Sex and social networking: the influence of male presence on social structure of female shark groups

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Marine predators such as sharks often form single-sex aggregations as part of their diel behavioral cycle. Such aggregations are potentially driven by contrasting reproductive and behavioral strategies between the sexes, leading to distinct sexual segregation. There is, however, no experimental evidence that such predator aggregations are governed by intrinsic social systems, demonstrating long-term temporal stability. Social network structure, temporal stability, and activity profiles were analyzed to examine the impact of introduced males on social structure of 4 captive groups of female catshark (*Scyliorhinus canicula*). Aside from foraging and habitat selection pressures, we question whether individual female sharks manage additional social demands that potentially influence activity budget and susceptibility to male harassment. Shark groups demonstrated marked differences in their tendency to aggregate in a unisex environment and concomitantly showed significant differences in social response to male presence. Dichotomy in social structure of the 4 groups revealed that well-connected individuals demonstrated greater resilience to male disturbance. Socially isolated females experienced greater levels of partner exchange, reduced temporal stability, and increased activity levels in the presence of males and control females. These results are the first to demonstrate the disruptive influence that male and novel females have on weak female shark social interactions; conversely, aggregations demonstrating relatively strong temporally stable social bonds (at least by some individuals) are particularly resilient to potential male harassment and novel (female) intruders. We highlight that additional 'social constraints' may have disparate influence on individuals occupying different structural positions within a network and may thus impact individual fitness unequally. *Key words:* aggregation, behavior, fish, network analysis, sexual segregation, shark, social structure. *[Behav Ecol 21:808–818 (2010)]*

Animals are driven to aggregate by a common requirement for resources, protection, and/or reproduction, and as such, gregariousness is a phenomenon widespread throughout the animal kingdom. Grouping behavior is common in both terrestrial and marine organisms, and individuals can derive a variety of benefits (and costs) from their close proximity to others. In some species, this might be the dissemination of useful foraging information, or in others, it may function to aid antipredator defense mechanisms. Conspecific interaction is therefore often characterized by consistent interindividual distances or a synchronization of activity (Krause and Ruxton 2002; Sumpter 2006). Individual participation in grouping behavior imposes a trade-off in behavioral strategies through the many biotic and abiotic selection pressures acting on each group member. Small gregarious marine and freshwater fish have proved ideal models in the past with which to study how the effects of these individual constraints act on overall group dynamics (Krause and Ruxton 2002; Lett et al. 2004). Specific selection pressures may also drive the evolution of differential male and female sexual strategies within conspecific aggregations (Wearmouth and Sims 2008).

Sex differences in behavior

In many animal societies, there are inherent differences in male and female investment in their progeny (Clutton-Brock and Parker 1995). In such societies, this can lead to differences in behavioral strategies between the sexes whereby males, who energetically invest little by way of gamete production and parental care, gain substantially greater genetic reward from mating events than females (Chapman et al. 2003). This high potential rate of reproduction may promote male behavioral strategies, which negatively impact female reproductive success (Magurran and Seghers 1994; Croft et al. 2003; Pilastro et al. 2003). Such differences in behavior between sexes may in some species be sufficient to fuel the spatial separation of the 2 sexes, leading to sexual segregation (Wearmouth and Sims 2008). In guppies (*Poecilia reticulata*), for example, sexual asymmetry in reproductive investment leads to male-biased movement between shoals (Croft et al. 2003), with high levels of sexual harassment causing females to actively select areas of high predation risk and low male presence (Darden and Croft 2008). Spatial segregation of the sexes is also apparent in elasmobranchs; mature female small-spotted catsharks (*Scyliorhinus canicula*) form single-sex aggregations in shallow labyrinthine caves in warmer coastal waters whereas males occupy deeper offshore habitat (Sims et al. 2001, 2006). Although evidence for sexual segregation in gregarious species is burgeoning, the proximate causes for segregation are largely speculative. Recent quantitative analyses, however, do indicate that male behavior impacts not only habitat selection and foraging in freshwater fish but also has implications for the development of familiarity and social structure in animal aggregations (Darden and Croft 2008; Darden et al. 2009).

The implications of different sexual strategies have been widely documented in the literature; however, little attention

has been paid to the differential impact such strategies may have on individuals. Variation in social preference or boldness, for example, influences the structure and dynamics of conspecific fish aggregations (Pike et al. 2008) and thus is equally likely to influence intersexual interaction in sexually segregating species. Differences in individual behavioral phenotype within an aggregation may therefore influence the extent to which any perturbation, whether it is the behavior of the opposite sex or otherwise, impacts their own reproductive success. The recent developments in animal social network analysis provide a vehicle for exploring these ideas in great detail.

Social structure

Biological social structures are often explained in terms of networks of direct and indirect interactions (Wey et al. 2008). There has been a recent flurry of interest surrounding social networks driven largely by increases in computational capacity and better analytical methods. This has resulted in social network analysis fast becoming an integral tool for understanding how individual behavior influences group decision making in social animal populations (Croft et al. 2008). Understanding the distribution of animals, information transfer, and spread of disease within particular species is greatly enhanced by examining social structure of animal aggregations (James et al. 2009). These biological networks are often highly dynamic and may be subject to a variety of biotic disturbances from intraspecific competition for food to intersexual harassment, and this may lead to behaviors promoting the constant assortment of individuals, each trying to optimize their own fitness. Hence, behavior of each individual group member can potentially affect the overall dynamic of a social network (Proulx et al. 2005; Pike et al. 2008).

To understand more fully the role an animal plays within a group of conspecifics, research requires fine-scale investigation and experimental manipulation of the social environment. For many aquatic animal systems, this is not possible due to numerous temporal, spatial, and physical constraints. For this reason, experimental research into the social behavior and group dynamics of fish has been almost exclusively confined to freshwater teleosts (Krause et al. 2000; Croft et al. 2005). The benefits of using such models are often the short life histories/generation times, high numbers of offspring, and small size at maturity. In contrast, elasmobranchs show k-selected characteristics in that they are long lived, slow to gain sexual maturity, frequently reach adult lengths of 1–2 m+, and consequently often occupy apex positions within their ecological niche. The behavioral decisions made by free-ranging sharks—whether they are social or otherwise—may therefore potentially impact their behavior for periods of years or even decades.

