

ESTIMATING CONTACT RATES OF HAWAIIAN MONK SEALS (*NEOMONACHUS SCHAUINSLANDI*) USING SOCIAL NETWORK ANALYSIS

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ABSTRACT: Understanding disease transmission dynamics, which are in part mediated by rates and patterns of social contact, is fundamental to predicting the likelihood, rate of spread, impacts, and mitigation of disease outbreaks in wildlife populations. Contact rates, which are important parameters required for epidemiologic models, are difficult to estimate. The endangered Hawaiian monk seal (*Neomonachus schauinslandi*) may be particularly vulnerable to morbillivirus outbreaks, due to its low abundance, lack of genetic diversity, and history of isolation from mammalian diseases. Morbillivirus epizootics have had devastating effects on other seal populations. We constructed social networks based on visual observations of individually identifiable monk seals associating onshore to estimate contact rates, assuming random mixing, and also to investigate contact patterns of different age and sex classes. Contact rates estimated from two island populations in 4 yr were remarkably similar, indicating any two individuals have about a one in 1,000 chance of making contact on any given day. Further, contact patterns within and among age and sex classes were statistically different from random. The methods we used could be broadly applied to empirically derive contact rates using association data. These rates are critical for epidemiologic modelling to simulate wildlife disease outbreaks and to inform science-based prevention and mitigation programs.

Key words: Association data, contact rates, Hawaiian monk seal, social network analysis.

INTRODUCTION

Infectious diseases are increasingly recognized as a threat to wildlife in general, and to endangered species conservation in particular (Dobson and Foufopoulos 2001; Schloegel et al. 2006; MacPhee and Greenwood 2013). Understanding disease transmission dynamics, which are in part mediated by rates and patterns of social contact, is fundamental to predicting the likelihood, rate of spread, impacts, and mitigation of disease outbreaks in wildlife populations (Craft 2015). Contact rates are singularly important parameters required for epidemiologic models, but their estimation is difficult (Anderson and May 1991; McCallum et al. 2001). Contact rates can be estimated from observed outbreak data, if available (Heide-Jorgensen and Harkonen 1992; Riley et al. 2003; Vynnycky and White 2010). An alternative is to estimate contact rates using association data from

individuals. One advantage of using social network data is that heterogeneous contact patterns (e.g., variation with sex or age) can be revealed, and these can profoundly influence disease transmission dynamics (Lloyd-Smith et al. 2005; Bansal et al. 2007).

The utility of network theory for characterizing disease transmission, coupled with the availability of accessible social network analysis software (Borgatti 2002; Csardi and Nepusz 2006; Butts 2008; Handcock et al. 2008), has facilitated the study of disease transmission. Animal association data used to populate networks include visual observation (Rushmore et al. 2014), mark-recapture (Perkins et al. 2009), radio telemetry (Cross et al. 2004; Porphyre et al. 2008), proximity-sensing telemetry (Böhm et al. 2009; Hamede et al. 2009), and the distribution of microbial genotypes among hosts (VanderWaal et al. 2014).

The Hawaiian monk seal (*Neomonachus schauinslandi*) is among the rarest of seals; approximately 1,200 individuals remain throughout the Hawaiian Archipelago, US (Carretta et al. 2014). Infectious disease is not limiting monk seal recovery (Aguirre et al. 2007). However, the species has extremely low genetic diversity (Schultz et al. 2009) and may have experienced limited exposure to mammalian diseases during millions of years of isolation in the Hawaiian Archipelago. Consequently, monk seals may be particularly vulnerable to disease outbreaks.

Morbilliviruses, specifically phocine distemper virus (PDV) and canine distemper virus, have caused mass die-offs of seals. In 1988, approximately 18,000 harbor seals, 70% of the population in Europe, died from PDV infection (Heide-Jorgensen and Harkonen 1992). A second outbreak in the North Sea in 2002 killed >20,000 harbor seals (Jensen et al. 2002). Outbreaks of canine distemper killed 5–10,000 Baikal seals (*Pusa sibirica*) in 1987–88 (Grachev et al. 1989) and 10,000 Caspian seals (*Pusa caspica*) in 2000 (Kennedy et al. 2000). Surveys for infectious disease indicate that Hawaiian monk seals have not been exposed to morbilliviruses (Aguirre et al. 2007).

