Vulnerability of a killer whale social network to disease outbreaks

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Emerging infectious diseases are among the main threats to conservation of biological diversity. 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. However, endangered animal populations are often small and to investigate the dynamics of small networks is a difficult task. 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 the network approach can be useful to study dynamical processes in very small networks.

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INTRODUCTION

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

In social mammals, disease dynamics is affected by patterns of contact among individuals [5]. 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 [6–8]. 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 dynamics in human societies, no previous study investigates the implications of this structure to disease outbreaks in animal populations. In this context, animal populations of endangered mammals provide a challenge to network approach, since these populations are often very small and how to investigate small networks has been pointed out as one of the leading questions in network research [9].

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

DATA COLLECTION

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

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A total of about 170 individually identified mammal-eating killer whales were recorded throughout British Columbia and Washington state since the 1970s [12] and new adult individuals are still occasionally documented. We recorded the social interactions of 58 individuals, but among them, 15 are members of groups that spend most of their time outside of our study area and during our sampling did not directly interact with individuals of the population studied. Those individuals are treated as possible sources of fluctuations in parameters used in our simulations of disease spreading. Our sample contains the social interactions of 43 mammal-eating killer whales, representing approximately 25% of the total identified population. Ideally, all individuals and social interactions in a network should be recorded. We assume that the sampled network is a good approximation of the real network [11]. Additional details of the data set and sampling methods have been previously presented [12].

KILLER WHALE SOCIAL NETWORK

Mammal-eating killer whales are one of the reproductively isolated forms of killer whales (*Orcinus orca*) that live along the Pacific coast of North America [12,14]. In the killer whale social network, individuals are represented by nodes and two individuals are connected by a link if they were recorded at least once in the same group, a "group" being defined as all whales acting in a coordinated manner (e.g., all traveling in the same direction at the same speed, often surfacing within 5–10 s of each other) and within visual range of the observers [17]. To characterize network topology, we described basic structural aspects of killer whale social network11 [11,18], including degree (number of links per node), average path length (the average number of links between two individuals), and the node's clustering coefficient C_i, defined as $C_i=2E_i/k_i(k_i-1)$, in which the k is the number of links that individual i have, $k(k-1)/2$ is the maximum number of links between the individuals that are linked to individual i (the neighbors of individual i), and E is the number of links between the neighbors of individual i actually recorded. Therefore, C_i varies from zero if the individual is not part of a cohesive group to one if the individual is part of a highly cohesive group.

In this form of killer whale, groups are usually small, containing an average of four individuals [17]. Some individuals are often observed together, such as adult females and their first-born males [12,19]. However, males and females without offspring temporarily associate with different groups [12,19], and groups often aggregate to hunt large marine mammals and perform social activities [17], leading to a complex social organization. To describe this variation in the strength of social interactions, we use the amount of time two individuals are observed together in a group. We quantify the temporal stability of the social interaction using the half-weight association index [20,21], defined as $w_{ij}=2r_{ij}/(r_i+r_j)$, in which w_{ij} is the value of half-weight association for killer whales i and j, r_{ij} is the number of times that killer whales i and j were recorded together, and r_i and r_j are the number of times that killer whale i and j were sampled, respectively. Therefore, this index scales from 0 (two individuals never recorded together) to 1 (two individuals always recorded together). Although this index may be affected by sampling, we believe that long-term duration of fieldwork (ten years) allows for an adequate characterization of disease spreading on the killer whale social network.

Disease simulations

We model the dynamics of disease spreading in the killer whale network using the susceptible-infected (SI) model [22], and include a factor f representing the fraction of individuals that is naturally nonsusceptible to the disease. One can also think of this problem as a site-bond percolation problem [23–25], where site dilution q relates to the fraction f of nonsusceptible individuals and bond dilution p to the probability for not transmitting the disease to nearest neighbors. Therefore, our simulations explore scenarios in which a disease may affect only a small part of the population ($f\rightarrow 1$) and others in which the entire population is vulnerable ($f\rightarrow 0$).

We start the spreading process from a single seed. For a given fraction f of nonsusceptible individuals, we perform extensive simulations as follows: at each time step, (1) disease spreads from an infected individual i to all healthy and susceptible animals j that directly interact with it with probability p equal to the half-weight index of association w_{ij}; (2) the individual i becomes noninfective, simulating death or the end of the infective period. The simulation stops at the time step t_{max} when all healthy and susceptible animals are infected or the disease spread is over. We count the number of individuals infected up to time t_{max}.

