

Familiarity, prior residency, resource availability and body mass as predictors of the movement activity of the European catfish

Ondřej Slavík¹ · Pavel Horký¹ · Matúš Maciak² · Marie Wackermannová¹

Received: 25 September 2014 / Accepted: 3 August 2015 / Published online: 21 August 2015
© Japan Ethological Society and Springer Japan 2015

Abstract When animals compete for resources, their competitive abilities and behavioural strategies can be expressed as changes in movement activity. Stress is an important predictor of activity, and the variability of this predictor reflects the impact of environmental and social factors, while the effects of stress are further influenced through individual behavioural syndromes. We examined the effects of social (familiar vs. unfamiliar and resident vs. intruder) and environmental (resource availability) factors and individual characteristics (body mass) on the movement activity of juvenile European catfish *Silurus glanis* (L.). Familiarity and prior residency decreased the movement activity of these catfish, whereas resource unavailability significantly increased the movement activity of intruders to a level 1.5 times greater than that of the residents. The occurrence of an interaction involving an individual whose body mass was higher than that of individuals from the opposite group predicted a low level of movement activity of this individual. These results suggest that familiarity, prior residency, and high body mass decrease stress from the limited availability of resources.

Keywords Movement activity · Prior residency · Familiarity · Body mass · Shelter · *Silurus glanis*

Introduction

When animals compete for resources, their competitive abilities and behavioural strategies can be expressed as changes in movement activity. This activity has been positively correlated with higher growth rate, larger size and shorter development (Werner and Anholt 1993), as more active animals frequently encounter more food (Olsson et al. 2002; Brodin 2008; Liebgold and Dibble 2011). The levels of activity can be explained as predictable animal behaviour in response to changes in the environmental conditions (MacArthur and Pianka 1966) and/or expression of individual personality consistent with time and across conditions (Sih et al. 2003, 2004; Brodin 2008; Conrad et al. 2011).

The relationship between the activity of animals and environmental conditions shows that level of activity correlates with geographical (Liebgold and Dibble 2011), seasonal (Valdimarsson et al. 1997; Benito et al. 2015) and diurnal variability (Alanära et al. 2001; Brännäs 2008). The activity of animals is further influenced through mutual interactions, and the level of activity reflects the social status of an individual (Gómez-Laplaza and Morgan 2003). Large and dominant individuals are active at times suitable for food intake and when predation risk is low, whilst subdominant individuals are diurnally active (Metcalfe et al. 1999; David et al. 2007) and have larger home ranges (Nakano 1995). Groups containing familiar individuals are more active and better at resource exploitation and predation avoidance compared with unfamiliar conspecifics (Höjesjö et al. 1998; Griffiths et al. 2004; Liebgold and Dibble 2011). Territory holders compete for the territory more actively with intruders than neighbours (Bookmythe et al. 2010), and active individuals more effectively defend the territory than less active conspecifics (Sikkel and Kramer 2005).

✉ Ondřej Slavík
oslavik@af.czu.cz

¹ Department of Zoology and Fisheries, Faculty of Agrobiological, Food and Natural Resources, Czech University of Life Sciences Prague, Kamýcká 129, Prague 6, Suchbátka 165 21, Czech Republic

² Department of Mathematical and Statistical Sciences, University of Alberta, 116 St. and 85 Ave., Edmonton, AB T6G 2R3, Canada

Consistent individual differences in activity have been observed for individuals in ecological situations in which the behavioural syndromes are measured (Réale et al. 2007; Conrad et al. 2011; Sih et al. 2012), e.g. in brook charr *Salvelinus fontinalis* (M.), suggesting two alternative feeding strategies based on high activity and consistent behaviour and/or low activity and plastic behaviour (McLaughlin et al. 1992; Wilson and McLaughlin 2007; Farwel and McLaughlin 2009). Activity is often a substitutive demonstration of an individual status, e.g. stress. Øverli et al. (2005) described the consistent behavioural traits of individuals in a group of rainbow trout *Oncorhynchus mykiss* (W.) selected for low and high cortisol response to stress, showing faster acclimatisation to novel environments and decreasing activity in the presence of intruders with low cortisol responses. Animals show decreased activity in the stressful presence of familiar predators (Brodin and Johansson 2004; Brodin et al. 2006) and/or dominant conspecifics (Rudolf 2007). Furthermore, different levels of activity accompanied with stress can be expected for residents and intruders, reflecting differences in motivation that can be won and/or lost (Wolf et al. 2007); intruders are expected to be more active, as these individuals are bolder, more exploratory and/or aggressive (Cote et al. 2010, 2015).

The aim of the present study was to analyse the movement activity in European catfish *Silurus glanis* (L.) as a response to multiple stressful factors. Europe's largest freshwater predator (Copp et al. 2009) lives in groups (Boulétreau et al. 2011), shows variability in movement activity across seasons and diurnal rhythms (Slavík et al. 2007), and displays individual differences in energy consumption (Slavík and Horký 2012) which are higher when fish are exposed to stressful contact with unfamiliar individuals (Slavík et al. 2011).

