Animal Behavior and Cognition
ABC 2026, 13(4):385-406
DOI: https://doi.org/10.26451/abc.13.04.04.2026
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Exploring Association and Social Networks Based on Proximity and Inter-Individual Interactions in a Group of Managed Care Killer Whales

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Citation – Themelin, M., Manitzas Hill, H. M., Robeck, T., Felice, M., & Dudzinski, K. M. (2026). Exploring association and social networks based on proximity and inter-individual interactions in a group of managed care killer whales. *Animal Behavior and Cognition, 13*(4), 385-406. https://doi.org/10.26451/abc.13.04.04.2026

Abstract – Killer whale societies have been investigated worldwide using association patterns and social network analysis. From residents living in enclosed matrilineal groups to the more flexible, fission-fusion-like groups, more details about killer whale societies continue to emerge. Despite these efforts, systematic investigation of inter-individual killer whale social exchanges remains sparse. Using frameworks established with *in situ* populations, we explored association and interactions networks of *ex situ* killer whales. Network analyses aligned with findings from *in situ* populations and showed that interaction networks were influenced by sex, and maybe age, whereas association networks were not. All individuals engaged socially with other group members and network analyses showed a well-connected group with no marginal individuals. Males were more central than females in both networks, which is contrary to other *in situ* studies, though our group composition might have impacted these findings. The youngest individual was more central and the oldest less central and less social in general, which aligns with other *in situ* observations. Overall, these results support two assumptions: 1) this group of *ex situ* killer whales generally exhibit social dynamics similar to *in situ* killer whales, though a few differences were observed, and 2) social management by the husbandry team for this group is in accordance with their individual association preferences. Group dynamics observed for these killer whales will inform the next phase of our longitudinal study focusing on social behaviors from underwater, which may allow insight into the evolution of both association and interaction networks for these killer whales over time.

Keywords – Killer whale, *Orcinus orca*, Social behavior, Sociality, Individual preference, Managed care, Social network analysis

The killer whale (*Orcinus orca*) is a cosmopolitan species with at least 10 identified ecotypes described globally based primarily on their foraging strategies, distribution, ecology, and morphology (de Bruyn et al., 2013). The best-known, most-studied populations include the Eastern North Pacific (ENP) killer whales with three ecotypes described: southern and northern residents (e.g., Bigg et al., 1990; Ford et al., 2000; Matkin et al., 2014; Tennessen et al., 2023), North Pacific Bigg's (i.e., transient, Baird & Dill, 1995; Ford & Ellis, 1999), and offshore (Dahlheim et al., 2008; Schorr et al., 2022). As research has expanded to additional killer whale populations so has our understanding of the unique nature of each of

these populations, including their social structures and association patterns. As an example, it is commonly acknowledged that killer whales live in matriarchal groups, yet, after accounting for the large variety of ecotypes and examining their idiosyncrasies, some groups closely resemble fission-fusion by showing more flexibility in their social dynamics (Ivkovich et al., 2020; Reisinger et al., 2017, Tixier et al., 2021).

In the ENP, the resident groups form stable matrilines comprised of an older female with her offspring and their offspring (Bigg et al., 1990). There is no dispersal (Ford et al., 2000; Matkin et al., 2014), and each clan has unique dialects with no common calls between clans (Deecke et al., 2000; Ford, 1989, 1991). Sympatric to the resident, the North Pacific Bigg's killer whales form small, ephemeral groups that feature both temporary and permanent dispersal by females (Baird & Whitehead, 2000; Ford & Ellis, 1999); it is unclear whether males overall disperse even though the mother-son association is often high and lifelong (Baird & Whitehead, 2000). Also, contrary to residents, the North Pacific Bigg's killer whales' group size and vocal habits seem highly correlated with their foraging ecology (Baird & Dill, 1996; Deecke et al., 2005). In the North Atlantic, Jourdain et al. (2024) showed that associations are flexible within and between social units that display ecological diversity with kinship as the main driver of social bonds within these killer whale groups rather than diet and foraging ecology. Contrary to the NPE groups, not much is known about southern hemisphere killer whales' ecology or social structure given the inaccessibility of their habitat and the cryptic habits of those populations (de Bruyn et al., 2013). The social structures of most of these ecotypes remain unknown, though stable social units have been identified for killer whales around the Crozet Islands (Guinet, 1991), but the decline of this population in the 1990s significantly altered the observed social structures (Busson et al., 2019).

The extant literature about the social activities of *in situ* killer whale populations has been based primarily on general behavioral categories and association patterns (i.e., time spent together or in proximity by two individuals), not on inter-individual exchanges. Research on killer whale association patterns have been conducted primarily on the well-studied North Pacific resident killer whale groups (e.g., Ellis et al., 2017; Ellis et al., 2021; Heimlich-Boran, 1986; Parsons et al., 2009; Weiss et al., 2021). Heimlich-Boran (1986) provided the first published exploration of association patterns based on age and sex of the individuals in dyads, although these analyses focused mostly on each dyad sex combination (i.e., male-male vs. mixed-sex vs. female-female) and did not compare them directly. Still, all associations were shown to be selective and not random. The mother-calf association was the most consistent and showed the highest of all association indices, with the birth of a second calf influencing the older calf's association with its mother. This latter observation contrasts with more recent work of sibling effect on an offspring association with its mother. Ellis et al. (2021) showed that even though both sexes remain in their natal groups (i.e., with the mother), there are differences between daughters and sons. For example, the association strength between mother and daughter decreases when the latter has her first calf whereas there is no change for a son. Interestingly, the mother-daughter association does not seem to be impacted if the mother has a calf, suggesting that daughters are driving the change in mother-daughter associations. Their study also indicated that when a mother dies, her offspring will associate more with siblings of the opposite sex and their grandmother (if alive) as compared with individuals who still have their mother. In accordance with other research (Weiss et al., 2021), the authors showed that associations are highly driven by kinship. Ellis et al. (2017) also confirmed that centrality (i.e., how well an individual is connected with other individuals of its social unit; Whitehead, 2008) impacts males more than females with males less centrally connected having a higher mortality risk, especially when resources are scarce. The explanation provided is that males (which likely need a greater food intake than females) are more at risk when the resources are low, thus their chances of finding food or the food-sharing opportunities are higher if they are more socially connected. While studies of association patterns in killer whales are important, association patterns might not represent the intricacies of their social lives as these patterns are based more on proximity than on actual inter-individual social exchanges. For example, when Weiss et al. (2021) examined both interaction (using contacts, i.e., direct interactions between two individuals) vs. association (i.e., time spent together by two individuals) networks in Southern resident killer whales using drones and physical contact exchanges between individuals for interaction measurements some differences emerged. The results of this study indicated that the interaction network might be influenced by the age and sex of the individuals involved,

whereas the association network was not, suggesting that females and males might use different socialization strategies. Their conclusion indicated that even though the gambit of the group hypothesis is applicable for some species (Danaher-Garcia et al., 2022), focusing on association patterns in closed groups of killer whales might conceal important components of their social lives.

Studies of *ex situ* killer whales can offer insight into behavioral exchanges between individuals, and provide non-invasive opportunities to better understand this species via investigative research into, for example, their physiology (Hedrick & Duffield, 1991; Kriete, 1995; Robeck & Nollens, 2013; Walker et al., 1988), metabolism (Kastelein et al., 2000; Kastelein et al., 2003; Kastelein & Vaughan, 1989; Kasting et al., 1989; Williams et al., 2011; Worthy et al., 2013), and behavior (Asper et al., 1988; Clark & Odell, 1999a, 1999b; Guarino et al., 2016; Martinez & Klinghammer, 1978; Sánchez-Hernández et al., 2019). From the very few behavioral studies conducted on *ex situ* killer whales, Sánchez-Hernández et al. (2019) were among the first to provide detail at the individual level as well as to describe killer whale affiliative, sexual, and agonistic interactions. More recently, Manitzas Hill et al. (2025) provided a detailed examination of *ex situ* killer whale activity budgets across a year with comparisons to *in situ* groups via the literature (e.g., Noren & Hauser, 2016), with similarities in the percent time spent in different broad behavioral categories evidenced. In the present paper, we expanded our analysis of the social interaction and proximity data collected by Manitzas Hill et al. to investigate the association and interaction networks between individuals of this *ex situ* killer whale group.