The susceptibility of Hawaiian monk seals to morbilliviruses is unknown, but the devastating effects these viruses can have on phocids and the endangered status of this species demonstrate the need to prepare for an epizootic in Hawaii. Phocine distemper virus-like virus and cetacean morbillivirus have been reported in several marine mammal species in the North Pacific (Duignan et al. 2014; Van Bressemer et al. 2014).

Estimating contact rates and evaluating heterogeneity in transmission patterns are key steps toward predicting the likely trajectory of disease outbreaks, and developing effective prevention or mitigation strategies. Because there has been no observed infectious disease outbreak in Hawaiian monk seals, we developed methods to estimate contact rates from observational data. We constructed social networks based on visual observations of individually identifiable seals

associating onshore to estimate overall contact rate and investigate contact patterns among different age and sex classes.

MATERIALS AND METHODS

Association data

Hawaiian monk seals are distributed in a metapopulation consisting of many subpopulations spanning the 2,500-km-wide Hawaiian Archipelago (Ragen and Lavigne 1999). Field studies have been ongoing for most subpopulations in the remote northwestern Hawaiian Islands since the early 1980s. Monk seals forage at sea, but they frequently return to land to rest. Females also give birth and nurse their pups on land. Thus, all individuals in a population can be monitored by beach surveys (Baker et al. 2006).

Monk seals were identified using plastic flipper tags, temporary pelage bleach marks, and natural markings (Harting et al. 2004). In the past, female monk seal mortality due to conspecific male aggression was a serious concern (Hiruki et al. 1993). To understand the social behavior involved and design mitigation measures, data were collected to document individuals observed in proximity to one another (Johanos et al. 1994, 2010). These data were repurposed in this study to construct social networks.

Association data were collected by researchers walking shorelines and identifying seals on the beach and nearshore waters (Johanos 2016). For each animal encountered, the identities of the two nearest neighbors within 10 m were recorded, unless there was another seal directly between them. These data were collected for several subpopulations and years. We analyzed only the most complete data sets that met the following criteria. First, we required that all seals in a subpopulation were detected over the course of a field season, using the criteria of Baker et al. (2006). Second, we chose long field seasons with numerous surveys conducted, to maximize the opportunity to observe associations. Third, the identity of observed associating seals could not always be ascertained during every sighting, for example, if identifying marks were not always visible. To minimize such missing data, we chose data sets for which the largest proportion of seals counted during surveys could also be identified. Finally, to minimize bias in the probability of detecting pairwise seal associations, we limited analysis to surveys during which researchers had been instructed to attempt to identify every animal seen on each survey.

Social network analysis

We used the R package *statnet* (Handcock et al. 2008). In *statnet* parlance, we considered individual seals “vertices,” and an observed association between any two vertices is termed an “edge.” The number of survey days during which the same two vertices (pair of seals) were observed associating is called the “edge strength.” Using *statnet* network objects to represent monk seal associations facilitated data visualization, calculation of standard network parameters, and estimation of contact rates. Some standard network statistics were calculated, including (Hawe et al. 2004):

- 1) density—the observed number of pairwise associations, or “edges,” observed divided by the total number of possible edges (if each individual were to associate with every other individual);
- 2) degree centrality—the number of direct associations each individual has to others; and
- 3) component structure—where a component is a group of interconnected nodes for which there exists at least one path from any individual to any other individual.

Contact rates under random mixing

Vynnycky and White (2010, p. xxvii) define the contact rate (β) as the “rate at which two specific individuals come into effective contact per unit time (equivalent to the per capita rate at which two specific individuals come into contact).” Effective contact is contact that would result in disease transmission if it occurred between an infectious and a susceptible individual. Morbilliviruses are typically transmitted horizontally by the respiratory route or by contact with oral, respiratory, and ocular fluids and exudates containing the virus (Duignan et al. 2014). We assumed that when two seals were observed within 10 m of one another at any point during a day, they experienced effective contact at some time during that day. Assuming random mixing of all individuals in the population, we derived the following equation to calculate the contact rate using seal association data:

$$\beta = \frac{2A}{DN(N-1)}, \quad (1)$$

where A is the total number of associations observed, D is the number of days observed, and N is the number of individuals in the population. The numerator is the total number of associations observed, doubled to account for the fact that each association involved two seals.

