

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 family groups for survival. In the northeastern Pacific, fish-eating, 'resident' killer whale populations are composed of matrilineal groups from which offspring do not disperse. We analysed the influence of various individuals' age, sex and matrilineal affiliation on their position in a social network. Here, we show that some matrilineal groups appeared to play more central roles than others in the network. Furthermore, juvenile whales, especially females, appeared to play 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 live-captures from the northeastern Pacific were likely to break the network graph into isolated groups. This finding raises concern regarding targeted takes, such as live-capture or drive fisheries, of matrilineal cetaceans.

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*; Coltman *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, matrifocal groups in which acoustic cues are used to discriminate among matrilineal groups (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 matrilineal groups 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 matrilineal groups. 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 matrilineal groups 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: $HWI = X / (X + Y_{A\text{alive}} + Y_{B\text{alive}}) / 2$, where X is the number of times individuals A and B were seen together, $Y_{A\text{alive}}$ is the number of times individual A was seen without B while B was alive, and $Y_{B\text{alive}}$ 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

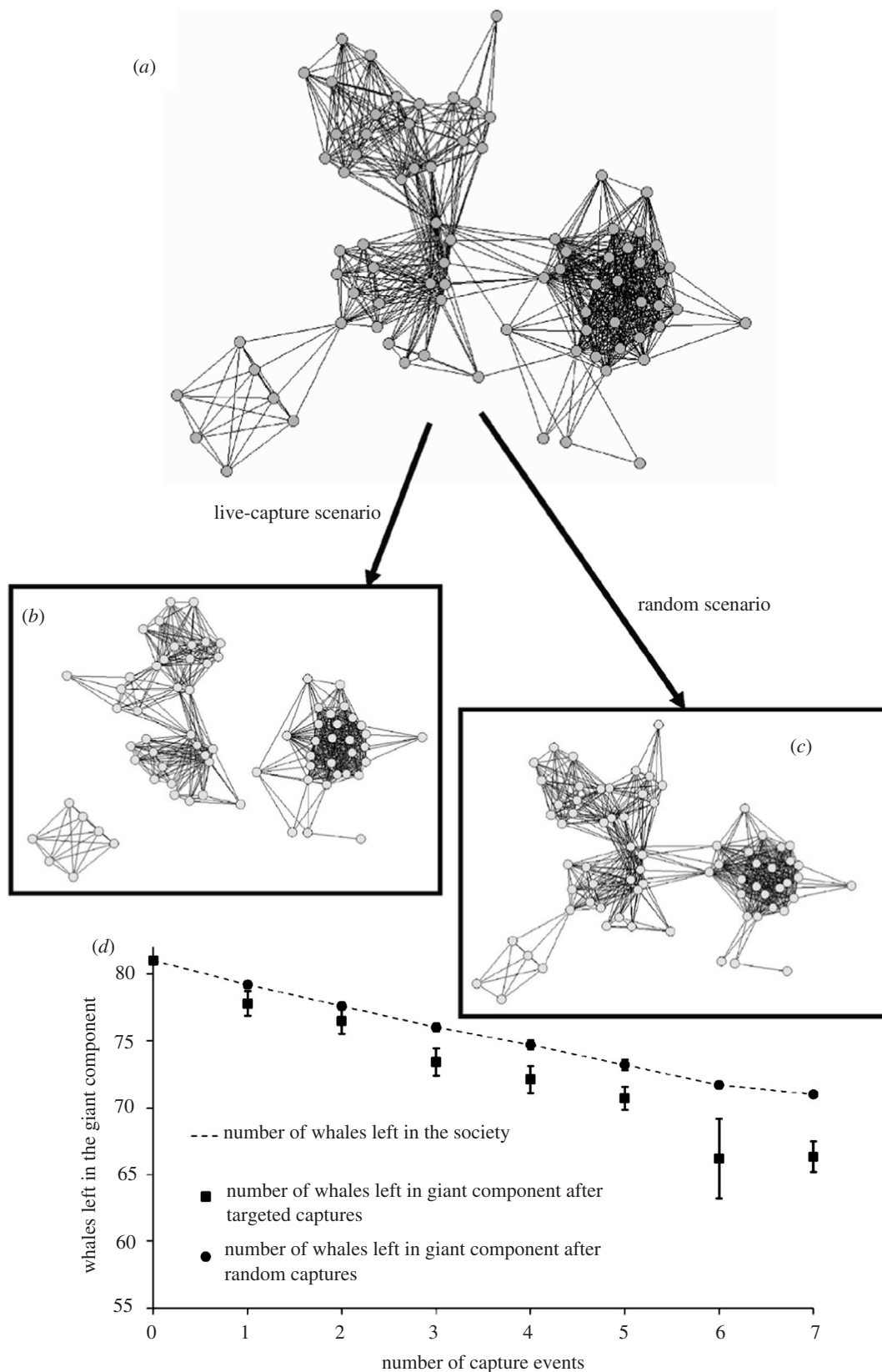


Figure 1. (a) A killer whale social network in which vertices are whales and edges are preferred companionship (i.e., a dyad's association index was higher than that expected by chance, HWI_{null}), and its fate under two different removal pressures. (b) The network was more likely to break down when 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 $\pm 1SE$.

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.

