



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

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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.

Significance statement

This study investigated the social personality axis in a wild population of juvenile lemon sharks. First, we demonstrated consistent individual differences in their tendency to socialize. Second, we showed that individuals maintained their differences over a four-month period in the wild. Finally, we found that individual social behaviors were maintained despite being tested in variable group compositions. These results highlight the importance of individuality in the social dynamic of a poorly investigated animal and suggest personality as an important aspect of juvenile lemon sharks' everyday life over a relatively long-term period.

Keywords Fission–fusion · Follower · Group phenotype · Leadership · Personality · Social dynamics

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Introduction

Animal personality, consistent individual differences in behavior across time and contexts, has been described in a broad spectrum of taxa (Gosling 2001; Sih et al. 2004; Réale et al. 2007) and is recognized as a fundamental aspect of ecology and evolution (Sih et al. 2012; Wolf and Weissing 2012). Furthermore, it is now understood that individual differences need to be incorporated within conservation management programs (Conrad et al. 2011; Mittelbach et al. 2014). However, a primary obstacle for many species, including large-bodied marine animals such as sharks, lies in the fact that not enough data exist to understand if and how the inclusion of personality could benefit such programs. This issue can be problematic considering the sensitivity of mega-fauna to anthropogenic harvest and overexploitation (e.g., Lewison et al. 2004; Estes et al. 2011). For example, sharks have only recently received attention from an individual-based behavioral standpoint (e.g., Huvneers et al. 2013; Vaudo et al. 2014; Matich and Heithaus 2015; Towner et al. 2016; Finger et al. 2017) and a behavioral consistency standpoint in the last few years (Jacoby et al. 2014; Wilson et al. 2015; Byrnes and Brown 2016; Byrnes et al. 2016a, b; Finger et al. 2016). In terms of consistency in individual social behavior, what little information there is remains unclear and in need of further study. For example, Jacoby et al. (2014) found consistent individual differences in social network position in a captive population of juvenile catsharks (*Scyliorhinus canicula*) but significance was lost once the group effect was controlled for. In contrast, Wilson et al. (2015) found no evidence of consistency in social network position in wild juvenile lemon sharks (*Negaprion brevirostris*).

Sharks are generally large-bodied, long-lived animals with a large brain to body mass ratio (Northcutt 1977; Yopak et al. 2007). They exhibit slow growth and reproduction rates, while occupying a relatively high trophic position (e.g., Stevens et al. 2000; Dulvy et al. 2014). As a result, sharks could be an interesting addition to smaller aquatic vertebrates (with relatively fast generational turnover) usually studied within the animal personality framework. For instance, while predation is often a factor underlying the evolution of social grouping, as frequently seen in teleost fishes (Krause and Ruxton 2002), some gregarious shark species such as the scalloped hammerhead (*Sphyrna lewini*; Klimley 1985) actually experience low risk of predation overall. It is then conceivable that alternative selective pressures shaped the evolution of social behavior in many shark species. As similar assumptions could be drawn for individual differences in sociability, it is important to further investigate personality in sharks. In addition, expanding this research to wild populations and long-term observations will help to determine the importance of personality to sharks' everyday life. Because sociability has already been described in different shark species (e.g., Myrberg and

Gruber 1974; Klimley 1985; Guttridge et al. 2009; Guttridge et al. 2011; Jacoby et al. 2012a; Mourier et al. 2012, 2017), it is a critical step for the development of better management programs. Indeed, the removal of particular personality types (Biro and Post 2008; Sutter et al. 2012; Biro and Sampson 2015) through fisheries might have unknown consequences for the food web, ecosystems and environmental management. For example, the documented risk posed by fishery targeting aggregations (Mucientes et al. 2009; Jacoby et al. 2012a), could conceivably select against social individuals (i.e., higher tendency to aggregate).

