Marine & Environmental Sciences Faculty Articles

Department of Marine and Environmental Sciences

5-25-2021

The effect of metabolic phenotype on sociability and social group size preference in a coral reef fish

Shaun S. Killen
University of Glasgow

Lauren E. Nadler
James Cook University, lnadler@nova.edu

Kathryn Grazioso
University of Miami

Amy Cox
The University of the West Indies

Mark I. McCormick
James Cook University

Find out more information about Nova Southeastern University and the Halmos College of Natural Sciences and Oceanography.

ORIGINAL RESEARCH

Ecology and Evolution
Open Access

WILEY

The effect of metabolic phenotype on sociability and social group size preference in a coral reef fish

Shaun S. Killen[1] [iD] | Lauren E. Nadler[2] | Kathryn Grazioso[3] | Amy Cox[4] |
Mark I. McCormick[2] [iD]

[1]College of Medical, Veterinary and Life Sciences, Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, UK

[2]Department of Marine Biology and Aquaculture, ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Qld, Australia

[3]Department of Marine Biology and Ecology, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL, USA

[4]Biological and Chemical Sciences, The University of the West Indies, St. Michael, Barbados

Correspondence
Shaun S. Killen, College of Medical, Veterinary and Life Sciences, Institute of Biodiversity, Animal Health and Comparative Medicine, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK.
Email: shaun.killen@glasgow.ac.uk

Present address
Lauren E. Nadler, Halmos College of Natural Sciences and Oceanography, Nova Southeastern University, Dania Beach, FL, USA

Abstract

Although individuals within social groups experience reduced predation risk and find food patches more consistently, there can be competition for food among group-mates. Individuals with a higher standard metabolic rate (SMR) may be less social, to prioritize food acquisition over defense, while a greater maximum metabolic rate (MMR) may modulate sociability through increased competitive ability. Therefore, in theory, individuals with a higher SMR may prefer smaller groups and those with greater MMR may prefer larger groups. We examined links among metabolic phenotype, sociability, and choice of group size in the redbelly yellowtail fusilier *Caesio cuning*. Individuals were exposed to three association tests: (a) a choice between two fish or zero fish; (b) a choice between five fish or zero fish; and (c) a choice between two fish and five fish. The first two tests quantified sociability while the third measured relative group size choice. Although there was no link between SMR and sociability, fish with a higher MMR were more social than those individuals with a lower MMR. While no correlation was found between MMR and group size choice, there was weak evidence that, if anything, individuals with a higher SMR preferred larger groups, contrary to our hypothesis. As *C. cuning* is an active fish that spends a large proportion of time operating above SMR, this result could suggest that the links between sociability and SMR may shift depending on a species' routine behavior. Links between sociability and MMR may arise if competitive ability allows individuals to obtain resources within groups. Although metabolic traits had no significant influence on group size choice, variation in food availability or predation risk could alter the effects of metabolism on group size choice.

KEYWORDS

competition, ecophysiology, foraging, group living, predator avoidance, teleost fish

1 | INTRODUCTION

Group living is widespread among animals due to the numerous benefits associated with predator avoidance, foraging, and reproduction (Krause & Ruxton, 2002; Ward & Webster, 2016). However, there are also a number of costs associated with group living. For example, although groups tend to find food patches more consistently than individual foragers (Ekman & Hake, 1988), groupmates will often compete for the limited food items discovered (Webster & Hart, 2006). This competition can lead to aggression within groups, as well as an unequal distribution of resources among groupmates (DeBlois & Rose, 1996). These costs and benefits may cause variable sociability (defined here as tendency to associate with conspecifics during nonaggressive interactions) within species, due to differences in individual needs, phenotypes, and perceived resource availability (Jolles et al., 2017; Killen, Fu, et al., 2016; Petkova et al., 2018; Réale et al., 2007).

At the proximate level, among-individual variation in sociability is likely influenced by the physiological phenotype of an animal, particularly factors associated with energy demand (Jolles et al., 2020). There is evidence that individuals with an intrinsically higher energetic demand are less social and more aggressive, spending more time away from conspecifics and rank higher in dominance hierarchies (Killen, Fu, et al., 2016; Killen et al., 2014; Metcalfe et al., 1995, 2016). These effects can also be stimulated when available food resources are scarce. Food-deprived individuals, for example, tend to be less social, likely because they prioritize noncompetitive access to food over the safety of remaining close to the group (Krause et al., 1999). These results highlight the complex relationships among sociability and factors such as energy demand, food availability, and competition. However, the degree to which these links can be broadly applied to social species across contexts, habitat types, and taxa requires further investigation.

Metabolic traits related to energy use may influence an individuals' sociability, but this relationship has yet to be explored. Maximum aerobic metabolic rate (MMR), for example, sets the upper bounds on an individual's aerobic scope (AS, capacity to support activities beyond basic maintenance) and is directly related to aerobic locomotor ability and potentially the ability to recover from burst-type anaerobic activity (Killen et al., 2015; Metcalfe et al., 2016; Norin & Clark, 2016). Given that AS and MMR can be positively associated with competitive ability (Killen et al., 2014), animals with a higher MMR may be more social if they are able to out-compete groupmates or be dominant within their social group. Hence, individuals with a higher AS and MMR may be able to maximize the benefits of sociality that come with ranking highly in the dominance hierarchy, due to greater success in interference competition (Isbell, 1991), including optimal positioning for defense and access to resources like food and shelter (Morrell & Romey, 2008). The minimum metabolic rate needed to sustain life (standard metabolic rate (SMR) in ectotherms and basal metabolic rate (BMR) in endotherms) dictates the lower bounds of AS (Careau et al., 2014; Chabot et al., 2016). Individuals with a high SMR or BMR may exhibit reduced sociability,

as they need to prioritize food acquisition over defense to meet their metabolic requirements through scramble competition (Cooper et al., 2016; Killen, Fu, et al., 2016; Whitehouse & Lubin, 1999).

