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Energetic costs of group-living? A reversed "group effect" in shoaling minnows (*Phoxinus phoxinus*)

Energetische Kosten des Gruppenlebens? Ein umgekehrter „Gruppeneffekt" bei schwarmbildenden Elritzen (*Phoxinus phoxinus*)

Martin Plath[1*], Adela Sarbu[2], Kaan Erkoc[2], David Bierbach[1], Jonas Jourdan[1] & Elke Schleucher[2]

[1]J.W. Goethe-University of Frankfurt, Department of Ecology & Evolution, Max-von-Laue-Straße 13, D-60438 Frankfurt am Main, Germany, mplath@bio.uni-frankfurt.de, *corresponding author
[2]J.W. Goethe-University of Frankfurt, Department of Animal Physiology, Max-von-Laue-Straße 13, D-60438 Frankfurt am Main, Germany

Summary: Group-living provides major benefits to the individual group members; e.g., teleost fishes often form shoals to reduce piscine and avian predation risk. A number of studies reported that shoal members can have a calming effect on individual fish, whereby individuals show typical stress responses (like increased oxygen consumption) in a lone compared to a grouped situation (the so-called "group effect"). We tested whether European minnows (*Phoxinus phoxinus*) also show such a group effect by comparing oxygen consumption (via respirometry) of individuals in a lone or grouped situation. Surprisingly, focal fish showed higher metabolic rates when a group was presented during respirometric measurements. Two alternative explanations for this effect seem possible: (a) presence of the group per se stressed the focal fish, or (b) being restricted to the respiratory chamber focal fish were stressed as they could not join the group. We predicted that, if hypothesis (b) was true, fish should show reduced metabolic rates when allowed to interact freely with a group, but should show increased metabolic rates if hypothesis (a) was true. As measuring individual oxygen consumption is impossible in free-ranging fish, we measured gill ventilation frequencies as a proxy of metabolic rates in a second experiment where focal fish were tested either alone, within a group, or, like in experiment one, with visual perception of a group. Again, metabolic rates were increased when focal fish could see a group nearby, but the increase was even higher when they could interact freely with the group. Thus, presence of the group per se might indeed elicit a stress response, and we tentatively argue this is due to costs arising from increasing competition among shoal members.

Keywords: Calming effect, competition, group-living, group effect, resting metabolism, shoaling

Zusammenfassung: Das Zusammenleben in Gruppen bietet Vorteile für die einzelnen Gruppenmitglieder. So bilden z.B. Knochenfische oftmals Schwärme, um das Risiko zu reduzieren, durch Raubfische und Vögel erbeutet zu werden. Mehrere Studien konnten zeigen, dass sich Schwarmbildung beruhigend auf einzelne Fische auswirkt. Dabei führt die Isolation zu typischen Stressreaktionen, die sich z.B. in einem erhöhten Sauerstoffverbrauch ausdrückt und in einer Schwarmsituation reduziert sind (der sogenannte „Gruppeneffekt"). Wir haben untersucht, ob auch Europäische Elritzen (*Phoxinus phoxinus*) einen Gruppeneffekt zeigen, wenn sie sich in einem Schwarm befinden. Dafür verglichen wir den Sauerstoffverbrauch (via Respirationstest) von isolierten Individuen und Individuen in einer Schwarmsituation. Überraschenderweise zeigten die Testfische höhere Stoffwechselraten, wenn ihnen während der Sauerstoffmessungen Artgenossen in unmittelbarer Nähe gezeigt wurden. Zwei Hypothesen könnten den Effekt erklären: (a) die Testfische wurden durch die Gruppe an sich gestresst oder (b) die Testfische waren gestresst, weil sie die Gruppe nicht erreichen konnten, da sie während der Messungen in der Respirationskammer festgehalten wurden. Wir sagten voraus, dass, wenn Hypothese (b) wahr wäre, die Fische eine reduzierte Stoffwechselrate zeigen sollten, sobald sie mit der Gruppe frei interagieren können. Zeigen sie jedoch auch dann eine erhöhte Stoffwechselrate, sollte dies Hypothese (a) unterstützen. Da die Messung des individuellen Sauerstoffverbrauchs in einer frei interagierenden Gruppe

