

# Vulnerability of a killer whale social network to disease outbreaks<sup>†</sup>

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## ABSTRACT

Emerging infectious diseases are among the main threats to conservation of biodiversity. A crucial task facing epidemiologists is to predict the vulnerability of populations of endangered animals to disease outbreaks. In this context, the network structure of social interactions within animal populations may affect disease spreading. Using network theory, we show that the social structure of an endangered population of mammal-eating killer whales is vulnerable to disease outbreaks. This feature was found to be a consequence of the combined effects of the topology and strength of social links among individuals. Our results uncover a serious challenge for conservation of the species and its ecosystem. In addition, this study shows that network approach can be useful to study dynamical processes in very small networks.

*Keywords: Orcinus, epidemics, small networks, sociality, transients, weighted networks.*

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## INTRODUCTION

Emerging infectious diseases are among the main threats to endangered populations and ecosystems<sup>1,2</sup>. Disease outbreaks are likely to promote ecological replacement between species<sup>3</sup>, cause local extinction of animal and plant populations, and affect the global survival of some species such as the thylacine (*Thylacinus cynocephalus*)<sup>1,4</sup>. In this context, a particular problem for conservation strategies is that an epidemic only becomes apparent after it has reached extreme levels<sup>4</sup>. Therefore, predicting the vulnerability of populations to epizootics can help to prevent the local extinction of endangered populations<sup>1</sup>.

In social mammals, disease dynamics is affected by patterns of contact among individuals<sup>5</sup>. Recently, studies focusing on human populations showed that by using a network theory framework we can infer the consequences of social structure on disease dynamics<sup>6-8</sup>. The structure of this network of contacts can influence the emergence of epidemics and therefore the viability of these populations. In spite of the importance of network structure for disease

1 dynamics in human societies, no previous study investigates the implications of this structure to  
2 disease outbreaks in animal populations. In this context, animal populations of endangered  
3 mammals provide a challenge to network approach, since these populations are often very small  
4 and how to investigate small networks has been pointed as one of the leading questions in  
5 network research<sup>9</sup>

6 Here, we used a network approach<sup>10,11</sup> to characterize the complex social organization of the  
7 endangered mammal-eating killer whales<sup>12</sup> and infer their vulnerability to disease epidemics.  
8 Mammal-eating killer whales prey upon marine mammals, and can potentially affect the structure  
9 of the coastal ecological community<sup>12,13</sup>. Currently, the recorded population of mammal-eating  
10 killer whales is in the low hundreds of individuals<sup>14</sup>. Levels of polychlorinated biphenyls (PCBs)  
11 in these whales are threateningly high<sup>15</sup> and they are exposed to a wide variety of pathogens<sup>16</sup>.  
12 We studied the vulnerability of a population of mammal-eating killer whales to epidemics using a  
13 generalized disease dynamic model to investigate if the killer whale social network is vulnerable  
14 to disease outbreaks and to understand the structural basis of the recorded vulnerability.

## 17 MATERIALS AND METHODS

### 19 Data collection

20 Our study is based on systematic observations of social interactions among killer whales  
21 around the southern tip of Vancouver Island, British Columbia, Canada and in adjacent areas of  
22 Washington State, U.S.A., from 1984 through 1996. Most (approximately 90%) of the encounters  
23 took place with good sighting conditions, and encounters were distributed both near shore and  
24 offshore throughout the study area, thus we believe that there should be no strong bias for  
25 sighting larger groups<sup>12</sup>. Individuals were identified photographically and (or) visually based on  
26 distinctive acquired and congenital characteristics of the dorsal fin and the saddle patch (a lightly  
27 pigmented area at the base of the dorsal fin). Only those encounters where all members of a  
28 group were identified were used in the analyses.

29 A total of about 170 individually identified mammal-eating killer whales were recorded  
30 throughout British Columbia and Washington state since the 70s<sup>12</sup> and new adult individuals are  
31 still occasionally documented. We recorded the social interactions of 58 individuals, but, among  
32 then, 15 are members of groups that spend most of their time outside of our study area and during  
33 our sampling did not interact with individuals of the population studied. Therefore, we removed  
34 these individuals from the analyses. Our sample contains the social interactions of 43 mammal-  
35 eating killer whales, representing approximately 25% of the total identified population. Ideally,  
36 all individuals and social interactions in a network should be recorded. We assume that the  
37 sampled network is a good approximation of the real network<sup>11</sup>. Additional details of the dataset  
38 and sampling methods have been previously presented<sup>12</sup>.

