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2 Digesting or swimming? Integration of the postprandial metabolism,
3 behavior and locomotion in a frequently foraging fish

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5 Li-Juan Nie, Zhen-Dong Cao and Shi-Jian Fu^{*}

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7 Laboratory of Evolutionary Physiology and Behavior, Chongqing Key
8 Laboratory of Animal Biology, Chongqing Normal University, Chongqing,
9 401331, China

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15 ^{*}Author to whom correspondence should be addressed,

16 Dr. Shi-Jian Fu,

17 E-mail: shijianfu9@cqnu.edu.cn

18 Tel and Fax: 862365910701

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20 ABSTRACT

21 Fish that are active foragers usually perform routine activities while digesting their food;
22 thus, their postprandial swimming capacity and related behavior adjustments might be
23 ecologically important. To test whether digestion affect swimming performance and
24 the relationships of digestion with metabolism and behavior in an active forager, we
25 investigated the postprandial metabolic response, spontaneous swimming activities,
26 critical swimming speed (U_{crit}), and fast-start escape performance of both fasted and
27 digesting (3 h after feeding to satiation) juvenile rose bitterling (*Rhodeus ocellatus*).
28 Feeding to satiation elicited a 50% increase in the oxygen consumption rate, which
29 peaked at 3 h after feeding and returned to the prefeeding state after another 3 h.
30 However, approximately 50% and 90% of individuals resumed feeding behavior at 2
31 and 3 h postfeeding, respectively, although the meal size varied substantially.
32 Digestion showed no effect on either steady swimming performance as suggested by
33 the U_{crit} or unsteady swimming performance indicated by the maximum linear
34 velocity in fast-start escape movement. However, digesting fish showed more
35 spontaneous activity as indicated by the longer total distance traveled, mainly through
36 an increased percentage of time spent moving (PTM). A further analysis found that
37 fasting individuals with high swimming speed were more inclined to increase their
38 PTM during digestive processes. The present study suggests that as an active forager
39 with a small meal size and hence limited postprandial physiological and
40 morphological changes, the swimming performance of rose bitterling is maintained
41 during digestion, which might be crucial for its active foraging mode and
42 anti-predation strategy.

43 Key words: digestion; competition, priority, swimming performance

1. Introduction

Feeding and swimming are two of the primary physiological activities of fish species. Feeding provides the energy for all physiological activities including swimming, whereas swimming capacity is closely related to the success of food capture. Fish usually perform routine activities while digesting their food (Fu et al., 2009); thus, changes in performance and behavior that result from digestion can have important ecological implications for wild fishes. The situation might be increasingly complicated in active foragers and/or in those fish species living in habitats with high swimming demands (e.g., high water velocity or predation stress) (Peng et al., 2014). The influence of digestion on swimming behavior in fish is poorly understood. It has been suggested that foraging behavior may be reduced with increasing levels of satiation (Gill and Hart, 1994, 1996), resulting in a decrease in spontaneous swimming speed with increasing satiation (Robinson and Pitcher, 1989; Asaeda et al., 2001). The decreased spontaneous activities may favor an efficient digestion process, more allocation of energy to growth, and a lower rate of encountering potential predators. However, for an active forager feeding on scattered low-energy food, the maintenance of postprandial activities might be ecologically important (Fu et al., 2009). Furthermore, some vital, routine tasks such as safeguarding territories and identification of potential predators which closely related to spontaneous swimming may also prevent a profound decrease of postprandial activities (Tudorache et al., 2009). Thus, the effect of feeding on spontaneous activities might differ among fish with different ecological habits (foraging mode, anti-predation strategy, etc.) and among environments with differences in flow regime, food abundance and/or predation stress.

