

1 **Rhythm of relationships in a social fish over the course of a full year in the wild**

2 **Short Title: Dynamics of Carp Social Networks**

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## 22 **Abstract**

23           Animals are expected to adjust their social behaviour to cope with challenges in their  
24 environment. Therefore, for fish populations, in temperate regions with seasonal and daily  
25 environmental oscillations, characteristic rhythms of social relationships should be pronounced. To date,  
26 most research concerning fish social networks and biorhythms has occurred in artificial laboratory  
27 environments or over confined temporal scales of days to weeks. By contrast, little is known about the  
28 social networks of wild, freely roaming fish, including how seasonal and diurnal rhythms modulate social  
29 networks over the course of a full year. The advent of high-resolution acoustic telemetry enables us to  
30 quantify detailed social interactions in the wild over time-scales sufficient to examine seasonal rhythms  
31 at whole-ecosystems scales. Our objective was to explore the rhythms of social interactions in a social  
32 fish population at various time-scales over one full year in the wild by examining high-resolution  
33 snapshots of dynamic social network. To that end, we tracked the behaviour of 36 adult common carp,  
34 *Cyprinus carpio*, in a 25 ha lake and constructed temporal social networks among individuals across  
35 various time-scales, where social interactions were defined by proximity. We compared the network  
36 structure to a temporally shuffled null model to examine the importance of social attraction, and  
37 checked for persistent characteristic groups (“friendships”) over time. The clustering within the carp  
38 social network tended to be more pronounced during daytime than nighttime throughout the year.  
39 Social attraction, particularly during daytime, was a key driver for interactions. Shoaling behavior  
40 substantially increased during daytime in the wintertime, whereas in summer carp interacted less  
41 frequently, but the interaction duration increased. Characteristic groups were more common in the  
42 summer months and during nighttime, where the social memory of carp lasted up to two weeks. We  
43 conclude that social relationships of carp change diurnally and seasonally. These patterns were likely  
44 driven by predator avoidance, seasonal shifts in lake temperature, visibility, forage availability and the  
45 presence of anoxic zones. The techniques we employed can be applied generally to high-resolution  
46 biotelemetry data to reveal social structures across other fish species at ecologically realistic scales.

## 47 Introduction

48 Animals are faced with continual exogenous oscillations of their environment and endogenous  
49 oscillations of their own physiology, over various timescales (Hastings, 2010). For example, all animals  
50 must cope with daily oscillations driven by the Earth's rotation around its axis, ~30 day oscillations  
51 driven by the lunar cycle and yearly oscillations driven by the Earth's elliptical orbit around the sun.  
52 Animals must also cope with internal oscillations driven by, for example, a heartbeat at very short time  
53 scales, or a reproductive cycle at longer, maybe even seasonal time scales. Furthermore, to feed and  
54 survive animals must also track the responses of their predators and prey to environmental oscillations  
55 (Vandermeer, 2004). Importantly, in ectotherms such as fish, ecosystem metabolism (e.g., productivity  
56 of resources and thermal environment) in the temperate zone reacts strongly to seasonal and daily  
57 changes in light and temperature, which causes periodic variation in the availability of food and the  
58 distribution of habitats (Hunt, Jardine, Hamilton, & Bunn, 2012; Stæhr & Jensen, 2007). Accordingly,  
59 animals must constantly respond to oscillations in their biotic environment throughout the food web as  
60 resource requirements and availability, danger and shelter, and reproductive opportunities oscillate  
61 across various frequencies to find food and shelter and avoid mortality.

62 Animals have adopted a number of physiological and behavioural strategies to cope with  
63 periodic fluctuations of the environment over time. The circadian clock, for example, is an inner  
64 oscillator synchronized with solar time that appears universally across taxa (Bernard, Gonze, Čajavec,  
65 Herzel, & Kramer, 2007; Dunlap, 1999; Edgar et al., 2012); it influences metabolism (Kohsaka & Bass,  
66 2007), hormones (Leatherland & McKeown, 1973) and ultimately behavior (Naylor, 1988). To survive  
67 resource fluctuations over yearly time-scales organisms may employ strategies like hibernation or other  
68 forms of metabolic depression (Ruf & Geiser, 2015). For most animals, and for ectotherms in particular,  
69 temperature is a critical resource they must adapt to (Magnuson, Crowder, & Medvick, 1979). In fishes,  
70 all biological processes are influenced by exogenously triggered temperature, including enzyme activity,  
71 metabolism, digestion, and feeding rate, leading to a strict dependency on warm waters to grow and  
72 reproduce (Conover & Present, 2016; Shultz, Reynolds, & Conover, 1996). In addition to modifying their  
73 physiology, animals also have the option to alter their behaviour in response to environmental changes  
74 (Holland, Brill, Chang, Sibert, & Fournier, 1992), which may take the form of migrating to more  
75 favourable habitats (Somveille, Rodrigues, & Manica, 2015), and importantly, animals may also change  
76 their response to other conspecifics by becoming more or less social (Monk et al., 2018).

77 There are costs and benefits to both pro-social and anti-social behaviour, which depend on an  
78 organism's environment and resource requirements (Monk et al., 2018; Snijders, Kurvers, Krause,  
79 Ramnarine, & Krause, 2018; Wiens, 1976). Group living can allow for increased predator avoidance  
80 (Foster & Treherne, 1981; Landeau & Terborgh, 1986; Pulliam, 1973), faster ability to find rare or mobile  
81 resources (Hills et al., 2015; Magurran & Higham, 1988; Pitcher, Magurran, & Winfield, 1982), increased  
82 ability to hunt large prey, and better conservation of resources (Gilbert, Robertson, Le Maho, Naito, &  
83 Ancel, 2006). However, living in groups also comes at the cost of sharing resources among conspecifics  
84 (Bertram, 1978) or increased transmission of parasites and pathogens (Côté, Poulin, & Zealand, 1985).  
85 Under certain conditions it is therefore, better to be solitary and defend a territory (J. Brown, 1968;  
86 Bryant & Grant, 1995) or behave nomadically (Eklöv, 1992). Hence, as the abiotic and biotic

87 environments as well as the internal physiological state of an animal oscillate we expect to observe  
88 periodic patterns in social behaviour across various time-scales. The behavioural reactions that occur  
89 most likely depend on the evolutionary adaptations of particular species, modified by local environmental  
90 conditions. For example, killer whales, *Orcinus orca*, increase their sociality with increasing resource  
91 abundance (Franks et al., 2012), while chacma baboons, *Papio hamadryas ursinus*, increase their  
92 sociality when resources become scarce (Henzi, Lusseau, Weingrill, Van Schaik, & Barrett, 2009). The  
93 environment-species interaction also dictates among population differences in social responses to the  
94 environment within the same species. For example banded killifish, *Fundulus diaphanus*, form larger  
95 groups when a predator is detected, but reduce their group size when food is available (Hoare, Couzin,  
96 Godin, & Krause, 2004).

