1   **Night reveals individuality in a shoaling fish**

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ABSTRACT

Many animals rely heavily on visual cues from their environment, and therefore show circadian rhythmicity in their behavioral activities. In group-living animals, individuals' activity rhythms must be synchronized not only with diel light-dark cycle but also with other group members. Increasing evidence has recently shown that circadian behaviors of animals are consistent within individuals and different between individuals, but the sources and consistency of diel activity variation in social context are less known. Using radio frequency identification (RFID) technology, we recorded individual moving activity of the Eurasian perch (*Perca fluviatilis*) in randomly formed groups through 10 full diel cycles in seminatural environment. We found diel changes in trait variability and repeatability estimates both within and between the groups: individual differences in activity were more repeatable in nighttime whereas group differences were more repeatable in daytime. The results suggest that collective group behavior in daylight obscures the expression of individuality, whereas the weak group effects in nighttime reveals a substantially wider continuum of individually consistent activity types. Our findings imply that 1) studying activity variation only on diurnal basis may underestimate the total activity variation among social individuals and may thus bias the repeatability estimates, and 2) accounting for diel variation in social effects may be essential for detecting ecologically realistic behavioral variation within and between animal groups. To conclude, this study highlights the complex interactions between circadian activity rhythms, individual behavioral differences, and group dynamics, and thereby provides new insights for understanding overall behavioral diversity in social animals.

Key words: circadian behavior, group repeatability, locomotor activity, nocturnal activity, social synchrony

INTRODUCTION

Many behavioral activities of animals are displayed in a rhythmic manner, and those related to circadian periodicity (~24 h dark-light cycle) have recently become an emerging theme in animal behavior and personality research. The biological rhythms of animals are typically adjusted by environmental cues, particularly by photoperiod entraining behavioral activities with local conditions, or more profoundly by circadian clock -mediated intrinsic physiological processes (Bell-Pedersen et al. 2005; Yerushalmi and Green 2009; Prokkola and Nikinmaa 2018). Growing evidence across animal taxa suggests that behaviors mediated by an individual's circadian rhythm are consistently different between individuals (Stuber et al. 2015; Refinetti et al. 2016; Alós et al. 2017). Diel activity patterns have thus been merged into the conceptual framework of animal personality (*i.e.* a correlated suite of individually *consistent* behaviors; Réale et al. 2007; Carere and Maestripieri 2013). However, the current evidence is mostly limited to reporting the existence of behavioral chronotypes, *i.e.* individual differences in traits associated with sleep/rest onset, duration and termination (Randler 2014; Stuber et al. 2014; Alós et al. 2017). A fundamental question that has remained unstudied is how the light rhythm shapes the between-individual variation in behavioral activity, and whether its consistency itself shows diel rhythmicity.

Many animals live in groups where the social environment induces diverse effects on individuals' activity patterns. The benefits of group-living include safety in numbers against enemies, and support in effective foraging (Ward and Webster 2016). However, gaining those benefits requires that the individuals' activity rhythms be synchronized among group members. While the local light rhythm typically predicts seasonal and diel changes in the activity of predators, parasites or prey, the social encounters and visual or olfactory cues from conspecifics are important stimuli that synchronize the activity rhythms amongst individuals (Davidson and Menaker 2003; Mistlberger and Skene 2004; Favreau et al. 2009). Social synchrony associates closely with behavioral conformity, when individuals tend to compromise between their own behavioral individuality and collective

group behavior (Sumpter 2010; Rands 2011). However, inter-individual variation in circadian behaviors are likely present also in social groups, and might relate to *e.g.* conflict reduction within hierarchical groups (Alanärä et al. 2001; Réale and Dingemanse 2010). Yet unexplored questions are whether and how living in a group affects the consistency of individuals' diel activity patterns.

The eco-evolutionary importance of intraspecific variation in a behavioral trait is usually based on its repeatability estimate, which sets the upper limit for its heritability and qualifies as a standard measure to statistically assess the consistency of different behavioral types (Bell et al. 2009). Although several studies have shown inter-individual variation in circadian behaviors, only very few have reported their repeatability (Alós et al. 2017; see also Niemelä and Dingemanse 2018). The repeatability estimates are context-dependent and affected by environmental conditions, and also by the temporal scale or the setup of a study (Bell et al. 2009, Killen et al. 2016). For example, to assess ecologically realistic repeatability for behavioral activity may require several days of monitoring until the animals habituate to the experimental conditions (Härkönen et al. 2014). In social animals, the amount of detectable between-individual variation may either decrease due to behavioral conformity (Magnhagen 2012) or increase due to conflict reduction (Hemelrijk and Wantia 2005), but also the groups themselves may differ consistently in behavior (Cronin 2015; Jolles et al. 2018). Thus, the validity and ecological relevance of commonly used individual behavioral tests for social animals have been questioned (Réale and Dingemanse 2010; Magnhagen 2012). For example, social animals studied in isolation may show arrhythmic and more variable circadian cycles than they would do in groups (Yerushalmi and Green 2009). Altogether, studying biological rhythms in social animals requires collecting data with frequent sampling around the clock, over many consecutive 24h cycles, and from individual animals in a social setting (*e.g.* Mistlberger and Skene 2004).