Previous work has observed individual variation in group size preference (Hoare et al., 2004; Martinez & Marschall, 1999), but the mechanisms underlying these differences are not well understood. The environment plays a key role in modulating choice of group size, with individuals tending to choose smaller groups when food is scarce and larger groups when they perceive danger (Hoare et al., 2000). In addition to having effects on sociability, individual physiological traits may have more nuanced effects on the preferred group size that an animal elects to join. An animal with a higher metabolic demand may, in theory, choose to join a relatively smaller group if given the option (Killen, Marras, et al., 2017). This shift to a smaller group would allow the animal to derive some modest benefits of group membership while minimizing the costs associated with resource sharing. There may be an optimal group size at which the variable costs and benefits of group membership are balanced (Brown, 1982; Markham et al., 2015; Sibly, 1983). However, much of the work to date on this topic has implicitly assumed that all individuals in a group or population are phenotypically homogenous. In reality, individuals may have context-specific optimal group sizes (Martinez & Marschall, 1999), in relation to their own metabolic demands or competitive ability (Metcalfe, 1986). Any effects of individual physiological traits on group size selection may be profound, but, so far, have not been empirically tested.

Understanding the role of metabolic phenotypes on sociability and group size preference is key to identify how individual variation in physiological traits may affect the formation and function of animal groups. Previous work has demonstrated that various aspects of morphology and behavior are important in assortment among and within social groups (Croft et al., 2003, 2005; Jones et al., 2010), with group composition in turn affecting overall group cohesion, coordination, and decision making (Herbert-Read, 2016; Herbert-Read et al., 2013). However, the role of metabolic traits in social group preference and assortment remains virtually unknown (Killen, Marras, et al., 2017). We studied these issues in the redbelly yellowtail fusilier *Caesio cuning*, a schooling, tropical, planktivorous coral reef fish species (photograph in Figure 1a). This species is commonly found foraging in the water column above shallow reefs in heterospecific schools of fishes from the families Caesionidae and Pomacentridae, in groups composed of a few individuals to several hundred individuals (Lieske & Myers, 1996; Quattrini et al., 2018). This natural variability in group size made this species an ideal candidate to better understand group size preference. While food is typically abundant on coral reefs, *C. cuning* experiences intense predation pressure and is a common prey item for a range of reef predators (Matley et al., 2018). In recent years, this species has experienced an increased frequency of tropical cyclone activity at the study site, which is likely to induce group fragmentation and reformation, thus making increased knowledge of the factors affecting sociability and group size preference particularly timely. Using a choice test methodology, we aimed to determine: (a) Whether the
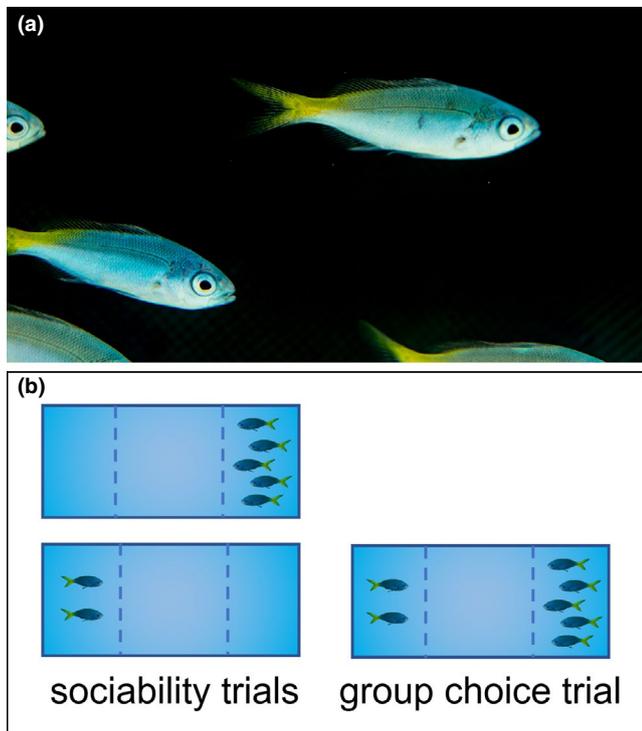
FIGURE 1 (a) The species used in the current study, the redbelly yellowtail fusilier *Caesio cuning*. (b) Schematic of the sociability and group choice assays used in the current study. Tanks are shown from above and not to scale. In each assay, a focal fish was placed in the middle section. Dashed lines represent perforated barriers between tank sections. Depending on the assay, the end sections would contain either a school of two fish, and school of five fish, or no fish. See Section 2 for details. Photo credit: Emmanuel Goncalves

tendency to choose a social or solitary context was related to SMR or MMR; and (b) Whether SMR or MMR affected group size choice. We hypothesized that individuals with a higher maintenance metabolism (i.e., SMR) would be less social and prefer smaller groups due to higher energetic demand. Conversely, those with a higher MMR would be more social and prefer larger groups, as they had a competitive advantage that would aid in maximizing the benefits of group living.

2 | METHODS

2.1 | Animal collection and maintenance

This study was conducted at the Lizard Island Research Station (LIRS), located in the Great Barrier Reef off the coast of tropical North Queensland (14°40′08″S; 145°27′34″E). All research was conducted under James Cook University Animal Ethics approval number A2103. Fish of unknown sex (as this species is not sexually dimorphic) from schools of juvenile *C. cuning* were collected by SCUBA divers from various reefs along the southern and eastern side of Lizard Island, using hand nets and barrier nets. All fish

captured were in good body condition, with no external evidence of predation attempts or issues with food shortage. Following collection, fish were measured using calipers; those fish 6–7 cm standard length were retained, while the remainder were released back to the site of capture. Size-matched fish were placed into 8 schools composed of 9 individuals. Individuals were maintained with the group with which they had been collected, in order to ensure that they had a baseline level of familiarity at the start of the experiment (Ward & Hart, 2003). As *C. cuning*, like many coral reef fishes, has a dispersing larval phase, social groups typically exhibit little to no genetic relatedness (Leis & Carson-Ewart, 2003). Schools were kept in 400-L round aquaria with a diameter of 110 cm, with continuous flow-through natural seawater (pumped from the lagoon in front of LIRS; conditions: 28°C, 35 psu, pH 8.15) and continuous aeration. For all experimentation described below, the same natural seawater source was used. All groups were allowed to acclimate to laboratory conditions for a minimum of 4 days following collection from the reef, before any experimentation was performed. Fish were fed newly hatched *Artemia* sp. followed by INVE Aquaculture food pellets twice daily to satiation. Each fish was tagged with an ~5 mm visual implant elastomer (VIE) tag so that all individuals could be individually identified throughout the duration of the study (Hoey & McCormick, 2006).