Site philopatry and nursery areas are common in many species of shark (Sims et al. 2001; Heupel and Simpfendorfer 2005; Chapman et al. 2009) periodically bringing together large numbers of adult and juvenile sharks. Under such conditions, it is probable that some degree of social organization or hierarchy may evolve. In comparison with teleost fishes, Chondrichthyes (sharks and rays) are characterized by a particularly high brain mass to body mass ratio (Northcutt 1977), this being one of the key attributes of social behavior in other large marine organisms, such as delphinids (Connor et al. 1998). This indicates that sharks also may be capable of cognitively complex behaviors, such as social systems, individual recognition, and dominance hierarchies (Myrberg and Gruber 1974; Sims 2003).

Small-spotted catsharks (S. canicula) are small benthic sharks, which are sexually monomorphic in body size, with both sexes achieving sexual maturity between 570–600 mm total length (Ford 1921). S. canicula demonstrate specific sexually segregated behavioral strategies, with females aggregating in shallow-water caves, a behavior potentially linked to the avoidance of males (Sims et al. 2001; Sims 2005). Acoustic telemetry has revealed that male catsharks occupy core areas of deep water during daylight hours with foraging excursions into warmer shallow waters at night (Sims et al. 2001; Sims et al. 2006). In the wild, male home ranges were found to overlap one another and were centered around tidal gyres and areas of high prey abundance (Sims et al. 2001). Therefore male–male interaction is plausible, but little is known about social behavior of male S. canicula. Putative male avoidance may cause females to refuge in shallow rocky substrata, where they often experience thermal conditions outside their optimum for growth (Wearmouth and Sims 2008). This species, which grows to a maximum length of 100 cm (Compagno et al. 2005), has been subject to previous behavioral experimentation due to its intermediate size and ability to survive and reproduce in captivity (Sims 2003). Although we are slowly beginning to develop an understanding of conspecific interactions in elasmobranchs (Guttridge et al. 2009), there is a distinct paucity of literature associated with social behavior in this taxa with detailed marine research restricted to the fission/fusion populations of sociable marine mammals (Clapham 1996; Connor et al. 1998; Lusseau 2003). This study aims to quantify captive shark (S. canicula) social networks under controlled and repeatable conditions. By manipulating the sex ratio, we aim to shed light on how male presence (of a species known to sexually segregate in the wild) may influence female social aggregation behavior. Specifically, we address the influence of males on (1) the structure of catshark networks, (2) the dynamics of female networks based on analyses of temporal stability, and (3) the activity budgets of females of different social connectivity.

MATERIALS AND METHODS

Experimental fish

Adult female small-spotted catsharks, S. canicula ($n = 16$), were collected during a 50-min survey trawl at station L4, in the English Channel (lat 50°15.53N, long 4°12.63W, off Plymouth) aboard a Marine Biological Association (MBA) research vessel in March 2007; 4 adult males were obtained several weeks later in April. A further 16 adult females were collected for a repeat experiment during a similar survey trawl at L4 in April 2009 with the addition of 4 adult males and 4 adult females collected in subsequent weeks for introduction into female catshark aggregations.

On land, the sharks were transported to the MBA Laboratory, Plymouth, UK (ca. 15-min journey), where they were weighed, measured, and marked with small identification tags. All S. canicula measured between 540–615 mm (total length, L_T) reducing the potential confounding effect of individual size on partner preference. In each year, sharks were separated into 2 groups (arenas 1, 2, 3, and 4, hereafter, A1–A4, respectively; $n = 8$ per arena) and were tagged with T-bar anchor tags (FD94; Floy Tag, Seattle, WA) on the posterior dorsal surface. For each of 4 different colored tags used, there was a left- and right-side orientation given to identify the 8 individuals within each of the 4 arenas. Length and mass measurements taken before and after experimentation indicated no deleterious effects on the catsharks health during captivity (e.g., mass loss). S. canicula have well-developed eyes, but scotopic vision rules out color perception in this species (Bozzano et al. 2001), suggesting that tag color had no effect on partner choice. All tagging adhered to institutional animal

welfare and U.K. Home Office guidelines as regulated under the Animals (Scientific Procedures) Act 1986 and was carried out by trained and licensed personnel.

Social network behavioral arenas

We observed catsharks in the same 2 circular fiberglass behavioral arenas for the duration of the 2007 and 2009 periods of data collection. Arenas were 1.83 m in diameter by 0.43 m in depth with a conical bottom, with a capacity of 2,242 l of seawater and a total possible "resting" area of 2.63 m². The water supply to the arenas was a semi-open recirculation system in which seawater was drawn through a course filter in the sublittoral zone of Plymouth Sound and pumped into a 67,500-l reservoir. Seawater from the reservoir passed through a commercial filtration system before entering each arena. Water was tested regularly for pH, ammonia, and nitrate concentration, and temperature control was maintained by passing the water through a chiller twice per week. Seawater in the arenas was subject to seasonal variation in temperature despite partial temperature control with the chiller; ambient water temperatures in MBA aquaria vary from 13 °C in winter to 19 °C in the summer. The seawater hall where arenas were located is lit by natural daylight and therefore behavioral arenas experienced a natural day/night cycle (ca. 14:10 h light:dark). The catsharks occupied the behavioral arenas for 7 days before data collection commenced to allow time for acclimation to test conditions. Catsharks were fed small pieces of white fish (130 g/arena) on a twice weekly discrete feeding schedule. Food was mixed with liposome enrichment and a commercial pellet and was equivalent to 2.5% of wet body mass per individual per feed (Sims and Davies 1994). Feeding events took place in the late afternoon following data collection.

Data collection

This comprised 2 methods: Partner preference and association patterns were recorded using a time series of visual scan samples, whereas data on activity patterns were collected by electronic G5 data (logging) storage tags (DSTs—Cefas Technology Ltd, Lowestoft, UK) attached to a subset of individuals within the group. DST data on activity were only collected in 2009 (groups A3 and A4) before which daylight activity was measured during visual scan samples. Wild female *S. canicula* utilize daylight hours resting in small groups in rocky substrata, including crevices and caves as part of the inactive phase of their diel cycle (Sims et al. 2001). Data collection periods were therefore 8 h per day, 5 days a week between the daylight hours of 08:00–17:00 h. Data were obtained from 13 scan samples per day per arena,

taken every 40 min through a small (20 × 20 cm) observation window and remained consistent between years. Temperature of the seawater in the behavioral arenas was recorded continuously every 5 min using iButton Thermochron temperature loggers (Maxim/Dallas Semiconductors, Dallas, TX). During each scan sample, active partner preference was recorded based on the orientation of the anterior half of the shark from the pelvic fin origin forwards, thus ruling out passive association between individuals. Strength of association was based on the frequency of samples in which individuals were observed resting together with individual behavioral repertoires produced by behaviors adhering to the parameters outlined in Table 1. These repertoires were useful for comparing the daily behavioral cycles of introduced male and female sharks with those of focal individuals in the networks.

