Are some sharks more social than others? Short- and long-term consistencies in the social behavior of juvenile lemon sharks

Jean Sebastian Finger https://orcid.org/0000-0002-4134-7073,
Tristan L. Guttridge,
Alexander D. M. Wilson,
Samuel H. Gruber,
Jens Krause https://orcid.org/0000-0002-1289-2857

1   **Are some sharks more social than others? Short and long-term consistencies in the social behavior**

2   **of juvenile lemon sharks**

3   Authors: J.S. Finger[1,2,3*], T.L. Guttridge[2], A.D.M. Wilson[4], S.H. Gruber[2], J. Krause[1,3]

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5   [1] Humboldt-Universität zu Berlin, Faculty of Life Sciences, Albrecht Daniel Thaer-Institut, Berlin,

6   Germany

7   [2] Bimini Biological Field Station Foundation, Bahamas

8   [3] Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

9   [4] School of Life and Environmental Sciences, University of Sydney, New South Wales 2006, Australia.

10

11   Correspondence:

12   J.S. Finger,

13   Bimini Biological Field Station Foundation,

14   9300 SW 99 St,

15   Miami FL 33176-2050, U.S.A.

16   js.finger@yahoo.fr

17   Orcid ID: orcid.org/0000-0002-4134-7073

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Abstract:

Despite substantial research interest in understanding individual-level consistency in behavioral attributes, significant knowledge gaps remain across traits and taxa. For example, relatively few studies have looked at social personality in large marine species such as elasmobranchs and whether or not individual differences in behavior are maintained in unstable social groups (i.e. fission-fusion dynamics). However, it is important to investigate this topic in other model species than the usually small species with short generation times typically investigated in these areas of behavioral ecology. Indeed, studies on ecologically diverse taxa could provide mechanistic insights into the emergence and maintenance of animal personality and dynamics of social groups in animals. In addition, understanding social behavior at the group- and individual-level could improve conservation management of these large animals with long generation times (e.g. removal of particular behavioral types by fisheries practices). Here, we investigated consistent individual differences in sociability in wild juvenile lemon sharks (*Negaprion brevirostris*) over both short- (4 to 18 days) and long-term (4 months) sampling periods. Individual sharks were observed in social groups and scored according to the number of social interactions performed during observations. Despite variable individual group compositions between repeated trials, sharks showed consistent individual differences in their social behavior over both time scales. These results suggest reduced plasticity and highlight individuality as an important explanatory variable for the social dynamics of juvenile lemon sharks. In addition, long term stability observed in this wild population demonstrates the importance of personality in the daily behavioral repertoire of juvenile lemon sharks. Our results are discussed in the context of other shark studies and taxonomic groups and potential avenues for future research are proposed.

44   **SIGNIFICANCE STATEMENT**

45   This study investigated the social personality axis in a wild population of juvenile lemon sharks. First, we

46   demonstrated consistent individual differences in their tendency to socialize. Second, we showed that

47   individuals maintained their differences over a four-month period in the wild. Finally, we found that

48   individual social behaviors were maintained despite being tested in variable group compositions. These

49   results highlight the importance of individuality in the social dynamic of a poorly investigated animal and

50   suggest personality as an important aspect of juvenile lemon sharks' everyday life over a relatively long-

51   term period.

52   Key words: Fission-fusion, follower, group phenotype, leadership, personality, social dynamics.

53

54   **INTRODUCTION**

55   Animal personality, consistent individual differences in behavior across time and contexts, has been

56   described in a broad spectrum of taxa (Gosling 2001; Sih et al. 2004; Reale et al. 2007) and is recognized

57   as a fundamental aspect of ecology and evolution (Sih et al. 2012; Wolf and Weissing 2012). Furthermore,

58   it is now understood that individual differences need to be incorporated within conservation management

59   programs (Conrad et al. 2011; Mittelbach et al. 2014). However, a primary obstacle for many species,

60   including large-bodied marine animals such as sharks, lies in the fact that not enough data exist to

61   understand if and how the inclusion of personality could benefit such programs. This issue can be

62   problematic considering the sensitivity of mega-fauna to anthropogenic harvest and overexploitation (e.g.

