Animal Behaviour xxx (2009) 1–9

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/yanbe

# 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.

ARTICLE INFO

*Article history:*
Received 1 October 2007
Initial acceptance 31 January 2008
Final acceptance 29 December 2008
Available online xxx
MS. number: A10870

*Keywords:*
association
conservation
endangered
killer whale
mammal
*Orcinus orca*
social dynamic
social structure

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.
© 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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.

0003-3472/$38.00 © 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2009.01.018

Please cite this article in press as: Parsons, K. M., et al., The social dynamics of southern resident killer whales and conservation implications for this endangered population, Animal Behaviour (2009), doi:10.1016/j.anbehav.2009.01.018

(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).

Please cite this article in press as: Parsons, K. M., et al., The social dynamics of southern resident killer whales and conservation implications for this endangered population, Animal Behaviour (2009), doi:10.1016/j.anbehav.2009.01.018

effects are also reflected by changes in the populations' ranging patterns and seasonal research effort, decreasing the frequency of encounters within the inshore waters. Because of the sparsity of non-summer encounters, data were restricted to summer (May–September) encounters to eliminate potential seasonal effects. All of the results presented hereafter refer to the analysis of the 1108 killer whale encounters (107 883 photographic identification records) photo-documented between May and September, 1975 through 2003.

*Annual Trends in the Strength of Intrapod Associations*

Annual estimates of the strength of association among whales were derived using the simple-ratio index of association (Cairns & Schwager 1987). This metric generates a statistically unbiased estimate of association (Ginsberg & Young 1992) in which the affiliation between each pair of individuals is estimated as a proportion of the total time spent together, where the number of encounters with both individuals is divided by the total number of encounters with either individual. A symmetric matrix of association between all pairs of identified whales was generated based on the number of sampling periods in which two individuals were both photographed during the same encounter. These pairwise association indexes were averaged across associates within pods to generate annual estimates of average intrapod rates of association. Likewise, association indexes among individuals belonging to different pods were averaged to generate annual estimates of interpod rates of association.

The length of the sampling period that defines association can have a significant effect when estimating the strength of associations; short sampling periods may underestimate the rate of association, whereas long sampling periods may artificially group individuals and consequently result in overestimates. The primary objective of the southern resident killer whale surveys was to photo-document each individual whale every year. As a result, the number of whales photographed during an encounter varied daily, and rarely were all whales photographed during an encounter. Therefore, the sampling period was set to a 7-day interval, where a given pair of whales was considered to have associated during the 1-week period irrespective of the number of joint encounters during that sampling period. Weekly sampling intervals proved long enough to allow the grouping of a few encounters (mean number of encounters per pod in 1 week = 1.76) over short time periods. This increased the probability of a representative photographic sampling of the individuals within groups and allowed us to assess long-term changes in associations among killer whales, while decreasing the effects of fine-scale transient changes in association and sampling effort variability between encounters and years.

Association indexes were calculated for each annual data set independently, and annual estimates of the average rate of association among pod members (intrapod) were derived for each of the three southern resident killer whale pods. All association analyses were performed using SOCPROG V.2 (http://myweb.dal.ca/hwhitehe/social.htm) run in the MATLAB computing environment. Trends in the strength of intrapod associations were assessed by comparing annual estimates of intrapod association. A change-point analysis was performed on the annual simple-ratio indexes to look for periods of significant change in intrapod association rates. The change-point analysis is based on the calculation of cumulative sums from the intrapod association indexes, which reflect the differences between the observed data values and the average rate of intrapod association over time. A change-point model was fitted to the data for each of the three pods independently, and to all three pods together as multiple observations over the same time series. Periods of significant change were assessed by performing a bootstrap analysis and calculating confidence intervals from the data. Change-point analysis and bootstrap confidence intervals (10 000 bootstrap samples) were calculated using Change-Point Analyzer (http://www.variation.com/cpa/).