97 To date, there have been few explorations into the temporal dynamics of animal social networks  
98 (Blonder, Wey, Dornhaus, James, & Sih, 2012; Pinter-Wollman et al., 2014), and none have been able to  
99 explore the dynamics across the full spectra of timescales expected within a full growing season in the  
100 temperate zone. The lack of long-term (i.e., multiple months), high-resolution animal social network  
101 data in the wild is a result of the immense challenge in collecting it at sufficient spatial-temporal  
102 resolutions (Krause et al., 2013). Most long-term datasets are generated through consistent periodic  
103 visual observations of interactions among identifiable animals (Henzi et al., 2009; Wittemyer, Douglas-  
104 Hamilton, & Getz, 2005). There is a particular lack of long-term social network data for fish because  
105 making long-term underwater observations has not been possible until recently. Initial work in the wild  
106 has however shown that certain fish species tend to be detected in groups of characteristic individuals  
107 (Hay & McKinnell, 2002; Klimley & Holloway, 1999; Ward et al., 2002; Wilson et al., 2014), but this  
108 pattern is not universal across species (Helfman, 1984). The lack of long term studies of fish in the wild is  
109 problematic because fish have been used widely as valuable model organisms to study social  
110 behaviours, such as shoaling (Wilson, Croft, & Krause, 2014), but most research in social behavior among  
111 fishes has occurred over short time periods of a few weeks, and often in non-naturalistic laboratory  
112 environments (Wilson et al., 2014). Evidence from non-human animal studies shows that social behavior  
113 is usually more dependent on ecology than taxonomy (Lefebvre, Palameta, & Hatch, 1996), raising  
114 doubts as to whether our lab-scale understanding is transferable to the wild (Sutter & Arlinghaus, et. al.,  
115 2012; Niemelä & Dingemanse, 2014). Consequently, very little is known with certainty about the  
116 relationships and social lives of wild-living fishes in large populations over long time-scales of multiple  
117 months in the wild.

118 Most species of fish must engage in social relationships for at least a portion of their life, for  
119 example during mating and shoaling for predator avoidance (Pitcher, 1986; Shaw, 1978). To increase  
120 fitness, many species socialize to establish hierarchies, exchange information and avoid predators  
121 (Seppälä, Karvonen, & Valtonen, 2008; Suboski & Templeton, 1989). Research in social learning has  
122 demonstrated a number of advanced social behaviors. For example, it has been shown that fish can  
123 learn escape routes from each other (C. Brown & Laland, 2002), infer social hierarchies by observing  
124 fights (Grosenick, Clement, & Fernald, 2007), recognize individual conspecifics (Griffiths & Magurran,  
125 1997), and when given conflicting social cues tend to value public information over immediate social  
126 information (Coolen, Ward, Hart, & Laland, 2005). More complex social behaviors such as cooperation,

127 establishment of partnerships and reciprocation of behaviors that require risk taking (Croft et al., 2006;  
128 Granroth-Wilding & Magurran, 2013; Milinski, Kulling, Kettler, & Bern, 1990), indicate that fish have well  
129 developed social cognition capabilities (Bshary, Gings, & Vail, 2014).

130 Today, with advanced computational methods and modern tracking technology, such as high-  
131 resolution, precise, acoustic telemetry it is possible to collect snapshots of social interactions at several  
132 second frequencies over years in the wild (Nathan et al., 2022; Baktoft, Zajicek, Klefoth, Svendsen, &  
133 Jacobsen, 2015; Guzzo et al., 2018; Krause et al., 2013), both underwater (Lennox et al., 2017) and in  
134 terrestrial environments (Wilmers et al., 2015). A suite of techniques are now available for constructing  
135 and analyzing social networks generated from acoustic data (Blonder et al., 2012; Finn et al., 2010;  
136 Jacoby & Freeman, 2016; Mourier, Brown, & Planes, 2017). With a full-year dataset containing high-  
137 resolution mobility traces of 36 common carp (*Cyprinus carpio*) in a small lake, we for the first time  
138 explore the “rhythm of relationships” in nature at a whole ecosystem scale for a fish. We ask a basic  
139 question: how do seasons and daytime modulate the social behavior of a fish species described as highly  
140 social from laboratory contexts (Huntingford et al. 2010)?

141 Wild common carp are long-lived, omnivorous, typically benthivorous, warmwater cyprinids,  
142 native to eastern Europe and Asia. The species has been domesticated for aquaculture purposes as early  
143 as 2000 years ago and globally introduced into the wild where it forms feral populations (Balon, 2004).  
144 Carp have permanently established widely across the freshwater ecosystems around the globe (Howes,  
145 1991; Parameswaran, Alikunhi, & Sukumaran, 1972; Vilizzi, 2012). They constitute a key fisheries  
146 resource for both commercial (FAO, 2018) and recreational fisheries (Arlinghaus & Mehner, 2003). Yet,  
147 appreciation of carp is not global. The species is also considered a pest in certain regions where it is  
148 originally non-native, such as North America (Bajer, Sullivan, & Sorensen, 2009), Australia (Taylor,  
149 Tracey, Hartmann, & Patil, 2012) and parts of Europe, such as Spain (Benito, Benejam, Zamora, & García-  
150 Berthou, 2015) as they can disturb aquatic macrophytes, leading to loss of water clarity and increased  
151 nutrient concentrations (Bajer et al., 2016). Accordingly, learning about the social behaviour of carp  
152 could help to improve both carp fisheries management (Klefoth, Skov, Kuparinen, & Arlinghaus, 2017),  
153 and eradication techniques (Bajer, Chizinski, & Sorensen, 2011).

154 The behaviour of carp is variable, both among populations (Hennen & Weber, 2014; Benito et  
155 al., 2015; Weber, Brown & Willis, 2016) and among individuals (Monk & Arlinghaus, 2017; Pollux, 2017).  
156 Increasing levels of domestication in stocked fish are known to increase the carp’s boldness (Klefoth,  
157 Skov, Krause, & Arlinghaus, 2012) and foraging activity and ingestion rates (Klefoth, Pieterek, &  
158 Arlinghaus, 2013). Carp are also known to be a social species, frequently found in groups (Bajer et al.,  
159 2011; Johnsen & Hasler, 1977; Osborne, Ling, Hicks, & Tempero, 2009), and can learn by social  
160 facilitation (Zion, Barki, Grinshpon, Rosenfeld, & Karplus, 2007). Carp are generally thought to occupy  
161 littoral habitats during the spring and summer and move to deeper waters to overwinter in larger  
162 groups (Armstrong et al., 2016; Johnsen & Hasler, 1977; Jones & Stuart, 2009; Penne & Pierce, 2008).  
163 Carp are also known to show marked diurnal behavioural patterns in the spring and summer months.  
164 For example, non-native carp that became established in a reservoir in the Ebro catchment in Spain  
165 were relatively inactive in deep hypoxic waters at nighttime, possibly refuging from nocturnal predators  
166 (in particular catfish, *Silurus glanis*), but became more active in shallow waters during the daytime

167 (Benito et al., 2015). By contrast, in other populations, carp have been observed to increase food  
168 consumption in the nighttime (Bajer, Lim, Travaline, Miller, & Sorensen, 2010; Proske, 1972), strongly  
169 indicating that diel patterns of behavior will vary with local ecological conditions.