We investigated the presence of consistent individual differences in the social behavior of wild juvenile lemon sharks by testing groups of six individuals. However, this study differs from those previously conducted in several aspects. First, this study assessed consistency over both short (4–18 days) and long-term (4 months) periods in wild sharks. Long-term observations have obvious benefits (Stamps and Groothuis 2010) but are rarely conducted on wild animal populations (Archard and Braithwaite 2010) and especially with such long-lived species. However, a major difficulty in generating long-term data sets is that individuals disperse or suffer mortality (Gruber et al. 2001), which can lead to different individuals being caught during a given sampling event. To account for this here, except for a subset of the data, individuals were haphazardly assigned to groups for retests, leading to variation in individuals' social environments (i.e., group composition). This approach provided the opportunity to determine if observed consistency in tendency to socialize can be attributed to individual differences and is not just a result of group effects and composition (Pritchard et al. 2001; Harcourt et al. 2009b; Kurvers et al. 2009; Cote et al. 2012). In addition, changing group composition while testing social personality in captivity reflected rapid changes in social partners commonly observed in juvenile lemon sharks in the wild (Guttridge et al. 2011; Wilson et al. 2015). Indeed, this aspect (among others) of their social dynamic has been shown to resemble that of wild guppies (*Poecilia reticulata*), a fish species demonstrating social fission-fusion behavior (Wilson et al. 2014, 2015). In summary, we tested the predictions that wild individual juvenile lemon sharks consistently differ in their social behavior over short- (5 to 18 days) and long-term (4 months) tests and further, in which these differences were robust to changes in group composition.

Method

Study site and sharks

This study was conducted on Bimini (20°–28°N, 72°–80°W), situated approximately 85 km east of the coast of Florida (USA) in The Bahamas. Wild juvenile lemon sharks from

two adjacent mangrove-fringed habitats (North Sound and Shark Land) were captured using gillnets (see Manire and Gruber 1991 for details) in June (7-day capture session) and November 2012 (3-day capture session). Upon capture, each individual was measured (pre-caudal length: PCL), sexed, and equipped with a unique color-coded tag (T-bar type, Floy Tag Manufacturing) for visual identification.

Lemon sharks were our test subject because they are a common, large coastal species in the western Atlantic. In some locations, they show long-term site attachment (approx. 3 years) allowing their capture and recapture over extended periods while living in their natural habitat (Morrissey and Gruber 1993; Dibattista et al. 2007; Chapman et al. 2009). In addition, they have been successfully used in semi-captive behavioral experiments (e.g., Guttridge et al. 2009; Finger et al. 2016).

Experimental setup

Sharks were housed in a large oval-shaped pen (10 × 5 m) constructed just offshore in the North Sound on sand bottom flats. They were given at least 4 days in the holding pen to acclimatize to captive conditions before beginning the experimental procedure. During holding time, they were fed every 3 days on a diet of fresh and frozen local fish (*Sphyræna barracuda*).

A channel (length, 4 m) linked the experimental pen to the holding pen. The circular experimental pen (diameter, 10 m) was equipped with a camera recorder placed 6 m above the center and operated by a system of ropes. A wooden tower (height, 3 m) was placed outside the pen to allow observations (Fig. 1).

The day before observation, six sharks, selected to reduce size difference (within PCL ± SD = 4.7 ± 2.73 cm), were ushered into the experimental pen, fed to satiation (to insure similarity of hunger level between individuals), and left overnight to acclimatize to their environment. Sex has been shown to have no influence on social dynamics of juvenile lemon sharks in Bimini (Guttridge et al. 2009, 2011) and was not considered further in the design of this experiment. On the day of observation, the swimming behavior of the six individuals was filmed for 20 min. Each individual was marked on their dorsal fins with unique color-coded tags to allow for subsequent identification and tracking during video analyses. Upon completion of filming, sharks were released or relocated to the holding pen to await further retesting (see below for test periods).

Test periods and group composition changes

During this study, two rounds of tests were carried out: June and November 2012. In June, individuals were tested only once ($N = 84$; 41 females and 43 males, mean pre-caudal

length ± SD = 51.8 ± 5.7 cm) and then released in their natural habitat. In November, all sharks ($N = 48$; 19 females and 29 males, mean pre-caudal length ± SD = 54.3 ± 6.1 cm) were tested twice (time between tests: 4 to 18 days; 8.5 ± 4.3 days), and of these individuals, 23 (14 females and 9 males) had been tested in June previously. Each observation session started at similar water depth (mean depth ± SD = 79 ± 12.4 cm), 1.5 h before or after a slack low tide.