nicht möglich ist, bestimmten wir in einem zweiten Experiment die Stoffwechselrate anhand der Atemfrequenz. Die Testfische wurden dabei entweder allein, mit einer Gruppe in Sichtweite oder mit einer Gruppe frei interagierend getestet. Auch hier war die Stoffwechselrate erhöht, wenn die Testfische die Gruppe nur visuell wahrnehmen konnten. Der Anstieg der Stoffwechselrate war sogar noch höher, wenn die Testfische frei mit der Gruppe interagierten. Die Anwesenheit der Gruppe scheint demnach in der Tat grundsätzlich eine Stressreaktion hervorzurufen und wir argumentieren, dass dies auf zunehmende Konkurrenz unter den Schwarmmitgliedern zurückzuführen ist.

Schlüsselwörter: Beruhigungseffekt, Konkurrenz, Gruppenleben, Gruppeneffekt, Ruhestoffwechsel, Schwarmverhalten

1. Introduction

Group formation (like shoaling behavior in fishes) provides major benefits to the individual group members in terms of protection from predators (Godin 1986, Pitcher & Parrish 1993, Krause & Ruxton 2002). Under predation risk, or in a novel environment, perceived safety-in-numbers can have a profound effect on individuals' oxygen consumption: In the guppy (*Poecilia reticulata*), for example, grouped fish show lower metabolic rates than individual fish (Teo & Chen 1993). Also in red-bellied piranha (*Pygocentrus nattereri*) ventilatory frequency (opercular rate) is lower in grouped fish, and grouped fish regain resting values sooner after a simulated predator attack than single fish (Queiroz & Magurran 2005). Likewise, Geyer & Mann (1939) reported lower individual metabolic rates when placing three perch (*Perca fluviatilis*) instead of one in a respiratory chamber. In addition, shoaling behavior provides individuals with fitness advantages that may include increased foraging efficiency and access to potential mates (Pitcher et al. 1982, Krause & Ruxton 2002). Shoaling fish find food more quickly, because the probability of locating food resources is proportional to the number of fish in the shoal (Morgan & Colgan 1987).

A comparison of 15 fish species suggested that reduced metabolic rates in grouped as compared to lone fish (the so-called "group effect") may be a general pattern (Parker 1973). This reduction is typically interpreted as a result of an interaction of a calming effect of shoal members (Parker 1973) and a possible hydrodynamic advantage that may occur when fish show synchronized swimming movements, i.e. schooling (Osborne 1961, Weihs 1973, Pitcher & Parrish 1993).

The first experiment of our present study concentrated on the calming effect and asked whether also European minnows (*Phoxinus phoxinus*, Cyprinidae) would exhibit reduced metabolic rates in a grouped situation. Surprisingly, we detected a strong increase in individual oxygen consumption when focal fish were surrounded by a group of conspecifics (see 3. Results). Generally, stress translates into increased metabolic rates in fishes (Elsasser et al. 2000, Schreck 2000, Barton 2002) and there are two possible explanations why fish were stressed in our first experiment: (a) presence of the group per se stressed the focal individuals due to perceived intraspecific competition (i.e., the associated risk of agonistic interactions among shoal members), or (b) focal individuals – being restricted to in the respiratory chamber – were stressed as they could not reach the group. If the second hypothesis was true, one would predict metabolic rates to decrease when focal individuals could interact directly with the group. However, when the group situation per se imposes stress on the focal individual, one would predict an even stronger increase in individual metabolic rates when in direct contact with shoal members. As measurements of individual oxygen consumption in a group are impossible, in our second experiment we measured opercular movement (opercular rates) as proxy for metabolic rates. Focal fish were tested in a lone situation, with a group in a separate compartment of the test tank (comparable to our first experiment) and while interacting freely with a group.

