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Original Article

Sex, synchrony, and skin contact: integrating multiple behaviors to assess pathogen transmission risk

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Direct pathogen and parasite transmission is fundamentally driven by a population's contact network structure and its demographic composition and is further modulated by pathogen life-history traits. Importantly, populations are most often concurrently exposed to a suite of pathogens, which is rarely investigated, because contact networks are typically inferred from spatial proximity only. Here, we use 5 years of detailed observations of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) that distinguish between four different types of social contact. We investigate how demography (sex and age) affects these different social behaviors. Three of the four social behaviors can be used as a proxy for understanding key routes of direct pathogen transmission (sexual contact, skin contact, and aerosol contact of respiratory vapor above the water surface). We quantify the demography-dependent network connectedness, representing the risk of exposure associated with the three pathogen transmission routes, and quantify coexposure risks and relate them to individual sociability. Our results suggest demography-driven disease risk in bottlenose dolphins, with males at greater risk than females, and transmission route-dependent implications for different age classes. We hypothesize that male alliance formation and the divergent reproductive strategies in males and females drive the demography-dependent connectedness and, hence, exposure risk to pathogens. Our study provides evidence for the risk of coexposure to pathogens transmitted along different transmission routes and that they relate to individual sociability. Hence, our results highlight the importance of a multibehavioral approach for a more complete understanding of the overall pathogen transmission risk in animal populations, as well as the cumulative costs of sociality.

Key words: **coinfection, contact networks, demography, disease transmission, multibehavior, social structure.**

INTRODUCTION

Social contact patterns among all individuals in a population fundamentally drive the propagation of directly transmitted pathogens (Cote and Poulin 1995), which has been identified as a major cost of sociality (Kappeler et al. 2015). These transmission processes, in interaction with pathogen life-history traits, determine population disease outcomes, such as outbreak size and duration, as well as the probability of an epidemic (Keeling and Eames 2005; Bansal et al. 2007). Importantly, populations are exposed to a suite of pathogens, often at the same time (Susi et al. 2015). Some pathogens can be transmitted across host species boundaries and through dormant or stable stages in the environment (Leu et al. 2010b; Silk et al. 2018a), decoupling the transmission route from host social contact networks. Here, we focus on directly transmitted parasites and pathogens as they directly relate to social contacts among host individuals. Directly transmitted pathogens are passed on along different routes through distinct contact behaviors, such as sexual (e.g., HIV; Attia et al. 2009) or droplet contact for the transmission of aerosolized pathogens (e.g., influenza; Lakdawala and Subbarao 2012). Importantly, all social contact types contribute to the overall disease risk of directly transmitted pathogens. Despite this, animal studies typically focus on one particular disease and one contact type only, which limits our insight into the overall risk of infection. In this study, we use social network methods to investigate potential pathogen transmission risk along three different behavioral routes and how these relate to demographic patterns of social associations. By examining multiple routes of transmission, we can better understand individual and population disease risks, as well as predict the cumulative costs of sociality during animal life histories.

Empirical animal studies, as well as mathematical models, have demonstrated a relationship between animal contact patterns and pathogen and parasite transmission risk (Leu et al. 2010b; Romano et al. 2016). For instance, in the brown spider monkey

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(*Ateles hybridus*), the amount of time spent in physical contact with others correlates with the parasite species richness found in the host individual (Rimbach et al. 2015). The link between social contact patterns and infectious disease risk is best quantified using network techniques (Croft et al. 2008). Contact networks allow for explicit consideration of complex interaction patterns among all individuals of a population and their integration into a disease context (Bansal et al. 2007). A connection (edge) is placed between two individuals (nodes) if they have an interaction capable of pathogen or parasite transmission. Doing this for all possible dyads forms a contact network of the population. Contact networks are used to model population-level processes and, therefore, allow the investigation of demographic effects.

Some recent studies have shown that heterogeneity in contact patterns, and hence individual transmission potential, can vary among demographic groups (Godfrey 2013; Silk et al. 2019). For instance, in bighorn sheep (*Ovis canadensis*), lambs have the highest interaction frequencies and interactions with infected mothers result in elevated mortality risk (Manlove et al. 2017). Demographic classes also differ in their trade-off among the basal organismal functions of maintenance, growth, immune system function, and reproduction, which may lead to differences in susceptibility among demographic classes (French et al. 2009). Contact patterns, and, hence, exposure risk, in interaction with susceptibility and acquired immunity can then translate to demography-dependent infection patterns (Bansal et al. 2010; White et al. 2018). However, demographic effects are rarely investigated across different contact networks. Insight into demographic effects on exposure risk will allow the identification of demographic groups most at risk in the event of pathogens entering a population. Such knowledge can prove essential in conservation efforts and disease management (Aiello et al. 2014).

