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Kleptoparasitism and aggressiveness are influenced by standard metabolic rate in eels

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ABSTRACT

Kleptoparasitism refers to either interspecific or intraspecific stealing of food already procured by other species or individuals. Within a given species, individuals might differ in their propensity to use such a tactic, in a similar manner to which they differ in their general level of aggressiveness. Standard metabolic rate is often viewed as a proxy for energy requirements. For this reason, it should directly impact on both kleptoparasitism and aggressiveness when individuals have to share the same food source. In the present study we first assessed the standard metabolic rate (SMR) of 128 juvenile European eels (*Anguilla anguilla*) by the determination of oxygen consumption. We then tested how the SMR could influence agonistic behavior of individuals competing for food in three distinct trials evenly distributed over three months. We demonstrate that SMR positively correlates with attacks (sum of bite and push events) in all trials. Similarly SMR correlated positively with kleptoparasitism (food theft), but this was significant only for the third trial (month 3). To our knowledge, the present study is the first reporting a link between kleptoparasitism and SMR in a fish species. This has ecological implications owing to the fact that this species is characterized by an environmental sex determination linked to early growth rate. We discuss theses findings in the light of the producer-scrounger foraging game.

1. Introduction

Foraging has been extensively studied by ecologists, ethologists and finally behavioral ecologists. Resources being (often) limited, many species compete for access to food [21], some of them snatching food items from other individuals (e.g [28]). The activity of obtaining food by using the investment of other foragers, called kleptoparasitism, has mostly been studied at the interspecific level [14, 20, 28]. Kleptoparasitism could be considered as a tactic of foraging strategy when it occurs at the intraspecific level. While this has been well described in birds (reviewed in [4]), kleptoparasitism between individuals of the same species has been scarcely described in fish. To date, intraspecific kleptoparasitism has been observed in three-spined sticklebacks, *Gasterosteus aculeatus* [33] and in European glass eels *Anguilla anguilla* [15]. Understanding processes that trigger its occurrence is puzzling since it might involves species' specific life history traits (*e.g.* social hierarchy, familiarity, [33]) as well as various behavioral and physiological mechanisms that are difficult to disentangle (*e.g.* aptitude to find food). In a previous study [15], food theft between glass eels (herein coined kleptoparasitism) has been considered a similar agonistic behavior than pushes, chases and nips. Whether kleptoparasitism during this experiment corresponded to a foraging tactic remains difficult to assess. Owing to the positive relationship between the real feeding needs and the occurrence of agonistic acts, the measure of standard metabolism is a possible way to address this question, assuming that measurement of individual metabolism is a proxy for motivation to feed [7, 27].

There are different ways to measure the individual's metabolism. Firstly, routine metabolism (RM) refers to ectotherms that are not in post-absorptive conditions and for which, spontaneous activities are allowed [5]. Conversely, the standard metabolic rate (SMR) represents the lowest rate of metabolism, measured at a particular temperature in the absence of muscular activity, food consumption and its subsequent processing [25]. In many fish species, metabolic rate correlates positively with aggressiveness. At the population level, a significant positive correlation between SMR and total aggressiveness was found in brown trout [34]. At the individual level, the social status is also well correlated with SMR. This has been demonstrated particularly in salmonid fish, where Metcalfe et al. [26] and Sloman et al. [32] showed that individuals with high SMR are more likely to be dominant than individuals with lower SMRs. Similarly, Cutts et al. [7], showed that aggressiveness correlates positively to SMR at the group level (discriminating groups with low, moderate or high SMR).

In eels, sex determination is influenced by the environment [8, 22], and early difference in growth rate has been identified as the major factor determining the future sex of individuals [18]. Eels that display the highest growth rate as juveniles develop as males and those with

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the lowest growth rate develop as females [18]. Hence, readily identifying individuals that monopolize disproportionate clutch of food, linked to their metabolism, could be promising to precociously detect individuals that would likely become males or females.

The purpose of the present study is i) to assess whether both kleptoparasitism and attacks are linked to the SMR of juvenile eels and ii) to evaluate to what extent food theft hails from the same behavior as push/bite aggressive acts. We finally discuss how this relates to the ecology of the species.

2. Materials and methods

Autumn and spring glass eels were respectively collected in November 2009 and April 2010 at the beginning of nocturnal floods and at similar tidal coefficients at the mouth of the Courant d'Huchet Estuary (Moliets, South-Western France, 43° 51′ N, 1° 23′ W). Sixty-four randomly chosen glass eels per season were subjected to the measurement of their metabolic rate through the determination of oxygen consumption.

2.1. Metabolic rate measurements

For this purpose, we used a micro-respirometer device composed of eight cylindrical respirometry chambers (diameter 13 mm, length 80 mm) fitted with a miniature circular oxygen sensor (type PSt3, Loligo Systems) linked to 2 oxymeters (Oxy4-mini PreSens, 4 canals each). Oxygen concentration was determined through optical measurements using optic fibers. An open system provided water to the respirometer chambers and in parallel, a re-circulated system maintained a current flow through the chamber (see Régnier et al. [30] for more details). At fixed time intervals, the open water system was turned off to measure the decrease in oxygen concentration due to glass eel oxygen consumption. To keep oxygen saturation above 80%, the open system was switched off during 20 min in order to record SMR. Then, the open system was switched on 20 min to bring the chamber oxygen level to saturation. A preliminary experiment (conducted by V. Bolliet) allowed fixing that time interval representing one cycle (20 min open system/20 min closed system).

