

Master's Thesis

**Group size influencing factors and social structure of
Indo-Pacific bottlenose dolphins (*Tursiops aduncus*)
in the Northern Egyptian Red Sea**



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Editorial Note

This document is the adapted version for online publication of the master's thesis submitted at the University of Zurich in May 2021. To protect privacy and future research interests, a section of the original appendix ("10.3 Collected data available for future studies") outlining potential follow-up studies was removed from this version. The scientific integrity and findings of the thesis remain entirely unaffected by this adjustment.

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Table of contents

1 Abstract	5
2 Introduction	6
3 Materials and methods	12
3.1 Data collection	12
3.1.1 Study site and population	12
3.1.2 Boat-based surveys	13
3.1.3 Underwater footage and photos	15
3.2 Data processing	18
3.3 Data analysis	19
3.3.1 Video analysis	20
3.3.2 Statistical analysis	21
3.3.3 Social network analysis	23
3.4 Ethical note	28
4 Results	29
4.1 Group size influencing factors	29
4.1.1 Activity state and (sub)group size	29
4.1.2 Calf number, season and group size	31
4.2 Social structure and distribution	33
4.2.1 Community structure and distribution at three reefs	33
4.2.2 Influence of sex on association strength	35
4.2.3 Influence of maternal relatedness on association strength	38
5 Discussion	40
5.1 Group size influencing factors	40
5.2 Social structure and distribution	45
6 Conclusion	50
7 Funding	51
8 Acknowledgements	51
9 References	53

10 Appendix	62
10.1 Supplementary figures and tables	62
10.2 Materials used for data collection/processing	68
10.2.1 Behavioural survey data sheet	68
10.2.2 Focal group follow data sheet	69
10.2.3 Extract of photo-ID catalogue	69

1 Abstract

Group living in animals provides various benefits, such as better protection from harmful biotic or abiotic factors, easier information access/transfer, increased foraging efficiency and higher reproductive success. With group living, also costs can arise such as intraspecific competition, increased parasite/disease transmission or higher detectability by predators. To overcome these costs and maximise the benefits of living in groups, animals have evolved diverse behavioural strategies. Species living in fission-fusion societies can do so by temporally dispersing into smaller groups. The Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) is a social marine mammal species that lives in fission-fusion societies, whereby a group (all individuals observed within 10 m of the next individual) usually consists of 5-15 individuals. However, not much is known about factors that can influence the group size. In this study, I investigated if the activity state, number of calves per group and season correlate with the size of (sub)groups. Besides boat-based observations, analysis of underwater footage gave a novel and detailed insight into subgroup size depending on the activity state. I found a significant correlation between activity state and (sub)group size. Additionally, calf number per group positively correlated with group size, which has been confirmed by several other bottlenose dolphin populations. Furthermore, this study investigated the social structure of Indo-Pacific bottlenose dolphins in the Northern Egyptian Red Sea. The group composition data were based on long-term photo-identification. Social network analysis was used to test whether sex and maternal kinship influence association strength on a dyadic level. Since intrasexual associations were stronger than intersexual ones, sex was identified as driver of sociality of Indo-Pacific bottlenose dolphins in the Northern Red Sea, which corroborates findings in other populations. To assess community structure at three frequently visited reefs, I applied a *multilevel* cluster detection algorithm. I could neither find any spatially restricted communities nor sex-biased distribution/philopatry, which contrasts with populations in Shark Bay, Western Australia. The large distribution can be attributed to the similar environmental conditions at the examined reefs in the Northern Red Sea. This study highlights the correlation of activity state and number of calves with group size and gives an insight into factors that shape sociality in Indo-Pacific bottlenose dolphins in the Northern Red Sea. The findings of this study are of high significance for future conservation efforts and the establishment of a sustainable dolphin-watching tourism in the Northern Red Sea.

2 Introduction

Sociality in the animal kingdom can only be understood by studying why animals form groups (Whitehouse & Lubin, 2005). Animal fitness depends on a range of behaviours: defence/protection from harmful biotic (e.g. parasitism and predation) or abiotic (e.g. unfavourable climatic conditions) factors, foraging and reproduction. From an evolutionary perspective, we expect that a successful social group (measured in average fitness of individual group members) fulfils protective (i.e. protection from predators and territory defence), foraging and reproductive functions of its group members in more successful way than individuals not belonging to a social group can do on their own (Whitehouse & Lubin, 2005).

For social animals, group living is not intrinsically beneficial because costs can arise that are not present when solitarily living, such as competition for food and mates, increased transmission risk of parasites and disease or higher detectability by predators (Alexander, 1974). The group size and social organisation of a species can be regarded as the outcome of an optimisation process that increases the benefits and reduces the costs as much as possible. Benefits and costs of living in a group vary with habitat. Hence, animal social structures are understood as trade-offs of species-specific requisites in a certain habitat. The interplay between group size/social organisation and ecological factors is even more complex, since lots of species have evolved behavioural strategies to decrease the costs of living in groups (Alexander, 1974).

Temporal dispersal into smaller groups is one strategy to overcome strong intraspecific competition in large groups (Kummer, 1971; van Schaik & van Hooff, 1983). Even though numerous species can split into smaller groups during the day, only a few species are used to regularly adapt their social structure in this way. Such species are part of fission-fusion societies, i.e. groups merge (fusion) and split (fission) by moving through the habitat (Kummer, 1971; van Schaik & van Hooff, 1983), which makes the group composition as well as the group size dynamic variables (Couzin, 2006). Species that live in fission-fusion societies include hyenas (*Hyaena brunnea*; Owens & Owens, 1978), giraffes (*Giraffa camelopardalis thornicrofti*; Bercovitch & Berry, 2012), spider monkeys (*Ateles fusciceps rufiventris*; Klein & Klein, 1977), chimpanzees (*Pan*

troglodytes; e.g. Nishida, 1968) as well as humans (*Homo sapiens*; Rodseth et al., 1991) and finally bottlenose dolphins (*Tursiops* sp.; Smolker et al., 1992).

The Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) is a social marine mammal species (*Cetacea, Odontoceti, Delphinidae*) (Connor et al., 2000). Adults can reach a length of 2.7 m and a weight up to 230 kg, while calves range from 0.8 to 1.5 m in size and 9-21 kg in weight (Shirihai & Jarrett, 2006). Indo-Pacific bottlenose dolphins have a slow life history with a life expectancy of 40-50 years, gestation period of twelve months, weaning age and interbirth interval of 3-6 years (Karniski, Krzyszczyk & Mann, 2018; Shirihai & Jarrett, 2006). Young individuals reach sexual maturity at the age of 8-12 years (Karniski, Krzyszczyk & Mann, 2018). This dolphin species preys on a wide range of fishes and cephalopods, especially squid (Amir et al., 2005). Their natural predators mainly are sharks but can also include orcas in certain areas (*Orcinus orca*) (Harwood & Hembree, 1987). Indo-Pacific bottlenose dolphins are distributed along the coasts of the Indo-Pacific (ranging from Indian waters, Southeast Asia, western, (south)eastern and northern Australia, New Caledonia, the Solomon Islands and South China up to Japan), the African east coast including South Africa and Madagascar, the Red Sea and the Persian Gulf (Shirihai & Jarrett, 2006). The species prefers shallow waters and inhabits lagoons, reefs as well as seagrass meadows in coastal proximity and even estuaries (WDC, 2019). Its near-shore distribution makes the species vulnerable to environmental degradation/habitat destruction, pollution (wastewater), hunting, boat traffic/underwater noise, intensive tourism, overfishing, bycatch and entanglement in fishing gear (IUCN status: NT) (WDC, 2019; Smith, 2012; IUCN Red List, 2021).

Not much is known about group size influencing factors in Indo-Pacific bottlenose dolphins. In the closely related common bottlenose dolphins (*Tursiops truncatus*), group size mainly correlates with habitat structure and activity state (Odell, 1976; Shane, 1977; Wells, 1978; Würsig, 1978). There is a trend of larger group size with increasing water depth and openness of the habitat (Odell, 1976; Shane, 1977; Wells, 1978; Würsig, 1978). This physiographically dependent trend is attributed to protection from predators as well as foraging techniques (Norris & Dohl, 1980; Wells, Irvine & Scott, 1980; Würsig, 1978). In shallow, coastal waters, the food resources associated with reefs or seagrass meadows are rather equally distributed, whereas in open

waters, fish shoals are the prevailing resource for the dolphins. Larger groups, in which more individuals can incorporate their senses in foraging, can raise the chance of cooperatively locating those patchy prey resources. Accordingly, larger groups in open waters provide a few of the identical functions as coastal habitats in relation to predator protection (Norris & Dohl, 1980; Wells, Irvine & Scott, 1980; Würsig, 1978).

The average group of Indo-Pacific bottlenose dolphins includes 5-15 individuals (Reeves et al., 2002). However, aggregations of up to 100 individuals have been observed in South African waters (Bouveroux et al., 2018). The largest recorded group size in the Northern Egyptian Red Sea has consisted of 68 individuals (Dolphin Watch Alliance (DWA), internal records). For Indo-Pacific bottlenose dolphins, much less data have been available about the relationship of activity state and group size than for common bottlenose dolphins. In Australian Indo-Pacific bottlenose dolphin populations, the socialising groups consisted of the largest number of individuals, followed by travelling and resting groups, while the smallest number of dolphins was observed during feeding (Möller, Allen & Harcourt, 2002; Kopps et al., 2013). Furthermore, larger groups were observed when calves were present (Möller, Allen & Harcourt, 2002). Eventually, group size was shown to vary with season, i.e. being largest during mating/calving season (Wiszniewski, Allen & Möller, 2009; Mann et al., 2000).

To acquire more knowledge about potential factors influencing group size in Indo-Pacific bottlenose dolphins, I investigated the following questions:

- 1) Does the (sub)group size depend on the activity state?
- 2) Does the number of calves per group correlate with group size?
- 3) Does the group size change with season?

I hypothesise in particular that sleeping subgroups are larger in size compared to socialising and playing subgroups as well as travelling groups. I predict a positive correlation of calf number per group and the total number of group members. Finally, larger groups are expected in the mating/calving peak season during spring/summer. In addition to the assessment of group size influencing factors, I analysed the social structure and distribution of Indo-Pacific bottlenose dolphins in the Northern Egyptian Red Sea to find potential similarities or differences with other populations in the world.

Indo-Pacific bottlenose dolphins form a complex fission-fusion society, where groups regularly change in size and composition (Smolker et al., 1992). Individuals join and leave the groups flexibly, with interactions that last from minutes to years (Connor et al., 2000). Fission-fusion dynamics reduce feeding competition and inbreeding in bottlenose dolphins as those flexible groups allow dolphins to disperse (Connor, Read & Wrangham, 2000; Tsai & Mann, 2013). Studies in Australia have reported sex-biased philopatry/dispersal: As generally true for many other mammalian species (Greenwood, 1980), the resident individuals (which are an integral part of the bottlenose dolphin community) are usually females, which are the more philopatric sex, whereas males, the more dispersing sex, more frequently immigrate and emigrate (Krützen et al., 2004b; Möller & Beheregaray, 2004). This is mirrored by bottlenose dolphins in Western Australia, where males have larger home ranges than females (Sprogis et al., 2016). The sex difference in home range size is attributed to male mating strategies, where alliances of males compete against each other over oestrous females that are separated from the rest of the group and coerced to mate (Scott et al., 2005). With larger home ranges, males could get more social opportunities, i.e. more available alliance partners, which then increases their reproductive success (Möller & Beheregaray, 2004). Females, on the other hand, rely more on the familiarity of resources (Greenwood, 1980). Independent of sex, home range size can also differ with habitat, correlating with predation risk and prey availability (Sprogis et al., 2016).

The bottlenose dolphin fission-fusion society is characterised by sexual assortment (Wells, Scott & Irvine, 1987; Smolker et al., 1992; Lusseau & Newman, 2004), i.e. females living in flexible groups consisting of kin (except from their dependent calves) and non-kin (Möller et al., 2006), whereas males form stable, lifelong bonded alliances, consisting of 2-4 individuals (so-called “buddies”) (Connor et al., 2000). The number of alliance members depends on the habitat (Fury, Ruckstuhl & Harrison, 2013). The alliances usually consist of unrelated, similarly aged adult males because the association with a conspecific of similar competitive ability rather than a relative is expected to provide higher reproductive benefits (Möller et al., 2001; Gerber et al., 2020).

In bottlenose dolphin populations, sexual segregation has been found outside the mating season, most likely that females can reduce the risk of aggressive male coercion (Fury, Ruckstuhl & Harrison, 2013; Connor, 2000). Females can form coalitions, often consisting of related individuals (Möller et al., 2006), to protect themselves and their dependent calves from harassing males (Connor et al., 2000). In bottlenose dolphin societies, male-female associations are mainly driven by the mating season and female reproductive state (Connor et al., 2000; Owen, Wells & Hofmann, 2002). However, constant male-female associations, which are not caused by geographic isolation, have been observed in southeastern Australian waters (Wiszniewski, Lusseau & Möller, 2010).

The “kin selection theory” states that individuals preferentially undergo association and cooperation with kin if the inclusive fitness benefits are higher than the costs (Hamilton, 1964). In most mammals, females stay within their natal group or area for their entire lives (Greenwood, 1980; Pusey & Packer, 1987). Thus, the opportunities for association with kin are high (Greenwood, 1980; Pusey & Packer, 1987). Also, in female bottlenose dolphins, kin often associate among each other; however, kinship is not a prerequisite for the membership in social clusters (Möller et al., 2006; Connor et al., 2019). There is also evidence that mother-offspring associations can decline after weaning, especially for sons to avoid inbreeding, even though there might still be substantial home range overlap (Tsai & Mann, 2013).

To receive an insight into the social structure and fission-fusion dynamics of the Indo-Pacific bottlenose dolphins in the Northern Red Egyptian Sea and since research has mainly focused on male alliance formation and not on female sociality, I asked:

- 4) Can spatially restricted communities be identified at the three frequently visited reefs Fanous, Shaab El Erg and Umm Usk and is there a sex-biased distribution pattern?
- 5) Are intrasexual associations stronger than intersexual ones?
- 6) Does offspring still more regularly associate with their mothers after weaning compared to unrelated animals among each other?

I hypothesise that bottlenose dolphin communities (community: subset of individuals that interact more frequently among each other compared to individuals outside the subset (Newman, 2018; Shizuka & Farine, 2016; Whitehead, 2008)) which are spatially restricted can be identified at all reefs. However, migrating individuals between the reefs and thus with a larger distribution, primarily males, are still observed. I predict that intrasexual associations are more stable compared to interactions that take place between males and females. Weaned females are expected to have higher association strengths with their mothers (according to Möller et al., 2006), whereas I expect weaned males to show weaker maternal associations compared to unrelated individuals associating among each other (according to Tsai & Mann, 2013).

To study the relationship of activity state and of subgroup size, I analysed long-term underwater footage collected between 2012 and 2020. To examine if calf number and season correlate with group size, I used long-term behavioural data of 2012-2020. To shed light on the social structure of the Indo-Pacific bottlenose population in the Northern Egyptian Red Sea, I analysed long-term photo-identification data from three different reefs between 2009 and 2020 by creating social networks. This study aims to receive a deeper insight into the complex social lives of the Indo-Pacific bottlenose dolphins in the Northern Red Sea, which will expand our knowledge about this species and its potential adaptations to different environments. The acquired knowledge about the behaviour and sociality of Indo-Pacific bottlenose dolphins in the Northern Red Sea is of importance to implement and improve conservation actions in the future.

3 Materials and methods

3.1 Data collection

3.1.1 Study site and population

I collected data from wild Indo-Pacific bottlenose dolphins in the Northern Red Sea, region El Gouna/Hurghada, Egypt (Figure 1). From the beginning of the long-term study in October 2009 until the end of 2020, 369 individuals have been identified in the population of the Northern Red Sea (DWA, internal records). There is an uncertainty term on this number because it is unknown if disappeared animals died or emigrated to non-studied areas or whether juveniles are the same individuals as weaned calves already in the photo-ID catalogue (extract in section 10.2.3) that lack marks, nicks or notches for identification (Costa, 2015; A. Ziltener, pers. comm.). This term has to be estimated in a future project assessing the abundance and distribution of the entire population (according to Costa, 2015).



Figure 1: Map of the study site in the Northern Egyptian Red Sea (DWA, 2021). The two reefs Shaab El Erg and Umm Usk, where the data collection took place in 2020, are circled in red. Circled in yellow is the reef of Fanous in the south, where no data were collected in 2020, but data of earlier years was analysed in the social network analysis (refer to section 4.2). The red star marks the location of El Gouna, the green one Hurghada.