Here, we investigated different types of social contact behavior as proxies for pathogen transmission along multiple direct transmission routes in a highly social marine mammal. The Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, forms complex fission–fusion societies with pervasive sex segregation (Galezo et al. 2018), and with associations and groups changing temporally, spatially, and in composition (Connor et al. 2000). In addition, long-term preferential social bonds exist among mother and calf and male alliance members. Mother–calf bonds are driven by extensive maternal investment. Approximately, after 4 years, when calves become increasingly independent and reach the juvenile state, interaction frequencies between mother and offspring decrease substantially, in particular, with male offspring (Smolker et al. 1992; Mann et al. 2000; Tsai and Mann 2013). Male alliances are strong, long-term stable social bonds among several males (Connor and Krützen 2015). These alliances are driven by male reproductive success as members of alliances are more successful at coercing females (Krützen et al. 2004; Wiszniewski et al. 2012). Juveniles, of both sexes, are variable in their interaction patterns and frequently interact with changing conspecifics (Krzyszczyk et al. 2017). These social complexities also reflect marked demographic differences in dolphin association patterns. Such demographic differences likely extend to other social contexts, including contacts that are relevant for pathogen transmission. This suggests divergent disease exposure risks among demographic groups and, ultimately, demographic differences in disease consequences.

The variety of behaviors in cetaceans provides multiple transmission pathways for a range of infectious diseases. For example, sexual contacts allow the transmission of the papillomavirus, which causes sexually transmitted infections (Van Bressem et al. 1999; Rehtanz et al. 2010), physical contact permits transmission of the poxvirus, causing skin infections (Van Bressem et al. 1999), and synchronous breathing allows for respiratory particle exchange, creating transmission pathways for the spread of respiratory pathogens, such as cetacean morbillivirus (Van Bressem et al. 2014) and *Brucella ceti* (Guzmán-Verri et al. 2012). Our study site Shark Bay, Australia, is a UNESCO World Heritage Site and a pristine environment; thus, its bottlenose dolphin population provides a healthy baseline for the study of disease-relevant behavior. However, two recent epizoological studies characterize the prevalence and demographic biases of a nonlethal skin infection known as tattoo-skin disease (likely caused by poxvirus) in the Shark Bay dolphin population (Powell et al. 2018, in press).

We used social networks to investigate how demography affected three discrete behaviors, each representing a transmission route for directly transmitted pathogens known to be present in cetacean populations (Van Bressem *et al.* 2009): 1) sexual contact relevant to transmission of sexually transmitted diseases; 2) physical skin contact relevant to transmission of skin diseases; and 3) synchronous breathing relevant to the transmission of respiratory infections. Importantly, we then determined the pairwise relationships between contact networks in order to understand coexposure risks and identify individuals and demographic groups that play an important role in the pathogen transmission across the population. In order to put the pathogen transmission probabilities into context of individual sociability, the propensity to interact with others, we also quantified 4) social associations among all dolphins based on spatial proximity. Our multibehavioral approach, which provides insight into exposure risk across several transmission modes and quantifies the risks of coexposure, further advances our understanding of the cumulative cost of sociality.

MATERIAL AND METHODS

Behavioral observation

Dolphin behavior was recorded as part of a long-term study at Shark Bay, Western Australia (25°47′S, 113°43′ E). Each year, from the start of the Austral winter to the end of spring (approximately mid-May to mid-December), the study tracks all resident members of a local population within a 300-km^2 study area. Our surveys are based on opportunistic sightings of dolphins in the study area. The presence of individuals and their behavior were recorded within the first 5 min of the sighting (Karniski et al. 2015). Dolphins were identified by photo ID based on distinctive body and dorsal fin markings (Bichell et al. 2018). The resulting data set includes detailed records on individual life histories, including sex, birth date, reproductive events, and individual behaviors, such as social interactions and their context. Our study is based on observations over 5 years. In a given year, we observed and included in our analysis a mean of 341 individuals (range: 306–382; Supplementary Table 1), consisting of a mean of 172 males (range: 152–203), 169 females (range: 147–186) and 279 adults (range: 240–314), 37 juveniles (range: 36–39), and 25 calves (range: 12–36). The research was conducted under the permit numbers IACUC 07-041, 10–023, and 13–069 and Department of Parks and Wildlife numbers SF-009876, SF-010347, SF-008076, SF-009311, and SF-007457.

Constructing contact networks

We used behavioral observations made during the period 2011–2015 and identified social contact between two individuals if they were observed interacting in a particular social context. We focused on four contact types—1) sexual contact, 2) skin contact, 3) synchronous breathing, and 4) social association—and constructed separate networks for each of those behaviors. Table 1 provides further detail about the behaviors that were included in each social context and examples of pathogens that spread along the represented transmission mode. In short, sexual contacts occur not only during mating but also in a nonreproductive context to mediate social relationships. All age and sex classes engage in sexual contacts, including between same-sex individuals (Mann 2006), and allow the transmission of sexually transmitted pathogens. Direct skin contact is typically affiliative and involves mostly rubbing, petting, and social play, which would allow the transmission of skin infections. Synchronous breathing is also an affiliative social behavior and occurs when two or more individuals coordinate their breathing during directional movement by surfacing together. In the process, respiratory vapor is exchanged and suspended respiratory pathogens can be transmitted. Finally, social associations were based on spatial proximity of individuals using a 10-m chain rule. All individuals within 10 m of another group member were considered to be associated (Karniski et al. 2015). For each behavioral context, we constructed five networks, one for each year, which accounts for possible transitions to successive age classes during the 5-year study. All yearly networks were unweighted networks with edges placed between two nodes if the pair interacted at least once in the respective behavioral context. We used unweighted networks in this analysis and did not distinguish between strong and weak ties because weak ties (i.e., edges with low weights) have been shown to be important in the context of pathogen or parasite transmission (Sah et al. 2018). Consequently, we calculated and analyzed each individual's *binary degree*, which quantifies the number of unique individuals each animal interacted with (Croft et al. 2008).