The G5 DSTs were programmed to measure pressure (depth) accurately to a resolution of ≤4 cm every 15 s and temperature (±0.1 °C) every 10 min for the duration of each deployment. For external attachment to the fish, tags were mounted on an epoxy resin base that was attached to the fish's dorsum using 2 subcutaneous T-bar anchor tags. Each tag mount was attached tightly at these 2 contact points to minimize slipping of the tag, the associated movement of which could cause irritation. Individuals were anaesthetized prior to tagging to reduce stress and lasting harm. The DST attachment procedures took approximately 3 min and were carried out by U.K. Home Office licensed personnel (for further details concerning anaesthetization and the DST attachment procedure, refer to Sims et al. 2006). Following the DST attachment procedure, fish recovery from anesthesia was facilitated by holding each fish at the surface of a tank with fast flowing seawater. Each individual was held into this fast flow of water, until it recovered strong swimming movements at which point it was either released into an arena or a holding tank.

To investigate social structure and temporal stability within the first 2 catshark groups (A1 and A2), 400 h of observations were recorded for both arenas (200 h per arena) over a period of 5 consecutive weeks. For the subsequent repeat experiment (A3 and A4), we extended the periods of manipulation and recovery from 1 to 2 weeks culminating in 880 h of observations (440 h per arena) over an 11-week period. During this time, egg-laying events occurred sporadically and usually at night. Like many oviparous fish species, these sharks exhibit no form of parental care, and therefore, eggs were removed immediately after data collection on each day. Female *S. canicula*, like other shark species, can store sperm for many months (Metten 1939), so these eggs (if fertilized) may not have been the product of matings made immediately prior to capture. Equally, female (fertilized) eggs produced in the time periods

Table 1

Definition of behaviors recorded during each scan sample in order to quantify individual behavioral repertoires

Behavior	Description	Score
Solitary resting	Resting > a head length from another individual.[a]	1
Solitary swimming	Swimming > a head length away from another individual.	2
Resting together (asymmetric)	Resting ≤ a head length from another individual.	3
Tactile resting (symmetric)	Resting with part of the fusiform body touching another individual or some pectoral bending.[b]	4

Following swimming was ruled out as a recorded behavior due to its infrequency.

[a] Head is defined as the tip of the snout to the last gill opening (Compagno et al. 2005).

[b] Resting individuals often lie with pectoral fins overlapping. The pectoral fins of *S. canicula* contain a number of unmyelinated nerve fibers called the corpuscular endings. These fibers are triggered by mechanical pressure and also body and fin movement and stretching of the skin. The receptors of these nerves are primarily regarded as proprioreceptors (Roberts 1978). The decision was therefore made to score 4 if the pectoral fins were bent against another individual and 3 if just overlapping.

following male introduction to the arenas may not necessarily have been a consequence of matings with captive males.

Social definition, treatment, and control

The presence or absence of an initial social structure, defined by differences in the distribution of association indices between the observed and a randomized data set (see "Statistical and data analyses"), was assessed during an initial 2-week period prior to any experimental manipulation. This period proved useful for identifying individuals occupying specific structural positions within the network (i.e., positions of high and low social connectivity, hereafter referred to as key and peripheral individuals). Following this period of social definition, 2 different pairs of male *S. canicula* were introduced to A1 and A2 sequentially for a week at a time. Staggered male introduction between arenas provided a control for external effects across independent replicates during continuous linear experimentation. Once social structure had been defined in A3 and A4, long-life DSTs were attached to 1 key and 1 peripheral female within each arena in order to analyze the effects of male and female introduction on the activity budget of individuals of differential social status. Scan samples resumed for an additional 2 weeks in A3 and A4 prior to any introductions to allow tagged individuals to acclimatize. Two males were then introduced to A3 and 2 females to A4 for a period of 2 weeks, followed by a 2-week recovery period. Introductions were then reversed, and a set of novel females and males were introduced to A3 and A4, respectively. Arenas A3 and A4 were also subject to an extra set of scan samples 2 months post experimentation to compare resultant social networks with those obtained immediately following capture. Total length (L_T) of each introduced male and female remained within the size range for the female sharks eliminating the effect of size differences on associative behavior. Introduced sharks were not floy-tagged but were easily identified from each other by characteristic coloration and/or spot markings. Following introductions, food provision was increased accordingly, and sharks were given 48 h to acclimatize to introductions before data collection commenced. Data collection was extended to incorporate the orientation and association of the new individuals.

Statistical and data analyses

Data were used to calculate association indices that were analyzed using SOCPROG 2.4 (Whitehead 2009). Developed primarily for the analysis of wild fission/fusion animal populations (e.g., cetaceans), SOCPROG was adapted here to define female catshark social structure based on symmetric tactile association behavior in captivity. SOCPROG 2.4 was used to create matrices of association indices, which were subject to permutation tests for significant pairs (dyads), network analyses, temporal analysis, and analyses of multiple association measures.

   Experimentation on captive association behavior ensures that each individual is recorded for every sample taken, without the need to make inference about the time individuals are not observed. The simple ratio index was therefore favored for the analysis of symmetric association data as it represents, most accurately, the degree of association between individuals within a captive population and without bias (Ginsberg and Young 1992). Symmetric association (restricted to behavior 4; Table 1) was based on tactile, and thus, reciprocal resting behavior between individual sharks and association indices was calculated as a simple estimate of the proportion of time that pairs of individuals were associating (Whitehead 1997). High values (close to 1) indicated individuals associate fre-

quently, and low values (close to 0) indicate that they rarely associate. The simple ratio index therefore produced a half matrix of symmetric association and is given as follows:

$$\text{Simple ratio index} = \frac{X}{X + Y_{ab} + Y_a + Y_b}$$

where X is the number of observations in which a and b were observed together in the same group, Y_{ab} is the number of sampling periods in which a and b were observed in separate groups, Y_a is the number of sampling periods in which only a was observed, and Y_b in which only b was observed (Ginsberg and Young 1992).

Preferred or avoided association

A randomization procedure described in Whitehead (2009) was used to determine whether there was a significant difference between the observed patterns of association within the 4 groups ($n = 8$), both before, during, and after manipulations, and those obtained from thousands of random permutations of the same data set. During the Monte Carlo permutation tests, the number of associations of each animal in each sampling period was kept at a constant with all groups being randomly permuted (Whitehead 2009). This null model favors a closed network where all individuals are recorded in every sampling period. Individuals were then randomly assigned within these fixed parameters, and the number of permutations was gradually increased until the P value stabilized at 60 000 permutations with 1000 flips of the data set per permutation (Whitehead 2009). The observed mean association index was calculated as the mean association of all possible dyads in each group ($n = 28$). This procedure was used to isolate pairs of individuals associating with or avoiding conspecifics more than would be expected under random association.