We examined the effects of individual characteristics (body mass), and social (familiar vs. unfamiliar, resident vs. intruder) and environmental factors (resource availability) on the movement activity of juvenile European catfish. We assumed that (1) level of activity decreases with increasing body mass, because large individuals are typically dominant and thereby exposed to lower social stresses, (2) familiar individuals will be more active because familiarity often reduces stress and prolongs resource exploitation, (3) the activity of residents will be reduced in the presence of intruders according to stress-induced intrusion, and (4) shelters are highly valuable resources; hence, their availability results in decreased activity.

Materials and methods

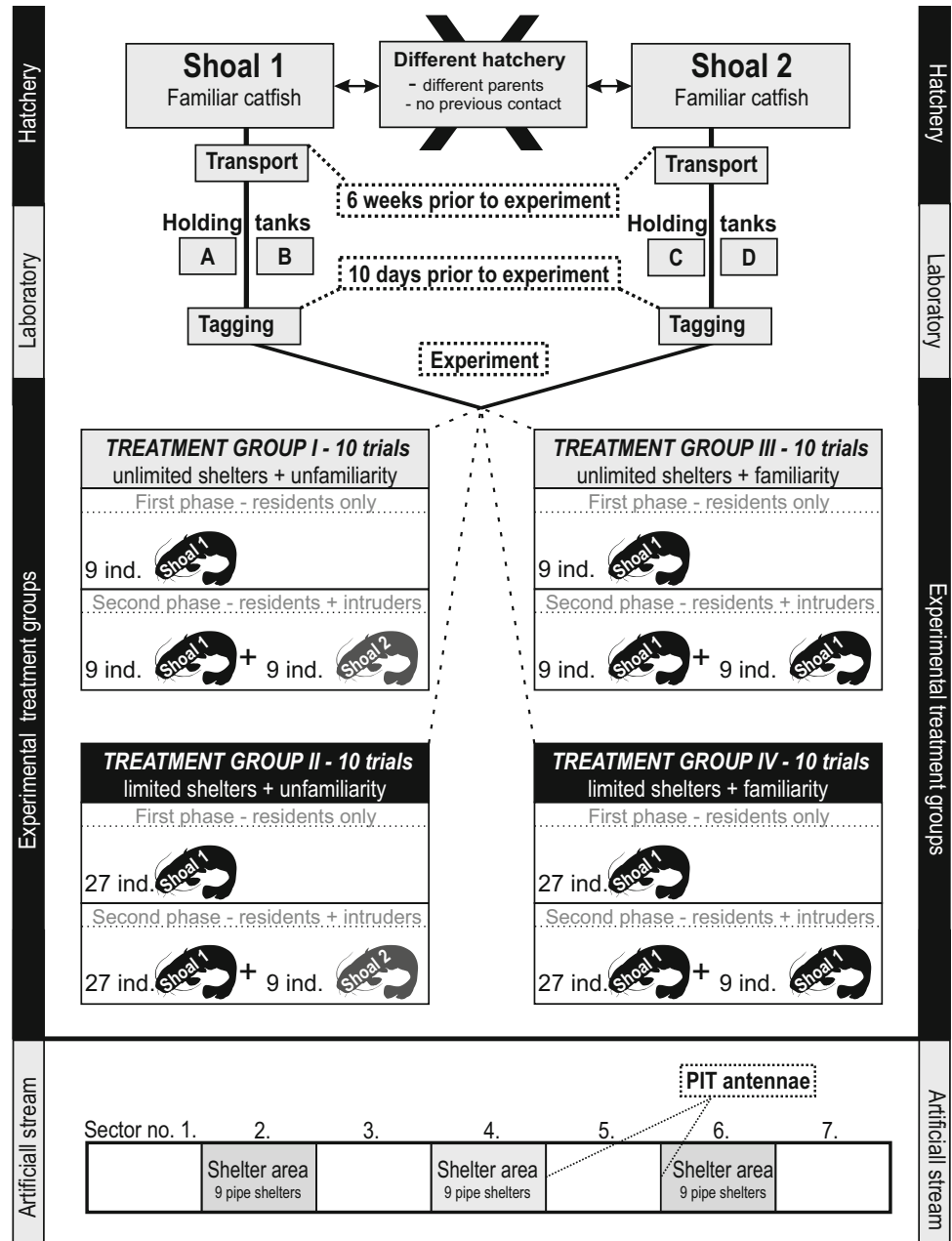
Study organisms used

The experiment was prepared and conducted according to valid legislative regulations (Law no. 246/1992, § 19, art. 1, letter c, filed with permit no. 26758/ENV/10-1092/620/10-PP6, registered by the Ministry of Environment of the Czech Republic). The fish used in the experiment were hatchery-reared juvenile catfish. Two shoals of European catfish unfamiliar with each other were obtained from different local fish suppliers (the first shoal from the Czech Fishery, Rybářství Třeboň, and the second shoal from the Rybářství Nové Hrady, Czech Republic) to ensure that the individuals belonging to the distinct shoals had never been in contact. A total of 1600 equal-sized fish (800 from each shoal) were transported from the hatcheries to the laboratory at the age of 4 months. The fish were transported under stable conditions in oxygenated tanks in an air-conditioned loading space, and the transport lasted approximately 2 h. No effect of the transport was found on the health or mortality of the fish.