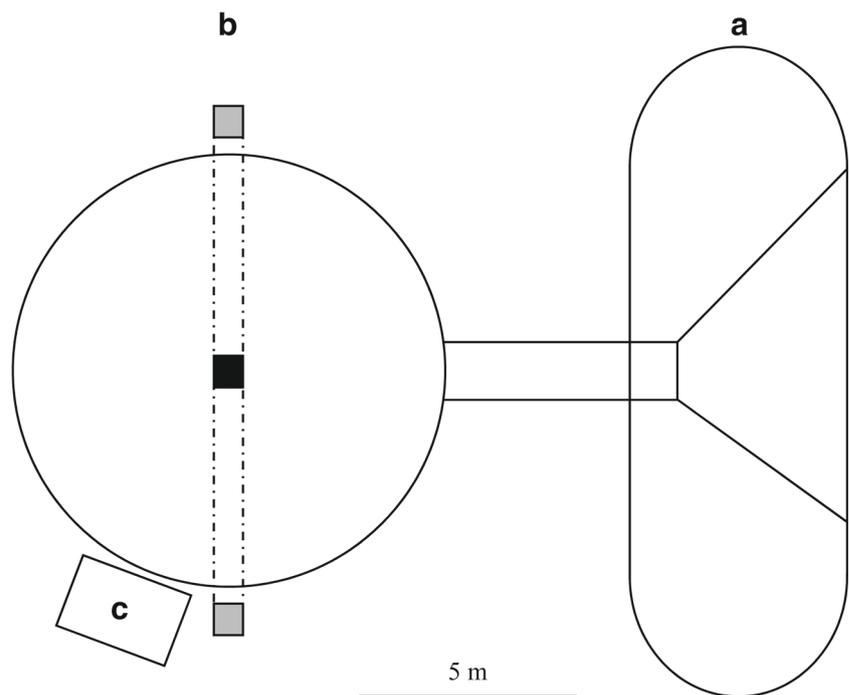
Group composition changes occurred haphazardly between June and November tests (23 individuals from 11 different groups from June were haphazardly allocated to 8 groups in November). Group mixing between test and retests in November consisted of exchanging half of a group (three individuals) with another half. Such mixing occurred for four groups ($N = 24$ individuals) whereas for four other groups, composition remained unchanged.

Social interaction observations

During video processing, data were recorded every 30 s, across 20-min observation sessions (thus 40 observations in total), each time the focal individual was recorded as social or asocial. Juvenile lemon shark social behavior is characteristically composed of following or paralleling with other individuals (see Table 1 for definitions). A leading event can be defined as occurring when one individual is being followed but is not paralleling or following another individual (Table 1). As a focal individual being followed might not reflect its wish to socialize, we considered only “active” events of social interaction (i.e., following and paralleling) as a social interaction performed by this individual. Resting and milling (see Table 1) were designated here as non-social events for two reasons. First, resting behavior in juvenile lemon sharks is not well understood and it has been shown that most (> 95%) social interactions occur during active swimming (Guttridge et al. 2009). Second, individuals were considered as social only when being notably influenced by another individual. Two (or more) individuals could cross paths but if neither of them modified their swimming movements then they were not considered to be interacting. Each individual’s social behavior score was obtained by summing the number of active social events (see below) over the 40 observations. All sharks in the arena were observed in this manner.

An algorithm was developed to quantify the social behaviors described above. This tool has also been used to analyze juvenile lemon sharks’ social behavior in another study (Keller et al. 2017). Briefly, for each of the 40 observations, this algorithm used position (coordinates of the tip of the snout) and orientation of the six individuals at time t , $t + 1$ and $t + 2$ s. Orientation was obtained relative to the previous point, therefore, at time t , orientation was obtained by adding a tracking point at $t - 1$ s. Tracking was completed manually by marking the snout of each shark using MtrackJ (Meijering

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)



et al. 2012) within ImageJ (Rasband 1997). Using these data, the algorithm calculated distances between individuals, along with the differences in orientation and position (front, behind, side by side) between sharks. Additional tracking ($t + 1$ and $t + 2$ s) was used to determine if overtaking occurred and if a dramatic turn of one shark (creating a large orientation difference at time t) influenced (i.e., following) other individuals (resulting in similar dramatic orientation change of the followers during $t + 1$ and $t + 2$). The resulting values obtained from these calculations allowed the algorithm to define each individual's social behavior as following (within social distance and behind another individual and similar orientation or influenced by this same individual), paralleling (within social distance and side by side or overtaking another individual and similar orientation than this same individual), or asocial (outside of social distance or not being influenced by other individuals). Upon completion, the algorithm provided the total number of social events over the 40 observations (paralleling and following; Table 1) as the individual social score in this investigation. The use of videos and this

algorithm to record and analyze behavioral data greatly reduced any potential observer bias.