Network analysis

Descriptive analyses of catshark social structure were produced by converting association matrices into descriptive sociograms that represent the network of links (and their relative strength) between all associating dyads. In a recent paper, Lusseau et al. (2008) argue that more traditional methods of network analysis such as binary (1:0) networks are inappropriate for analyzing animal social networks. Therefore, SOCPROG 2.4 treats the association matrix as a weighted network to produce values for average path length, eigenvector centrality, and weighted degree for each individual or node of the network. The average path length (i.e., the shortest number of nodes between 2 individuals) describes the extent to which any member of a network can reach other members of that network (Newman 2003). Eigenvector centrality is proportional, between 0 and 1, and assigns relative importance to each node (or individual) within a network based on the number of highly connected nodes an individual is associated with. The weighted degree, often referred to as strength, is simply the sum of association indices of any individual with all other individuals. It is noteworthy to reiterate here that these measures are derived purely from symmetric tactile behavior and will thus be weighted by the association index. Such measures not only provide some indication of the strength of social structure at a specific point in time but also allow us to assess the relative importance we might attach to an individual and its overall influence on a social network.

Temporal stability and activity analyses

Lagged association rates (LARs) and null association rates (NARs) were calculated for associations between all individuals and were plotted continuously against time lag, using

the moving average method (Whitehead 2009). LAR is an estimate of the probability that individuals associating at one point in time will be interacting at t time units later (Whitehead 1997). The NAR indicates the expected LAR given random association. Different models of temporal stability were simultaneously fitted to our observed data. These models best reflected the more plausible social components adhering our networks. The temporal dynamics of these networks were then indicated by the smallest quasi-Akaike information criterion (QAIC; Whitehead 2007). Unless otherwise stated, there was substantial support for all models based on a ΔQAIC value of between 0 and 2 (Whitehead 2009). In order to assess the precision of estimates made for a LAR, the jack-knife procedure was adopted (Sokal and Rohlf 2003), whereby analysis was rerun progressively omitting one sampling period at a time. Jack-knifing was set to occur for every fifth sampling period as sampling periods were nonindependent of one another. Furthermore, the coefficient of variation was used to describe the fluctuation in amplitude of the LAR allowing inference to be made into small-scale changes in stability of female social structure.

Activity pattern data from the DST vertical profiles (A3 and A4 only) were analyzed and corrected using a custom-written analysis program (Dive Analysis v5, MBA). All individual depth profiles were corrected and calibrated to fluctuations in atmospheric pressure through data obtained from the Plymouth Marine Laboratory meteorological station. Recalibration of the DST data was also applied every 6 h to control for tag drift in baseline pressure readings. Vertical displacement measures obtained from the depth profiles were tested for normality using the Anderson–Darling test, which found that the data were not normally distributed. A General Linear Model (GLM) followed by a Tukey test was used to determine significant differences in vertical displacement (activity) between treatments. Due to the large sample size of the activity pattern data (total move steps of key and peripheral individuals in A3 and A4, $n =$ 229 075), GLM was considered to be quite robust, even though the data were not normally distributed (Zar 1999). These statistics were carried out using MINITAB release 15 (Minitab Inc., State College, PA).

RESULTS

Social structure

The social structure of 4 groups ($n = 8$) of female catshark (*S. canicula*) were monitored and analyzed during March to April 2007 and April to July 2009. Although it is difficult to age mature sharks without analysis of the vertebra, individuals were sized matched as closely as possible. With data restricted to symmetric (or tactile) association, the permutation test showed a strong difference from random association in all groups for the 2-week period in which initial social structure was described. Time-depth profiles of individuals tagged with pressure (depth)-sensitive DSTs indicated that individuals resumed regular diel activity patterns 48 h after the DST attachment procedure. Furthermore, network analyses revealed that tagged individuals maintained their relative positions of high (key) and low (peripheral) connectivity, allowing us to use the 2-week period post-tagging as our new baseline social structure. Using a 2-sided significance level for dyads ($P > 0.95$ and $P < 0.05$), all 4 groups of captive sharks recorded >20 out of a possible 28 significant dyads (a pair of individuals observed associating with or avoiding one another more frequently than expected from random assortment). Under such random assortment, the expected number of significant dyads was 1.4, equal to 5% of the total number of symmetric dyads. The test for preferred or avoided association showed that

Table 2

Permutation test for preferred and avoided association over the 2-week period prior to manipulation

| Data set | Mean association index | | P value |
	Observed	Randomized	
A1	0.34270	0.42953	<0.001
A2	0.15741	0.21538	<0.001
A3[a]	0.18706	0.25780	<0.001
A4[a]	0.16506	0.23714	<0.001

The null hypothesis of no preferential association in this period is therefore rejected.

[a] Indicates arenas in which a key and a peripheral female were tagged with G5 long-life DSTs

during the initial period of social definition, there was a significant difference between the observed mean association and the randomized mean association (Table 2). Interestingly, the randomized mean was greater than the observed mean association, suggesting that avoidance behavior was more prevalent than association. However, it also suggests that fairly strong association was restricted to just a few individuals, even in a captive environment. Nonetheless, preference and avoidance behavior between individuals in all groups occurred significantly more often than would be expected by chance from random association.

Strikingly, there was a high level of structural variation between each of the 4 social networks highlighting the fact that groups were characterized by differences in individual preference for association or indeed different behavioral phenotypes (see sociograms, Fig. 1). Network metrics, however, reveal similarities in structure between arenas 1 and 3 (A1 and A3) and arenas 2 and 4 (A2 and A4), and therefore, it is useful to discuss these 2 sets of arenas separately. A1 and A3 showed distinct structural variation in which association was influenced by 3 or 4 strongly connected key females (B, C, E, and H in A1 and C, D, and E in A3). Social heterogeneity was reflected by the broad range of weighted degree and average path length within these groups (A1: weighted degree range, 0.76–3.21; average path length range, 1.90–8.48. A3: weighted degree, 0.75–2.00; average path length, 0.89–3.18). By contrast, A2 and A4 represented more homogeneous social networks (A2: weighted degree range, 0.71–1.58; average path length range, 0.77–1.78. A4: weighted degree, 1.02–1.78; average path length, 1.56–2.56). These were characterized by a lower overall mean association with greater mixing between individuals, thus illustrating the clear differences in strength of association between individuals across arenas (Figure 1). From the outset, A1 and A3 appeared to represent stronger social structures than A2 and A4 with females observed aggregating in larger mean group sizes ($\pm$standard error [SE]: A1 = 2.87 $\pm$ 0.11, A3 = 2.45 $\pm$ 0.02, A2 = 1.85 $\pm$ 0.03, and A4 = 2.30 $\pm$ 0.02). These structural trends not only had implications for the long-term stability of associations (see temporal analyses) but also appeared amplified by the introduction of male sharks.