Dividing by D gives the number of associations (or contacts) per day, and dividing by N gives the per capita number of contacts per day. Finally, dividing again by $N-1$ yields the rate at which two specific individuals come into contact per unit time (because an individual cannot contact itself, $N-1$ is the number of other individuals each seal could potentially contact).

Class-specific contact rates

The foregoing assumed all seals randomly encountered one another, such that a single β would apply to all individuals. To explore patterns in social behavior among various age and sex classes of seals, we also estimated class-specific β values. Based on visually assessed size and other morphologic features, monk seals were assigned a size class each year in which they were observed. Size class serves as a proxy for approximate grouped ages. Pups are young of the year, juveniles are typically 1–2 yr old, subadults are typically 3–4 yr old, and adults are ≥ 5 yr old. We examined evidence for heterogeneous contact within and between eight age and sex classes (i.e., males and females of the four size classes).

The contact rate between individuals of class i and j , β_{ij} , is:

$$\beta_{ij} = \frac{A_{ij}}{DN_i N_j}, \quad (2)$$

where A_{ij} is the number of associations that individuals of class i were observed to have with individuals of class j . Analogous to Equation 1, Equation 2 gives the rate at which a specific individual of class i encounters a specific individual of class j per unit time. In this case, dividing first by N_i and D obtains the average number of contacts an individual of class i has with individuals of class j per day. To obtain β_{ij} , we also divide by the number of individuals in class j , N_j .

Note that in this interclass-specific equation, we do not double the numerator as in Equation 1. In this case, the numerator is the total number of contacts that class i individuals have with class j individuals. By definition, only one player in these associations is type i . In contrast, in the formulation of β under random mixing, all individuals were treated as one class, so each association involved two individuals of the same class, and doubling the tally is correct. Finally, note that within-class associations (β_{ii}) are analogous to the overall random mixing β :

$$\beta_{ii} = \frac{2A_{ii}}{DN_i(N_i-1)}. \quad (3)$$

Contact rates may be density dependent or frequency dependent (McCallum et al. 2001).

Under density dependence, the expected total number of contacts an individual has per unit time is a function of the total population size or density. Under frequency dependence, the number of contacts an individual has is constant regardless of population density. Density-dependent contact is typically assumed in wildlife and plant disease models, whereas frequency dependence is often assumed for human disease (Vynnycky and White 2010). We assume density-dependent contact occurs in Hawaiian monk seals. In the context of estimating class-specific contact rates, then $\beta_{ij} = \beta_{ji}$.

We evaluated differences among class-specific contact rates using a permutation test to preserve the “clumping” of observed seal associations. The frequency distribution of unique pairings (the distribution of number of days when each possible pairing of individuals was observed associating) was randomly permuted 10,000 times across all possible seal pairs without regard to age and sex class. For each permutation, we calculated class-specific contact rates and built a distribution of rates that would be expected if the distribution of associations were random with respect to class. We compared each observed class-specific contact rate to the randomly permuted distributions. The permutation test captured the heterogeneity in association frequency among pairs, and specifically evaluated whether this heterogeneity was related to classes.

Correcting for missing identities and duplicate associations

When researchers observed two seals in association, occasionally the identity of one or both could not be obtained. Age class and sex of unidentified seals were recorded when known. Additionally, there were cases when the same two seals were recorded associating twice within a day. Failing to account for associations involving unidentified seals would negatively bias estimates of contact rates, while inclusion of duplicate associations within a day would positively bias contact rates (as the latter were defined as daily rates).

We excluded duplicate associations among identified pairs on the same day. When unidentified seals were involved, it was not possible to recognize duplicate sightings. Thus, we reduced the tally of associations involving at least one unidentified seal by the proportion of duplicates observed among associations involving fully identified seals.

Correcting the class-specific contact rates required apportioning associations (in which the size or sex of at least one seal was unknown) to specific classes for calculation of the A_{ij} values in Equation 2. Associations involving unknown size

or sex were assigned to known classes according to the proportion of class-specific associations observed among fully identified pairs of seals. For example, suppose 10 associations were observed between adults of unknown sex and subadult males. Further, suppose among the identified seals, subadult male associations with adults were composed of 60% associations with adult males and 40% with adult females. Then we would assign 6 and 4, respectively, of the associations between subadult males and adults of unknown sex to adult males and females, respectively. Having thus distributed all associations involving unidentified seals to age and sex classes, we then reduced their number, as shown earlier, by the proportion of duplicates observed among associations involving fully identified seals. These values were added to the number of class-specific associations observed among identified seals to obtain the corrected A_{ij} values (Eq. 2).