### 40 Killer whale social network

41 Mammal-eating killer whales are one of the reproductively isolated forms of killer whales  
42 (*Orcinus orca*) that live along the Pacific coast of North America<sup>12,14</sup>. In the killer whale social  
43 network, individuals are represented by nodes and two individuals are connected by a link if they  
44 were recorded at least once in the same group, a “group” being defined as all whales acting in a  
45 coordinated manner (e.g., all travelling in the same direction at the same speed, often surfacing  
46 within 5–10 s of each other) and within visual range of the observers<sup>17</sup>.

1 In this form, groups are usually small, containing an average of four individuals<sup>17</sup>. Some  
 2 individuals are often observed together, such as adult females and their first-born males<sup>12, 18</sup>.  
 3 However, males and females without offspring temporarily associate with different groups<sup>12, 18</sup>,  
 4 and groups often aggregate to hunt large marine mammals and perform social activities<sup>17</sup>,  
 5 leading to a complex social organization. To describe this variation in the strength of social  
 6 interactions, we use the amount of time two individuals are observed together in a group. We  
 7 quantify the temporal stability of the social interaction using the half-weight association index<sup>19</sup>,  
 8<sup>20</sup>, defined as  $w_{ij} = 2r_{ij} / (r_i + r_j)$ , in which  $w_{ij}$  is the value of half-weight association for killer  
 9 whales  $i$  and  $j$ ,  $r_{ij}$  is the number of times that killer whales  $i$  and  $j$  were recorded together, and  $r_i$   
 10 and  $r_j$  are the number of times that killer whale  $i$  and  $j$  were sampled, respectively. Therefore,  
 11 this index scales from 0 (two individuals never recorded together) to 1 (two individuals always  
 12 recorded together). Although this index may be affected by sampling, we believe that long-term  
 13 duration of fieldwork (10 years) allows an adequate characterization of social networks patterns.  
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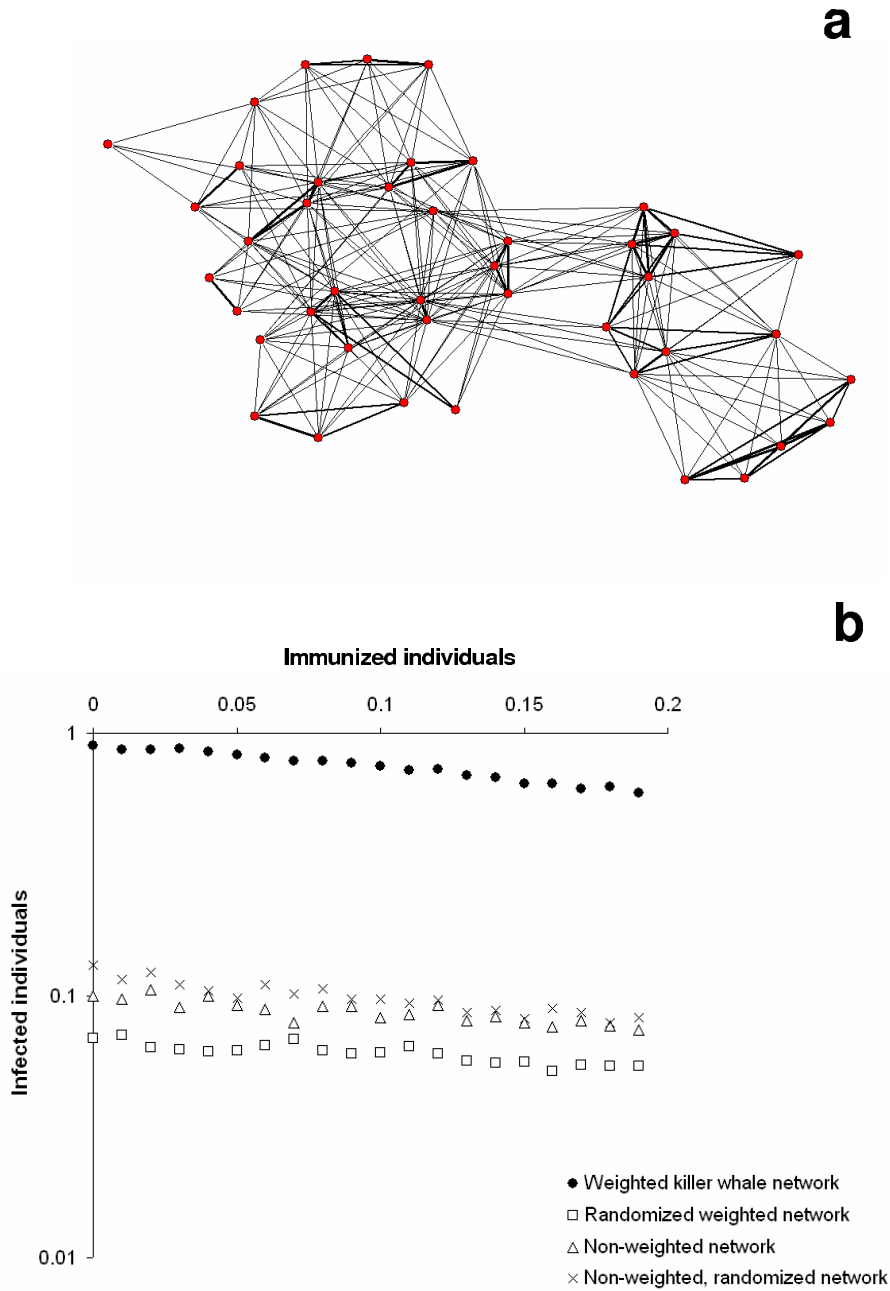
### 15 **Disease simulations**