The fundamental aim of this study was to gain better understanding of the sources and consistency of circadian activity variation in social animals. We used a predominantly day-active and naturally shoaling freshwater fish, the Eurasian perch (*Perca fluviatilis*) as a model species. We

97   monitored the moving activity of 320 individuals in eight randomly formed groups over ten

98   consecutive 24h diel cycles. We recorded individual movements in large semi-natural enclosures

99   under natural light rhythm with a state-of-the-art radio frequency identification (RFID) system. Using

100 the high-precision dataset, we extracted activity traits that would capture the daily total variation in

101 activity among the study fish, and specifically under contrasting light conditions (diurnal vs.

102 nocturnal activity). We applied linear mixed models to quantify trait variances and adjusted

103 repeatability estimates at individual- and group-level. Our leading hypothesis was that the light

104 rhythm shapes the proportion of total variance attributable to between-individual differences through

105 the strength of group effects. First, we tested if the detectable between-individual activity variation

106 differs under conditions typically presuming either social synchrony or asynchrony (*i.e.* light vs. dark,

107 respectively). Based on the assumption on stronger behavioral conformity in daylight than in

108 darkness, we predicted lower between-individual than between-group variability in diurnal activity

109 (see Magnhagen 2012), and that the overall variability in activity in darkness is lower than in daylight.

110 Second, we tested if the groups express more repeatable differences in diurnal than nocturnal activity.

111 We further assumed that the high social synchrony in daylight leaves proportionally less variance to

112 be explained by between-individual differences in diurnal activity than in nocturnal activity.

113

114 **MATERIAL AND METHODS**

115 *Model species*

116 The Eurasian perch is a native freshwater fish in the Northern Hemisphere and has been widely used

117 as model species in behavioral ecology. The perch is a highly social fish that forms relatively large

118 shoals, particularly at a young age. When shoaling, the behaviors of individual perch are influenced

119 by social environment, but individual differences persist regardless of high social coordination

120 (Magnhagen 2012). However, the general movements of perch are driven particularly by feeding

121 motivation influenced by light and temperature but also by predator avoidance and prey abundance

122 (Heermann et al. 2013; Nakayama et al. 2018). The piscivorous perch are visual predators and thus

123 they usually show higher activity in daylight and crepuscular conditions than in darkness (Ylönen et

124 al. 2007). In darkness the shoals break up, and perch are observed to rest on the bottom (Imbrock et

125 al. 1996). However, the typical circadian activity pattern varies across seasons. It is less rhythmic

126 during long-day conditions in the summer, and elevated levels of nocturnal activity have been found

127 in summer and early fall (Jacobsen et al. 2002; Nakayama et al. 2018).

128

129 *Experimental setup*

130 We performed the study at Kainuu Fisheries Research Station (KFRS, www.kfrs.fi, location 64°24'

131 N, 27°50' E) of the Natural Resources Institute Finland. Our study fish comprised F_1 progeny of wild

132 Eurasian perch (n = 300; 100–500 g in body weight) originating from Lake Oulujärvi. We assumed

133 the potential truncation of behavioral variation due to the trapping of the parent fish irrelevant for this

134 study. The offspring produced at KFRS in May 2012 were raised with natural food resources in a

135 seminatural forest pond (6.5 ha) through two growth seasons 2012–2013. There were no other

136 piscivorous fish species in the pond, but in addition to potential cannibalism, the juveniles were

137 naturally exposed to terrestrial predators (*e.g.* birds, mustelids). In September 2013, the pond was

138 drained and ca. 17 000 perch (a mean weight of 10 g) were harvested and habituated to flow-through

139 hatchery conditions (details in Härkönen et al. 2017). The fish were maintained under a natural

140 temperature regime and artificial lighting following natural changes in photoperiod. The fish were

141 fed during the daytime with minced prey fish (smelt *Osmerus eperlanus*) and the diet was

142 supplemented with commercial dry feed pellets (VERONESI VITA 1.0 / 1.5 / CIRCUIT 1.7,

143 Raisioagro, Finland) *ad libitum*.

144 In September 2015, 320 perch (at age 3+) were randomly dip-netted from the holding

145 tanks and anesthetized with a standard solution of benzocaine (40 mg l^{-1}) for processing. The fish

146 were measured (1 mm), weighed (0.1 g), and a 12.0 mm half-duplex passive integrated transponder

147 (HDX PIT) tag (OregonRFID Inc. USA) was implanted under the skin next to the dorsal fin. The

148 mean fish size (SD, range) was 165.5 mm (20.4 mm, 125.0 – 229.0 mm) and 50.0 g (22.5 g, 18.6 –

149 139.9 g). After processing, the fish were observed in large tanks (15 m^2) for a week to ensure full

150 recovery from the tagging.