2.2 | Estimation of metabolic rates

Four focal fish were randomly chosen from each school to estimate metabolic rate ($n = 32$ fish total). Fish were fasted for approximately 24 hr before being measured for oxygen uptake. MMR was measured after exhaustive exercise by manually chasing individual fish in a circular tank (30 cm diameter) with a water depth of 10 cm. This method assumes that maximum rates of oxygen uptake are achieved during the recovery from the bout of exhaustive anaerobic exercise (Norin & Clark, 2016; Reidy et al., 1995) and have been shown to give similar estimates of MMR when compared to other methods (Killen, Norin, et al., 2017). Fish swam rapidly throughout this protocol, using burst-type swimming, until complete exhaustion (average time to exhaustion = 99.8 ± 6.50 s). Fish were then exposed to air for 1 min, before being transferred into individual cylindrical 370 ml acrylic respirometry chambers connected to an intermittent-flow respirometry system (Steffensen, 1989; Svendsen et al., 2016). The time between the end of the air exposure and sealing of the chamber was always less than 10 s. Opaque barriers were placed between chambers to prevent visual contact between fish in adjacent chambers. Water oxygen content was quantified once every 2 s using a Firesting 4-channel oxygen meter and associated sensors (PyroScience GmbH, Aachen, Germany). Respirometers were placed within an aerated, rectangular, temperature-regulated water bath (29.0 ± 0.5°C) and were shielded from disturbance and direct lighting by an opaque plastic blind. Water mixing within each respirometer was achieved with a peristaltic pump that moved water through the chamber and around an external circuit of gas-impermeable

tubing. Every 7 min, an automated flush pump would switch on for 3 min to flush chambers with oxygenated water, and, when switched off, sealed the respirometers to allow the decline in oxygen content to be analyzed, from which the rate of oxygen uptake was calculated. Fish remained in the same respirometry chambers overnight to allow the measurement of SMR. Individuals were then removed from the respirometer at around 07.00 the following day, having remained in the respirometers for approximately 17–19 hr in total.

To estimate MMR, we calculated rates of oxygen uptake for each 3 min time interval throughout the first 30 min of recovery immediately following the exhaustive exercise; MMR (mg O_2 hr^{-1}) was taken as the highest rate of aerobic metabolism during this period. Whole-animal SMR (mg O_2 hr^{-1}) was estimated as the lowest 20th percentile of measurements taken throughout the measurement period (Chabot et al., 2016). The first 5 hr of confinement in the chambers was excluded from analyses of SMR because the oxygen consumption of fish was often elevated at this time. Both SMR and MMR have previously been shown to be repeatable in the short term (Norin & Malte, 2011), and therefore, these measurements would be indicative of metabolic rate at the time of testing. To correct for background bacterial oxygen uptake, three baseline measures were conducted before and after the fish's measurements in the empty chamber. The amount of background oxygen uptake was then subtracted from the measures in each chamber at each time point, assuming a linear increase in bacterial activity over time (Rodgers et al., 2016). After each experimental run, all respirometers and tubing were thoroughly cleaned with diluted bleach and rinsed with hot water.

2.3 | Sociability and choice of group size

Fish were tested for social behaviors beginning three days after the estimation of metabolic rates. Each focal individual underwent three variations of a binary choice test (Jolles et al., 2017; Jones et al., 2010; Killen, Fu, et al., 2016; Krause et al., 1999; Nadler et al., 2016; Rahn et al., 2015), with approximately 24 hr between each test: (a) a choice between associating with two fish or zero fish; (b) a choice between five fish or zero fish; and (c) a choice between two fish and five fish (Figure 1b). For each focal fish, the sequence of trials was randomized. The first two tests represented estimates of baseline sociability, while the third test measured relative group size choice (Agrillo et al., 2008; Buckingham et al., 2007; Gómez-Laplaza et al., 2018; Gómez-Laplaza & Gerlai, 2016; Hager & Helfman, 1991). The stimulus schools used in each of these three tests were composed of fish from within their social groups, so as to not confound association preferences with varying degrees of familiarity (Ward & Hart, 2003). Prior to each trial, fish were fasted for a minimum of 7 hr prior to testing. Tests of sociability and group size were conducted in an elongated rectangular arena (30 cm × 90 cm) filled with water to a height of 8 cm. A transparent partition was located 11 cm from either end of the arena, such that the arena was effectively divided into three sections: Two end sections to contain stimulus

schools and one larger central zone to contain the focal fish. Each partition also had small holes to allow the passage of olfactory cues between zones. The entire arena was surrounded by an opaque white tent to minimize external disturbance. In preparation for a test, appropriately-sized stimulus schools (composed of two or five fish) were carefully removed from their holding tank (avoiding air exposure) and placed into randomly determined end-zones. The focal fish was similarly placed into the central chamber but contained within a transparent cylinder that also contained a small piece of coral. After a five-minute acclimation period, the cylinder was lifted and the fish was allowed to fully explore the arena. The coral was left in place in the center of the arena, because pilot trials had shown fish to be reluctant to move within the central chamber without this small piece of structure in place. The trial then continued for 20 min and was video-recorded from above at 25 frames per second (Sony Handicam HD). Between each trial, the test arena was drained and refilled.

Videos were analyzed for space use (movement speed while in motion and time spent motionless) using Ethovision XT 10 (Noldus). The threshold for movement was considered to be 0.25 cm/s rather than zero, to avoid tracking software detection errors around the fish center of mass. For sociability trials (schools of either two or five fish vs. zero fish), the distance between the focal fish and the stimulus school was quantified for each frame of the video (25 frames per second). For the group choice trials (five fish vs. two fish within the same arena), the cumulative time spent within 2 body lengths of each stimulus school (calculated for each focal fish by drawing a line down the fish's midline from snout to tail on a still frame image in ImageJ (Schneider et al., 2012), then using this length measurement to define the zone in Ethovision), as well as the time spent in the middle section of the arena (outside of the two body length zone of either school size) were recorded. The two tests were scored differently, as there was only one zone of interest in the sociability trials (containing either two or five fish) versus two zones of interest in the group choice trials (with a choice between groups of two or five fish). School size preference was quantified by calculating the absolute time difference spent in proximity to each school size (measured in seconds). Values for all behavioral metrics were aggregated in two ways: (a) into means for 5-min bins for initial analyses, and (b) into means for the entire second half of each trial (see Section 2.4).