The data collection in the field focused on individuals that inhabit the reefs of Shaab El Erg and Umm Usk (distance between the two reefs ca. 18 km; red circles in Figure 1), which are valuable meeting points for different behaviours, especially for sleeping and resting, but also for socialising, playing and rubbing against various substrates (Ziltener, Wright & Kreicker, 2015; Ziltener & Kreicker, 2013; Ziltener, Kreicker & Gross, 2015; Kreicker & Ziltener, 2017). The data were collected from the research vessel by using behavioural data sheets (refer to section 10.2.1) and photo-identification (according to Würsig & Würsig, 1977). Additional behavioural data were collected by underwater filming during snorkelling and scuba diving (according to Confédération

Mondiale des Activités Subaquatiques (CMAS) scientific diver and Verein Deutscher Sporttaucher (VDST) guidelines). The field data were collected between 13th February and 16th March 2020 as well as between 19th August and 27th September 2020. The observation took place at daytime from 07:00 am to 05:00 pm. In total, data were collected on 28 offshore days (February/March: 13 days resulting in 15 surveys, August/September: 15 days resulting in 24 surveys). More offshore days in this total period of 80 days were not possible due to unfavourable weather conditions (strong wind and wave action) and an already occupied research vessel. In the water, the dolphins were observed 0-4 hours per day depending on environmental conditions (wind, waves and current), behaviour of the dolphins (avoidance of snorkellers/divers), human disturbance (tourist boats chasing dolphins) and the appearance of other marine species, such as blacktip reef sharks (*Carcharhinus melanopterus*).

3.1.2 Boat-based surveys

After the dolphin group had been identified according to the 10 m chain rule (two individuals are in the same dolphin group if they are within 10 m of each other or within 10 m of another dolphin, ad infinitum; Smolker et al., 1992), the boat-based survey began and was conducted for at least 5-15 min before going into the water, if possible. 39 surveys (12 in Shaab El Erg and 10 in Umm Usk; 1-3 (0-2 at Shaab El Erg and Umm Usk) surveys per offshore day depending on dolphin sightings) were conducted in 28 days of fieldwork. Just 22 out of the 39 conducted surveys took place in Shaab El Erg or Umm Usk because either no dolphins were sighted at those two reefs, we did an overnight safari with a route that also included other reefs or there were bad weather conditions that hindered us from driving to the far north to reach Umm Usk. At those two reefs, the total sample size was 322 dolphins (the same individual can be sampled several times over various surveys), thereby 1-39 dolphins were observed per survey. Each survey (refer to section 10.2.1) was marked by date, time and survey number, if multiple surveys were done on the same day.

The recorded survey parameters included (refer to section 10.2.1):

- **Group size** (total number of individuals per survey, can consist of only one individual; according to 10 m chain rule (Smolker et al., 1992))
- **Number of calves** (in infant or echelon position (Mann & Smuts, 1998))
- **Behaviour/activity state**
 - ➔ Predominant activity state: first 5 min of survey recorded (focal group continuous sampling): if the activity state is common to $\geq 50\%$ of the dolphin group for $\geq 50\%$ of the 5 min interval (as done in Shark Bay, Western Australia; M. Krützen, pers. comm.)
 - ➔ Second activity state either observed in first 5 min or later
 - ➔ **Sleep/rest, socialise, play, travel, forage**
- **Geographic movement direction** (north, east, south, west etc.)
- **Movement type**
 - ➔ **Straight:** individuals in parallel orientation, moving in one general direction (within 45°)
 - ➔ **Meander:** individuals in parallel orientation, frequently changing direction (varying more than 45°)
 - ➔ **Mill:** non-directional/no net movement, individuals surface facing various directions; Stockin et al., 2008). Individuals in a milling assemblage are generally stationary over an area; however, assemblages can also move at any speed.
- **Group spread** (modular distance between group members)
 - ➔ **Very tight/mother-calf pairs** (< 0.3 m distance between dyad), **tight** (group members 0.3-2 m apart), **moderate** (2-5 m), **spread** (5-10 m)
- **Speed**
 - ➔ **Very slow** (< 1 km/h), **slow** (1-2 km/h), **cruising** (2-3 km/h), **moderate** (3-4 km/h), **fast** (4-6 km/h), **blasting** (> 6 km/h)
- **Environmental factors**
 - ➔ **Water temperature** (measured at surface), **water depth**, **wind strength** (Beaufort scale), **wind direction**, **habitat type** (lagoon, reef or open water)

Compared to other behaviours, not much data have been collected on travelling dolphins since the data collection mainly took place stationary at the two reefs Shaab El Erg and Umm Usk and travelling mainly takes place in the open water (Kreicker & Ziltener, 2017). Because of the short daylength during wintertime (07:00 am to 05:00

pm), we mostly arrived at the reef when the dolphins were already there and had to depart before the dolphins left the reef. Thus, we missed a lot of travelling events (A. Ziltener, pers. comm.). However, in case the dolphins left the reef earlier or we coincidentally met travelling dolphins along the way to/from the reef, we did a focal group follow (according to Karniski et al., 2015; refer to section 10.2.2) together with photo-identifications of the group members until the group was lost or all individuals were identified (continuous sampling) (A. Ziltener, pers. comm.). Moreover, very few data have been collected about foraging because Indo-Pacific bottlenose dolphins in the Northern Red Sea forage in the late afternoon and at night (Kreicker & Ziltener, 2017) when it is too dark to observe them. Cameras attached to the bodies of the animals would provide an insight into the foraging behaviour at those late hours; however, those cameras have not been allowed in Egypt yet. Hydrophones, which would be useful in detecting foraging behaviour, are prohibited to use for research purposes in Egyptian waters (A. Ziltener, pers. comm.).

According to Würsig and Würsig (1977), information about the group composition was collected by using the mark-recapture method (photo-identification with the camera *Canon EOS 5D Mark IV* from the boat). Herewith, individual marks, nicks and notches on the dorsal fin give an insight about the dolphin identity (name) and therefore demographic parameters assigned to the individual, such as sex (determined by presence of dependent calves in infant/echelon position (Mann & Smuts, 1998) for adult females, or during underwater observation of uro-genital slit, extruded penis or body shape of adults), age class (correlated with body size) and female reproductive state (age class of dependent calf; Möller & Harcourt, 2008) as well as first registration date/location and health condition (A. Ziltener, pers. comm.). The individual dolphin identity was determined by comparing the photographs of the dorsal fins with the photo-ID catalogue created by DWA (extract in section 10.2.3).

3.1.3 Underwater footage and photos

Besides the observation from the boat, we got an additional insight into the dolphin behaviour with underwater footage (A. Ziltener, pers. comm.) recorded with the *GoPro Black Hero 5/8* video camera. Per survey, animals were filmed for an average length of 15-45 min (min. 0 min, max. 150 min). With 31 underwater surveys this summed up to a total video material of about 15.5 h.

Water visibility in the Northern Red Sea is around 30 m but can be less with strong currents and wind (A. Ziltener, pers. comm.). Together with the absence of large and potentially dangerous shark species at the reefs, these conditions are ideal for dolphin underwater research. We normally went into the water from the mooring place of the research vessel to avoid disturbance of the dolphins by engine noise. Nevertheless, when the dolphins were deep inside the lagoon, far away from the mooring place, we slowly approached them with the rubber boat. The rubber boat stopped with enough distance from the animals that we could slowly slide into the water. When we encountered active dolphins underwater, they usually approached and scanned us. The common observation distance lay within 10 m (ca. 3 m on average), but the dolphins could come even much closer (10 cm or less). According to our behavioural observations, we could say that the dolphins recognised us individually (A. Ziltener, pers. comm.). After that short welcoming phase, we followed the group (if we could keep up with their speed, certainly not during travelling) and did not interfere with their behaviours because they are habituated to human divers and snorkellers (A. Ziltener, pers. comm.). This was supported by the sleeping behaviour of the dolphins: They usually did not wake up and were not disturbed because of our presence, i.e. no avoidance or reaction such as scanning or opening of closed eye, and swam very close to us, which was regarded as trust towards us researchers (A. Ziltener, pers. comm.).

With underwater observation, it is much easier to estimate the age of a dolphin because the number of speckles on the ventrum can be recorded (Krzyszczuk, 2013). The sex of an animal can be confirmed by seeing the uro-genital slit. Underwater, the health condition of an animal (e.g. wounds or fungi on skin, broken jaw, fishing gear entanglement) can be documented more precisely than from the boat. Finally, there are some underwater behaviours which cannot be observed from the surface such as rubbing behaviour on different substrates, nursing, playing with different species and objects because sometimes the dolphins do not come up to the surface with the object (A. Ziltener, pers. comm.).

A dolphin group is characterised by dynamic organisation and fissions into smaller social units, called subgroups (according to Daura-Jorge et al., 2005). A subgroup was defined as an assemblage of dolphins (or just one individual) that is separated by 5-10 m from another assemblage (or another individual) that is said to be in the same group,

according to the 10 m chain rule (A. Ziltener, pers. comm.; Smolker et al., 1992). The observation of the subgroup continued until subgroup changed its composition (exchange of individuals) or was lost (according to López, 2006). The size of these subgroups can be recorded more easily with underwater footage than from the boat. It was unlikely to record all subgroups at the time with underwater footage because most of the time, just two researchers are in the water (A. Ziltener, pers. comm.). However, since underwater video material of already multiple hours at the same reefs has been collected since 2012, repeated measurements of the same individuals could be assumed. Thus, these underwater video data give an additional insight into the relationship of behaviour and subgroup size.

Additionally, the overall group size (all individuals observed in the group during the survey, according to the 10 m chain rule (Smolker et al., 1992), i.e. sum of all subgroup sizes), observed from the boat, was backed up underwater when observing large groups of ≥ 20 individuals since it was possible to miss an individual or count double in the usually short time interval when the animals came to the surface. The successful determination of group size also depended on environmental conditions (flat sea and good water visibility favoured) and the behaviour (easier to count individuals during sleep because of the cohesive group structure and coordinated movement; refer to ethogram in Table 1) (A. Ziltener, pers. comm.).

Finally, the dolphin identity was backed up with underwater photo-identification (by using the *Olympus Stylus TG-2* photo camera; Würsig & Würsig, 1977). Underwater photo-identification also allowed to identify individuals with clean dorsal fins, mainly juveniles and calves, because more body parts can be seen underwater. Thus, potential marks, nicks, notches or scars on the fluke and pectoral fins were captured more easily than from the boat. By looking at other body parts than the dorsal fin, underwater photo-identification also reduced the risk of assigning a new ID to an individual that had already existed in the ID catalogue and whose dorsal fin changed a lot since the last sighting as a result of a fight with conspecifics, shark attack, boat collision or entanglement in fishing gear (A. Ziltener, pers. comm.).

Additionally, drones would be useful for cetacean research (M. Krützen, pers. comm.). The continuous recording in the bird's eye view gives a good overview of group

cohesiveness/spread and thus fission-fusion dynamics. Thanks to the good water visibility in the Red Sea, the member numbers of large, spread groups and all subgroups as well as the behaviours near the surface of all (sub)group members could be recorded simultaneously. Drone footage would also give an insight into novel research questions such as unravelling group leadership. The caused disturbance by drone use is said to be even smaller than underwater research and especially than the moving boat. However, drones are not allowed for research purposes in Egypt yet (A. Ziltener, pers. comm.).

3.2 Data processing

Before the social network analysis (refer to section 3.3.3), the selected data had to be processed. If the location of the survey, i.e. which reef, was unsure and could not be confirmed with GPS coordinates, the survey was excluded from the analysis. For the data of 2009-2018, the photo-identification had already been done by the DWA team, whereas for 2019 and 2020, I did the photo-identification with the DWA photo-ID catalogue myself. IDs were only used for the analysis if they were confirmed with photo-identification, meaning individuals seen by eye and just written down on the data sheet was not sufficient. Two surveys at the same reef on the same day were kept in the final data set, not merged and regarded as two independent data points if the groups consisted of different individuals that did not interact with each other (according to 10 m chain rule; Smolker et al., 1992). This data processing also enabled independent data points for the behavioural data (avoiding pseudo-replication when recording calf numbers and group sizes; refer to questions 2 and 3) and video data (refer to question 1) (M. Krützen, pers. comm.). Samples from the same reefs on following days did not cause a problem for independence of data points since the groups of the Indo-Pacific bottlenose dolphins in the Northern Red Sea usually change their sizes and compositions over night or even on the same day, a characteristic of animals living in fission-fusion societies (A. Ziltener, pers. comm.; Connor et al., 2000).

Finally, the survey ID data had to be in the correct format in the *comma-separated values* (CSV) file (ID name as column name, each row was a survey/grouping event filled with 0 (ID not present) and 1 (ID present)). If the number of confirmed photo-identified individuals exceeded the recorded group size, the group size was adapted to the number of identified individuals. If the number of photo-identified animals was

lower than the group size, the number of calves (if it was higher than the photo-identified calf number) was based on the information of the behavioural data sheet since calves were quite easily detectable from the boat thanks to smaller body size and infant/echelon position with their mothers, especially while sleeping (A. Ziltener, pers. comm.; Mann & Smuts, 1998).

3.3 Data analysis

Table 1: Ethogram as basis for the video analysis.

Sleep	Sleep is characterised by unilateral eye closure (Lyamin et al., 2008; caused by unihemispheric slow waves (Rattenborg, Amlaner & Lima, 2000)), continuous, rather slow (2-3 km/h, but sometimes up to 4 km/h) movement with regular, peduncle or tail-out dives and low activity (no jumping or fluke slapping) (A. Ziltener, pers. comm.). Furthermore, the tight/cohesive (individuals < 2 m apart) (sub)group formation does not show any signs of foraging/socialising/playing and vocalising (on a frequency audible to human ear) during sleep. Sleeping behaviour includes synchronous/coordinated movement (straight or meander) including short and regular surfacing to breathe mostly 3-4 times before diving for an extended period (1-3 min; Ziltener, Wright & Kreicker, 2015; Fumagalli, Cesario & Costa, 2019). For mother-calf pairs, sleeping includes nursing (A. Ziltener, pers. comm.).
Rest	In the Northern Red Sea, on (sub)group level, we define “resting” when dolphins in the awaking/falling asleep phase show signs of socialising (especially petting) or a quick human interaction (scanning or explicitly turning head towards human) or body rubbing on substrates (e.g. sponges/gorgonia) while ≤ 50 % of the (sub)group are still sleeping deeply. The resting dolphins can still slowly swim in a relatively tight (sub)group formation, but often can also pursue slightly different directions in loose formations (less cohesive/coordinated than sleeping). On (sub)group level, “resting” is yet defined as an intermediate/transition activity state between (inactive) sleeping and (active) socialising/playing/substrate rubbing, a behaviour of low activity that likely would be called “snoozing” in humans (A. Ziltener, pers. comm.).
Socialise	Social behaviours include (physical) contact among conspecifics, such as social playing, chasing, leaping (entire body breaks water surface), displays (e.g. penis erection), aggressive behaviours (mounting (open beak)/jaw clapping, fluke slapping on the surface (splashing), S position; A. Ziltener, pers. comm.), contact swimming, petting (one dolphin rubs another individual with its fluke or flippers; Mann & Smuts, 1998), rubbing (whole bodies on each other), genital inspections and mating (Christiansen et al., 2010; Krzyszczyk et al., 2017; Smith, 2012). Social behaviours are frequently accompanied by vocalising (M. Krützen, pers. comm.). Creating bubbles with the blowhole is also regarded as a form of socialising observed in mating, presumably a form of non-verbal communication. However, bubbles can also be a form of deep exhaling when coming up to the surface (A. Ziltener, pers. comm.).
Play	Playful, close, and often physical interactions with something else than conspecifics: live species, such as humans, turtles, rays, pufferfish, moray eels, jellyfish and dead/abandoned objects, e.g. coral pieces, shells, algae, rubbish and fishing ropes (adapted from Steiner, 2011).
Travel	The travelling dolphin group is persistently (min. 1 min) moving in parallel orientation (directional movement, not varying more than 45 °), swimming near the surface with short diving intervals and a travel speed of > 4 km/h (Christiansen et al., 2010; Smith, 2012; A. Ziltener, pers. comm.).

3.3.1 Video analysis

For reasons of consistency, the recording person of the analysed underwater videos was always A. Ziltener, except for the videos in 2020, where she was not in the water, I recorded them myself. First, of each survey from 2012 to 2020, one video was randomly selected (by the *sample* function in the statistical program *RStudio* (version 1.3.959; Field, Miles & Field, 2012)). I analysed the videos from 2012 to 2019, in addition to the ones of 2020 collected during my field stay, to assess the relationship of behaviour and subgroup size on a broader, long-term scale. No consistent video recording was available from 2009 to 2011. Because of quality reasons, *GoPro* videos were preferred, but if not available in a specific survey, also videos recorded with the *Olympus Stylus TG-2/4* or *Panasonic Lumix DMC-FH25* camera were analysed. After randomly selecting the videos to analyse, the number of videos per year differed. In 2017, there was the smallest video number to analyse (16). To equalise the numbers of analysed videos per year, 16 out of the initially chosen videos were selected per year (also done with the *sample* function in *RStudio*). To have the same number of videos analysed for every season (36 each per “spring” (March–May), “summer” (June–August) and “autumn” (September–November) and “winter” (December–February)), the video selection mentioned above was not entirely random. Since the data collection had not always taken place equally distributed over the years, it was not always possible to have exactly four videos per season in each year.

Continuous focal subgroup sampling with 1 min intervals was used for the video analysis. An initial testing phase revealed that after three minutes, generally no more new information regarding activity state and subgroup size was gained since no clearly stable activity state periods over time could be defined. To save time, just the first three minutes of each selected video (only if the video was at least 1 min in total length) were analysed because the average length of all analysed videos was about 3 min. If the video was less than 3 min in length, the video material after a full minute was only analysed if it lasted ≥ 30 seconds, e.g. the third minute of a 02:30 min long video was analysed as opposed to a 02:29 min long video, since the first 30 s of a new interval could still be influenced by the previous interval (M. Manser, pers. comm.). As 144 videos were analysed, this added up to a total amount of 432 min of analysed video material.