69 Locomotion in fish can be described as steady or unsteady swimming. Steady
70 swimming is defined as swimming in a straight line at a constant speed (Blake 1983;
71 Videler 1993). It is important to hold position in a flow and to seek suitable habitats,
72 among other functions (Plaut 2001; Kieffer 2010; Fu et al., 2013). Both steady
73 swimming and digestion are assumed to be metabolized aerobically and hence may
74 compete for oxygen during postprandial swimming specifically in low oxygen
75 environments (Jourdan-Pineau et al., 2010; Zhang et al., 2012). Thus, the competition
76 between digestion and swimming during postprandial locomotion has drawn the
77 attention of scientists (Alsop and Wood, 1997; Thorarensen and Farrell, 2006;
78 Altimiras et al., 2008; Fu et al., 2009; Jourdan-Pineau et al., 2010). The steady
79 swimming performance indicated by the critical swimming speed (U_{crit} , the water
80 speed at which a fish can no longer maintain position, also called the maximum
81 sustainable swimming speed) showed no change after feeding in fish species such as
82 common carp (*Cyprinus carpio*) (Pang et al., 2011) and the European sea bass
83 (*Dicentrarchus labrax*) (Altimiras et al., 2008; Jourdan-Pineau et al., 2010). In
84 contrast, the U_{crit} has been reported to decrease from 10% to 30% in fish species such
85 as Chinese bream (*Parabramis pekinensis*) (Peng et al., 2014), goldfish (*Carassius*
86 *auratus*) (Pang et al., 2011), rainbow trout (*Oncorhynchus mykiss*) (Alsop and Wood,
87 1997) and Chinook salmon (*Oncorhynchus tshawytscha*) (Thorarensen and Farrell,
88 2006). The ecological benefit and cost of maintaining a steady swimming
89 performance while digesting may vary among fish species with divergent ecological
90 habits and/or species that favor different habitats (Yan et al., 2013). It might be the
91 selective agents underlying the differences of response of U_{crit} to digestion, whereas
92 the physiological mechanisms used by different fish species remain largely unknown.
93 Thus, the investigation of postprandial changes in swimming performance, behavior

mode and other physiological performances from an integrative perspective in more fish species might provide useful information.

Unsteady swimming involves maneuvers, acceleration and deceleration (Blake, 1983; Videler, 1993) and is a major component of spontaneous swimming activity, which includes common behaviors such as safeguarding territories, searching for food, avoiding predators and mating. Among them, the fast-start escape swimming response is a form of burst swimming of less than approximately 1 s in duration that is considered to be fueled anaerobically (Webb, 1986; Domenici and Blake, 1997; Walker et al., 2005). The propulsive performance of the fast-start response can be evaluated through quantified distance-time parameters, such as maximum forward velocity ($V_{\max}$) and maximum linear acceleration ($A_{\max}$) during the fast-start escape movement (see review by Domenici and Blake, 1997). Theoretically, there is no metabolic competition between digestion and the fast-start escape response. However, several feeding-elicited morphological consequences such as increased mass and changes in body shape may negatively affect fast-start performance. The relationship between feeding and fast-start has only been investigated in an ambush predator, southern catfish (*Silurus meridionalis*), in which feeding to satiation resulted in a profound impairment in the fast-start response (Yan et al., 2015). The decreased fast-start performance while digesting is reasonable because southern catfish usually consume large meals, hide without moving while digesting, and have low predation stress. The effects of feeding on the fast-start response in active foraging fish species and its relationships with other physiological activities and behaviors need further investigation.

The maintenance of both steady and unsteady swimming performance and the corresponding adjustment of behavior mode might be closely correlated with each

other and are ecologically important in active fish species. Thus, in the present study, we aimed to test whether feeding affects the performance of steady and unsteady swimming and whether such effects may be related to postprandial behavioral changes. We selected a small, frequently foraging fish, the rose bitterling (*Rhodeus ocellatus*), as an experimental model. Rose bitterlings prefer still bodies of water such as ponds and lakes but also occupy rivers with slow flow. These fish usually swim and forage in areas with high predation stress. To achieve our goal, we first measured the postprandial metabolic response as indicated by oxygen consumption rate ($\dot{M}O_2$) after a satiating meal to characterize the digestive process of this fish. Then, we measured the latency and degree of regained appetite after a satiating meal to qualitatively determine its foraging mode. Lastly, we measured the spontaneous physical activities, U_{crit} and fast-start response of fish during fasting and digesting (3 h after feeding, when postprandial metabolism peaks).