170 Our objective was to explore the social relationships of a population of carp over one full year at  
171 a whole ecosystem scale, and to identify the relevant time-scales of carp social behavior in the wild  
172 under realistic ecological scales. To that end, we recorded three-dimensional positions of carp in a  
173 whole-lake using high resolution acoustic telemetry, and inferred the temporal social network of carp by  
174 logging proximity events. We describe how seasons and daytime influence both mobility and social  
175 behavior, perform statistical tests to assess the degree to which time spent together is explained by  
176 social attraction given that other ecological factors (e.g., local food availability) may drive co-location of  
177 two individuals, and finally study the social network at varying time-scales to measure the persistence of  
178 community structure over time. Having found that there is significant local clustering in the social  
179 network, we investigate whether these groups, or communities, that emerge on short time-scales and  
180 give rise to local clustering, persist over time. By analyzing the persistence of clustering over time we  
181 aim to get at the more fundamental question which is whether there is social memory in the system that  
182 drives the groups of fish to meet repeatedly.

## 183 **Methods**

### 184 **Study site**

185 Kleiner Döllensee (52°59'41.9"N, 13°34'56.4"E) is a 25 ha lake in northern Brandenburg,  
186 Germany, classified as eutrophic with a total phosphorous concentration of 38  $\mu\text{g L}^{-1}$  at spring overturn.  
187 The average depth during the study period was 4.4 m, while the maximum depth is 7.8 m and the secchi  
188 depth was  $1.97 \pm 0.61$  m (mean  $\pm$  standard deviation). Reeds (*Phragmites australis*) form a belt of  
189 growth around the lake. Between May and October the lake stratifies turning layers below ca. 4 m  
190 anoxic (See figures SI1 and SI2). Kleiner Döllensee hosts 14 fish species typical for mesotrophic to slightly  
191 eutrophic natural lakes in German lowlands (Eckmann, 1995). Top predators include introduced  
192 European catfish (*Silurus glanis*), and native northern pike (*Esox lucius*) and Eurasian perch (*Perca*  
193 *fluviatilis*). Carp competitors include an abundant populations of large common bream (*Abramis brama*),  
194 tench (*Tinca tinca*), rudd (*Scardinius erythrophthalmus*), roach (*Rutilus rutilus*) and white bream (*Blicca*  
195 *bjoerkna*). Through recent nutrient increases, the submerged macrophyte coverage has been declining  
196 in the lake and is now restricted to near shore locations and macrophytes taller than 10 cm covered  
197 9.2% of the lake area.

### 198 **Telemetry system**

199 The lake has been equipped with 20 submerged (~2 m) high-resolution acoustic telemetry receivers  
200 (WHS 3050; 200 kHz; Lotek Wireless Inc., Newmarket, Ontario, Canada) distributed at fixed locations  
201 throughout the lake (described in detail in Baktoft et al. 2015). The system allows whole-lake positional  
202 telemetry in 3-D at high spatio-temporal resolution with several position fixes per minute depending on  
203 transmitter burst rates (Baktoft et al. 2015). Location datapoints are estimated by hypertriangulation of  
204 ultrasonic signals originating from surgically implanted transmitters. Median location accuracy



205 throughout the lake is 3.1 m (Baktoft et al., 2015). Macrophytes, known to strongly attenuate acoustic  
206 signals, were scarce during the study period; thus we can reason that most signal loss occurred when  
207 the fish swam among the reed close to shore. However, significant decreases in data yield did occur over  
208 some periods in warmer summer months, indicating improved telemetry performance during the cooler  
209 periods of the year (Fig. 2A). Average across the year data yield was about 40%. For a full description of  
210 the system and its performance see Baktoft et al., (2015).

## 211 **Carp population**

212 All carp recorded in the dataset were hatchery born and bred in earthen ponds as is typical in  
213 many European fisheries where carp are stocked after being raised in pond aquaculture. In June 2014,  
214 91 carp with transmitters implanted (0.3% to 2.2% body mass) were released to Kleiner Döllnsee. Due to  
215 tag loss, known to be a prevalent problem in carp tagging (Daniel, Hicks, Ling, & David, 2009; Økland,  
216 Hay, Naesje, Nickandor, & Thorstad, 2003), an additional 24 tagged carp were released in September  
217 2014. Of these 115 carp known to have been introduced to the lake, between 25-36 ( $540 \pm 79$  cm total  
218 length, mean  $\pm$  standard deviation; see Fig S11 for individual level data) were successfully monitored  
219 throughout all of 2015 for an entire year (Fig. 1). The rest experienced transmitter loss. Tagging-induced  
220 mortality was extremely low as revealed by recaptures that had lost tags but were alive.

221 For transmitter implantation, carp were anaesthetized using a 9:1 EtOH:clove oil solution added  
222 at  $1\text{ mL L}^{-1}$  (Carl Roth, Karlsruhe, Germany). All surgical tools and acoustic telemetry tags were sterilized  
223 with a mixture of tap-water and 7.5% povidone-iodine (PVP; Braunol<sup>®</sup>; B. Braun, Kronberg, Germany)  
224 before each transmitter implantation. We implanted the transmitters (model MM-M-TP-16-50,  
225 dimension: 16 by 85 mm, wet weight: 21 g; Lotek Wireless, Newmarket, Canada) into the body cavity  
226 (see (Klefoth, Kobler, & Arlinghaus, 2008) for procedures), and each fish received 4–5 sutures using PDS-  
227 II adsorbable monofilament suture material and FS-1 3–0 needles (Ethicon, USA). Following recovery  
228 from surgery the fish were immediately released into the study lake. The burst frequency of the  
229 transmitters was five seconds, and the transmitters were equipped with a temperature sensor,  
230 recording once per minute, and a pressure sensor to record depth at all other transmissions.

## 231 **Inferring social networks**

232 Because we did not directly measure social interactions between fish, we had to infer it using  
233 mobility traces. In the current analysis, we used persistent proximity as a proxy for contact. We  
234 employed several post-processing techniques to increase accuracy and data yield to produce the best  
235 reconstruction of the temporal contact network as possible. First, we resampled the location data from  
236 5 s to 15 s to remove noise and recover potentially lost measurements by applying a 30 s median filter in  
237 15 s increments across the location trajectory of each fish. We then measured pairwise distance in each  
238 time-bin, resulting in  $\frac{N(N-1)}{2}$  time series of inter-fish distance. Each series would have some missing  
239 values which we linearly imputed by up to 30 minutes. To get the times at which links were on and off  
240 we thresholded the distance series at 10 m. Finally, we applied a filter which removed singleton contact  
241 events and clustered consecutive ones with short breaks (up to 5 minutes). Figure 5 shows two

242 examples of distance time series, how we threshold them and how that results in a link activity time  
243 series.

