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Social network correlates of food availability in an endangered population of killer whales, *Orcinus orca*

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For the majority of social species, group composition is dynamic, and individuals are interconnected in a heterogeneous social network. Social network structure has far-reaching implications for the ecology of individuals and populations. However, we have little understanding of how ecological variables shape this structure. We used a long-term data set (1984–2007) to examine the relationship between food availability and social network structure in the endangered southern resident killer whales. During the summer months individuals in this population feed primarily on chinook salmon, *Oncorhynchus tshawytscha*, which show annual variation in abundance. We tested the hypothesis that temporal variation in chinook salmon will correlate with variation in social network structure. Using a null model that controlled for population demography, group size and sampling effort, we found a significant relationship between the connectivity of the social network and salmon abundance, with a more interconnected social network in years of high salmon abundance. Our results demonstrate that resource availability may be an important determinant of social network structure. Given the central importance of the social network for population processes such as the maintenance of cooperation and the transmission of information and disease, a change in social network structure caused by a change in food availability may have significant ecological and evolutionary consequences.

For the vast majority of social species, group composition is dynamic and individuals move between social groups leading to a highly interconnected social network. Who interacts with whom and the local and global population social structures have implications for central issues in ecology and evolution (Krause & Ruxton 2002; Croft et al. 2008). For example population social structure is central to the way animals exploit their environment (Hoelzel 1993; Baird & Dill 1996), gene flow (Piertney et al. 1999; Matocq & Lacey 2004; Wolf & Trillmich 2008), frequency-dependent selection (Nowak & May 1992; Lieberman et al. 2005), and information transfer and disease transmission (Watts & Strogatz 1998; Cross et al. 2004). Describing the social structure of populations and unravelling the mechanisms and ecological factors underpinning this is therefore a key research focus in ecology and evolution.

Insights into the evolution of sociality have been gained by analysing social structure based on group size and composition, particularly by comparing traits among populations (or species) living under different ecological conditions (Crook 1965; Jarman 1974; Seghers 1974). This body of work has demonstrated that an important determinant of population social structure is the distribution and availability of resources. For example, the size of the group is often limited by the quality and quantity of food available (Caraco & Wolf 1975; Baird & Dill 1996). Such patterns have been found across a range of taxa, with groups generally being larger when food is more abundant (many antelope species: Jarman 1974; spider monkeys, *Ateles geoffroyi*, and chimpanzees, *Pan troglodytes*: Chapman et al. 1995; various primates: Janson & Goldsmith 1995; badgers, *Meles meles*: Kruuk & Parish 1982; ants, *Veromessor pergandei, Pogonomyrmex rugosus, Pogonomyrmex californicus*: Bernstein 1975). While such studies have focused on the level of the

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group, we know very little about how the social dynamics (e.g. the stability of social relationships) are influenced by the ecological environment and the implications of this for the social connectivity of the population.

The social organization of a population is based upon the nature and strength of interactions between individuals (Gowans et al. 2001). Using a network approach to investigate such social connectivity in populations provides us with quantitative metrics to describe the social structure at different levels of organization from the individual up to the whole population (Lusseau 2003, 2007; Lusseau & Newman 2004; Croft et al. 2006, 2008; Madden et al. 2009). Social network analysis of animal populations has been applied in many ways; examples include disease and parasite transmission (Corner et al. 2003; Guimarães et al. 2007; Böhm et al. 2008; Godfrey et al. 2009; Drewe 2010), cooperative and behavioural assortative interactions between individuals (Croft et al. 2006, 2009), to gain understanding of social organization (Gowans et al. 2001; Leu et al. 2010), information transfer (Krützen et al. 2005; Hoppitt et al. 2010), the influence of individuals on a network (Darden et al. 2009; Jacoby et al. 2010) and the role individuals play within the network (Lusseau & Newman 2004; Lusseau 2007). At present the relationship between the social network structure of a population and food availability is poorly understood. The little work that has been done suggests that food availability may play an important role in shaping social network structure. For example, in a study on female chacma baboons, *Papio hamadryas ursinus*, Henzi et al. (2009) found that when food was scarce, associations became more polarized into both constant and casual associations. In experiments on European shore crabs, *Carcinus maenas*, Tanner & Jackson (2011) demonstrated that when resources were clumped individuals aggregated into cohesive, stable subgroups. Moreover, recent work on Atlantic killer whales by Beck et al. (2011) showed that the strength of associations among matrilines differed between populations that had different foraging specializations.