Relationship between behavior and demography

To understand the relationship between behavior and demography, we developed regression models for each behavior with demographic covariates. We used a generalized linear mixed model (GLMM) with a Poisson distribution, and binary *degree* as the response variable, as described above. We controlled these models for sampling effort and tested statistical significance with permutation null models to account for the nonindependence of network-derived data (Farine and Whitehead 2015).

Demographic-specific transmission risks

For the demographic covariates, we included sex and age as categorical predictors with two (male or female) and three levels (calf, juvenile, or adult), respectively. The composition of the study population in each year is shown in Supplementary Table 1. Sexes were determined by sightings of the genital area or by the repeated association with a dependent calf (Mann and Smuts 1998). The birth years of all individuals were known and used to determine the age for each year of the study (calf: 0–4 years, juvenile: 5–10 years, adult: >10 years). This approach controlled for any transition to the next age category. Models that also included the interaction term between sex and age did not have greater explanatory power (ΔAICc < 2).

Incorporating sampling effort

Our surveys were based on opportunistic encounters of the dolphins, although we have full coverage of our core study area. This did not allow us to standardize our sampling effort among individuals. Instead, we included three sampling variables into our linear mixed models that accounted for possible effects of the sampling regime, which has been suggested to improve model coefficient values and reduce type II errors (Farine 2017). We also included *year* as a random effect to account for repeated measures. First, sampling frequency or effort can influence the number of edges

Table 1

Social contexts. Behaviors that were included in each context and the associated pathogen transmission mode

	Social context	Included behaviors	Transmission mode	Pathogen example
	Sexual contact	Mounting, rostro-genital contact, genital inspection	Sexual transmission	Papillomavirus
	Skin contact	Rubbing, petting, social play	Contact transmission	Poxvirus
	Synchronous breathing	Coordinated breathing	Aerosolized pathogen transmission (droplet contact)	Morbillivirus, *Brucella ceti*
	Social association	Spatial proximity (10 m, chain rule)		

and/or nodes that are observed in a given time period. Further, the proportion of edges sampled has been shown to affect network measures, including, for example, mean degree (Perreault 2010). The relationship between sampling effort and the proportion of edges and nodes recorded is nonlinear. That is, with increasing sampling effort, the probability of recording new edges or nodes decreases and can be modeled using a logarithmic relationship. In networks constructed using empirical data, we do not know the proportion of edges that were sampled. Nevertheless, we can account for this through the direct relationship with sampling effort. In our model, we did this by including the number of days (*obs.days.freq*) each individual was observed in each year. Second, the time interval between consecutive observation days can affect the probability of whether individuals are observed interacting with the same or different dyadic partners or have joined or left groups (Haddadi et al. 2011). Therefore, we included the mean number of days between consecutive observation days (*obs.days.dur*) for each individual and year. Third, some individuals were sampled multiple times per day. We further controlled for oversampling of certain individuals by adding the mean number of times (*obs.norm*) each individual was observed per day in a given year into our model. We used a 1-year time scale for the construction of our networks so that demographic transitions and among-year changes in social dynamics were accounted for. Based on the structure of our linear mixed model, the time scale of our degree estimates is per (sampled) day and could be aggregated across an average infectious period for a disease of interest. We assumed a logarithmic relationship between each of the three sampling variables and the response. We also scaled the sampling variables by dividing by the square root of the mean square a standard technique to standardize variables that are on different scales while not centering them. Finally, if the model was overdispersed, we added an observation level random effect ($1|obs$; Harrison 2014) to the below model. The model structure was:

$$\begin{aligned}\text{degree} = \text{sex} + \text{age} + \log(\text{obs.days.freq}) \\ + \log(\text{obs.days.dur} + 1) + \log(\text{obs.norm}) + (1|\text{year})\end{aligned} \tag{1}$$

Statistical significance testing using permutation tests

To determine whether our network data are differently structured than expected at random (Farine and Whitehead 2015), we tested our hypotheses based on null models constructed by multiple permutations of the empirical data within each year. We analyzed all behaviors separately. For each permutation, we randomly rewired all edges in each yearly network and derived node degree values for all individuals. We then reran the same GLMM as we did for the observed data. We repeated the randomizations 1000 times and calculated P-values (P_{rand}) for each fixed effect by comparing the coefficient estimate of the model for the observed data to the distribution of the coefficients for randomized data. We had three age categories and used Tukey's test followed by randomizations as described above to determine significant differences among all age categories. Because each iteration of the randomized data contained the same number of individuals and interactions as the observed data, our analysis accounted for potential significant effects resulting from different study group sizes and their interactions in a given year and behavior. We considered effects to be significant if the coefficients of the observed data fell outside the 95% range of the random coefficient distribution and calculated two-sided P-values following Farine (2017).