244 Based on individual temperature and location measurements of the  $N = 36$  carp we computed,  
245 for each fish,  $i$ , on each day the local temperature,  $T_i$ , the distance from shore,  $d_i$ , the Shannon entropy,  
246  $S_i = -\sum_m c_m \log c_m$ , where  $c_m$  is the fraction of time spent in lake area  $m$  (when the lake is split into 10 m x 10  
247 m cells), the velocity,  $v_i$ , and the depth,  $h_i$ . From the inferred social network we measured for each pair,  
248  $n$ , the average interaction duration,  $\tau_n^+$ , the average time between interactions,  $\tau_n^-$ , and the interaction  
249 probability,  $p_n$ . Quantities were estimated separately for daytime and nighttime once per solar cycle and  
250 reported as population averages, denoted by dropping the node/link index.

251 We, furthermore, measured the local clustering coefficient as a population average for each  
252 monthly aggregated social network split into day and night. The average local clustering in a network is  
253 bounded between zero and one, and reflects the tendency for triangles, or triads, to form in the  
254 network (Saramäki, Kivelä, Onnela, Kaski, & Kertesz, 2007). Intuitively, if a node has a high local  
255 clustering coefficient its neighbors are highly interconnected. Triads are indicative of community  
256 structure and informs about social behavior at the group-scale (Wasserman & Faust, 1994; Scott, 2000).

### 257 **Null model of social attraction**

258 Since our inferred social network builds on the assumption that co-location equates interaction,  
259 it is natural to wonder how much of that interaction is due to “social attraction” – meaning very broadly  
260 that fish go to specific places because there are other fish there – and how much is due to the  
261 environment driving the fishes to visit the same places at the same times. Indeed, it is plausible that the  
262 population is entirely non-social and any co-location is due to similar resource use (e.g., habitat choice).  
263 To assess the impact of social attraction on interaction, we created a shuffled dataset using a null model  
264 that time-shifts the mobility trace of each fish independently by a random number of whole days  
265 between zero and six. In the shuffled dataset, any potential correlation in the location traces of two  
266 individuals due to their social attraction was broken (Spiegel, Leu, Sih, & Bull, 2016). The data with  
267 individually shifted mobility tracks then modeled a mobility pattern where each pair swims entirely  
268 independent of each other, effectively breaking location dependencies that may have existed due to  
269 social attraction. Hence, we got an estimate of the background level of that statistic due to habitual  
270 space use. This was, furthermore, a very strong null model since some fraction of fish pairs would be  
271 shifted the same amount (statistically:  $7 (1/7)^2 = 14.3\%$ ), thus not removing all inter-pair dependency.  
272 Effect sizes would therefore be slightly underestimated. We then measured and compared the raw  
273 number of interactions as well as the average local clustering coefficient in the real and shuffled data.  
274 We used this null model because, intuitively, if carp were truly non-social and only interacted when they  
275 happened to use the same areas simultaneously, randomizing the data in this fashion would likely yield  
276 the same amount of co-location events. The only assumption that this null model makes is that key  
277 resources which drive mobility do not fluctuate significantly on the scale of days. See (Spiegel et al.,  
278 2016) for an in-depth discussion of the null model.



279 Finally, we acknowledge that a stronger statistical approach would have been to produce many  
280 (thousands) of such shuffled datasets with this null model and report average effect sizes as well as  $p$ -  
281 values associated with each effect. For the current dataset this was not computationally feasible, since  
282 we inferred interactions by querying the distance between every pair in every time-step, which  
283 yields  $\frac{N(N-1)}{2} \cdot 2.1 \cdot 10^6$  timesteps  $\approx$  1.3billion queries (or  $\sim$ 2 days of computing time using 56 2.60GHz  
284 processors) per shuffled dataset.

## 285 **Timescale Analysis to Identify Communities**

286 We conducted a computational experiment where we measured how the number of  
287 communities changed when we incrementally split each monthly social network into multiple shorter  
288 aggregates. Specifically, we first aggregated all interactions in a four week window within a given month  
289 and weighted links by the number of interactions between two fish that exceeded the background level  
290 of interaction (number of interactions in the null data). We then broke this network into two two-week  
291 networks each mapping the interactions in their given window. We continue breaking up the networks  
292 into an increasing number of temporally shorter networks until the window size was one hour and the  
293 number of networks was 24 h/day  $\cdot$  28 days=672. In each iteration we ran the community detection  
294 algorithm Infomap (Rosvall, Axelsson, & Bergstrom, 2009) on the networks and recorded the number of  
295 communities that had three or more members. In the results, we report the average and standard error  
296 of the mean across slices for each aggregation level.

## 297 **Results**

### 298 **Behavioral trends during day and night across the year**

#### 299 **Behaviour was variable across the season, while strong shoaling was a daytime winter phenomenon**

300 We observed high variation across most individual and social behaviors across the year. This  
301 variation was largely due to the fish shoaling in deep waters at the center of the lake during daytime in  
302 colder months. We saw differences in swimming speed (Jan. avg.: 1.03 m/s, June avg.: 0.51 m/s) depth  
303 (Jan. avg.: 5.15 m, June avg.: 1.48 m) and distance from shore (Jan. avg.: 103.38 m, June avg.: 40.22 m).  
304 Moreover, we found that indicators of social interactions in the colder months were elevated, such as  
305 time spent together (Jan. avg.: 12.22 minutes, June avg.: 9.32 minutes), and interaction probability (Jan.  
306 avg.: 0.154, June avg.: 0.042). In colder months there was also a great difference between social  
307 indicators during day and night, which we interpret as a strong signal that shoaling is indeed a daytime  
308 phenomenon in this population. Figure 2 contains a full summary of these results. In warmer months  
309 starting late March, as the lake stratified (Figure S12), deep waters turned anoxic forcing the carp closer  
310 to the surface. We observed already in late February that interaction probability and duration of  
311 interaction during daytime decreased, while time between interactions increased overall. This means  
312 that shoaling ceased before deeper water layers turned anoxic in spring and over the summer. Shoaling  
313 in daytime re-appeared gradually during the fall and peaked again in December.

#### 314 **Behavioral differences between day and night were seasonal**

315           Across all the behavioral and social indicators we studied, we only observed high variation over  
316 daytime during the winter, but not in the other seasons. Comparing the time-series of  $p$  (interaction  
317 probability) for January with July, it is clear that social interactions were a periodic function of daytime  
318 only in the winter, whereas they were far more sporadic in the summer (Fig. 2D). A notable exception,  
319 though not directly an indicator of behavior, was data yield. Here, we observed the opposite: in winter,  
320 roughly the same amount of location measurements were successful across the solar cycle, whereas in  
321 summer, the fish were significantly easier to detect (higher yield) at night (Fig. 2A). This is surprising  
322 because we simultaneously observed the carp to swim closer to the shore during the night (lowered  $d$ ,  
323 Fig. 2B), where we would expect more signal attenuation due to reed growth, suggesting that the carp  
324 actively swam in denser vegetation during daytime in the summer, moving to the sublittoral areas  
325 during night where detectability increased.