Male introduction

The introduction of males to our behavioral arenas caused differential change across female networks (Figure 1). Pairs of introduced males demonstrated highly correlated behavioral repertoires to one another based on frequencies of recorded behaviors (Table 1) across arenas in both 2007 and 2009 (A1 and A2: Pearson's $r = 0.971$, $n = 4$ and $P < 0.05$; A3
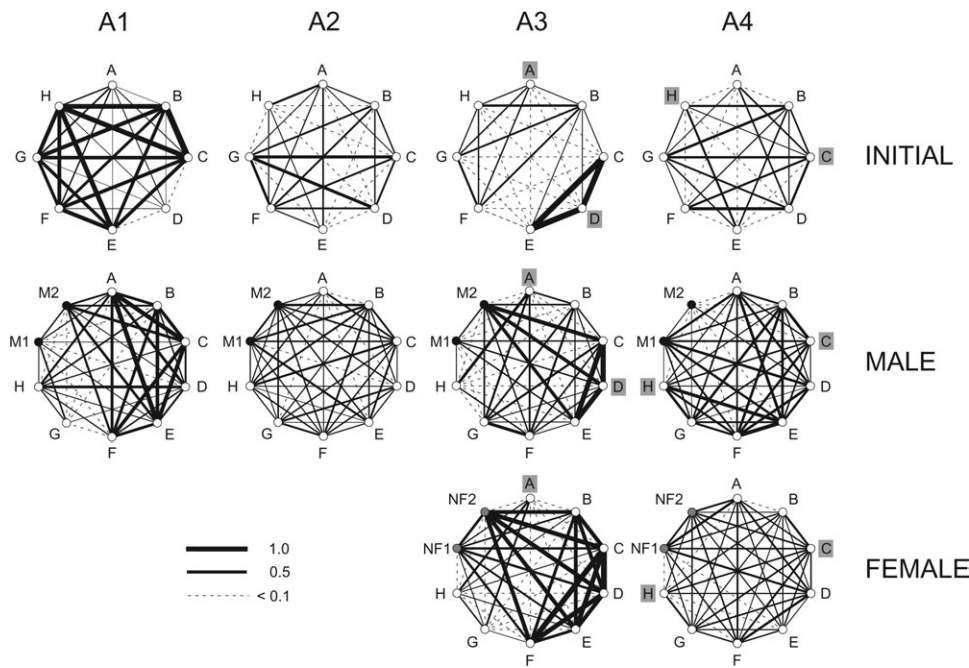
Figure 1
Symmetric sociograms (with relative tie weighting) across 4 arenas, showing the tactile resting behavior of female catsharks (white nodes), for initial social structure and the social structure during the introduction of male (black nodes) and novel female sharks (gray nodes, A3 and A4). Shaded labels indicate key and peripheral sharks tagged with DSTs (Note: There was only 1 functioning tag during female introduction to A3).

and A4: Pearson's $r = 0.948$, $n = 4$ and $P = 0.05$). Therefore, female response to male introduction was deemed to be reflective of female behavioral phenotype not differential male behavior. Across arenas, the introduction of males appeared to influence females differently depending on the strength of their initial social ties. As we might expect, there was a greater dichotomy in individual response to males in the groups, demonstrating increased social heterogeneity (A1 and A3) with key individuals remaining highly connected despite a slight reduction in overall mean association. An examination of the network measures (eigenvector centrality, weighted degree, and average path length) indicated that these highly connected individuals maintained the skewed distribution of the network when males were introduced. Furthermore, examination of the response of A1 and A3 reveals that social ties to 1 of the 2 males in each arena were kept to a minimal, <0.2, and the social ties of peripheral females increased in their weighted degree. This response was characterized by increases in eigenvector centrality ($\pm$SE) for peripheral individuals across both heterogeneous arenas (A1 female D: 0.10 [$\pm$0.02]–0.29 [$\pm$0.03] and A3 female F: 0.10 [$\pm$0.02]–0.24 [$\pm$0.02]) and had implications for the dynamics of these social networks (see temporal and activity analyses). SEs were bootstrapped using 1000 replicates.

Male introduction produced much more uniform effects within the arenas showing less structural variation in sociality. The average weighted degree of social ties increased in A2 (1.1–1.28) and A4 (1.16–1.86), suggesting more numerous associations between both female and male sharks. Increased mean association was driven by high levels of partner assortment and increased mixing. Key and peripheral individuals were no longer obvious and 3 out of the 4 males introduced to A2 and A4 became fully integrated into the social network (Figure 1). During scans samples, 2 instances of males chasing females were witnessed (D.M.P.J.) with no intrasexual chasing observed at any other time. These descriptive analyses demonstrate that females with strong social ties were more resilient to the potential disturbance posed by male presence.

Conversely, males had a much more disruptive effect on the weaker female networks.

Temporal stability and activity analyses
The analysis of LAR for initial structure and structure during male introduction lends further support to the differential social responses to male presence. LAR and its associated lag were calculated over 400 associations for all temporal analyses. These analyses revealed that A1 and A3 maintained consistent levels of temporal stability well above the NAR throughout the initial period of social definition (Figure 2a,c). This indicates that individuals were associated more often than would be expected by random for periods of up to 2 weeks or more. By contrast, arenas 2 and 4 demonstrated much lower LARs with trends decreasing toward random (null) over the same period of time (Figure 2b,d). This would suggest that temporal stability is stronger in an aggregation with more well-connected individuals, a trend reflected by the smaller amplitude of LARs for the groups showing greater social heterogeneity. The best-fitting model for all arenas during social definition consisted of 2 levels of casual acquaintances: $a3 \times \exp(-a1 \times \text{td}) + a4 \times \exp(-a2 \times \text{td})$, where td represents time lag and $a1$, $a2$, $a3$, and $a4$ the exponential parameters of the model (Whitehead 2009).