In this study we explored how food availability may impact population social network structure of the southern resident killer whales, which exhibit strong social bonds (Mesnick et al. 1999; Williams & Lusseau 2006) and are organized into highly stable, matrilineal social units (Bigg et al. 1990). The southern resident killer whale community is a highly interconnected, closed population (Fig. 1), with no dispersal by males or females from the maternal group. Southern resident killer whales occur in the coastal waters of British Columbia and Washington State throughout the year; however, they are seen most frequently from June to September (Fig. 2) when they feed on migrating salmonids (Olesiuk et al. 1990; Ford & Ellis 2006). Chinook salmon, *Oncorhynchus tshawytscha*, comprise the largest proportion of their diet during this time, supplemented with chum salmon, *Oncorhynchus keta*, sockeye salmon, *Oncorhynchus nerka*, pink salmon, *Oncorhynchus gorbuscha*, ling cod, *Ophiodon elongatus*, and Pacific halibut, *Hippoglossus stenolepis* (Ford & Ellis 2006). Recent work by Ford & Ellis (2006) and Hanson et al. (2010) shows that from June to September chinook salmon makes up more than 90% of the southern resident killer whales' diet. There is well-documented temporal variation in the abundance of chinook salmon (Fig. 3). These fluctuations may be caused by a combination of anthropogenic impacts and El Niño conditions affecting the survival of juvenile salmon (Slaney et al. 1996; Lackey 2003; Beacham et al. 2008). Previous research found that declines in chinook salmon abundance are correlated with reduced killer whale reproductive success (Ward et al. 2009) and higher mortality rates (Ford et al. 2010). We examined the impact that a change in food availability may have on a population's social dynamics. We predicted that in times of low salmon abundance the population will be socially fragmented, as individuals would have to spend more time foraging over a wider area, thus limiting the opportunity for social interactions.

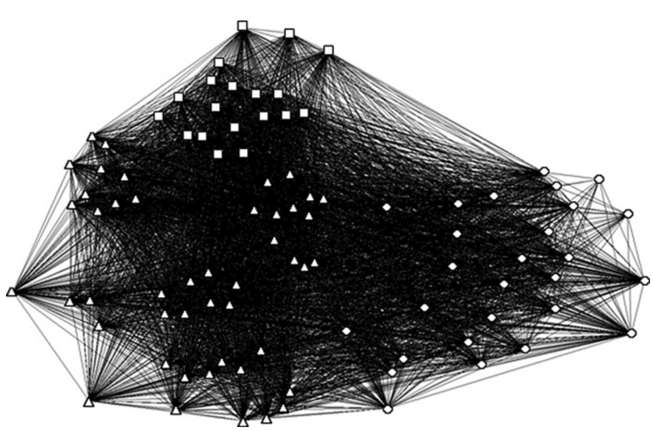

Figure 1. An example of the densely connected social network structure showing all HWI associations during the high salmon periods (15 June to 15 August) for 2007 (J pod (○), K pod (□) and L pod(△)). Figure drawn using network visualization software, UCInet (Borgatti et al. 2002).

METHODS

Data Collection

From 1984 to 2007 sightings of southern resident killer whales were documented by photographic census throughout the year by the Center for Whale Research, San Juan Island, WA, U.S.A. (48.551130°N, 123.075633°W). All observations were carried out from boats (9 m trimaran and 5.5 m Boston Whaler). During each sampling day, every individual killer whale encountered was photographed by trained staff using Canon or Nikon SLR cameras with 300 mm fixed lenses (1984–2004) or with Canon or Nikon DSLR cameras with fixed 300 mm or 80–200 mm lenses (2003–2007). Sampling was limited to conditions suitable for photoidentification: no rain and relatively calm sea state (less than Beaufort 4). Individuals were identified by their unique fin shapes, saddle patches and the presence of any nicks or scratches, and sexed using the distinctive pigmentation patterns around the genital slits (Ford et al. 2000). We used data from 15 June to 15 August each year which is in the middle of the time when the chinook salmon are most abundant and form the major part of the southern resident killer whales' diet (Hanson et al. 2010). During this time observations were made on a total of 536 sampling days (mean $\pm$ SD $= 22.33 \pm 9.13$ days/year) and a total of 10 208 unique photographs were taken which were of sufficient quality for accurate identification. Every individual encountered was identified and included in subsequent analysis, regardless of age or sex.

Animals travelling together will usually occupy the same channels of water (i.e. will not take different routes around an island). To define social associations we followed the methods presented in Parsons et al. (2009), which recognizes that individuals within acoustic proximity have the opportunity to interact. We assumed that all animals photographed within acoustic range (approximately 10 km; Miller 2006) were part of the same group. Every attempt was made to photograph all individuals present, which was facilitated by the fact that killer whales travel in close physical proximity (Bigg et al. 1990; Ford et al. 2000; Parsons et al. 2009).

To estimate chinook salmon abundance we used data provided by the Pacific Salmon Commission (www.psc.org). During the study period (15 June–15 August) the southern resident killer whales