Specifically, we addressed the following questions: What are the association and interaction networks for this population, and how do they relate to each other, using demographic variables such as centrality of individual killer whale and sex? In the current study, we constructed two networks, one based on proximity (association network) and one based on inter-individual social exchanges (interaction network), which were then compared to each other to investigate the social exchanges of these *ex situ* killer whales and better understand their relationships. These network analyses can inform their husbandry team about the social management quality of this group, offer avenues with which to enhance sociality and sociability, while also fostering knowledge about killer whale social dynamics that could be applied to *in situ* populations. Given that information on *in situ* populations' social interactions is currently limited, the results examining our *ex situ* killer whale group dynamics can help create protocols appropriate to both settings to allow more direct comparisons. This knowledge could augment conservation and management goals and tools applicable to endangered populations.

Methods

Ethics Statement

Approval to conduct this study was granted by the SeaWorld Parks Animal Research Use Committee, an internal IACUC committee. All coding analyses were from video data only, and video data were collected in a non-invasive manner from cameras mounted above each pool that did not influence animal actions, interactions, or behavior. Because all observations were from video data that were non-invasively collected, an IACUC approval was not required.

Study Site and Animals

This study was conducted from video data collected at SeaWorld California (SWC) from April 2022 to January 2023, as part of an ongoing, longitudinal study begun in 2022. SWC offers a five-pool habitat of 24,605 m^3, including two visitor-viewable pools (public areas) and a back area restricted to trainer access. The public areas consist of a large semi-circular pool for public presentation and an oval pool with underwater viewing. The back area includes two rectangular same-size pools as well as a medical pool with a lifting floor. Pools are interconnected by 10 gates allowing for various pool combination accessible to the animals. See Manitzas Hill et al. (2025) for details regarding the facility layout. Our study group included 8-9 killer whales (9 in April and June 2022, 8 for the remainder of the study period). Individual killer whales

were identified by dorsal fin and fluke shapes. Animal sexes were equally represented (1:1). Ages ranged from 9–56+ years during the observation period (Table 1), though age categories were quite homogenous with primarily sexually mature individuals, one juvenile male, and a post-reproductive female (Manitzas Hill et al., 2025). All individuals were born in managed care, except COR and ULY for which the ages provided are estimated (indicated by "~" in Table 1). Besides KAL, NAK, and MAK (i.e., siblings, Table 1), all individuals were unrelated.

Table 1

Study Animals' Age and Sex

Name/Code	Age (y)	Sex
COR	~56	F
ORK	33	F
SHO	29	F
KAL*	17	F
ULY	~44	M
KEE	29	M
NAK*†	21	M
IKA	19	M
MAK*	9	M

Note. Ages listed as of April 2022 *Siblings. †Nakai was only present in April and June 2022.

Video Data Collection & Analysis

Each of the five pools had at least one high-resolution Power-Over-Ethernet overhead camera, allowing full topside coverage of the entire habitat with 8-10 camera angles. A 72-h period of continuous day-time video was exported every two months between April 2022 and January 2023. Each day-time footage was segmented into three five-hour time blocks per pool to facilitate data storage: from 0600 to 1100, from 1100 to 1600, and from 1600 to 2100. A total of 1,843 h of video was exported, see Manitzas Hill et al. (2025) for details related to video export dates, cameras placement, and export processes.

Video data were event sampled following a scan sample protocol using BORIS (version 7.13.9, Friard & Gamba, 2016). Ten scans, one scan per minute at the top of each minute (i.e., 10-min observation period), were completed at the top of each hour for each pool with each time block coded independently. For each pool, each 10-min observation was conducted at the exact same time to account for equal representation of each killer whale (i.e., each individual was counted once per scan). The first and last 10-minute observation periods were dependent on available daylight, with the first observation starting at either 0600 or 0700 and the last observation starting between 1800 and 2000 (at the top of the hour). Accounting for all camera angles, all pools, and all 10-min observation periods, a total of 311.7 h of video were analyzed. See Manitzas Hill et al. (2025) for more details regarding BORIS coding. One co-author coded all videos, while a second co-author also coded 2% of videos for inter-reliability with a 99% match. For the main coder, intra-reliability was assessed with a concordance index calculated averaging 0.99 (for details, see Manitzas Hill et al., 2025).

For the overall study (including Manitzas Hill et al., 2025 and the present study), 10 behaviors were used to record each animal's behavior for each scan: attention to trainer(s), attention to environment, resting, play/exploration, rubbing, social, pattern (i.e., a sequence of behaviors that is repeated at least two times in a raw while the animal is not swimming), swimming pattern (i.e., the repeated sequence of behaviors is performed while the animal is swimming), not applicable/not visible (NA/NV), and training (see Manitzas Hill et al., 2025 for detailed definitions). As all 10-min observation periods were fixed in time, training could happen during the scans and if so, the animals were recorded as "in training". For each of these behaviors and for each scan, spatial proximity between individuals was recorded as "in proximity", "solo", or "unidentified". Individuals were considered "in proximity" if they were within an adult body length of one another and the identities of the animals were noted. Individuals were considered "solo" if no

other individual was visible within an adult body length of them. "Unidentified" was used in situations for which proximity could not be properly assessed, like when animals were swimming at the bottom of the pool and not clearly visible or one individual was in a blind spot.

In the present study, we used proximity data and social behaviors data from our long-term longitudinal study at SWC to build an association network and an interaction network for this killer whale group. The association network was solely based on scans spent in proximity of one another and the interaction network was based on scans spent in direct social exchanges between individuals (i.e., any interactions, duo swims, or group swims, see below). These social exchanges corresponded to the "social" behavior from Manitzas Hill et al. (2025), which included duo swims, group swims, and interactions. Duo swims included all recordings in which two individuals swam within an adult female body length of each other in the same direction, no matter their relative positioning (i.e., in a pair swimming position or not, based on Themelin & Dudzinski, 2025). Group swims included all recordings of three or more killer whales swimming together in the same direction within an adult female body length of one another following a chain rule.

Interactions included all events where two or more killer whales directed their behavior(s) toward each other, with some of the following actions: chase or circle swim one another, make contact with one another, or interact with the same object together. Interactions were categorized based on components observable from the surface, i.e., angle and speed of approach, reciprocity between individuals, and responses of each individual involved in the interaction(s). Interactions were defined as affiliative when angles of approach were oblique or side-to-side, with slow to medium speeds, and involved reciprocity in each individual action toward one another. Affiliative interactions could also include rubbing on each individual's body but whereas any rubbing would be affiliative, not all interactions had to include rubbing to be categorized as such. Interactions were defined as agonistic based on a perpendicular or full head-to-head approach, medium to high speeds, and might have included one individual swimming away from the other, though this was not a requirement of the agonistic definition. Since observations were made from the surface, sun glare, water displacement and distortion, and splashes caused by some interactions sometimes prevented classification into any category. These interactions were simply recorded as "Other Interaction". Only five scans included agonistic interactions (all part of the same event) and six scans included "other" interactions were recorded. The five agonistic scans were not counted in the calculation of the indices (see below) for the individuals involved. The six "other" scans were considered neutral, i.e., without positive or negative components, and were included in the calculation of the indices for the individuals involved. To avoid any confusion between our "interaction" network (including also duo and group swims data) and our social behavior "interaction", we will use the term "social" network instead of "interaction" network.