63   Lewison et al. 2004; Estes et al. 2011). For example, sharks have only recently received attention from an

64   individual-based behavioral standpoint (e.g. Huveneers et al. 2013; Vaudo et al. 2014; Matich and

65   Heithaus 2015; Towner et al. 2016; Finger et al. 2017) and a behavioral consistency standpoint in the last

66   few years (Jacoby et al. 2014; Wilson et al. 2015; Byrnes and Brown 2016; Byrnes et al. 2016a, b; Finger

67   et al. 2016). In terms of consistency in individual social behavior, what little information there is remains

68   unclear and in need of further study. For example, Jacoby et al. (2014) found consistent individual

69   differences in social network position in a captive population of juvenile catsharks (*Scyliorhinus canicula*)

70   but significance was lost once the group effect was controlled for. In contrast, Wilson et al. 2015 found no

71   evidence of consistency in social network position in wild juvenile lemon sharks (*Negaprion brevirostris*).

72   Sharks are generally large-bodied, long-lived animals with a large brain to body mass ratio (Northcutt

73   1977; Yopak et al. 2007). They exhibit slow growth and reproduction rates, while occupying a relatively

74   high trophic position (e.g. Stevens et al. 2000; Dulvy et al. 2014). As a result, sharks could be an

75   interesting addition to smaller aquatic vertebrates (with relatively fast generational turn-over) usually

76   studied within the animal personality framework. For instance, while predation is often a factor underlying

77   the evolution of social grouping, as frequently seen in teleost fishes (Krause and Ruxton 2002), some

78   gregarious shark species such as the scalloped hammerhead (*Sphyrna lewini*; Klimley 1985) actually

79   experience low risk of predation overall. It is then conceivable that alternative selective pressures shaped

80   the evolution of social behavior in many shark species. As similar assumptions could be drawn for

81   individual differences in sociability, it is important to further investigate personality in sharks. In addition,

82   expanding this research to wild populations and long-term observations will help to determine the

83   importance of personality to sharks' everyday life. Because sociability has already been described in

84   different shark species (e.g. Myrberg and Gruber 1974; Klimley 1985; Guttridge et al. 2009; Guttridge et

85   al. 2011; Jacoby et al. 2012a; Mourier et al. 2012, 2017), it is a critical step for the development of better

86   management programs. Indeed, the removal of particular personality types (Biro and Post 2008; Sutter et

87   al. 2012; Biro and Sampson 2015) through fisheries might have unknown consequences for the food web,

88   ecosystems and environmental management. For example, the documented risk posed by fishery targeting

89   aggregations (Mucientes et al. 2009; Jacoby et al. 2012a), could conceivably select against social

90   individuals (i.e. higher tendency to aggregate).

91   We investigated the presence of consistent individual differences in the social behavior of wild juvenile

92   lemon sharks by testing groups of six individuals. However, this study differs from those previously

93   conducted in several aspects. First this study assessed consistency over both short (4-18 days) and long-

94   term (4 months) periods in wild sharks. Long-term observations have obvious benefits (Stamps and

95   Groothuis 2010) but are rarely conducted on wild animal populations (Archard and Braithwaite 2010) and

96   especially with such long-lived species. However, a major difficulty in generating long-term data sets is

97   that individuals disperse or suffer mortality (Gruber et al. 2001), which can lead to different individuals

98   being caught during a given sampling event. To account for this here, except for a subset of the data,

99   individuals were haphazardly assigned to groups for retests, leading to variation in individuals' social

100   environments (i.e., group composition). This approach provided the opportunity to determine if observed

101   consistency in tendency to socialize can be attributed to individual differences and is not just a result of

102   group effects and composition (Pritchard et al. 2001; Harcourt et al. 2009b; Kurvers et al. 2009; Cote et al.