2. Methods

2.1. Origin, maintenance and handling of test fish

Juvenile European minnows (*Phoxinus phoxinus*, Cyprinidae) were obtained from a commercial breeder (Fischzucht Rhönforelle GmbH & Co. KG, Gersfeld, Germany) in 2009. Experiments were conducted between May and September 2010. Fish were raised and maintained in 300 l mixed-sex stock tanks at 15 °C water temperature at the Animal Care Facility of the University of Frankfurt. Water was filtered and aerated and thus oxygen-saturated (several measurements read around 7.8 mg $O_2 \cdot l^{-1}$). At the time of the experiments, n = 37 adult minnows were available, which were not in reproductive condition during the time of experimentation.

All fish were fed twice daily with commercial flake and pellet food, once in the morning (so test fish were satiated) and once in the late afternoon (after tests were completed). Stock tanks were equipped with stones and terracotta tubes as shelter and the bottom was covered with natural gravel. Fish were repeatedly caught with a dip-net and gently transferred to a different maintenance aquarium; thus, all test fish were familiar to the general procedure of netting and entering a novel environment. Fish used as stimulus shoal were taken from the same tank as the focal fish. Although focal fish were used only once per experiment, some fish were reused in our second experiment, in which case at least two days had passed until retesting.

2.2. Experiment 1: Oxygen consumption in different social contexts

In a first step, we determined whether test fish during our experiments would show any obvious stress response without a stimulus shoal present. We compared individual oxygen consumption in light and darkness and hypothesized that a stress response would lead to higher values during the light treatment, while values in darkness should reflect their routine metabolic rate (RMR). In a second step, we compared the response of individual minnows to the visual presentation of a stimulus shoal outside of the respiratory chamber.

O_2-consumption of fish was measured in an open-flow respirometry system (for a detailed description see KÖHLER et al. 2011), consisting of a cylindrical respiratory chamber (diameter 5.7 cm, length 22 cm, volume 0.56 l), placed in a plastic tank (56 x 25 x 15.5 cm) filled with water and attached to a tubing system with O_2-saturated water of 15 °C running at a constant flow rate of 2.5 $l \cdot h^{-1}$. Flow rate was continuously monitored and controlled by a valve and a flow-meter [ROTA Type K12/G1831/77 (WEHR–2), accuracy ±1.6 %]. Directly before and after the respirometry chamber, O_2-content was measured by two oxygen electrodes (Oxi 315i, WTW; accuracy: ±0.5 %), which were built into the system in sealed, custom-made cuvettes. Oxygen electrodes were calibrated before each measurement against water vapor saturated air by inserting the sensor in the OxiCal-SL container provided by the manufacturer. Flow conditions in the measuring cuvettes were kept constant by magnetic stirrers. The whole set-up was covered with brown cardboard, so that any disturbance from the outside was reduced to a minimum, however, during the light treatments light was provided by overhead fixtures (room illumination).

Test fish were placed into the respirometry chamber and before any measurement was started, test fish were allowed to settle for 20 min. Oxygen consumption rates were then recorded over a period of 10 min, provided steady-state readings from the electrodes. For the comparison of metabolic rates in light and darkness we tested n = 20 individuals (body mass: 8.48±1.23 g; standard length, SL: 83.6±5.46 mm) as described above and repeated measurements while the respiratory chamber was covered entirely with aluminum foil and light was turned off. To test for an effect of social context, focal fish (n = 27; body mass: 8.69±1.43 g; SL: 83.6±7.94 mm) were tested under light conditions as described before. Then, six conspecifics (body mass: 8.07±0.86 g; SL: 82.5±2.81 mm) were haphazardly taken

from the stock tank and introduced into the test tank surrounding the respiratory chamber. After the 20 min habituation phase measurements were repeated for another 10 min period. Once a test was completed, focal fish were weighed to the nearest 0.1 g using a Sartorius PT 600 scale (accuracy: ±0.1 %) and measured for standard length to the nearest full millimeter.