2. Materials and methods

2.1. Experimental animals and acclimation

Juvenile rose bitterlings (*Rhodeus ocellatus*) (N = 206, see Table 1 for body size) were obtained from a local pond and kept in tanks containing 25 ± 1 °C de-chlorinated, fully aerated tap water for 2 weeks before the experiment. The photoperiod was maintained at 14 L:10 D, and the dissolved oxygen level was kept above 90% saturation. One-tenth of the water in the tank was replaced daily with freshwater. Throughout the experimental period, the fish were fed once daily (at 09:00 am) to satiation with a commercial frozen sludge worm (*Tubifex tubifex*). The uneaten food and feces were removed with a siphon 30 minutes after feeding.

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145 2.2. Experimental design

146 Experiment I (Feeding metabolism test). After 2 d of fasting, 15 individuals were
147 selected for measurement of the postprandial metabolic response after a satiating meal
148 of sludge worm.

149 Experiment II (Resumption of appetite test) Sixty individuals were selected and
150 offered a satiating meal (sludge worm). Then, five groups of 12 individuals were
151 randomly selected after 1, 2, 3, 4 and 48 h, and another meal was offered. Then,
152 whether and how much each individual ate was recorded.

153 Experiment III (Spontaneous swimming test) Thirty-three fish after 2 d of fasting
154 and 38 digesting fish (2–3 h after feeding, when postprandial metabolic rate peaked
155 according to experiment I) were selected for observation of spontaneous swimming
156 activities.

157 Experiment IV (Fast-start escape response test). Twenty fasting and 20 digesting
158 individuals were selected for measurement of the fast-start escape response.

159 Experiment V (U_{crit} test). Ten fasting (48 h postfeeding) and 10 digesting individuals
160 were selected for measurement of U_{crit} .

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162 2.3. Experimental facilities and measurements

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164 2.3.1 Measurement of postprandial metabolic response

165 To investigate the postprandial $\dot{M}O_2$ responses in rose bitterling, after 24 h of fasting,
166 15 fish were individually moved to a continuous-flow respirometer with a water
167 temperature of $25 \pm 0.5^\circ\text{C}$ (see structure in Fu et al., 2005) and acclimated for another
168 24 h. Then, $\dot{M}O_2$ was measured 7 times at 1 h intervals to determine the prefeeding

$\dot{M}O_2$. Then, each fish was fed a satiating meal of sludge worm (approximately 1.4% of body mass). Afterward, the $\dot{M}O_2$ was measured at 1 h intervals for 12 h, ensuring that all of the fed fish completed digestion. The following formula was used to calculate the $\dot{M}O_2$ ($mg\ O_2\ kg^{-1}\ h^{-1}$) according to previous studies (Clark et al., 2013; Norin et al., 2016):

$$\dot{M}O_2 = \Delta O_2 \times v / m \quad (1)$$

ΔO_2 is the difference in dissolved oxygen level ($mg\ L^{-1}$) between the experimental chamber and a control chamber (chamber without fish), v is the water flow rate in the experimental chamber ($L\ h^{-1}$), and m is the body mass of the fish (kg). The dissolved oxygen level was measured at the outlet of the chamber using an oximeter (HQ40d, Hach Company, Loveland, CO, USA) which was calibrated daily during experiment. The flow rate of water through the respirometer chamber was measured at the outflow point from each chamber.

