (shaun.killen@glasgow.ac.uk).
458
459 **Experimental model and subject details**
460 *Animal model*
461 Approximately 180 common minnows were collected from the River Kelvin, Glasgow, United
462 Kingdom (55° 51' 59.99" N -4° 18' 60.00" W) using large dip-nets. Animals were in a non-
463 reproductive state and thus sex was unable to be identified. Sex was therefore not included as a
464 factor in analyses but was unlikely to affect results given that individuals were non-reproductive at
465 the time of experiments. In addition, individuals were randomly assigned to test groups (as
466 described below) and so males and females should have been equally distributed among groups and
467 time points in relation to feeding. To reduce capture bias at the time of collection from the wild,
468 shallow-side channels along the river were used to initially herd fish before capture. Fish were
469 maintained in the laboratory in four stock tanks (640 mm L x 620 mm W x 330 mm H) in
470 recirculating, aerated freshwater at 13°C. All tanks had pebble substrate, artificial plants, and plastic
471 tubes for environmental enrichment and were maintained on a 12 L:12 D photoperiod. All
472 individuals were fed daily using commercial feed (flakes) and bloodworm. Fish were held in these
473 conditions for approximately 4 months before starting experiments (at this point, fish mass = 2.7 ±
474 0.09 (s.e.m.) g; total length = 6.74 ± 0.07 cm). Before experiments, however, individuals were
475 deprived of food for a minimum of 36 h. The maintenance, handling, and non-lethal experiments
476 conducted on fish during this study were carried out in strict accordance with the Home Office
477 legislation (Project Licence Number: 60/4461) in the United Kingdom.
478
479 **Method details**
480 *Protocol Overview*
481 The overall protocol consisted of three main parts, details of which are given below. First, the
482 standard and maximum metabolic rates (SMR and MMR, respectively) of individual minnows (n =
483 130) were estimated from rates of oxygen uptake ($\dot{M}_{O_2}$) using using intermittent-closed
484 respirometry. Secondly, and approximately 3 weeks later, these same fish were used in group
485 behavioural trials within a swimming flume (6 fish per group). These trials were video recorded and
486 later analysed to estimate the spatial position of individual fish. Positions were estimated for each
487 fish before, during, and after a period of feeding in which drifting food items (bloodworms) were
488 injected into the flume. The total number of food items eaten by each fish was also quantified. In
489 these behaviour trials, each individual fish was tested twice (about 2 weeks between trials), with
490 each trial being performed with a different set of conspecifics. Behaviour was recorded for 45 groups
491 in total. Due to a small number of mortalities, some individuals were not used in both trials. Only
492 individuals that were exposed to all trials and metabolic trait measurements were used in statistical
493 analyses (n = 123 fish). Thirdly, a different set of minnows were measured for $\dot{M}_{O_2}$ in the 40 h
494 following feeding on different amounts of food items. The data from these trials were used to
495 construct a predictive equation (see Results) of the rise in $\dot{M}_{O_2}$ induced by feeding (i.e. the 'specific
496 dynamic action'; SDA) in relation to the amount of food eaten and the time since feeding. This
497 equation was then applied to fish used in the behavioural trials within the swim flume, to estimate
498 the percentage of remaining aerobic scope each fish would have possessed according to food it had
499 consumed and the timing of the observations.
500
501 *Estimation of metabolic rates*
502 Fasted fish were carefully removed from their holding tanks using a dip-net. Maximum metabolic
503 rate was measured after exhaustive exercise for a 2 min duration by manually chasing individual fish
504 in a circular tank (50 cm diameter) with a water depth of 10 cm. All fish were exhausted after this

505   time period and would not swim with further stimulation. This method assumes that maximum $\dot{M}_{O_2}$
506   is achieved during the recovery from the bout of exhaustive and partially anaerobic exercise, which
507   is generally well supported [38, 39]. After complete exhaustion, fish were immediately transferred
508   into individual cylindrical 96 mL glass respirometry chambers connected to an intermittent-closed
509   respirometry system; the time until transfer was always less than 10 s [40, 41]. Water oxygen
510   content in the respirometry chambers was quantified once every 2 s using a FireStingO$_2$ 4-channel
511   optical oxygen meter and associated sensors and software (Pyro Science GmbH, Aachen, Germany).
512   The respirometry chambers were kept in a 50 L rectangular experimental tank which was aerated
513   and temperature regulated to 13°C. The setup was shielded from disturbance and direct lighting by
514   an opaque plastic blind. Water mixing within each respirometry chamber was achieved with a
515   peristaltic pump that moved water through the chamber and around an external circuit of gas-tight
516   tubing. An automated flush pump allowed the chambers to switch between being flushed with fresh
517   and fully aerated water for 3 min, and then switched off for 8 min, during which time the chambers
518   were sealed to allow the decrease in oxygen content to be analysed to indicate the rate of oxygen
519   uptake ($\dot{M}_{O_2}$). To estimate MMR, we calculated $\dot{M}_{O_2}$ for each 2 min time interval throughout the first
520   20 min of recovery immediately following the exhaustive exercise, and MMR (mg O$_2$ h^{-1}) was taken
521   as the highest $\dot{M}_{O_2}$ during this period.

523   After measurement of MMR, fish remained in the same respirometry chambers overnight to allow
524   the estimation of SMR. Individuals were then removed from the respirometry chambers at around
525   09:00 the following day, having remained in the respirometry chambers for approximately 20 h in
526   total. The fish were then lightly anaesthetised using benzocaine, given a unique combination of
527   coloured visible implant elastomer tags (Northwest Marine Technology Inc., Shaw Island, USA) to
528   allow individual identification when in groups, measured for wet mass and total length, and returned
529   to their holding tanks for 4 days before continuing with the remainder of the study. Whole-animal
530   SMR (mg O$_2$ h^{-1}) was estimated as the lowest 10th percentile of measurements taken throughout the
531   measurement period [42]. The first 5 h of confinement in the chambers was excluded from analyses
532   of SMR because the $\dot{M}_{O_2}$ of the fish was often elevated at this time. Aerobic scope (AS) was
533   calculated as the difference between MMR and SMR. Before and after fish $\dot{M}_{O_2}$ measurements,
534   three full respirometry cycles were run with empty chambers to measure any background $\dot{M}_{O_2}$ by
535   bacteria. The increase in this background respiration from start to end of a respirometry trial was
536   assumed to be linear and was subtracted from each measure of $\dot{M}_{O_2}$ by individual fish.