2.4 | Statistical analysis

All analyses were conducted using R v. 3.6.1 (R Core Team, 2019) using the package lme4 (Bates et al., 2016) with p-values produced using the package "lmerTest" (Kuznetsova et al., 2017). An initial analysis indicated an effect of time in the arena for some response variables (Figure S1; Table S1), so subsequent analysis used only behavior collected during the second half of each trial (i.e., data from the first 15 min were deemed acclimation time and not considered). This procedure is comparable to findings by O'Neill et al. (2018), who found that activity of feral fishes was elevated for up to 10 min

in behavioral assays after individuals were placed in a novel arena. Next, two separate models were constructed. The first was an LME, to examine factors affecting sociability. This model included data for 32 fish from eight groups, with each fish tested for sociability in two treatments, that is, in the presence of groups composed of two or five stimulus fish. This model included log-transformed mean distance from conspecifics as the response variable (two observations per fish—one from each sociability trial), body mass (g), SMR (mg O_2 hr^{-1}), MMR (mg O_2 hr^{-1}), and treatment (two fish or five fish) as explanatory variables, and individual fish nested within group as a random effect (to account for non-independence of fish housed in the same social group and the repeated measure of individuals). The second model was an LME to examine factors affecting choice of group size ($n = 31$ fish from eight groups; one fish was unable to be scored for group size choice because of a recording malfunction). This model included the difference in time spent in proximity to the two stimulus schools when presented simultaneously as the response variable (one observation per fish), body mass (g), SMR (mg O_2 hr^{-1}), MMR (mg O_2 hr^{-1}), and log-transformed mean distance to conspecifics in the sociability trials as explanatory variables, and group as a random effect (to account for non-independence of fish housed in the same social group). All models initially contained all two-way interactions; these interactions were removed sequentially when nonsignificant, starting with those terms with the lowest t-value, and the models re-analyzed. Interactions were retained in models if their removal resulted in a poorer model (significantly larger Akaike information criterion (AIC) value as indicated by likelihood ratio tests, LRT). To verify that the residuals conformed to the model assumptions of linearity, homoscedasticity, and normality of residuals, residual-fit and quantile–quantile plots were examined visually. As previously noted, measures of mean proximity to conspecifics in the sociability assays needed to be log-transformed to meet the assumption of homoscedasticity. Model r^2 values were determined using the MuMIn 1.9.13 package for R (Bartoń, 2013). This included marginal r^2 (r^2_m) and conditional r^2 (r^2_c), which indicate the variance explained by fixed factors and by both fixed and random factors, respectively (Nakagawa & Schielzeth, 2013). p-values are generally imprecise in model outputs and are arbitrary when used as definitive thresholds for declaring statistical significance (Boos & Stefanski, 2011; Halsey et al., 2015). Thus, for all models, we treat p-values as a continuous measure providing an approximate level of evidence against the null hypothesis (Fisher, 1959).

For use in figures, metabolic traits were standardized to a common body mass of 8.0 g (the mean mass of all focal fish used in the study), by first calculating the residuals of an ordinary least squares regression of the following form:

$$\log_{10}MR = b + a\log_{10}M + \epsilon \quad (1)$$

where MR is either SMR or MMR, M is body mass (g), a and b are constants and ϵ is the residual variation (Figure S2). The residuals of this regression were added to the fitted value for an animal of 8.0 g to obtain adjusted estimates of SMR and MMR.

3 | RESULTS

3.1 | Sociability and metabolic traits

Individual fish exhibited wide variation in sociability, with mean distance from the stimulus school showing an approximate 10-fold variation among individuals during exposure to schools of conspecifics. There was strong evidence that fish with a higher MMR were more social, whether they were exposed to two or five fish (Figure 2; Table 1). SMR had no link with sociability (Table 1). Among individuals, SMR and MMR were not correlated (Pearson correlation with mass-adjusted values, $r = .095$, $p = .62$).

3.2 | Group size choice

Although fish with a higher SMR showed some tendency to associate more frequently with the larger school, this effect was not statistically significant (Figure 3; Table 2). Neither MMR nor sociability affected the time that individuals spent with either school size when given a choice between schools (Table 2).

4 | DISCUSSION

The study provides insight into how individual variation in physiological and behavioral traits is relevant in the context of group living. In particular, MMR played a role in dictating individual variation in sociability. However, contrary to previous work, the current study found no observable effect of SMR on sociability or group size choice. These results therefore suggest that the role of MMR and SMR in sociability and group size choice may shift depending on the
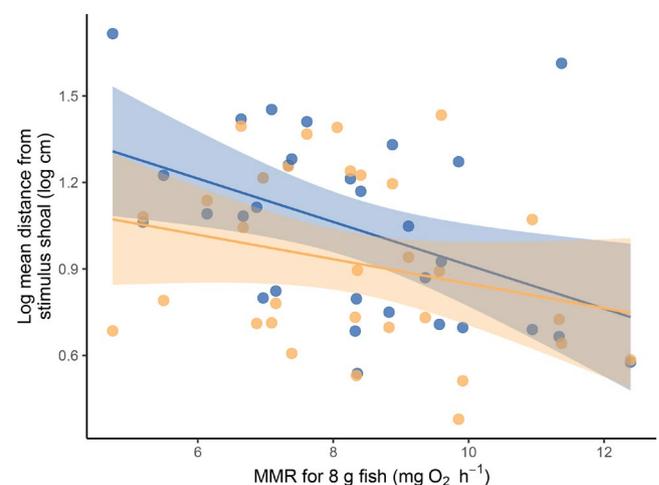

FIGURE 2 Links between mass-adjusted (to an 8 g animal) maximum metabolic rate (MMR) in redbelly yellowtail fusilier and sociability, measured as the mean distance from a stimulus school of either two fish (blue points) or five fish (yellow points). Each data point represents one individual. Lines represent linear regression with 95% confidence intervals (shaded areas)

	Estimate	*SE*	*df*	*t*	*p*	r^2_m	r^2_c
Log distance from conspecifics (log cm)							
Intercept	1.569	0.301	27.67	5.211	<.0001	.166	.218
Mass	0.047	0.046	24.68	1.009	.323		
SMR	−0.238	0.235	25.90	−1.014	.320		
MMR	−0.057	0.021	24.68	−2.699	.012		
School size							
Five	−0.118	0.073	27.93	−1.615	.118		