Social interactions across behavioral contexts and the risk of coexposure

In order to understand the risk of coexposure to multiple pathogens transmitted along different transmission routes, we investigated whether dyadic interaction frequencies of adult individuals were consistent across behavioral contexts. That is, whether pairs of individuals that were strongly connected in one network were also strongly connected in the other networks capturing different transmission routes. In order to test these edge-based hypotheses, we constructed a weighted summary network across the 5-year study period for each behavioral context. We conducted pairwise comparisons to assess the relationship between two contact networks while accounting for sex similarity effects, which is sex-assortative behavior. The edge weights represented the simple ratio interaction index (SRI) for each dyad, which is the total number of interactions relative to the number of observations of the dyad. The simple ratio index is a relative measure, which takes the number of observations of the dyad into account, and, hence, allows direct comparison of edge weights across individuals and behavioral contexts with different observation frequencies. In contrast to our degree analysis above, this avoids the need to include sampling variables to account for the sampling regime.

We then conducted a multiple regression quadratic assignment procedure (MRQAP) with double semipartialling. One contact network was the dependent matrix and the second contact network and the sex similarity matrix were the two independent matrices. The sex similarity matrix identified social contacts as occurring between two males, male and female, or two females. This allowed us to determine the association between the interaction patterns of the two contact networks while controlling for a potential effect of sex assortativity. We then transformed the weighted networks into binary networks and analyzed them with the same MRQAP procedure. Together, this elucidates whether individuals tended to interact with the same individuals (binary networks) and at similar interaction frequencies across behavioral contexts (weighted networks).

We used the same approach to determine the relationship between individual sociability and transmission risk. Fewer individuals were concurrently part of all four networks than in our pairwise comparison. Among the four behaviors, sexual contact data were sparse, in large part, because such behaviors are infrequent (Mann 2006) and, thus, were excluded from our analysis to allow for a larger sample size. A total of 94 individuals showed all three behaviors. Similar to the above, we conducted an MRQAP with the social associations as the dependent matrix and skin contact and synchronous breathing as the two independent matrices.

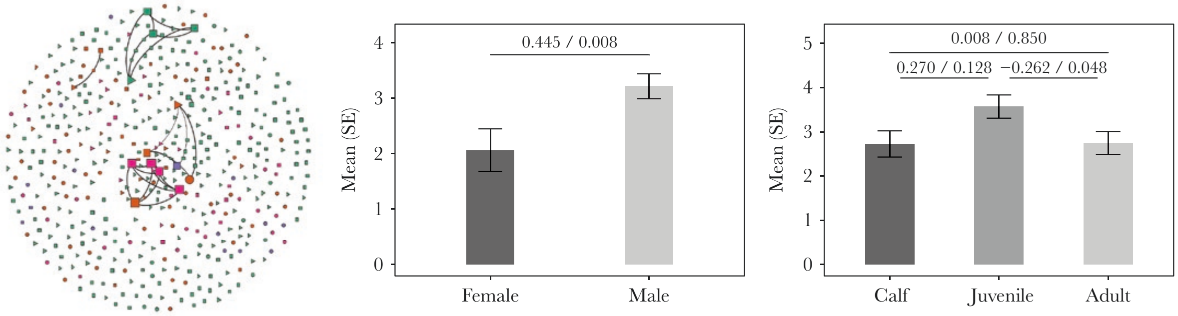
We used the R packages *igraph* (Csardi and Nepusz 2006) for social network analysis, *asnipe* (Farine 2013) for the MRQAP analysis, and the package *lme4* (Bates *et al.* 2015) for the majority of statistical modeling. We considered alpha values of 0.05 as statistically significant.

RESULTS

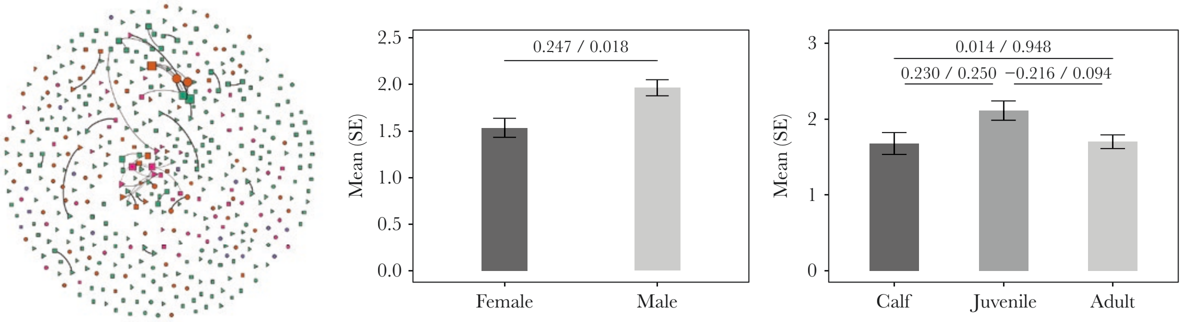
Demography-dependent transmission risks

We determined demographic effects in each of the four contact networks. Each network described a different social context (sexual contact, skin contact, synchronous breathing, and social association). In the social association network, which represented the general sociability, males were significantly more strongly connected