RESULTS

One monk seal association data set was superior to all others and was the primary subject of analysis. At Laysan Island in 1991, 250 seals were identified, and discovery curves indicated that the entire population was identified (Baker et al. 2006). The field season was approximately 4 mo, during which systematic surveys with recorded associations were conducted on 103 d. We documented 3,635 pairwise associations, and both seals involved were identified in 85% of these cases. Three other data sets (Laysan in 1992 and 1993, and Lisianski Island in 1992) existed for which all individuals were enumerated; however, considerably fewer surveys were conducted in those instances, and a lower proportion of associations had both seals identified (range 73–79%). These data sets were analyzed primarily to ascertain whether results were consistent with those from Laysan in 1991.

Among the four data sets examined, all measures of network connectivity increased with the number of days of observation (12–103 d; Table 1). The data set with the highest number of observation days (Laysan in 1991) had the highest density, highest mean degree centrality, and the lowest number of components. All these statistics ranked in the same order as the number of observation days.

TABLE 1. Descriptive summary statistics on social networks and contact rates (β) of Hawaiian monk seals (*Neomonachus schauinslandi*) at two locations, Laysan and Lisianski Islands, in the northwestern Hawaiian Islands, USA. Contact rates were calculated assuming random mixing among all individuals. The component rows indicate the size of components (i.e., the number of seals within them) and number of components (in parentheses). All network statistics are based upon associations in which both seals were identified. However, contact rate estimates are corrected for both duplicate associations observed the same day and associations in which one or both seals were not identified.

Variable	Laysan	Laysan	Laysan	Lisianski
Year	1991	1992	1993	1992
Number of seals	250	270	254	213
Survey days	103	91	54	12
Start date	5 April	30 March	19 April	24 May
End date	22 July	24 July	19 June	15 July
Total edges	1,898	1,175	662	229
Edges \times edge strengths	3,075	1,870	1,434	271
Density	0.061	0.033	0.021	0.010
Components	246 (1)	251 (1)	234 (1)	157 (1)
	1 (4)	1 (19)	1 (20)	3 (2)
				2 (6)
				1 (38)
Degree centrality				
Mean	15.2	8.7	5.2	2.2
Median	14	8	4	2
Minimum	0	0	0	0
Maximum	48	31	22	8
SD	8.7	6.5	4.0	1.73
β (corrected)	0.001122	0.000769	0.001097	0.001260

Contact rates were measured per unit time, and therefore they should not be sensitive to the number of observation days. Consistent with this, the contact rates (assuming random mixing) estimated for the four data sets were remarkably similar, although they were collected in different years and in two different island populations (Table 1). The coefficient of variation among the four estimates was 0.20.

Most associating pairs of seals were only observed together on one or a few occasions. For the most complete (Laysan in 1991) data set, pairs were seen together on as many as 41 d. However, 82% of pairings occurred only once, and 98% occurred fewer than five times. Of 35 cases in which pairings were observed five or more times, 32 involved adult females associating with pups. The remaining three cases involved a pair of weaned pups, an adult male and adult female, and an adult female

and subadult male. Similar patterns were consistently observed among all data sets.

Estimates of class-specific contact rates indicated that seals do not mix randomly; rather, some age-sex groups tend to associate more or less with their own class or with others (Table 2). Permutation tests demonstrated that many of the observed contact rates were statistically significantly different from random mixing, with some age-sex classes interacting more, and some less, than would be expected (Fig. 1). The permutation tests were necessarily restricted to the subset of associations in which the identity of both seals was known. As such, the contact rates examined using the permutation tests were not corrected for associations in which one or both seals were not identified (as was the case in Table 2). These corrections increased the calculated contact rates but resulted in very minor changes in the relative magnitude of class-specific rates. For example, the correla-

TABLE 2. Matrix of estimated age and sex class-specific contact rates (β_{ij}) of Hawaiian monk seals (*Neomonachus schauinslandi*) at Laysan Island in 1991. Values indicate the daily rate at which a specific individual of class i associates with a specific individual of class j . Because we assume density-dependent mixing, $\beta_{ij} = \beta_{ji}$, only the upper triangle of the matrix is shown. Column and row headings indicate the age-sex classes (A = adult, S = subadult, J = juvenile, P = pup; F = female, M = male). Values are corrected for associations where one or both seals were not identified and for estimated duplicate associations recorded on the same day.