151   To quantify components of behavioral variation under natural light rhythm, we

152 performed a 10-day experiment on 2 – 12 October 2015. We assigned the perch randomly to eight

153 groups of 40 individuals and released the fish in seminatural outdoor enclosures (see Fig. 1 for

154 details). The body length did not vary significantly between the replicate groups (One-way ANOVA:

155 $F_{7, 319} = 0.890$, $P = 0.515$). We recorded the movements of PIT-tagged individuals continuously with

156 RFID system recording the antenna bypasses 9 times per second (see details in Vainikka et al. 2012).

157 In the study site, the photoperiod varies greatly according to the season potentially affecting the perch

158 activity pattern. We performed the experiment right after the autumnal equinox, when the day and

159 night periods are equal in length: at the onset of the experiment, sunrise was at 7:19 and sunset at

160 18:36, and at the end of the experiment, the respective times were 7:49 and 18:00.

161   The water running in the enclosures came from the adjacent Lake Kivesjärvi. It is a

162 humic, mesotrophic lake with water color (CNS, mean ± SD) of 103.2 ± 41.3 mg/l Pt and turbidity

163 of 1.1 ± 0.4 FNU (mean values 2006-2016; Surface waters – water quality database by the Finnish

164 Environment Institute and the Centre for Economic Development, Transport and the Environment).

165 The temperature of the incoming water varied naturally regarding the seasonal conditions (the range

166 of daily measurements 6.9°C – 10.6°C). The gravel bottom and incoming water provided natural prey

167 items during the experiment, including plankton, benthos and occasionally small-sized prey fish

168 (smelt, roach *Rutilus rutilus* and ruffe *Gymnocephalus cernua*). The incoming water from the lake

169 may have also transferred highly diluted olfactory cues of common day- and night-active predators

170 (pike *Esox lucius* and burbot *Lota lota,* respectively; Ylönen et al. 2007).

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Data analyses

The high precision movement data were recorded automatically using computers connected to RFID antennae to detect ecologically realistic behavioral variation without human disturbance or observer bias. All the signal detections were first processed using PIT Data software package (http://pitdata.net/) to calculate section crosses (see Fig. 1) for each individual per hour (*i.e.* for 243 hours). An individual was removed from further analyses if no signal detection was recorded ($n = 3$) or the tag stopped operating ($n = 4$) during the experiment. To produce applicable behavioral variables for further analyses, the one-hour resolution data were processed using custom algorithms included in AV Bio-Statistics software (developed by A.V.). We calculated three activity scores describing general moving activity within different temporal slots. An individually repeated measure of *total activity* was calculated as the mean of hourly antenna bypasses within each 24h cycle. The data were processed accordingly to separate *diurnal activity* and *nocturnal activity* based on the closest full hour of sunset and sunrise (see above). The obtained activity scores do not provide any information on individual behavior between the signal detections (*e.g.* resting, feeding or sheltering). To obtain a variable that would capture the differences in individual activity types among individuals, we calculated a *circadian score* as the proportion of an individual's diurnal activity to the total activity within each full diel cycle.

We analyzed the effect of fish size on overall variation in each activity variable (*i.e.* on 10 repeated measures for ln-transformed *total activity*, *diurnal activity*, *nocturnal activity* and *circadian score*) by fitting linear mixed-effects models (GLMM) in SPSS 22.0 for Windows (IBM Corp. Released 2014). To account for repeated measures of individuals, subject identity was entered as a random effect (incl. random intercept). We added a random group-effect, which not only represented the differences between randomly created social groups but also included uncontrolled differences between the seminatural enclosures (*e.g.* food availability and distribution of sheltering structures, among other "tank effects"). The influence of total body length and weight were tested

197   separately with mean-standardized values to facilitate meaningful comparison of the models. Owing

198   to lower AIC, we present only the models with the body length.

199   We fitted LMM-based models to the data to obtain size-adjusted repeatability estimates

200   (R_{adj}) for temporal consistency of individual- and group-level variation in the behavioral variables

201   using the package 'rptR' in *R* version 3.5.1 (R Core Team 2017; Stoffel et al. 2017). In a typical

202   experimental setup for estimating individual repeatability, the behavioral variation among study

203   subjects is assessed as the variance attributable to between individual differences compared to the

204   total variation including also the within-individual variance (Dingemanse and Dochtermann

205   2013). Based on variance components, behaviors that show relatively low within-individual variance

206   compared to high between-individual variance are more repeatable. In our group setup, the total

207   variance additionally included the variance due to between-group differences. Our model-based

208   estimates at individual-level thus represent the typical behavioral repeatability, *i.e.* the unstandardized

209   variance component that is attributable to between-individual differences relative to the total

210   variance, while group-level estimates represent the proportion of variance explained by the between-

211   group differences. To quantify the uncertainty of model-based repeatability estimates, all estimations

212   including 95% confidence intervals (CIs) were based on bootstrapping with 1000 resamples. We

213   assessed the statistical significance of the repeatability estimates by means of likelihood ratio tests

214   (LRT). We considered two estimates of repeatability significantly different if their CIs did not overlap

215   with another or zero (Payton et al. 2003).