103   2012). In addition, changing group composition while testing social personality in captivity reflected rapid

104   changes in social partners commonly observed in juvenile lemon sharks in the wild (Guttridge et al. 2011;

105   Wilson et al. 2015). Indeed, this aspect (among others) of their social dynamic has been shown to

106   resemble that of wild guppies (*Poecilia reticulata*), a fish species demonstrating social fission-fusion

107   behavior (Wilson et al. 2014, 2015). In summary, we tested the predictions that wild individual juvenile

108   lemon sharks consistently differ in their social behavior over short (5 to 18 days) and long-term (4

109   months) tests and further, that these differences were robust to changes in group composition.

110

111   **METHOD**

112   *Study site and Sharks*

113   This study was conducted on Bimini (20° - 28°N, 72° - 80°W), situated approximately 85 km east of the

114   coast of Florida (USA) in The Bahamas. Wild juvenile lemon sharks from two adjacent mangrove-fringed

115   habitats (North Sound and Shark Land) were captured using gillnets (see Manire and Gruber 1991 for

116   details) in June (7-day capture session) and November 2012 (3-day capture session). Upon capture, each

117   individual was measured (pre-caudal length: PCL), sexed and equipped with a unique color-coded tag (T-

118   bar type, Floy Tag Manufacturing) for visual identification.

119   Lemon sharks were our test subject because they are a common, large coastal species in the western

120   Atlantic. In some locations, they show long-term site attachment (approx. three years) allowing their

121   capture and recapture over extended periods while living in their natural habitat (Morrissey and Gruber

122   1993; Dibattista et al. 2007; Chapman et al. 2009). In addition, they have been successfully used in semi-

123   captive behavioral experiments (e.g. Guttridge et al. 2009; Finger et al. 2016).

124   *Experimental set-up*

125   Sharks were housed in a large oval-shaped pen (10 x 5 m) constructed just offshore in the North Sound on

126   sand bottom flats. They were given at least four days in the holding pen to acclimatize to captive

127   conditions before beginning the experimental procedure. During holding time, they were fed every three

128   days on a diet of fresh and frozen local fish (*Sphyraena barracuda*).

129   A channel (length, 4 m) linked the experimental pen to the holding pen. The circular experimental pen

130   (diameter, 10 m) was equipped with a camera recorder placed 6 m above the center and operated by a

131   system of ropes. A wooden tower (height, 3 m) was placed outside the pen to allow observations (Fig. 1).

132   The day before observation, six sharks, selected to reduce size difference (within PCL ± SD = 4.7 ± 2.73

133   cm), were ushered into the experimental pen, fed to satiation (to insure similarity of hunger level between

134   individuals) and left overnight to acclimatize to their environment. Sex has been shown to have no

135   influence on social dynamics of juvenile lemon sharks in Bimini (Guttridge et al. 2009, 2011) and was not

136   considered further in the design of this experiment. On the day of observation, the swimming behavior of

137   the six individuals was filmed for 20 minutes. Each individual was marked on their dorsal fins with unique

138   color-coded tags to allow for subsequent identification and tracking during video analyses. Upon

139   completion of filming, sharks were released, or relocated to the holding pen to await further retesting (see

140   below for test periods).

141 *Test periods and group composition changes*

142 During this study, two rounds of tests were carried out: June and November 2012. In June, individuals

143 were tested only once (N=84; 41 females and 43 males, mean pre-caudal length $\pm$ SD = 51.8 $\pm$ 5.7 cm)

144 and then released in their natural habitat. In November, all sharks (N=48; 19 females and 29 males, mean

145 pre-caudal length $\pm$ SD = 54.3 $\pm$ 6.1 cm) were tested twice (time between tests: 4 to 18 days; 8.5 $\pm$ 4.3

146 days), and of these individuals, 23 (14 females and 9 males) had been tested in June previously. Each

147 observation session started at similar water depth (mean depth $\pm$ SD = 79 $\pm$ 12.4 cm), 1.5 hr before or after

148 a slack low tide.