By analysing the selected underwater videos, the parameters activity state and subgroup size were determined and added to a *Microsoft Excel* (*Microsoft 365*, version 2016) spreadsheet. With the video analysis, the numbers of individuals, i.e. subgroup size(s), in a group showing certain activity state(s) were identified since mostly it was not likely that the entire group showed the predominant activity state (which was observed from the boat at the beginning of the survey) at the same time, e.g. some individuals still slept, whereas others were already socialising/petting. However, if all individuals showed the same activity state in the group and were within 5 m from the next individual (according to subgroup definition; A. Ziltener, pers. comm.), the subgroup size was equal to the group size in that case. The subgroup size and the corresponding activity state were recorded in 1 min intervals. When the same subgroup size – activity state combination was observed twice within one interval, but obviously with a different subgroup composition, it was recorded again. Two events of the same subgroup size – activity state combination within the same interval were also recorded when the activity state of the same subgroup changed temporarily, but finally reached the initial activity state again.

For specification of the ethogram (Table 1), in the video analysis, “sleep” was defined on (sub)group level as activity state when > 50 % of the subgroup were continuously moving with no signs of other activity states, such as socialising, and the socialising minority of the subgroup still showed coordinated movement with the sleeping subgroup (approximately same direction). Otherwise, if the socialising individuals were not moving with the sleeping subgroup anymore, the two activity states were regarded as “sleep” and “socialise” for two different subgroups.

3.3.2 Statistical analysis

The statistical analysis was done in the statistical program *RStudio* (version 1.3.959; Field, Miles & Field, 2012). The data sets (spreadsheets) were imported as CSV files.

Activity state and (sub)group size

To address question 1, the relationship of (sub)group size (count response variable) and activity state (categorical explanatory variable) was examined. The activity state was a factor with six levels (total sample size = 838): “play” (n = 195), “socialise” (n = 95), “play/socialise” (n = 73; an intermediate activity state where in the same subgroup,

individuals were dynamically socialising and playing in turn), “rest” (n = 121), “sleep” (n = 254) and “travel” (n = 100). The data were based on the video analysis (to detect subgroup sizes of dolphins showing various activity states) and boat-based surveys (to record the group size (if estimated range, taken average (rounding down for uneven numbers))). Also, “travel” data of 2010-2020 were exclusively provided by the boat-based surveys since this behaviour is hard to record in the water because of higher speed compared to other behaviours (A. Ziltener, pers. comm.). Since “travel” data were already recorded between 2010 and 2011, where no video data for all the other activity states was available, I controlled for that time difference by including “year” as a categorical explanatory variable (additive effect). I applied a generalised linear model (GLM), two-way analysis of variance (ANOVA) with Poisson distribution, since the response variable was a positive integer without a known maximum (Field, Miles & Field, 2012). In the Poisson GLM, the canonical link function is the natural logarithm (log link; inverse link: $e^{\cdot}$ (exponential)).

Calf number, season and group size

In questions 2 and 3, the relationship of overall group size (response variable), number of dependent (before weaning) calves (count explanatory variable; covariate) and season (categorical explanatory variable; predictor) was investigated. Season was a factor with the four categories “spring” (Mar–May), “summer” (Jun–Jul) and “autumn” (Sep–Nov) and “winter” (Dec–Feb). The data were based on the boat-based surveys (number of calves; if there was an estimated range for the overall group size, the average was taken (rounding down for uneven numbers)) and underwater photo-ID information (to confirm number of calves). The sample size was 144 data points (one data point per analysed video for question 1). As a model, I applied an analysis of covariance (ANCOVA) with an additive effect between the two explanatory variables and Poisson distribution (GLM) because the response variable was a positive integer without a known maximum (Field, Miles & Field, 2012).

For all three questions, the prerequisite of the Poisson distribution was not fulfilled because the mean and the variance were not equal (refer to Tables 3 & 4; Field, Miles and Field, 2012). Thus, I changed the *R* “family” argument from “poisson” to “quasipoisson” to account for the data overdispersion (dispersion parameter > 1) and estimate the dispersion parameter more precisely. The comparisons of the selected

GLMs with the null models (explanatory variables removed) were based on two-tailed likelihood ratio tests. I applied the *R* function *Anova(glm_model_name, type="III")* because the order of the predictor(s) and covariate mattered. Thus, the predictor(s) and covariate were evaluated simultaneously (type III (simultaneous) sums of squares) (Field, Miles & Field, 2012). In question 1 and 3, when looking at the different levels of the categorical variables “activity state” and “season”, the t- and p-values were based on the separate comparisons of each level with the null hypothesis that claimed that each separate level would be equal to 0, i.e. having no effect on the response variable (refer to Tables 3 & 4). For all statistical analyses, the statistical significance was set at the 5 % level.

3.3.3 Social network analysis

Social network analysis (SNA) is a powerful tool to assess population dynamics (Snijders et al., 2017). On a dyadic level, factors that influence social associations may be identified (Newman, 2018; refer to questions 5 and 6). On a larger community scale, SNA allows cluster detection, which can give an insight into social organisation and structure (community structure analysis; Newman, 2018; refer to question 4).

I used to the “gambit of the group” approach, which is commonly used in SNA of cetacean social structures (Whitehead and Dufault, 1999). This approach is built on the following assumption: Individuals that are clustered together in a group, do also interact among each other. “Gambit of the group” is supported if “(1) all, or almost all, interactions take place within groups, and (2) interactions are similar and take place at a uniform rate between all pairs within a group” (quoted from Whitehead and Dufault, 1999).

The association index/coefficient measures the proportion of time two individuals (a dyad) spend with each other (Hoppitt & Farine, 2018). Most frequently, the Half Weight Index (HWI; Cairns & Schwager, 1987) or the Simple Ratio Index (SRI; Ginsberg and Young, 1992) have been used as association indices to study cetacean social structure. In this study, SRI was preferred over HWI since no clear bias existed (e.g. in large groups (≥ 20 individuals), where often less than 50 % of the individuals are photo-identified (Karczmarski et al., 2005; Hoppitt & Farine, 2018)) even though many

juveniles were not possible to identify since they lack marks, nicks or notches as identification characteristics (A. Ziltener, pers. comm.).

All SRI calculations were executed by using the *R* package *asnipe* (Farine, 2013) according to the mathematical formula of the SRI (Ginsberg & Young, 1992):

$$SRI = \frac{x}{x + y_{AB} + y_A + y_B}$$

x is the number of grouping events, i.e. surveys, in which both individuals A and B were observed in association. y_A refers to the number of surveys where individual A was seen, but B was not. Accordingly, y_B is the number of surveys in which individual B was observed, but A was not. y_{AB} describes the number of surveys where A and B were encountered but did not associate. SRIs range from 0 (a dyad was never observed in association) to 1 (a dyad was always seen together).

The entire SNA was conducted in *RStudio* (version 1.3.959; Field, Miles & Field, 2012). The *R* package *igraph* was used to create all network plots (Csárdi & Nepusz, 2006).

Data structure

The SNA was conducted to evaluate the fission-fusion dynamics on an individual and community level over time by using long-term data about group composition at three spatially separated meeting points (for several behaviours: Ziltener, Wright & Kreicker, 2015; Ziltener & Kreicker, 2013; Ziltener, Kreicker & Gross, 2015; Kreicker & Ziltener, 2017) with similar environmental conditions (A. Ziltener, pers. comm.). Those meeting points included the three reefs Fanous, Shaab El Erg and Umm Usk (refer to Figure 1). Since 2015, almost no data have been collected in Fanous since it is the reef that is located most in the south and takes a long time to reach from the research basis (which was transferred from Hurghada to El Gouna in 2015). Thus, the group compositions in Fanous were investigated from 2009 to 2014. From 2016, data in Umm Usk, the reef most in the north, have been regularly collected, whereas for Shaab El Erg data were available over the whole period of 2009 to 2020. In total, there were 413 grouping events (Fanous: $n = 142$, Shaab El Erg: $n = 216$, Umm Usk: $n = 55$) grouping events, of which 21 (one Umm Usk survey had to be excluded because of unclear group composition) were collected in my presence in 2020. The data of the SNA were

based the photo-ID information during the entire observation time of the survey (from the boat and underwater). In rare cases, there might have been some individuals that never associated with each other because of the possibility of preceding departure of a few individuals before others arrive, especially in longer survey durations. However, photo-ID data only based on the first 5 min of the survey would include a high risk of missing IDs and thus associations, especially in large groups (A. Ziltener, pers. comm.).

Data preparation

Three CSV files were imported into *RStudio*: The IDs of the dolphins present in the surveys (group-by-individual matrix with all grouping events of the individual interactions), the meta data of the surveys (reef and year) and the demographic information about the various IDs. The demographic data set included the parameters sex and maternal relatedness (mother identity determined on a behavioural basis while dependent calf was sleeping/resting in infant or echelon position (Mann & Smuts, 1998)). The original data set (group-by-individual matrix) for all three reefs over the whole time period of 2009-2020 contained 251 individuals. Dependent calves were excluded from the data set to prevent association index bias since the expected SRI for mother-calf pairs is 1 (Mann et al., 2000). Thus, the final data set for all three reefs from 2009 to 2020 consisted of 178 individuals: 90 males, 73 females and 15 individuals of unknown sex.

Community structure and distribution at three reefs

For question 4, I examined whether communities may be identified whose distributions are spatially restricted to the three different reefs (residents) over the whole period of 2009-2020. The community structure was assessed by calculating the modularity score Q (Newman, 2004). Q is defined as the proportion of edges (connections/associations between nodes/individuals) that appear within communities, relative to the proportion expected in case all edges were set randomly. A meaningful community subdivision can most probably be found if $Q \geq 0.3$ (Newman, 2004). The community structure analysis was based on SRIs provided by the *R* package *asnipe* (Farine, 2013). For the small networks ($n \leq 1000$) in this study, the *Louvain/multilevel* community/cluster detection algorithm was used to graphically identify those communities (provided by the *R* package *igraph*; Csárdi & Nepusz, 2006) based on

the modularity score (Yang, Algesheimer & Tessone, 2016; Blondel et al., 2008). Individuals that were sighted less than five times were excluded from the data analysis to avoid potential bias of association indices (S. Marfurt, pers. comm.).

Additionally, I applied a multinomial logistic regression (GLM with logit link function) to detect a possible trend of sex-biased distribution/philopatry. The number of visited reefs (1, 2 or 3) was the response variable and sex (male or female) the predictor. I assessed if males were less philopatric than females, i.e. if males have a larger home range restricted to the three assessed reefs. The data of the model were based on the numbers of identified individuals that were sighted at least once at one of the three reefs. Dependent calves and individuals of unknown sex excluded from the analysis. The sample size was 163 (90 males and 73 females). The number of individuals for all reef and time combinations are listed in Table 2.

Table 2: Number of sighted individuals, divided by sex, depending on reef and year.

Reef	Year	Males	Females	Unknown	Total	M/F ratio (%)
Fanous	2009-2014	54	44	1	99	55/45
Umm Usk	2016-2020	46	33	4	83	58/42
Shaab El Erg	2009-2014	53	49	4	106	52/48
Shaab El Erg	2016-2020	49	37	4	90	57/43
Shaab El Erg	2009-2020	70	58	8	136	55/45
All three	2009-2020	90	73	15	178	55/45

Influence of sex on association strength

In question 5, the association strengths, measured by the SRIs, of male-male, female-female and male-female interactions were compared to test whether the association strengths of intra- and intersexual interactions differ. I did three (one per reef) pairwise Mantel tests (non-parametric matrix correlation test; Mantel, 1967) with 10'000 node permutations (to avoid non-independence of the data) based on a two-tailed Pearson's χ^2 test (by using the *R* package *vegan*; Oksanen et al., 2018) to assess the correlations of the SRI association matrices with the "sex similarity" matrices for every dyad, where a either 1 (female-female dyad), 2 (male-male dyad) or 3 (mixed male-female dyad) was assigned to the dyads. Individuals that were sighted less than five times were excluded from the data analysis to avoid potential bias when comparing association indices (S. Marfurt, pers. comm.).

Influence of maternal relatedness on association strength

In question 6, to determine the dyadic association strengths between weaned calves and their mothers compared to unrelated individuals (all dyads except identified mother-weaned calf associations), I conducted three permutation-based Mantel tests (according to question 5). The SRIs for every dyad of the association matrices were tested against “maternal relatedness similarity” matrices, where either a 0 (individuals not related), 1 (mother-daughter dyads) or 2 (mother-son dyads) was assigned to the dyads. I tested the influence of maternal relatedness on the association strength based on behavioural observations since genetic analyses are not feasible in the Egyptian Red Sea owing to governmental guidelines (A. Ziltener, pers. comm.).

At the reefs Fanous, Shaab El Erg and Umm Usk, I analysed data of 13 weaned calves (six males and seven females). Due to the small sample size of maternally related individuals, explained by the lack of genetic data, I excluded individuals from the analysis that were seen less than three rather than five times (J. Evans, pers. comm.). Caused by missing genetic data, only individuals were included in the data set that were still dependent calves when first sighting them and could be identified again after weaning, which was only possible with marks, nicks or notches present prior to weaning. Other potential reasons for losing individuals after weaning are dispersal to another area or (unconfirmed) death (A. Ziltener, pers. comm.). Already before weaning, around 50 % of the calves in the Northern Red Sea die (DWA, internal records; 44 % calf mortality in Shark Bay, Western Australia; Mann et al., 2000).

With the three permutation-based Mantel tests for questions 5 and 6, one per reef, I did a restricted randomisation to avoid preferred association bias (swap of dolphin identities among grouping events at the same reef, but not between reefs) because I expected that there were dolphins which do not visit all three reefs (no geographic overlap and thus no opportunity to associate) (J. Evans & S. Marfurt, pers. comm.). All Mantel tests were conducted at the significance level of 5 %.

3.4 Ethical note

The data collection in the Egyptian Red Sea was non-invasive, i.e. only behavioural data were collected, and hence no ethical approval of the planned fieldwork was needed. It was justifiable to collect data on wild Indo-Pacific bottlenose dolphins since the research vessel stuck to the guidelines of the voluntary code of conduct when approaching the dolphins (DWA, 2020). To avoid/minimise a disturbance of the animals and thus also bias of the data, the dolphins were only approached from the side and followed parallel to the movement direction, not closer than 50 m and 200 m during the main sleeping/resting time (09:00 am – 01:00 pm). The Egyptian Ministry of Environment (EEAA) and the Red Sea National Park Authority on site have been informed about the ongoing studies and approved them as well as the Red Sea Governor.

4 Results

4.1 Group size influencing factors

4.1.1 Activity state and (sub)group size

Activity state had a highly significant effect on (sub)group size (likelihood ratio test (LRT): $\chi^2_{(5)} = 568.93$, $p < 0.001$). Travelling groups were largest in size (mean = 9.90; Table 3 & Figure 2) compared to the subgroups in the other activity states. Besides travelling groups, subgroups of sleeping individuals were clearly larger (mean = 7.76; Table 3 & Figure 2) compared to the other activity states. Additionally, travelling and sleeping (sub)groups also showed much larger variances opposed to the subgroups of the other activity states (Table 3 & Figure 2). The activity states “rest” (mean = 3.26), “socialise” (mean = 3.43) and “play/socialise” (mean = 2.92) led to subgroups of similar small sizes (all medians = 3; Table 3 & Figure 2). Finally, it was shown that playing individuals are part of the smallest (sub)groups (mean = 1.34; Table 3 & Figure 2) and mostly consisting of just one individual (median = 1). The residual deviance was 1932.32 (residual degrees of freedom = 822). Independent of activity state, the (sub)group size mean was 4.96 (median = 3) and ranged from 1 to 42 (variance = 30.02) (Appendix Figure 2).