216

217   **RESULTS**

218   The continuously tracked perch displayed a clear diel pattern in the mean moving activity through 10

219   diel cycles (Fig. 2). The LMMs revealed statistically significant positive effects of body length on all

220   activity scores (*Total activity* b ± SE = 0.251 ± 0.028, $F_{1,\ 295.813} = 77.487$, $P < 0.001$; *Diurnal activity*

221   b ± SE = 0.051 ± 0.024, $F_{1,\ 295.596} = 4.635$, $P = 0.032$, and *Nocturnal activity* b ± SE = 0.382 ± 0.039,

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222    $F_{1, 262.249} = 95.864$, $P < 0.001$). The *circadian score* decreased with body length ($b \pm SE = -0.055 \pm$

223   0.007, $F_{1, 291.248} = 69.610$, $P < 0.001$), 291, in *i.e.* the proportion of *nocturnal activity* increased with

224   body size. Therefore, all repeatability estimates were adjusted with respect to body length. All size-

225   adjusted repeatability estimates presented in Table 1 were statistically significant (LRT: $P < 0.001$),

226   revealing that the perch expressed temporally consistent activity variation among both individuals

227   and shoals.

228   On average, the perch were less active in daylight, and the overall variation in moving activity

229   was substantially greater at night (Table 1, Fig. 2). Consequently, there was a difference in how the

230   total variation in *diurnal activity* and *nocturnal activity* was distributed between individuals and

231   groups (Table 1, Fig. 3). The individual-level repeatability in *nocturnal activity* was higher than the

232   group-level repeatability, while the opposite difference was found in *diurnal activity*. The high

233   variation among individuals in *nocturnal activity* resulted in the highest individual-level repeatability

234   estimate ($R_{adj} = 0.40$, 95% CI 0.308 to 0.500) whereas the repeatability of *diurnal activity* was

235   significantly lower ($R_{adj} = 0.22$, 95% CI 0.143 to 0.305). The group-level point estimate for

236   repeatability was higher for *diurnal activity* ($R_{adj} = 0.35$) than for *nocturnal activity* ($R_{adj} = 0.21$), but,

237   due to overlapping CI's, this difference was not considered statistically significant.

238   The between-individual variation in *circadian scores* was significantly repeatable (R_{adj}

239    $= 0.35$), indicating predictable differences among individuals in their tendency for diurnal vs.

240   nocturnal activity. Based on individual mean scores, 21 % of the perch were proportionally more

241   active in daylight, while 79 % were more active in nighttime. We illustrate the activity differences

242   between these circadian behavioral types in Figure 4. For example, the fish exhibiting a consistently

243   high total activity through the experiment displayed higher activity in nighttime, while low activity

244   types were more active in daylight. The group-level variance in circadian scoring was substantially

245   low, and only 10 % of the total variation was explained by consistent differences between the groups

246   (Table 1).

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DISCUSSION

The moving activity of perch showed clear circadian rhythmicity, but there were also systematic changes in variability and repeatability estimates of the behavioral activity between day and night. To be more specific, the decomposition of total variance in the activity scores revealed a diel turnover in the proportion of variance attributable to between-individual *vs.* between-group differences: the individual differences were more repeatable in nighttime whereas the group differences were more repeatable in daytime. The relatively low variability in *diurnal activity* between individuals in a group together with the proportionally high between-group variability supported our predictions of social synchrony at daylight, and aligned with the earlier findings by Magnhagen and Bunnefeld (2009) on group conformity. The randomly formed groups, *per se*, showed repeatable differences particularly in *diurnal activity* that persisted regardless of the consistent individual differences within the groups. Unexpectedly, the perch showed great total variability in *nocturnal activity* between individuals whereas the group-level differences were smaller than in daytime. This indicates that the individuals remained differently active once they scattered for the night. Altogether, our main results imply that high conformity in daylight may obscure the expression of individual differences in a behavior, whereas stronger individuality becomes detectable in the nighttime once the group effects weaken.

Fish generally express social behavior by synchronizing their locomotor activity, and, accordingly, the individual perch appeared to conform to the average moving activity of the group in daylight. This is common in animals that use social information for avoidance of predators or parasites, foraging and consensus decision-making on movements (Webster and Laland 2012; Aplin et al. 2015; Ramos et al. 2015). Despite the high degree of behavioral conformity, individuality in diurnal activity was not entirely lost in groups, which is in line with earlier studies on perch personality (Magnhagen 2012; Kekäläinen et al. 2014). The study perch also expressed repeatable between-group differences particularly in diurnal activity. In addition to uncontrolled tank effects,

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the between-group differences can be provoked by the phenotypic differences among individuals (Pinter-Wollman et al. 2012; Herbert-Read et al. 2013; Cronin 2015). The consistent group differences may emerge if the groups differ in the average behavior of their members (Carere et al. 2018), or alternatively if the groups differ in the behavioral composition (Brown et al. 2014). For example, bold and explorative behaviors of group leaders can contribute to foraging and collective behavior of the whole group (Pruitt et al. 2013; Aplin et al. 2014), whereas groups with a more effective leadership can move consistently faster or more cohesively than the others (Couzin et al. 2005; Jolles et al. 2017). Accordingly, bold and explorative individuals tend to occupy the front positions of the perch shoals (Magnhagen and Bunnefeld 2009; Härkönen et al. 2016), and it should be further studied if behavioral differences between the shoal leaders could explain the higher group repeatability during the daytime than in nighttime.