### 326 **In summer, interactions are less frequent but more persistent**

327           In warmer months, when the deep zones of the lake become anoxic and the food was  
328 concentrated in the littoral zone, the carp had little to gain foraging-wise from swimming at the lake  
329 centre or in the deep water in the lake centre. Instead, they resided in the shallow waters alongside the  
330 shore where they could seek protection from predators among the food-rich reeds without investing  
331 much energy in mobility (lowered  $d$ ,  $S$ , and  $v$ , Fig. 2B). This introduced a technical inconvenience as reed  
332 attenuated acoustic signals, which caused the data yield to drop substantially during summer (Fig. 2A).  
333 Despite this, we can report the somewhat surprising result that during the summer when carp  
334 associated strongly with the vegetated littoral zone, they interacted less often (lowered  $p$ , Fig. 2C) but  
335 also spend less time apart between interactions (lowered  $\tau^-$ , Fig. 2C). Additionally,  $\tau^+$ , which we should  
336 expect to drop across the summer due signal attenuation, appeared, although noisy, stable throughout  
337 the year. This suggests that inside the reed, fish were interacting in small persistent groups.

### 338 **Social attraction or co-use of suitable habitats?**

#### 339 **Social attraction was a key driver of social interactions**

340           We found that across the year, there were one to six times more interactions in the real data  
341 than in the shuffled data (Fig. 3B). This is strong evidence that social attraction was, in most months of  
342 the year, a key driving mechanism for proximity interaction of carp. The effect sizes were greatest at the  
343 start of the year in winter and decreased towards autumn. The overall number of interactions in the real  
344 data dropped as well (Fig. 3A, note that y-axis is log-scaled). We also observed that effect sizes were  
345 larger during daytime than at night (Fig. 3B). This indicates that nightly mobility (or *stationarity*) took  
346 place in the same locations over at least a week and was less driven by where other fish spend their  
347 nights.

#### 348 **Elevated local clustering revealed tight knit community structure**

349           We found that clustering was higher during daytime than at nighttime in most months (Fig. 3).  
350 Clustering varied over the year, where we observed a decline in clustering from winter through summer  
351 and then an increase from autumn to winter, where by December, clustering had returned to the same  
352 level as in January, in spite of the number of interactions being many times smaller. Nighttime clustering

353 also varied periodically in synchrony with the seasons. We measured the effect size of clustering by  
354 comparing to our null model, and observed that the effect sizes decreased over the year, to the point  
355 where we could not confidently state that any of the observed local clustering was due to social  
356 attraction. At the same time, however, the local clustering was just as high at the end of the year as it  
357 was in the beginning, leading us to reason that over the year the fish grew more habitual, visiting the  
358 same few locations every day at regular times.

## 359 **Network structure at varying time-scales**

### 360 **Social memory varied over the year**

361 If the carp population had no collective social memory they would not form clusters, but instead  
362 mix randomly, and any emerging communities in the interaction network would be due to simultaneous  
363 space use. We studied the interaction networks that emerged when aggregating over time-windows of  
364 different duration (subtracting the corresponding random network produced by the null model), and  
365 measured the number of communities with three or more members as a proxy for the use of social  
366 memory in interactions (Fig. 4). We reason that when it is possible to aggregate over a long time window  
367 and still obtain a number of communities, there is a high degree of social memory in the population.  
368 Furthermore, the longest aggregation that does not wash out communities is a good estimate of the  
369 time-scale of social memory. We found that social memory was significantly more time-persistent in the  
370 summer where, for example, the number of detected communities at night peaked at the two week  
371 aggregation for months May and August. Reversely, in winter months like January and December, the  
372 network mixed on very short time-scales. This is not surprising, as we know this mixing happened due to  
373 shoaling, however, since the fish only shoaled during daytime we were surprised to find that that this  
374 mixing to a large extent persisted into the night.

### 375 **Night communities were numerous and had longer time-scales**

376 In nine out of 12 months, the number of communities during the night was higher than in  
377 daytime. This is not surprising because the fish interacted much more during the day, which caused  
378 mixing between existing groups on shorter time-scales. Curiously, however, the measured time-scales  
379 (aggregation time where number of communities peaks and then drops) of nightly communities were in  
380 many cases longer than those of day communities.

## 381 **Discussion**

382 We observed that the social behaviour of a population of carp was highly dynamic across daily  
383 and seasonal scales, where the clustering and social memory was oscillating based on interactions  
384 between diurnal and seasonal rhythms. Thus, inferring social network information from time snapshots  
385 of data in selected weeks or months can lead to biased conclusions. Our analysis also showed that the  
386 groups of carp were indeed aggregating because of social attraction and the carp were likely to spend  
387 time in characteristic groups with the same individuals for up to two weeks particularly during the  
388 nighttime in the summer, indicative of pronounced social memory. We finally observed higher clustering  
389 during the daytime than the nighttime, and surprisingly large shoals of actively moving carp in the

390 wintertime during daytime, which as discussed below is likely a response to environmental conditions in  
391 the lake and the origin of the fish. Methodologically, our analysis can serve as a template for future  
392 investigations into the causes and consequences of social behaviour in the wild as more high-resolution  
393 movement data in the wild begins to emerge. Our findings can also help inform both sampling design  
394 (Bajer & Sorensen, 2012; Muška et al., 2018) or removal strategies (Bajer et al., 2011; Carl, Weber &  
395 Brown, 2016) for common carp in the wild.