Group Management

During the study period, some individual killer whale personalities and inter-individual interactions precluded two killer whales from being grouped together and therefore, prevented all animals to be housed together with access to all pools at the same time. Thus, the SWC killer whale husbandry team managed the group daily, shifting individuals into fluctuating 'social groupings' for different periods of time with varying pool access. For this study, we defined social grouping as a group of 1 to 6 killer whales, grouped together by the husbandry team with specific pool access identified. The husbandry team changed social groupings throughout each day, and from one day to another, based on each individual killer whale's preferences and/or care practices needed (Manitzas Hill et al., 2025). These individual preferences are based on observations by the husbandry team of inter-individual interactions both outside of and during training sessions, where each killer whale might more readily express willingness to be with specific individuals. Once in these social groupings, the animals were free to spend time with any individuals available (i.e., grouped with them). Pool access or availability referred to the pools accessible to a social grouping for the time this group was together. Pool availability varied from 1 to 4 pools for a social grouping, with pool D always used in combination with other pool(s) access (Manitzas Hill et al., 2025).

Statistical & Network Analyses

To better understand the relationships that connect the individuals in our study group, two types of indices were calculated to build our networks. The first was based on proximity data to calculate a coefficient of association (COA) between each pair of individuals to be used to build the association network. Every time two individuals were recorded as "in proximity", they were considered associated. Since social groupings were managed by the husbandry team, all individuals were not available to one another during each scan, although all individuals were located and identified at all times. Thus, each COA was calculated for a specific dyad AB, only taking into account when individual A and individual B were grouped together in the same social grouping. Our COA was based on the simple ratio index (Cairns & Schwager, 1987; Whitehead, 2008, 2009) and since all individuals could be identified at all times, i.e., yA = yB = 0 (Cairns & Schwager, 1987; Whitehead, 2008, 2009), the following formula was used:

$$COA = \frac{x}{x + yAB} = \frac{x}{gAB}$$

where x is the number of scans A and B are in proximity, i.e., associated, and yAB is the number of scans both A and B are in the same social grouping but not associated. The simplified formula includes gAB where $gAB = x + yAB$, i.e., the number of scans in which A and B were part of the same social grouping, no matter their proximity.

The second index was a social rate (SR) was used to build the social (interaction) network. For a dyad AB, it was based on the number of scans individual A and individual B were engaged in social exchanges (i.e., duo swims, group swims, or interactions) when both A and B were part of the same social grouping. Agonistic interactions were not included in SR calculation, which removed 1 to 5 scans for each of the following individuals: COR, KAL, ORK, and MAK. The social rate was calculated as follows:

$$SR = \frac{socAB}{gAB}$$

where $socAB$ was the number of scans A and B were engaged in social exchanges with one another, and gAB was the number of scans A and B were part of the same social grouping.

Both indices ranged from 0 (never associated or never involved in social exchanges when grouped together) to 1 (always associated or always involved in social exchanges when grouped together). To investigate any sex effect on the COA and SR indices, linear mixed-effect models (LMMs) were executed in R (version 4.5.0; R Core Team, 2024), via RStudio (version 2024.12.1+563; Posit team, 2025), using the *{nlme}* package (Pinheiro et al., 2023; Pinheiro & Bates, 2000) and *PermTest* function from the *{pgirmess}* package (Giraudoux, 2024) for p-value calculation with 1,000 Monte Carlo simulations. LMMs were conducted independently on both indices using sex as a fixed factor and individual as a random factor to account for repeated measures. These analyses were conducted on both the raw and adjusted COA and SR (see below). Also, to investigate the effect of the dyads' sex combinations (i.e., Female-Female, Female-Male, Male-Male) on the COA and SR values, LMMs were also conducted in R using the *{stats}* package and *PermTest* function from the *{pgirmess}* package (Giraudoux, 2024) for p-value calculation with 1,000 Monte Carlo simulations. LMMs were still performed independently on both indices using sex combination as a fixed factor.

UCINET (version 6.809; Borgatti et al., 2002) was used for network analyses. First, Quadratic Assignment Procedure (QAP) correlation was run to compare the association and social networks. Then, centrality measures, i.e., weighted degree, eigenvector centrality, and betweenness, were calculated for each matrix. These are common measures of centrality used during social network analyses (Whitehead, 2008), calculated for an individual X with the other individuals of the social unit, i.e., the social groupings in our case. In a weighted network, degree centrality (or strength, Barthélemy et al., 2005) is simply the sum of all association indices between X and its associates (Whitehead, 2008). Eigenvector centrality measures

how well X is connected to others but also how well X close associates are themselves well connected in the network (Whitehead, 2008, 2009). Betweenness refers to the number of shortest paths between individuals passing through individual X (Whitehead, 2008).

Considering the constraints of our data set, with each dyad not observed for the same number of scans, one dyad (IKA-ULY) observed in the same social grouping for only 20 scans showing the maximum indices (1 for both COA and SR), and one individual (NAK) only present in April and June 2022, all network analyses were conducted on three types of matrices for each network (i.e., COA and SR): the raw data, the adjusted data for IKA-ULY (indices of 1), and the adjusted data for IKA-ULY and removing NAK. This approach was taken to evaluate the influence of the strong indices between IKA and ULY on both networks and allow preventing these indices to have too much weight on centrality measures and afterward analyses. To adjust the indices of 1 observed for IKA-ULY, both COA and SR were given values of two standard deviations over the mean for both networks (new values for IKA-ULY: COA = 0.558 and SR = 0.458). All centrality measures were conducted on each type of matrices (i.e., raw, adjusted for IKA-ULY, adjusted for IKA-ULY and NAK removed) for each network.

Using RStudio (Posit team, 2025), and the *{coin}* package (Hothorn et al., 2006), we then tested the different centrality measures of both networks for any potential sex effect running Fisher-Pitman permutation tests. Due to the homogeneity of our age categories, age effect was not investigated statistically, though differences observed potentially related to age will be discussed.

Results

Overall, 261 h of raw video footage were coded (i.e., counting one angle per pool), with 241 10-min observations completed, representing 2,410 scans. As each scan contained 8-9 entries, i.e., one per individual killer whale, the full data set consisted of 20,150 entries in total. Over the range of social grouping combinations possible (246 for 8 killer whales including the two never grouped together, and 492 for 9 killer whales), 74 different social groupings were observed during the study, highlighting the husbandry team's decisions to respect some preferred individual affiliations. NAK was present for April and June 2022 sessions and involved in 165 social events. NAK's data were retained for all analyses as he engaged (in each social category) with each individual in the group.

As the dyad IKA-ULY was observed only over 20 scans during which they were always associated and engaged in social exchanges, their COA and SR values were 1. To investigate the influence of such values on the interpretation of the centrality measures for both networks, we calculated centrality measures on the raw COA/SR matrices and on an adjusted matrices for which IKA-ULY's COA/SR were adjusted to equal two standard deviations over the mean. Also, as NAK was present only early in the study but was associated and engaged in social exchanges regularly, we also calculated the centrality measure on the adjusted matrices for IKA-ULY removing NAK from the network. These measures on the different matrices showed that the weight of the link between IKA-ULY influenced the interpretation of centrality measures for other individuals, changing completely who was the most central individual. They also showed that the presence or absence of NAK in the network did not seem to influence the centrality measures of other individuals. Thus, only the results from the adjusted matrices for IKA-ULY, keeping NAK in the network, will be presented in the results section. The results from the other matrices are presented in the Supplemental Material (raw matrices in Table S1 to S3 with sociograms on Figure S1; adjusted values for IKA-ULY removing NAK from the network in Table S4 to S6 with the sociograms in Figure S2), though all results will be considered for the discussion about this population's networks.