Table 3: Statistical parameters divided by activity state. The model coefficient (estimate) as well as upper and lower confidence interval (CI) of the Poisson GLM are exponentiated/back-transformed. Standard errors (SE) of the model are stated on log link scale. All p-values are significant. All the model parameters of the different activity states are in relation to the year 2010 as reference. Sample size (n), variance, mean and median (sub)group size are given for each activity state.

	n	Estimate	SE	t	p (> t)	2.5 % CI	97.5 % CI	Variance	Mean	Median
Play	195	0.57	0.26	-2.10	< 0.05	0.33	0.94	0.61	1.34	1
Socialise	95	2.51	0.14	6.77	< 0.001	1.92	3.27	4.65	3.43	3
Play/Socialise	73	2.05	0.15	4.73	< 0.001	1.52	2.76	1.52	2.92	3
Rest	121	2.41	0.13	6.71	< 0.001	1.87	3.12	6.46	3.26	3
Sleep	254	5.53	0.11	15.83	< 0.001	4.50	6.88	35.45	7.76	6
Travel	100	8.51	0.12	17.59	< 0.001	6.73	10.84	69.20	9.90	7

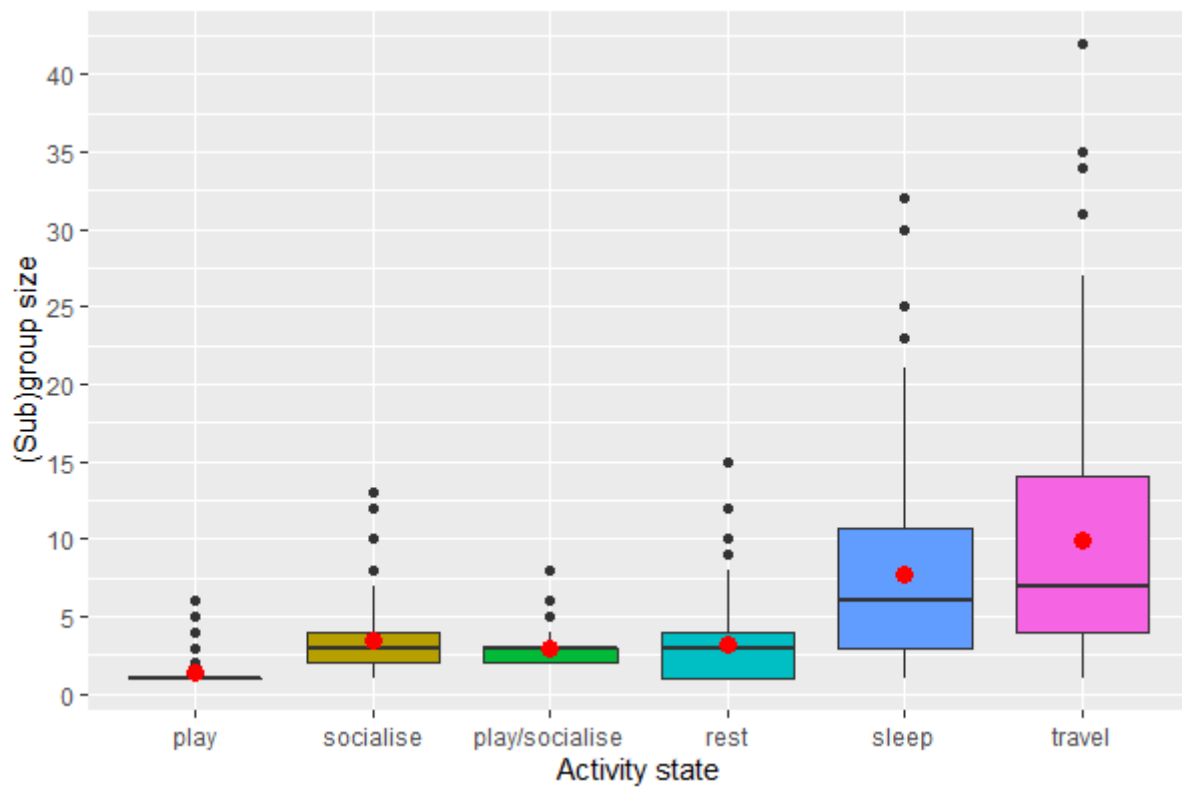


Figure 2: Relationship of activity state and (sub)group size. The box is the interquartile range (IQR), bounded at the bottom of the box through the first quartile (25th percentile) and at the top through the third quartile (75th percentile). The upper whisker expands from the third quartile to the largest value not more than + 1.5·IQR, accordingly for the lower whisker: max. - 1.5·IQR from the first quartile. The small black dots outside the boxes represent extreme values, whereas the large red dots are the (sub)group size means for each activity state.

4.1.2 Calf number, season and group size

Overall group size (total number of individuals in the group, including calves, according to 10 m chain rule (Smolker et al., 1992)) correlated significantly with the number of dependent calves per group (LRT: $\chi^2_{(1)} = 62.85$, $p < 0.001$). There was a positive, almost linear relationship between number of calves and overall group size (slope = 1.27), i.e. the more calves were present in the group, the larger the group size was (Figure 3 & Table 4). Mean calf number per group was 1.78 (median = 1; Table 4) and ranged from 0 to 9 (Appendix Figure 4).

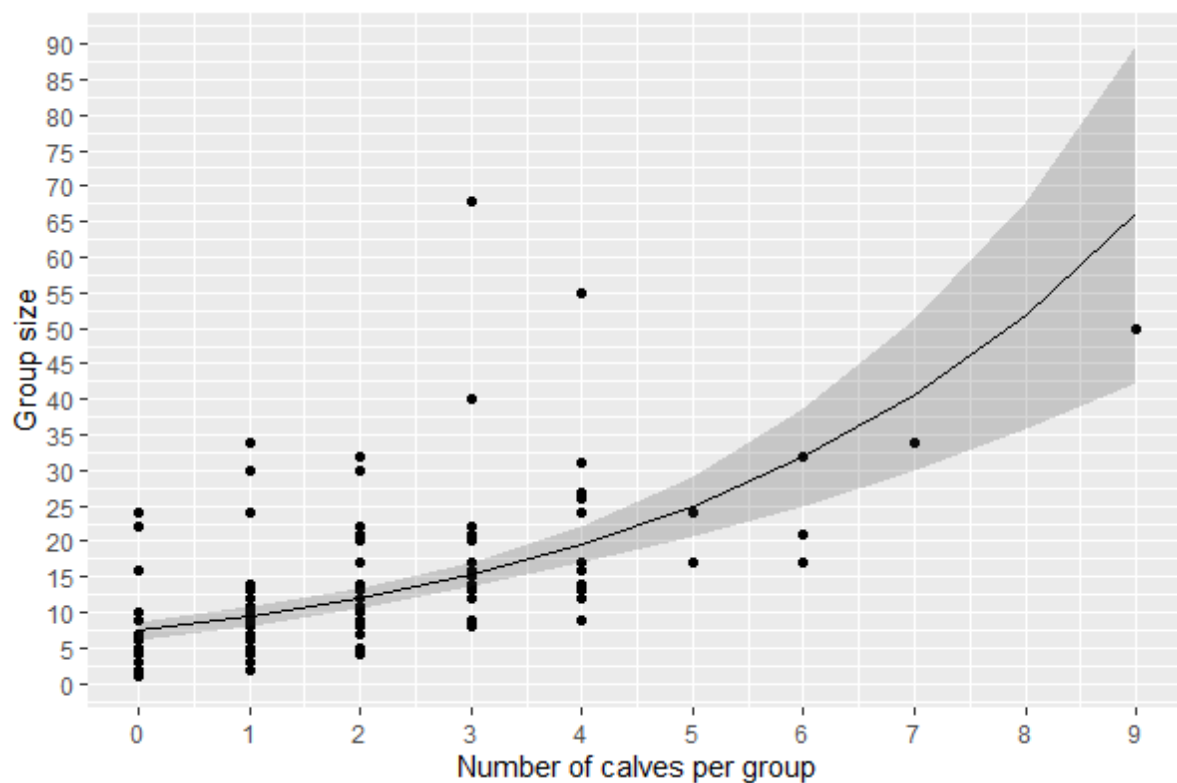


Figure 3: Relationship of calf number per group and overall group size. The x-axis shows the number of dependent calves per group. The y-axis displays the overall group size, i.e. total number of individuals per group, including calves.

Although season did not have a statistically significant effect on the overall group size (LRT: $\chi^2_{(3)} = 6.58$, $p = 0.09$), there was a trend. Larger groups were observed in spring (mean = 14.00) and summer (mean = 15.56) than in autumn (mean = 10.94) and winter (mean = 9.61) (Figure & Table 4). The residual deviance was 671.04 (139 residual degrees of freedom). Independent of season, the overall group size had a mean of 12.53 (median = 10) and ranged from 1 to 68 (variance = 116.40) (Appendix Figure 5).

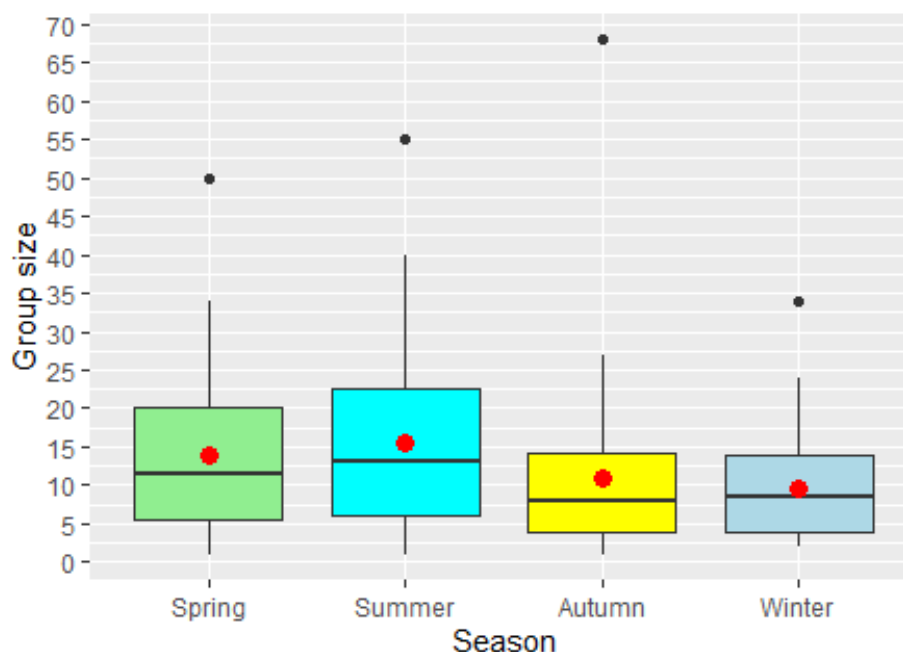


Figure 4: Relationship of season and overall group size. The box is the interquartile range, bounded at the bottom of the box through the first quartile (25th percentile) and at the top through the third quartile (75th percentile). The lengths of the upper and lower whiskers correspond to $\max. \pm 1.5 \cdot \text{IQR}$. The small black dots outside the boxes represent extreme values, whereas the large red dots within the boxes are the group size means for each season.

Table 4: Statistical parameters of calf number per group (covariate) and season (predictor), divided into the four categories spring, summer, autumn and winter. The model coefficient (estimate) as well as upper and lower confidence interval (CI) of the Poisson GLM are exponentiated/back-transformed. Standard errors (SE) of the model are stated on log link scale. Sample size (n), variance, mean and median group size are given for each season. Additionally, the total sample size ($n = 144$), variance, mean and median of the calf number per group is given.

	n	Estimate	SE	t	p (> t)	2.5 % CI	97.5 % CI	Variance	Mean	Median
Spring	36	7.67	0.14	14.32	< 0.001	5.76	10.06	117.26	14.00	11.5
Summer	36	1.21	0.15	1.27	0.21	0.90	1.63	143.97	15.56	13
Autumn	36	0.84	0.17	-1.03	0.31	0.61	1.17	141.43	10.94	8
Winter	36	0.86	0.18	-0.89	0.38	0.60	1.20	49.86	9.61	8.5
Calves	144	1.27	0.03	8.53	< 0.001	1.20	10.06	2.60	1.78	1

4.2 Social structure and distribution

4.2.1 Community structure and distribution at three reefs

When keeping both males and females in the data set, the *multilevel* community detection algorithm (Blondel et al., 2008) identified five communities in Shaab El Erg ($Q = 0.17$, $n = 92$ individuals; Figure 5), three in Fanous (modularity $Q = 0.19$, $n = 66$; Appendix Figure 6), four in Umm Usk ($Q = 0.14$, $n = 36$; Appendix Figure 7) and six communities for the whole area (all three reefs together) over the entire time period from 2009 to 2020 ($Q = 0.20$, $n = 113$; Figure 6). However, since all the modularity scores were below the value of 0.3, these community subdivisions were regarded as not meaningful according to Newman (2004).

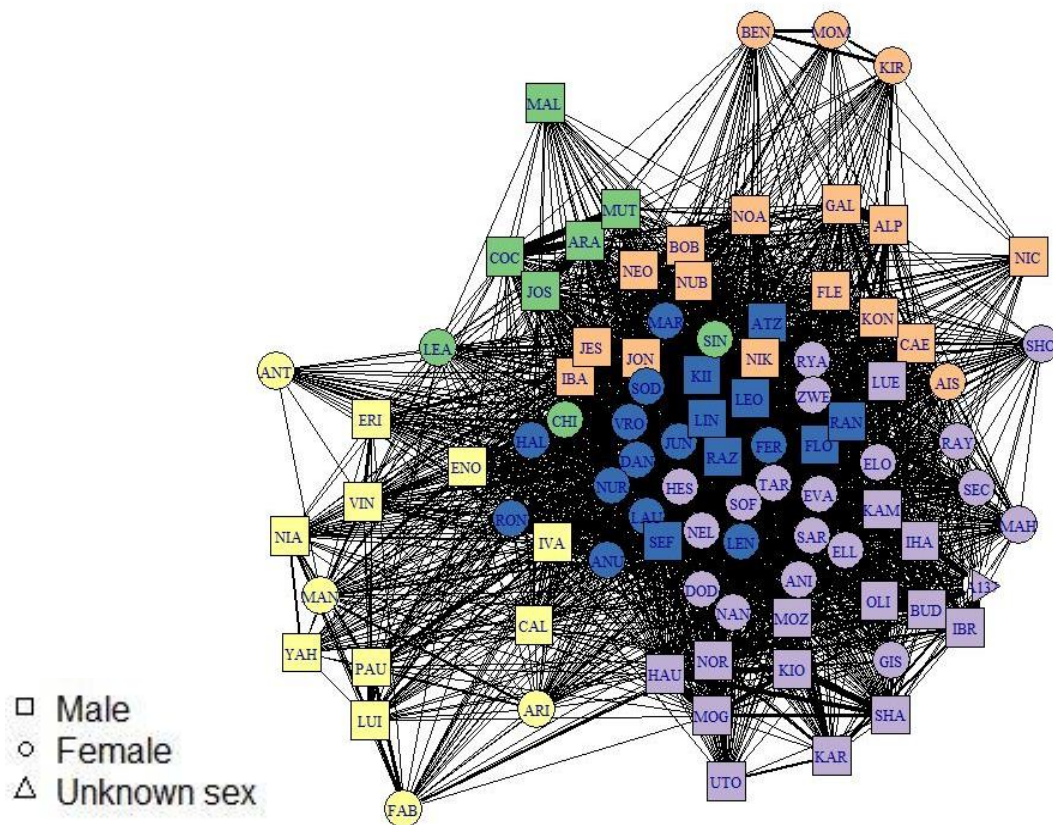


Figure 5: Network plot showing community memberships in Shaab El Erg, 2009-2020.

The nodes are coloured according to community memberships. Males are displayed as squared and females as circled nodes. Individuals of unknown sex are shaped as triangles. Thickness of the edges corresponds of the association strengths between the nodes.

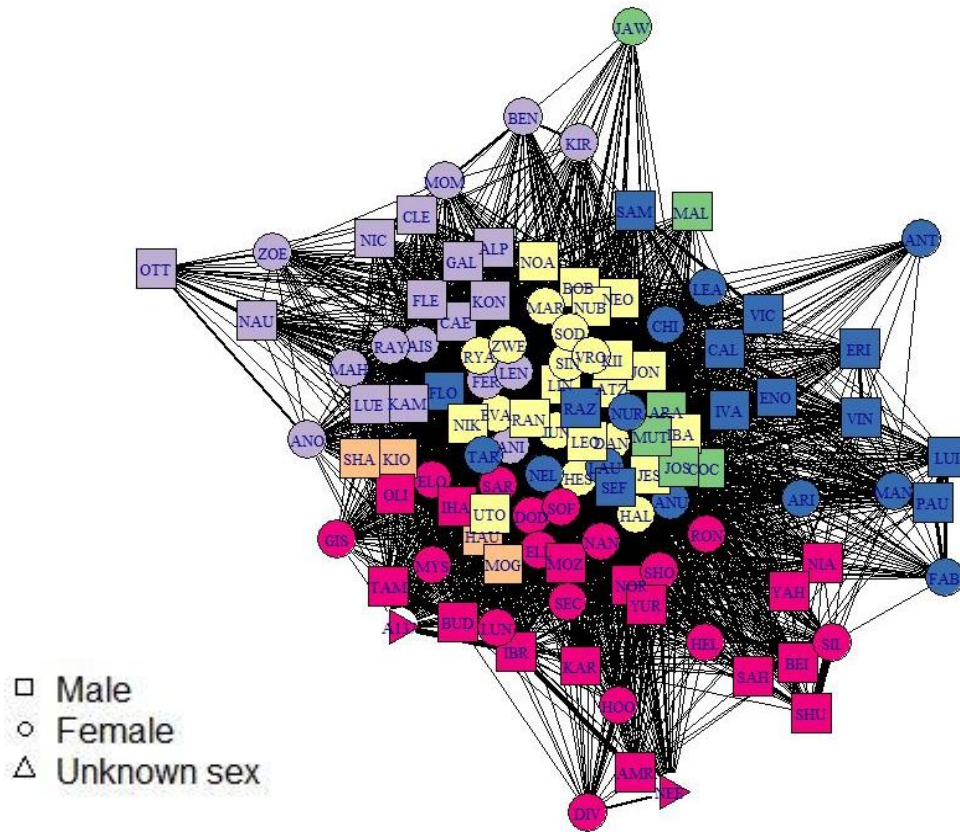


Figure 6: Network plot illustrating community memberships in the whole area (all three reefs Fanous, Shaab El Erg and Umm Usk) from 2009 to 2020. The communities are differentiated by colour. Males are displayed as squared and females as circled nodes. Individuals of unknown sex are shaped as triangles. Thickness of the edges corresponds of the association strengths between the nodes.