The fish were subsequently kept in 4 separate holding tanks (1000 L each, initial density 3.8 kg m^{-3} , i.e., 400 individuals per tank) for 6 weeks prior to the start of the experiment. Each holding tank (A, B, C, and D; Fig. 1) contained individual shelters made of pipes (diameter 5 cm; length 20 cm) that were interconnected to form a honeycomb-like structure (for details, see Slavík et al. 2012). All individuals could inhabit their own shelter, as the number of shelters was higher than the number of fish. Hence, the frequency and intensity of aggressive behavior were low, and the experimenter did not need to intervene to prevent the escalation of interactions to injurious fighting. The fish were fed ad libitum on food pellets (Biomar Group, Denmark, <http://www.biomar.com>) distributed across the whole tank, providing free access to food to all individuals twice a day. The fish were kept under a natural photoperiod, maintaining the same regime to which they had become accustomed in the hatchery. The water was purified using biological filters with an integrated UV steriliser (Pressure-Flo 5000; Rolf C. Hagen, <http://www.lagunaponds.com>). The water temperature, dissolved oxygen and pH were controlled automatically (HOBO data logger; Onset Computer, Bourne, MA, USA).

The fish were tagged 10 days prior to the start of the experiment. The fish were anaesthetised with 2-phenoxyethanol (0.2 ml L^{-1} ; Merck KGaA, Germany) and then measured (standard length LS; mean 102 mm, range 84–128 mm) and weighed (mean body mass 9.6 g, range

Fig. 1 Experimental design and the artificial stream. Repetitions of trials involved the regular rotation of European catfish *Silurus glanis* (L.) from different holding tanks used as residents or intruders to minimise the ‘fish origin’ effect on the results



4–18 g). No size differences between the shoals of fish were detected (standard length $p > 0.87$, $n = 1600$; body mass $p > 0.71$, $n = 1600$). Passive integrated transponders (PIT; Trovan ID 100, 0.1 g in air, 12 mm 2.1 mm; EID Aalten, Aalten, Netherlands) were inserted into the abdominal cavity using a syringe. This method has been successfully used in behavioural experiments (Alanära et al. 2001). No adverse effects of PIT implantation or anesthesia were observed.

All experimental fish (1600 individuals) survived, and, after the experiment, fish were released under the control of Fish Management Authorities into the fish ponds with extensive production management.

Experimental design

The laboratory experiment was conducted between September 1 and December 6, 2011, in an oval artificial stream (see Slavík et al. 2011 for details). For the purpose of this experiment, only one-half of the stream was used (5.25 m long, 0.49 m wide and 0.32 m deep). This segment was divided into 7 subunits using 8 equidistant PIT antennae. A set of 9 interconnected pipe shelters was placed within 3 of the 7 subunits in an alternating pattern (a no-shelter unit followed by a shelter unit and so on; Fig. 1). Pipe shelters have been shown to be an important resource for juvenile catfish (Slavík et al. 2012). We simulated

natural stream conditions in terms of opportunities to swim freely around the shelters, even if they were occupied. We were unable to distinguish between a fish that was directly within a shelter and a fish that was simply near the shelter. Mesh was placed over the outer antennae to prevent fish from escaping from the observed stream segment. The antennae (inner area 0.49 m × 0.25 m) were designed to serve as frames to detect fish swimming through them. The antennae were connected to a recorder that stored the detection information (PIT tag code, date, time and antenna number) in its internal memory. The handling conditions were comparable to those in the holding tanks, and the water quality and flow were controlled by 2 Pressure-Flo 5000 units (60 L/min each). This arrangement generated a visible current (0.01 m s⁻¹) circulating through the stream; however, the fish did not have to swim continuously to maintain their positions. The average temperature, dissolved oxygen content, pH, and conductivity throughout the entire experiment were 19.51 ± SD 0.22 °C, 6.53 ± SD 0.18 mg L⁻¹, 7.24 ± SD 0.14, and 307 ± SD 5.4 μS cm⁻¹, respectively.