396 We found highly variable social behaviour of our carp population in the wild over the course of a  
397 full year. The carp aggregated in somewhat deeper zones in wintertime in agreement with previous  
398 natural history knowledge of the species (Armstrong et al., 2016; Bajer et al., 2011; Bauer & Schlott,  
399 2004; Gusar, 1989; Johnsen & Hasler, 1977; Penne & Pierce, 2008; Taylor et al., 2012), however, these  
400 zones did not encompass the deepest points of the lake. Previous work in other systems with low  
401 resolution telemetry has reported carp were largely sedentary during the wintertime with only localized  
402 activity (Bauer & Schlott, 2004; Johnsen & Hasler, 1977; Jurajda et al., 2016; Penne & Pierce, 2008), in  
403 stark contrast to the high levels of daytime activity we observed during winter in Kleiner Döllnsee.  
404 Elevated levels of overwintering activity of carp are usually attributed to stressors, such as low oxygen  
405 (Bauer & Schlott, 2004), movement of humans on the ice surface (Johnsen & Hasler, 1977), or predators  
406 (Adámek, Sukop, Moreno Rendón, & Kouřil, 2003). In our study, hypoxic conditions was an unlikely  
407 stressor as Kleiner Döllnsee is well oxygenated in the wintertime. Moreover, the fish were not manually  
408 tracked eliminating human on-ice activity as a possible disturbance. Therefore, reasons for the  
409 surprisingly active shoaling behaviour are likely related to “hypothetical” predator avoidance behavior  
410 shown by the introduced carp in their new, unfamiliar environment particularly during daytime in  
411 response to visual predators. Shoaling is a common response to predation risk (Pitcher, 1986) as it offers  
412 increased predator detection probability (Godin, Classon, & Abrahams, 1988) and dilution of risk  
413 (Queiroz & Magurran, 2005), and shoaling can confuse predators (Krakauer, 1995). The carp we tracked  
414 were still likely responsive to predation risk despite the fact that they were large enough to escape the  
415 threat of predation from most predators in the lake (Gaeta et al., 2018). Possible predators include  
416 European catfish (Carol, Benejam, Benito, & García-Berthou, 2009), great cormorants (*Phalacrocorax*  
417 *carbo*) (Adámek, Kucerova & Roche, 1999) or mustelids such as the European otter (*Lutra lutra*)  
418 (Adámek et al., 2003; Britton, Pegg, Shepherd, & Toms, 2006). Indeed, carp in a reservoir were observed  
419 to spend their nights in deep hypoxic waters, which was also speculated to be a response to a  
420 population of wels catfish present in the reservoir, which hunt nocturnally (Benito et al., 2015). We  
421 found that the carp reduced their shoaling behaviour in the second winter in our study, after they were  
422 more familiar with the (rather low predation) risks of the novel environment, which lends further  
423 support to the idea that daytime winter shoaling in the first winter after introduction to their new  
424 environment was likely a predator-avoidance response driven by unfamiliarity with possible predation  
425 threats during daytime in winter. We expect that carp should behave cautiously in a novel lake  
426 environment, despite a lack of strong predation risk due to their larger size (Lorenzen, 2000). The anti-  
427 predator behaviour could become fixed from early life experience or from the evolutionary past  
428 (Blumstein, 2006; Magurran, 1990; Swaney, Cabrera-Álvarez, & Reader, 2015). When compared to  
429 behaviour in a controlled laboratory environment conducted in large tanks, carp have been observed to  
430 behave highly cautiously after introduction to a predator free semi-natural pond environment of

431 comparable size, where the fish reduced their visits to open feeding sites (Klefoth et al., 2012). In the  
432 case of the experiment by Klefoth et al. (2012) water from a nearby lake was flowing through the semi-  
433 natural ponds, and therefore the carp were likely exposed to chemical cues signalling that predators  
434 could be present. Hence, it is reasonable that the fish tracked in our experiment, which were recently  
435 introduced to the lake, could be behaving cautiously, despite a low actual predation risk. After learning  
436 about the true predation threat in the lake was likely low (in fact no otters were recently seen in the  
437 lake and cormorant predation is low too), the carp likely behaved less cautiously in the second winter  
438 and reduced their daytime social behavior substantially.

439         The carp were more likely to shoal in the daytime than the nighttime throughout most of the  
440 year. As the daytime clustering corresponded with offshore movements, into riskier habitat outside  
441 plant refuges, the daytime clustering may partially be explained as a response to visual predators such  
442 as cormorants (White et al., 2008) or pike (Eklöv, 1992) that actively hunt during daytime in the study  
443 lake (Kobler et al., 2008). Diurnal migrations, in particular diurnal vertical migrations, are also a well  
444 known behavioural response displayed by many smaller bodied fish species, macroinvertebrates and  
445 zooplankton, where individuals balance bioenergetic efficiency, foraging opportunities and predation  
446 risk, by sheltering in deeper water and foraging in shallower waters when predators are less active  
447 (Mehner, 2012). Some cyprinids have also been observed to migrate horizontally on a daily scale  
448 (Kubečka, 1993; Nakayama et al., 2018), as we observed the carp doing in our study. Similar to the carp,  
449 common bream (Schulz & Berg, 1987) and freshwater drum, *Aplodinotus grunniens* (Rypel & Mitchell,  
450 2007), have been observed to move from littoral habitats during the night to pelagic habitats during the  
451 daytime. Further a whole fish assemblage in a Czech reservoir aggregated in the pelagic during the  
452 daytime and spread out in the littoral during the nighttime (Muška et al., 2013, 2018). Other small  
453 cyprinid species have been observed to migrate horizontally in the opposite direction to our tracked  
454 carp, sheltering in the littoral during the daytime and foraging in the pelagic at nighttime (Haertel &  
455 Eckmann, 2002; Nakayama et al., 2018). The ultimate mechanism for diurnal horizontal migrations and  
456 in which direction they occur in these species is not known, but it is expected to also relate to a tradeoff  
457 between resource availability and predation risk (Rypel & Mitchell, 2007; Schulz & Berg, 1987; Shoup,  
458 Boswell, & Wahl, 2014). Hence, in the summertime the carp may be foraging in the littoral habitat  
459 during the night-time, avoiding predation risk from the pelagic catfish (Benito et al., 2015; Carol,  
460 Zamora, & García-Berthou, 2007) and foraging in more pelagic habitat during the daytime, while forming  
461 shoals to reduce perceived predation risk from pike or otters.

462         We found longer-lasting and smaller groups of fish during the summertime, in particular during  
463 the nighttime. Our comparisons to a null model of behaviour (Spiegel et al., 2016) indicated that these  
464 clusters were not driven by attraction to similar locations at similar times, but were truly a result of  
465 attraction to the individual carp. We found that the carp during the summertime had a pronounced  
466 social memory, showing preferences to interact with certain individuals for up to two weeks.  
467 Importantly, two weeks is longer than it took the twelve days for guppies, *Poecilia reticulata*, to learn  
468 and retain the identity of conspecifics (Griffiths & Magurran, 1997); hence it is likely that the carp were  
469 able to remember the identities of their conspecifics. Furthermore, although the carp spent their days  
470 mixing in larger groups, they tended to spend the nights together in smaller characteristic groups. Carp

471 anglers have long noted that carp have “friends”, as many have observed that after catching one specific  
472 individual carp a second individual is predictably captured (Hearn, 2000). In juvenile fish preferred  
473 interactions have can be based on kinship (Piyapong et al., 2011); however, kinship is typically not the  
474 case in adult fish (Croft et al., 2012; Russell, Kelley, Graves, & Magurran, 2004), and therefore it is likely  
475 that the groups we observed were not based on kinship. In the summer months, Kleiner Döllensee is  
476 productive and resource-rich; however, the spatiotemporal distribution of food is patchy across the  
477 lake. In such patchy environment, carp should benefit from information sharing (Monk et al., 2018) to  
478 find resources faster. Indeed, when feed bags were introduced into a lake the whole population of carp  
479 were able to find a feed bag within four nights, much faster than possible by individual private searching  
480 (Bajer et al., 2010), suggesting social learning and other forms of communication (e.g., chemical  
481 communication through excretion; Brönmark, & Hansson, 2000). Therefore, we suggest that the small  
482 groups of carp we found in the summer may provide them with valuable information regarding resource  
483 distribution in the lake. Carp are also quick to learn from trained demonstrators (Karplus et al., 2007;  
484 Klefoth et al., 2012; Zion et al., 2007), and can retain socially learned information for at least one year  
485 as, population-wide catch rates were found to decline for an entire year after angling a pond despite  
486 most individuals in the population never having been captured (Beukema, 1970).