Social distance

Previous studies used a maximum social distance of either one (Wilson et al. 2015) or four body lengths (Guttridge et al. 2011) when considering social interactions of juvenile lemon sharks in semi-wild or wild conditions. In contrast, 2.5 body lengths between individuals were found to be best in our experimental setup. This value was observed as being the maximum distance at which individuals performed following behavior during preliminary video analyses (distance was calculated using coordinates of sharks in videos and absence or presence of social interaction was determined by two observers).

A comparison between social distances (i.e., 1, 2.5, and 4 body lengths) showed that below 2.5 body lengths, a large number of associations were missed but above 2.5 body lengths only very few were added.

Table 1 Social behavior of juvenile lemon sharks. Each of these behaviors is only considered when individuals are within 2.5 body lengths of each other. Table modified from Guttridge et al. (2011)

Behavioral state	Definition	Included as social score
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

Algorithm reliability

To control for the reliability of this algorithm, four videos that were processed through the algorithm were also analyzed manually. Observers, naïve to the algorithm, were asked to describe each individual social behavior as describe above (to mimic analyses by the algorithm). Social scores obtained from manual observations and the above algorithm were highly correlated (Spearman's rank correlation: $r_s = 0.96$, $N = 24$, $P < 0.001$) and did not differ significantly (Wilcoxon paired test: $V = 138.5$, $P = 0.71$, $N = 24$). We therefore concluded that the algorithm showed results highly similar to those obtained through manual observation and could therefore be confidently applied to the full data set.

Short- and long-term tests

To test short-term consistency, analyses were performed within the November period overall, then we divided this period into groups of mixed and non-mixed composition. To test long-term consistency, analyses were performed between observations from June and November. We took the first trial of November tests instead of the average between the two trials to minimize the potential of confounding effects (due to habituation, familiarity development, etc.).

Correlation and permutations

To investigate consistent individual differences in social behavior, we first used Spearman rank correlation analyses within the different subsets of data described above. If a significant correlation was found (for short-term or long-term data), a permutation analysis was performed. For permutation analyses, individual social scores were randomly sampled from the social groups they were tested in. Therefore, a shark could be assigned only a social score from another shark (or his own) from the same social group. This was applied to June, November first, and November second trials. Using this randomly permuted data, correlation tests were performed between trials (e.g., correlation between permuted June and permuted November first trial for long-term tests) and the Spearman's rho estimations extracted. This step was repeated 10,000 times to obtain a distribution of randomly simulated rho for each correlation we were interested in. This distribution was then compared to the observed rho (estimated from original data) by extracting the proportion of simulated rho greater than the observed rho (thereafter referred to as P). If P was found to be smaller or equal to 0.025, we deemed our observed correlation significant which was used as a demonstration of consistent individual differences. These within-group permutations were necessary to control for a potential effect of pseudo-replication created by testing individuals in groups (Croft et al. 2011) and the possibility that any observed

consistency could be due to consistent differences in overall group behavior between trials.

Repeatability

To provide a repeatability score of sociability along with a 95% confidence interval, the full data set (all trials included) was analyzed using a linear mixed model with individual ID as random factor and sex, size, capture location (i.e., nursery), time in pen before trial, and period of observation (June, November) as fixed effects. Social score was normalized using a square root transformation. Normalization of the data allowed the use of the function exactRLRT from the RLRsim package (Scheipl et al. 2008) to test significance of the random term (i.e., individual ID). Repeatability was calculated according to Nakagawa and Schielzeth (2010). The 95% confidence interval was calculated using the confint function from lme4 package (Bates et al. 2015). These analyses were performed on the overall data set. All analyses were performed in R v3.2.3 (R Core Team 2015).