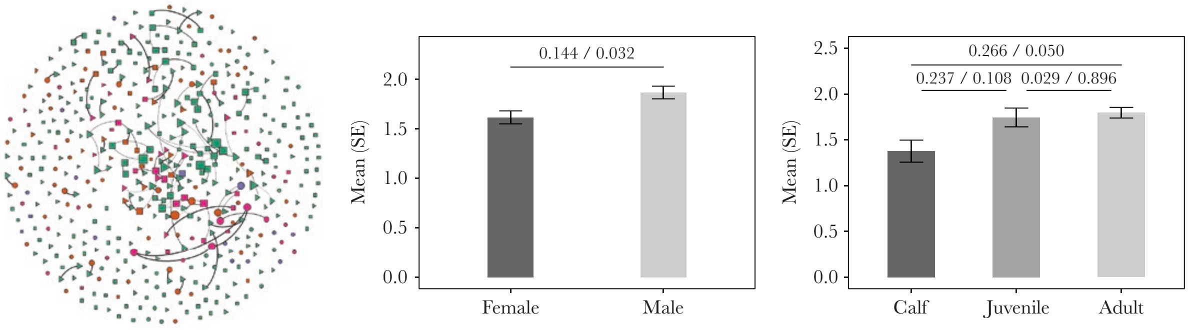
(a) Sexual contact network



(b) Skin contact network



(c) Synchronous breathing network



(d) Social association network

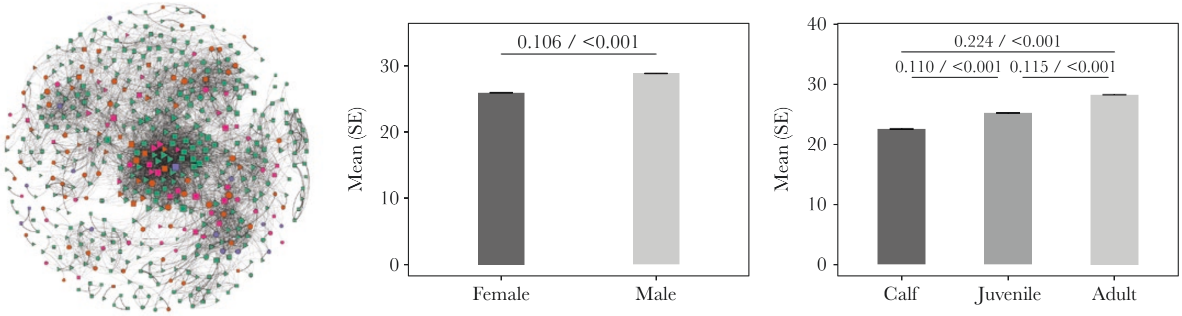


Figure 1

The network graphs show contact data in 2013 as an illustrative example. Node shape illustrates sex: square: male; triangle: female; circle: unknown. Node colors illustrate age: orange: calf; pink: juvenile; green: adult; violet: unknown. (a),(b), and (c) are disease-relevant contacts, (d) shows general sociability. The middle and right panels show the degree values (marginal mean, SE) for the demographic groups, as well as the results of the GLMM. The coefficient values of the GLMM analyzing the empirical network, separated by / and P_{rand} values of the permutation test, illustrate the statistical difference between demographic groups. Residual degrees of freedom in our models were 54, 229, 512, and 1330 from sexual contact through to social associations.

(i.e., had a higher degree) than females and connectivity significantly increased with age. All coefficient values of the GLMM analyses and P_{rand} values of the integrated permutation tests are presented in Figure 1. The other three social contexts represented three pathogen transmission routes. Similar to the baseline sociability, we found that, across all three transmission behaviors, males were also more strongly connected than females (Figure 1). Age effects were not consistent and differed across social contexts. For instance, juveniles were more strongly connected than adults in the sexual contact network and, similarly, in the skin contact network, although the latter finding was not significant ($P_{\mathrm{rand}} = 0.094$). In contrast, in the synchronous breathing network, adults and, to some extent, juveniles ($P_{\mathrm{rand}} = 0.108$) showed higher degree values than calves.

Social interactions across behavioral contexts and the risk of coexposure

For the MRQAP analysis, which uses summary networks across the 5-year period, we considered only adults because younger individuals could transition between age classes during the 5 years and because we did not find a consistent age effect across behavioral contexts in the demographic analysis described above. We also only considered adults that had been observed showing both behaviors included in the respective pairwise comparison.

Using pairwise comparisons of the summary networks, we determined that dyadic connectivity was consistent across behavioral contexts among adults. That is, dolphin dyads that engaged in one type of social behavior also likely engaged in other types. It suggests the existence of coexposure risks across several pathogen transmission routes in the bottlenose dolphin. This was the case both for weighted as well as binary networks (Table 2). We controlled for sex-assortative behavior in our analysis, which is whether edges were between two males, male and female, or two females, and did not find any significant effect of the sex similarity matrix.

Finally, we investigated the relationship between different transmission contact networks and individual sociability. We found that the skin contact network, as well as the synchronous breathing network, was significantly correlated with the association network. As before, this was the case for both weighted and binary networks. This expands the above analyses to individual sociability and illustrates that individuals that were well connected in the background sociality network (social associations) were also well connected in the pathogen transmission contact networks (Table 3). The relationship was particularly strong between the weighted synchronous breathing and social association networks, which, to some extent, may be due to both behaviors being observed more frequently than the skin contact behavior.