Each day, eight glass eels were placed in metabolic chambers at 4 p.m. and recording started thereafter (one oxygen measurement per minute). Glass eels were acclimated for 16 h, and SMR was established in the morning (*i.e.* 8 a.m. to 12 a.m.). Thus, the first sixteen hours were dedicated to acclimatization and the following 4 h (6 cycles) were dedicated to the recording of resting oxygen consumption. Then the fish were removed from the tubes and control sessions (3 cycles without glass eels) were carried out in order to evaluate the error associated to the measuring device plus the error linked to potential microbial respiration. Mean slope of oxygen consumption for each individual was calculated on the basis of the three weakest measuring cycles (from 6 cycles), assuming a generalized linear model (calculations performed using R software; see Régnier et al. [30] for more details). The SMR ($mm^3O_2 \cdot h^{-1}$) was calculated as the difference between slopes of measuring sessions and control sessions. This operation took place over 8 consecutive days, for each season, and allowed the SMR measurements of 64 individuals for each season.

2.2. Biometric measurements

All individuals (128 individuals evenly distributed in 16 aquariums: 8 per aquarium) were lightly anesthetized (eugenol1 / 10 in alcohol, 0.3 $ml \cdot L^{-1}$), measured (±0.5 mm) and weighed after blotting (sartorius CP 153 balance, ±1 mg). This allowed the calculation of the relative (*i.e.* weight specific) SMR (rSMR) expressed in $mm^3O_2 \cdot h^{-1} \cdot g^{-1}$, per fish. Following these measurements, the fish were individually marked using four different colors (red, yellow, blue and orange) of visible implant elastomer (VIE tag, Northwest Marine Technology, Inc, Shaw Island, WA, USA.) implanted subcutaneously on either the ventral or the dorsal area.

2.3. Behavioral observations

In autumn and spring, eight aquaria of 50 cm long, 25 cm wide and 25 cm high were filled up to an outflow located at 15 cm above the aquarium floor using thermo-regulated freshwater from the Nivelle River in open water circulation (see [17] for a detailed description of aquarium design). The photoperiod regime was 12 h L/12 h D with 30 min of dawn (07.00–07.30) and dusk (19.00–19.30). Light intensity was maintained at 27 μW cm^{-2} during the L period (day) and 0 μW cm^{-2} during the D period (night). Groups of eight individuals were then placed in each aquarium. The behavior of each individual, with known rSMR, was then monitored over time.

Direct behavioral observations were conducted over three distinct 11-day trials (one per month over 3 months) as described in Geffroy and Bardonnet [15]. Feeding started at the first trial (26 days after capture), on 14th December 2009 and 13th April 2010 for autumn and spring recruits, respectively. During each trial (11 days, Table 1), the fish were observed directly for 9 days divided into two periods of 5 and 4 consecutive days, separated by two days of break, which were devoted to video recording to monitoring diel activity (these results were reported elsewhere, *i.e.* [17]). In glass eels, agonistic interactions, including food theft, occur only during the feeding period and are easy to monitor [1]. Fish were observed in the afternoon (1.00 p.m. to 4.30 p.m.), from 70 cm away from the front of each aquarium; this is a sufficient distance to avoid disturbance in this species with low visual acuity [29]. Each group of fish was observed for 20 min to count aggressive acts between individuals. Food items (live bloodworms, BW) were delivered one by one, by dropping them from above the aquarium, during the 20 min of monitoring. Each time a BW was consumed, another one was added to the aquarium. Three specific behaviors were identified: “nose push”, where the focal fish pushes the body of the eating individual; “bite” delivered by the focal fish towards the eating individual; “theft”, where the focal individual grabs the BW from the mouth of another individual. All these acts were recorded using a vocal recorder by the same observer (BG). Between trials, the glass eels were fed *ad libitum* with BW.

2.4. Statistical analysis

The correlation between “thefts” and “attacks” (sum of push and bite) was investigated using the Pearson product-moment correlation coefficient (r). Generalized linear mixed models (GLMM) were used to study the relationship between rSMR and both “thefts” and “attacks”, where the group (aquarium) was considered as a random variable. In a previous study, we showed, using the same individuals, that spring recruits were generally more aggressive than autumn recruits [15]. For the present study, which aims at detecting a link between rSMR and both “thefts” and “attacks” at the individuals level, the season factor was thus included in the GLMM as a random effect, since the rSMR of

Table 1
Mean number of blood worms eaten during the experiment for both autumn and spring glass eels, recorded during and between trials.

	Autumn		Spring	
	Duration (days)	Mean number of blood worms consumed	Duration (days)	Mean number of blood worms consumed
Trial 1	11	12.5	11	15.7
Between	10	49.5	17	66.6
Trial 2	11	118.7	11	127.3
Between	18	304.4	17	243.8
Trial 3	11	171	11	155.6