2.3.2. Measurement of appetite recovery

The appetite experiment was performed in a cylindrical tank ($\Phi = 25\ cm$) with a 10 cm water depth. Briefly, 60 fish that showed normal feeding activity during the acclimation period were selected, transferred to individual experimental observation tanks, and acclimatized for 48 h. Next, each fish was offered a satiating meal. Then, after 1, 2, 3, 4 and 48 h of fasting, 12 fish were selected and offered another meal, and whether and how much each individual ate was recorded.

2.3.3. Measurement of spontaneous swimming activity

For fasting fish, 38 fish subjected to fasting for 2 d were transferred to individual circular observation chambers ($\Phi = 25\ cm$) and acclimatized for 8 h. The water depth was kept at 10 cm. Then, the spontaneous activity of each fish was recorded for 1 h by video cameras connected to a computer. For digesting fish, 33 fish subjected to fasting

for 2 d were transferred to observation chamber and acclimatized for 5.5 h and then offered a satiating meal. Next, the spontaneous activity of each fish was recorded for 1 h, beginning 2.5 h after feeding (when postprandial $\dot{M}O_2$ peaked). All the videos were then analyzed with EthoVision XT 9 software (EthoVision XT 9, Nodus, Netherlands). The total distance moved during the entire observation period (DM, cm), percentage of time spent moving (PTM, %) and the average swimming speed during movement ($cm\ s^{-1}$) were calculated.

2.3.4. Measurement of U_{crit}

A Brett-type swimming tunnel respirometer (Brett, 1964) was used to measure U_{crit} (see detail in Penghan et al., 2014). A circulating water flow was generated in the tunnel (total volume, 3.5 L) by an acrylic propeller attached to a variable speed pump. A honeycomb screen was secured at each end of the swimming chamber to reduce turbulence and to ensure uniform water velocity across the swimming chamber. A video camera was used to calibrate the water velocity to the voltage output from the pump controller. The fish were placed downstream of the propeller in a swimming chamber with a $20\ cm^2$ cross-sectional area. The water temperature in the swimming chamber was controlled within $\pm 0.2^\circ C$ using a water bath connected to a stainless steel heat exchanger. U_{crit} was calculated for individual fish using Brett's equation (Brett, 1964):

$$U_{crit} = V + (t / T) \Delta V \quad (2)$$

where V is the highest speed at which the fish swam during the full time period of the experiment ($cm\ s^{-1}$), ΔV is the velocity increment ($1\ body\ length\ s^{-1}$; $6\ cm\ s^{-1}$), T is the prescribed period of swimming per speed (20 min), and t is the time during which the fish swam at the final speed (min).

The U_{crit} was measured at $25\ ^\circ C$. The fish, after either 2 d of fasting or a satiating

meal, were individually introduced into the swimming respirometry tunnel and held for 2 h at a slow water velocity (approximately 6 cm s^{-1}) for recovery. Then, the water speed was increased by 6 cm s^{-1} every 20 min until the fish became exhausted. Testing was terminated when the fish failed to move off the rear honeycomb screen of the swimming chamber for 20 s (Lee et al., 2003).

2.3.5. Measurement of the fast-start escape response

The fast-start response was measured with a device developed by the Laboratory of Evolutionary Physiology and Behavior, Chongqing Normal University. The device included a high-speed camera (A504K, Basler; $500 \text{ frames} \cdot \text{s}^{-1}$) and a Light Emitting Diode (LED) matrix light source and sink (engraved with 1 cm^{-1} grid lines on the bottom) (Yan et al., 2013). Before fast-start measurement, 40 fish after 48 h fasting were dorsally marked with titanium oxide at their centers of mass. The duration of the entire process was less than 30 s, and fish were allowed to recover for 4 hours after the procedure (Yan et al., 2015). Then, 20 fish were individually transferred to the acclimation zone of the fast-start escape experimental system and allowed to rest for another 1 h. The remaining 20 fish were offered a satiating meal, transferred to the acclimation zone of the fast-start escape experimental system at 1.5 h after individual feeding, and allowed to rest for another 1 h. The depth of the water in the tank was 10 cm. Either a fasting or a digesting fish was then introduced into the filming zone through an alleyway. Escape responses were elicited by an electrical impulse ($0.75 \text{ V} \cdot \text{cm}^{-1}$; $50 \text{ m} \cdot \text{s}$) administered when the fish maintained a position at the center of the filming zone. The high-speed camera was used to record the entire escape process (time span: 2 s). The resulting sequence images were then digitized with TpsUtil and TpsDig software (<http://life.bio.sunysb.edu/morph>) to define the track of the center of mass in the locomotion performed by the fish during its escape response. The