Table 2

Social interactions across behavioral contexts and coexposure risk in adults. We identified the relationships between networks using MRQAPs with one type of social behavior as the dependent matrix and the other social behavior type and sex similarity as the independent matrices. Significance values were calculated based on randomizations shown as P_{rand}

Dependent network	Independent network	Coefficient	P_{rand}
Weighted networks			
Sexual contact	Skin contact	0.999	**0.004**
	Sex similarity	−0.011	0.879
Sexual contact	Synchronous breathing	0.732	**0.019**
	Sex similarity	−0.050	0.470
Skin contact	Synchronous breathing	0.550	**<0.001**
	Sex similarity	0.001	0.393
Binary networks			
Sexual contact	Skin contact	0.428	**0.028**
	Sex similarity	0.017	0.868
Sexual contact	Synchronous breathing	0.419	**0.024**
	Sex similarity	−0.049	0.626
Skin contact	Synchronous breathing	0.246	**<0.001**
	Sex similarity	0.002	0.437

DISCUSSION

Demography-dependent transmission risks

Our study provides empirical evidence of divergent demographic effects on social network centrality (node degree) across four behavioral contexts. Importantly, three of the four behavioral contexts each represent a direct pathogen transmission route and the fourth reflects individual sociability. The routes include sexual transmission and contact transmission, as well as droplet transmission of aerosolized pathogens. We found differences between male and female centrality across all four contexts, with males consistently more strongly connected and, hence, more exposed. Furthermore, individual network connectivity among adults was consistent across all three distinct pathogen transmission routes, as well as the sociability network. Differences among age classes depended on the transmission route. Our results suggest demography-driven disease implications in bottlenose dolphins, with diverging effects for males and females, and transmission route-dependent effects for different age classes.

Focusing on the social association network first, males interacted with more conspecifics than females. One explanation for sex-dependent network connectivity can be derived from the social organization and sex-specific mating strategies in bottlenose dolphins (Mann et al. 2000; Connor and Krützen 2015). At Shark Bay, males form two-level social alliances with other males, usually pairs and trios on the first level and super-alliances (alliances between first-level alliances) on the second level (Connor and Krützen 2015). Male alliances compete for females and individual reproductive success is linked to alliance membership (Krützen et al. 2004; Wiszniewski et al. 2012). In contrast, female reproductive success is driven by access to ecological resources and protection of the offspring (Emlen and Oring 1977; Mann et al. 2000; Frère et al. 2010a). Consequently, females do not form comparable alliances, are more variable in their sociability, and tend to spend more time

Table 3

Relationship between sociability and exposure risks in adults. We identified the relationship using MRQAPs with the social association network as the dependent matrix and the skin contact and synchronous breathing network as the independent matrices

Dependent network	Independent network	Coefficient	P_{rand}
Weighted networks			
Social association	Skin contact	0.138	**<0.001**
	Synchronous breathing	0.975	**<0.001**
Binary networks			
Social association	Skin contact	0.512	**<0.001**
	Synchronous breathing	0.585	**<0.001**

alone, as foraging is a solitary activity (Galezo et al. 2018), or alone with their calf. Most females predominantly interact with their calf, while some females also interact with other females, including their juvenile or adult offspring (Mann et al. 2000; Frère et al. 2010b). Beyond our annual networks, that is, for periods that comprise multiple interbirth intervals, it is conceivable that female centrality may increase over time because offspring enter the population and interact with their mother and other females. In contrast, male centrality may remain stable as calves and juveniles usually avoid adult males (Stanton et al. 2011; Krzyszczyk et al. 2017). These processes could obscure the clear sex-dependent connectivity we showed in annual social association networks and highlights the importance of the study period.

Beyond the social association network, males were also more widely connected than females in the three disease-relevant contact networks. This suggests that, within dolphin groups, individuals not only associate with each other (spatial proximity) but also engage in other affiliative social behaviors. This notion is shown by our MRQAP analyses, which demonstrated that adult relationships and the relative interaction frequencies were consistent across behavioral contexts. Dolphins, like many highly gregarious mammals, establish and maintain their social bonds through tactile, as well as sexual interactions, including among same-sex individuals (Mann 2006; Kaplan and Connor 2007). Synchronous breathing is most often observed when dolphins move in the same direction (Sakai et al. 2010) and occurs mostly within groups that travel together. We suggest that it facilitates group cohesion, and may be indicative of close social bonds, similar to skin and sexual contacts. Taken together, we hypothesize that the formation of alliances in males but not females, and the formation of female–calf bonds, could explain the observed sex differences in connectivity. In particular, we suggest that the larger group size of male alliances and super-alliances compared to female–calf pairs could drive the consistently greater male network connectivity across behavioral contexts. However, we acknowledge that our hypothesis is based on group size and individual connectivity and not assortativity.

We also found an age effect in some of our networks. Juveniles and adults were connected to more individuals than calves both in the synchronous breathing and social association network. Again, we suggest that this age effect is driven by the social organization. Calves spend the majority of their time in association with their mother (Mann and Smuts 1999; Mann et al. 2000; Gibson and Mann 2008) and both adjust their dive behavior to each other's presence (Miketa et al. 2018), resulting in synchronous breathing (Mann and Smuts 1999; Sakai et al. 2010). Hence, we argue that, during both behaviors, calves of both sexes closely follow their mother's behavior, resulting in comparable and relatively low network connectivity. Then, with increasing age, and decreasing dependency on their mother, individuals, especially males (Krzyszczyk et al. 2017), expand their social network connections. Therefore, the observed age effect could be driven by the strong mother–calf bond and could indirectly reflect the sex differences discussed above.