Data availability The data sets analyzed during the current study are available in the open science framework repository, <https://osf.io/7w4mx/>. The algorithm used in this study is not publicly available but could be available from the corresponding author on reasonable request. This is to prevent potential misuse of this non-friendly-user code only adapted to the swimming characteristics of the juvenile lemon sharks.

Results

Consistency in social behavior was found over short-term periods of several days (Spearman rank correlation: $r_s = 0.43$, $N = 48$, $P < 0.001$; Fig. 2a) and long-term periods of 4 months (Spearman rank correlation: $r_s = 0.52$, $N = 23$, $P = 0.01$; Fig. 2b). The consistency found here was not caused by differences in overall group behavior (permutation analyses: short-term tests: $P = 0.005$; long-term tests: $P = 0.0088$).

Within short tests, those that did not experience any changes in group composition did not show consistent differences in social behavior (Spearman rank correlation: $r_s = 0.39$, $N = 24$, $P = 0.057$), whereas individuals that experienced a mixing of groups did (Spearman rank correlation: $r_s = 0.43$, $N = 24$, $P < 0.05$; permutation analyses: $P = 0.0094$). However, individuals from the short-term non-mixed group showed consistent individual differences as well, when one outlier (see Fig. 3a) was removed (Spearman rank correlation: $r_s = 0.58$, $N = 23$, $P < 0.01$).

Overall, juvenile lemon sharks demonstrated repeatability in their social behavior (repeatability = 0.49; CI: [0.36, 0.51]; RLRT = 16.578, $P < 0.001$) when controlling for size, sex,

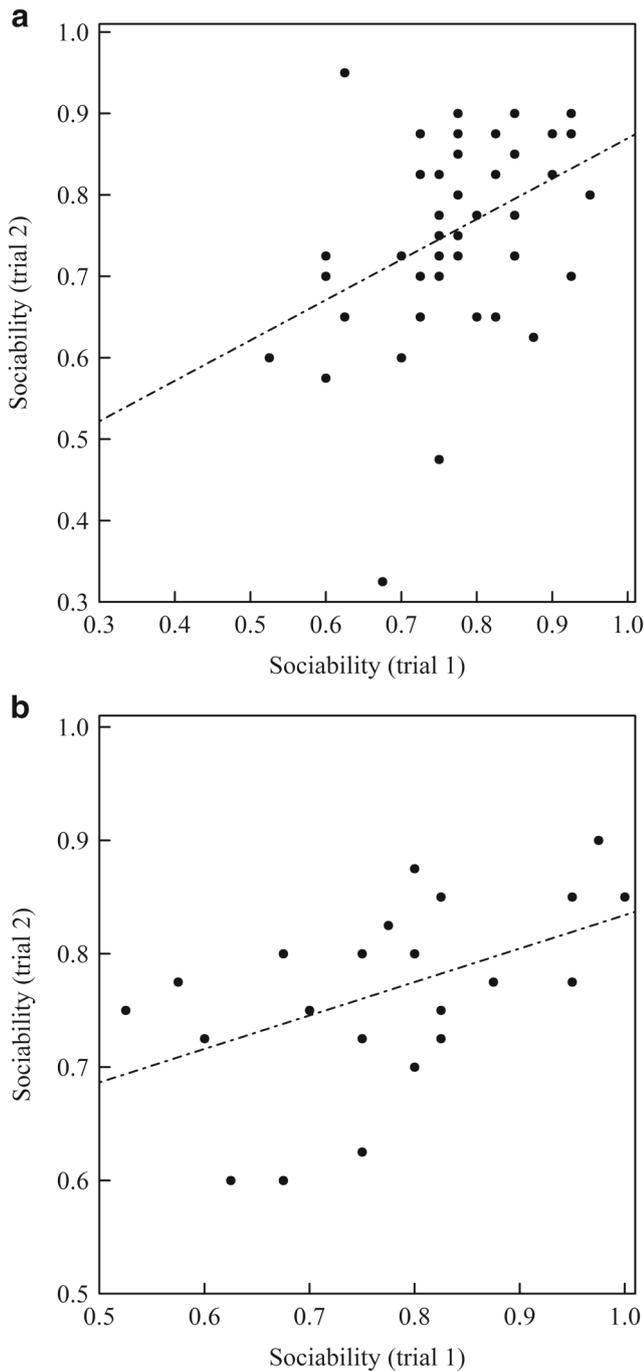


Fig. 2 Comparison of sociability score for juvenile lemon sharks in Bimini, Bahamas between trial 1 and trial 2 for short-term (a) and long-term (b) test retests

location of capture, time in captivity before observations and period of testing.