149 Group composition changes occurred haphazardly between June and November tests (23 individuals from

150 11 different groups from June were haphazardly allocated to 8 groups in November). Group mixing

151 between test and retests in November consisted of exchanging half of a group (3 individuals) with another

152 half. Such mixing occurred for 4 groups (N=24 individuals) whereas for 4 other groups composition

153 remained unchanged.

154 *Social interaction observations*

155 During video processing, data were recorded every 30 seconds, across 20-minute observation sessions

156 (thus 40 observations in total); each time the focal individual was recorded as social or asocial. Juvenile

157 lemon shark social behavior is characteristically composed of following or paralleling with other

158 individuals (see Table 1 for definitions). A leading event can be defined as occurring when one individual

159 is being followed but is not paralleling or following another individual (Table 1). As a focal individual

160 being followed might not reflect its wish to socialize, we considered only "active" events of social

161 interaction (i.e. following and paralleling) as a social interaction performed by this individual. Resting and

162 milling (see Table 1) were designated here as non-social events for two reasons. First, resting behavior in

163 juvenile lemon sharks is not well understood and it has been shown that most (>95%) social interactions

164 occur during active swimming (Guttridge et al. 2009). Second, individuals were considered as social only

165 when being notably influenced by another individual. Two (or more) individuals could cross paths but if

166 neither of them modified their swimming movements then they were not considered to be interacting.

167 Each individual's social behavior score was obtained by summing the number of active social events (see

168 below) over the 40 observations. All sharks in the arena were observed in this manner.

169 An algorithm was developed to quantify the social behaviors described above. This tool has also been

170 used to analyze juvenile lemon sharks' social behavior in another study (Keller et al. 2017). Briefly, for

171 each of the 40 observations, this algorithm used position (coordinates of the tip of the snout) and

172 orientation of the six individuals at time *t*, *t*+1 and *t*+2 second. Orientation was obtained relative to the

173 previous point, therefore, at time t, orientation was obtained by adding a tracking point at t-1 second.

174 Tracking was completed manually by marking the snout of each shark using MtrackJ (Meijering et al.

175 2012) within ImageJ (Rasband 1997). Using these data, the algorithm calculated distances between

176 individuals, along with the differences in orientation and position (front, behind, side by side) between

177 sharks. Additional tracking (t+1 and t+2 seconds) was used to determine if overtaking occurred, and if a

178 dramatic turn of one shark (creating a large orientation difference at time t) influenced (i.e. following)

179 other individuals (resulting in similar dramatic orientation change of the followers during t+1 and t+2).

180 The resulting values obtained from these calculations allowed the algorithm to define each individual's

181 social behavior as following (within social distance and behind another individual and similar orientation

182 or influenced by this same individual), paralleling (within social distance and side by side or overtaking

183 another individual and similar orientation than this same individual) or asocial (outside of social distance

184 or not being influenced by other individuals). Upon completion, the algorithm provided the total number

185 of social events over the 40 observations (paralleling and following; Table 1) as the individual social score

186 in this investigation. The above algorithm was used to standardize data collection and reduce potential

187 observer bias.

188 *Social distance*

189   Previous studies used a maximum social distance of either one (Wilson et al. 2015) or four body lengths

190   (Guttridge et al. 2011) when considering social interactions of juvenile lemon sharks in semi-wild or wild

191   conditions. In contrast, 2.5 body lengths between individuals were found to be best in our experimental

192   setup. This value was observed as being the maximum distance at which individuals performed following

193   behavior during preliminary video analyses (distance was calculated using coordinates of sharks in videos

194   and absence or presence of social interaction was determined by two observers).

195   A comparison between social distances (i.e. 1, 2.5 and 4 body lengths) showed that below 2.5 body

196   lengths, a large number of associations were missed but above 2.5 body lengths only very few were added.