538   *Metabolic cost of feeding (SDA)*
539   The increase in $\dot{M}_{O_2}$ following feeding (i.e. the SDA response) was measured using the intermittent-
540   closed respirometry setup described above. In this case, however, fish were fed a set amount of
541   bloodworms immediately before being placed within the respirometry chambers. Pilot studies
542   revealed that minnows would not eat food that was directly injected into the respirometry
543   chambers, thus fish were fed before placement into the chambers. Individuals (separate fish from
544   those used in previous swimming trials and measurements of metabolic attributes) were fasted for 4
545   days to elevate hunger levels and ensure that each fish would eat all of their assigned food during
546   trials. From one of the 4 holding tanks, individuals were randomly selected and assigned to receive
547   either 0, 3, 6, 9, or 12 bloodworms (covering the range of food items consumed by fish in the
548   schooling trials; detailed below). The fish receiving 0 bloodworms acted as a control for handling
549   involved in transfer to the respirometry chambers. Fish were fed their prescribed amount of food in
550   a temperature-regulated tank kept at 13°C. Once each fish had eaten the desired number of food
551   items, they were immediately placed into the respirometry chamber and $\dot{M}_{O_2}$ was measured as
552   described above for the next 40 h. In total, 32 fish were measured for $\dot{M}_{O_2}$ in these feeding trials (n =
553   6 individuals per feeding level; n = 8 control individuals). For the calculation of SMR in these
554   individuals, the lowest 10th percentile of data was used after oxygen consumption had reached a

555   clear baseline; data collected while $\dot{M}_{O_2}$ was still elevated due to feeding was not used for the

556   calculation of SMR (all fish had reached a plateau in their $\dot{M}_{O_2}$ within 11 h). To account for any

557   effects of handling during feeding or transfer to the respirometry chambers during the period over

558   which SDA was measured, the mean $\dot{M}_{O_2}$ for the control fish was subtracted from all fed individuals.

559

560   For subsequent analyses, meal sizes were also quantified in terms of the percentage body mass each

561   fish consumed. This was achieved by weighing samples of 20 bloodworms (blotted dry to remove

562   excess water) and using the mean mass of these, divided by the total number of blood worms per

563   sample, as an estimate of the mass of one bloodworm.

564

565   *Spatial positioning and feeding of schooling fish*

566   Measurements of fish behaviour in swimming schools (Movie S1) were performed in a 30 L

567   Steffensen-type swimming tunnel (Loligo Systems, Viborg, Denmark), designed to cause fish to swim

568   at controlled speeds in non-turbulent water with a uniform velocity profile. Water in the tunnel was

569   regulated to 13°C and the tunnel had a working (swimming) section that was 45 cm long, 14 cm

570   wide, and 14 cm high. During group trials, the speed of the tunnel was set to 13 cm s^{-1} (~2 body

571   lengths s^{-1}) to ensure individuals swam aerobically with a steady pace.

572

573   To begin a trial, six individuals that had been fasted for 36 h were carefully removed from their

574   holding tanks with dip-nets. This shoal size was chosen because it allowed the intake of food per

575   individual to be easily quantified and it prevented crowding within the flume. To reduce capture

576   bias, individuals were selected by eye then pursued until capture. Fish were then introduced as a

577   group to the working section of the swim tunnel and water velocity was gradually increased from 0

578   to 13 cm s^{-1}. Each school was then allowed to settle in the swim tunnel for 30 min prior to

579   conducting any behavioural observations. Following this period, the behaviour of the schools was

580   recorded using a camera (GoPro Hero4, GoPro, California, USA) positioned directly above the swim

581   tunnel. Specifically, trials were recorded during 10 min intervals starting at: (1) 10 min before the

582   introduction of food; (2) during a feeding period; (3) 20 min following the conclusion of feeding; (4)

583   40 min following feeding; and (5) 60 min following feeding. During the feeding period, individual

584   bloodworms were injected (using a 10 mL syringe) into the flow of the swim tunnel in a randomised

585   location through one of five pieces of aquarium tubing. The tube used for each injection was

586   determined using a random number generator. The aquarium tubing was inserted halfway into the

587   honeycomb flow straightener at the front of the swimming section and was not visible to the fish

588   (Figure S1). During the injection of food, the fish were shielded from the experimenter in order to

589   minimise stress or any cues that would signal the onset of incoming food. During the feeding period,

590   a total of 30 bloodworms were introduced into the flow of the tunnel with approximately 8 s

591   between injections. This number of food items ensured that there was enough food for some, but

592   not all, individuals within the school to become satiated, if there was a heterogeneous level of food

593   intake among fish within a school. Additional control trials (8 groups with 6 fish each) were

594   conducted in which fish were not fed at time 0, but were still video recorded at −10, 0, 20, 40 and 60

595   min. The fish used for these trials were different fish than those used in the treatment trials, and

596   each control fish was tested in one trial.

597

598   All videos were later analysed to quantify: (1) the number of food items consumed by each

599   individual, and (2) the spatial positioning behaviour of individuals within schools during each time

600   period. To determine positioning, still frames of each recording were analysed at 30 s intervals. The

601   fish in each frame (identified by their unique elastomer tag) were ranked according to their

602   proximity to the front of the school according to the position of their snout (Figure S1). This

603   produced 20 observations per individual per trial for each of the five time intervals described above

604   (i.e. 100 observations per individual per group trial).

605

Quantification and statistical analyses

All models were produced using R v. 3.4.0 (R Development Core Team 2016) using the function lmer in package lme4 [43]. Outputs of statistical analysis are mentioned where appropriate in the Results. Additionally, outputs for all models are presented in Tables S1-S5. Before inclusion in statistical models, all metabolic attributes (SMR, MMR, and AS) were standardised to a common body mass (2.7 g, the mean mass of all fish in the study at the time of metabolic rate measurements) using the residuals of the relationships between the log-transformed value of each variable and log body mass (see Figure S1). For all models in which AS is described as being used as an explanatory variable, separate models were also constructed which instead used MMR as an index of aerobic capacity. All model outputs are given in Tables S1-S5, however in the Results section specific values refer to models that used AS. Importantly, the use of either MMR or AS in models did not affect conclusions. Similarly, in cases where meal size (as a percentage of body mass) was used as an explanatory variable, alternative models were run using the absolute number of food items as an index of food intake. Again, all models are given in Tables S1-S5, but Results refer to models using meal size as a percentage of body mass, and conclusions were not affected by the use of either meal size or number of food items eaten in models.

