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The social dynamics of southern resident killer whales and conservation implications for this endangered population

K.M. Parsons[a,b,*], K.C. Balcomb, III[b,1], J.K.B. Ford[c,2], J.W. Durban[d,3]

[a] Northwest Fisheries Science Center, National Marine Fisheries Service, Seattle, WA, U.S.A.
[b] Center for Whale Research, Friday Harbor, WA, U.S.A.
[c] Fisheries & Oceans Canada, Pacific Biological Station, Nanaimo, BC
[d] NMML, Alaska Fisheries Science Center, National Marine Fisheries Service, Seattle, WA, U.S.A.

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Quantitatively characterizing the social structure of a population provides important insight into the forces shaping key population processes. Moreover, long-term social dynamics provide an avenue for understanding population-level responses to changes in socioecological conditions. This is particularly true for species that show natal philopatry and highly stable hierarchically structured social units, such as the piscivorous resident killer whales of the northeast Pacific. The southern resident killer whale population is a small, demographically closed population, comprising three commonly recognized pods (J, K and L pods), that has recently been listed as endangered throughout its range in both Canadian and U.S.A. waters. In this study, we quantitatively assessed social structure in this population from 29 years of photo-identification data to characterize significant temporal changes in sociality. Preferential affiliation among killer whales within both genealogical matrilines and pods was supported by two different analytical methods and, despite interannual variability, these social clusters persisted throughout the study. All three pods experienced fluctuations in social cohesion over time, but the overall rate of intrapod affiliation was consistently lowest within L pod, the largest of the southern resident pods. The most recent increase in fluidity within social units, occurring in the mid to late 1990s, was coincident with a significant decline in population size, suggesting a possible common response to external stressors. Quantifying these trends in social structure is the first step towards understanding the causes and consequences of long-term changes in killer whale social structure.

Sociality reflects the balance between the selective forces causing and maintaining social groups, and the detriments associated with group living (Crook & Gartlan 1966; Alexander 1974; Clutton-Brock & Harvey 1977; Bertram 1978; Lott 1984; Packer et al. 1990; Gowans et al. 2007). The costs of group living include such factors as increased competition and aggression, increased parasitism or disease transfer, while the benefits include social foraging, group vigilance and cooperative care of young. Social groups develop and persist when the driving forces enhance the fitness of individuals in groups above and beyond that of solitary individuals, despite the inherent costs of living in larger groups. However, sociality evolves under the influence of ecological constraints, which vary across both time and space and can affect both the size and persistence of social units (Crook 1970; Emlen & Oring 1977; Wrangham 1980; Wrangham et al. 1993; Chapman et al. 1995; Wittemyer et al. 2005). The organization of individuals into social groups can be characterized by the empirical assessment of social structure within a population.

Social structure can be defined by the pattern of relationships between individuals (Hinde 1976; Whitehead & Dufault 1999; Kappeler & van Schaik 2002). At the most basic level, these relationships are defined by the day-to-day interactions among individuals and, as such, they shape many key population processes. This class of interactions not only affects competition for resources (including mating opportunities) and information transmission (e.g. Whiten 2000; Rendell & Whitehead 2001), learned behaviours (Giraldeau et al. 1994) and disease (Altizer et al. 2003; Cross et al. 2004; Keeling & Eames 2005), but also shapes patterns of gene flow and opportunities for cooperative behaviour and reciprocity

* Correspondence and present address: K. M. Parsons, NMML, Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sandpoint Way NE, Seattle, WA 98115, U.S.A.
E-mail address: kim.parsons@mail.com (K.M. Parsons).
[1] K. C. Balcomb, III is at the Center for Whale Research, Box 1577, Friday Harbor, WA 98250, U.S.A.
[2] J. K. B. Ford is at Fisheries & Oceans Canada, Pacific Biological Station, Nanaimo, BC V9T 6N7, Canada.
[3] J. W. Durban is at the NMML, Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sandpoint Way NE, Seattle, WA 98115, U.S.A.

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(Alexander 1974; Whitehead 1997). As such, social structure determines many integral processes and offers insights into population dynamics and socioecological interactions.

Social structure can be characterized by quantifying the interactions between individuals in terms of their nature, spatiotemporal patterning and longevity (e.g. Symington 1990; Connor et al. 1992; Whitehead 1997, 1999; Baird & Whitehead 2000; Wronski & Apio 2006). Such descriptors rely upon long-term observational data and the ability to identify individual animals over extended periods by their persistent natural or artificial markings. Long-term observational studies have provided unique insight into the social structure of groups within several large mammal populations (e.g. Packer et al. 1990; Baird & Whitehead 2000; Fernando & Lande 2000; Durant et al. 2004; Sinha et al. 2005; Wittemyer et al. 2005; Sundaresan et al. 2007), and have proved invaluable in assessing conservation priorities and modelling extinction risks for social species (e.g. Vucetich et al. 1997). Social structure largely determines the interacting members of a population, shaping not only the breeding pattern but also the behavioural plasticity of a population. As such, social systems can shape the impact of prey dynamics and inflate the importance of demographic stochasticity (Keane et al. 1994; Vucetich et al. 1997). Furthermore, incorporating social structure into extinction or risk assessment models is essential for accurately evaluating the persistence of social species. These effects can be particularly dramatic for species or populations with highly restricted natal dispersal.