To classify ‘prior residency’, 2 phases that were identical for all treatment groups were defined. In the first phase, individuals considered to be ‘residents’ were released into the artificial stream and left there for the following 24 h (beginning at 0800 hours). The data from the first phase of the experiment were not used for further analyses. In the second phase, other individuals considered to be ‘intruders’ were introduced into the artificial stream. The second phase was the experimental phase and lasted for the following 24 h. Different ‘environmental factors’ were defined by the number of available shelters in the artificial stream (resource availability). In the unlimited shelter availability treatment group, there were 27 pipe shelters and 18 individuals (9 first phase + 9 second phase) in the artificial stream, whereas in the limited shelter availability treatment group, there were 27 pipe shelters and 36 individuals (27 first phase + 9 second phase). In each trial, the repetitions were performed by regularly rotating fish from different holding tanks as residents or intruders to minimise the ‘fish origin’ effect on the results. Individual fish were not used in the experiment repeatedly. In the familiar treatment group, the individuals added during the second phase of the experiment as intruders were familiar with the residents (i.e., they were all from the same shoal and holding tank); in the unfamiliar treatment group, they were not. Combining the different features led to 4 experimental treatment groups (Fig. 1), each of which was repeated ten times. Forty individual trial repetitions under the different ecological and familiarity conditions were conducted, resulting in the use of 1080 catfish during the entire experiment. In total, we logged over 3 million recordings of catfish movements. Subsequently, the data

were reduced to a dataset containing 1080 data points (one activity value per each individual fish per 24 h, see below). These data were used in the final statistical analyses.

Statistical analyses

Statistical analyses were performed using R software v.2.11.1 (R Development Core Team, Vienna, 2010). First, the PIT transmitters were used to obtain a raw data sample consisting of more than 3 million separate measurements, each of which included the ID number of the antenna, the ID number of the fish passing through that antenna, and the time. Additional explanatory variables were used to document necessary information on each trial setting (trial repetition, resource availability, familiarity, and prior residency), a fish-specific characteristic (body mass), and certain characteristics based on the individual and the opposite group (for example, the ratio between the individual’s body mass and the mean body mass of individuals from the opposite group). These data introduced unbalanced and irregular longitudinal time profiles for every individual catfish. These profiles were used to compute a total number of antennae passes per each minute based on a one-minute grid. These values (i.e., 1440 values within 24 h) were averaged for each individual to obtain the ‘individual movement activity’ value, one per subject. The individual movement activity was used as a dependent variable. The grid averaging step excludes the dependence occurring within repeated measurements. Additionally, the 1-min grid was chosen as optimal to stabilise the variance and to normalise the data.

Several different modelling approaches were tested. The GLM regression modelling framework was then applied, and a model for Gaussian data with a logarithmic link was proposed. We used the logarithmic link rather than transforming the response using logarithms to preserve the original interpretation of the activity. The final model was selected from other competing models (all two way interactions were tested) always according to a better Akaike’s Information Criterion (AIC) value considering the model with lower AIC to fit the data better (Burnham and Anderson 1998). The AIC of the final model was 27.5 and the range of the ΔAIC comparing it’s fit with other models was 7.3–58.9.

The final model had the following form:

$$\log[\text{EIMA}] = \mu + \Delta_S + \phi_F + \alpha_N + \omega_1 \times \log[\text{BodyMass}] + \omega_2 \times \text{grMeanBodyMass} + [\Delta \times \alpha]_{S \wedge N}$$

where EIMA is an Expected Individual Movement Activity value predicted by the model. The parameter μ is an intercept term for the reference category (unlimited shelters, resident fish and unfamiliarity). Additional intercept

corrections for non-reference categories are introduced via, Δ_S , ϕ_F and α_N . The model also introduces 2 slope parameters, ω_1 and ω_2 , to express a dependence on the logarithm of the individual’s body mass ‘log[BodyMass]’ and the ratio between the individual’s body mass and the mean body mass of the individuals in the opposite group ‘grMeanBodyMass’. The interaction term $[\Delta \times \alpha]_{S \wedge N}$ between shelter availability and prior residency corrects for the intercept term if the model refers to an intruder under the limited-shelter treatment group. The parameter estimates, together with the standard error estimates and the appropriate significance tests (classical *t* test *p* values common for the GLM framework), are given in Table 1. All other explanatory variables considered by the experiment but not listed in the table (for example, a factor covariate for trial repetitions) that were tested in the model building stage as non-significant or did not improve model fit according to AIC were removed from the table.

Results

The expected individual catfish movement activity was dependent on familiarity, prior residency, and body mass as well as on the resource availability (Table 1; Fig. 2). Unfamiliar fish and intruders displayed a higher level of movement activity than familiar conspecifics and residents, i.e. familiarity and prior residency decreased the movement activity of the juvenile catfish. Movement activity generally increased under the resource availability of unlimited shelters; however, the movement activity of residents and intruders differed. The model predicted a slightly lower level of movement activity in residents than in intruders. Moreover, if the shelters were limited, this difference increased significantly to a value 1.5 times greater than that associated with unlimited shelters (Table 1; Fig. 2), i.e. *n* intruders further increased their activity compared with residents if the shelters were limited. Nevertheless, the movement activity of the fish was also significantly

influenced by body mass and the ratio between an individual’s body mass and the mean body mass of the fish from the opposite group (see also Fig. 2). If a catfish was substantially larger than the mean body mass of the opposite group, its movement activity decreased to the minimum irrespective of the ecological conditions, familiarity, and prior residency. Conversely, we observed that the smaller an individual was relative to the mean body mass of the opposite group, the higher the influence of the treatment group was on its activity.