Most visually oriented animals, including the perch, usually show diurnal activity, and sleep/rest during the night (Siegel 2008). Thus, it was somewhat surprising that nighttime produced substantially greater diversity in activity among the perch compared to daytime. Group-living animals may modify their activity rhythms to balance the trade-off between the antipredator benefits and the costs of increased feeding competition (Vainikka et al. 2005). In this study, high overall nocturnal activity may relate to predator-free experimental design, since the absence of predators is known to increase nocturnal activity even in diurnal species (Carnevali et al. 2016). Nocturnal foraging may also reduce the competition over food but it also reduces the feeding efficiency (Alanärä et al. 2001). This study was conducted in mid-fall when decreasing temperatures and shortening day length may limit food availability. Elevating (nocturnal) activity levels when visibility is low and/or food is limited may increase the encounter probability with prey. Body size and energy levels often contribute to the activity differences among individuals through feeding motivation (Sih et al. 2015). Accordingly, variation in all activity scores, including the proportion of nocturnal activity, correlated positively with perch size. Large perch are shown to adopt alternative strategies to allocate more time

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297 to foraging (Jacobsen et al. 2015), whereas elevated levels of nocturnal activity may relate to fulfilling

298 the increased foraging demands (Nakayama et al. 2018).

299 The perch expressed different activity types assessed as showing higher activity either in

300 daytime or in nighttime. This preference was consistent within individuals and different between

301 individuals ($R_{adj} = 0.35$), but also least affected by group-level effects. Individual fish may have

302 preferences for diurnal or nocturnal activity (Reebs 2002): for example Závorka et al. (2016) showed

303 that salmonid individuals that are inactive in diurnal conditions may be highly active in nocturnal

304 conditions. In some fish species, social environment modifies individual activity rhythms. The sea

305 bass (*Dicentrarchus labrax*) tested alone are active in nighttime, but in a group they adopt a diurnal

306 activity rhythm (Anras et al. 1997), whereas rainbow trout (*Oncorhynchus mykiss*) are almost

307 exclusively diurnal when tested in isolation, but may display both diurnal and nocturnal activity in

308 groups (Chen et al. 2002a; Chen et al. 2002b). Our study showed that individuality in diel activity

309 rhythm may be expressed in groups. The consistency of diel activity differences among the study

310 perch also suggests that different activity rhythms can be under natural selection. In theory, individual

311 specialization on separate activity times could increase fitness by reducing intraspecific competition

312 for foraging opportunities (Brännäs and Alanärä 1997; Alanärä et al. 2001) but also expose

313 individuals differentially to *e.g.* day- and night-active predators (Ylönen et al. 2007). Further studies

314 are needed to understand how individually different activity rhythms within groups add variation to

315 other personality dimensions and life history, and how those link to fitness in different ecological and

316 evolutionary contexts.

317

318 **Conclusions**

319 Modern technological applications have made it feasible to shift from individual behavioral tests in

320 laboratory towards studying animals under more ecologically realistic conditions. Using an RFID

321 system built in large seminatural enclosures, we found that the Eurasian perch expressed individually

consistent behavioral activity under natural light rhythm, but that individual repeatability was the highest in nighttime while group repeatability was the highest in daytime. The results imply that accounting for the diel variation in social effects may be essential to detect realistic behavioral variation among group-living individuals. Altogether, this study highlights how meaningful interpretation of behavioral heterogeneity from ecological datasets requires understanding of potential interactions between natural activity rhythms, individual behavioral differences, and group dynamics.

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491 **Tables and table legend**

492

493 **Table 1**. LMM-based, size-adjusted variance and repeatability estimates (with 95 % confidence

494 intervals) for individuals and groups in all behavioral variables. All repeatability estimates are

495 statistically significant at the level of $P < 0.001$.

| Variable	Estimation for ID		Estimation for Group	
	Var	*R$_{adj}$*	*Var*	*R$_{adj}$*
Total activity	7.00 [5.76 – 8.20]	0.31 [0.22 – 0.42]	7.36 [1.57 – 17.30]	0.33 [0.10 – 0.52]
Diurnal activity	2.84 [2.31 – 3.39]	0.22 [0.14 – 0.31]	4.59 [0.97 – 10.0]	0.35 [0.10 – 0.55]
Nocturnal activity	23.60 [19.60 – 27.90]	0.40 [0.31 – 0.50]	12.20 [2.41 – 26.90]	0.21 [0.05 – 0.38]
Circadian score	0.03 [0.02 – 0.03]	0.35 [0.30 – 0.41]	0.01 [0.00 – 0.02]	0.10 [0.02 – 0.21]