No sex-biased distribution/philopatry could be identified since the distribution at the three reefs did not significantly differ between males and females (LRT: $\chi^2_{(2)} = 4.04$, $p = 0.13$, residual deviance = 353.77, residual degrees of freedom = 322). In summary, neither the males (every individual was found at two reefs on average (SE = 0.04)) nor the females (mean $\pm$ SE = 1.97 ± 0.04) could either be identified as the more dispersing or philopatric sex.

4.2.2 Influence of sex on association strength

There was a statistically significant effect of sex-dependent association type on the association strength with intrasexual (male-male or female-female) associations being stronger than intersexual (male-female) ones (Mantel tests: Fanous: $p < 0.001$, $n = 66$ individuals; Shaab El Erg: $p < 0.001$, $n = 92$; Umm Usk: $p = 0.001$, $n = 36$). In Fanous, the male-male associations were strongest on average (mean simple ratio index (SRI) $\pm$ SE = 0.106 ± 0.004), followed by female-female (0.091 ± 0.003) and male-female (0.069 ± 0.001) associations (Figure 7 & Appendix Figure 9). The same pattern occurred in Umm Usk: On average, male-male (mean SRI $\pm$ SE = 0.218 ± 0.009) associations were stronger than female-female (0.168 ± 0.01) and male-female ones (0.155 ± 0.004) (Figures 8 & 9). In Shaab El Erg, female-female bonds were stronger on average (mean SRI $\pm$ SE = 0.084 ± 0.002) than male-male ones (0.071 ± 0.002), also with intersexual bonds being the weakest (0.064 ± 0.001) (Figure 10 & Appendix Figure 10).

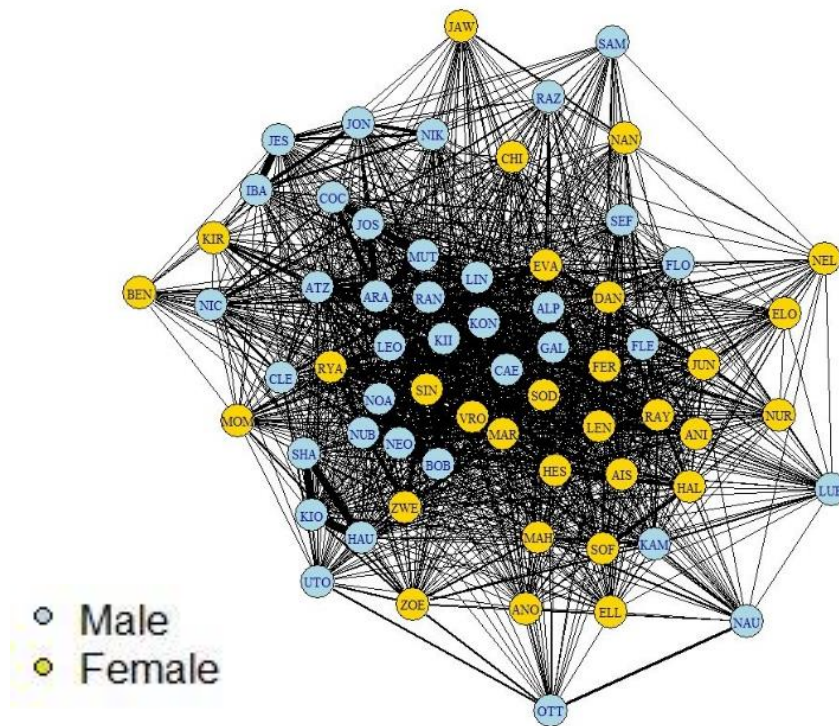


Figure 7: Network plot showing sex-dependent association strengths in Fanous, 2009-2014 ($n_{\text{males}} = 36$, $n_{\text{females}} = 30$). Males are displayed as light blue nodes and females as golden ones. Thickness of the edges represents association strength. According to the clustering pattern, assortment dependent on sex can easily be recognised.

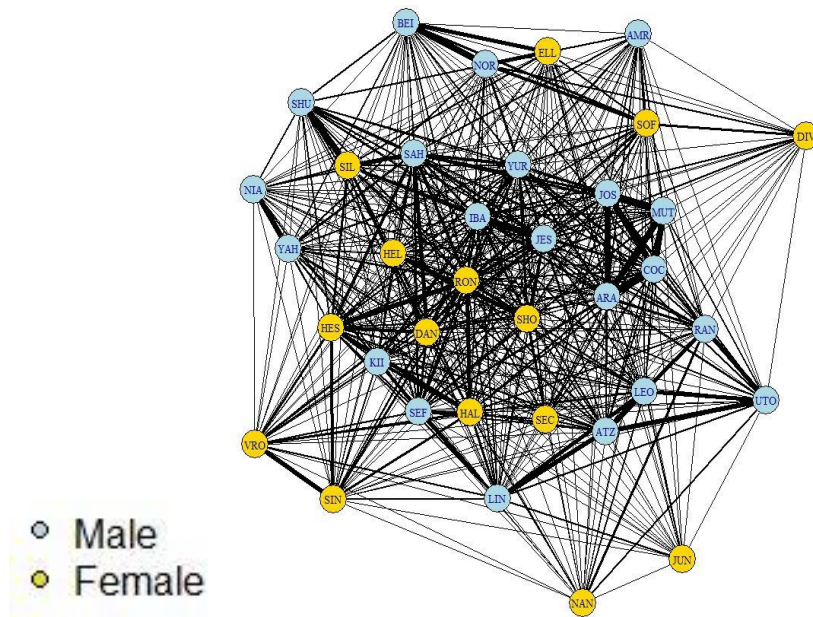


Figure 8: Network plot showing sex-dependent association strengths in Umm Usk, 2016-2020 ($n_{\text{males}} = 21$, $n_{\text{females}} = 15$). Males are displayed as light blue nodes and females as golden ones. Thickness of the edges represents association strength. Association strengths between individuals of the same sex were generally higher.

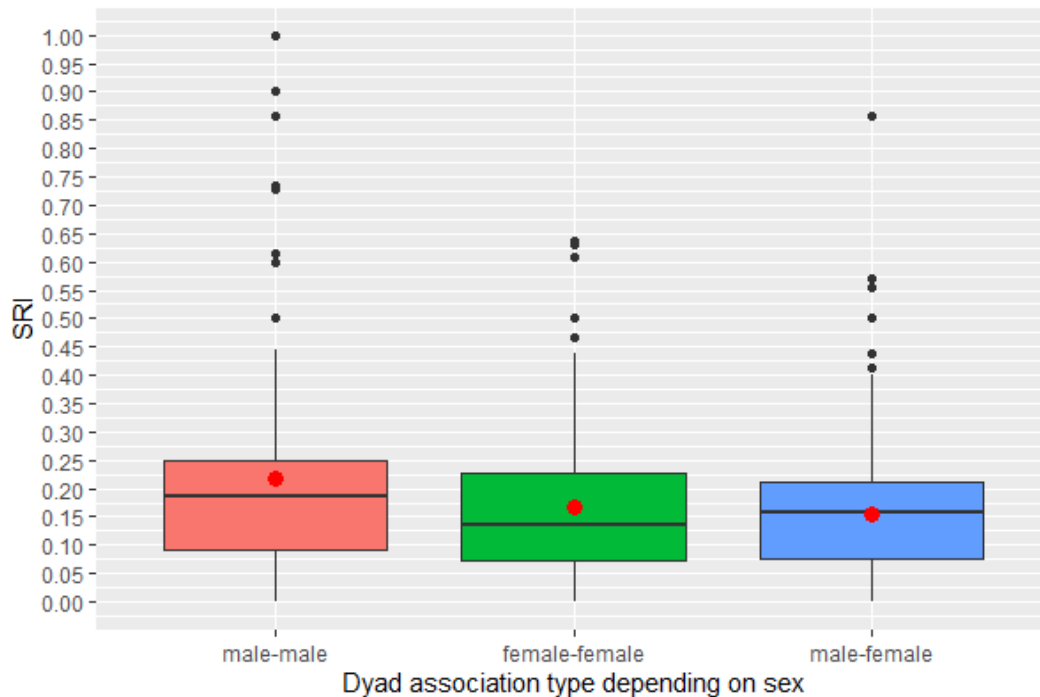


Figure 9: Association strengths for male-male, female-female and male-female dyads in Umm Usk, 2016-2020 ($n_{\text{males}} = 21$, $n_{\text{females}} = 15$). The SRI is shown on the y-axis: 1 means that a dyad is observed every time, 0 means that a dyad never associated. The box is the interquartile range, bounded at the bottom of the box through the first quartile (25th percentile) and at the top through the third quartile (75th percentile). The lengths of the upper and lower whiskers correspond to $\max. \pm 1.5 \cdot \text{IQR}$. The small black dots outside the boxes represent extreme values, whereas the large red dots within the boxes are the SRI means for the three association type categories.

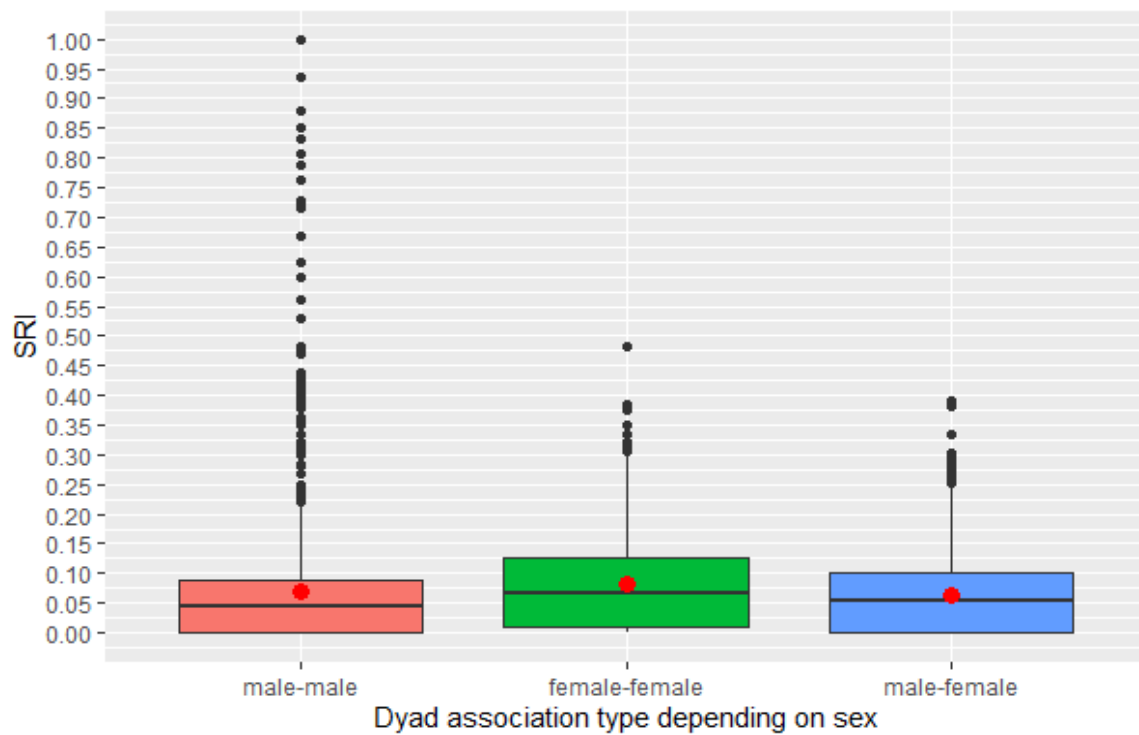


Figure 10: Association strengths for male-male, female-female and male-female dyads in Shaab El Erg, 2009-2020 ($n_{\text{males}} = 50$, $n_{\text{females}} = 41$). The SRI is shown on the y-axis: 1 means that a dyad is observed every time, 0 means that a dyad never associated. The box is the interquartile range, bounded at the bottom of the box through the first quartile (25th percentile) and at the top through the third quartile (75th percentile). The lengths of the upper and lower whiskers correspond to $\max. \pm 1.5 \cdot \text{IQR}$. The small black dots outside the boxes represent extreme values, whereas the large red dots within the boxes are the SRI means for the three association type categories.

4.2.3 Influence of maternal relatedness on association strength

Association strength was not significantly influenced by maternal relatedness (Mantel tests: Fanous: $p = 0.05$, $n = 80$ individuals; Shaab El Erg: $p = 0.23$, $n = 101$; Umm Usk: $p = 0.08$, $n = 54$). Nevertheless, at all three reefs, the association strength of maternally related females was higher on average compared to unrelated individuals. In Fanous, weaned females (mean $SRI \pm SE = 0.142 \pm 0.035$, $n = 6$) associated more with their mothers than males (0.106 ± 0.052 , $n = 2$) as well as unrelated individuals among each other (0.069 ± 0.001) (Figure 11). The same pattern was observed in Umm Usk, where the association strength was highest between maternally related females (mean $SRI \pm SE = 0.288 \pm 0.122$, $n = 2$), followed by weaned males associating with their mothers (0.182 , $n = 1$) and unrelated animals (0.138 ± 0.003) (Appendix Figure 11). In Shaab El Erg, daughters (mean $SRI \pm SE = 0.113 \pm 0.026$, $n = 5$) showed stronger associations with their mothers after weaning compared to unrelated individuals (0.063 ± 0.001) (Figure 12). Weaned sons associated less with their mothers (0.048 ± 0.011 , $n = 5$) than unrelated individuals among each other (Figure 12). Despite not being statistically significant, maternal relatedness was identified as an additional factor besides sex that potentially affects the association strength of Indo-Pacific bottlenose dolphins in the Northern Red Sea.

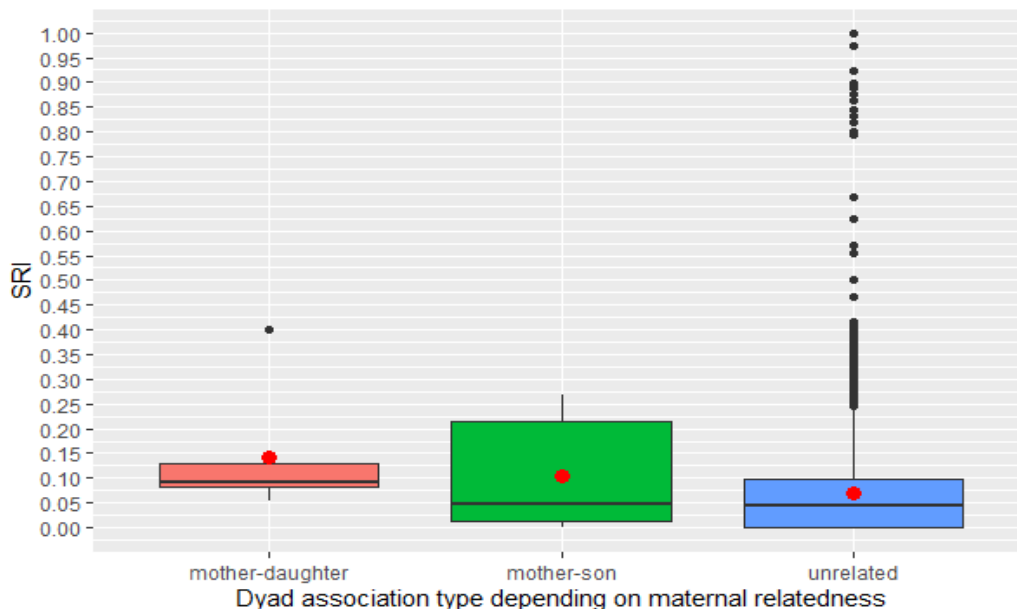


Figure 11: Association strengths for maternally related females (mother-daughter dyads), maternally related males (mother-son dyads) and unrelated individuals in Fanous, 2009-2014. The SRI is shown on the y-axis: 1 means that a dyad is observed every time, 0 means that a dyad never associated. The box is the interquartile range, bounded at the bottom of the box through the first quartile (25th percentile) and at the top through the third quartile (75th percentile). The lengths of the upper and lower whiskers correspond to $\max. \pm 1.5 \cdot IQR$. The small black dots outside the boxes represent extreme values, whereas the large red dots are the SRI means for the three association type categories.