	AF	AM	SF	SM	JF	JM	PF	PM
AF	0.0005899	0.0012386	0.0007888	0.0013023	0.0006123	0.0005343	0.0033783	0.0040921
AM		0.0008408	0.0008181	0.0010579	0.0006608	0.0007345	0.0003611	0.0002068
SF			0.0004810	0.0019775	0.0012097	0.0015938	0.0006439	0.0007183
SM				0.0037691	0.0014576	0.0015328	0.0009854	0.0007004
JF					0.0006984	0.0011458	0.0003748	0.0004326
JM						0.0011734	0.0006055	0.0007392
PF							0.0042627	0.0026343
PM								0.0014702

tion coefficient (r) for corrected and uncorrected contact rates at Laysan in 1991 was 0.99. As noted previously, in 85% of associations at Laysan in 1991, both seals were identified. Because higher proportions of unidentified seal associations and less observation effort occurred in the other data sets, class-specific contact rates were likely more uncertain than at Laysan in 1991. Nevertheless, the ranks of class-specific contact rates estimated from associations where both seals were identified were highly correlated among all data sets (Table 3). Correlations among the actual estimates (as opposed to ranks) were more variable (Table 3), largely due to an unusually large contact rate estimate among subadult males associating with each other at Laysan in 1993. These results suggest the association patterns observed among age-sex classes were consistent over time and at both islands. Degree-centrality statistics further revealed differences among the age-sex classes (Table 4).

DISCUSSION

Our estimates of Hawaiian monk seal contact rates will be used in epidemiologic models to inform disease outbreak prevention and response plans. Moreover, the social network analysis results and estimates of contact rates are largely consistent with

qualitative impressions of Hawaiian monk seal social behavior. Monk seals are not highly gregarious, nor are they thigmotactic, and they do not form dense aggregations onshore as do some pinnipeds. Rather, they tend to rest singly or in small groups. Further, monk seals are sedentary on land and often spend hours resting in the same area. Social network patterns, accordingly, indicate that individual seals tend to associate with a small proportion of the total population. In the most thoroughly observed population, seals only associated with an average of 15 others in a population of 250, over 103 d. Network density was only 0.06 for this data set. Estimated contact rates among all four data sets examined (Table 1) suggest that any two individuals had about a one in 1,000 chance of making contact on any day.

Despite the low network density, the social network component structure revealed that essentially the entire population was interconnected. In the Laysan 1991 population, there was one large component consisting of 246 individuals, and four components of one individual. The four individuals included an adult seen only once when dead, and three pups that died at a young age or were born late in the observation period. These pups were all seen in association with mothers, but only incidentally, not during one of the systematic surveys from which the social network was constructed. The fact that a