The factors affecting the position of fish within groups was assessed using a linear mixed effects model (LME) with mean position (within a given time period and trial) as the dependent variable, body mass, SMR, AS (or MMR), and time post-feeding (categorical with five levels: −10, 0, 20, 40, and 60) as fixed factors, and fish ID nested within group and trial number (either trial one or two for an individual fish) as random factors. Repeatability (R) of individual positioning within schools across and within time periods (before, during, and after feeding) was calculated as adjusted (consistency) repeatability using the variance components from this first LME model [44]. The amount of food eaten by each individual while swimming in groups was analysed using a second LME model with the number of food items obtained as the dependent variable, mass, SMR, AS (or MMR), and position as fixed effects, and fish ID, group number, and trial number as random effects. Within-context repeatability for individual positioning within each time period, as well as repeatability of food captured during feeding, across the two trials was calculated using the variance components from this second LME model.

To examine the effects of feeding on the amount of AS available for swimming, a predictive multiple regression was constructed from the data for fish measured for $\dot{M}_{O_2}$ following feeding. This model used $\dot{M}_{O_2}$ as the response variable, and meal size (in terms of percentage body mass), time post-feeding, and body mass as explanatory variables (see Results). Before inclusion in statistical models, the predicted percentage of AS remaining was standardised to a common body mass (2.7 g, the mean mass of all fish in the study at the time of metabolic rate measurements) using the residuals of the relationships between percent remaining AS and body mass. After applying this model to fish in the swimming trials, the predicted percentage of AS remaining after feeding was analysed using an LME with standardised percentage of remaining AS as the dependent variable, mass, meal size (or number of food items), SMR, AS (or MMR), and time as fixed effects, and fish ID nested within group and trial number as random effects. Finally, the change in position between the feeding period (time 0 min) and 60 min post-feeding for each individual was analysed using an LME with the change in position as the dependent variable, mass, meal size (percentage body mass or food items eaten), standardised percentage AS remaining, and time as fixed effects, and fish ID nested within group and trial number as random effects. For all models, model selection proceeded by using maximum likelihood estimation, dropping variables one by one, starting with the variables with smallest t values. Variables were kept in the model if their removal resulted in significantly larger Akaike information criterion value as indicated by likelihood ratio tests. The assumptions of homoscedasticity and normality of residuals were confirmed by visual inspection of residual-fit plots and Q-Q plots. To conform to model assumptions, mass, SMR, MMR, and AS were $\log_{10}$-transformed.

657
658   Significance testing was employed to provide some indication of the strength of evidence for
659   observed patterns, along with model r^2 values using the MuMIn 1.9.13 package for R [45]. This
660   included marginal r^2 (r^2_m) and conditional r^2 (r^2_c), which indicate the variance explained by fixed
661   factors and by both fixed and random factors, respectively [46]. P-values are generally imprecise in
662   model outputs and are arbitrary when used as thresholds for declaring statistical significance and
663   problematic and limiting in several ways [47, 48]. Thus, for all models we treat p-values as a
664   continuous measure providing an approximate level of evidence against the null hypothesis [49].
665
666   **Data and software availability**
667   All data are available in the Mendeley Data Repository (http://dx.doi.org/10.17632/8g955t3r9g.1).
668
669   **Movie S1. Sample video of a group of minnows within the swim flume, feeding on drifting food**
670   **items. Related to Figure 1 and STAR Methods.**