Discussion

In the present study, laboratory observations were used to demonstrate differences in the movement activity of juvenile catfish facing stressful social and environmental conditions. The results showed that when a catfish is substantially larger than the mean body mass of the opposite group, the movement activity of the catfish is decreased to the minimum, irrespective of the social and environmental conditions. We speculated that the social and environmental factors were weak, facilitating the manifestation of individual differences with respect to the behavioural syndromes theory (Sih et al. 2003; Carter et al. 2013). Considering that a low level of movement activity represents success in competition for shelters, lower movement activity with higher body mass supports this assumption. Activity was associated with boldness (Brodin 2008; Conrad et al. 2011), and considering the fact that bold individuals grow faster (Koolhaas et al. 1999), are in better condition (Brown et al. 2007), and reach higher social status (Dahlbom et al. 2011), large catfish can be suggested as bold individuals in the present study. In contrast, smaller conspecifics with a higher level of activity might represent reactive individuals that are more sensitive to stress (Øverli et al. 2005). These results indicate that high body mass, presumably interconnected with boldness and dominance, suppresses reactions to external factors and affect the

Table 1 Parameter estimates with corresponding standard errors and *p* values for the model

Parameter description	Non-reference category	Model notation	Parameter estimate	Standard error	<i>p</i> value of the test
Intercept	–	μ	–2.3313	1.3267	0.0792
Shelter availability	Limited shelters	Δ_S	–0.6339	0.0946	0.35 e ^{–10}
Residency	No	α_N	0.6814	0.0755	<e ^{–16}
Social familiarity	Familiar	ϕ_F	–0.1614	0.0481	0.0008
Log[body mass]	–	ω_1	0.9394	0.2945	0.0015
grMeanBodyMass	–	ω_2	–1.2788	0.2961	1.73 e ^{–5E}
Shelter availability × residency	Limited shelters and intruders	$[\Delta \times \alpha]_{S \wedge N}$	0.4115	0.1152	0.0004

Parameter estimates are given by maximum likelihood estimation and *p* values are obtained using a classical *t* test common for GLM regression framework

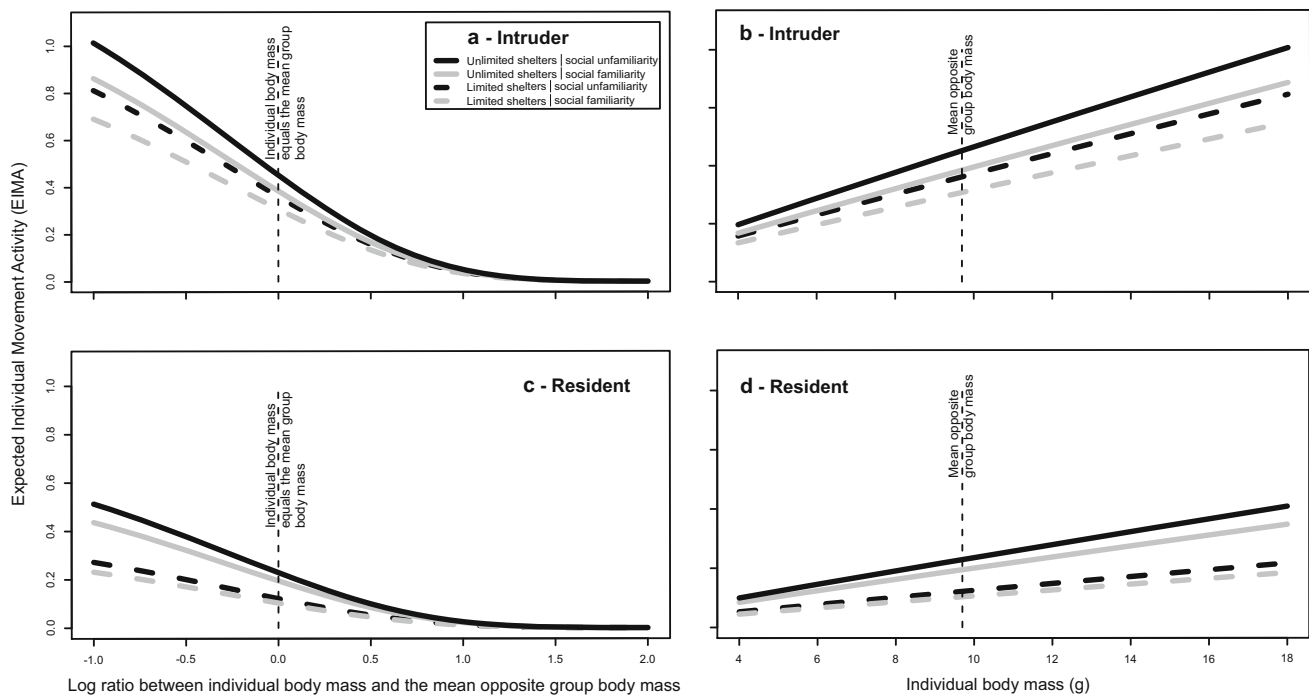


Fig. 2 Expected individual movement activity (EIMA) values plotted against the logarithm of the ratio between individual body mass and the mean opposite group body mass (a) and individual body mass (b) for intruders and, analogously, for residents (c, d). Four different treatment groups are distinguished (unlimited shelters, unfamiliarity