16 Our simulations are not associated with any specific disease in order to maintain the  
 17 generality of our results. We model the dynamics of disease spread in the killer whale network  
 18 using the classical susceptible-infected (SI) model<sup>21</sup>, but have incorporated a fraction  $f$  of  
 19 individuals that is naturally non-susceptible to the disease. Therefore, our simulations explore  
 20 scenarios in which a disease may affect only a small part of the population ( $f \rightarrow 1$ ) to scenarios  
 21 in which the entire population is vulnerable ( $f \rightarrow 0$ ).

22 In the initial condition of our model there is a single, infected individual. The initial  
 23 condition and stochastic fluctuations may profoundly affect processes occurring in small  
 24 networks<sup>22</sup>, such as the killer whale network studied here ( $n = 43$  individuals). To circumvent this  
 25 problem we perform an intensive set of simulations. For a given fraction  $f$  of non-susceptible  
 26 individuals, we perform 50 simulations using a given individual  $i$  as the first infected individual.  
 27 We repeat this procedure until all individuals are used as the first infected individual.

28 At the each time step, (1) disease spreads with probability equal to their half-weight index of  
 29 association from an infected individual  $i$  to all healthy and susceptible animals that directly  
 30 interact with it; (2) the individual  $i$  becomes non-infective, simulating death or the end of the  
 31 infective period. The simulation stops when no healthy and susceptible animal is infected in a  
 32 given time step. Then, the final number of infected animals (including infective and non-  
 33 infective) is recorded.

34 To understand the basis of the observed vulnerability, we perform similar sets of simulations  
 35 in networks in which (1) interactions were randomly distributed among individuals (controlling  
 36 for the effects of the observed patterns of interactions); (2) interactions were assumed to be  
 37 equivalent and the probability of a healthy and susceptible animal be infected were  $1/k$ , in which  
 38  $k$  is the number of individuals that interact with the infected animal (controlling for the effects of  
 39 the interaction weight); (3) assuming both (1) and (2), such as in classical epidemiological  
 40 models<sup>7, 8, 23, 24</sup>, controlling for both the patterns of interactions and the interaction weight.  
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 3 **Figure 1.** The structure and vulnerability of the social network of mammal-eating killer whales. (a) The social  
 4 network in which the width of links is proportional to the weight or strength of social interaction ( $w_{ij}$ ), quantified  
 5 using the half-weight index of association. (b) The average proportion of infected individuals after simulation of  
 6 disease spreading ( $n = 2150$  simulations, 50 replicates assuming that a given individual is the first infected  
 7 individual). Simulations were performed using different fractions of non-susceptible individuals and four different  
 8 scenarios: (1) the real weighted social network, (2) the network in which interactions are randomized among  
 9 individuals (preserving the weight of interactions), (3) the network in which all links have the same weight  
 10 (preserving the topology), and (4) a random network assuming that all links have the same weight (as in classical  
 11 epidemiological models). (see text for further details).  
 12