2.3. Experiment 2: Opercular ventilation rates in different social contexts

The test tank for our measurement of opercular rates (60 x 30 x 30 cm) was filled to a level of 20 cm with aged tap water of 15°C. The water of the test tank was aerated throughout and illumination was provided by two 100 Watt neon tubes installed on the ceiling of the experimental room. All sides except the front wall were covered by black plastic foil to avoid any disturbance from the outside. To videotape the focal individual's opercular ventilation rates we placed a camera (JVC GR-D725E) in front of the test tank.

Each trial consisted of three treatments, simulating three different social contexts. The order of the three treatments was balanced, i.e., one third of the trials started with treatment one, one third with part two, etc. At the beginning of each trial focal fish (n = 15; body mass: 9.01±1.15 g; standard length, SL: 85.5±6.60 mm) could acclimate to the novel test tank for 10 min, after which we videotaped the focal fish for 3 min. In the first treatment, the focal fish was alone. For the second treatment, we divided the test tank by a removable, transparent Plexiglas™ sheet in two equal halves. We introduced a group of familiar conspecifics (seven to eight individuals, body mass: 8.23±0.83 g; SL: 81.25±4.33 mm) into the opposite compartment and repeated videotaping of the focal fish. During the third treatment, no Plexiglas sheet was installed, so all fish could interact directly. Focal fish could be identified and tracked in this treatment as the entire sequence of testing was videotaped (JVC GR-D725E). Each treatment was preceded by a 10 min habituation period to avoid confounding effects arising from the handling process. Ventilation rates were later established as opercular ventilation rate, determined as the frequency at which the operculum was lifted (count per min), which can be used as an indicator of oxygen consumption.

2.4. Statistical analysis

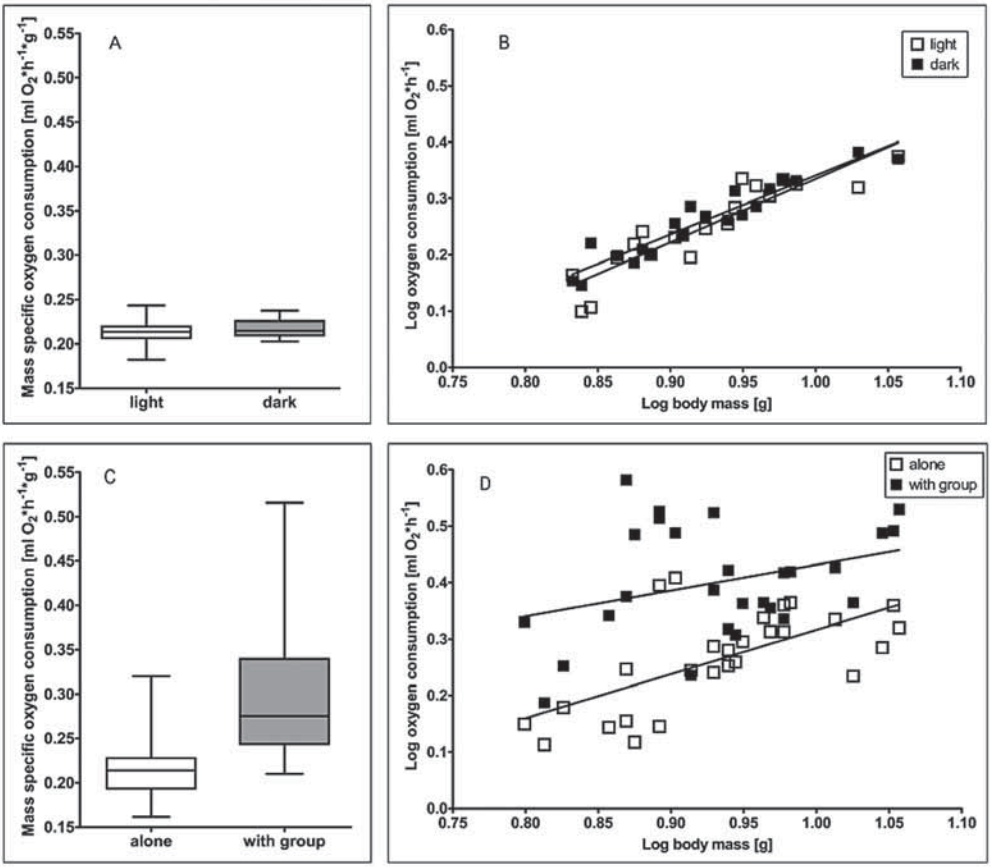
We expected all physiological measures determined herein to strongly co-vary with body mass (Clarke & Johnston 1999, White et al. 2006). However, all experiments were designed in a way that repeated measurements of the same test subjects were taken, so we did not need to include body mass in our statistical analyses when testing for treatment effects. We used non-parametric tests throughout, as Kolmogorov-Smirnoff tests indicated that data were not normally distributed. Oxygen consumption rates from experiment 1 were compared between treatments using Wilcoxon signed-rank tests, while data from experiment 2 were compared in a Friedman repeated measures ANOVA. For display purpose, data on oxygen consumption were depicted both as mass-specific values [ml $O_2 \cdot h^{-1} \cdot g^{-1}$] (figs 1A, B), but also the conventional way of plotting $\log_{10}$-transformed O_2-consumption against $\log_{10}$-transformed body mass (figs 1C, D) is shown.