Conversely, in the sexual and skin contact networks, juveniles were more strongly connected than adults. Bottlenose dolphins develop social relationships from an early age through tactile and sexual interactions, which could explain our findings. This is similar to many other species with a complex social organization, where offspring learn and establish social relationships early in their life (Holekamp and Smale 1991). In particular, during the juvenile period, young dolphins practice their social skills and further develop short and long-term social affiliations (Krzyszczyk et al. 2017). Practicing social skills may also result in conflict and juveniles have been shown to have the highest prevalence of new tooth-rake scarring (Lee et al. 2019). Hence, the practice period may drive the peak connectivity of juveniles in the sexual and skin contact network, followed by reduced connectivity as adults, again.

Disease implications of demographic differences

The network structure is an important driver of pathogen transmission (Sah et al. 2017, 2018), and individual infection has been shown to scale with node connectedness (Leu et al. 2010b; Rimbach et al. 2015). Furthermore, the relationship between social contact patterns and infection by directly transmitted pathogens can be modulated through variable susceptibility among individuals. For instance, demographic classes can differ in their susceptibility due to their divergent trade-off among basal organismal functions of maintenance, growth, reproduction, and immune system function (French et al. 2009), as well as due to passive maternal immunity (Kallio et al. 2006) or acquired immunity through previous exposure (Sadd and Schmid-Hempel 2006). Regarding the risk of exposure, we suggest that the contact network structures in our study population could translate to demographic effects on outbreaks of wildlife diseases. Recently reported age effects on skin disease prevalence in bottlenose dolphins (Powell et al. 2018) support this notion. In particular, due to their greater connectedness, as shown above, male bottlenose dolphins would be more exposed to becoming infected by pathogens. Importantly, the consistency of our results across all contact networks means that males would be generally at a greater risk to be exposed to pathogens that are transmitted along these different transmission routes. Concurrently, males would also play a greater role in spreading pathogens through the population. This is similar to findings in yellow-necked mice (*Apodemus flavicollis*) where males influence helminth transmission more strongly than females (Ferrari et al. 2004) and in European badgers where male connectivity across space is thought to explain the male bias in infection rates (Silk et al. 2018b). Male-biased parasite burden is a common phenomenon and has been linked to transmission relevant behavioral differences between males and females (Godfrey 2013). Beyond contact patterns, other intrinsic factors can also affect disease spread, including sex-biased transmission risk per contact, immune response, and infection period (Zuk and McKean 1996; Perkins et al. 2008). Hence, the greater exposure risk in males is particularly remarkable since susceptibility is generally heightened in males through the immune suppressive effects of testosterone (Zuk and McKean 1996; Grear et al. 2009). Nevertheless, the combined risk of exposure, which we showed here, and, by extension, the combined costs of pathogen transmission along multiple transmission routes, appears to be offset by the benefits of higher reproductive success among alliance members compared to males that are not in alliances (Krützen et al. 2004). Thus, males may compromise health to maximize reproductive success. Females and their calves, in contrast, have reduced pathogen transmission risk by interacting with fewer conspecifics.

Social interactions across behavioral contexts and the risk of coexposure

We showed that network connectivity was consistent across behavioral contexts representing pathogen transmission modes. Using binary networks, we showed that individuals tended to interact with the same conspecifics in multiple contexts. Then, the weighted networks showed that pairwise connectivity (edge weight) was comparable across behaviors. That is, pairs of individuals with strong social bonds had high interaction frequencies in all behavioral contexts. Together, this suggests the likelihood of coexposure to multiple pathogens in bottlenose dolphins. Well-connected individuals are particularly at risk to be coexposed, but they also pose a manifold transmission risk to the population.

In particular, we showed notably high MRQAP coefficients between the sexual contact and skin contact network (0.999; Table 2), as well as between the social association and synchronized breathing network (0.975; Table 3). We argue that this is driven by the functional parallels between these pairs of behaviors. Sexual and tactile contacts establish and maintain social bonds (Mann 2006; Kaplan and Connor 2007) and, indeed, tactile interactions and skin contact can be common during sexual contact. However, these behaviors are different because skin contact excludes the genital area. Nevertheless, sexual contact could represent a coexposure risk. Similarly, social associations and synchronous breathing also share functional parallels as both facilitate group movement (Sakai et al. 2010). The two parallels suggest that the paired behaviors are more likely to co-occur and, hence, to be observed together, which could contribute toward the high MRQAP coefficients. Similarly, synchrony is also important during other social interactions, such as skin and sexual contact. This could explain the large coefficient values between the contact networks of these behaviors and synchronous breathing.

In a disease context, the co-occurrence and functional parallels between pairs of behaviors suggest a high likelihood of coexposure to pathogens transmitted along those contact routes. Coexposure, in interaction with individual susceptibility, could then lead to coinfection. However, research is lacking on how individuals trade-off immunological responses to multiple pathogens and how that affects susceptibility and, ultimately, coinfection with different pathogens (Hawley and Altizer 2011). In addition to cross-immunity, infected individuals may also change their behavior and, for instance, reduce activity and interindividual contact behavior, thereby reducing exposure and, hence, transmission potential (Poulin 2018). Nevertheless, coinfections with multiple viruses have been reported in dolphins, for instance, coinfection with the herpes virus (sexual transmission) and morbillivirus (likely droplet transmission during synchronized breathing; Soto et al. 2012). Our results allow predictions of pathogen coexposure risk depending on their transmission route. For instance, they suggest a high probability of coexposure to papillomavirus (sexually transmitted; Rehtanz *et al.* 2010) and to poxvirus (transmitted through skin contact; Van Bressem et al. 1999; MRQAP coefficient 0.999) and, to a lesser extent, to morbillivirus (droplet transmission during synchronized breathing; Van Bressem et al. 2014; MRQAP coefficient 0.732). Similarly, our results suggest that individuals with high social association frequencies are more likely to become infected with respiratory diseases because they are likely to also show high frequencies of synchronized breathing with their social associates.