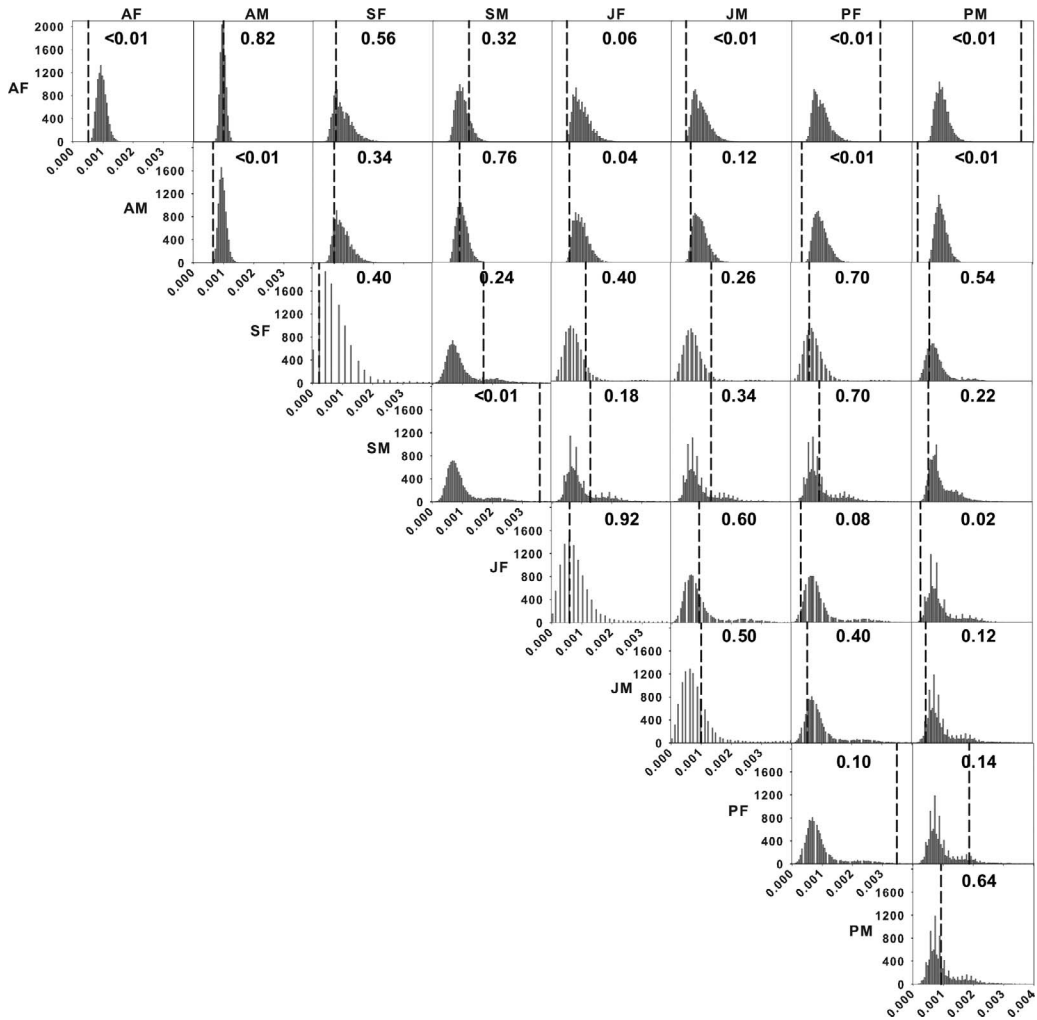


FIGURE 1. Distribution (bars) of 10,000 randomly permuted contact rates of Hawaiian monk seals (*Neomonachus schauinslandi*) at Laysan Island, Hawaii, USA, in 1991, assuming random mixing with regard to age and sex class. Headings indicate the age-sex classes (A=adult, S=subadult, J=juvenile, P=pup; F=female, M=male). The vertical dashed line spanning the height of each plot indicates observed contact rates among and within classes, calculated using only observed associations wherein both seals were identified (thus they differ from values reported in Table 2). Values indicate the two-tailed *P*-values of the observed contact rates based upon percentiles of the random distributions.

contact pathway existed between any two individuals in the population has implications for disease spread. We must anticipate that a pathogen introduced to a susceptible monk seal population has the potential to infect every individual. Note that the other data sets yielded less connected networks with more isolated seals; however, this was almost certainly because the number of survey days was lower (Table 1).

TABLE 3. Correlation coefficients (*r*) of age and sex class-specific contact rates for Hawaiian monk seals (*Neomonachus schauinslandi*) estimated from four data sets: Laysan Island in 1991, 1992, and 1993, and Lisianski Island in 1992. Standard and rank correlation coefficients are shown, the latter in parentheses.

	Laysan 1992	Laysan 1993	Lisianski 1992
Laysan 1991	0.93 (0.91)	0.61 (0.85)	0.84 (0.75)
Laysan 1992		0.83 (0.97)	0.66 (0.74)
Laysan 1993			0.18 (0.68)

TABLE 4. Summary degree centrality statistics by age and sex class for Hawaiian monk seals (*Neomonachus schauinslandi*) at Laysan Island, Hawaii, USA, in 1991, showing mean, SD, and minimum and maximum number of individuals with which each seal was observed associating. *N* is the number of individuals in each age and sex class in the population.