Note: Individual fish nested within group was included as a random effect. For the factor "school size," the treatment of a school size of two is the reference category.
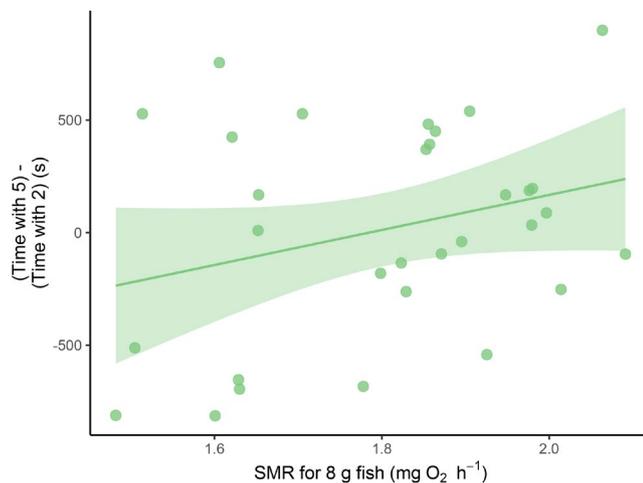

FIGURE 3 Links between mass-adjusted (to an 8 g animal) standard metabolic rate (SMR) in redbelly yellowtail fusiliers and absolute difference in time spent with a school of five fish versus a school of two in school choice trials. Each data point represents one individual. Lines represent linear regression with 95% confidence intervals (shaded areas)

life history of the species examined or the context with which individuals are presented with social choices.

Individual *C. cuning* with a higher MMR were more social, as evidenced by greater cohesion with the stimulus school. MMR sets the upper limit on the capacity to perform oxygen-consuming physiological tasks such as growth, digestion, and locomotor activity (Killen, Norin, et al., 2017) and is generally associated with increased energy demand due to greater spontaneous activity and higher costs to maintain the metabolic machinery for peak performance (Auer et al., 2017; Biro & Stamps, 2010; Killen, Glazier, et al., 2016). Despite this typical correlation, in this study, SMR and MMR showed no evidence of a correlation, as has been shown in other species (Norin & Clark, 2016), suggesting that SMR and MMR can have independent links to sociability in this species. One plausible explanation for the positive correlation between MMR and sociability is that a high MMR may confer a competitive advantage when resources are shared (Webster & Hart, 2006) or better allow an individual to occupy its preferred spatial position or role within a group (Killen et al., 2012, 2014). This advantage would allow an individual to minimize the potential costs of resource sharing imposed by group membership, while simultaneously maximizing the benefits of grouping, such as safety from predators. While the protocol for estimating MMR used in the current study (i.e., the chase protocol) typically provides comparable measurements to swim tunnel respirometry (Killen, Marras, et al., 2017), notably, there may be variation among species in terms of the exact values that are produced by each method (Andersson et al., 2020; Rummer et al., 2016). In the current study, variation among individuals, with regard to the effectiveness of this protocol, could modulate the correlations between MMR and behavior. Therefore, future work could examine how the choice of measurement protocol affects MMR values and correlation with other traits at the individual level.

The results with SMR diverged from findings in previous studies. The reasons for this discrepancy are unclear but suggest that links between sociability and metabolic demand may vary among species and contexts. Killen, Fu, et al. (2016), for example, observed lower sociability in juvenile qingbo carp with a higher metabolic rate, while Cooper et al. (2016) observed similar results with threespine sticklebacks. However, unlike qinbo carp or sticklebacks, *C. cuning*, in particular, is a highly athletic and active species (Hamner et al., 1988). This type of lifestyle typically entails spending a large proportion of its time functioning at active metabolic rates well above SMR (Killen et al., 2010). Therefore, social fishes that frequently exceed their SMR through routine processes may exhibit a stronger relationship between their sociability and their upper constraints on metabolic rate, while sociability in lower-activity species may be more strongly linked to their minimum metabolic needs. Killen, Fu, et al. (2016) also examined sociability in fish with varying SMR at longer time intervals since last feeding than the methodology employed in this study. Hence, stronger connections between SMR and sociability may be observed if food is withheld for longer time periods, as fish with a higher SMR would intrinsically become hungry more quickly than individuals with a lower SMR phenotype given their higher energy demand. Future research comparing species with varying life histories would aid in teasing apart the connections among sociability and metabolic rate.

Contrary to predictions, there were no obvious links between metabolic traits and choice of group size in this species. As the

TABLE 2 Results of linear mixed-effects models examining the factors influencing the time spent closer to a school of five fish instead of a school of two fish, when allowed to make an active choice

	Estimate	SE	df	t	p	r^2_m	r^2_c
Δ Time (s)							
Intercept	−440.53	410.60	25.00	−1.073	.294	.089	.089
Mass	−50.84	54.07	25.00	−0.940	.356		
SMR	361.52	258.66.56	25.00	1.398	.174		
MMR	19.75	26.05	25.00	0.758	.456		
Log sociability	31.19	190.04	25.00	0.164	.871		

Note: The response variable "Δ Time" was calculated using the difference between the time spent near the school of five fish and the time near the school of two fish. Group was included as a random effect. "Sociability" is the mean distance from conspecifics from the two sociability assays (one assay with two stimulus fish and the other with five stimulus fish).

stimulus groups were placed into the same sized end sections of the experimental arena, stimulus groups of different sizes could have exhibited differences in density, and, therefore, these results could also be indicative of variability in preference for group density or cohesion. Prior studies have shown that reduced food availability can cause fish to prefer smaller group sizes with lower cohesion, presumably because individuals begin to prioritize the acquisition of food over the group safety (Ford & Swearer, 2013; Hoare et al., 2004). Theoretically, the costs and benefits of a particular group size should modulate individual tendency to associate with a group, with an optimal group size maximizing individual fitness (Hager & Helfman, 1991; Markham et al., 2015; Martinez & Marschall, 1999). As each individual joins a group, their proportional contribution to group safety is less than the cost they impose in terms of resource sharing, and so net benefits are maximized at some intermediate group size (Killen, Marras, et al., 2017). If an individual has a relatively high metabolic demand, however, they plausibly would have a smaller optimal group size compared to an individual with a lower metabolic demand. As such, we hypothesized that fish with a higher metabolic demand would choose to associate with smaller groups to reduce competition for discovered food items. Yet, this trend was not observed here. If anything, individuals with higher SMR showed a slightly increased tendency to associate with larger groups. This trend warrants further investigation, but, potentially, fish with a higher SMR might prioritize a greater consistency in finding food patches (Ekman & Hake, 1988), even if there is then competition with groupmates once food is located. In addition, the group sizes used in this study were always smaller than those with which the fish had been housed or would belong to in nature, and future work should investigate the response to larger stimulus group sizes.