Both male and female manipulations appeared to affect the temporal stability of female networks, evident by increases in the amplitude of the LAR. During male introduction, however, temporal stability remained nonrandom throughout A1 and A3 despite the downward trend of the model (Figure 2e,g). A2 and A4 particularly had considerably reduced LARs from the outset with temporal stability lasting approximately 1 week (65 samples) prior to male introduction. Male disruption was apparent in both these arenas with A2 showing an increase in amplitude of LAR causing temporal stability to be reduced to just over 1 day (15 samples). A4 remained very close to the null but the downward trend, and level of association was exaggerated further. This is consistent with our network analysis, which indicates greater random mixing and partner assortment in arenas 2 and 4. Aside from A1, which maintained the same model in accordance with the QAIC, A2 and A3 were
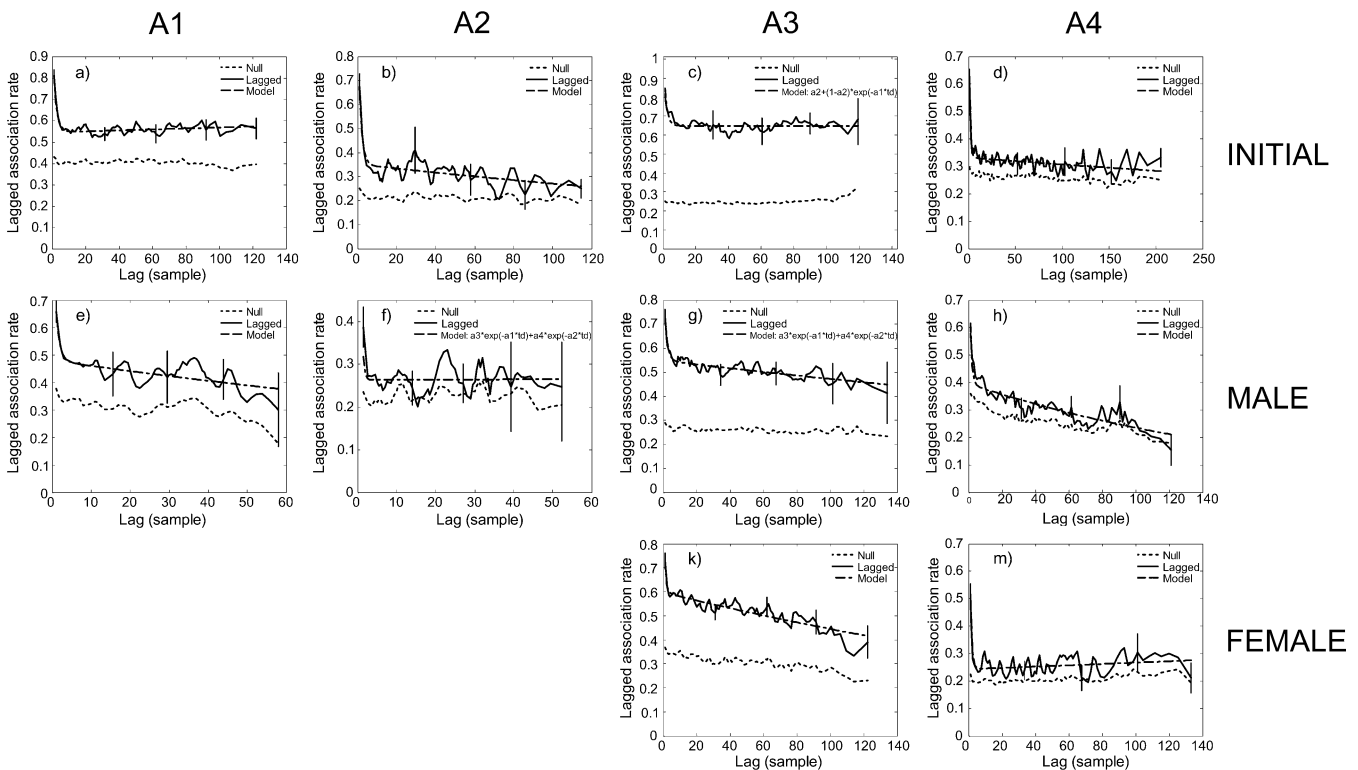
Figure 2
LAR (with jack-knifed estimates of precision) for initial social structure of females in arenas 1–4 and the structure during male and female introduction. Unless otherwise stated, the most frequent model to best fit the data was the "2 levels of casual acquaintances." ΔQAIC indicated substantial support for each model with the exception of (h) and (k), which had values of ΔQAIC >10. All LAR analyses were on symmetric associations and excluded any data from introduced individuals. Note: Scale of the *x* axis for male introduction. A1 and A2 (e and f) = 0–60 (1 week) and A3 and A4 (g and h) = 0–120 (2 weeks)—see "MATERIALS AND METHODS."

better explained by a model consisting of rapid dissociation and 2 levels of casual acquaintance. With a ΔQAIC >10, there was no support for any of the models in A4, so the original model was selected as it had the smallest QAIC value.

The analysis of activity profiles for arenas A3 and A4 revealed further insights into the potential fitness implications associated with occupying different structural positions within shark social networks, assuming increased activity impacts fitness and thus reproductive success. The results of the GLM indicate the significant differences in vertical displacement of individuals occupying positions of high and low social connectivity (Figure 3). There is clear evidence that all tagged individuals were sensitive to change in group composition and particularly the removal of male and female individuals after a treatment. Activity increased significantly for all tagged sharks during recovery periods with the exception of peripheral female A (A3) following female removal (A3: peripheral—$F_4 = 183.47$, $P < 0.001$; A4: key—$F_4 = 121.91$, $P < 0.001$, peripheral—$F_4 = 1981.88$, $P < 0.001$). Aside from key individual D (A3), which was very strongly associated initially, all tagged individuals responded to male introduction by significantly increasing their activity ($P < 0.001$) from the initial period of social definition. Similarly, peripheral females in each arena significantly increased activity levels in response to the introduction of novel females.

Female control
To control for putative effects of adding novel individuals to our behavioral arenas, female *S. canicula* were introduced to arenas 3 and 4. The heterogeneous social structure of A3

responded to novel female introduction with an increase in mean association with key individuals maintaining their positions of structural importance. Peripheral individuals tagged with DSTs responded to both male and female introduction by significantly increasing their activity (A3: $F_4 = 183.47$, $P < 0.001$ and A4: $F_4 = 1981.88$, $P < 0.001$: Figure 3b,d) implying a greater susceptibility to disruption of any kind by the more weakly connected females. The weaker social network in A4 maintained a much lower level of mean association (0.155) during female introduction, and social ties remained homogeneous between all group members, including novel females. There was no significant change in mean activity of the key individual in this group during female introduction. Despite partial water temperature control with a chiller, we were unable to prevent a gradual increase in seasonal temperature during experimentation. This was due to the high turnover of water required to maintain experimental sharks optimally (full exchange of tank water, 2242 l/h). Temperature increases were ~1 °C in 2007 (A1 and A2; 5 weeks) and ~4 °C in 2009 (A3 and A4, 11 weeks). Consistent results across individuals occupying positions of different social connectivity and the alternation of our treatments suggest that our results were the product of significant behavioral changes and were not driven by gradual changes in temperature.

