A killer whale social network is vulnerable to targeted removals

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Individuals play various roles in maintaining social integrity of mammalian populations. However, many models developed for managing wildlife resources assume that all individuals are equal. Killer whales are social animals that rely on relationships within and among female groups for reproduction and survival. In the northeastern Pacific, fish-eating, 'resident' killer whale populations are composed of matrilines from which offspring do not disperse. We analysed the influence of various individuals' ages, sex and matrilineal affiliation on their position in a social network. Here, we show that some matrilines appeared to play more central roles than others in the network. Furthermore, juvenile whales, especially females, played a central role in maintaining network cohesion. These two key findings were supported subsequently by simulating removal of different individuals. The network was robust to random removals; however, simulations that mimicked historic targeted removals of different individuals to their social network. Anthropogenic removal targeting particular matrilines implicitly and particular age–sex classes explicitly could cause different population-level effects than random culling.

Keywords: social network; anthropogenic impact; sociality; live capture; by-catch; matriline

1. INTRODUCTION

The consequences for a mammalian society of removing individuals (through natural mortality, culling or live-captures) will vary with the role that individuals play. For example, African elephants (Loxodonta africana) use acoustic cues to discriminate among family groups. The oldest individuals in female groups have been shown experimentally to possess superior ability to discriminate among contact call types and this increase in social cohesion and information exchange may lead to higher reproductive success for social groups led by older females than younger ones (McComb et al. 2001). Preferential poaching of matriarchs (for their tusks) is thought to reduce the information available to female social groups (McComb et al. 2001). Trophy hunting similarly skews the reproductive success of bighorn sheep (Ovis canadensis; Colman et al. 2003) by removing rams with larger horns. Human activities can alter key features of animal populations, such as their socioecology and their population biology. Assuming that all individuals play similar social roles in their population can have unanticipated consequences on the dynamics of wildlife populations.

There might be parallels to these anthropogenic influences in killer whale (Orcinus orca) societies. Like African elephants, fish–eating killer whales in the northeastern Pacific live in stable, matrilineal groups in which acoustic cues are used to discriminate among matrilines (Ford 1989; Deecke et al. 2000). However, the functional role of different age–sex classes in killer whale societies has not been studied extensively. The extraordinarily strong fidelity of fish–eating killer whales to their natal units suggests an important and potentially variable contribution of different individuals to their social network. Anthropogenic removal targeting particular matrilines implicitly and particular age–sex classes explicitly could cause different population-level effects than random culling.

Live-capture fisheries of killer whales occurred in the northeastern Pacific from 1962 to 1972 (Bigg & Wolman 1975), and may have played a role in the current at-risk status of the targeted populations. The topic is of ongoing concern to conservation and management globally: a live-capture fishery for 10 killer whales began recently in the waters off far east Russia (Preliminary evidence suggests that this population’s social structure and small size is similar to that of fish–eating killer whale communities of the coastal northeastern Pacific (International Whaling Commission 2005).

We used information on the social structure of the ‘northern resident’ killer whale community off north-eastern Vancouver Island, Canada to examine the role of different life-history characteristics in maintaining cohesion of their social network. We also simulated the consequences to this population of removing 10 individuals.

2. MATERIAL AND METHODS

(a) Network construction

Association data were recorded at 15-min intervals, from 08.00 to 20.00 h in July and August, 1995–2003, near Robson Bight (Michael Bigg) Ecological Reserve (50.5°N, 126.2°W). Individual and group composition was determined using acoustic cues (Ford 1989), by comparing natural markings on dorsal fins to a photo-identification catalogue (Ford et al. 2000), and through a process of elimination to infer identity of less recognizable individuals within matrilines. There were 14,288 group sightings, defined as animals within 10 body lengths of one another, acting in a coordinated manner. We restricted association data to the component of the population that used the area most frequently, that is individuals observed more than 150 times and for which we could reliably estimate association indices. While adjacent 15-minute scans are unlikely to be statistically independent, our sampling was geographically restricted, which minimized potential for pseudoreplication. Repeated observations of freely associating whales were necessary to quantify variation in relative strength of associations. The censored dataset represents 81 whales from a population that numbered 203 in 2003. These whales spanned all age–sex classes and represented 13 of the 34 matrilines in the population. A half-weight index, corrected for deaths and births, was calculated for each dyad, a matrix of 81×81 whales, based on whether the two whales had been seen together: 