In the eastern North Pacific behaviourally divergent and reproductively isolated killer whale, *Orcinus orca*, lineages (or ecotypes) exist in sympatry (Bigg 1982). Among these are the piscivorous so-called 'resident' killer whales that travel in relatively large groups commonly referred to as pods; a term used to describe groups of whales found to occur together during at least 50% of documented encounters over a period of several years (Bigg et al. 1990). Long-term observations indicate that pods are most often composed of several matrilineal units (clusters of adult females and their offspring related to a common female ancestor; Bigg et al. 1990). These resident-type killer whales show the most extreme form of restricted dispersal, characterized by natal philopatry of both sexes (Bigg et al. 1987, 1990). The social unity produced by a lack of dispersal from the natal group creates a scenario in which the population may be particularly vulnerable to both demographic and environmental stochasticity (Guimaraes et al. 2007). Examining temporal patterns in the social structure within such populations provides key baseline data that can be used to evaluate socioecological interactions and model the potential impact of future events.

The Southern Resident Killer Whale Population

The southern resident killer whale population is a small, demographically closed population consisting of fewer than 100 whales. Population members occur commonly throughout the coastal waters of southern British Columbia and Washington State, with peak frequency in inshore waters during the summer months (Ford et al. 2000). Since the early 1970s, this population has been photographically censused on an annual basis using the natural variability both in the shape of the dorsal fin, and the area of pigmentation immediately posterior to the dorsal fin (the saddle patch) to reliably identify each individual killer whale (Bigg 1982; Bigg et al. 1987). In most years the population was enumerated from the annual photographic identification census data. For rare years in which the census was incomplete because of variability in funding, field seasons or effort, population size was adjusted retrospectively. This photo-identification approach has provided the data necessary to monitor annual changes in population size and demographics, data which have most recently provided the basis for listing the southern resident killer whale population as endangered under the Canadian Species at Risk Act (SARA) and the U.S. Endangered Species Act (ESA). Photo-identification records have also generated longitudinal association data spanning more than three decades, providing unique insight into this matrifocal society. Here, we examined the temporal trends in the stability of the three commonly recognized southern resident killer whale pods (J, K and L pods), and the associations among individual matrilines. We also used novel analytical approaches to examine temporal changes in social stability over three decades, and explored the social dynamics of this population.

METHODS

Individual-based Photo-identification Data

A relational database was compiled of all existing photographic records for the southern resident killer whales by combining records maintained by the Center for Whale Research, WA (CWR) and those from the Pacific Biological Station, Fisheries and Oceans Canada (DFO). These data referenced every killer whale photograph by date, time and location, thereby providing a longitudinal resighting history for each whale, and a list of associates for each whale during each encounter. The compiled data consisted of 1366 different killer whale encounters composed of 118 704 individual identification records, spanning all years between 1967 and 2003. By pod, the number of encounter weeks ranged from 300 to 365, and the number of photo-documented groups ranged from 575 to 652 per pod (Table 1). Recognizing that interindividual visual and acoustic proximity provides the opportunity for interaction and the transmission of information among whales, a group was defined simply as all killer whales within sight, showing some degree of coordinated behaviour and within acoustic range (approximately 10 km; Miller 2006). An encounter referred to a group of whales photographed at a particular date, time and location. Our analyses assume that animals that were spatially close and photographed within the same group were associating. This assumption is based on the anticipation that the whales' communication capabilities enable them to select among potential associates. Evaluating associations among individual whales with reference to random expectations will identify patterns of repeated nonrandom affiliations that indicate preferred associations.

To assess long-term trends and interannual changes in social cohesion within the population, we restricted all analyses to those years with the most consistent data sampling. Killer whale grouping patterns may experience seasonal changes in response to changes in prey type and distribution; however, such seasonal

Table 1
Numbers of groups, sample periods and individuals used in analyses for three southern resident killer whale pods

	J pod	K pod	L pod
Number of groups	652	575	593
No. weekly sample periods	365	300	303
Average no. groups/week	1.71	1.80	1.76
No. individual whales	37	31	89
Average±SD annual pod size	19.00±1.71	16.66±1.47	48.28±5.48
Average±SD annual rate of intrapod association	0.627±0.13	0.591±0.15	0.413±0.094
No. years when associations significantly correlated with matriline identity	21/29	15/29	29/29

Association based on matriline identity was tested using a Mantel test where significance was estimated at the level of $P < 0.05$ (annual P values for each pod are not presented).