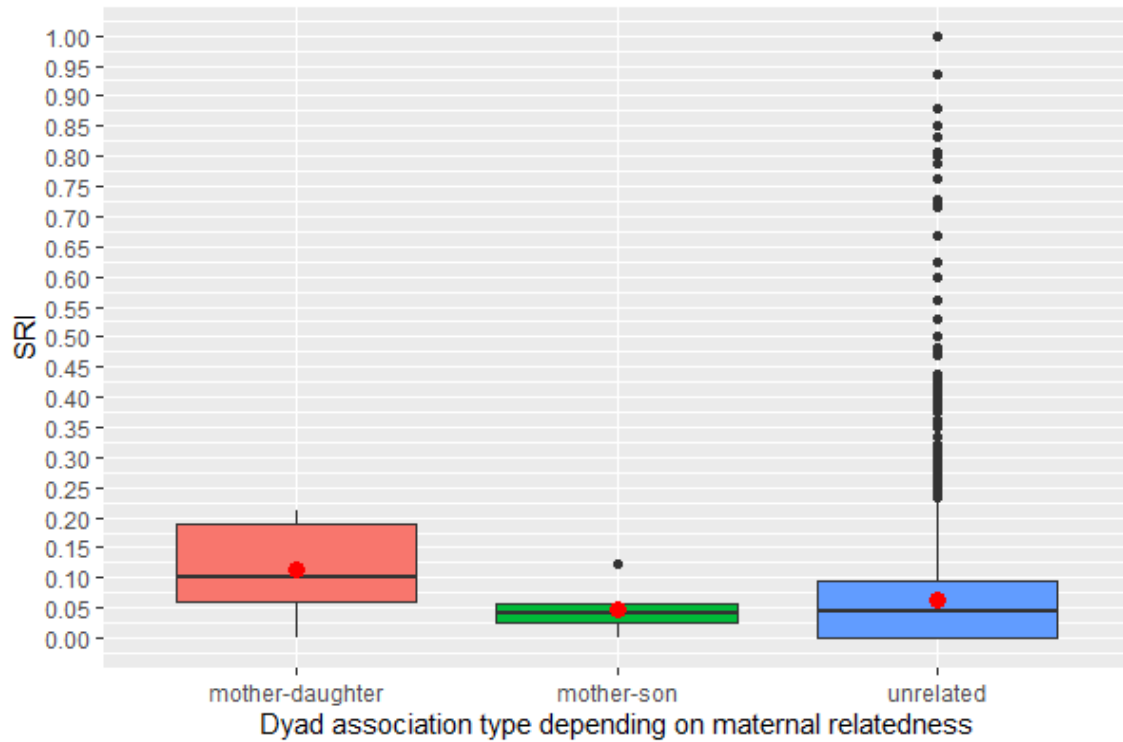


Figure 12: Association strengths for maternally related females (mother-daughter dyads), maternally related males (mother-son dyads) and unrelated individuals in Shaab El Erg, 2009-2020. The SRI is shown on the y-axis: 1 means that a dyad is observed every time, 0 means that a dyad never associated. The box is the interquartile range, bounded at the bottom of the box through the first quartile (25th percentile) and at the top through the third quartile (75th percentile). The lengths of the upper and lower whiskers correspond to max. $\pm 1.5 \cdot \text{IQR}$. The small black dots outside the boxes represent extreme values, whereas the large red dots within the boxes are the SRI means for the three association type categories.

5 Discussion

The aim of this study was to examine factors that might influence group size and give an insight into the social structure of the Indo-Pacific bottlenose dolphin population in the Northern Egyptian Red Sea. I found that activity state as well as calf number correlate significantly with group size. Additionally, there was a trend that group size was influenced by season. I showed that sex and potentially also maternal relatedness influence the strength of social bonds.

5.1 Group size influencing factors

As predicted, sleeping subgroups were significantly larger in size than socialising and playing subgroups. This can be attributed to the fact that sleep is an activity state characterised by a potentially dangerous reduction in environmental awareness/responsiveness (Lima et al., 2005). Thus, the risk of being attacked or predated is much higher during sleep (Lima et al., 2005) and a larger number of individuals provides a higher overall vigilance (according to the “many eyes hypothesis” (Powell, 1974) or “detection effect” (Dehn, 1990)), which reduces predation risk. Moreover, in a larger subgroup, every individual can afford spending less time in active vigilance (Roberts, 1996) and allocate more time to sleep leading to a higher fitness (Pollard & Blumstein, 2008).

With reduced environmental awareness, larger subgroups might not only provide an advantage in quicker detection of a potential danger such as a predator (Dehn, 1990), but also responding earlier to a disturbance in general, e.g. in the context of unregulated dolphin watching/swimming tourism, as often seen in the Egyptian Red Sea. Hence, the “detection effect” (Dehn, 1990) may not just be applied on predator-prey interactions but can also provide an explanation why the sleeping subgroups can be quite large in the presence of human disturbance (Constantine, Brunton & Dennis, 2004). A large group is expected to react earlier to a disturbance thanks to overall increased vigilance (Dehn, 1990), which may reduce the stress for each individual (M. Manser, pers. comm.). As a potential reverse effect, larger subgroups are assumed to be detected more easily (Alexander, 1974) and thus attracted by more tourists, which increases the disturbance level on the dolphins again.

There was a much higher variance of sleeping subgroups, which ranged from 1 to 32 individuals in size, compared to the other activity states, except travelling. Small sleeping subgroups were also observed, sometimes consisting of a single individual that has to sleep as well (Lima et al., 2005). To investigate if a small overall group size (all individuals observed in the group during the survey, according to the 10 m chain rule (Smolker et al., 1992), i.e. sum of all subgroup sizes) was the only reason for small sleeping subgroups (because with a small overall group size, it is more likely that the subgroups are also smaller), I calculated the proportion of individuals in a subgroup divided by the overall group size (subgroup size as a percentage of overall group size: subgroup % group). Subgroup % group of “sleep” also had a very large variance (min. = 3 %, max. = 100 %) (refer to Appendix Figure 1). The small values are most likely explained by individuals that are still or already asleep, whereas the awake rest of the group split into other subgroups to socialise or play in proximity.

Resting subgroups were smaller (median = 3) than sleeping subgroups (median = 6). Resting dolphins have approximately the same mean subgroup size as socialising individuals (also median = 3). On subgroup level, this can at least partly be explained by the ethogram (refer to Table 1) since in resting subgroups ≥ 50 % of the dolphins are socialising. Small resting subgroups may indicate that the environmental awareness may be higher than during sleep (Dehn, 1990; Lima et al., 2005). Thus, animals that are not fully asleep seem to be less reliant on the protective effect of larger groups (Dehn, 1990).

Against the prediction, travelling groups were slightly larger in size than sleeping subgroups on average. The same outcome resulted in a study in common bottlenose dolphins in Australian waters (Lear & Bryden, 1980). The Indo-Pacific dolphins in the Northern Red Sea travelled as an entire group and did not split into subgroups (because when leaving a certain spot, the entire group would split into two, a leaving and a staying group), which in contrast is possible for sleeping dolphins. The large variance of “travel” can be explained by the large variety of group sizes (min. = 1, max. = 42).

Travelling led to larger gatherings compared to playing and socialising. This is in contrast to studies in Australian waters, where socialising groups were significantly

larger in size than travelling groups (Möller, Allen & Harcourt, 2002; Kopps et al., 2013). The opposite result I found may be explained by the different sampling approach. Usually in cetacean research, as done in Möller, Allen & Harcourt (2002) and Kopps et al. (2013), the activity state determination is based on boat surveys where the predominant activity state is documented. Thus, the entire group is assigned to this predominant activity state. With underwater observation, we can easily detect individuals that deviate from the predominant activity state and subgroup formation. Our approach therefore gives an additional insight into the dynamic lives of Indo-Pacific bottlenose dolphins and I found that social gatherings are generally, if we look at them in detail, quite small and consist of few individuals (median = 3). Social behaviours such as petting, but also mating sometimes, can take place between just two or three individuals, which is another reason for social gatherings of few individuals (Mann & Smuts, 1988; Saayman, Tayler & Bower, 1973). As in common bottlenose dolphins (Bearzi, Notarbartolo-di Sciara & Politi, 1997), social gatherings of large subgroups are mainly observed during the mating and calving peak season in the Northern Red Sea (A. Ziltener, pers. comm.).

Dolphins show a high level of cognitive and behavioural complexity and a pronounced exploratory behaviour, already from young age (Reiss & Marino, 2001; López-Marulanda et al., 2019). Play behaviour is not dependent on other conspecifics and can take place alone (Janik, 2015), which was confirmed by the subgroup size assessment for playing individuals in this study. The playing subgroups were small (min. = 1, max. = 6) and usually consisting of one individual; however, playing can often build up to a social act by raising the attention of other conspecifics (Janik, 2015). There were incidents, where disentangling the behaviours of playing and socialising was difficult, because play often leads to a social encounter where conspecifics are socialising with each other, alternately with playing with other species or objects (Janik, 2015; A. Ziltener, pers. comm.). Hence, the mean subgroup size of the intermediate activity state “play/socialise” lies between “play” and “socialise”.

A study of Indo-Pacific bottlenose dolphins in southeastern Australian waters also found a significant correlation of activity state and the group size (Möller, Allen & Harcourt). Additionally, it was shown that at different locations along the same coastline the group sizes correlating with the activity states, can vary. These differences were

attributed to different social factors of the two study populations, e.g. the proportions of reproductive females (Möller, Allen & Harcourt, 2002). In the closely related common bottlenose dolphin, various studies also found different outcomes regarding the relationship of activity state and group size depending on the environment (Lear & Bryden, 1980; Shane, 1977). It leads me to the conclusion that the partly conflicting results of my study compared to Möller, Allen and Harcourt (2002) might not be entirely explained by the alternative sampling approach of recognising subgroups more easily in underwater observation, but also by differing population and habitat structures between the Red (lack of estuarine environments) and the Tasman Sea.

The hypothesised positive correlation between calf number per group and overall group size was confirmed. Larger groups with increasing number of calves have also been observed in Indo-Pacific dolphins inhabiting southeastern Australian waters (Möller, Allen & Harcourt, 2002) as well as in various populations of the closely related common bottlenose dolphin (Wells, Scott & Irvine, 1987; Bearzi, Notarbartolo-di-Sciara & Politi, 1997; Vermeulen, Holsbeek & Das, 2015). In Indo-Pacific bottlenose dolphins in southeastern Australia, the larger group size with calves being present was attributed to increased calf assistance, lower maternal investment and higher predator protection (Norris & Dohl, 1980). According to the “detection effect” (Dehn, 1990), a larger group size could not only reduce the predation risk for the calves and their mothers, but also the risk of being disturbed by human activities in the context of mass tourism, as observed in the Northern Red Sea, during important behaviours such as nursing (A. Ziltener, pers. comm.).

In the Northern Red Sea, the proportion of females that have already reproduced is 20.6 % of the entire population. This proportion is represented by the ratio of calf number to overall group size of approximately 1:5 (refer to Figure 3; if calf number ≥ 5 , uncertainty quite large (broad confidence interval) because of few data points). Thus, in the Northern Red Sea, in contrast to southeastern Australia (Möller, Allen & Harcourt, 2002), instead of mechanisms such as calf assistance and higher predator protection, the positive correlation of calf number and overall group size may just be explained by the demographic group composition: If more reproductive females are part of the group, the number of calves in the group is expected to increase linearly. However, to confirm those social mechanisms such as calf assistance and increased

predator protection for calves do not have an influence on group formation in the Northern Red Sea, further studies need to focus on behavioural interactions on an individual level.

Eventually, there is a trend of Indo-Pacific bottlenose dolphin groups in the Northern Red Sea being larger in spring and summer compared to autumn and winter. I explain this trend by the mating/calving peak season, which takes place between May and July (A. Ziltener, pers. comm.). Larger group sizes during mating/calving season have also been observed in populations in southeastern Australian and in Shark Bay, Western Australia (Wiszniewski, Allen & Möller, 2009; Mann et al., 2000). Larger groups in the calving season provide a protected environment where early postnatal development and learning can take place (Wells, Scott & Irvine, 1987). As in common bottlenose dolphins (Hanson & DeFran, 1993), I expect that more social encounters, which are observed often and intensely during mating and calving season, can lead to larger group sizes. In another dolphin species, such as the Indo-Pacific humpback dolphin (*Sousa chinensis*), a seasonal increase in group size, attributed to reproductive activity, has been recorded as well (Karczmarski, Cockcroft & McLachlan, 1999).

Besides reproductive activity, ecological constraints varying with season, e.g. air/water temperature, rainfall, food availability, can influence group size in the animal kingdom (Bräger, 1992; Shane, 1990; Korstjens, Verhoeckx & Dunbar, 2006). Howler (*Alouatta palliata*) and spider monkeys (*Ateles geoffroyi*), two neotropical primate species, have been shown to differ in group size depending on seasonally available food resources (Chapman, 1990; Korstjens, Verhoeckx & Dunbar, 2006). In African lions (*Panthera leo*), season has an influence on prey size as well as capture efficiency and therefore determines the group size range, where the energetic requirements of individual group members are met, i.e. maximising individual fitness (Caraco & Wolf, 1975). To allow a firm conclusion about the influence of season on group size in Indo-Pacific bottlenose dolphins in the Northern Red Sea, future studies should investigate on a finer, monthly scale what and how seasonal environmental factors, e.g. water temperature, influence group size.

5.2 Social structure and distribution

Against my prediction, neither female nor male Indo-Pacific bottlenose dolphins inhabiting the Northern Red Sea could be identified as being the more philopatric or dispersing sex. However, bisexual philopatry, i.e. substantial habitat overlap, has also been observed for a population in Shark Bay, Western Australia (Connor et al., 2000; Tsai & Mann, 2013) and in common bottlenose dolphins in Sarasota Bay, Florida, USA (McHugh et al., 2011). Fission-fusion dynamics and flexibly splitting into smaller groups reduce intraspecific competition and can facilitate bisexual philopatry, where bottlenose dolphins can gain fitness benefits from familiar associates, including kin, and resources in the habitat (Tsai & Mann, 2013). Similar patterns have been reported in birds such as red-winged black birds (*Agelaius phoeniceus*; Beletsky & Orians, 1989) and cliff swallows (*Petrochelidon pyrrhonota*; Brown, Brown & Brazeal, 2008).

One third of the animals that were found at least in one reef, visited all three reefs and thus had a home range of approximately 175 km². For males, this lies in the range of what has been observed in a population in Bunbury, Western Australia (Sprogis et al., 2016). In Shark Bay, males can even have a larger home range (Randić, et al., 2012). Females in the Northern Red Sea spread over larger area than their conspecifics in Bunbury (Sprogis et al., 2016). The actual home range of the dolphins in the Northern Red Sea is most likely larger since the data analysis only focused on three reefs. The lack of spatially restricted communities and large distribution (two thirds of the animals found at the three reefs visited at least two reefs) can be explained by the similar environmental conditions and habitat structures at the three reefs Fanous, Shaab El Erg and Umm Usk. Thus, the dolphins are well adapted to all the three reef habitats to fulfil their ecological needs (Costa, 2015). Even when the community detection algorithms were just based on data of individuals of the same sex, no clearly meaningful community subdivisions were identified. This is in contrast to Shark Bay, where strong sexual segregation has been reported (Fury, Ruckstuhl & Harrison, 2013; Connor, 2000; M. Krützen & S. Marfurt, pers. comm.). Compared to Shark Bay, only few coercion events of males against females have been documented at the reefs, which might be a potential reason for the lack of strong sexual segregation in the Northern Red Sea (A. Ziltener, pers. comm.). In the Australian humpback dolphin (*Sousa sahulensis*), another cetacean species, distinct social communities based on residency patterns were also not identified (Hunt et al., 2019).

According to my prediction, sex was shown to influence the association strength of Indo-Pacific bottlenose dolphins in the Northern Red Sea with intrasexual associations being significantly stronger than intersexual ones. In Australian waters around Shark Bay (Smolker et al., 1992; Connor et al., 2000; Krützen et al., 2004a) and Port Stephens (Möller et al., 2001 & 2006), Indo-Pacific bottlenose dolphins also prefer to associate with conspecifics of the same sex, which is explained by the different reproductive strategies of males and females. Adult males form strong same-sex alliances whose members cooperate to sequester females for mating opportunities (Connor, Smolker & Richards, 1992; Smolker et al., 1992). Females may benefit from associating with other females because of calf protection/assistance, sharing similar foraging tactics (and thus increased access to food sources) and affiliative behaviours that reduce stress during male harassment (Wrangham & Rubenstein, 1986; Gibson & Mann, 2008; Mann et al., 2012; Connor, Mann et al., 2006). Sexual segregation has also been reported in common bottlenose dolphins (Wells, Irvine & Scott, 1987; Wells, 1991). Strong intrasexual associations have also been observed outside the genus *Tursiops* in cetaceans. In Australian humpback dolphins, higher assortative associations have been reported among individuals of the same sex (Hunt et al., 2019). Preferred intrasexual affiliations are not restricted to cetaceans, but have also been reported in great apes, such as chimpanzees, where not only males but also females formed distinct clusters (Wakefield, 2013).

As predicted, at two reefs, male-male associations were stronger on average than female-female and male-female interactions. Strong male-male associations are explained by stable, long-term alliance formation to improve access to oestrous females (Connor et al., 2000; Möller et al., 2001; Scott et al., 2005). The extreme values of large SRI values in the unrelated (refer to section 4.2.3) and male-male dyads (refer to boxplots in section 4.2.2) can be explained by the fact that those strong-bonded male alliances mostly consist of unrelated, similarly aged individuals (Möller et al., 2001; Gerber et al., 2020). The mean association strengths of male-male associations differed depending on the reef. In Umm Usk, the reef with the smallest number of individuals, the mean association strength was largest, whereas in Shaab El Erg, the reef with the highest number of individuals, the mean association strength was lowest. Since the number of male alliances consisting of adult males were equal

at all three reefs, the reefs with more males in total have a higher number of males that do not (yet) belong to a stable male alliance, e.g. juveniles (Galezo et al., 2020; Gerber et al., 2020), which decreases mean association strength. Moreover, the different sex ratios at the different reefs (refer to Table 2) may explain the differences in association strengths between male-male and female-female associations: The differences were larger in Umm Usk (58 % males and 42 % females) compared to the other two reefs, where the sex ratio was more similar (55 % males and 45 % females).