Discussion

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

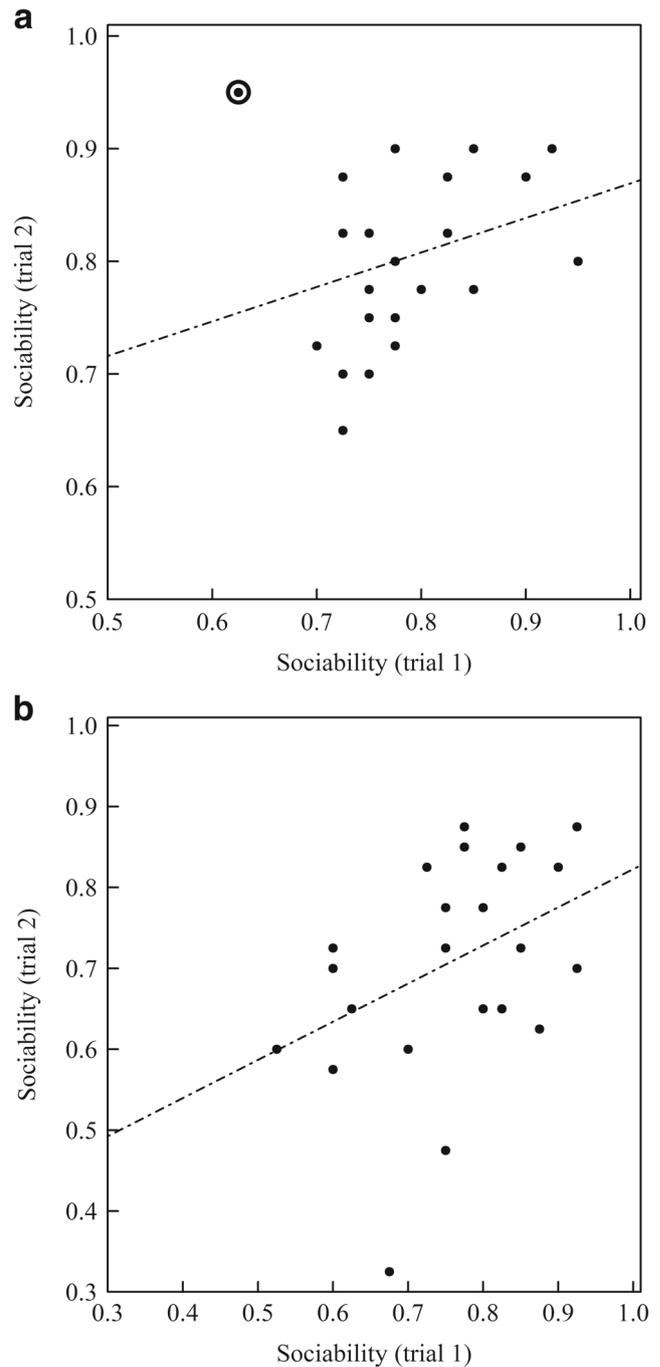


Fig. 3 Comparison of sociability scores between trial 1 and trial 2 for short-term showing individual juvenile lemon sharks (Bimini, Bahamas) that experienced no change (a) and change (b) in group composition between test and retests. The circle identifies a potential outlier mentioned in the text above

sharks consistently differed from each other in some aspects of their social behavior despite being tested in groups (see Webster and Ward 2011 for mechanisms having the potential to suppress individual differences) over a 4-month period. Overall, we found a repeatability of 0.49, which is relatively high (see Bell et al. 2009) and consistent with other studies of

wild populations (Bell et al. 2009). In addition, consistent individual differences were still maintained despite changes in group composition. The later result indicates that, at least in the juvenile lemon shark population studied, individual social behavioral types play an important part in the social dynamics of these animals and could have a strong impact on their social behavior in the wild.