197   *Algorithm reliability*

198   To control for the reliability of this algorithm, 4 videos that were processed through the algorithm were

199   also analyzed manually. Observers, naïve to the algorithm, were asked to describe each individual social

200   behavior as describe above (to mimic analyses by the algorithm). Social scores obtained from manual

201   observations and the above algorithm were highly correlated (Spearman's rank correlation: $r_s = 0.96$,

202   N=24, P<0.001) and did not differ significantly (Wilcoxon paired test: V=138.5, P=0.71, N=24). We

203   therefore concluded that the algorithm showed results highly similar to those obtained through manual

204   observation and could therefore be confidently applied to the full data set.

205   *Short and long-term tests*

206   To test short-term consistency, analyses were performed within the November period overall, then we

207   divided this period into groups of mixed and non-mixed composition. To test long-term consistency,

208   analyses were performed between observations from June and November. We took the first trial of

209   November tests instead of the average between the two trials to minimize the potential of confounding

210   effects (due to habituation, familiarity development etc.).

211   *Correlation and permutations*

212　To investigate consistent individual differences in social behavior, we first used Spearman rank

213　correlation analyses within the different subsets of data described above. If a significant correlation was

214　found (for short-term or long-term data) a permutation analysis was performed. For permutation analyses,

215　individual social scores were randomly sampled from the social groups they were tested in. Therefore, a

216　shark could be assigned only a social score from another shark (or his own) from the same social group.

217　This was applied to June, November first and November second trials. Using this randomly permuted

218　data, correlation tests were performed between trials (e.g. correlation between permutated June and

219　permutated November first trial for long-term tests) and the Spearman's rho estimations extracted. This

220　step was repeated 10,000 times to obtain a distribution of randomly simulated rho for each correlation we

221　were interested in. This distribution was then compared to the observed rho (estimated from original data)

222　by extracting the proportion of simulated rho greater than the observed rho (thereafter referred to as P). If

223　P was found to be smaller or equal to 0.025, we deemed our observed correlation significant which was

224　used as a demonstration of consistent individual differences. These within-group permutations were

225　necessary to control for a potential effect of pseudo-replication created by testing individuals in groups

226　(Croft et al. 2011) and the possibility that any observed consistency could be due to consistent differences

227　in overall group behavior between trials.

228　*Repeatability*

229　To provide a repeatability score of sociability along with a 95% confidence interval, the full data set (all

230　trials included) was analyzed using a linear mixed model with individual ID as random factor and sex,

231　size, capture location (i.e. nursery), time in pen before trial and period of observation (June; November) as

232　fixed effects. Social score was normalized using a square root transformation. Normalization of the data

233　allowed the use of the function exactRLRT from the RLRsim package (Scheipl et al. 2008) to test

234　significance of the random term (i.e. individual ID). Repeatability was calculated according to Nakagawa

235　and Schielzeth (2010). The 95% confidence interval was calculated using the confint function from lme4

236   package (Bates et al. 2015). These analyses were performed on the overall data set. All analyses were

237   performed in R v3.2.3 (R Core Team 2015).

238

239   **RESULTS**

240   Consistency in social behavior was found over short-term periods of several days (Spearman rank

241   correlation: r_s=0.43, N=48, P<0.001, Fig. 2a) and long-term periods of four months (Spearman rank

242   correlation: r_s=0.52, N=23, P = 0.01, Fig. 2b). The consistency found here was not caused by differences

243   in overall group behavior (permutation analyses: short-term tests: P=0.005; long-term tests: P=0.0088).

244   Within short tests, those that did not experience any changes in group composition did not show consistent

245   differences in social behavior (Spearman rank correlation: r_s=0.39, N=24, P=0.057,) whereas individuals

246   that experienced a mixing of groups did (Spearman rank correlation: r_s=0.43, N=24, P<0.05; Permutation

247   analyses: P=0.0094). However, individuals from the short-term non-mixed group showed consistent

248   individual differences as well, when one outlier (see Fig. 3a) was removed (Spearman rank correlation:

249   r_s=0.58, N=23, P<0.01).