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 HWI = \frac{X + (Y_{A_{\text{const}}} + Y_{B_{\text{const}}})/2}{X + Y_{A_{\text{const}}} + Y_{B_{\text{const}}}}
\]

where \(X\) is the number of times individuals A and B were seen together, \(Y_{A_{\text{const}}}\) is the number of times individual A was seen without B while B was alive, and \(Y_{B_{\text{const}}}\) is the number of times individual B was seen without A while A was alive. The social network of individuals seen often in the area was constructed based...
on preferred companionship. Preferred companionships were defined as individuals seen together in groups more often than one would expect from random association: i.e. pairs with HWI greater than HWI_{null} (Whitehead 1995) were kept in the social network (figure 1a). The null HWI was determined from the average number of associates a whale had (10) and the number of whales from which it could choose (80). Thus, dyads with HWI higher than 0.125 were retained as preferred companionships.

Figure 1. (a) A killer whale social network in which vertices are whales and edges are preferred companionship (i.e., a dyad’s association index was higher than that expected by chance, HWI_{null}), and its fate under two different removal pressures. (b) The network was more likely to break down when ten whales were removed using a realistic live-capture scenario (six out of ten attempts), than in (c) when the removed whales were selected randomly (zero out of ten attempts). (d) This weakness resulted in fewer whales being linked together in a cluster after removal attempts using the live-capture scenario, error bars are \pm 1SE).
3. RESULTS

All whales were connected in one social network that comprised several inter-connected clusters (figure 1a). The 81 whales were linked by 740 preferred companionships. Whales from the same matriline were most likely to associate with one another (matrilineal mixing pattern defined using standard assortativity coefficient (Newman 2002): \( r = 0.289 \pm 0.0082 \)), while sex and age of whales did not play important roles in the association pattern observed (sex, \( r = 0.019 \pm 0.0266 \); age, \( r = -0.049 \pm 0.0150 \)).

The model including matriline membership and sex–age classes best explained the observed variation in betweenness (difference in AIC with next best model was 20, which included matriline alone). While the matriline parameter was significant, the sex–age class parameter was not, although there was a non-significant tendency for younger individuals to have higher betweenness values. The same model explained the variation in degree, but in this case both parameters were significant. Juveniles and sexually immature females had higher degree values (difference in AIC with next best model was 50, which only included matriline). Future work should address issues of independence of scan samples and whether network measures are affected by sampling frequency and unequal capture probability of individuals. We have addressed these concerns by removing rarely seen animals from the analyses, but that filtering process removed data that could facilitate analyses to explore social and aggregative factors that drive grouping behaviour in killer whales.

The social network was more likely to fragment under targeted captures than during random removal (figure 1b,c). This led to fewer whales being included in one connected network after 10 whales were removed using the realistic live-capture scenario than during random removals (figure 1d; \( F_{1,19} = 4.9 \), \( p = 0.04 \); targeted = 64 whales left on average; random = 71 whales).

4. DISCUSSION

Like human social networks, a killer whale social network is vulnerable to attacks that target vertices with high betweenness and degree values (Holme et al. 2002). The network we describe evaluated preferred companionships; chance encounters between whales also occurred, which could form the basis for future preferred companionships in cases where whales were removed. The latency of the observed fragmentation is therefore unknown, but can be assumed to increase as the number of individuals removed over short time periods also increases.

Different matrilines appeared to play different roles in this killer whale social network, because matriline membership was the major contributor to the variation in both centrality measures. We collected association information in an important foraging area for a subset of the population. This discrepancy in matrilineal contribution to the network may reflect differences in local adaptation of different matrilines. This has important implications for other species such as sperm whales and long-finned pilot whales, which are or have been subjected to intense hunting pressure in various regions, and are also matrifocal species. The drive fishery technique used to hunt pilot whales and the strong sexual segregation of sperm whales, increase the possibility of removing many members of a matriline at once. Recent studies show that different sperm whale matrilines will have different foraging success under different climatic conditions (Whitehead & Rendell 2004), highlighting that matriline-based knowledge or foraging specializations could become lost during hunts where a whole matriline might be completely removed. Anthropogenic activities that target family groups represent an ecological challenge to which killer whale societies are not adapted and such removals could impact the viability of targeted populations. It is therefore important to collect information about the role of various individuals and natal groups in a population before live-capture programs start. Our findings also suggest that the social structure of populations cannot be disregarded from management plans that promote the recovery of depleted species. Our attempt to integrate sociality into a live-capture fishery for killer whales raises serious concerns about removals that target clusters of closely related...
animals, and indeed, any management procedure that treats all individuals in a network as generic.

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