As mentioned above, social personality has already been investigated in sharks (Jacoby et al. 2014; Wilson et al. 2015). However, our study differs from these other investigations in several important points. First, despite using the same species and age criterion, Wilson et al. (2015) did not find consistency in the social proxies they used. While these contrasting results might be attributed to dissimilarities between populations, there are also several methodological discrepancies between Wilson et al.'s study and ours (e.g., sampling method/frequency and smaller sample size). A convergence of methods to investigate consistent individual differences in these two juvenile lemon shark populations would be useful. Indeed, the possibility to compare between populations might lead to important insights into causes of emergence and maintenance of animal personality. Second, our investigation differs from Jacoby et al.'s (2014) study in which consistent individual differences in the social behavior of juvenile catsharks were detected. While they maintained the composition of social groups in their experiments, we allowed it to vary between trials in ours. This was an important aspect of our experimental design for two reasons. First, we believe that our approach reflects natural social mixing between individuals likely to occur in juvenile lemon shark nurseries. Second, it indicated that our observed results were not caused by consistent overall group differences. Similarly, keeping group composition constant between trials to investigate social personality in the catshark (Jacoby et al. 2014) may blur the distinction between individual and group behavior differences as causes for Jacoby et al.'s observation. This concern is reinforced by the fact that individual catsharks (*Scyliorhinus canicula*) prefer certain individuals over others (Jacoby et al. 2012b) which might influence individual social tendency based on group composition. However, in contrast to juvenile lemon sharks, in catsharks not mixing group composition and allowing affinity to develop reflects their ecology during early life stages. Indeed, they are a sedentary species, which hatch in egg clusters, display high site fidelity and are therefore expected to have a pre-determined and relatively stable social environment (D.M.P. Jacoby personal communication). Therefore, mixing group composition in this system might not be relevant to describe the social dynamic of juvenile catsharks in the wild. This highlights the importance to carefully consider the ecology and natural behavior of the species if one is interested in understanding the consequences of individual differences in behavior in the wild. Nevertheless, the contrast between these two species provides interesting

systems to investigate social dynamics in two alternative social systems. Here again, converging methods in future work could be highly beneficial in our understanding of animal personality and social systems in animals. This overall illustrates an unexpected diversity in shark social systems that could provide interesting data if further studied.

Cote et al. (2012) gave individual mosquitofish (*Gambusia affinis*) a choice between shoals of different sizes and compositions in binary choice experiments and found that despite an effect of these two characteristics, individual differences in sociability were still detectable. Even though our investigation differs in several ways including the choice to let individuals interact together, our results are in agreement with the maintenance of individual differences despite social context changes. It is important to note a relative similarity of what is considered as a social interaction. Indeed, in a binary choice experiment, observers record only "active" attempts of socializing from the focal individual. Similarly, in our experiment, we recorded a behavior as social only when the focal individual actively interacted. Being followed by another individual was not considered as social which led to classify leading as asocial, in contrast to the commonly used gambit of the group, for instance. We believe that this treatment of leading events could be related to the distinction between effective (an individual able to impose its preferences) and intrinsic leaders (the tendency of an individual to pursue its own preference) discussed by Johnstone and Manica (2011). However, instead of imposing other individuals to follow, it seems that an intrinsic leader becomes an effective leader only in the presence of followers. This, in turn, suggests that some aspects of individual behavior are relatively fixed even in groups and could play an important part in the dynamic of social groups (Harcourt et al. 2009a; Laskowski and Bell 2014). However, further tests are needed to investigate this hypothesis in juvenile lemon sharks. It could, for instance, be done by experimentally changing group compositions based on known social personality types and observe how cohesion is impacted (e.g., social network measures and group size), especially in an "extreme" social environment (e.g., only asocial individuals). Continuing this work to understand the influence of individuality on social group dynamic is important as it remains poorly understood. Results from the literature indicate that this is dependent on context and/or species (e.g., Magnhagen and Staffan 2005; Magnhagen and Bunnefeld 2009; Magnhagen 2012; Castanheira et al. 2013; Brown and Irving 2014). For instance, Magnhagen and Staffan (2005) found that in perch (*Perca fluviatilis*), the boldness score of individual young of the year perch was strongly modified by other group members. On the other hand, Magnhagen and Bunnefeld (2009) found that in 1-year-old perch, individual boldness was also expressed while tested in groups. Interestingly, Magnhagen (2012) suggested that the maintenance of individuality in perch social groups might depend on the experience of