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Antibodies		
N/A		
Bacterial and Virus Strains		
N/A		
Biological Samples		
N/A		
Chemicals, Peptides, and Recombinant Proteins		
N/A		
Critical Commercial Assays		
N/A		
Deposited Data		
Raw data	This paper	Table S2
Experimental Models: Cell Lines		
N/A		
Experimental Models: Organisms/Strains		
Common minnow	Wild caught (River Kelvin, UK)	*Phoxinus phoxinus*
Oligonucleotides		
N/A		
Recombinant DNA		
N/A		
Software and Algorithms		
R version 3.4.0	R Core Team	https://www.r-project.org/
Other		
N/A		
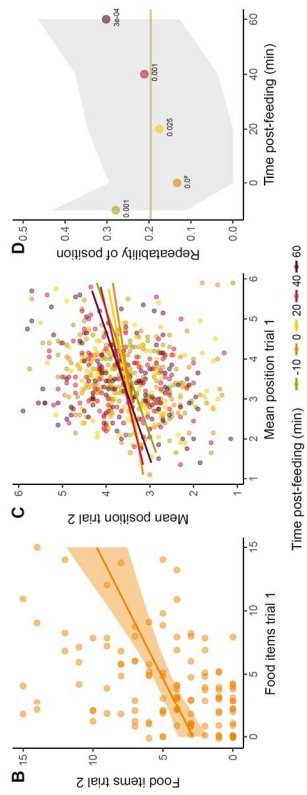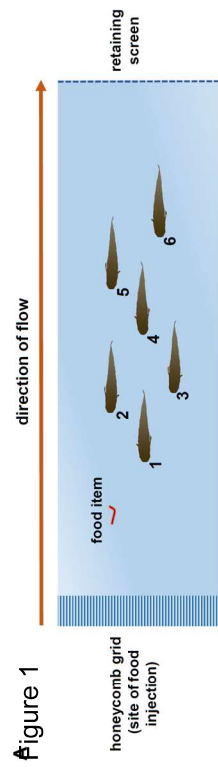
Figure 1
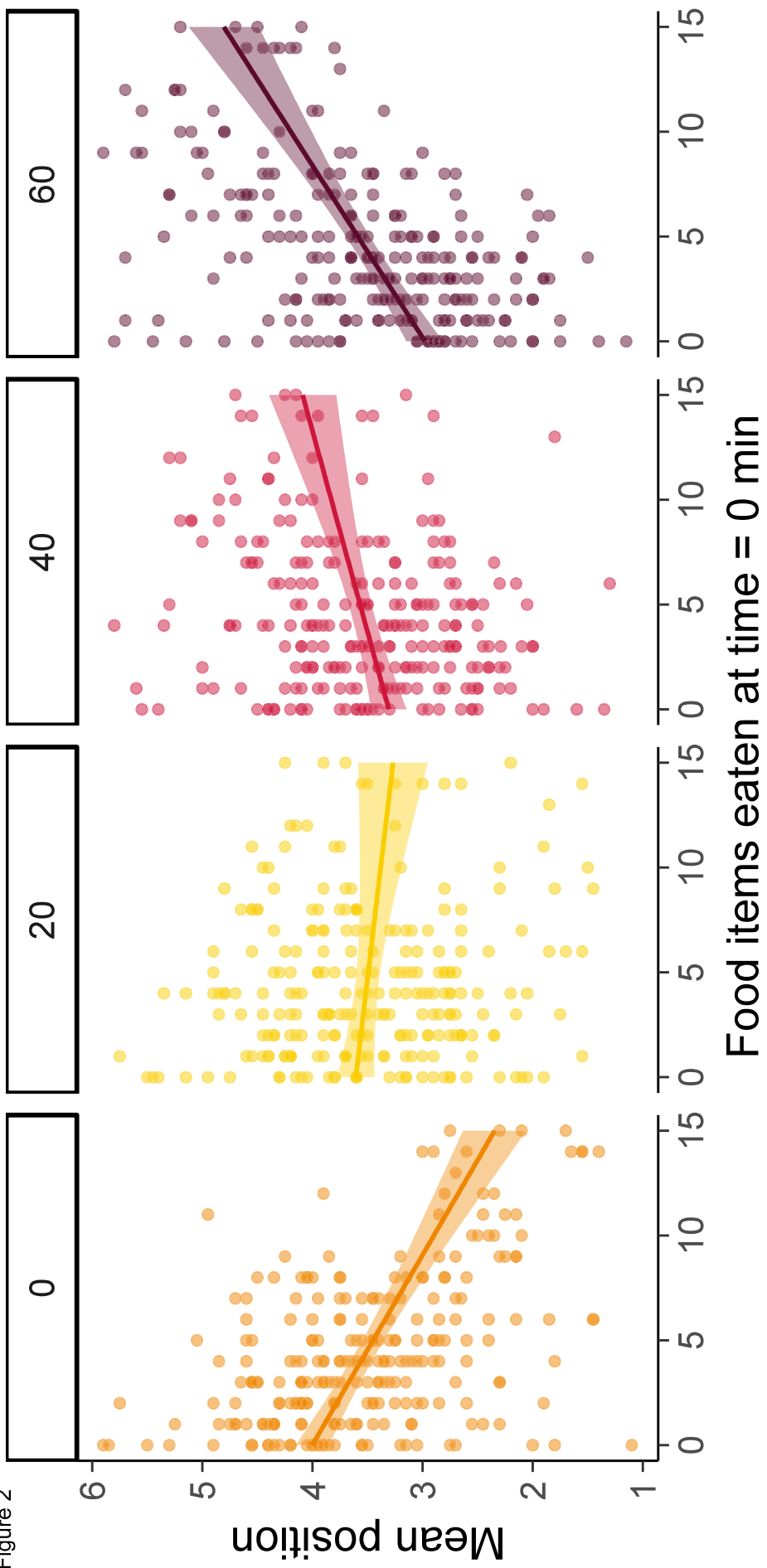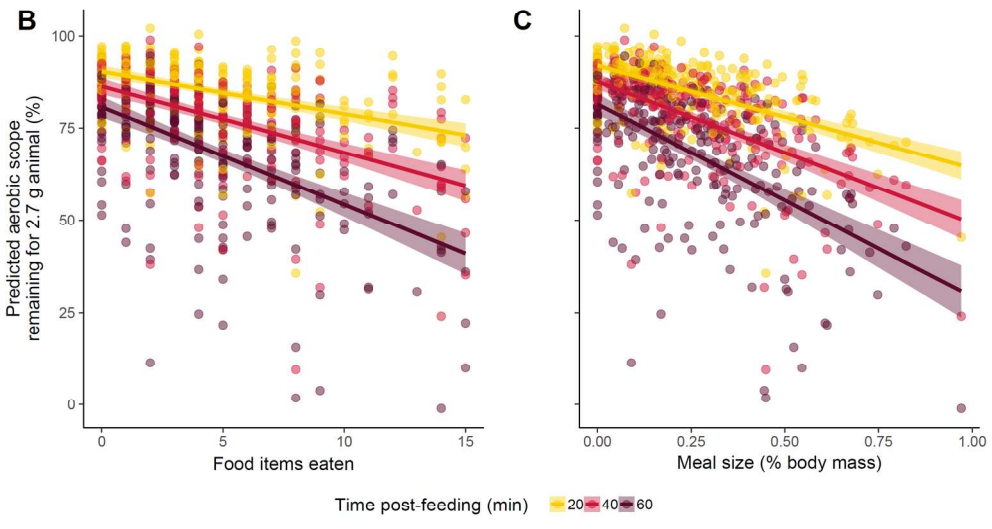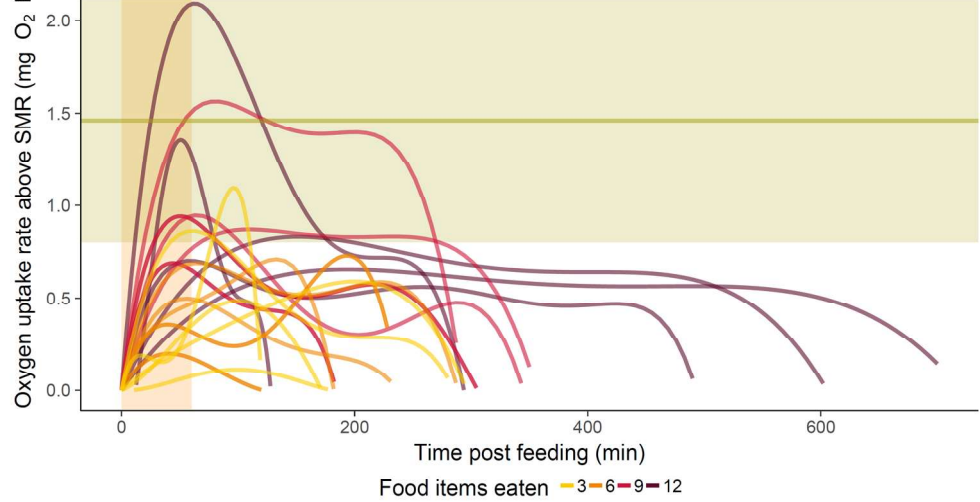
Figure 2