In Shaab El Erg, female-female dyads showed on average even stronger associations than male-male dyads. This result is surprising since females are said to form more flexible and less stable groups than males (Smolker et al., 1992). Of the three assessed reefs, Shaab El Erg is the geographically most central one and visited by most individuals, i.e. 80 % of the females visiting the three reefs occurred in Shaab El Erg, and if an individual visited more than one reef, it always occurred in Shaab El Erg. Thus, the chance for overlapping home ranges in Shaab El Erg compared to the other two reefs is higher. If females encounter each other more often, the chance of establishing more stable bonds may be higher. However, further studies should be conducted at other reefs in the Northern Red Sea and on an individual level to confirm if female-female interactions are stronger and more stable than previously thought.

With the inclusion of male-female associations, there were no meaningful community subdivisions at the three examined reefs. However, it is possible that there would be meaningful community subdivisions during the mating peak season since it has been shown that male-female associations of bottlenose dolphins in Western Australia and Florida mainly occur in the mating season (Connor et al., 2000; Owen, Wells & Hofmann, 2002). Thus, it needs further investigation whether there is also a seasonal influence on the fission-fusion dynamics of Indo-Pacific bottlenose dolphins in the Northern Red Sea.

Because of the small sample size, it will be difficult to make a statistically supported statement about the importance of maternal kinship on the social association strength before the permission of genetic sampling in the Egyptian Red Sea. Due to missing genetic sampling, the data must be interpreted with caution since the dyads that were regarded as “unrelated” (all dyads except identified mother-weaned calf associations)

could actually be related because those individuals were already weaned when first encountering them (and thus maternal kinship was not identifiable on a behavioural basis) or might not have been recognised anymore because their dorsal fins changed tremendously. However, since there was a trend of maternally related females showing stronger associations compared to unrelated individuals, I assume that maternal relatedness is a factor that can shape female sociality of Indo-Pacific bottlenose dolphins in the Northern Red Sea. This is consistent with Australian populations in Port Stephens and Shark Bay, where maternally related females associated more often than would be expected by chance (Möller et al., 2006; Frère et al., 2010). With ongoing association after weaning, daughters develop similar foraging tactics as their mothers (Mann & Sargeant, 2003) and gain indirect fitness benefits by assistance the mother in calf rearing, according to the “kin selection theory” (Hamilton, 1964), which has also been reported in cooperative breeders such as meerkats (*Suricata suricatta*; Clutton-Brock et al., 2001).

Other toothed whale species such as Australian bottlenose/Burrnun dolphins (*Tursiops australis*; Diaz-Aguirre et al., 2020), short-beaked common dolphins (*Delphinus delphis*; Zanardo et al., 2016) and sperm whales (*Physeter macrocephalus*; Gero, Engelhaupt & Whitehead, 2008) were also shown to have strong associations among related females. Besides toothed whales, high association rates of maternally related females are found in several other species in the animal kingdom, such as greater horseshoe bats (*Rhinolophus ferrumequinum*; Rossiter et al., 2002) crested macaques (*Macaca nigra*; Kerhoas et al., 2016), baboons (*Papio cynocephalus*; Silk, Alberts & Altmann, 2003; Silk et al., 2009), giraffes (*Giraffa camelopardalis*; Carter et al., 2013) and African elephants (*Loxodonta africana*; Goldenberg, Douglas-Hamilton & Wittemyer, 2016).

After weaning, sons associate less with their mothers than daughters do (Samuels, 1996), mainly to avoid inbreeding (Tsai & Mann, 2013). Therefore, it is surprising that at two reefs Fanous and Umm Usk in the Northern Red Sea, mother-son associations were stronger on average than associations of unrelated individuals. However, for those two reefs, due to data restrictions, a shorter time period was assessed than for Shaab El Erg. Thus, the sample sizes were smaller and all weaned sons in the data set were still juveniles. In Shark Bay, it has been reported that male juveniles, before

reaching the adulthood and forming stable alliances with other unrelated males, can regularly associate with maternally related conspecifics (30 % of mean intersexual association strength) (Gerber et al., 2020), which may explain the increased association strength of mothers and sons at those reefs in the Northern Red Sea. Those related conspecifics are said to be their mother's associates, i.e. sisters, which can lead to indirect association with their mothers. To find out whether juvenile males associate primarily with their mothers or sisters, social networks need to be analysed on an individual, behavioural level in future research projects.

6 Conclusion

This study demonstrates that multiple factors shape the complex social structure of Indo-Pacific bottlenose dolphins in the Northern Egyptian Red Sea. The activity state was identified to significantly correlate with the (sub)group size. The travelling groups were largest in size, followed by sleeping subgroups. Since sleep is characterised by a reduction in environmental awareness, the predation risk is much higher during sleep (Lima et al., 2005). According to the “detection effect”, more individuals detect the predator earlier and enable other individuals to reduce their own vigilance (Dehn, 1990; Roberts, 1996). Additionally, the hypothesised positive correlation between calf number per group and overall group size was confirmed. These findings are of importance for the implementation of a sustainable dolphin-watching tourism: When encountering large groups, it is likely that the group is either asleep and/or consists of calves. Thus, it is more vulnerable and should be approached more carefully (Christiansen et al., 2010; Stensland & Berggren, 2007). There was evidence that sex drives sociality of Indo-Pacific bottlenose dolphins in the Northern Red Sea. Intrasexual associations being stronger than intersexual ones is explained by the different reproductive strategies of males and females (Connor, Smolker & Richards, 1992; Smolker et al., 1992). Unexpectedly, at one reef in the Northern Red Sea, female-female associations were even stronger on average than male-male ones. Thus, female-female associations might be more stable than previously thought. However, this hypothesis is yet to be confirmed by assessing female sociality on an individual level in the entire distribution area in the Northern Red Sea. The lack of spatially restricted communities and large distribution of the population in the Northern Red Sea implies that future conservation actions should not just focus on a single reef but aim to implement larger marine protected areas with restricted tourism. Since group size and composition are critical determinants of fission-fusion dynamics (Gowans, Würsig & Karczmarski, 2007), this study not only expands our knowledge about group size influencing factors and the social structure of Indo-Pacific bottlenose dolphins in the Northern Egyptian Red Sea, but potentially also sheds light on fission-fusion societies of other cetaceans and terrestrial mammal species.

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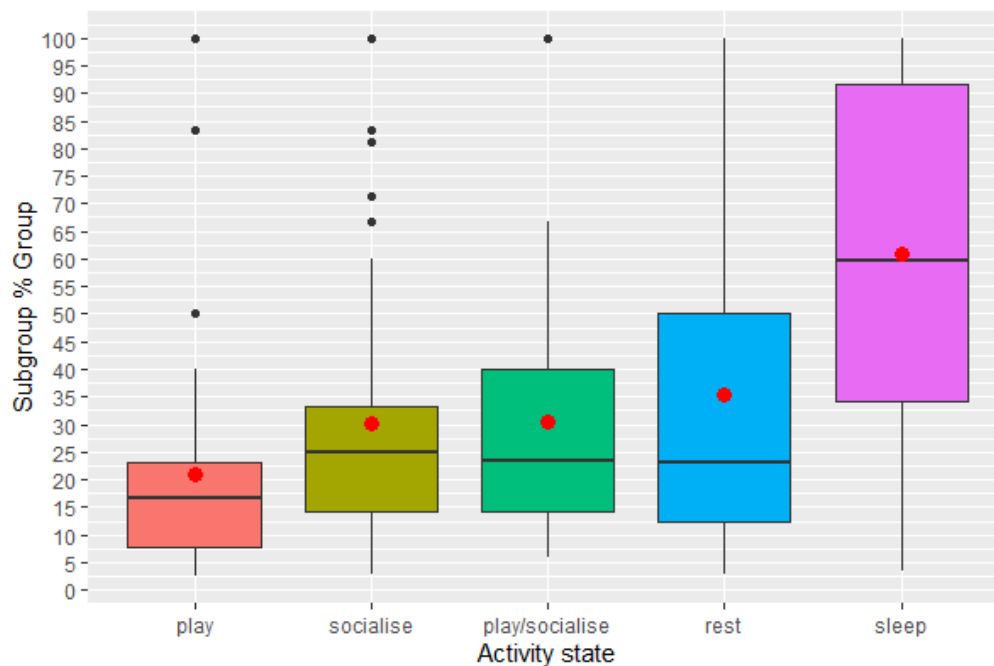
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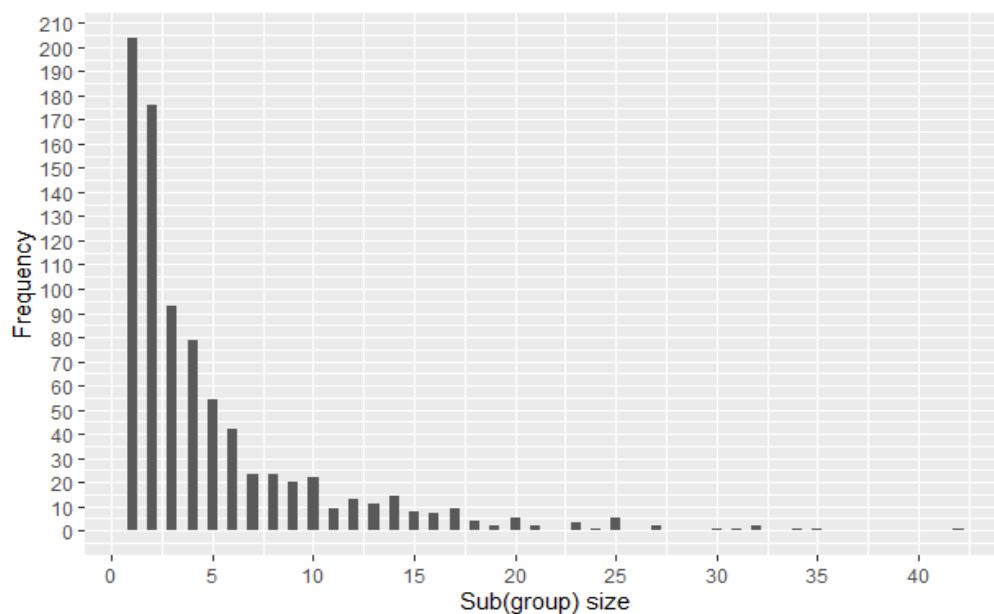
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10 Appendix

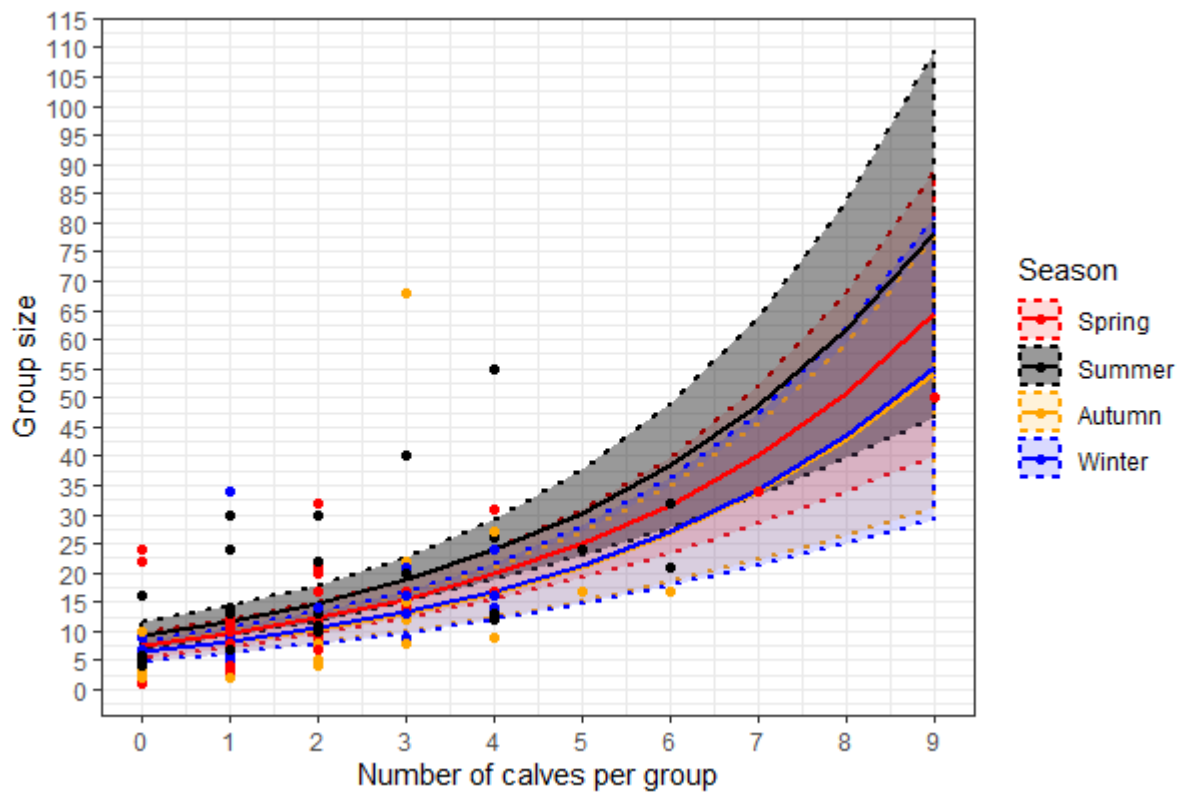
10.1 Supplementary figures and tables



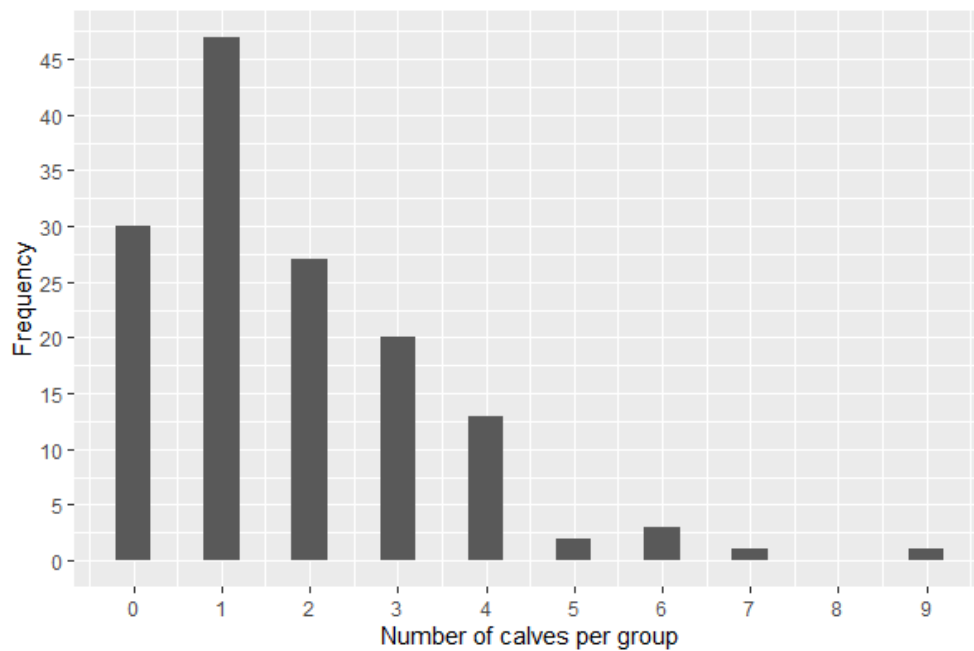
Appendix Figure 1: Relationship of activity state and subgroup size as a percentage of overall group size (subgroup % group). The box shows the interquartile range, bounded at the bottom of the box through the first quartile (25th percentile) and at the top through the third quartile (75th percentile). The lengths of the upper and lower whiskers correspond to $\max. \pm 1.5 \cdot \text{IQR}$. The small black dots outside the boxes represent extreme values, whereas the large red dots within the boxes are the means for each activity state.



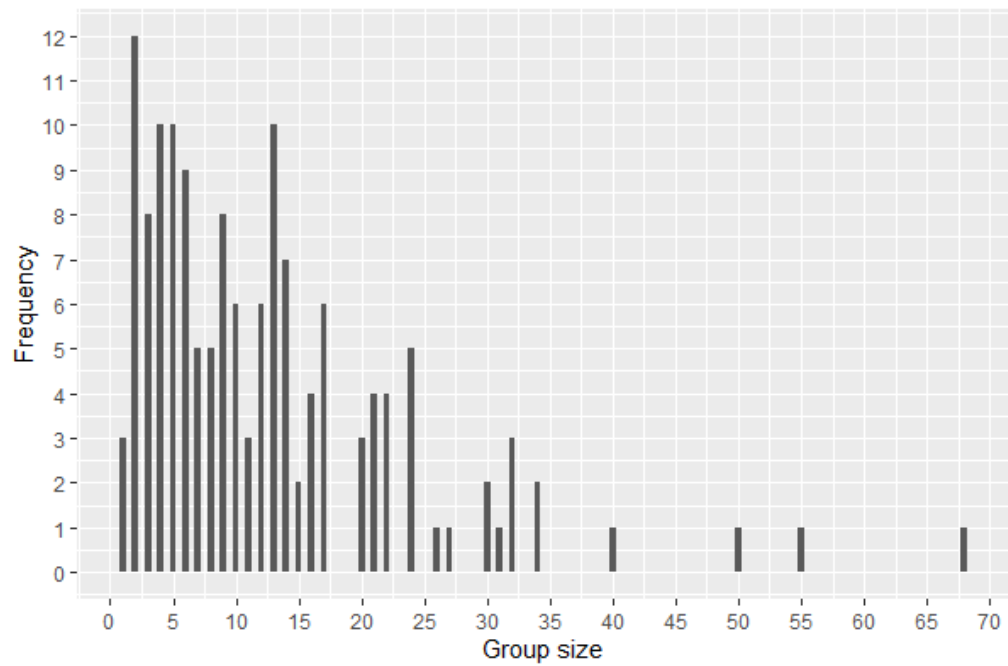
Appendix Figure 2: Frequency distribution of (sub)group size. The x-axis shows the size of the (sub)group. The y-axis displays the number of observations. The frequency distribution is right skewed.