## 1 RESULTS

2  
3 In a network with  $n = 43$  individuals such as in this killer whale network, the maximum  
4 possible number of interactions is  $n(n-1)/2 = 903$ . We recorded 253 interactions among 43  
5 individuals, totalizing 28% of possible interactions, leading to  $11.8 \pm 4.8$  interactions per  
6 individual, mean  $\pm$  SD. The observed interactions usually had, on average, an intermediary  
7 weight ( $\bar{w}_{ij} = 0.40 \pm 0.39$ ), but 17 pairs of individuals show maximum weight ( $w=1$ ), indicating  
8 long-term interaction between individuals. On average,  $2.06 \pm 0.85$  interactions separate two  
9 randomly selected individuals, indicating that there is a small path connecting any pair of  
10 individuals.

11 We found that the killer whale social network (Fig.1a) showed a strong potential for the  
12 emergence disease outbreaks. In simulations assuming that all individuals are susceptible to the  
13 simulated diseases, up to 90% of individuals were infected (Fig. 1b). The fraction of individuals  
14 infected is higher than 50% even if the 20% of individuals are immune to the disease (Figure 1b).  
15 The strong vulnerability observed in real networks was almost ten times higher than observed in  
16 disease simulations performed in the three network models (Figure 1b).

## 17 18 19 DISCUSSION

20  
21 Our study describes for the first time the vulnerability of an animal social network to disease  
22 dynamics; we show that the population of mammal-eating killer whales analyzed here is  
23 vulnerable to disease outbreaks. Our results suggest that a large fraction of the killer whale  
24 population studied may be affected by a disease spreading through the social interactions between  
25 individuals. The failure of theoretical networks to lead to similar patterns of disease dynamics  
26 suggests that the observed vulnerability is a consequence of the combined effects of both the  
27 topology (i.e., the distribution) and the interaction strength of social links in killer whales.  
28 Therefore, even for small populations as the studied here, classical epidemiological models that  
29 assume that two randomly selected individuals have a constant probability of interact and that all  
30 social interactions are equivalent are not adequate<sup>25</sup>. Previous studies demonstrate that topology  
31 may contain information of the build-up of small networks<sup>22</sup>. Here, we contribute to the  
32 development of one of central themes of network theory, the study of small networks<sup>9</sup>, by  
33 showing that aspects of network structure (topology and interaction strength) affect dynamic  
34 processes such as diseases spreading in small networks.

35 In the context of the conservation of mammal-eating killer whales, our study suggests even  
36 endangered species in which individuals live in seemingly small and isolated groups, interacting  
37 with a few individuals, may be threatened to disease outbreaks that may affect almost the entire  
38 population. It is important to note that in natural conditions the disease transmission is probably  
39 compensated by the benefits derived from social interactions, such as hunting efficiency<sup>17</sup> and  
40 food share<sup>26</sup>. However, the same may not be true in reduced populations in which the immunity  
41 of individuals is already challenged by contaminant loads<sup>15</sup>, or facing recently introduced  
42 pathogens<sup>1</sup>.

43 The observed deviation between the predictions of classical epidemiological models and our  
44 simulations suggests that the development of new monitoring and prevention policies are pivotal  
45 to the conservation and management of killer whales. These policies should be associated with  
46 the identification of potentially dangerous pathogens<sup>16</sup> and to the continuous monitoring of

1 health conditions of individuals in order to detect epidemics at early stages. Previous studies  
 2 focusing on the spread of disease in human social networks propose that biased policies toward  
 3 certain groups of individuals may be more efficient to control disease outbreaks<sup>27-29</sup>. In mammal-  
 4 eating killer whales, our results suggest that individuals that show strong interactions with a  
 5 number of individuals are likely to be the most important to the observed epizootic dynamics.  
 6 Thus, special attention should be devoted to mature females, since they are likely to associate  
 7 with a number of individuals and establish long-term interactions with their offspring, even after  
 8 the individuals disperse from the original group<sup>12</sup>.

9 We emphasize that the approach described here may help to provide new insight into the  
 10 vulnerability of other social mammals. Because of the importance of top predators such as  
 11 mammal-eating killer whales to the long-term maintenance of ecological communities<sup>13, 30, 31</sup>, we  
 12 suggest that future studies should focus social, endangered top predators that are likely to be  
 13 threatened by epizootics, such as lions (*Panthera leo*), African wild dogs (*Lycaon pictus*) and  
 14 hyenas (*Crocuta crocuta*)<sup>32</sup>.

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