(b) The role of individuals in the social network

We tested whether sex, age, or matriline of individuals influenced their network centrality. We explored which whales tended to achieve higher 'betweenness' and 'degree'; network measures commonly used to determine the centrality of individuals. The higher the betweenness (Freeman 1977), the more often an individual is found between clusters in the network graph. In other words, betweenness quantifies how much of a bottleneck an individual creates (Lusseau & Newman 2004). The degree of an individual is a measure of how much influence an individual has on its peers: the more individuals that a whale is linked to, the more individuals it can affect. The degree of an individual is measured by counting the number of associates a whale has (number of edges). We tested, using generalized linear models (in SPSS 12.0; SPSS, Inc.), whether sex-age class (juveniles, sexually immature male, sexually immature females, sexually mature males, sexually mature females and post-reproductive females) or matriline could explain the variance observed in these two centrality measures. These sex-age classes were developed because male and female killer whales have different reproductive biology: males become sexually mature later than females, and females become senescent past their 50's (Olesiuk *et al.* 1990). Therefore, these classes were more relevant for this species than considering age and sex separately. (It is worth noting, however, that considering sex and age separately yielded similar results.) For each centrality measure, we tested the effect of each whale's characteristics and their interactions and determined which model provided the most parsimonious explanation for the variance observed, using Akaike's information criterion (AIC).

(c) The effects of targeted and random removals

We modelled the effect of targeted removals by eliminating individuals in a manner consistent with a historic live-capture fishery and then comparing these effects to random removals of the same magnitude. We determined the number of whales to remove at each event from capture probabilities obtained from previous live-capture programs (likelihood to capture one whale was 0.57; 2 whales, 0.29; 3 whales, 0.14) (Bigg & Wolman 1975). Our simulations mimicked live-capture preferences for matriline, age and sex of whales during targeted removals (four females and two males aged between 4 and 10, and two females and two males aged between 10 and 20), while we randomly selected individuals captured during an event for random removals. We assessed the likelihood that the network would break down into isolated clusters after each type of removal event (targeted versus random). To do so, we counted how many whales were left interconnected in the largest cluster (giant component, figure 1d) after each removal event. This was repeated 10 times.

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 matriline 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.

We thank BC Parks and their contractors for permission to use the sightings data, which were collected largely by David Briggs, Cheryl Ciccone and R.W. We thank Robert L. Brownell, Volker Deecke, Graeme Ellis, John K. B. Ford, M. E. J. Newman, Paul M. Thompson, Hal Whitehead and two anonymous reviewers for constructive comments. Data collected by G. Ellis and J. K. B. Ford (Cetacean Research Program, Fisheries and Oceans Canada) were used to describe the northern resident killer whale population. Whale and Dolphin Conservation Society and the Humane Society of the United States provided additional funding for the analysis. R.W. was responsible for the association data, and together with D.L. designed the study. D.L. designed and carried out the analyses.

- Bigg, M. A. & Wolman, A. A. 1975 Live-capture killer whale fishery, British Columbia and Washington State, 1962–72. *J. Fish. Res. Board Canada* **32**, 1213–1221.
- Coltman, D. W., O'Donoghue, P., Jorgenson, J. T., Hogg, J. T., Strobeck, C. & Festa-Bianchet, M. 2003 Undesirable evolutionary consequences of trophy hunting. *Nature* **426**, 655–658. (doi:10.1038/nature02177)
- Deecke, V. B., Ford, J. K. B. & Spong, P. 2000 Dialect change in resident killer whales: implications for vocal learning and cultural transmission. *Anim. Behav.* **60**, 629–638. (doi:10.1006/anbe.2000.1454)
- Ford, J. K. B. 1989 Acoustic behavior of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Can. J. Zool.* **67**, 727–745.
- Ford, J. K. B., Ellis, G. M. & Balcomb, K. C. 2000 *Killer whales: the natural history and genealogy of *Orcinus orca** in British Columbia and Washington State. Vancouver, Canada: University of British Columbia Press.
- Freeman, L. C. 1977 A set of measures of centrality based upon betweenness. *Sociometry* **40**, 35–41. (doi:10.2307/3033543)
- Holme, P., Kim, B. J., Yoon, C. N. & Han, S. K. 2002 Attack vulnerability of complex networks. *Phys. Rev. E* **65** art. no.-056109
- International Whaling Commission 2005 Report of the scientific committee.
- Lusseau, D. & Newman, M. E. J. 2004 Identifying the role that animals play in their social networks. *Proc. R. Soc. B* **271**, S477–S481. (doi:10.1098/rspb.2003.2622)
- McComb, K., Moss, C., Durant, S. M., Baker, L. & Sayialel, S. 2001 Matriarchs as repositories of social knowledge in African elephants. *Science* **292**, 491–494.
- Newman, M. E. J. 2002 Assortative mixing in networks. *Phys. Rev. Lett.* **89** art. no.-208701
- Olesiuk, P., Bigg, M. A. & Ellis, G. 1990 Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Rep. Int. Whaling Comm.* Special Issue **12**, 209–244.
- Whitehead, H. 1995 Investigating structure and temporal scale in social organizations using identified individuals. *Behav. Ecol.* **6**, 199–208.
- Whitehead, H. & Rendell, L. 2004 Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. *J. Anim. Ecol.* **73**, 190–196. (doi:10.1111/j.1365-2656.2004.00798.x)