As mentioned above, the link between metabolic traits and group size choice may be labile and vary with context. Stronger trends could emerge between group size choice and metabolic traits if fish were fasted for longer time periods prior to trials or presented with a predator cue during trials to simulate a threat. Possibly, both stimulus school sizes in current study were simply below the optimal group size for this species, thus making any differences in group size choice among phenotypes difficult to detect. Future work would ideally provide individuals with a choice of a

greater range of group sizes or to examine group size preference and fission-fusion dynamics in free-ranging animals of known physiological phenotypes (Couzin, 2006; Kelley et al., 2011; Killen, Marras, et al., 2017). These approaches are logistically challenging but would be the next step in understanding the role of metabolic traits on group size preference for individual fish at larger spatial scales and with larger group sizes. In addition, while SMR and MMR are both repeatable over the timeframe examined in the current study (Norin & Malte, Kelley2011), repeatability in these traits may decline over longer time periods (White et al., 2013). Future work should examine how within- and among-individual variation in SMR and MMR affect their correlations with behavioral traits such as sociability and group size preference (by performing multiple measures of SMR and MMR per individual), and how these associations vary across different timescales.

In conclusion, we found that individuals with a higher maximum rate of aerobic metabolism were more likely to associate with conspecifics and that, contrary to previous work, SMR had no link to sociability. Also contrary to predictions, we observed that metabolic traits have no influence on group size preference, within the range of group sizes examined, although there may be a slight tendency for individuals with a higher SMR to prefer larger groups. This work is among the first studies to examine how individual variation in metabolic traits affects individual decision making when potentially joining a group of conspecifics, and along with the few other studies in this area (Killen, Fu, et al., 2016) reveals that such influences are likely to be context-dependent and variable among species with differing lifestyles.

CONFLICT OF INTEREST

AUTHOR CONTRIBUTION

Shaun S. Killen: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Software (equal); Validation (equal); Visualization (equal); Writing-original draft (equal); Writing-review & editing (equal). **Lauren E. Nadler:** Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing-review & editing (equal). **Kathryn Grazioso:** Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing-review & editing (equal). **Amy Cox:** Investigation (equal); Methodology (equal); Writing-review & editing (equal). **Mark I. McCormick:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

ORCID

Shaun S. Killen https://orcid.org/0000-0003-4949-3988
Mark I. McCormick https://orcid.org/0000-0001-9289-1645

REFERENCES

Agrillo, C., Dadda, M., Serena, G., & Bisazza, A. (2008). Do fish count? Spontaneous discrimination of quantity in female mosquitofish. *Animal Cognition*, *11*, 495–503. https://doi.org/10.1007/s10071-008-0140-9

Andersson, M. L., Sundberg, F., & Eklöv, P. (2020). Chasing away accurate results: Exhaustive chase protocols underestimate maximum metabolic rate estimates in European perch Perca fluviatilis. *Journal of Fish Biology*, *97*(6), 1644–1650.

Auer, S. K., Killen, S. S., & Rezende, E. L. (2017). Resting versus active: A meta-analysis of the intra-and inter-specific associations between minimum, sustained, and maximum metabolic rates in vertebrates. *Functional Ecology*, *31*, 1728–1738.

Bartoń, K. (2013). *MuMIn: Multi-model inference. R package version 1.9.* 13. The Comprehensive R Archive Network (CRAN), Vienna, Austria.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Grothendieck, G., Green, P., & Bolker, M. B. (2016). *Package 'lme4'.* R Package Version 1.1-10.

Biro, P. A., & Stamps, J. A. (2010). Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends in Ecology & Evolution*, *25*, 653–659. https://doi.org/10.1016/j.tree.2010.08.003

Boos, D. D., & Stefanski, L. A. (2011). P-Value precision and reproducibility. *The American Statistician*, *65*(4), 213–221. https://doi.org/10.1198/tas.2011.10129

Brown, J. L. (1982). Optimal group size in territorial animals. *Journal of Theoretical Biology*, *95*, 793–810. https://doi.org/10.1016/0022-5193(82)90354-X

Buckingham, J. N., Wong, B. B. M., & Rosenthal, G. G. (2007). Shoaling decisions in female swordtails: How do fish gauge group size? *Behaviour*, *144*, 1333–1346. https://doi.org/10.1163/156853907782418196

Careau, V., Buttemer, W. A., & Buchanan, K. L. (2014). Developmental stress can uncouple relationships between physiology and behaviour. *Biology Letters*, *10*, 20140834. https://doi.org/10.1098/rsbl.2014.0834

Chabot, D., Steffensen, J. F., & Farrell, A. P. (2016). The determination of standard metabolic rate in fishes. *Journal of Fish Biology*, *88*, 81–121. https://doi.org/10.1111/jfb.12845

Cooper, B., Adriaenssens, B., & Killen, S. S. (2018). Individual variation in the compromise between social group membership and exposure to preferred temperatures. *Proceedings of the Royal Society B*, *285*, 20180884. https://doi.org/10.1098/rspb.2018.0884

Croft, D., Arrowsmith, B., Bielby, J., Skinner, K., White, E., Couzin, I., Magurran, A., Ramnarine, I., & Krause, J. (2003). Mechanisms underlying shoal composition in the Trinidadian guppy, *Poecilia reticulata*. *Oikos*, *100*, 429–438.

Croft, D. P., James, R., Ward, A. J. W., Botham, M. S., Mawdsley, D., & Krause, J. (2005). Assortative interactions and social networks in fish. *Oecologia*, *143*, 211–219. https://doi.org/10.1007/s00442-004-1796-8

Couzin, I. D. (2006). Behavioral ecology: Social organization in fission–fusion societies. *Current Biology*, *16*(5), R169–R171. https://doi.org/10.1016/j.cub.2006.02.042

DeBlois, E. M., & Rose, G. A. (1996). Cross-shoal variability in the feeding habits of migrating Atlantic cod (*Gadus morhua*). *Oecologia*, *108*, 192–196. https://doi.org/10.1007/BF00333231

Ekman, J., & Hake, M. (1988). Avian flocking reduces starvation risk: An experimental demonstration. *Behavioral Ecology and Sociobiology*, *22*, 91–94. https://doi.org/10.1007/BF00303543

Fisher, R. A. (1959). *Statistical Methods and Scientific Inference* (2nd ed.). Hafner Publishing Co.