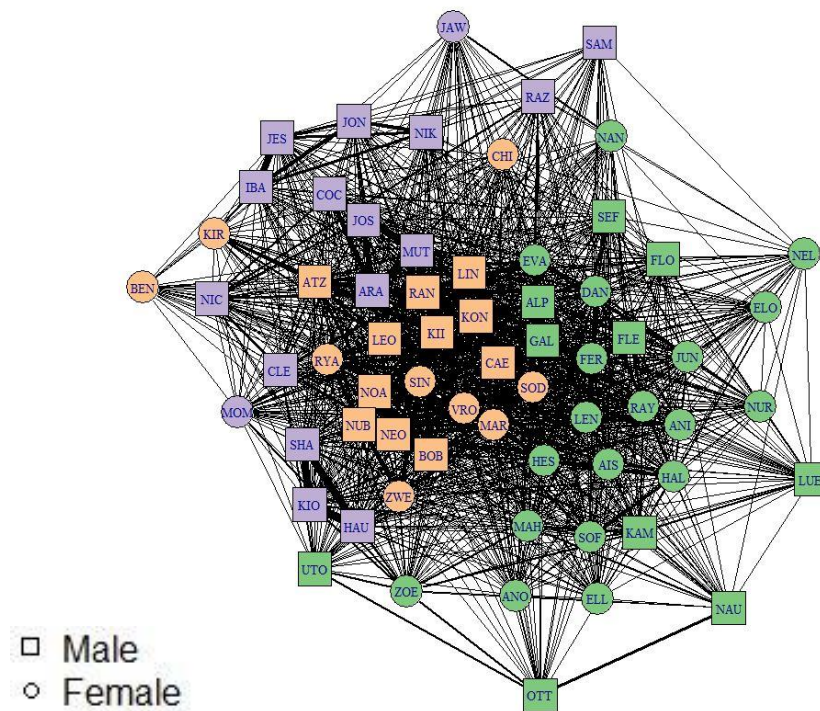
Appendix Figure 3: Relationship of calf number per group (covariate), season (predictor) and overall group size. The x-axis shows the number of dependent calves per group. The four regression slopes correspond to the four different seasons (see colour legend in graph). The y-axis shows the overall group size, i.e. the total number of individuals per group.



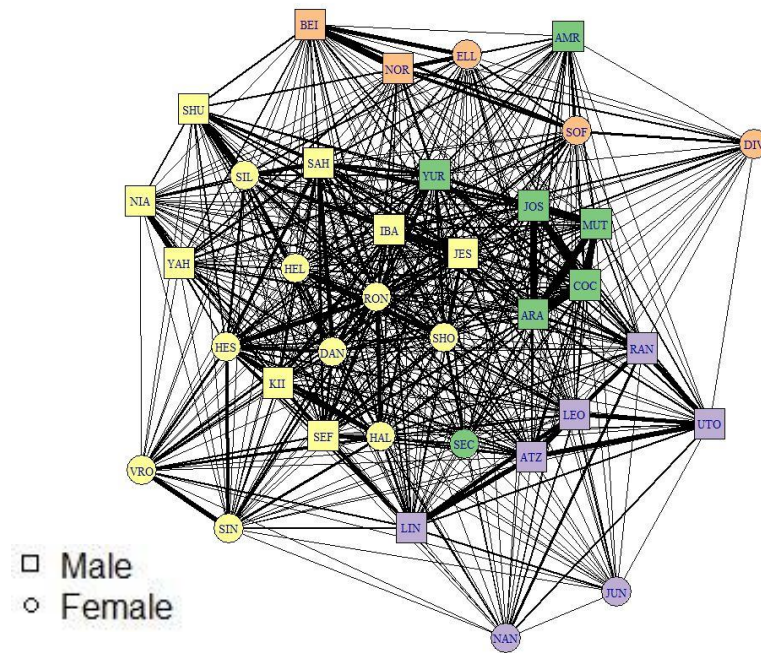
Appendix Figure 4: Frequency distribution of calf number per group. The x-axis shows the number of dependent calves per group. The y-axis displays the number of observations. The frequency distribution is right-skewed.



Appendix Figure 5: Frequency distribution of overall group size. The x-axis shows the total number of individuals per group. The y-axis displays the number of observations. The frequency distribution is right-skewed.



Appendix Figure 6: Network plot showing community memberships in Fanous, 2009-2014 ($Q = 0.19$, $n = 66$). The communities are differentiated by colour. Males are displayed as squared and females as circled nodes. Thickness of the edges represents association strength.



Appendix Figure 7: Network plot showing community memberships in Umm Usk, 2016-2020 ($Q = 0.14$, $n = 36$). The communities are differentiated by colour. Males are displayed as squared and females as circled nodes. Thickness of the edges represents association strength.

Appendix Table 1: Numbers of individuals occurring at different numbers of reefs depending on sex.

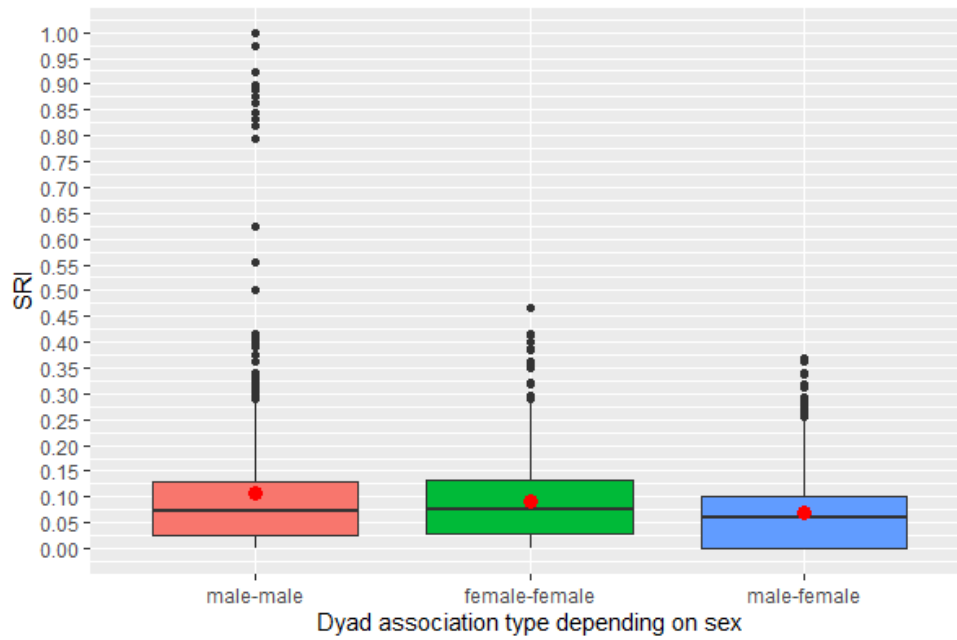
	1	2	3	Total
Males	28	34	28	90
Females	29	17	27	73
Total	57	51	55	163

Appendix Table 2: Percentages of male and female individuals divided by the number of reefs they occur.

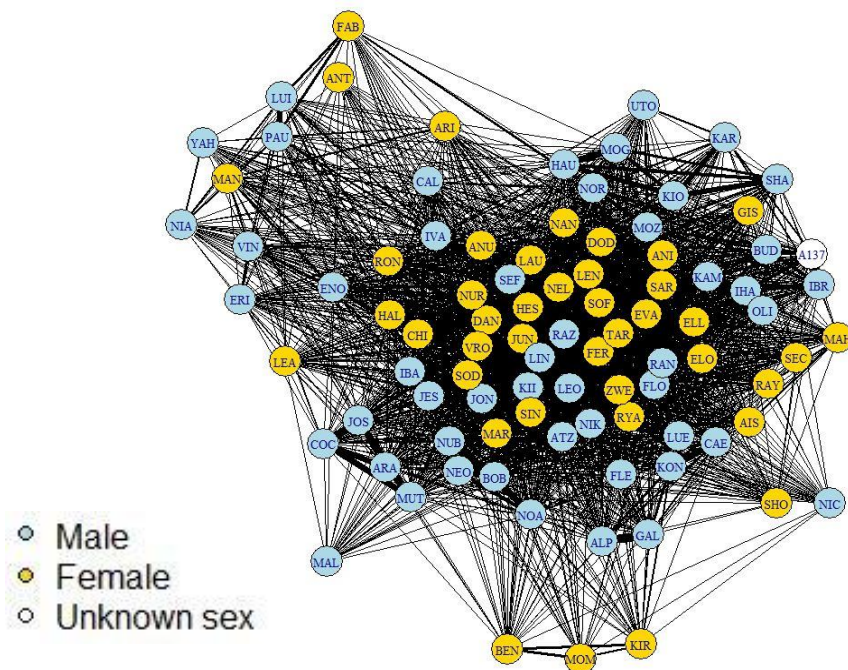
	1	2	3	Total
Males	31 %	38 %	31 %	100 %
Females	40 %	23 %	37 %	100 %
Total	35 %	31 %	34 %	100 %



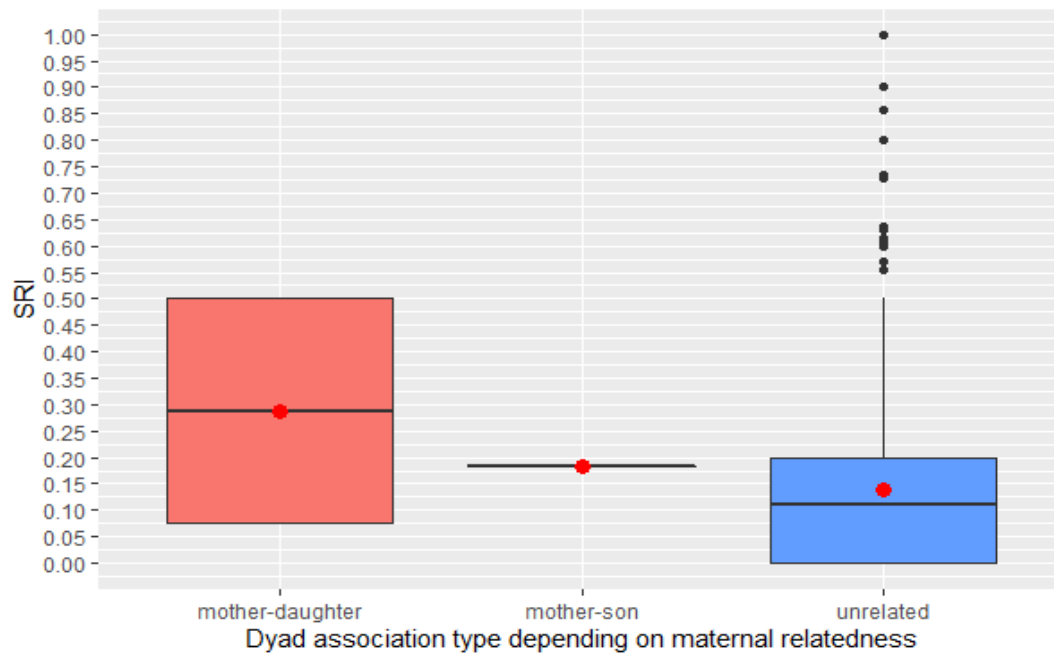
Appendix Figure 8: Pie charts displaying percentages of male and female individuals divided by the number of reefs they occur. The different colours correspond to the number of visited reefs according to the legend in the graph.



Appendix Figure 9: Association strengths for male-male, female-female and male-female dyads in Fanous, 2009-2014 ($n_{\text{males}} = 36$, $n_{\text{females}} = 30$). The SRI is shown on the y-axis: 1 means that a dyad is observed every time, 0 means that a dyad never associated. The box is the interquartile range, bounded at the bottom of the box through the first quartile (25th percentile) and at the top through the third quartile (75th percentile). The lengths of the upper and lower whiskers correspond to $\max. \pm 1.5 \cdot \text{IQR}$. The small black dots outside the boxes represent extreme values, whereas the large red dots within the boxes are the SRI means for the three association type categories.



Appendix Figure 10: Network plot showing sex-dependent association strengths in Shaab El Erg, 2009-2020 ($n_{\text{males}} = 50$, $n_{\text{females}} = 41$). Males are displayed as light blue nodes and females as golden ones. White nodes correspond to individuals of unknown sex. Thickness of the edges represents association strength. According to the clustering pattern, assortment dependent on sex can be recognised.



Appendix Figure 11: Association strengths for maternally related females (mother-daughter dyads), maternally related males (mother-son dyads) and unrelated individuals in Umm Usk, 2016-2020 ($n_{\text{total}} = 54$, $n_{\text{daughters}} = 2$, $n_{\text{sons}} = 1$). SRI is shown on the y-axis: 1 means that a dyad is observed every time, 0 means that a dyad never associated. The box is the interquartile range, bounded at the bottom of the box through the first quartile (25th percentile) and at the top through the third quartile (75th percentile). The lengths of the upper and lower whiskers correspond to $\max. \pm 1.5 \cdot \text{IQR}$. The small black dots outside the boxes represent extreme values, whereas the large red dots are the SRI means for the three association type categories.

10.2 Materials used for data collection/processing

10.2.1 Behavioural survey data sheet

Internal document by Shark Bay Dolphins, adapted by Dolphin Watch Alliance

Survey # (& Focal Follow #):										Data entry: (date/initials)		
Date:	Depth	GPS	Habitat	Substrate	# Boats in proximity	Boat activity around dolphins						
Observer:		North	1Lagoon	1Reef	50-100m:	# Boats:				All ID? y/n		
Boat:	Temp		2Reef edge	2Sand	100-200m:	Snorkelers set: y/n				All identifiable? y/n		
Time 1st ID:		East	3Reef	3Seagrass	>200m:	Divers set: y/n				All photo/ID? y/n		
Time depart:	BFT		4Open water	4other		Ds crossed: y/n				# IDs 1st 5 min		
Reason depart: 5 D L R O			Location:		Sother						Total (before depart)	
ID codes or names; Place animals that arrive > 5 min in parentheses												
Arrivals (IDs and times):												
Departures (IDs and times):												
PARTY DATA during r st 5 min: Circle all predominant, check all occurrences. Put later data in notes!												
Activity	Spread(m)	Surface info	Speed (kts)	Group foraging	Socialize see UW obs.	ID	BP (calf ID)	BP after 5min				
Rest	Vit<.3	rg pp	Vtr <1	Spread td/pd			: y / n	: y / n				
Travel	Tig .3-2	td lp	Str 1-2	bird mill			: y / n	: y / n				
Socialize	Mod 2-5	pd hs	Ctr 2-3	lp&pp feed			: y / n	: y / n				
Forage	Spr 5-10	rs snag	Mtr 3-4	snack party			: y / n	: y / n				
Play	Wsp > 10	rt	Ftr 4-6				: y / n	: y / n				
Unknown			Btr >6									
Check and note ID				NOTES								
Display? Type												
Sync surf?												
Spy hop?												
Vocal.?Type												
Bubbles?Type												
Bow ride?												
Object play?												
Species play?												
Dive1 (min, ID):				Dive2:		Dive3:		Snorkel:				
Note				Underwater observation				Gorgoning y/n				
IDs of close associations (Vit<.30)								IDs:				
Sync surf?								Nursing				
								IDs:				
								Photos:				
								Videos:				
ID1= Actor ID2=Recipient												
Socialize	ID of Initiator	ID 1	ID 2	ID 1	ID 2	Individual or Interaction	ID 1	ID 2	Rubbing	ID	Fecal sample#	ID
pet			bep			hup			Leather coral		F1	
rub			hth			hro			Sponge			
krb			hj			hfu			Sand		Vomit# V1	ID
prb			hds			hfd			Seagrass			
crb			ndg			bup			Object play	ID	Vocalization	ID
hrb			gou			osd					Whistles	
bon			mou			lob					Echolocation	
sex			erection			sus			Species play	ID	Bubbles (Type)	
						mo						
						ic						

Label unknowns: 1AF (adult female), 1AM (adult male), 1AxX (adult unk. sex), 1JF (juv fem), 1JM (juv male), 1JX (juv unk. sex), 1CF (calf fem), 1CM (calf male), 1CX (calf unk. sex), 1XX (no size info), mother calf pairs 1AF 1CX, 2AF 2CX..

10.2.2 Focal group follow data sheet

Internal document by Shark Bay Dolphins, adapted by Dolphin Watch Alliance

Focal Follow #:		Date:	
GPS/Location (Start&End):		BFT& Wind direction:	
Habitat:		Glare:	
Substrate:		Sighting condition:	
Focal ID(s):			
Time	Group size	Behavior (IDs, subgroups, nearest neighbors, spread, surface info, speed, travelling direction, arrivals&depart..)	Notes (e.g boat activity, (GPS) location, Environm.)

10.2.3 Extract of DWA photo-ID catalogue



Laura



Lino



Marry



Moga



Rya



Sefa



Ferdinand



Vroni



Zwerg