250   Overall, juvenile lemon sharks demonstrated repeatability in their social behavior (repeatability= 0.49; CI:

251   [0.36, 0.51]; RLRT=16.578, P<0.001) when controlling for size, sex, location of capture, time in captivity

252   before observations and period of testing.

253

254   **DISCUSSION**

255   In this study, we explored the presence of a social personality trait in wild juvenile lemon sharks. In doing

256   so we found that sharks consistently differed from each other in some aspects of their social behavior

257   despite being tested in groups (see Webster and Ward 2011 for mechanisms having the potential to

258   suppress individual differences) over a four-month period. Overall, we found a repeatability of 0.49,

259 which is relatively high (see Bell et al. 2009) and consistent with other studies of wild populations (Bell et

260 al. 2009). In addition, consistent individual differences were still maintained despite changes in group

261 composition. The later result indicates that, at least in the juvenile lemon shark population studied,

262 individual social behavioral types play an important part in the social dynamics of these animals and could

263 have a strong impact on their social behavior in the wild.

264 As mentioned above, social personality has already been investigated in sharks (Jacoby et al. 2014;

265 Wilson et al. 2015). However, our study differs from these other investigations in several important points.

266 First, despite using the same species and age criterion, Wilson et al. (2015) did not find consistency in the

267 social proxies they used. While these contrasting results might be attributed to dissimilarities between

268 populations, there are also several methodological discrepancies between Wilson et al.'s study and ours

269 (e.g. sampling method/frequency and smaller sample size). A convergence of methods, to investigate

270 consistent individual differences in these two juvenile lemon shark populations would be useful. Indeed,

271 the possibility to compare between populations might lead to important insights into causes of emergence

272 and maintenance of animal personality. Second our investigation differs from Jacoby et al.'s (2014) study

273 in which consistent individual differences in the social behavior of juvenile catsharks were detected.

274 While they maintained the composition of social groups in their experiments, we allowed it to vary

275 between trials in ours. This was an important aspect of our experimental design for two reasons. First, we

276 believe that our approach reflects natural social mixing between individuals likely to occur in juvenile

277 lemon shark nurseries. Second it indicated that our observed results were not caused by consistent overall

278 group differences. Similarly, keeping group composition constant between trials to investigate social

279 personality in the catshark (Jacoby et al. 2014) may blur the distinction between individual and group

280 behavior differences as causes for Jacoby et al's observation. This concern is reinforced by the fact that

281 individual catsharks (*Scyliorhinus canicula*) prefer certain individuals over others (Jacoby et al. 2012b)

282 which might influence individual social tendency based on group composition. However, in contrast to

283 juvenile lemon sharks, in catsharks not mixing group composition and allowing affinity to develop reflects

284   their ecology during early life stages. Indeed, they are a sedentary species, that hatch in egg clusters,

285   display high site fidelity and are therefore expected to have a pre-determined and relatively stable social

286   environment (D.M.P. Jacoby personal communication). Therefore, mixing group composition in this

287   system might not be relevant to describe the social dynamic of juvenile catsharks in the wild. This

288   highlights the importance to carefully consider the ecology and natural behavior of the species if one is

289   interested in understanding the consequences of individual differences in behavior in the wild.

290   Nevertheless, the contrast between these two species provides interesting systems to investigate social

291   dynamics in two alternative social systems. Here again, converging methods in future work could be

292   highly beneficial in our understanding of animal personality and social systems in animals. This overall

293   illustrates an unexpected diversity in shark social systems that could provide interesting data if further

294   studied.