487         Recognizing specific individuals by social memory may provide additional foraging benefits to  
488 the carp in our study. Familiarity in general is known to provide fitness benefits (Seppä, Laurila,  
489 Peuhkuri, Piironen, & Lower, 2011), in particular via the increased foraging success through directed  
490 social learning as fish may learn better from familiar individuals (Swaney et al., 2015). Hence, knowing  
491 and following the most productive foragers in the population should be beneficial, especially in the  
492 context of producer scrounger dynamics, where some individuals may be generally better at finding new  
493 food sources through private information, while other individuals tend to follow those individuals to find  
494 food (Caraco & Giraldeau, 1991). As well, carp are known to show consistent inter-individual differences  
495 in foraging rate (Pollux, 2017) and individual variation in diet (Mehner et al., 2018) and taste preferences  
496 (Kasumyan, 2000). Consequently, certain individual fish may have better information regarding certain  
497 food sources within the patchy resource distribution in a natural lake, providing fitness benefits to  
498 sociality during resource-rich environmental conditions in the warmer periods of the year.

499

## 500 **Conclusion**

501         We found that carp adjust their social behaviour following several timescales of oscillation,  
502 where yearly and daily oscillations very likely respond to variation in perceived predation risk and  
503 resource availability, moderated by the benefits of social interactions. Despite a low realized threat of  
504 predation in our study lake given the large size of the tagged carp, the fish displayed cautious behaviour  
505 after introduction into a novel environment, particularly during the day and in winter by revealing strong  
506 tendencies of shoaling. Further, the carp displayed pronounced social interactions based on social  
507 attraction with the community organization being non-random and based on a social memory. These  
508 findings strongly indicated that carp are able to recognize one another and to take advantage of  
509 familiarity during productive phases in warmer months of the year. To our knowledge, our work is



510 among the first year long high-resolution analyses of animal social networks in the wild. Our analysis  
511 may serve as a methodological template for future analyses into the rhythm of relationships in other  
512 species and taxa.

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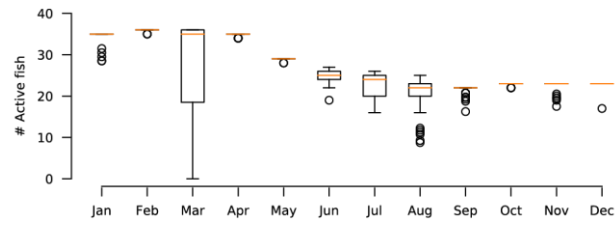
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881 **Tables and Figures**

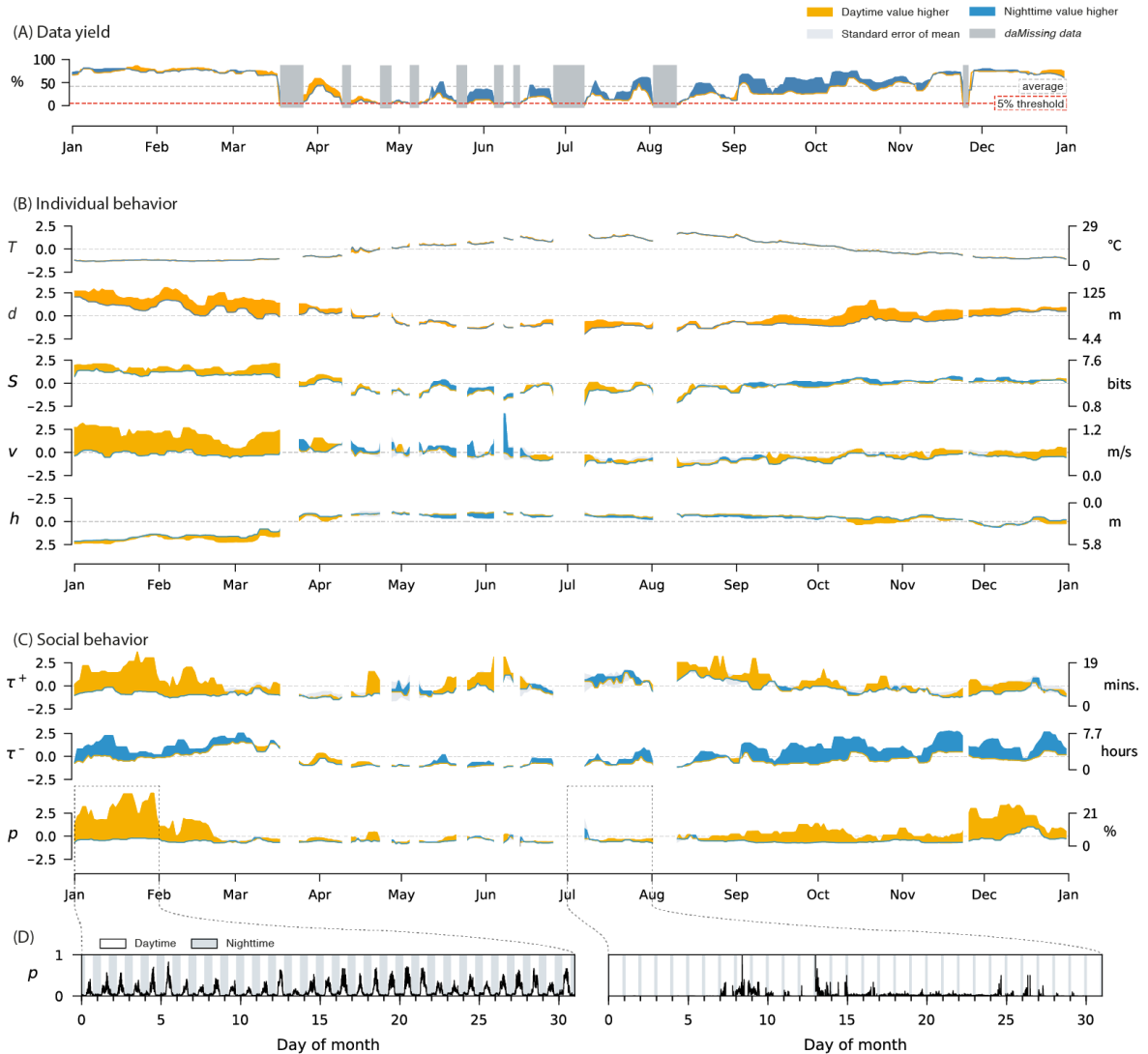
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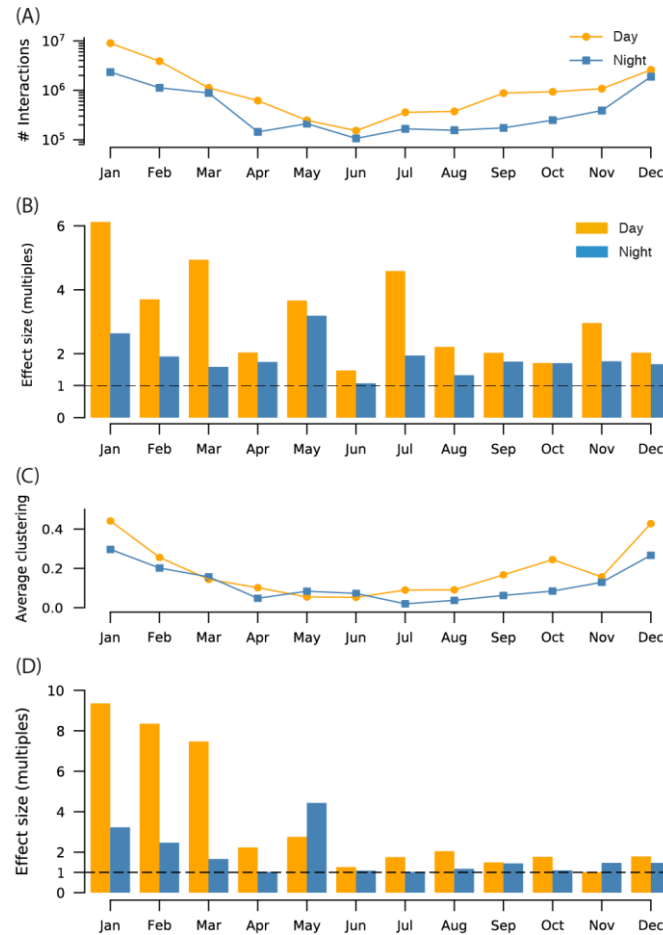
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885 FIG. 1. Distribution of number of fish with successfully recorded mobility on each day, across  
886 the year. At the beginning of the year 36 fish are active and at the end of the year 23 are active.