Ford, J. R., & Swearer, S. E. (2013). Two's company, three's a crowd: Food and shelter limitation outweigh the benefits of group living in a shoaling fish. *Ecology*, *94*, 1069–1077. https://doi.org/10.1890/12-1891.1

Gómez-Laplaza, L. M., Díaz-Sotelo, E., & Gerlai, R. (2018). Quantity discrimination in angelfish, Pterophyllum scalare: A novel approach with food as the discriminant. *Animal Behaviour*, *142*, 19–30. https://doi.org/10.1016/j.anbehav.2018.06.001

Gómez-Laplaza, L. M., & Gerlai, R. (2016). Short-term memory effects on crossing the boundary: Discrimination between large and small quantities in Angelfish (Pterophyllum scalare). *PLoS One*, *11*, e0162923. https://doi.org/10.1371/journal.pone.0162923

Hager, M. C., & Helfman, G. S. (1991). Safety in numbers: Shoal size choice by minnows under predatory threat. *Behavioral Ecology and Sociobiology*, *29*, 271–276. https://doi.org/10.1007/BF00163984

Halsey, L. G., Curran-Everett, D., Vowler, S. L., & Drummond, G. B. (2015). The fickle P value generates irreproducible results. *Nature Methods*, *12*(3), 179–185. https://doi.org/10.1038/nmeth.3288

Hamner, W. M., Jones, M. S., Carleton, J. H., Hauri, I. R., & Williams, D. M. (1988). Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. *Bulletin of Marine Science*, *42*, 459–479.

Herbert-Read, J. E. (2016). Understanding how animal groups achieve coordinated movement. *Journal of Experimental Biology*, *219*, 2971–2983. https://doi.org/10.1242/jeb.129411

Herbert-Read, J. E., Krause, S., Morrell, L., Schaerf, T., Krause, J., & Ward, A. (2013). The role of individuality in collective group movement. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20122564.

Hoare, D., Couzin, I. D., Godin, J.-G., & Krause, J. (2004). Context-dependent group size choice in fish. *Animal Behaviour*, *67*, 155–164. https://doi.org/10.1016/j.anbehav.2003.04.004

Hoare, D. J., Ruxton, G. D., Godin, J.-G.-J., & Krause, J. (2000). The social organization of free-ranging fish shoals. *Oikos*, *89*, 546–554. https://doi.org/10.1034/j.1600-0706.2000.890314.x

Hoey, A. S., & McCormick, M. I. (2006). Effects of subcutaneous fluorescent tags on the growth and survival of a newly settled coral reef

fish, *Pomacentrus amboinensis* (Pomacentridae). In *Proceedings of the 10th International Coral Reefs Symposium 2006* (pp. 420–425).

Isbell, L. A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, 2, 143–155. https://doi.org/10.1093/beheco/2.2.143

Jolles, J. W., Boogert, N. J., Sridhar, V. H., Couzin, I. D., & Manica, A. (2017). Consistent individual differences drive collective behavior and group functioning of schooling fish. *Current Biology*, 27, 2862–2868.e7. https://doi.org/10.1016/j.cub.2017.08.004

Jolles, J. W., King, A. J., & Killen, S. S. (2020). The role of individual heterogeneity in collective animal behaviour. *Trends in Ecology and Evolution*, 35, 278–291. https://doi.org/10.1016/j.tree.2019.11.001

Jones, K. A., Croft, D. P., Ramnarine, I. W., & Godin, J.-G.-J. (2010). Size-assortative shoaling in the guppy (*Poecilia reticulata*): The role of active choice. *Ethology*, 116, 147–154.

Kelley, J. L., Morrell, L. J., Inskip, C., Krause, J., & Croft, D. P. (2011). Predation risk shapes social networks in fission-fusion populations. *PLoS ONE*, 6(8), e24280. https://doi.org/10.1371/journal.pone.0024280

Killen, S. S., Atkinson, D., & Glazier, D. S. (2010). The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. *Ecology Letters*, 13, 184–193. https://doi.org/10.1111/j.1461-0248.2009.01415.x

Killen, S. S., Fu, C., Wu, Q., Wang, Y.-X., & Fu, S.-J. (2016). The relationship between metabolic rate and sociability is altered by food-deprivation. *Functional Ecology*, 30(8), 1358–1365. https://doi.org/10.1111/1365-2435.12634

Killen, S. S., Glazier, D. S., Rezende, E. L., Clark, T. D., Atkinson, D., Willener, A. S., & Halsey, L. G. (2016). Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. *American Naturalist*, 187(5), 592–606. https://doi.org/10.1086/685893

Killen, S. S., Marras, S., Nadler, L., & Domenici, P. (2017). The role of physiological traits in assortment among and within fish shoals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160233. https://doi.org/10.1098/rstb.2016.0233

Killen, S. S., Marras, S., Steffensen, J. F., & McKenzie, D. J. (2012). Aerobic capacity influences the spatial position of individuals within fish schools. *Proceedings of the Royal Society B: Biological Sciences*, 279, 357–364. https://doi.org/10.1098/rspb.2011.1006

Killen, S. S., Mitchell, M. D., Rummer, J. L., Chivers, D. P., Ferrari, M. C. O., Meekan, M. G., & McCormick, M. I. (2014). Aerobic scope predicts dominance during early life in a tropical damselfish. *Functional Ecology*, 28, 1367–1376. https://doi.org/10.1111/1365-2435.12296

Killen, S. S., Norin, T., & Halsey, L. G. (2017). Do method and species lifestyle affect measures of maximum metabolic rate in fishes? *Journal of Fish Biology*, 90, 1037–1046. https://doi.org/10.1111/jfb.13195

Killen, S. S., Reid, D., Marras, S., & Domenici, P. (2015). The interplay between aerobic metabolism and antipredator performance: vigilance is related to recovery rate after exercise. *Frontiers in Physiology*, 6, 111.

Krause, J., Hartmann, N., & Pritchard, V. L. (1999). The influence of nutritional state on shoal choice in zebrafish, *Danio rerio*. *Animal Behaviour*, 57, 771–775. https://doi.org/10.1006/anbe.1998.1010

Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford University Press.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82(13), 1–26.

Leis, J. M., & Carson-Ewart, B. M. (2003). Orientation of pelagic larvae of coral-reef fishes in the ocean. *Marine Ecology Progress Series*, 252, 239–253. https://doi.org/10.3354/meps252239

Lieske, E., & Myers, R. (1996). *Coral Reef Fishes: Caribbean, Indian Ocean and Pacific Ocean including the Red Sea*. Princeton University Press.