maximum linear velocity ($V_{\max}$, cm s^{-1}) and maximum acceleration rate ($A_{\max}$, m s^{-2}) of the center of mass during the escape response were measured (Yan et al., 2015).

2.4. Data analysis

SPSS version 17.0 was used for data analysis. All values are presented as the means $\pm$ S.E. $P < 0.05$ was used as the level of statistical significance. The effect of postfeeding time on $\dot{M}O_2$ in experiment I was determined using a one-way repeated-measures analysis of variance (ANOVA). The percentage of individuals that showed feeding behavior in experiment II was determined using the Chi-square test, while the difference in meal size was tested using one-way ANOVA. The effects of digestion on spontaneous activity, U_{crit} and fast-start escape response were tested using t-tests. All data used for ANOVA and t-tests were checked by One-sample Kolmogorov-Smirnov test and Levene's test for the normality and heteroscedasticity, respectively. The relationship among variables of spontaneous activity was also evaluated by a regression.

3. Results

3.1. The postprandial metabolic response

The $\dot{M}O_2$ increased significantly immediately after feeding and peaked with a value of approximately 150% of that of the prefeeding level at 3 h postfeeding, followed by a return to the fasting level at 6 h postfeeding (Fig. 1).

3.2. Resumption of appetite

Four, six, 11 and 11 out of 12 experimental fish ate the diet at 1, 2, 3, and 4 h,

respectively, after a previous feeding bout, whereas all fish ate the diet after 48 h of fasting (Fig. 2A). However, the ingestion levels of fish at 1 or 2 h after feeding were significantly lower than those of fish allowed 3 and 4 h of recovery. Furthermore, 48 h fasting fish showed a much higher ingestion level compared to 3 or 4 h postprandial fish (Fig. 2B).

3.3. Effects of digestion on spontaneous swimming activity

There was no significant difference in the average velocity of spontaneous swimming activity (Fig. 3A), whereas the PTM (Fig. 3B) of digesting fish was significantly higher than that of fasting fish. Thus, the DM (Fig. 3C) in digesting fish was significantly longer than that of fasting fish during the whole observation period.

Within either fasting or digesting fish, both PTM and velocity were significantly positively correlated with DM (Fig. 3D, E). The relationship between PTM and DM could be described as $Y = 3.768X - 14.168$ ($R^2 = 0.929$, $N = 33$, $P < 0.001$) in digesting fish and as $Y = 2.749X - 1.657$ ($R^2 = 0.735$, $N = 38$, $P < 0.001$) in fasting fish (Fig. 3D). The relationship between DM and velocity could be described as $Y = 15.816X - 65.292$ ($R^2 = 0.368$, $N = 33$, $P < 0.001$) in digesting fish and as $Y = 5.717X - 0.593$ ($R^2 = 0.252$, $N = 38$, $P = 0.001$) in fasting fish (Fig. 3E). Furthermore, a positive correlation was observed in digesting fish ($Y = 2.676X - 0.835$ ($R^2 = 0.161$, $N = 33$, $P = 0.021$)) but not in fasting fish (Fig. 3F).

3.4. Effects of digestion on U_{crit} and fast-start escape response

There were no significant differences between fasting and digesting fish in U_{crit} , V_{max} or A_{max} (Table 2).