We did not find any effect of sex similarity in any of our network correlations. This indicates that neither males nor females showed sex-assortative interaction frequencies that were scaled to observation frequencies. This is somewhat surprising given the social alliance structure in males but not females. This could be due to the aggregation of all contacts into one 5-year summary network for each behavior. Social contact structures, including sex-assortative behavior, can vary in a seasonally dependent manner. For instance, seasonal ecological and social factors, such as the availability of resources (Spiegel et al. 2015) and mating opportunities (Leu et al. 2011), have been shown to influence social interaction frequencies and social network structure in lizards. This explanation is particularly intuitive in relation to our analysis of sexual contact behavior. Reproduction in our study population is moderately seasonal (September–January; Mann et al. 2000), suggesting that sexual interactions between males and females are also more frequent during these months as gestation is approximately 12 months (Mann et al. 2000). However, sexual contact also maintains long-term social relationships within the sexes, in particular, among males (Mann 2006; Kaplan and Connor 2007) and is possibly more frequent during the remaining part of the year. Together, the multiple functions of sexual contact behavior, beyond reproduction, could explain why we did not find any evidence for sex assortativity in sexual contact behavior. Furthermore, this explanation could also expand to all four behaviors that we observed given the strong positive relationship among them. Future work on sex-assortative behavior and, in particular, its dynamic over time would provide further insight into the complexities of bottlenose dolphin sociality.

CONCLUSION

We showed that demography influenced the social network structure in the bottlenose dolphin population at Shark Bay across four different behavioral contexts. Three of these networks were based on behaviors that represented distinct routes for directly transmitted pathogens. Basic principles of epidemiology and pathogen transmission apply both in aquatic and terrestrial environments (McCallum et al. 2004). In particular, direct transmission processes through social contacts, which we investigated in the present study, are comparable and have been successfully modeled for both environments (Murray 2009). It suggests that our findings are informative for scholars of disease dynamics beyond the aquatic environment. While we do not consider indirect transmission routes in this study, this can be studied in the future.

In our study, individuals that were well connected in the network of one behavioral context were also well connected in the other two contexts. We hypothesize that the consistently higher pathogen transmission risk among males across all transmission pathways, and among adults and, to some extent, juveniles for droplet infections through synchronous breathing behavior, is driven by the male alliance structure and the mother–calf bond. This has two important implications. First, it suggests that the divergent reproductive strategies in males and females, and, hence, sexual selection, drive the demography-dependent transmission risk for pathogens using a multitude of transmission routes. Second, when networks are structured into highly cohesive groups with fewer interactions between groups, this can result in more localized infections affecting a smaller proportion of social groups and decreasing the likelihood of a population-wide major outbreak (Sah et al. 2017). Whether the population-level social structure in bottlenose dolphins reduces disease implications on the population level remains to be investigated. Here, we focused on the individual level and also showed that highly sociable individuals are likely to be coexposed to pathogens that are transmitted along different transmission routes. Our study lacked empirical data on pathogen infections and did not allow us to investigate actual coinfection patterns. Collecting such data is rarely possible in large marine mammals, although there is promising progress in the development of new biological sampling techniques (Mann and Karniski 2017), which may provide important insights in the future. Nevertheless, our study highlights the importance of characterizing the baseline contact structure of multiple contact types in order to make predictions of potential infection spread. Furthermore, it also allows the comparison against changes in contact structure following infection and reduced health.

In the present study, we provide insights into demographic effects on disease risks across multiple pathogen transmission routes. The cost of sociality has been clearly linked to pathogen transmission (Kappeler et al. 2015). Here, we suggest that investigating pathogen transmission in a multibehavioral context could offer a more comprehensive understanding of the evolution of sociality. We argue that this is due to the probability of coinfections and the possibility of transmission route-dependent disease implications.

Finally, our study also provides important insights into the conservation of populations that experience disease outbreaks. Intervention efforts on the individual level, for example, through vaccination or removal of individuals, have been suggested to be more effective if they target highly connected individuals or individuals that connect communities (Sah et al. 2017). Our results suggest that focusing intervention efforts on adult males in our study population would yield the greatest benefit. Furthermore, we have also shown that the contact patterns in two pathogen transmission networks (skin contact and synchronous breathing) strongly correlate with the social association patterns. In wildlife species, social association patterns can be identified more readily than contact behaviors that occur less frequently. Our results highlight that social associations could be used as a proxy to deduce contact patterns that are relevant for the transmission of diseases, allowing conservationists to identify highly connected individuals more readily to assist in informed intervention efforts.

SUPPLEMENTARY MATERIAL

Supplementary data are available at Behavioral Ecology online.

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