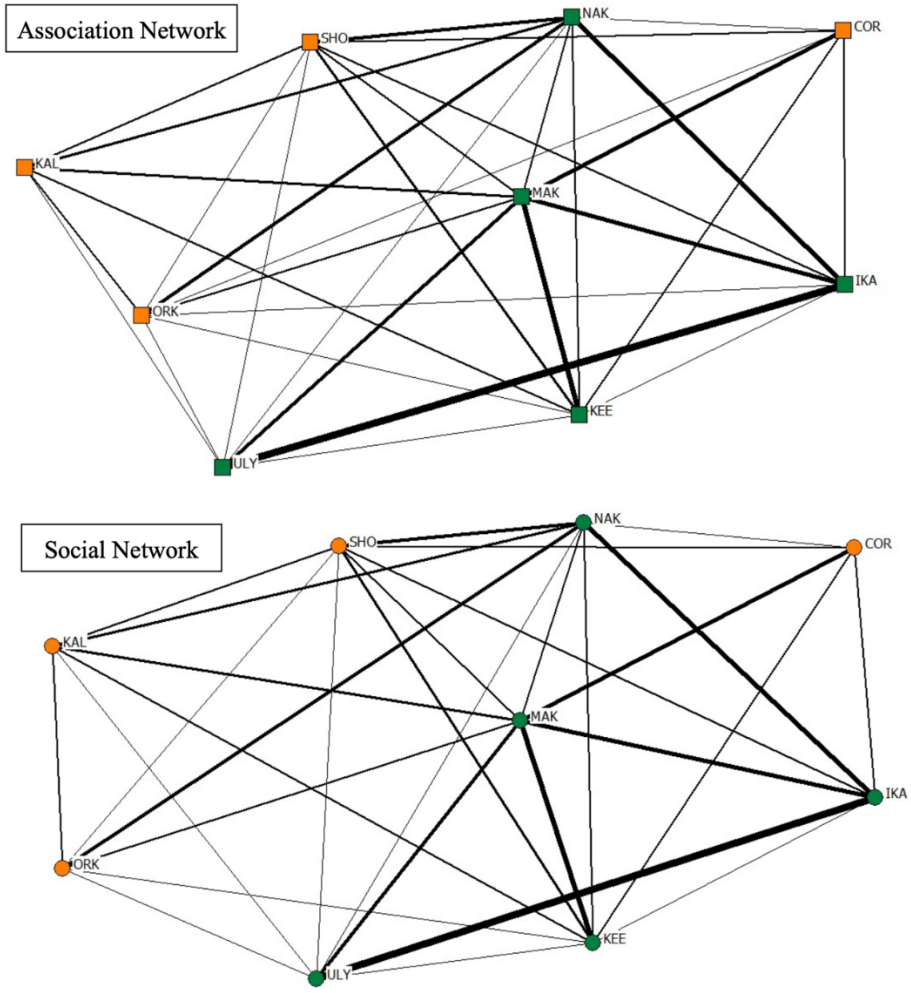
The COAs and SRs for each dyad based on the adjusted values for IKA-ULY keeping NAK in the networks are presented in Tables 2 and 3. We tested the correlation between the two matrices (i.e., COA and SR networks) and QAP correlation results showed both networks were highly correlated ($r = 0.87$, $p < .001$; Figure 1). The sociograms of both networks are presented in Figure 1. The results of the LMM did not show significant differences between sexes on the COAs ($\bar{X}_{FEM} \pm SD_{FEM} = 0.155 \pm 0.108$, $N = 4$; $\bar{X}_{MAL} \pm SD_{MAL} = 0.203 \pm 0.148$, $N = 5$) but showed significant differences ($p = .008$) for the SR, with males showing higher values than females ($\bar{X}_{FEM} \pm SD_{FEM} = 0.057 \pm 0.059$, $N = 4$; $\bar{X}_{MAL} \pm SD_{MAL} = 0.120 \pm 0.123$,

$N = 5$). Looking at sex combination effects for both networks, only the social network showed significant differences. Male-Male dyads showed significantly higher SR than both Female-Female ($p = .039$; $\bar{X}_{MM} \pm SD_{MM} = 0.165 \pm 0.150$, $N = 10$; $\bar{X}_{FF} \pm SD_{FF} = 0.033 \pm 0.026$, $N = 6$), and Female-Male dyads ($p = .023$; $\bar{X}_{MM} \pm SD_{MM} = 0.165 \pm 0.150$, $N = 10$; $\bar{X}_{FM} \pm SD_{FM} = 0.072 \pm 0.070$, $N = 19$) (Figure 2).

Centrality measures for both COA and SR networks (Table 4) were investigated for sex differences. The Fisher-Pitman permutation tests (Table 5) showed males had significantly higher weighted degree ($\bar{X}_{MAL} \pm SD_{MAL} = 0.936 \pm 0.269$, $N = 5$; $\bar{X}_{FEM} \pm SD_{FEM} = 0.440 \pm 0.083$, $N = 4$) and eigenvector centrality ($\bar{X}_{MAL} \pm SD_{MAL} = 0.405 \pm 0.102$, $N = 5$; $\bar{X}_{FEM} \pm SD_{FEM} = 0.184 \pm 0.038$, $N = 4$) for the social network (i.e., SR). Although males showed higher centrality values than females for the association network (i.e., COA), this difference was not significant.

Figure 1

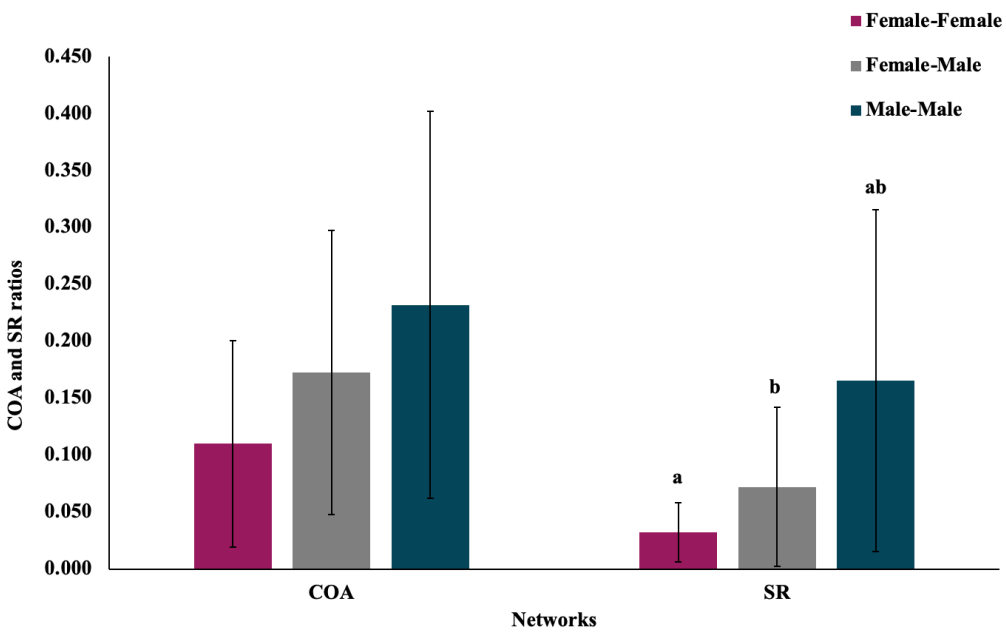
Sociograms of the Association and Social Networks of the SWC Killer Whales Based on Adjusted Measures for Ika-Uly, Keeping Nak in the Network



Note. Association network based on COA values, square nodes, top image. Social network based on SR values, circle nodes, lower image. The graphs were created using NetDraw from UCINET (Borgatti et al., 2002). Orange nodes = Females, Green nodes = Males. The thickness of the edges represents the weight of the link (i.e., COA or SR, respectively). The nodes are arranged using non-metric multidimensional scaling. COR-ULY are not linked because they were never observed in the same social grouping. For all other dyads, an absence of link represents the absence of proximity or social exchanges between the individuals.