predation. Unfortunately, most of the experiments focusing on personality in a social context tested other personality axes than sociability (e.g., boldness or exploration). A direct comparison with our study is therefore difficult but these differences between investigations are interesting. If further studied in teleost fishes and sharks, comparative work could lead to a better understanding of overall social group behavior in animals (Wolf and Krause 2014; Farine et al. 2015) while emphasizing the importance of behavioral type into group dynamics.

Contrary to expectation, individuals that experienced the same group composition between tests showed a lack of consistency. A potential explanation would be an unforeseen familiarity development during the experimental procedure. This has been demonstrated to influence social interactions in this species (Keller et al. 2017) and in catsharks (Jacoby et al. 2012b). A simpler explanation might, however, be the influence of one outlier and indeed once removed consistency was found.

Long-term stability of personality traits has been described in other animals (Koski 2011; Beleyur et al. 2015; Debeffe et al. 2015; Wuerz and Krüger 2015) including fish (King et al. 2013; Boulton et al. 2014; Castanheira et al. 2016; Vrtelova et al. 2016). However, only a few studies have demonstrated long-term consistency of social behavior in wild populations (see for instance: Cote and Clobert 2007; Aplin et al. 2015), as shown here in juvenile lemon sharks. These are interesting results when contrasted with a study by Nakayama et al. (2013), describing that the individual tendency to follow is experimentally changeable (i.e., using reward) in the three-spined stickleback (*Gasterosteus aculeatus*). If the tendency to follow is plastic and can change depending on experience, one can ask how individual differences are maintained over a long period in the wild (e.g., positive feed-back loop, highly stable environments). Trying to experimentally modify the tendency to follow in juvenile lemon sharks would be an interesting first step in this direction. The demonstration of such long-term consistency is also ecologically important. Indeed, even if a 4-month period is relatively short compared to the age of maturity in this species (sexual maturity is reached at 12 years old; Brown and Gruber 1988), the first 3 years of life (ontogenetic stages of this investigation) represents a critical life history period for juvenile lemon sharks, due to their high natural mortality (Gruber et al. 2001; Dibattista et al. 2007). Finding individual behavioral consistency during this period suggests that personality could have an impact on everyday life of juvenile lemon sharks. One logical next step would be to investigate the ecological consequences of long-term consistency in juvenile lemon sharks. Nevertheless, longer term tests are still required to confidently conclude that individual differences are indeed stable over the entire three-year period during this life stage. Such long-term studies are overall rare and absent for elasmobranchs. It is, therefore, important to

extend such research to further populations and species to better understand stability and the ecological consequences of personality in these animals. This would overall benefit the study of animal personality by giving insights into the emergence and maintenance of individual differences (e.g., Dall et al. 2004; Stamps 2007; Wolf et al. 2007; Bergmuller and Taborsky 2010; Dingemanse and Wolf 2010).

Overall, this study has shown that individual juvenile lemon sharks vary in their tendency to socialize in a consistent manner. Consistency was maintained despite changes in group composition. These results indicate a potential strong impact of individuality on group behavior. It could be rewarding to extend this approach to other taxa and investigate in which circumstances consistency takes over plasticity in the tendency to socialize. Furthermore, the fact that these variations between individuals persist through relatively long-time periods suggests that personality is an important aspect of sharks' behavior that could have both ecological and evolutionary impacts. Finally, these results show that the behavioral complexity of sharks (and other elasmobranchs) is underestimated and that this taxonomic group deserves more attention.

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Compliance with ethical standards

Ethical statement No sharks died during the experiments, and all were released at their site of capture with their color tags removed. Handling (e.g., size/sex determination and tagging) was performed within 5 min to minimize stress. All procedures were approved by the Department of Marine Resources, Bahamas (Permit no: MAF/LIA/22). No steps required anesthetizing the animals as this would increase handling time, increasing the stress on the animal.

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

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

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