295   Cote et al. (2012) gave individual mosquitofish (*Gambusia affinis*) a choice between shoals of different

296   sizes and compositions in binary choice experiments and found that despite an effect of these two

297   characteristics, individual differences in sociability were still detectable. Even though our investigation

298   differs in several ways including the choice to let individuals interact together, our results are in agreement

299   with the maintenance of individual differences despite social context changes. It is important to note a

300   relative similarity of what is considered as a social interaction. Indeed, in a binary choice experiment,

301   observers record only "active" attempts of socializing from the focal individual. Similarly, in our

302   experiment, we recorded a behavior as social only when the focal individual actively interacted. Being

303   followed by another individual was not considered as social which led to classify leading as asocial, in

304   contrast to the commonly used gambit of the group, for instance. We believe that this treatment of leading

305   events could be related to the distinction between effective (an individual able to impose its preferences)

306   and intrinsic leaders (the tendency of an individual to pursue its own preference) discussed by Johnston

307   and Manica (2011). However, instead of imposing other individuals to follow, it seems that an intrinsic

308   leader becomes an effective leader only in the presence of followers. This, in turn, suggests that some

309   aspects of individual behavior are relatively fixed even in groups and could play an important part in the

310   dynamic of social groups (Harcourt et al. 2009a; Laskowski and Bell 2014). However, further tests are

311   needed to investigate this hypothesis in juvenile lemon sharks. It could, for instance, be done by

312   experimentally changing group compositions based on known social personality types and observe how

313   cohesion is impacted (e.g. social network measures and group size), especially in an "extreme" social

314   environment (e.g. only asocial individuals). Continuing this work to understand the influence of

315   individuality on social group dynamic is important as it remains poorly understood. Results from the

316   literature indicate that this is dependent on context and/or species (e.g. Magnhagen and Staffan 2005;

317   Magnhagen and Bunnefeld 2009; Magnhagen 2012; Castanheira et al. 2013; Brown and Irving 2014). For

318   instance, Magnhagen and Staffan (2005) found that in perch (*Perca fluviatilis*) the boldness score of

319   individual young of the year perch was strongly modified by other group members. On the other hand,

320   Magnhagen and Bunnefeld (2009) found that in 1-year-old perch individual boldness was also expressed

321   while tested in groups. Interestingly, Magnhagen (2012) suggested that the maintenance of individuality in

322   perch social groups might depend on the experience of predation. Unfortunately, most of the experiments

323   focusing on personality in a social context tested other personality axes than sociability (e.g. boldness or

324   exploration). A direct comparison with our study is therefore difficult but these differences between

325   investigations are interesting. If further studied in Teleost fishes and sharks, comparative work could lead

326   to a better understanding of overall social group behavior in animals (Wolf and Krause 2014; Farine et al.

327   2015) while emphasizing the importance of behavioral type into group dynamics.

328   Contrary to expectation, individuals that experienced the same group composition between tests showed a

329   lack of consistency. A potential explanation would be an unforeseen familiarity development during the

330   experimental procedure. This has been demonstrated to influence social interactions in this species (Keller

331   et al. 2017) and in catsharks (Jacoby et al. 2012b). A simpler explanation might, however, be the influence

332   of one outlier and indeed once removed consistency was found.

333   Long-term stability of personality traits has been described in other animals (Koski 2011; Beleyur et al.

334   2015; Debeffe et al. 2015; Wuerz and Kruger 2015) including fish (King et al. 2013; Boulton et al. 2014;

335   Castanheira et al. 2016; Vrtelova et al. 2016). However, only a few studies have demonstrated long-term

336   consistency of social behavior in wild populations (see for instance: Cote and Clobert 2007; Aplin et al.

337   2015), as shown here in juvenile lemon sharks. These are interesting results when contrasted with a study

338   by Nakayama et al. (2013), describing that the individual tendency to follow is experimentally changeable

339   (i.e. using reward) in the three-spined stickleback (*Gasterosteus aculeatus*). If the tendency to follow is

340   plastic and can change depending on experience, one can ask how individual differences are maintained

341   over a long period in the wild (e.g. positive feed-back loop, highly stable environments). Trying to

342   experimentally modify the tendency to follow in juvenile lemon sharks would be an interesting first step

343   in this direction. The demonstration of such long-term consistency is also ecologically important. Indeed,

344   even if a four-month period is relatively short compared to the age of maturity in this species (sexual

345   maturity is reached at 12 years old; Brown and Gruber 1988), the first three years of life (ontogenetic

346   stages of this investigation) represent a critical life-history period for juvenile lemon sharks, due to their