Figure 2

Effect of Sex Combinations on COA and SR Values



Note. Error bars represent standard deviation. LMM for COA: N.S. LMM for SR: a and b depict significant differences with following *p*-values: a = .039 and b = .023.

Table 2

Coa Values for Each Killer Whale Dyad Based on Grouping Possibilities

	IKA	KAL	KEE	MAK	NAK	ORK	SHO	ULY
COR	*0.280*	0.000	0.063	***0.330***	0.176	0.007	*0.194*	*NA*
IKA		0.000	0.043	0.291	***0.328***	0.027	*0.216*	**0.558**
KAL			0.094	***0.394***	*0.306*	0.135	*0.213*	0.075
KEE				***0.409***	0.130	0.096	*0.235*	0.115
MAK					0.148	0.141	*0.181*	*0.270*
NAK						***0.376***	*0.233*	0.029
ORK							0.112	0.024
SHO								0.033

Note. IKA-ULY presents the adjusted value based on two standard deviations over the mean of the raw COA (raw COA: $\bar{X} + 2SD$ = 0.193 + 2 x 0.183). Italicized values represent COA over the mean, bold-italicized values represent COA over the mean and one standard deviation, and bold values represent COA over the mean and two standard deviations. For this network: $\bar{X} \pm SD = 0.180$ ± 0.135, N = 9. For COR-ULY, NA indicates COA calculation was not possible as these two individuals were never part of the same social grouping.

Table 3

SR Values for Each Killer Whale Dyad Based on Grouping Possibilities

	IKA	KAL	KEE	MAK	NAK	ORK	SHO	ULY
COR	0.061	0.000	0.047	***0.253***	0.008	0.000	0.050	*NA*
IKA		0.000	0.032	***0.231***	***0.303***	0.000	*0.096*	**0.458**
KAL			0.078	*0.105*	*0.118*	0.051	0.057	0.016
KEE				***0.278***	0.067	0.022	*0.101*	0.002
MAK					0.074	0.045	0.054	*0.180*
NAK						*0.188*	*0.157*	0.029
ORK							0.037	0.016
SHO								0.005

Note. IKA-ULY presents the adjusted value based on two standard deviations over the mean of the raw SR (raw SR: $\bar{X} + 2SD$ = 0.107 + 2 x 0.175). Italicized values represent SR over the mean, bold-italicized values represent SR over the mean and one standard deviation, and bold values represent SR over the mean and two standard deviations. For this network: $\bar{X} \pm SD$ = 0.092 ± 0.104, N = 9. For COR-ULY, *NA* indicates SR calculation was not possible as these two individuals were never part of the same social grouping.

Table 4

Centrality Measures for each Individual and Both Networks

	Degree		Eigenvector centrality		Betweenness	
	COA	SR	COA	SR	COA	SR
COR^{F}	1.050	0.419	0.279	0.208	0	0
KAL^{F}	1.217	0.425	0.301	0.164	0	0
ORK^{F}	0.918	0.359	0.224	0.141	**0.533**	0
SHO^{F}	1.417	0.557	0.325	0.222	**0.533**	**1.1**
IKA^{M}	1.743	1.181	0.398	**0.532**	0.167	0.2
KEE^{M}	1.185	0.627	0.292	0.260	**0.533**	**1.1**
MAK^{M}	**2.164**	**1.220**	**0.456**	0.458	**0.533**	**1.1**
NAK^{M}	1.726	0.944	0.372	0.366	**0.533**	**1.1**
ULY^{M}	1.104	0.706	0.292	0.409	0.167	0.4

Note. Association network = COA. Social network = SR. Bold fonts represent the highest values for each centrality measure for each network. Centrality measures were calculated on the adjusted values for IKA-ULY. Individuals' sex is denoted by ^{F} for females and ^{M} for males.

Table 5

Fisher-Pitman Permutation Tests' Results for Each Centrality Measure for Both Networks Based on Sex

	Degree		Eigenvector Centrality		Betweenness	
	Z	*P*	*Z*	*P*	*Z*	*P*
COA	-1.361	.179	-1.316	.216	-0.733	.446
SR	-2.259	**.023**	-2.373	**.016**	-1.416	.142

Note. Bold fonts represent significant p-values ($p < .05$).

Discussion

While individual contribution to social exchanges in a group is yet to be fully understood for either *in situ* or *ex situ* killer whales, examining association patterns and social exchange rates offer an avenue to assess the role(s) of sex, age, and individual on these networks. The social exchanges observed in this study led to the calculation of a social rate (hereafter referred to as *interaction* to facilitate comparison to the literature) to better evaluate the strength of each dyadic relationship. Additionally, our long-term dataset of this group's general behaviors (Manitzas Hill et al., 2025) and proximity data allowed us to calculate COAs

for each dyad. Published research suggests that associations are not random in cetacean species, as preferential associations are typical in *in situ* social groups (e.g., Bigg et al., 1990; Danaher-Garcìa et al., 2019; de Stephanis et al., 2008; Degrati et al., 2019; Lusseau et al., 2003; Möller et al., 2006; Reisinger et al., 2017). Although we did not test for random associations, the great variability observed between dyads for both COA and SR values support the presence of preferred associations and interactions for these *ex situ* killer whales, like previously reported for *in situ* social groups. Comparison of these two networks confirmed that animals who associated with one another also interacted, as has been confirmed recently for smaller delphinids (Danaher-Garcìa et al., 2022).

Differences between female and male COAs were not found, though males showed somewhat higher values. In contrast, significant differences in SR were confirmed with males exhibiting higher values than females in general. These results are consistent with previous work (e.g., Weiss et al., 2021) showing association networks are not influenced by sex but interaction networks might vary between the sexes depending on the behavior on which the latter is based. Additionally, Weiss et al. (2021) suggested that individuals of different sex and age might have different social strategies in resident killer whales, influencing their interaction network. Our results support these findings as there was no sex combination effect for the COAs but there was one for the SRs. Although our sample size is small compared to other studies, our results showed male-male dyads had significantly higher SR values than any other dyads. This sex-based dyadic preference could relate to previous work for *in situ* populations in which Heimlich-Boran (1986) described male killer whales as having more "valuable" relationships, based on more direct interactions versus being observed in the same group, than females. Relationship quality has been investigated in other species (Fraser et al., 2008; Fraser & Bugnyar, 2010; Majolo et al., 2010; McFarland & Majolo, 2011), including dolphins (Themelin et al., 2020), with preliminary results showing more valuable relationships in male-male dyads. Relationship quality examination relies on social behavior exchanges and would be worth exploring in killer whales once these exchanges have been studied in greater detail.

The effect of our small sample size was particularly visible when comparing the raw and adjusted matrices for both networks. As IKA-ULY were observed in only 20 scans in the same social grouping and were associated and engaged in social events for those 20 scans, this dyad had the maximum values for both indices. When examining the raw data for centrality measures, IKA was generally the most central individual, which was not expected. After adjusting the COA and SR for that dyad, other patterns of centrality emerged, still showing IKA as highly central overall, but with MAK as most central. Though the relationship between IKA-ULY seems strong, the small number of scans for this dyad requires more observations to better understand their relationship and the position of both individuals in this social group.