black solid line; unlimited shelters, familiarity grey solid line; limited shelters, unfamiliarity black dashed line; limited shelters, familiarity grey dashed line). A vertical line is plotted for a ratio equal to zero. This value indicates that the individual's body mass equals the mean body mass of the opposite group

results of competition. This effect is strong, particularly in combination with the motivation to defend a valuable territory (Stokkebo and Hardy 2000; Kokko et al. 2006), represented by shelter availability in this case.

Despite information that familiarity typically increases movement activity (Liebgold and Dibble 2011), the results showed that familiarity predicted low movement activity. This finding corresponds with previous studies showing that familiar fish more effectively exploit resources (Höjesjö et al. 1998; Griffiths et al. 2004), because the recognition of social partners facilitates the avoidance of ineffective time and energy use, injury, and/or predation risk (Giraldeau and Caraco 2000; Griffiths and Ward 2011). Correspondingly, the familiarity of juvenile catfish has been associated with low movement activity resulting from the advantageous characteristic of the recognition of social partners in a group. Furthermore, the results showed that the asymmetric relationship between resident and intruder was associated with differences in movement activity, indicating a lower level of movement activity of residents with no respect to changes in resource availability during the experiment, expressed as shelter limitation. Thus, resource limitation plays a fundamental role in processes in natural systems (Murdoch 1994; Turchin 1999), and its direct influence is associated with a critical degree of resource saturation (Osenberg et al. 2002). Shelters also

represent highly contested resources (Sultana et al. 2013). Ford and Swearer (2013) showed that shelter limitation was the best predictor of mortality in coral reef fish. In the present study, we examined the effect of shelter limitation as a saturated critical resource of the activity of catfish. Unlimited shelter availability induced higher movement activity in juvenile catfish. Note that experimental animals typically display an initially intensive response to a novel environment, with subsequent habituation and a gradual decline in activity (Gómez-Laplaza and Morgan 2003). In contrast, the tendency of the intruders to further significantly increase activity compared with residents when the per capita availability of shelters is low suggests that intruders also show increased activity resulting from unfavourable environmental conditions. As reported, residents are predicted to prevail in defence of highly valuable territory (Stokkebo and Hardy 2000; Humphries et al. 2006; Gherardi 2006; Takeuchi 2006). Because per capita shelter availability was the only variable environmental condition in the present experiment, we speculated that residents succeed in defence of valuable territories, i.e. the residents are more invested in shelter defence, whereas intruders are more invested in searching for shelter. This investment by the intruders has been associated with higher movement activity. The lower movement activity of residents can also be considered in terms of differences in

status in the social hierarchy. For example, Rosell et al. (2008) reported the over-domination of resident root vole *Microtus oeconomus* males in pairwise interactions. In the present study, we observed asymmetry in the movement activity of residents and intruders: the residents showed a lower level of activity, which might represent successful territorial defence. Although the outcome of competition for resources is affected by the complexities of the various factors with less apparent structure (Kokko et al. 2006), the results indicated that competition is accompanied by a lower level of movement activity by residents than by intruders.

Thus, the results presented here are consistent with previous studies describing the relationship between social experience and animal behaviour. Correspondingly, as familiarity is beneficial for resource exploitation, we recorded a lower movement activity of familiar catfish needed for shelter occupancy. Furthermore, the asymmetric relationship between residents and intruders was accompanied by differences in movement activity, with a lower level of movement activity shown by the residents. These findings are consistent with theories predicting the success of residents defending their territories when using the advantage of prior residency and higher motivation for the defence of valuable resources. These social (familiarity/unfamiliarity, resident/intruder) and environmental factors (resources availability) have been suggested as weak, demonstrating individual differences represented as body mass. High individual body mass predicted low movement activity, irrespective of the social and environmental conditions. Thus, the results of the present study highlight a role for individual characteristics in shaping the behavioural responses of catfish to external factors.

Acknowledgments This work was supported by the Czech Science Foundation (No. 13-05872S). The authors sincerely thank anonymous referees for critical evaluation and valuable comments on the manuscript. In addition, the authors wish to thank M. Fort for his assistance during the experimental period, and A. Slavikova for the help with earlier versions of the manuscript.