Although temporal stability remained nonrandom during female introduction to A3 (Figure 2k), a downward trend, compounded by lack of support for the model of 2 levels of casual acquaintances, suggested that there were increased levels of mixing. This mixing, however, appeared to result from
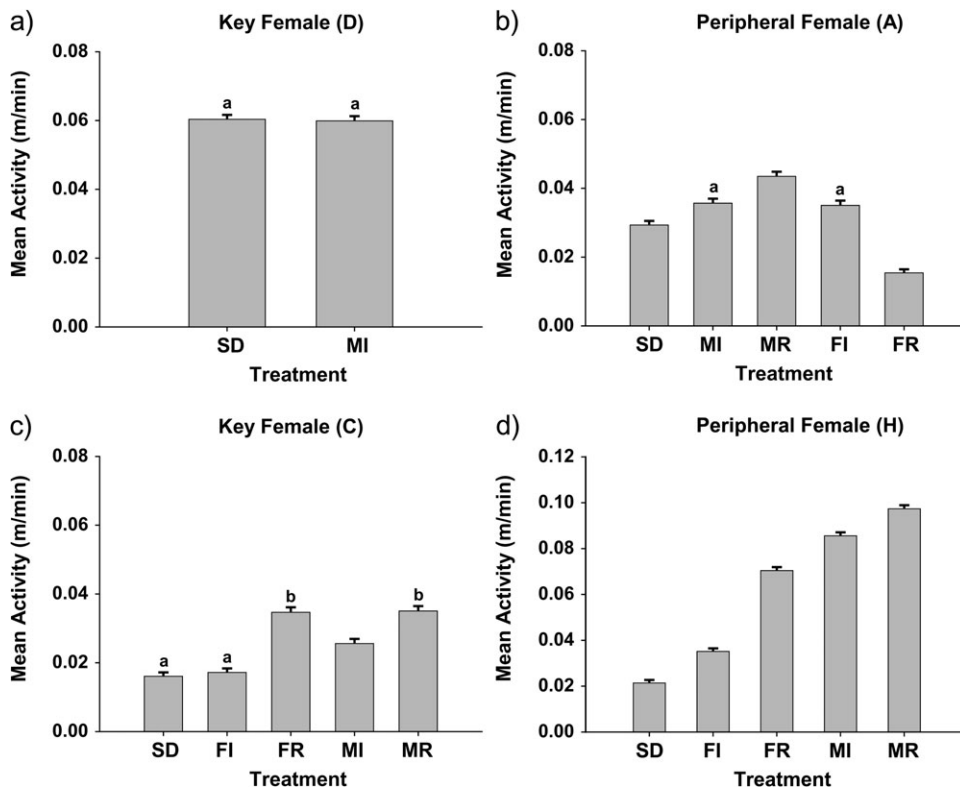
Figure 3
Mean activity (error bars indicate SE) of key and peripheral female in a strongly dichotomous social network A3 (a–b) and a more homogeneous network A4 (c–d) during each treatment. SD = social definition, MI = male introduction, MR = male recovery, FI = female introduction, and FR = female recovery. Treatments with the same lower case letters indicate no significant difference at $P < 0.05$ level. There was limited activity data for the key individual D (a) due to the tag being shed after MI.

the formation of additional and strong dyadic ties between increasing numbers of individuals, including our novel females (mean association increased from 0.191 to 0.268; Figure 1). The temporal stability of A4 remained short term and virtually random, a product of low levels of overall association. In contrast to the introduction of males, however, there was some support for the model of 2 levels of casual acquaintances, and this model indicated an increase in temporal stability over time and away from the NAR. We demonstrate, therefore, that although female introduction influenced the behavior of our focal shark groups, this influence produced increased levels of mean association and the formation of new dyadic bonds incorporating group mates and novel individuals.

One week of scan samples was taken 2 months after the end of experimentation in 2009. These data indicated that approximately 5 months on, similar network structures for A3 and A4 were being maintained by 2 out of 3 of the original highly connected key females (initial tie strength and 5 months on; A3 E – D: 0.84 and 0.69 and A4 F – C: 0.26 and 0.45). This supports the idea that marine fish also probably possess individual behavioral phenotypes (Pike et al. 2008) and adds further weight to our suggestion that long-term temporally stable associations are an important factor in structuring aggregation events in *S. canicula*.

DISCUSSION

Shark social networks, like other animal networks, appear structured by nonrandom association between specific individuals. A high degree of variation in network properties appears to reflect interindividual social preferences, with disturbance to these networks affecting individuals unequally depending on the strength of their social affiliations.

Under captive conditions, the replicated networks demonstrated substantial structural variation and considerable dif-

ferences in temporal stability. In the wild, however, it is probable that aggregations of *S. canicula* obey much more dynamic laws and fluctuations in composition, and therefore, captive networks were subjected to manipulation of group composition and sex ratio. Consistent with literature on behavioral phenotypes in freshwater teleost fish (Pike et al. 2008), individuals appeared to be characterized by persistent preferences for social and asocial behavior. Temporally, stable networks (A1 and A3) were maintained by a few strongly connected individuals producing a skewed distribution of social interaction. Long-term association was maintained in these networks, and peripheral females became more interconnected with the addition of male sharks. Less stable networks, however, consisted primarily of weakly associated individuals who tended to distribute their interactions more evenly. Substantial male integration into such weaker network structures (A2 and A4) caused already fragile temporal stability to fall below random after approximately 1 day and increased mixing and partner exchange elevated activity levels of peripheral females. Activity profiles revealed that all individuals—with the exception of the most strongly connected individual (key female D in A3)—showed significantly increased activity in response to male presence. Recovery periods, where group composition returned to $n = 8$ from $n = 10$, also initiated increased activity rates, regardless of the treatment. Weakly associated sharks in both homogeneous and heterogeneous networks appeared to respond to any form of disruption (males and novel females) more acutely then their more strongly connected conspecifics, suggesting potential benefits to maintaining persistent refuge partners.