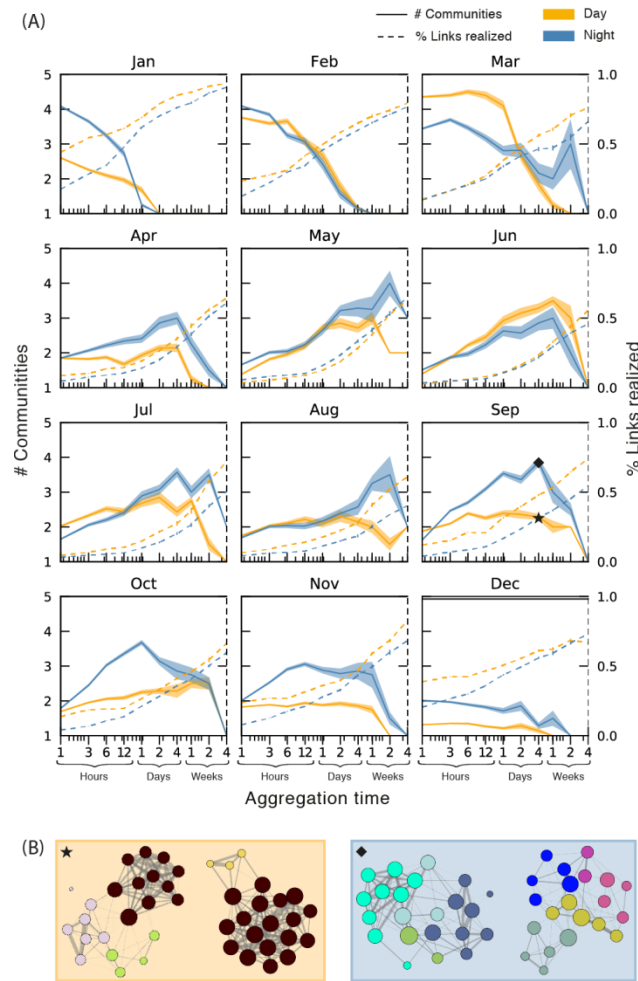
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**FIG. 2. Seasons and daytime modulate individual and social behavior.** (A) Percentage successful location measurements across the year. Using a 5% threshold we label the periods marked in grey as missing data. Notice how these periods are missing in panels (B) and (C). (B) Individual behavioral indicators computed from location data, including temperature,  $T$ , distance from shore,  $d$ , spatial entropy,  $S$ , velocity,  $v$ , and depth,  $h$ . All values in panels (B) and (C) are population averages. Deviations are represented as the average standard error of the mean of day and night, which rarely exceeds the absolute difference between day and night. The left set of axes are standardized values representing standard deviations from the mean, and the right give the actual values. (C) Social behavioral indicators measured at the level of pairs. We measure social activity in terms of the typical interaction duration,  $\tau^+$ , time between interactions,  $\tau^-$ , and interaction probability,  $p$ . (D) Example of how  $p$  varies rhythmically throughout January and July.



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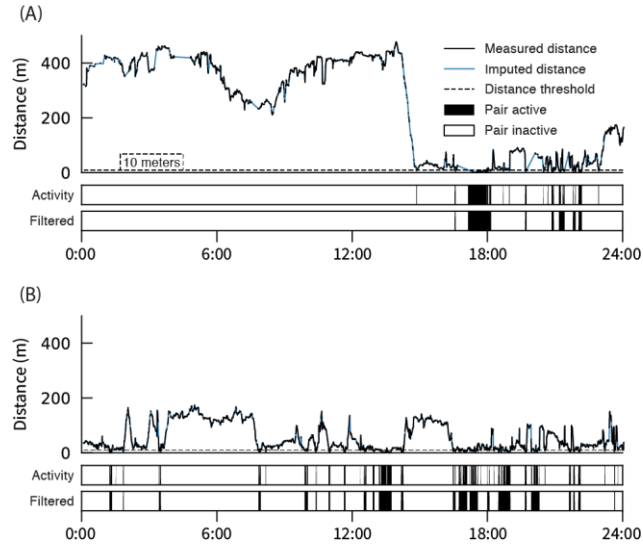
**FIG. 3. Effect sizes compared to shuffled data.** (A) Number of interactions observed during day and night in the real data over the year. Note the y-axis is log-scaled. There are many times more interactions during daytime, and a decrease in total number of interactions observed over the year. (B) The effect size of number of interactions in the real data as compared to the shuffled data (count of real divided by count of shuffled). The dashed line signifies a one-to-one ratio and therefore no effect. (C) Average network clustering coefficient. (D) Effect size of clustering.



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914 **FIG. 4. Number of communities at different levels of aggregation.** (A) Number of communities  
915 (3 or more members) and percentage of realized links as a function of aggregation time for  
916 each month. Each has its own y-axis. Shaded regions surrounding the solid lines are standard  
917 errors. The x-axis is log-scaled. (B) Four example networks, two for day (left) and two for night  
918 (right), with communities detected (coloured separately) by the Infomap algorithm [18]. Each is  
919 an aggregate over four days in September, the references marked with a star and a diamond on  
920 the corresponding curves in (A).

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924 **FIG. 5. Inferring proximity network with distance threshold.** (A) and (B) show how distance  
925 between two different pairs of fish vary throughout the same day. The dashed line at *Distance* =  
926 10 m is the threshold we enforce to get the activity series shown below, which we filter to  
927 produce the bottom series.