3. Results

3.1. Experiment 1: Oxygen consumption in different social contexts

Individual oxygen consumption was determined as 1.80±0.31 ml $O_2 \cdot h^{-1}$ in light and 1.85±0.29 ml $O_2 \cdot h^{-1}$ in darkness (Wilcoxon signed-rank test: z =–1.23, P = 0.22, n = 20). Likewise, mass-specific values were established as 0.21±0.02 ml $O_2 \cdot h^{-1} \cdot g^{-1}$ in light and 0.22±0.01 ml $O_2 \cdot h^{-1} \cdot g^{-1}$ in darkness (Wilcoxon signed-rank test: z = –1.16, P = 0.25, n = 20; fig. 1A). Hence, we did not find any difference between individual oxygen consumption when tested under light and dark conditions.

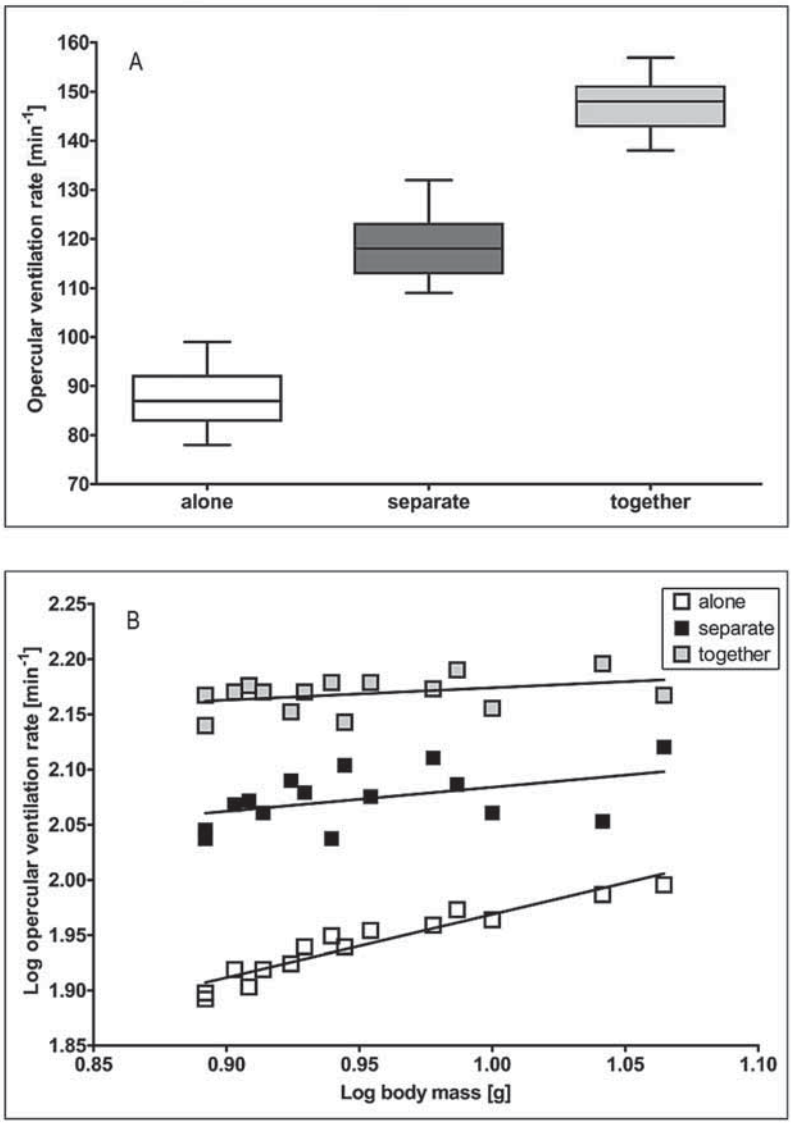
Our main question was, whether individual minnows alter their metabolic rates upon pre-