To understand the structural basis of the observed vulnerability, we perform similar sets of simulations in networks in which (1) links were randomly distributed among individuals (controlling for the effects of the observed distribution of links among individuals); (2) links were assumed to be equivalent and the probability of a healthy and susceptible animal be infected were $1/k$, in which k is the number of individuals that interact with the infected animal (controlling for the effects of the interaction weight); (3) assuming both (1) and (2), such as in classical epidemiological models [6–8,26] and therefore controlling for both observed distribution of links and interaction weight).

RESULTS

The killer whale network has a core of 43 individuals, resulting on a maximum possible number of $n(n-1)/2=903$ links. We recorded $L=253$ links representing 28% of all possible links, leading to an average of 12 links per individual $\langle k\rangle=11.77\pm4.75$ (mean $\pm$ standard deviation). The minimum number of links recorded for an individual was $k=4$, whereas the two more connected individuals interact with more than 50% of individuals ($k=23$). The probability that a random network with the same number of individuals and links as that of the killer whale network has at least an individual with 23 links is very small [$<10^{-3}$, predicted using binomial distribution with parameters n and $2L/n(n-1)$]. Therefore, random links among individuals did not repro-

duce the existence of highly connected individuals as observed in a killer whale network. The observed interactions usually had, on average, an intermediary weight ($\bar{w}_{ij}$ $=0.40\pm0.39$), but 17 pairs of individuals show maximum weight ($w=1$), indicating long-term interaction between individuals. On average 2 links separate two randomly selected individuals, indicating that there is a small path p connecting any pair of individuals ($p=2.06\pm0.85$). In fact, the largest recorded path between two individuals was 4 links. The average clustering coefficient of the killer whale network, $\langle C\rangle$ $=0.32\pm0.07$, was not different from expected for a random network with the same number of nodes and links $\langle C_R\rangle$ $=2L/n(n-1)=0.28$. However, this is a result of the masquerading effect of five individuals that show very small clustering ($\langle\langle C_i\rangle=0.17$). The majority of individuals (32 individuals, 88.3%) are part of cohesive groups ($C_i>C_R$), whereas in a random network, we should expect that 50% of the individuals will show ($C_i>C_R$). The probability that a random network with the same number of individuals and links as that of the killer whale network has at least 32 individuals with $C_i>C_R$ is very small ($<10^{-6}$, predicted using binomial distribution with parameters n and 0.5). Therefore, the killer whale network shows small-world properties, combining small path length and high clustering [18].

We found that the killer whale social network [Fig. 1(a)] showed a strong potential for the emergence disease outbreaks. In simulations assuming that all individuals are susceptible to the simulated diseases, up to 90% of individuals were infected [Fig. 1(b)]. The fraction of individuals infected is higher than 50% even if the 20% of individuals are immune to the disease [Fig. 1(b)]. The strong vulnerability observed in real networks was higher than observed in disease simulations performed in the three network models, especially in the models in which interactions are equivalent [Fig. 1(b)]. Thus, our results support the relevance of the interplay between topology and dynamics of social interaction for the spreading of infectious diseases in the killer whale community.