Overall, regardless of the COA/SR adjustment in analyses, males showed generally higher centrality than females for all centrality measures in both networks. These differences were significant only for the interaction network (i.e., SR), which is contrary to the findings of Weiss et al. (2021) in which females were more central than males. Yet, this major difference between our study and theirs is not surprising when examining the particular characteristics of each study group. Weiss et al. focused on J pod of the Southern resident killer whale (SRKW) population, with a significantly larger sample size (22 individuals in 2019) compared to our study. More importantly, the strongest associations in SRKW occur between mothers and their offspring (Ellis et al., 2021), with maternal kinship driving the association patterns, given that this population forms stable matrilines with no offspring dispersal (Bigg et al., 1990; Parson et al., 2009). As shown by Weiss et al., physical contact exchanges were influenced by kinship, and mother-offspring pairs largely contributed to their interaction rates as centrality was higher among females and young individuals. There were nine mother-offspring pairs in the SRKW J pod and none in our study group, which likely contributed to the observed difference.

Additionally, drawing comparisons with any studies on wild populations is rather difficult as the basis of our indices' calculations are not the same. Weiss et al. (2021) is the only available study incorporating physical contact between killer whales to evaluate an interaction network. Since physical contact could not be confirmed from the surface in the current study, interaction rate was based on social events between individuals during scheduled scans sampled over 10-minute observation periods. Also, all

other studies on social network analysis in killer whales are based on associations, with group (i.e., "associates") defined generally using a 10-meter chain rule, considering all individuals observed in the same group as associated. Here, our "associations" are defined using effective proximity between individuals based on an adult female body length, which means individuals that would have been considered "associated" in the wild were not in our study. The particularities of our sampling protocol and our definitions are more likely to underestimate our association and interaction indices compared to other killer whale studies.

Looking more closely at the centrality measures for both networks, MAK was the most central individual, showing higher gregariousness (i.e., tendency to form associations with other individuals, Pepper et al., 1999), higher connections to other well-connected individuals, and being a key individual connecting other group members. MAK's higher centrality could be related to his age, as he was the youngest member of the group, much like the *in situ* population Weiss et al. (2021) observed in which younger individuals also presented higher centrality measures. Similarly, although calculated based on associations and not interactions, Williams and Lusseau (2006) reported that betweenness was higher for younger individuals than older. Dudzinski et al. (2025; in review) did not examine centrality or betweenness for group members; however, their study confirmed the influence and value of offspring to a social group with tighter spacing between individuals (i.e., close proximity), increased activity levels and social affiliation (i.e., PSP and contact exchanges), and more play observed in groups with more and younger pre-weaned calves. Thus, young animals seem to play an important role to the dynamics of delphinid social groups, though it requires more investigation to understand their position in both matriarchal and fission-fusion societies.

As killer whale social groups are usually considered matriarchal with higher centrality values observed for females (Weiss et al., 2021; Williams & Lusseau, 2006), we were interested in the centrality measures' variability of the females in our group considering they were less central than males. The two 30-year-old females (SHO & ORK) showed the highest centrality compared to the oldest (+56 y) and the youngest (~17 y) ones. Specifically, SHO showed higher values for all centrality measures and showing comparable values to males. Interestingly, ORK showed the lowest values for weighted degree and eigenvector centrality, but comparable betweenness to SHO. The oldest female in the group (COR), though showing comparable weighted degree to the others (i.e., gregariousness), was overall the least central. This pattern is consistent with Weiss et al.'s (2021) observations of age being negatively correlated with centrality, and the general tendency for older individuals to be less social. Finally, the youngest female (KAL) showed comparable values to SHO, though very low betweenness. These results suggest that the differences observed in centrality between males and females might be due to our group's age composition. Specifically, while this *ex situ* group was composed of mostly adults, age differences between mid-aged (30-year-olds) and older individuals might have influenced the observed centrality for female killer whales.

While the killer whales in the current study consisted of six unrelated individuals and three siblings (KAL, MAK, NAK), which deviated greatly from observations of resident killer whale populations (Ellis et al., 2017; Ellis et al., 2021; Weiss et al., 2021), this composition and our results may not be so different if compared to more fission-fusion-like killer whale populations (Baird & Whitehead, 2000; Ford & Ellis, 1999; Reisinger et al., 2017). For example, the Marion Island killer whales have social units that include both related and unrelated individual and seem to show more flexibility than in resident killer whale populations. Also, considering that maternal kinship and/or foraging ecology are the primary drivers for killer whale social structures in most populations (Baird & Whitehead, 2000; Baumgartner et al., 2025; Beck et al., 2012; Bigg et al., 1990; Foster et al., 2012; Jourdain et al., 2024), it is not surprising to see differences in our study group. Indeed, individuals in managed care are provided with food, which reduces the impact of diet on their sociality. This difference might be even more important for males in which network centrality has been linked to their survival, especially during years of low resource availability (Ellis et al., 2017). Considering males in our study are provisioned and do not have to rely on others to find food or opportunities to share food and there are no offspring in the current social grouping, these differences might explain the more central position of our males as compared to *in situ* populations (Ellis et al., 2017).

Overall, all killer whales in our study group were seen socially engaged with several group members. Even individuals that showed low levels of social engagement with others were not particularly solitary, showing comparable gregariousness to other group members. Although there seems to be preferential associations and interactions between individuals with some dyads not engaging at all (e.g., COR-KAL and KAL-IKA), no marginal individuals were found, and all individuals were well inter-connected in both networks. Beside IKA-ULY, the strongest links for both networks were observed between KEE-MAK, KAL-MAK, and COR-MAK, as well as IKA-NAK and KAL-NAK. Interestingly, the three related individuals (i.e., siblings) in our group are part of these strongest bonds. Ellis et al. (2021) reported that siblings of the opposite sex show higher association levels with each other when their mother is no longer in the group. Our results are somewhat consistent with their findings as KAL's strongest connections were with MAK and NAK, although the connection to their sister was not the strongest association observed for either male. Also of interest, for both KAL-MAK and KAL-NAK, the SRs were much lower than expected from the observed COAs, showing that even though these dyads did spend time together, they did not particularly engage socially. This finding is consistent with other observations of social exchanges among kin in bottlenose dolphins, with non-kin sharing more pectoral fin contacts (Dudzinski & Ribic, 2017) and performing more PSPs (DCP unpublished data, 2019-2025) together than kin.

The strength of the current study is its application of association metrics that are used to assess *in situ* populations, which enables comparisons between killer whale social groups in different settings. Also, identifying central individuals in any group using social network analyses is a tool for the conservation of critically endangered *in situ* populations and for management of *ex situ* groups. Knowing the identity of these central or key individuals allows effective and targeted management of a group if and when these individuals are lost. However, like all studies, the findings must be considered with caution given the small sample of killer whales in the study group analyzed. Social network analyses conducted with *in situ* populations are usually based on partial, if not entire populations (i.e., SRKW studies). That said, our roughly equal sex ratio allowed for a microcosm assessment of sex differences in both networks. The homogenous age categories precluded statistical analysis of the effect of age on COA and SRs values, and centrality measures observed. The few observations related to age of the youngest male and oldest female are therefore anecdotal, and additional research is needed with other *ex situ* killer whale groups to examine the effect of age on killer whale sociality.