496

Figure legends

498
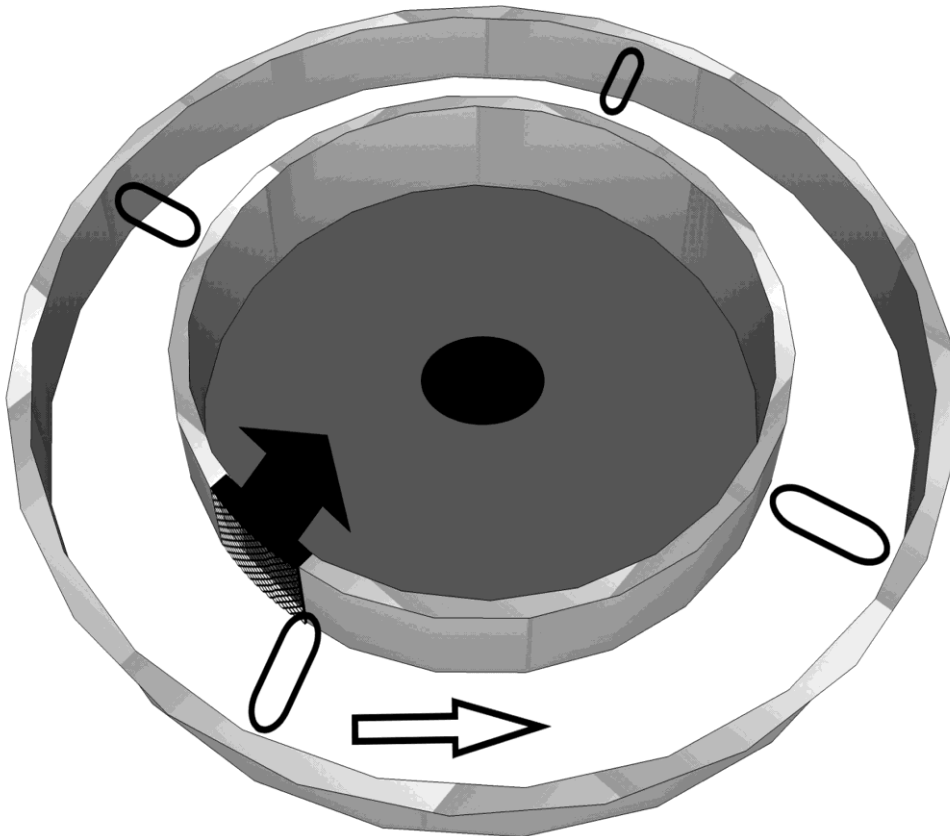
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500   Figure 1. An illustration of a seminatural enclosure ($n = 8$) used in the behavioral experiment. Outer

501   circumference of the channel is 30.1 m, inner circumference 21.4 m, and width 1.5 m. Water depth

502   is on average 0.3 m. The white arrow indicates the direction of the water flow (ca. 0.11 m $\times$ s^{-1} / 55 l

503    $\times$ s^{-1}) and the position of the water inlet. The black arrow indicates the water running out of the

504   system. The bottom of the streams is fully layered with approximately 20 cm of gravel (size 10–20

505   mm) and pebbles (20–100 mm). In addition, four concrete masonry units (size 200 x 500 mm) were

506   scattered on the bottom to provide shelter for the fish. Four plastic loops divide the channel into four

507   sections (distance between two loops 6.5 m). Each loop is equipped with an RFID-antenna and