4. Discussion

Juvenile rose bitterlings showed a postprandial metabolic profile typical of those in previous studies in other fish species, i.e., an increase immediately after feeding, followed by a slow return to prefeeding status (Wang et al., 2012). However, the 50% postprandial metabolic increase and 6 h of duration were among the lowest values reported for all studied cyprinid fish species (Fu et al., 2009; Zhang et al., 2012). After a satiating meal, one-third of individuals at 1 h after feeding and almost all individuals (11 out of 12 individuals) at 3 h after feeding showed bouts of feeding behavior, even though the postprandial metabolism was still running at its peak level. This suggested that the appetite of the rose bitterling is more closely related to the fullness of the digestive tract rather than to the feeding metabolic state, which may be highly adaptive to its frequent foraging mode. However, the profoundly smaller meal size compared to that of fish fasted for 48 h indicated that there was still some undigested food left in digestive tract at the earlier time points. This is similar to results from the spotted dogfish (*Scyliorhinus canicula*) suggesting that the return of appetite is more closely related to digestive tract fullness than to the level of postprandial metabolism (Sims and Davies, 1994). However, a study in rainbow trout (*Oncorhynchus mykiss*) suggested that oxygen consumption may constrain its food intake (Saravanan et al., 2013). Thus, whether the appetite constrained by digestive fullness and postprandial metabolism may vary among fish species with different foraging modes.

The spontaneous activities were measured at c. 3 h after feeding in the present study because we assumed that behavior might show the strongest impairment at postprandial metabolic peak. Swimming speed during spontaneous activity showed no significant decrease, in contrast to the results of previous studies in fish species such

as three-spined stickleback (*Gasterosteus aculeatus*) (Gill and Hart, 1994, 1996), herring (*Clupea harengus*) (Robinson and Pitcher, 1989), and topmouth gudgeon (*Pseudorasbora parva*) (Asaeda et al., 2001). By contrast, digesting bitterlings showed even higher DM than fasting fish. This increase in DM was consistent with the appetite experiment, which showed that almost all individuals consumed another meal after 3 h of digestion. The unexpected result that spontaneous activities showed no decrease during digestion in rose bitterling is possibly due to the frequent foraging mode of these fish, which means that rose bitterling need to feed while digesting a small amount of food in a single meal (like most other cyprinids, it has no stomach and instead has a swollen esophagus) (Wu, 1982). Further analysis indicated that the increased DM after feeding was primarily due to the elevated PTM during digestion of some individuals with high speed during fasting. This suggested that rose bitterlings may elevate their foraging activity to obtain more food when food availability is high rather than down-regulating their behavior to save energy or decrease the rate of encountering its predators (Asaeda et al., 2001; Fu et al., 2009). However, the increased spontaneous activity might also contribute to physiological behaviors other than foraging, which may be suppressed by 48 h of fasting in the present study but released along with the secretion of corticosterones after a satiating meal (Kotz, 2006; Gingerich et al., 2010). Because we measured all variables after 3 h of digesting, further study on how spontaneous activity changes immediately after ingestion might provide additional useful information.

Although fish rely on anaerobic metabolism to different degrees while reaching U_{crit} (Nelson et al., 1996), U_{crit} is highly correlated with the maximum oxygen uptake capacity and is widely accepted as an indicator of aerobic swimming performance. Thus, the U_{crit} might decrease during digestion due to competition for oxygen.