Lastly, there is a dearth of data from *in situ* killer whales with which to compare our rich dataset. The handful of studies focusing on killer whale social network analyses (Ellis et al., 2017; Ellis et al., 2021; Ivkovich et al., 2020; Forster et al., 2012; Jourdain et al., 2024; Weiss et al., 2021) use different protocol and association measurements, making direct comparisons between both settings challenging at best. Most studies of *in situ* killer whales primarily focus research at the group-level comparing social units (Bigg et al., 1990; Ivkovich et al., 2020; Reisinger et al., 2017) rather than on dyadic interactions within a social unit. Though Weiss et al. (2021) provided a good starting point for *in situ*/*ex situ* comparisons, harmonization of methods used in both settings is needed for direct comparisons. Still, this study allowed us to better understand the position of each individual in this group of *ex situ* killer whales and confirmed the good management of social groupings by the husbandry team in accordance with the inter-individual relationships observed. The second phase of our ongoing, longitudinal study of this group of *ex situ* killer whales includes examination of inter-individual exchanges from underwater; following a protocol that has been proven for smaller dolphin comparisons (Dudzinski, 2010; Dudzinski et al., 2009, 2010; Themelin et al., 2020), videos from underwater and drone perspectives of *in situ* killer whales will be directly compared to *ex situ* killer whale data.

Acknowledgements

Thank you to the training team at SeaWorld California (SWC) who assisted with behavior discussion topics, video export(s), and killer whale identifications. Thank you to N. Danaher-Garcia, DCP, for advice on statistical analyses with UCINET. Thank you to B. Brown for assistance with early data

analyses. All reviewed data were from video records collected non-invasively that did not require IRB or IACUC oversight. This study was approved by the SWC research committee and administration. Thank you to K. Steinman for help with logistics and to K. Flaherty Clark and C. Dold at SeaWorld for their support.

Author Contributions: MT: Conceptualization, Methodology, Investigation, Software, Formal Analysis, Validation, Writing - Original Draft, Review & Editing; HMH: Conceptualization, Formal Analysis, Validation, Writing - Review & Editing; TR: Conceptualization, Funding Acquisition, Writing - Review & Editing, Supervision, Facility; MF: Software, Writing - Review & Editing, Resources; KMD: Conceptualization, Methodology, Investigation, Funding Acquisition, Resources, Data Curation, Writing - Review & Editing, Project Administration

Funding: Funding for this research was provided by United & Entertainment and the Dolphin Communication Project. This article represents contribution #136 from DCP and SeaWorld Parks technical contribution number 2025-3.

Conflict of Interest: The authors declare no conflict of interest.

Data Availability: Data can be made available on reasonable request to the Dolphin Communication Project, via the corresponding author.

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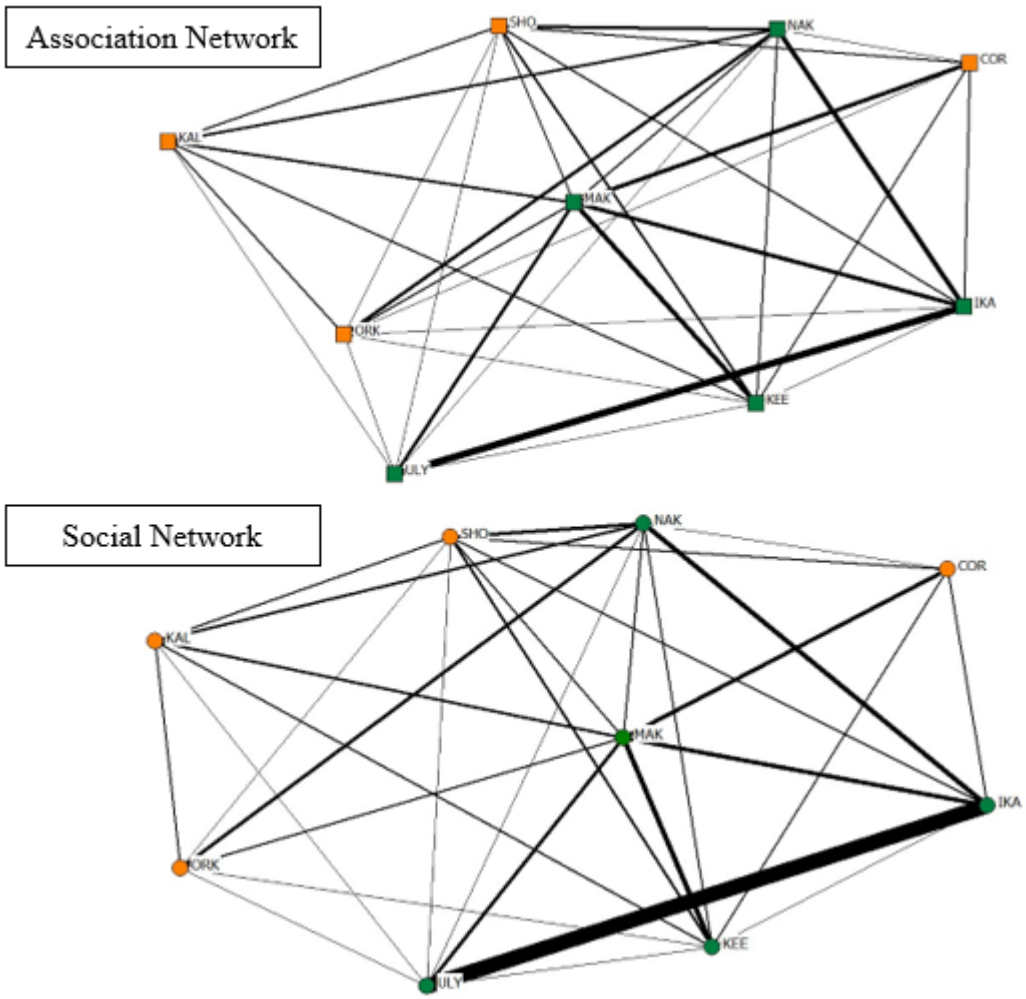
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Supplementary Materials

Figure S1

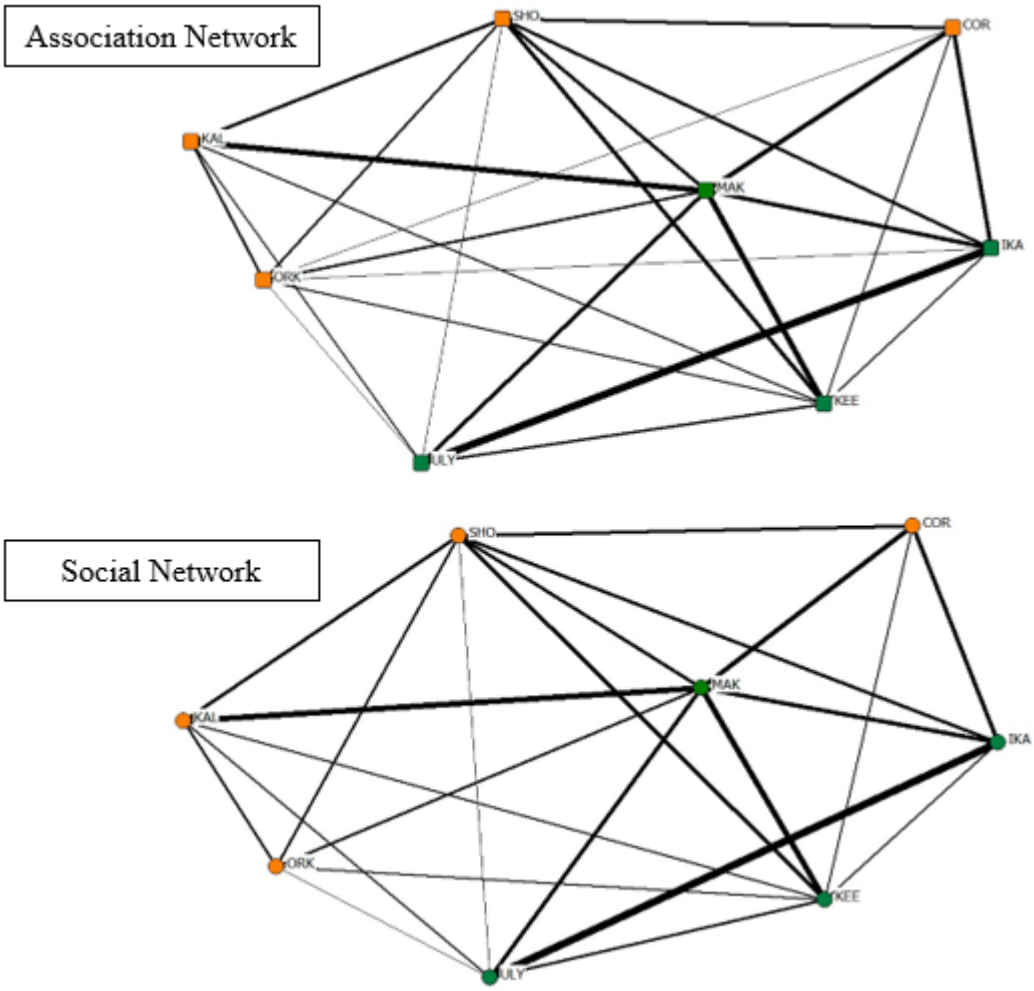
Sociograms of the Association and Social Networks of the SWC Killer Whales Based on Raw COA and SR Values