Figure 3

Figure 4
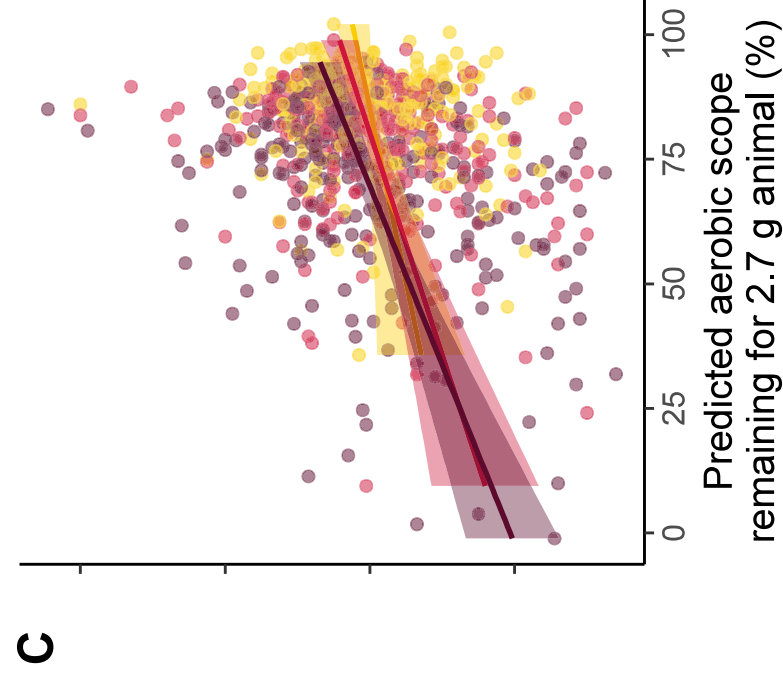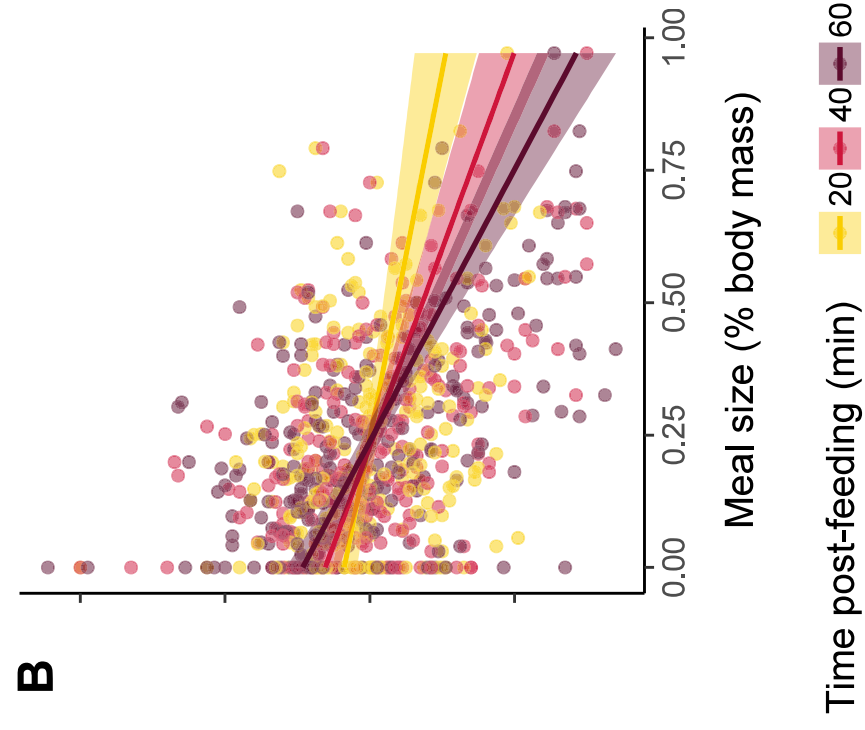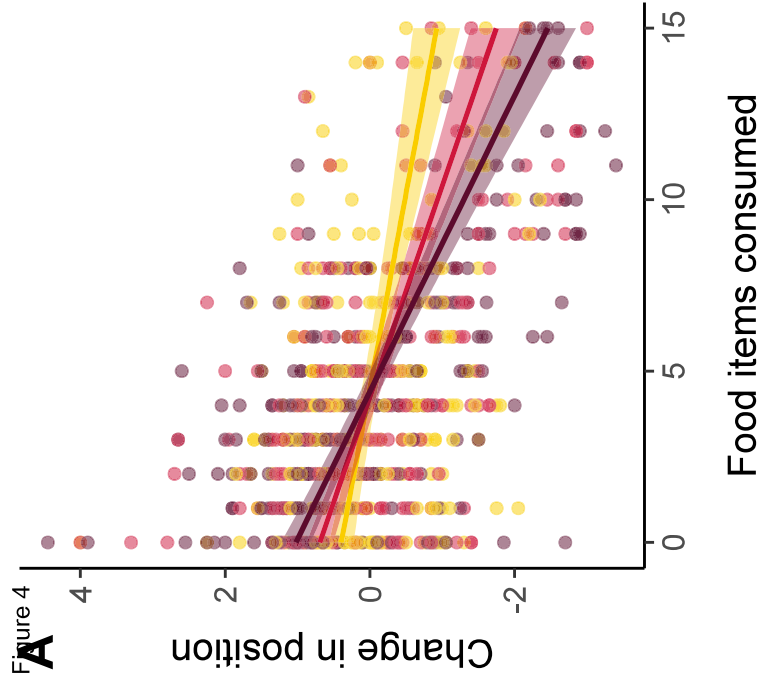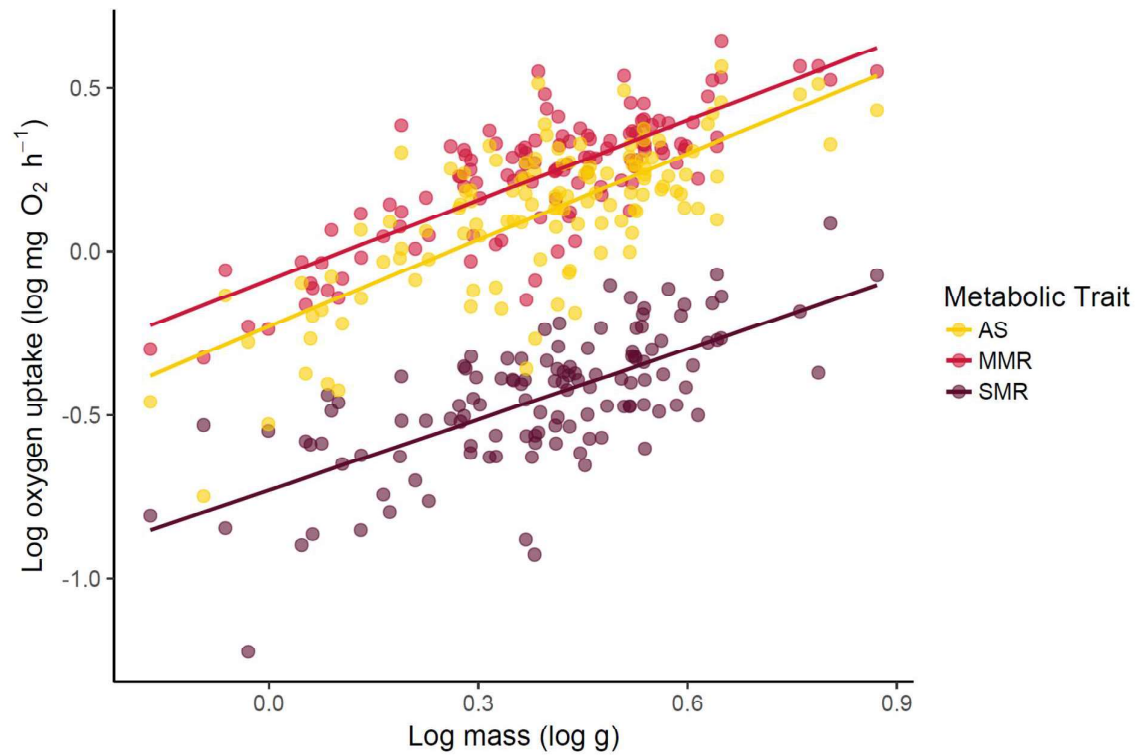
Figure S1. Relationship between metabolic traits measured in common minnows and body mass. Related to mass-standardisation of variables described in STAR Methods. SMR = standard metabolic rate; MMR = maximum metabolic rate; AS = aerobic scope. Regression equations are as follows: log SMR = -0.732 + 0.721(log mass), r^2 = 0.470, $p < 0.0001$; log MMR = -0.087 + 0.813(log mass), r^2 = 0.638, $p < 0.0001$; log AS = -0.227 + 0.878(log mass), r^2 = 0.532, $p < 0.0001$.
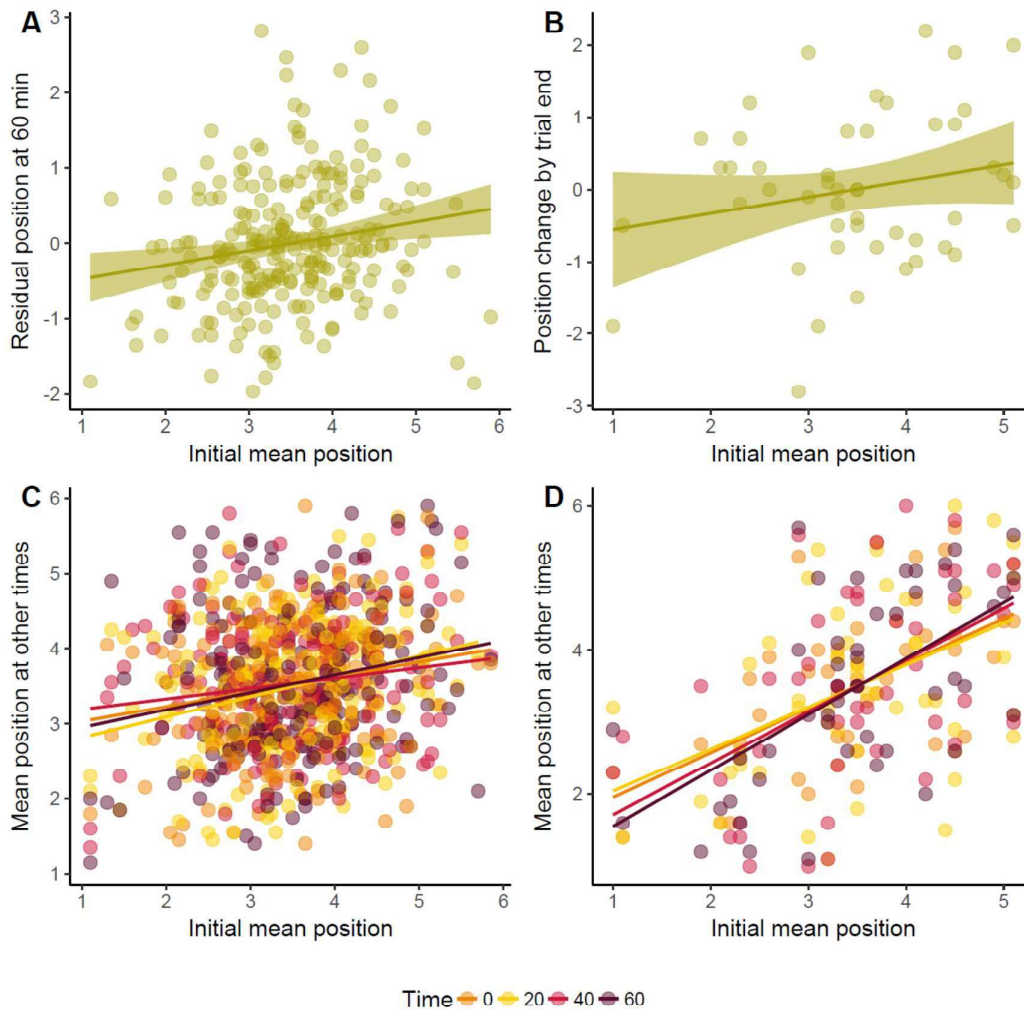
FIGURE S2. Changes in spatial position during trials were not due to fish at the front early in the trial becoming fatigued (independent of food intake) or the result of only being able to move toward the back. Related to Figure 4. (A) For treatment trials, the relationship between residual positon at 60 min (after controlling for the total number of food items consumed) and initial spatial position at the beginning of the trial. (B) For control trials in which fish were not fed (8 groups of 6 fish each, with each fish tested one time in one group), the relationship between total change in mean position during the course of the trial and the initial position of each individual (10 minutes before time 0, the point at which fish would have been fed in treatment trials). (C) For treatment trials, spatial positioning of individuals at various times post-feeding, in relation to their initial position 10 minutes before feeding; (D) Spatial positioning during control trials in which fish were not fed (8 groups of 6 fish each, with each fish tested one time in one group) at various times in relation to the position of fish when the trial first began (10 minutes before time 0). Point are coloured according to the variable "Time", which represents the time in relation to when fish would have been fed in the treatment trials (i.e. time 0, and at 20, 40, and 60 min after this time). In all panels, each data point = 1 individual fish. For visual reference, lines in each panel represent linear regression through points; shaded area is 95% CI for regression. Model outputs are given in Table S6.