347   high natural mortality (Gruber et al. 2001; Dibattista et al. 2007). Finding individual behavioral

348   consistency during this period suggests that personality could have an impact on everyday life of juvenile

349   lemon sharks. One logical next step would be to investigate the ecological consequences of long-term

350   consistency in juvenile lemon sharks. Nevertheless, longer term tests are still required to confidently

351   conclude that individual differences are indeed stable over the entire three-year period during this life

352   stage. Such long-term studies are overall rare and absent for elasmobranchs. It is, therefore, important to

353   extend such research to further populations and species to better understand stability and the ecological

354   consequences of personality in these animals. This would overall benefit the study of animal personality

355   by giving insights into the emergence and maintenance of individual differences (e.g. Dall et al. 2004;

356   Stamps 2007; Wolf et al. 2007; Bergmuller and Taborsky 2010; Dingemanse and Wolf 2010).

357   Overall, this study has shown that individual juvenile lemon sharks vary in their tendency to socialize in a

358   consistent manner. Consistency was maintained despite changes in group composition. These results

359   indicate a potential strong impact of individuality on group behavior. It could be rewarding to extend this

360   approach to other taxa and investigate in which circumstances consistency takes over plasticity in the

361   tendency to socialize. Furthermore, the fact that these variations between individuals persist through

362   relatively long-time periods suggests that personality is an important aspect of sharks' behavior that could

363   have both ecological and evolutionary impacts. Finally, these results show that the behavioral complexity

364   of sharks (and other elasmobranchs) is underestimated and that this taxonomic group deserves more

365   attention.

366

371   **Compliance with ethical standards**

372   **Ethical statement** No sharks died during the experiments, and all were released at their site of capture

373   with their color tags removed. All manipulations (e.g. size/sex determination and tagging) were performed

374   within five minutes to minimize stress. All procedures were approved by the Department of Marine

375   Resources, Bahamas (Permit no: MAF/LIA/22). No steps required anaesthetizing the animals as this

376   would increase manipulation time, increasing the stress on the animal.

380   **Conflict of interest** The authors declare that they have no conflict of interest.

381   **Ethical approval** All applicable guidelines for the care and use of animals were followed.

382

383   **DATA AVAILABILITY**

384 The datasets analyzed during the current study are available in the open science framework repository,

385 https://osf.io/7w4mx/. The algorithm used in this study is not publicly available but could be available

386 from the corresponding author on reasonable request. This is to prevent potential misuse of this non-

387 friendly-user code only adapted to the swimming characteristics of the juvenile lemon sharks.

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Figure legend

Fig. 1 Schematic of the experimental setup in Bimini, Bahamas with holding pen (A) separated into compartments containing size-matched sharks, linked to the experimental pen (B), via channel. On both sides of the social pen, there are two vertical wooden posts (brown squares) linked by ropes (dashed lines) used to raise and slide the camera (black box) above the center of the experimental pen. Identification of individuals and camera operation are performed from a wooden tower (C)

Fig. 2 Comparison of sociability score for juvenile lemon sharks in Bimini, Bahamas between trial 1 and trial 2 for short-term (a) and long-term (b) test retests

604   **Fig. 3** Comparison of sociability scores between trial 1 and trial 2 for short-term showing individual

605   juvenile lemon sharks (Bimini, Bahamas) that experienced no change (a) and change (b) in group

606   composition between test and retests. The circle identifies a potential outlier mentioned in the text above

Behavioral State	Definition	Included as social score

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621   **Table 1** Social behavior of juvenile lemon sharks. Each of these behaviors is only considered when

622   individuals are within 2.5 body lengths of each other. Table modified from Guttridge et al. (2011)

Following	An individual mimics trajectory of followed individual.	Yes
Paralleling	Individuals swimming side by side either at similar speed or while overtaking/being overtaken.	Yes
Milling	Individuals swimming in a non-coordinated manner.	No
Leading	Being followed but not paralleling or following another individual.	No

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