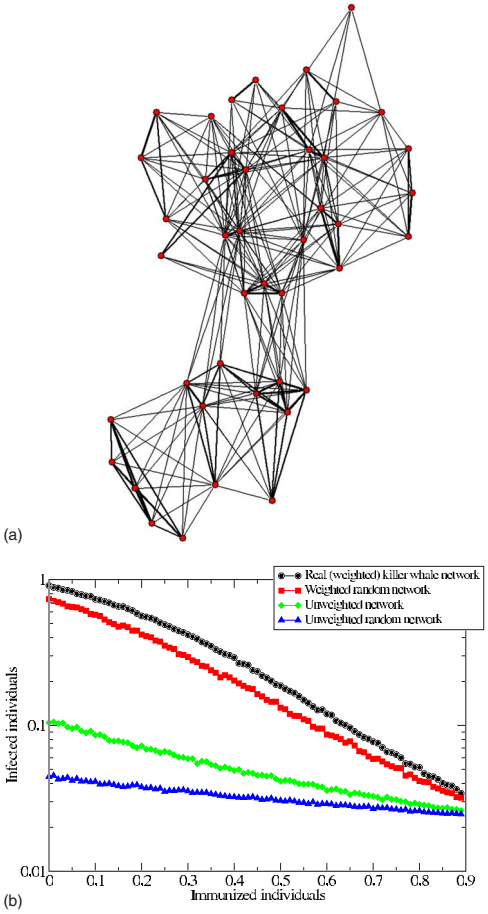

FIG. 1. (Color online) The structure and vulnerability of the social network of mammal-eating killer whales. (a) The social network in which the width of links is proportional to the weight or strength of social interaction (w_{ij}), quantified using the half-weight index of association. (b) The average proportion of infected individuals after simulation of disease spreading ($n=2150$ simulations, 50 replicates assuming that a given individual is the first infected individual). Simulations were performed using different fractions of nonsusceptible individuals and four different scenarios: (1) the real weighted social network, (2) the network in which interactions are randomized among individuals (preserving the weight of interactions), (3) the network in which all links have the same weight (preserving the topology), and (4) a random network assuming that all links have the same weight (as in classical epidemiological models). (See text for further details.)

DISCUSSION

Our study describes for the first time the vulnerability of an animal social network to disease dynamics; we show that the population of mammal-eating killer whales analyzed here is vulnerable to disease outbreaks. Our results suggest that a large fraction of the killer whale population studied may be affected by a disease spreading through the social interactions between individuals. The failure of theoretical networks in which links are equivalent and/or distributed randomly among individuals to lead to similar patterns of disease dynamics suggests that the observed vulnerability is a consequence of the combined effects of both the topology (i.e., the distribution) and the interaction strength of social links in killer whales. Therefore, even for small populations as studied here, classical epidemiological models that assume that two randomly selected individuals have a constant probability of interacting and that all social interactions are equivalent are not adequate [27]. In fact, we showed that the killer whale social network has nonrandom structural patterns that include the presence of some highly connected individuals, small path length, and high clustering. In addition, previous studies demonstrate that topology may contain information of the buildup of small networks [28,29]. Therefore, we contribute to the development of one of the central themes of network theory, the study of small networks [9], by showing that aspects of network structure (topology and interaction strength) affect dynamic processes such as diseases spreading in very small networks.

In the context of the conservation of mammal-eating killer whales, our study suggests that even endangered species in which individuals live in seemingly small and isolated groups, interacting with a few individuals, may be threatened

to disease outbreaks that may affect almost the entire population. Although there is no available data to test our predictions, there is (1) a wide variety of pathogens that attack killer whales [16], (2) the population shows high levels of contamination by PCBs, increasing the vulnerability of individuals [15], and (3) the population of other top predators were locally or globally extinct due to pathogens [1,4]. It is important to note that in natural conditions the transmission of disease is probably compensated by the benefits derived from social interactions, such as hunting efficiency [17] and food sharing [30]. However, the same may not be true in reduced populations in which the immunity of individuals is already challenged by contaminant loads [15], or facing recently introduced pathogens [1].

The observed deviation between the predictions of classical epidemiological models and our simulations reinforce the importance of topology for dynamics within complex networks [11]. Previous studies focusing on the spread of disease in human social networks propose that biased policies toward certain groups of individuals may be more efficient to control disease outbreaks [31–33]. In mammal-eating killer whales, our results suggest that individuals that show strong interactions with a number of individuals are likely to be the most important to the observed epizootic dynamics. Thus, special attention should be devoted to mature females, since they are likely to associate with a number of individuals and establish long-term interactions with their offspring, even after the individuals disperse from the original group [12]. These strategies should be associated with the identification of potentially dangerous pathogens [16] and to the continuous monitoring of health conditions of individuals in order to detect epidemics at early stages.

We emphasize that the approach described here may help to provide new insight into the vulnerability of other social mammals. Because of the importance of top predators such as mammal-eating killer whales to the long-term maintenance of ecological communities [13,34,35], we suggest that future studies should focus social, endangered top predators that are likely to be threatened by epizootics, such as lions (*Panthera leo*), African wild dogs (*Lycaon pictus*), and hyenas (*Crocuta crocuta*) [36].

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