508   connected to a computer that continuously records signal detections from the bypassing PIT-tagged
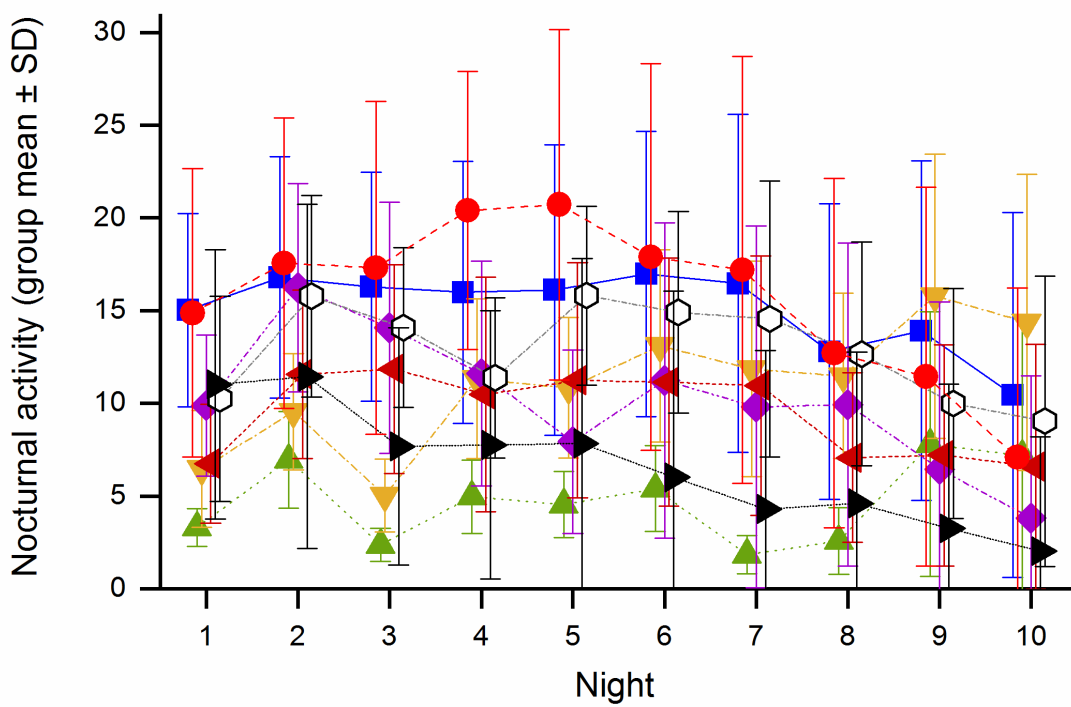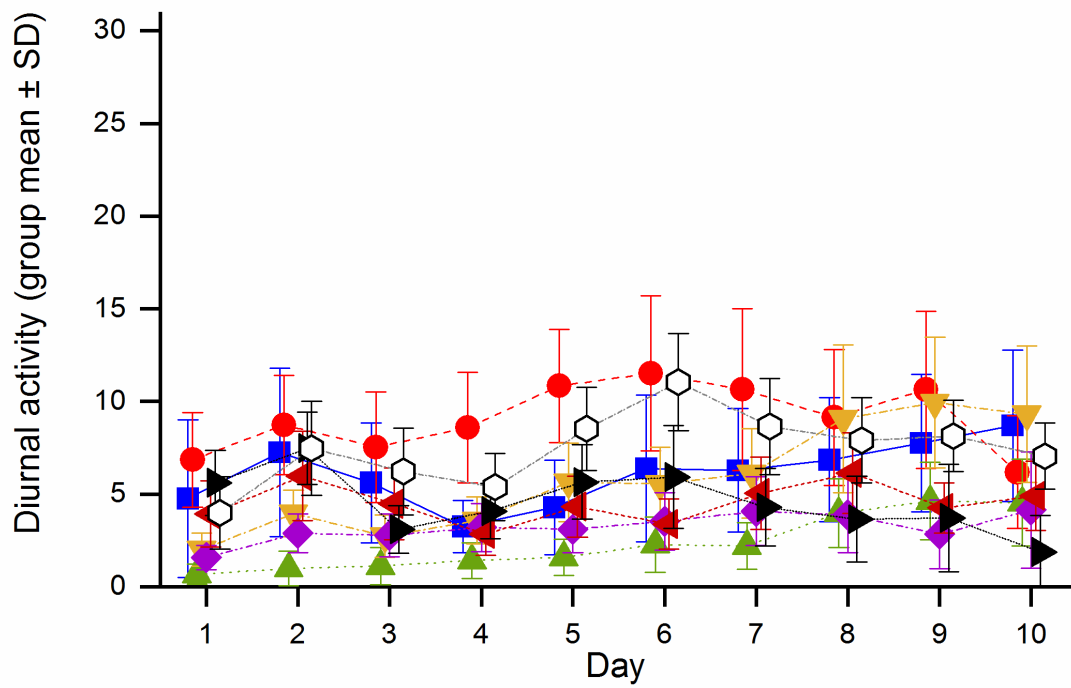
509   fish.