Figs 1A-D: Metabolic rates of European minnows (*Phoxinus phoxinus*) during the respirometric measurements (experiment 1). In the first treatment, focal fish were tested in light (open) and darkness (gray) (**A+B**) while in the second treatment, focal fish were tested in light but either in absence (open) or presence of a stimulus shoal (black) (**C+D**). **A** and **C** show mass-specific O_2-consumption rates (ml $O_2 \cdot h^{-1} \cdot g^{-1}$) while **B** and **D** show the relationship between metabolic rate [log(ml $O_2 \cdot h^{-1}$)] and body mass [log(g)]. Boxplots depict the median, the 25-75 % (box) and the 5-95 % range of the data (whiskers).

Abb. 1A-D: Metabolismusraten von Elritzen (*Phoxinus phoxinus*) während der respirometrischen Messungen in Experiment 1. Die Testfische wurden während der ersten Behandlung alleine im Hellen (offene Symbole) oder im Dunkeln (schwarze Symbole) getestet (**A**+**B**). Während der zweiten Behandlung wurden die Testfische im Hellen entweder alleine (offen Symbole) oder in Gegenward einer Artgenossen-Gruppe (graue Symbole) getestet (**C**+**D**). Die Teilabbildungen **A** und **C** zeigen den massenspezifischen O_2-Verbrauch (ml $O_2 \cdot h^{-1} \cdot g^{-1}$), während **B** und **D** den Zusammenhang zwischen Metabolismusrate [log(ml $O_2 \cdot h^{-1}$)] und Körpergewicht [log(g)] der Testfische wiedergeben. Boxplots zeigen den Median, den 25-75 %- (Box) und den 5-95 %-Bereich der Daten (Whiskers).

sentation of a stimulus shoal. Oxygen consumption increased significantly from 1.87±0.36 ml $O_2 \cdot h^{-1}$ to 2.58±0.58 ml $O_2 \cdot h^{-1}$ when a stimulus shoal was presented outside of the respiratory chamber (Wilcoxon signed-rank test: z = -4.52, $P < 0.001$, n = 27). The same pattern emerges when considering mass-specific consumption rates (treatment 1: 0.22±0.04 ml $O_2 \cdot h^{-1} \cdot g^{-1}$; treatment 2: 0.30±0.08 ml $O_2 \cdot h^{-1} \cdot g^{-1}$; z = -4.52, $P < 0.001$, n = 27; fig. 1B). Thus, oxygen consumption during the part of the tests involving a stimulus shoal increased to 141±37 % of the oxygen consumption recorded in the solitary situation. The relationship between



Figs 2A-B: Metabolic rates of European minnows (*Phoxinus phoxinus*) based on opercular ventilation rates (experiment 2). Ventilation rates (min^{-1}) were measured when the focal fish were either alone (open), could see a stimulus shoal in a neighboring tank (black), or had physical contact to the other shoal members (gray). Mean ventilation rates are given in (**A**) while the relationship between ventilation rates [log(min^{-1})] and body mass [log(g)] is shown in (**B**). Boxplots depict the median, the 25-75 % (box) and the 5-95 % range of the data (whiskers).