The behavioral decisions adopted by slow-growing late-maturing elasmobranchs have potentially far reaching consequences for individuals that may live for several decades. The decision to form long-term social ties, developed through

repeated interactions (and potentially social recognition), is therefore likely to be of some ecological importance among apex marine predators occupying a highly variable spatiotemporal environment. Indeed, the benefits of associating with familiar conspecifics have been highlighted in a number of fish (Swaney et al. 2001; Ward and Hart 2003) and terrestrial animals (Moscovice and Snowdon 2006; Pinter-Wollman et al. 2009). Thus, the pressures driving such decisions in predators are probably substantial and the consequences significant. Individuals in gregarious species of elasmobranch may contend with additional social constraints imposed by a requirement to maintain information exchange, interindividual distance, or other collective behaviors (Sumpter 2006). In addition, such constraints may be heavily influenced by intersexual conflict derived from asymmetric reproductive investment. Increased competition between males can then result in different behavioral strategies between the sexes potentially, leading to segregation of the sexes and/or single-sex aggregation events (Clutton-Brock and Parker 1995; Pilastro et al. 2003; Wearmouth and Sims 2008).

Adult female catsharks (S. canicula) spend approximately 60–70% of their time aggregating in shallow inshore rocky crevices during the daylight resting phase of their diel cycle (Sims et al. 2001). These refuge sites are generally small with individuals tightly packed inside, for example, in one location (Lough Hyne, Southwest Ireland), limiting the number of females per refuge to between 3 and 13 sharks (Sims et al. 2001). Female S. canicula adopt different behavioral strategies to males, and little overlap is evident between respective activity areas (Sims et al. 2001, 2006). Indicative of many species, male reproductive strategy promotes numerous and frequent mating with multiple receptive partners, a strategy which in sharks particularly, could negatively impact female fitness due to the aggressive nature and energetic expense of mating events (Pratt and Carrier 2001). Female sharks, however, may counter this behavior by storing sperm until fertilization is required (Metten 1939). Indeed, this is consistent with behavioral and physiological evidence that female S. canicula frequently change refuge location en masse, store sperm, and delay fertilization (Sims 2005). Thus refuging behavior has been attributed, in part, to female avoidance of mating events during egg-laying and gestation periods (Sims 2003, 2005). This study is the first to investigate the direct effects of male behavior on female social structure in a predatory species of shark known to sexually segregate in the wild (Sims et al. 2001). We demonstrate that these refuge aggregations are likely to be maintained by nonrandom association between specific individuals with the capacity to form relatively stable long-term social bonds. Examination of the strength and stability of these bonds within a controlled captive environment provides an important insight into the ecological plasticity of these aggregations.

The permutation test for preferred or avoided association demonstrated that 4 groups of wild female catsharks ($n = 8$ per group) showed distinct social structures (significant at the $P < 0.001$ level) after just 3 weeks in captivity. This illustrates the potential importance of social interactions in this species and is consistent with theories that the large brain mass to body mass ratios found in elasmobranchs are conducive to the formation of complex social structures in gregarious species of shark (Northcutt 1977). Clearly, studying social behavior in captivity places specific restrictions on the movement and behavior of the experimental animals. The size of the behavioral arena will, to some degree, favor association over nonassociation because the potential for individuals not to associate is greatly reduced by space limitations. In this study, however, individual S. canicula chosen at random for each arena

showed considerable differences in their tendency to aggregate with one another indicated by the differences in the initial mean group size. Given the mean association index was lower than the expected mean in our random model, the dimensions of the behavioral arenas were considered sufficient to allow individuals to both associate with and avoid certain conspecifics. This was evident by the marked structural variation in the strength of dyadic links between individuals (thicknesses of lines; Figure 1) and by the variation in levels of temporal stability across the behavioral arenas (Figure 2). The putative causes of such variation remain unclear but may include levels of prior association in the wild or genetic relatedness of group members. Although these ideas provide interesting avenues for future research, the temporal data provided here strongly support recent work advocating behavioral phenotypes within fish aggregations (Pike et al. 2008), whereby variation in group structure is dictated by differences in behavior at the level of the individual (Magurran 1993). Furthermore, it reinforces current suggestions that familiarity may confer substantial benefits in social animals and to fish in particular (Ward and Hart 2003).

Although an animal's movement and distribution are often closely linked to their mating system (Croft et al. 2003), an individual's energy budget is dictated by a trade-off in behavioral strategies influenced by a variety of biotic and abiotic perturbations, whether it be competition for food, habitat selection, or mate availability (Sims et al. 2006; Darden and Croft 2008). The activity profiles presented here in response to social perturbation provide energetic support for the differential impact of disturbance on individuals of varying social connectivity. The limited replication of tagged individuals, however, encourages greater investigation in order to fully evaluate the extent to which individual variation compounds the effects of novel conspecifics on activity budget.

In summary, female refuge aggregations of small spotted catsharks (S. canicula) show significant nonrandom social structure adhered by strongly associated individuals. These aggregations provide further support that group stability is dictated by individuals aiming to maximize their own fitness, giving rise to individual variability within aggregations (Tyler and Rose 1994). Furthermore, manipulation of the sex ratio within each group shows that there are perhaps additional constraints on wild female S. canicula as a result of increased activity by less well-associated individuals in search of more socially stable refuge aggregations. Although there have been considerable advances in the telemetry and remote tracking of free-ranging sharks (Sims 2003), there is a distinct lack of specific quantitative research into the most influential factors determining social structure of marine predators (Wearmouth and Sims, 2008). This is despite the need to understand what factors act to structure natural predator populations, and how and why these may alter realized distribution patterns of species that, in the case of sharks, are currently exploited at unsustainable rates (Baum et al. 2003). The results of this study contribute to this understanding by analyzing the strength and dynamics of social interactions within aggregations of apex predators. We assess, under changing conditions, the likelihood that populations may be structured according to sexual interactions and/or sex differences in behavior. For some species of shark in particular, determining how widespread sexual segregation is, and whether this also initiates female-only aggregations, will be important for conservation because spatially focused fisheries may concentrate on one sex over another in certain areas, potentially exacerbating population declines (Wearmouth and Sims 2008; Mucientes et al. 2009). The outcome of this study also has implications for appraising the welfare of captive male–female groups of sharks in public display aquaria. Shark mating is usually highly

aggressive and can result in serious wounding of females by males (Pratt and Carrier 2001). If males disrupt female social groups through potential sexual harassment and no appropriate refugial habitats are available, it is open to question whether keeping male and female sharks together is best welfare practice in cases where the ratio of males to females is not at least very low.

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