	estimate	s.e.	df	t	p	r^2_m	r^2_c
model with AS as a fixed factor							
intercept	3.239	0.169	190.70	19.165	< 0.0001	0.129	0.427
log mass (log g)	0.695	0.252	239.70	2.757	0.006		
food items	-0.041	0.014	751.00	-2.811	0.005		
log SMR (log mg O_2 h^{-1})	-0.255	0.249	240.00	-1.026	0.306		
log AS (log mg O_2 h^{-1})	-0.016	0.237	240.00	-0.067	0.947		
time (min)							
0	0.364	0.094	976.00	3.890	0.0001		
20	-0.032	0.094	976.00	-0.338	0.735		
40	-0.331	0.094	976.00	-3.530	0.0004		
60	-0.659	0.094	976.00	-7.027	< 0.0001		
food items x time (min)							
0	-0.080	0.016	976.00	-5.026	< 0.0001		
20	0.0076	0.016	976.00	0.480	0.631		
40	0.082	0.016	976.00	5.162	< 0.0001		
60	0.152	0.016	976.00	9.517	< 0.0001		
model with MMR as a fixed factor							
intercept	3.238	0.194	219.30	16.710	< 0.0001	0.129	0.427
log mass (log g)	0.694	0.253	249.70	2.756	0.006		
food items	-0.041	0.014	751.30	-2.816	0.005		
log SMR (log mg O_2 h^{-1})	-0.252	0.246	240.00	-1.024	0.306		
log MMR (log mg O_2 h^{-1})	-0.003	0.312	240.10	0.000	0.999		
time (min)							
0	0.364	0.094	976.00	3.890	0.0001		
20	-0.032	0.094	976.00	-0.338	0.735		
40	-0.331	0.094	976.00	-3.530	0.0004		
60	-0.659	0.094	976.00	-7.027	< 0.0001		
food items x time (min)							
0	-0.080	0.016	976.00	-5.026	< 0.0001		
20	0.008	0.016	976.00	0.480	0.631		
40	0.082	0.016	976.00	5.162	< 0.0001		
60	0.152	0.016	976.00	9.517	< 0.0001		

TABLE S1. Results of linear mixed effects models examining factors affecting the mean position of individual fish within swimming schools. Related to Figure 2. SMR = standard metabolic rate; MMR = maximum aerobic scope; AS = aerobic scope. Note that each of SMR, MMR, and AS were standardised to a common mass of 2.7 g (the mean mass of all fish in the study at the time of oxygen uptake measurements) before use in models. The term 'mass' refers to body mass at the time of the group swimming trials in the flume. Separate models were constructed to use either MMR or AS as indices of aerobic capacity. For each model, fish ID nested within group and trial number (each fish was tested twice in two different groups) were used as random effects.

	estimate	s.e.	t	p	r^2
response: peak oxygen uptake					
intercept	-1.325	0.645	-2.056	0.055	0.599
log mass (log g)	3.067	0.775	0.959	0.001	
log SMR (log mg O_2 h^{-1})	-0.373	0.392	-0.952	0.355	
meal size (%)	1.019	0.324	3.146	0.006	
intercept	-0.589	0.518	-1.139	0.271	0.557
log mass (log g)	1.614	0.530	3.044	0.007	
log SMR (log mg O_2 h^{-1})	-0.311	0.414	-0.750	0.463	
food items	0.063	0.024	2.678	0.016	
response: time at peak (min)					
intercept	67.659	123.729	0.547	0.592	0.056
log mass (log g)	4.153	148.685	0.028	0.978	
log SMR (log mg O_2 h^{-1})	-41.370	75.282	-0.550	0.590	
meal size (%)	16.094	62.202	0.259	0.799	
intercept	110.034	94.222	1.168	0.259	0.056
log mass(log g)	-34.078	96.498	-0.353	0.728	
log SMR (log mg O_2 h^{-1})	-21.589	75.436	-0.286	0.778	
food items	-1.037	4.302	-0.241	0.812	
response: time until return to SMR (min)					
intercept	-190.4	253.700	-0.751	0.463	0.509
log mass (log g)	455.0	304.900	1.492	0.154	
log SMR (log mg O_2 h^{-1})	-105.5	154.400	-0.683	0.504	
meal size (%)	484.9	127.500	3.802	0.001	
intercept	115.134	195.502	0.589	0.564	0.498
log mass (log g)	-214.013	200.226	-1.069	0.300	
log SMR (log mg O_2 h^{-1})	-102.991	156.523	-0.658	0.519	
food items	33.041	8.926	3.702	0.002	

TABLE S2. Results of general linear models examining factors affecting oxygen uptake following feeding in minnows. Related to Figure 3A. SMR = standard metabolic rate. For each response variable, separate models were constructed to use either meal size (% body mass) or number of food items consumed as indices of food intake.