Age class	Sex	Mean	SD	Minimum	Maximum	<i>N</i>
Adult	Female	14.5	7.3	0	31	73
	Male	15.4	8.7	1	48	89
Subadult	Female	17.3	10.2	1	32	10
	Male	24.2	10.6	7	47	20
Juvenile	Female	13.8	6.6	6	27	12
	Male	14.9	10.2	2	30	13
Pup	Female	13.1	6.7	0	22	13
	Male	9.3	6.0	0	22	20

Estimates of contact rates from association data are credible inasmuch as they derive from observed behavior. Nevertheless, converting associations into effective contact for disease transmission may result in positive or negative bias owing to assumptions about the representativeness of observations and the transmissibility of pathogens. Our analysis was primarily motivated by the need to assess the potential spread of a morbillivirus, which is known for high transmissibility through respiratory or physical contact routes (Appel et al. 1981). We therefore assumed that any two seals observed within 10 m of one another at any time during a day would have effective contact at some point during that day. This may have positively biased estimated contact rates if some associating seals remained sufficiently far apart throughout the day that the typical respiratory route of transmission could not occur. The annual cycle of birth, nursing, estrus, mate competition, and mating in Hawaiian monk seals is asynchronous compared to many pinnipeds, but most of these activities (some of which clearly result in elevated associations) occur in spring and summer. Our association data were collected during these seasons (Table 1), which could also positively bias our estimated contact rates.

Several other considerations would tend to lead to negative bias in our estimation of contact rates. Seal associations were recorded just once daily as observers walked by. As

noted previously, Hawaiian monk seals tend to be sedentary on land, such that a daily instantaneous record might capture a large portion of associations. Nevertheless, some proportion of shorter-term associations was undoubtedly missed. Similarly, all observations occurred on land, and we assumed there was no effective contact at sea. This is reasonable because monk seals are solitary foragers, although they have been recorded socializing in the water (Parrish et al. 2000). Much of the social interaction likely occurs underwater when seals are holding their breath. This would naturally limit respiratory transmission, yet it seems likely that at least some effective contact occurs at sea. For example, monk seals mate in the water (Johanos et al. 1994). These considerations suggest that our estimates of contact rates should be considered provisional. Still, they represent a viable reference for exploring potential disease spread in this species.

Contact patterns varied significantly among age and sex groups. One pattern revealed in Figure 1 was well known prior to the analysis—adult females and pups have a high association rate. Monk seal mothers fast and remain nursing and protecting their pups for 5–7 wk after birth (Johanos et al. 1994). Upon weaning, mothers break this strong association. While this finding was trivial, other patterns revealed aspects of Hawaiian monk seal social behavior that were not previously apparent and may be important for predicting

and mitigating spread of disease. Departures from random mixing between age and sex classes are difficult to interpret. An admixture of unilateral or mutual attraction, avoidance, aggression, or indifference could explain both higher and lower contact rates than would be expected under random mixing. Thus, definitive conclusions about what drives these association patterns are elusive, yet some informed speculation is possible given existing knowledge of the species mating system and other social behavior.

Adult females clearly showed an affinity for the pups they were nursing, but they seemed to strongly avoid one another. The monk seal mating system is likely characterized by promiscuity (Stirling 1983), estrus is not synchronized among females, and adult males compete to attend females near estrus on the beach and in the water where they mate (Johanos et al. 1994, 2010). Interestingly, the contact rate between adult males and females, representing males of all ranks and females in various points in their reproductive cycle, was very near that expected under random mixing (Fig. 1). Adult male monk seals “cruise” shorelines and briefly inspect and sometimes interact with seals resting on the beach. This often involves close interactions likely to constitute effective contact. While some of these events were recorded during surveys, because of their brief nature, many were undoubtedly not observed, representing another source of potential negative bias in estimated contact rates.

Subadult males emerged as a remarkably social group. Their observed contact rates among themselves and other seal classes exceeded the mode of the expected distribution in six of eight cases (Fig. 1). Further, they were involved in five of the top 10 highest observed contact rates within and among age and sex classes (Table 2). We suspect that this elevated sociality reflects that male reproductive success in this species depends on social skills in terms of competition with other males and gaining access to females. Subadult males are approaching social reproductive maturity and likely devote more time and energy to social interaction than do other age and sex

classes. Contact rates of subadult males with one another were on par with that between adult females and pups (Table 2). Finally, the average degree centrality of subadult males was the highest of any class (Table 4).

Whatever the reasons for the patterns observed, it is clear that monk seals exhibit heterogeneous contact patterns with respect to age and sex. Our approach for evaluating statistically significant differences among groups could be applied in other species whenever association data with group information are available. Whether the statistical departures from random mixing are sufficient to greatly influence the spread of a pathogen through the population would be best determined through epidemiologic modelling. Variables such as the age and sex of the first infected individual, and conditions such as the age-sex structure of the vulnerable population would modulate the impact of class-specific contact rates.

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