Furthermore, the increased body mass and morphological change might increase the drag force when swimming and hence decrease the swimming efficiency. However, in the present study, the steady swimming performance suggested by U_{crit} showed no change after feeding. This is due to the small meal size, which produced little effect on the body morphology and hence swimming efficiency. Although we did not measure metabolic rate in this study, a previous report indicated that steady swimming could elicit an increase in $\dot{M}O_2$ of more than 500% (Yan et al., 2013). Thus, the small metabolic increase elicited by digestion showed a negligible effect on the scope of aerobic metabolism used for swimming. This situation is similar to that of active cyprinids such as grass carp (*Ctenopharyngodon idellus*), which possess a low digestive capacity, leading to little change in postprandial locomotor performance, which benefits its frequent grazing behavior (Fu et al., 2009). Alternatively, the cardio-respiratory system of rose bitterlings may be highly flexible, enabling it to meet the oxygen demands of both digestion and locomotion, a situation similar to that of common carp (*Cyprinus carpio*) (Pang et al., 2011). The feeding showed no effect on any of the measured variables related to the fast-start escape response, which may also be due to the small meal size. Small meals might be crucial for the rose bitterling's anti-predator strategy because the spontaneous activities and thus the encounter rate may be increased during digestion. The effect of feeding on the fast-start response has only been investigated in southern catfish, in which a meal size of 25% of its body mass, but not a meal of 12.5% body mass, negatively affected the fast-start response (Yan et al., 2015). Again, the measurement of fast-start behavior immediately after feeding might be useful in this species due to its rapid digestive process.

In conclusion, as a frequent forager in still water with high predation stress, rose

bitterling showed a low meal size but a rapid return of appetite. Feeding showed no effect on either steady or unsteady swimming performance, as feeding (and hence digestion) results in little change in metabolism. The physiological mechanism and behavioral and ecological relevance of elevating spontaneous activity via spending more time and distance in moving require further investigation. Nevertheless, the withholding of most of its locomotion performance while digesting might be ecologically important as selection favors high demands for foraging, digesting and swimming performance according to the foraging mode and high-predation habitat of the rose bitterling.

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Figure captions

Fig. 1. The postprandial $\dot{M}O_2$ response after a satiating meal (c. 1.4% body mass) in juvenile rose bitterling (Mean $\pm$ S.E., N = 15). a, b, c, d, values without a common lowercase letter indicate a significant difference ($P < 0.05$).

Fig. 2. Effects of period after a satiating meal on the percentage of individuals resuming feeding behavior (A) and on the meal size (% body mass) (B) in juvenile rose bitterling (Mean $\pm$ S.E., N = 12). a, b, c, values without a common lowercase letter indicate a significant difference ($P < 0.05$).

Fig 3. The effects of digestion on average velocity during movement, percentage of time spent in moving (PTM) and total distance moved (DM) during the observation period and their relationships in juvenile rose bitterlings (Mean $\pm$ S.E., N = 38 and 33 for fasting and digesting fish). a, b, values without a common lowercase letter indicate a significant difference ($P < 0.05$).

Table 1. The body size of experimental fish used in the present study (Mean $\pm$ S.E.)

	Feeding metabolism	Resumption of appetite	Spontaneous activity		Critical swimming speed		Fast-start escape response	
			Fasting	Digesting	Fasting	Digesting	Fasting	Digesting
n	15	60	38	33	10	10	20	20
Body weight (g)	1.36 $\pm$ 0.07	1.29 $\pm$ 0.02	1.33 $\pm$ 0.05	1.33 $\pm$ 0.05	1.22 $\pm$ 0.04	1.24 $\pm$ 0.05	1.24 $\pm$ 0.08	1.13 $\pm$ 0.03
Body length (cm)	3.95 $\pm$ 0.05	3.95 $\pm$ 0.02	3.98 $\pm$ 0.05	3.98 $\pm$ 0.05	3.98 $\pm$ 0.05	3.94 $\pm$ 0.06	3.95 $\pm$ 0.08	3.81 $\pm$ 0.03

Table 2. Effects of digestion on critical swimming speed and fast-start escape performance in juvenile rose bitterling.

	Fasting	Digesting
U_{crit} (cm s ⁻¹)	42.71 ± 1.59	41.23 ± 2.27
V_{max} in fast-start (cm s ⁻¹)	127.79 ± 10.12	115.89 ± 63.39
A_{max} in fast-start (m s ⁻²)	177.19 ± 14.81	153.54 ± 10.92

Figure 1

Figure 2

Figure 3