Note. Association network based on raw COA values (Table S1), square nodes, top image. Social network based on raw SR values (Table S2), circle nodes, lower image. The graphs were created using NetDraw from UCINET (Borgatti et al., 2002). Orange nodes = Females, Green nodes = Males. The thickness of the edges represents the weight of the link (i.e., COA or SR, respectively). The nodes are arranged using non-metric multidimensional scaling. COR-ULY are not linked because they were never observed in the same social grouping. For all other dyads, an absence of link represents the absence of proximity or social exchanges between the individuals.

Figure 2

Sociograms of the Association and Social Networks of the SWC Killer Whales Based on the Adjusted Matrices of COA and SR Values for IKA-ULY, Removing NAK from the Network



Note. Association network based on the adjusted matrix for IKA-ULY, removing NAK from the network (Table S4), square nodes, top image. Social network based on the adjusted matrix for IKA-ULY, removing NAK from the network (Table S5), circle nodes, lower image. The graphs were created using NetDraw from UCINET (Borgatti et al., 2002). Orange nodes = Females, Green nodes = Males. The thickness of the edges represents the weight of the link (i.e., COA or SR, respectively). The nodes are arranged using non-metric multidimensional scaling. COR-ULY are not linked because they were never observed in the same social grouping. For all other dyads, an absence of link represents the absence of proximity or social exchanges between the individuals.

Table S1

Raw COAs for Each Dyad Based on Social Grouping Possibilities

	IKA	KAL	KEE	MAK	NAK	ORK	SHO	ULY
COR	0.280	0.000	0.063	0.330	0.176	0.007	0.194	NA
IKA		0.000	0.043	0.291	0.328	0.027	0.216	1.000
KAL			0.094	0.394	0.306	0.135	0.213	0.075
KEE				0.409	0.130	0.096	0.235	0.115
MAK					0.148	0.141	0.181	0.270
NAK						0.376	0.233	0.029
ORK							0.112	0.024
SHO								0.033

Note. IKA-ULY grouped together for 20 scans. For this network: $\bar{X} \pm SD = 0.193 \pm 0.183$, $N = 9$.

Table S2

Raw SRs for Each Dyad Based on Social Grouping Possibilities

	IKA	KAL	KEE	MAK	NAK	ORK	SHO	ULY
COR	0.061	0.000	0.047	0.253	0.008	0.000	0.050	NA
IKA		0.000	0.032	0.231	0.303	0.000	0.096	1.000
KAL			0.078	0.105	0.118	0.051	0.057	0.016
KEE				0.278	0.067	0.022	0.101	0.002
MAK					0.074	0.045	0.054	0.180
NAK						0.188	0.157	0.029
ORK							0.037	0.016
SHO								0.005

Note. IKA-ULY grouped together for 20 scans. For this network: $\bar{X} \pm SD = 0.107 \pm 0.175$, $N = 9$.

Table S3

Centrality Measures for Each Killer Whale Calculated in UCINET (Borgatti et al., 2002) Based on the Raw COAs (Table S1) and SRs (Table S2)

	Degree		Eigenvector centrality		Betweenness	
	COA	SR	COA	SR	COA	SR
COR^F	1.050	0.419	0.251	0.110	0	0
KAL^F	1.217	0.425	0.250	0.076	0	0
ORK^F	0.918	0.359	0.184	0.068	**0.533**	0
SHO^F	1.417	0.557	0.282	0.123	**0.533**	**1.1**
IKA^M	**2.185**	**1.723**	**0.494**	**0.654**	0.167	0.2
KEE^M	1.185	0.627	0.251	0.125	**0.533**	**1.1**
MAK^M	2.164	1.220	0.414	0.303	**0.533**	**1.1**
NAK^M	1.726	0.944	0.325	0.244	**0.533**	**1.1**
ULY^M	1.546	1.248	0.420	0.607	0.167	0.4

Table S4

Adjusted Matrix for IKA-ULU, Removing NAK from the Network. COAs for Each Dyad Based on Social grouping Possibilities

	IKA	KAL	KEE	MAK	ORK	SHO	ULY
COR	0.280	0.000	0.063	0.330	0.007	0.194	NA
IKA		0.000	0.043	0.291	0.027	0.216	0.558
KAL			0.094	0.394	0.135	0.213	0.075
KEE				0.409	0.096	0.235	0.115
MAK					0.141	0.181	0.270
ORK						0.112	0.024
SHO							0.033

Note. IKA-ULY adjusted based on two standard deviations over mean on the raw COA. NAK removed from the network. For this network: $\bar{X} \pm SD = 0.171 \pm 0.141$, $N = 8$.

Table S5

Adjusted Matrix for IKA-ULY, Removing NAK from the Network. SRs for Each Dyad Based on Social Grouping Possibilities

	IKA	KAL	KEE	MAK	ORK	SHO	ULY
COR	0.061	0.000	0.047	0.253	0.000	0.050	NA
IKA		0.000	0.032	0.231	0.000	0.096	0.458
KAL			0.078	0.105	0.051	0.057	0.016
KEE				0.278	0.022	0.101	0.002
MAK					0.045	0.054	0.180
ORK						0.037	0.016
SHO							0.005

Table S6

Centrality Measures for Each Killer Whale Calculated in UCINET (Borgatti et al., 2002) Based on the Adjusted IKA-ULY Values for COA (Table S4) and SR (Table S5), and NAK Removed from the Networks

	Degree		Eigenvector centrality		Betweenness	
	COA	SR	COA	SR	COA	SR
COR^{F}	0.874	0.411	0.302	0.262	0	0
KAL^{F}	0.911	0.307	0.285	0.139	0	0
ORK^{F}	0.542	0.171	0.163	0.072	**0.65**	0
SHO^{F}	1.184	0.4	0.331	0.187	**0.65**	**1.417**
IKA^{M}	1.415	0.878	0.423	0.531	0.2	0.25
KEE^{M}	1.055	0.56	0.33	0.289	**0.65**	**1.417**
MAK^{M}	**2.016**	**1.146**	**0.522**	**0.530**	**0.65**	**1.417**
ULY^{M}	1.075	0.677	0.362	0.475	0.2	0.5

Note. Bold fonts represent the highest values for each centrality measure for each network. Individuals' sex is denoted by ^{F} for females and ^{M} for males.