References

- Alanärä A, Burns MD, Metcalfe NB (2001) Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. *J Anim Ecol* 70:980–986
- Benito J, Benejam L, Zamora L, García-Berthou E (2015) Diel cycle and effects of water flow on activity and use of depth by common carp. *Trans Am Fish Soc* 144:491–501. doi:10.1080/00028487.2015.1017656
- Booksmythe I, Jennions MD, Backwell PRY (2010) Investigating the ‘dear enemy’ phenomenon in the territory defence of the fiddler crab, *Uca mjoebergi*. *Anim Behav* 79:419–423
- Boulétreau S, Cucherousset J, Villéger S, Masson R, Santoul F (2011) Colossal aggregations of giant alien freshwater fish as a potential biogeochemical hotspot. *PLoS ONE* 6:e25732. doi:10.1371/journal.pone.0025732
- Brännäs E (2008) Temporal resource partitioning varies with individual competitive ability: a test with Arctic charr *Salvenius alpinus* visiting a feeding site from a refuge. *J Fish Biol* 73:524–535. doi:10.1111/j.1095-8649.200801941.x
- Brodin T (2008) Behavioral syndrome over the boundaries of life—carryovers from larvae to adult damselfly. *Behav Ecol* 20:30–37. doi:10.1093/beheco/arn111
- Brodin T, Johansson F (2004) Conflicting selection pressures on the growth/predation risk trade-off in a damselfly. *Ecology* 85:2927–2932
- Brodin T, Mikolajewski DJ, Johansson F (2006) Behavioral and life history effects of predator diet cues during ontogeny in damselfly larvae. *Oecologia* 148:162–169
- Brown C, Jones F, Braithwaite VA (2007) Correlation between boldness and body mass in natural populations of the poeciliid *Brachyrhaphis episcopi*. *J Fish Biol* 71:1590–1601
- Burnham KP, Anderson DR (1998) Model selection and inference: a practical information—theoretic approach. Springer, New York
- Carter AJ, Feeney WE, Marshall HH, Cowlishaw G, Heinsohn R (2013) Animal personality: what are behavioural ecologists measuring? *Biol Rev* 88:465–475
- Conrad JL, Weinersmith KL, Brodin T, Saltz JB, Sih A (2011) Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *J Fish Biol* 78:395–435
- Copp GH, Britton JR, Cucherousset J, García-Berthou E, Kirk R, Peeler E, Stakénas S (2009) Voracious invader or benign feline? A review of the environmental biology of European catfish *Silurus glanis* in its native and introduced ranges. *Fish Fish* 10:252–282. doi:10.1111/j.1467-2979.2008.00321.x
- Cote J, Clobert J, Brodin T, Fogarty S, Sih A (2010) Personality-dependent dispersal: characterisation, ontogeny and consequences for spatially structured populations. *Philos Trans R Soc Lond B* 365:4065–4076. doi:10.1098/rstb.2010.0176
- Cote J, Fogarty S, Tymen B, Sih A, Brodin T (2015) Personality-dependent dispersal cancelled under predation risk. *Proc R Soc Lond B* 280:20132349. doi:10.1098/rspb.2013.2349
- Dahlbom SJ, Lagman D, Lundstedt-Enkel K, Sundström LF, Winberg S (2011) Boldness predicts social status in zebrafish (*Danio rerio*). *PLoS ONE* 6(8):e23565. doi:10.1371/journal.pone.0023565
- David BO, Closs GP, Crow SK, Hansen EA (2007) Is diel activity determined by social rank in a drift-feeding stream fish dominance hierarchy. *Anim Behav* 74:259–263. doi:10.1016/j.anbehav.2006.08.015
- Farwel M, McLaughlin RL (2009) Alternative foraging tactics and risk taking in brook charr (*Salvenius fontinalis*). *Behav Ecol* 20:913–921. doi:10.1093/beheco/arp059
- Ford JR, Swearer SE (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
- Gherardi F (2006) Fighting behavior in hermit crabs: the combined effect of resource-holding potential and resource value in *Pagurus longicarpus*. *Behav Ecol Sociobiol* 59:500–510
- Giraldeau L-A, Caraco T (2000) Social foraging theory. Monographs in behavior and ecology. Princeton University Press, Princeton
- Gómez-Laplaza LM, Morgan E (2003) The influence of social rank in the angelfish, *Pterophyllum scalare*, on locomotor and feeding activities in a novel environment. *Lab Anim* 37:108–120
- Griffiths SW, Ward A (2011) Social recognition of conspecifics. In: Brown C, Laland K, Krause J (eds) Fish cognition and behavior, 2nd edn. Blackwell, Oxford, pp 186–216
- Griffiths SW, Brodmark S, Höjesjö J, Jonsson JI (2004) Coping with divided attention: the advantage of familiarity. *Proc R Soc Lond B* 271:695–699