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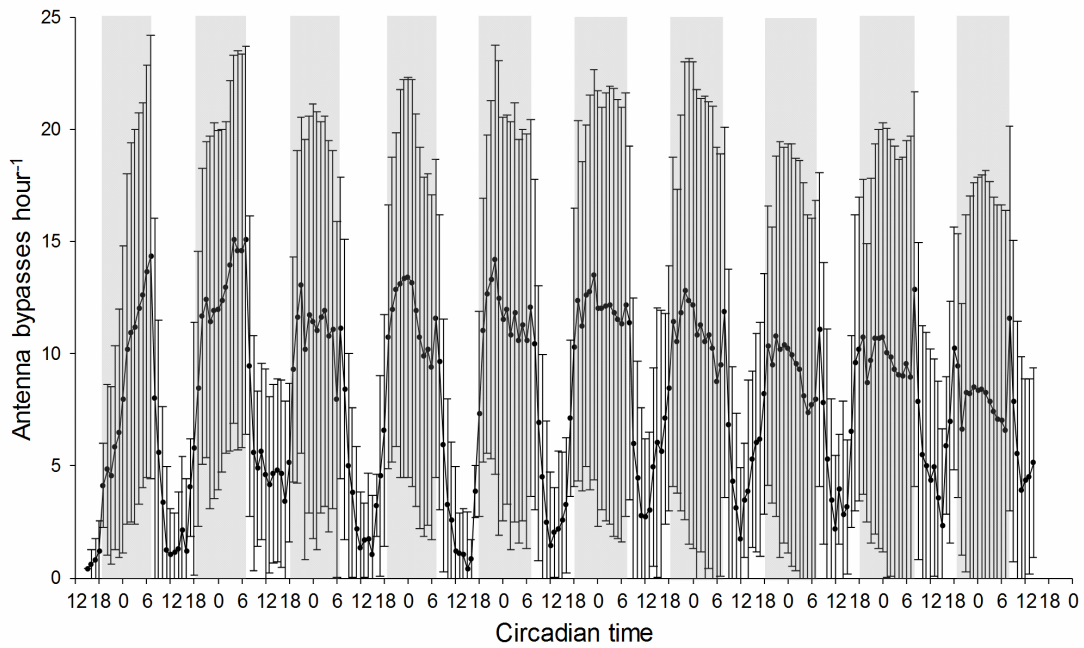
Figure 2. Circadian activity pattern of the study perch ($n = 313$) represented as mean number ($\pm$ SD)

of hourly signal detections through 10 diel cycles. Shaded areas indicate the periods from sunset to

sunrise.

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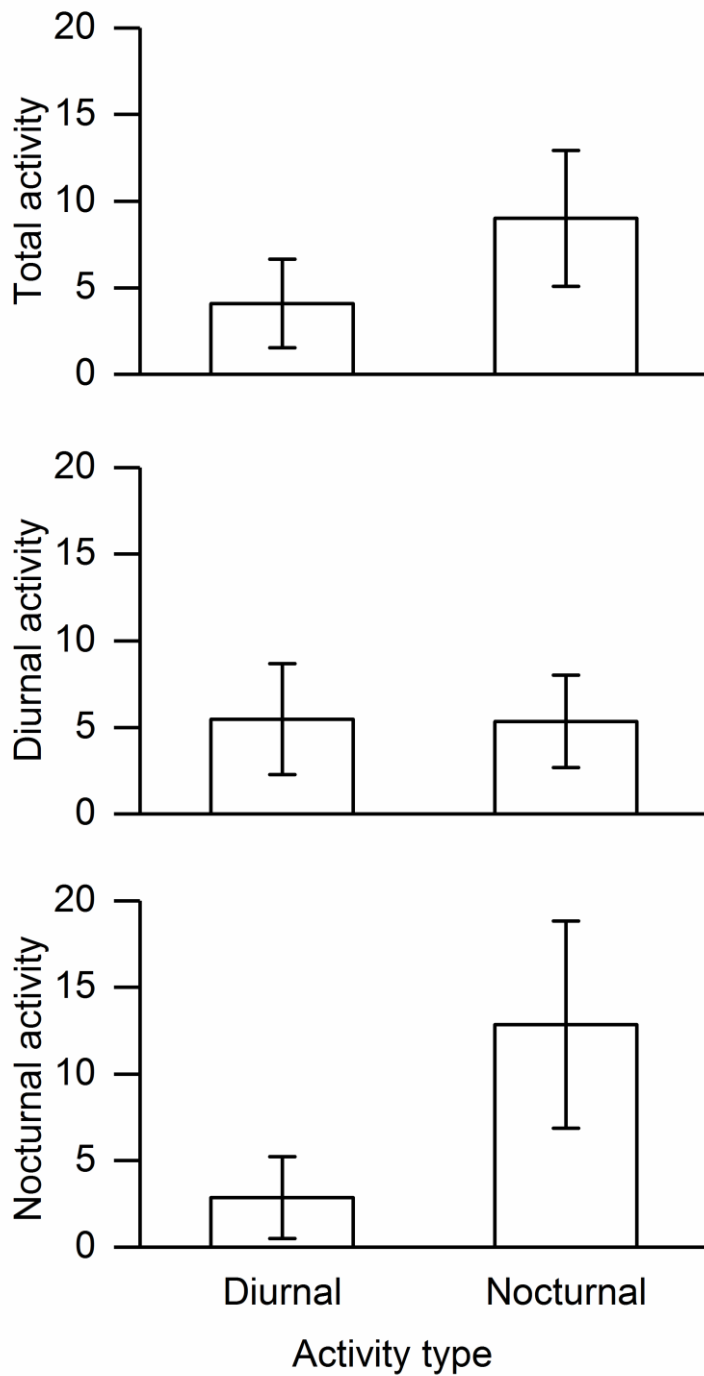
Figure 3. Diurnal and nocturnal activity variation between and within the eight study shoals (group mean ± SD) through 10 diel cycles.

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Figure 4. Differences in individual mean activity scores (± SD) between the activity types. The activity types are based on circadian scoring describing whether an individual was proportionally more active diurnally or nocturnally.