Abb. 2A-B: Metabolismusraten von Elritzen (*Phoxinis phoxinus*) basierend auf der Atemfrequenz während der drei Versuchssituationen in Experiment 2. Die Atemfrequenz (min^{-1}) wurde gemessen, während der Versuchsfisch entweder allein war (weiß), den Stimulusschwarm in einem benachbarten Becken sehen konnte (schwarz) oder physischer Kontakt zu den anderen Schwarmmitgliedern möglich war (grau). Die durchschnittliche Atemfrequenz ist in Abbildung **A** gezeigt und der Zusammenhang zwischen Metabolismusrate [log(min^{-1})] und Körpergewicht [log(g)] in Abbildung **B**. Boxplots zeigen den Median, den 25-75 %- (Box) und den 5-95 %-Bereich der Daten (Whiskers).

log-transformed oxygen consumption and log-transformed body mass in the comparison of metabolic rates in light and darkness showed that oxygen consumption increased in a linear fashion with increasing body mass (light: a = 1.13, b = 0.16, R^2 = 0.83; dark: a = 1.05, b = 0.19, R^2 = 0.90; fig. 1C). A similar pattern was observed in the comparison between the lone situation and the situation where a stimulus shoal was presented (alone: a = 0.78, b = 0.34, R^2 = 0.42; with group: a = 0.46, b = 0.93, R^2 = 0.10; fig. 1D).

3.2. Experiment 2: Opercular ventilation rates

Ventilation rates differed significantly among social contexts (Friedman test: χ^2 = 30.00, df = 2, P < 0.001, n = 15) and increased from 87.5±6.4 opercular beats per min (mean±SD) in treatment 1 (solitary fish), over 118.6±7.0 beats per min in treatment 2 (stimulus shoal was presented in an adjacent compartment), to 147.5±5.3 beats per min in treatment 3, where all fish interacted freely (fig. 2A). The mean (±SD) relative increase (compared to treatment 1) was to 136±9 % in treatment 2, and to 169±11 % in treatment 3. A linear regression showed that log-transformed opercular ventilation rates slightly increased with log-transformed body mass (alone: a = 0.57, b = 25.12, R^2 = 0.91; separate: a = 0.22, b = 74.13, R^2 = 0.20; together: a = 0.10, b = 114.82, R^2 = 0.14; fig. 2B).

4. Discussion

An influence of group size on metabolic costs has been found in several fish species (Parker 1973, Itazawa et al. 1978, Smatresk & Herreid 1980, Klyashtorin & Salikzyanov 1981, Ross et al. 1992). A calming effect was reported, e.g., for Eurasian perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*), in which oxygen consumption rates of isolated fish were twice as high as that of individuals in groups of eight fish, with intermediate values in groups of four fish (Schleuter et al. 2007). Accordingly, specific growth rates were reported to be 3.5 times as high in groups of four ruffe (Schleuter & Eckmann 2006) as compared to single fish (Henson & Newman 2000). In our current study we detected a completely different pattern in grouped European minnows: Individual oxygen consumption and gill ventilation frequencies strongly increased when focal fish faced a group situation, most strongly when allowed to interact freely with a group.

In our first experiment, we did not find a significant difference between individual oxygen consumption in light and darkness. If the lone situation per se induced stress responses in the focal fish one could expect higher consumption rates during the light treatment and reduced consumption due to a calming down of the test fish in darkness, which would then represent the rotuine metabolic rate (RMR). However, our test fish did not show a stress-induced response in the lone situation whether tested in light or darkness.