	estimate	s.e.	df	t	p	r^2_m	r^2_c
model with meal size as a fixed factor							
intercept	80.178	2.311	68.30	34.700	< 0.0001	0.799	0.937
log mass (log g)	-32.091	2.772	240.50	-11.578	< 0.0001		
meal size (%)	-32.581	2.452	369.80	-13.287	< 0.0001		
log SMR (log mg O_2 h^{-1})	-11.716	2.884	240.00	-4.053	< 0.0001		
log MMR (log mg O_2 h^{-1})	80.068	3.645	240.00	21.974	< 0.0001		
time (min)							
40	-4.299	0.601	488.00	-7.149	< 0.0001		
60	-10.307	0.601	488.00	-17.139	< 0.0001		
meal size (%) x time (min)							
40	-10.661	1.923	488.00	-5.533	< 0.0001		
60	-25.558	1.923	488.00	-13.265	< 0.0001		
model with food items as a fixed factor							
intercept	69.077	2.320	123.20	29.780	< 0.0001	0.791	0.946
log mass (log g)	-10.623	3.101	241.00	-3.427	0.0007		
food items	-1.661	0.137	330.30	-12.104	< 0.0001		
log SMR (log mg O_2 h^{-1})	-12.938	3.021	240.00	-4.286	< 0.0001		
log MMR (log mg O_2 h^{-1})	78.748	3.810	240.00	20.671	< 0.0001		
time (min)							
40	-3.966	0.545	488.00	-7.272	< 0.0001		
60	-9.509	0.545	488.00	-17.433	< 0.0001		
food items x time (min)							
40	-0.650	0.093	488.00	-6.993	< 0.0001		
60	-1.560	0.093	488.00	-16.766	< 0.0001		

TABLE S3. Results of linear mixed effects models examining the estimated percentage of aerobic scope remaining after feeding, after accounting for the approximate costs of digestion and meal assimilation. Related to Figure 3B and 3C. SMR = standard metabolic rate; AS = aerobic scope. Note that each of SMR and AS were standardised to a common mass of 2.7 g (the mean mass of all fish in the study at the time of oxygen uptake measurements) before use in models. The term 'mass' refers to body mass at the time of the group swimming trials in the flume. Separate models were constructed to use either meal size (% body mass) or number of food items consumed as indices of food intake. For each model, fish ID nested within group and trial number (each fish was tested twice in two different groups) were used as random effects.

	estimate	s.e.	df	t	p	r^2_m	r^2_c
model with food items as a fixed factor							
intercept	0.494	0.183	282.40	2.697	0.0074	0.310	0.722
log mass (log g)	-0.230	0.367	243.10	-0.627	0.531		
food items	-0.085	0.017	404.00	-4.935	< 0.0001		
time (min)							
40	0.297	0.086	487.30	3.446	0.0006		
60	0.627	0.086	487.20	7.279	< 0.0001		
food items x time (min)							
40	-0.075	0.015	487.20	-5.089	< 0.0001		
60	-0.144	0.015	487.20	-9.820	< 0.0001		
model with meal size as a fixed factor							
intercept	1.163	0.200	278.70	5.803	< 0.0001	0.279	0.710
log mass (log g)	-1.648	0.352	243.10	-4.681	< 0.0001		
meal size (%)	-1.468	0.322	425.00	-4.559	< 0.0001		
time (min)							
40	0.264	0.090	487.30	2.924	0.0036		
60	0.575	0.090	487.10	6.385	< 0.0001		
meal size (%) x time (min)							
40	-1.246	0.289	487.20	-4.315	< 0.0001		
60	-2.455	0.289	487.10	-8.504	< 0.0001		
model with remaining AS as a fixed factor							
intercept	-1.581	0.376	253.60	-4.204	< 0.0001	0.150	0.700
log mass (log g)	-1.605	0.395	241.80	-4.060	< 0.0001		
remaining AS (%)	0.028	0.004	485.60	7.564	< 0.0001		
time (min)							
40	0.151	0.064	593.50	2.373	0.0179		
60	0.432	0.084	730.70	5.156	< 0.0001		

TABLE S4. Results of linear mixed effects models examining factors affecting the change in mean position of individual fish after feeding in swimming schools. Related to Figure 4. SMR = standard metabolic rate; AS = aerobic scope. Note that each of SMR and AS were standardised to a common mass of 2.7 g (the mean mass of all fish in the study at the time of oxygen uptake measurements) before use in models. The term 'mass' refers to body mass at the time of the group swimming trials in the flume. Separate models were constructed to use either meal size (% body mass) or number of food items consumed as indices of food intake. The percentage of AS remaining was not included in models with food intake because of the strong correlations between variables. For each model, fish ID nested within group and trial number (each fish was tested twice in two different groups) were used as random effects.

	estimate	s.e.	df	t	p	r^2_m	r^2_c
residual position at 60 min							
intercept	-0.917	0.302	152.10	-3.034	0.003	0.042	0.295
log mass (log g)	0.649	0.383	153.33	1.695	0.092		
initial position	0.171	0.066	240.54	2.592	0.010		
mean position during control trials							
intercept	0.004	0.511	143.59	0.008	0.993	0.375	0.610
log mass (log g)	-0.052	0.416	45.00	-0.125	0.901		
initial position	1.002	0.142	141.60	7.067	< 0.0001		
time (min)							
0	1.335	0.569	184.00	2.344	0.02		
20	1.459	0.569	184.00	2.563	0.011		
40	1.000	0.569	184.00	1.757	0.081		
60	0.780	0.569	184.00	1.371	0.172		
initial position x time (min)							
0	-0.389	0.157	184.00	-2.416	0.017		
20	-0.417	0.157	184.00	-2.651	0.009		
40	-0.285	0.157	184.00	-1.813	0.071		
60	-0.225	0.157	184.00	-1.431	0.154		
change in position during control trials							
intercept	-0.796	0.561		-1.419	0.163	0.045	
log mass (log g)	0.197	0.645		0.306	0.761		
initial position	0.217	0.156		1.382	0.174		

TABLE S5. Summary of analyses demonstrating that changes in position are not due to individuals spending more time at the front of the group or having nowhere to move besides moving backward. Related to Figure 4 and Figure S2. The first linear mixed effects model examines the relationship between residual position at 60 min post-feeding (after correcting for total food items consumed) and initial position occupied by fish at the beginning of trials. Model also included fish ID, group, and trial number as random factors. The second linear mixed effects model examines factors affecting the mean position occupied by fish during control trials in which individuals were not fed over a 70 min time period. Model also included fish ID nested within group as a random factor. The final model is a general linear model examining factors affecting change in positioning in fish during control trials in which individual were not fed, over a 70 min time period.