- Höjesjö J, Jonsson JI, Petersson E, Järvi T (1998) The importance of being familiar: individual recognition and social behavior in sea trout (*Salmo trutta*). *Behav Ecol* 9:445–451
- Humphries EL, Hebblethwaite AJ, Batchelor TP, Hardy IC (2006) The importance of valuing resources: host weight and contender age as determinants of parasitoid wasp contest outcomes. *Anim Behav* 72:891–898
- Kokko H, López-Sepulcre A, Morell LJ (2006) From hawks and doves to self-consistent games of territorial behavior. *Am Nat* 167:901–912
- Koolhaas JM, Korte SM, De Boer SF, van der Vegt BJ, van Reenen CG, Hopster H, de Jong IC, Ruis MAW, Blokuis HJ (1999) Coping styles in animals: current status in behavior and stress-physiology. *Neurosci Biobehav R* 23:925–935
- Liebgold EB, Dibble CJ (2011) Better the devil you know: familiarity affects foraging activity of red-backed salamanders, *Plethodon cinereus*. *Anim Behav* 82:1059–1066
- MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. *Am Nat* 100:603–609
- McLaughlin RL, Grant JWA, Kramer DL (1992) Individual variation and alternative patterns of foraging movements in recently-emerged brook charr, *Salvelinus fontinalis*. *Behaviour* 120:286–301
- Metcalfe NB, Fraser NHC, Burns MD (1999) Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *J Anim Ecol* 68:371–381
- Murdoch WW (1994) Population regulation in theory and practice. *Ecology* 75:271–287
- Nakano S (1995) Individual differences in resource use, growth and emigration under influence of a dominance hierarchy in fluvial red-spotted masu salmon in a natural habitat. *J Anim Ecol* 64:75–84
- Olsson O, Bruun M, Smith H (2002) Starling foraging success in relation to agricultural land-use. *Ecography* 25:363–371
- Osenberg CW, St Mary CM, Schmitt RJ, Holbrook SJ, Chesson P, Byrne B (2002) Rethinking ecological inference: density dependence in reef fishes. *Ecol Lett* 5:715–721
- Øverli Ø, Winberg S, Pottinger TG (2005) Behavioral and neuroendocrine correlates of selection for stress responsiveness in rainbow trout—a review. *Integ Compar Biol* 45:463–474. doi:10.1093/icb/45.3.463
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal temperament within ecology and evolution. *Biol Rev* 82:291–318
- Rosell F, Gundersen G, Le Galliard J-F (2008) Territory ownership and familiarity status affect how much male root voles (*Microtus oeconomus*) invest in territory defence. *Behav Ecol Sociobiol* 62:1559–1568
- Rudolf V (2007) Consequences of stage-structured predators: cannibalism, behavioral effects, and trophic cascades. *Ecology* 88:2991–3003
- Sih A, Kats LB, Maurer EF (2003) Behavioural correlations across situations and the evolution of antipredator behavior in a sunfish–salamandre system. *Anim Behav* 65:29–44
- Sih A, Bell A, Johnson JC (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol* 19:372–378
- Sih A, Cote J, Evans M, Fogarty S, Pruitt J (2012) Ecological implications of behavioural syndromes. *Ecol Lett* 15:278–289. doi:10.1111/j.1461-0248.2011.01731.x
- Sikkel PC, Kramer DL (2005) Territory revisits reduce intrusion during spawning trips by female yellowtail damselfish, *Microspathodon chrysurus*. *Anim Behav* 71:71–78. doi:10.1016/j.anbehav.2005.03.028
- Slavík O, Horký P (2012) Diel dualism in the energy consumption of the European catfish *Silurus glanis*. *J Fish Biol* 81:2223–2234
- Slavík O, Horký P, Bartoš L, Kolářová J, Randák T (2007) Diurnal and seasonal behaviour of adult and juvenile European catfish as determined by radio-telemetry in the River Berounka, Czech Republic. *J Fish Biol* 71:104–114. doi:10.1111/j.1095-8649.2007.01471.x
- Slavík O, Pešta M, Horký P (2011) Effect of grading on energy consumption in European catfish *Silurus glanis*. *Aquaculture* 313:73–78
- Slavík O, Maciak M, Horký P (2012) Shelter use of familiar and unfamiliar groups of juvenile European catfish *Silurus glanis*. *Appl Anim Behav Sci* 142:116–123
- Stokkebo S, Hardy ICW (2000) The importance of being gravid: egg load and contest outcome in a parasitoid wasp. *Anim Behav* 47:339–350
- Sultana Z, Takaoka J, Koga T (2013) Resource value differentially affects fighting success between reproductive and non-reproductive seasons. *J Ethol* 31:203–209
- Takeuchi T (2006) Matter of size or matter of residency experience? Territorial contest in a Green hairstreak, *Chrysoyephyrus smaragdinus* (Lepidoptera: Lycaenidae). *Ethology* 112:293–299
- Turchin P (1999) Population regulation: a synthetic view. *Oikos* 84:153–159
- Valdimarsson SK, Metcalfe NB, Thorpe JE, Huntingford FA (1997) Seasonal changes in sheltering: effects of light and temperature on diel activity in juvenile salmon. *Anim Behav* 54:1405–1412
- Werner EE, Anholt BR (1993) Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *Am Nat* 142:242–272
- Wilson ADM, McLaughlin RL (2007) Behavioral syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations. *Anim Behav* 74:689–698
- Wolf M, van Doorn S, Leimar O, Weissing FJ (2007) Life-history trade-offs favour the evolution of animal personalities. *Nature* 447:581–585