To measure oxygen-consumption rates, focal fish were tested while residing in the respiratory chamber and thus could not reach the group that was placed in the surrounding tank. Visual cues may play an important role in the group effect; e.g., Shlaifer (1939) and Wirtz & Davenport (1976) showed that goldfish (*Carassius auratus*) and blennies (*Blennius pholis*) would change their metabolic rates if a mirror was positioned so that fish could see their reflections. One could argue that the increase in oxygen consumption may be caused by focal fish attempting (but failing) to reach the group. However, if so, one would predict fish to show reduced metabolic rates in treatment 3 of experiment 2 where they could interact freely with all group members. This was not the case though, and ventilation rates were even higher than when the group was visually presented (treatment 2 of experiment 2).

Theoretically, our findings of increased metabolic rates when confronted with a group of conspecifics could be explained by an increase in the focal individual's activity level when in sight of a group (treatment 2 of experiments 1 and 2) or when residing within a group (treatment 3 of experiment 2). However, the video recordings from experiment 2 suggest that this

was not the case, and it also seems unlikely that metabolic rates were affected by activity levels in experiment 1 (at least not to the extent observed here), as the respiratory chamber largely restricted fish movement. Likewise, SCHLEUTER et al. (2007) found differences in activity to explain only a part of the variance in metabolic rates when comparing single and grouped fish. Some ostariophysan fishes, including European minnows, have epidermal club cells that when ruptured release an odorant (Schreckstoff) which induces alarm responses in conspecifics and some heterospecific species (VON FRISCH 1941, CHIVERS et al. 2007). For example, MATHIS & SMITH (1993) demonstrated that fathead minnows (*Pimephales promelas*) showed a 48 % increase in shoaling tendency and an 18 % increase in shelter use following exposure to Schreckstoff. It is possible that the release of even small amounts of alarm substances from damaged tissue caused by even the gentlest netting procedures could result in an increase in opercular rate. However, as the three treatments in experiment 2 were performed in balanced order (see 2. Methods), an effect of Schreckstoff can be ruled out to explain our results. Taken together, our present results therefore suggest an effect of the presence of conspecifics on individuals' metabolic expenses (see also SHLAIFER 1939, PARKER 1973).

But why did metabolic rates increase when (familiar) group-living European minnows were within a group situation? Beside numerous benefits, group-living also imposes costs arising from several mechanisms including increased competition for food, space, mating partners or other resources, and increased risk of disease transmission (PULLIAM & CARACO 1984, RANTA et al. 1993, KRAUSE & RUXTON 2002, LOYS RICHARDS et al. 2010). For example, in situations where costs of increased food competition outweigh the benefits of shoaling (e.g., in starved fish), reduced shoaling is commonly observed, probably because starved individuals are more affected by competition from shoal members (REEBS & SAULNIER 1997, KRAUSE et al. 1999, PLATH & SCHLUPP 2008).

Even though all test fish were fed to satiation before the tests, we argue that competition within minnow shoals (and the associated perceived risk of agonistic interactions among shoal members) is what causes the pattern observed here. Qualitatively, we did not observe overt aggression in any of our experiments; still, we argue that competition within minnow shoals leads to a certain level of stress among group members that manifested in increased metabolic rates.

ORPWOOD et al. (2008) found European minnows to respond to the presence of predatory pike (*Esox lucius*) by forming larger shoals (see also MAGURRAN & PITCHER 1987), but only in structurally simple habitats, while minnows maintained small shoal size in structurally complex habitats. In other words: When habitat complexity allows individuals to seek shelter individually, the aforementioned cost-benefit trade-off of group formation is shifted in favor of increasingly solitary behavior. European minnows are known to make use of refuges when they are not active (FROST 1943, GREENWOOD & METCALFE 1998) and sheltering – while abandoning shoal formation – is also regularly seen in our maintenance aquaria.

Overall, it seems that minnow shoals are highly dynamic and individuals may behave almost solitarily when resting (i.e., hiding inside vegetation or under stones; FROST 1943, GREENWOOD & METCALFE 1998), but form more or less dense shoals when moving in the open water column. Shoaling, or facultative schooling, however, are primarily responses to predation threat (PITCHER 1973, MAGURRAN & PITCHER 1987), while costs arising from competition within shoals can easily go unnoticed, unless metabolic rates are being considered, as was done in this study.

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