Markham, A. C., Gesquiere, L. R., Alberts, S. C., & Altmann, J. (2015). Optimal group size in a highly social mammal. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 14882–14887. https://doi.org/10.1073/pnas.1517794112

Martinez, F. A., & Marschall, E. A. (1999). A dynamic model of group-size choice in the coral reef fish *Dascyllus albisella*. *Behavioral Ecology*, 10, 572–577. https://doi.org/10.1093/beheco/10.5.572

Matley, J. K., Maes, G. E., Devloo-Delva, F., Huerlimann, R., Chua, G., Tobin, A. J., Fisk, A. T., Simpfendorfer, C. A., & Heupel, M. R. (2018). Integrating complementary methods to improve diet analysis in fishery-targeted species. *Ecology and Evolution*, 8, 9503–9515. https://doi.org/10.1002/ece3.4456

Metcalfe, N. (1986). Variation in winter flocking associations and dispersion patterns in the turnstone *Arenaria interpres*. *Journal of Zoology*, 209, 385–403. https://doi.org/10.1111/j.1469-7998.1986.tb03600.x

Metcalfe, N. B., Taylor, A. C., & Thorpe, J. E. (1995). Metabolic rate, social status and life-history strategies in Atlantic salmon. *Animal Behavior*, 49, 431–436. https://doi.org/10.1006/anbe.1995.0056

Metcalfe, N. B., Van Leeuwen, T. E., & Killen, S. S. (2016). Does individual variation in metabolic phenotype predict fish behaviour and performance? *Journal of Fish Biology*, 88, 298–321. https://doi.org/10.1111/jfb.12699

Morrell, L. J., & Romey, W. L. (2008). Optimal individual positions within animal groups. *Behavioral Ecology*, 19, 909–919. https://doi.org/10.1093/beheco/arn050

Nadler, L. E., Killen, S. S., McCormick, M. I., Watson, S., & Munday, P. L. (2016). Effect of elevated carbon dioxide on shoal familiarity and metabolism in a coral reef fish. *Conservation Physiology*, 4, cow052. https://doi.org/10.1093/conphys/cow052

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews*, 85, 935–956. https://doi.org/10.1111/j.1469-185X.2010.00141.x

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142.

Norin, T., & Clark, T. D. (2016). Measurement and relevance of maximum metabolic rate in fishes. *Journal of Fish Biology*, 88, 122–151. https://doi.org/10.1111/jfb.12796

Norin, T., & Malte, H. (2011). Repeatability of standard metabolic rate, active metabolic rate and aerobic scope in young brown trout during a period of moderate food availability. *Journal of Experimental Biology*, 214, 1668–1675. https://doi.org/10.1242/jeb.054205

O'Neill, S. J., Williamson, J. E., Tosetto, L., & Brown, C. (2018). Effects of acclimatisation on behavioural repeatability in two behaviour assays of the guppy *Poecilia reticulata*. *Behavioral Ecology and Sociobiology*, 72, 166. https://doi.org/10.1007/s00265-018-2582-7

Petkova, I., Abbey-Lee, R. N., & Lovlie, H. (2018). Parasite infection and host personality: Glugea-infected three-spined sticklebacks are more social. *Behavioral Ecology and Sociobiology*, 72, 173. https://doi.org/10.1007/s00265-018-2586-3

Quattrini, F. G., Bshary, R., & Roche, D. G. (2018). Does the presence of an odd individual affect group choice? *Behavioral Ecology*, 29, 855–861. https://doi.org/10.1093/beheco/ary062

R Core Team (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rahn, A. K., Hammer, D. A., & Bakker, T. C. M. (2015). Experimental infection with the directly transmitted parasite Gyrodactylus influences shoaling behaviour in sticklebacks. *Animal Behaviour*, 107, 253–261. https://doi.org/10.1016/j.anbehav.2015.07.004

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82, 291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Reidy, S. P., Nelson, J. A., Tang, Y., & Kerr, S. R. (1995). Post-exercise metabolic rate in Atlantic cod and its dependence upon the method

of exhaustion. *Journal of Fish Biology*, *47*, 377–386. https://doi.org/10.1111/j.1095-8649.1995.tb01907.x

Rodgers, G. G., Tenzing, P., & Clark, T. D. (2016). Experimental methods in aquatic respirometry: The importance of mixing devices and accounting for background respiration. *Journal of Fish Biology*, *88*, 65–80. https://doi.org/10.1111/jfb.12848

Rummer, J. L., Binning, S. A., Roche, D. G., & Johansen, J. L. (2016). Methods matter: Considering locomotory mode and respirometry technique when estimating metabolic rates of fishes. *Conservation Physiology*, *4*(1), cow008. https://doi.org/10.1093/conphys/cow008

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671–675. https://doi.org/10.1038/nmeth.2089

Sibly, R. M. (1983). Optimal group size is unstable. *Animal Behaviour*, *31*, 947–948. https://doi.org/10.1016/S0003-3472(83)80250-4

Steffensen, J. (1989). Some errors in respirometry of aquatic breathers: How to avoid and correct for them. *Fish Physiology and Biochemistry*, *6*, 49–59. https://doi.org/10.1007/BF02995809

Svendsen, M. B. S., Bushnell, P., & Steffensen, J. F. (2016). Design and setup of intermittent-flow respirometry system for aquatic organisms. *Journal of Fish Biology*, *88*, 26–50. https://doi.org/10.1111/jfb.12797

Ward, A. J. W., & Hart, P. J. B. (2003). The effects of kin and familiarity on interactions between fish. *Fish and Fisheries*, *4*, 348–358. https://doi.org/10.1046/j.1467-2979.2003.00135.x

Ward, A., & Webster, M. (2016). Sociality. In *Sociality: The behaviour of group-living animals*. Springer.

Webster, M. M., & Hart, P. J. (2006). Kleptoparasitic prey competition in shoaling fish: Effects of familiarity and prey distribution. *Behavioral Ecology*, *17*, 959–964. https://doi.org/10.1093/beheco/arl037

White, C. R., Schimpf, N. G., & Cassey, P. (2013). The repeatability of metabolic rate declines with time. *Journal of Experimental Biology*, *216*(10), 1763–1765. https://doi.org/10.1242/jeb.076562

Whitehouse, M. E. A., & Lubin, Y. (1999). Competitive foraging in the social spider *Stegodyphus dumicola*. *Animal Behaviour*, *58*, 677–688. https://doi.org/10.1006/anbe.1999.1168

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.