*Examining the Significance of Social Units*

Long-term behavioural observations on this killer whale population have supported the existence of a hierarchical female-based system of social structure, wherein matrilines are composed of individuals related to a living or ancestral female, and each of the three larger pods are composed of varying numbers of matrilines (Bigg 1982; Heimlich-Boran 1986; Bigg et al. 1990). Intermediary units, referred to as subpods (Bigg et al. 1987, 1990), are occasionally recognized within some of the larger southern resident pods. Subpods are generally composed of one to several matrilineal units that associate with a high degree of regularity. We used the long-term photographic association data to examine the temporal stability of these larger social units over the study's 29 years. For the purpose of our data analyses, we applied the strictest definition of a 'matriline', including only genealogies known by relatedness through female kin, excluding genealogies identified as 'probable' or 'possible' in the published identification catalogues (Ford et al. 1994, 2000). We calculated a mean association index both among pods and among matrilines, based on the individual resighting data. The Mantel test (Schnell et al. 1985) was used to test the null hypothesis that associations within and between pods (or matrilines) are similar, and whales do not preferentially associate with kin at these two hierarchical classes. Statistical significance was estimated by permuting associations between classes 10 000 times using the random permutation routine executed in SOCPROG.

The preferential association of related whales was also explored by examining the identity of whales in photographs containing multiple identifiable whales. Assuming that close physical proximity and surfacing synchrony is a prerequisite for two whales to be photographed simultaneously, and this proximity presents the opportunity for interaction among whales, photographic frames containing multiple whales may reflect socially significant patterns of association. We explored this by examining the identities of multiple whales within single photographic frames, and comparing their pod and matriline memberships. Although nearly all identification photographs were taken with a 300 mm telephoto lens, both photographic effort (e.g. number of photographers) and media (film versus digital) varied over the 29-year study period. In addition, metadata were not always readily available to identify multiple photographs taken within a single surfacing sequence. To control for identical sequential photographs and pseudoreplication, all CWR photographs were indentified and sorted by encounter, then photographs containing more than one whale were subsampled to include only unique photographs (i.e. unique combinations of whales) within each encounter. A similar approach was adopted by Bigg et al. (1990), where photographic sequences were used to gain information on the strength of social bonds among resident killer whales.

*Modelling Social Clusters Using a Bayesian Mixture Model*

A Bayesian mixture model (BMM) was 'blindly' fitted to the photographic identification data to identify social units, assuming no prior knowledge of pod affiliations. The Bayesian framework enabled uncertainty about both the number and the composition of social clusters to be analysed and it communicated these uncertainties as direct probability statements (e.g. Wade 2000). To examine interannual changes in the number of social clusters

Please cite this article in press as: Parsons, K. M., et al., The social dynamics of southern resident killer whales and conservation implications for this endangered population, Animal Behaviour (2009), doi:10.1016/j.anbehav.2009.01.018

within the population, we used the matriline identity of individual whales as our data unit. As above, individuals whose genealogy was uncertain and previously identified as 'possible' or 'probable' (Ford et al. 1994, 2000) were assigned to their own matriline to avoid artificially preclustering the data.

For each year separately, we summarized the encounter histories of the matrilines as a binary matrix taking the values 1 or 0, depending whether or not each matriline was identified in each encounter. These binary data were modelled as Bernoulli random variables, where the underlying density of the encounter probabilities was modelled as arising from a mixture of distributions, and clusters of matrilines with similar encounter histories were identified from their component distribution. Specifically, we modelled the logistic function of the encounter probabilities to proceed from a mixture of normal component distributions, and the clusters were defined by the hyper-parameters specifying the mean and variance of each of the component distributions (Escobar & West 1995). Temporal variability within components was specified by a Gamma prior distribution for component variances, which was centred on one with one degree of freedom to allow a range of possible values. The component means were assumed to be normally distributed about zero (because of the logistic transform of encounter probabilities), and the variability between components was controlled by a Gamma distribution with mean of 1 and a *df* of 1, to allow differences between components to emerge. This mixture formulation allowed the identification of clusters representing groupings with different temporal transitions in encounter probabilities over time.

To facilitate computation and inference about cluster allocations, we introduced indicator variables, one for each matriline, to indicate which component in the mixture generated the vector of encounter probabilities for each matriline (Neal 2000). We used Markov Chain Monte Carlo (MCMC; Brooks 1998) sampling to make repeated draws from the model, and the cluster allocation attached to each matriline was taken over the candidate values assigned at each iteration of the chain. Variability in the sampled values represented uncertainty about cluster membership, which was communicated as direct probability statements based on the relative frequency of values in the MCMC sample. A key feature of the approach is that the number of clusters was not specified, but instead the number of non-empty clusters was estimated from a maximum ceiling value ($C$) of 10 clusters by adopting a Dirichlet process prior for the distribution of mixing proportions (Escobar & West 1995; Dey et al. 1999). The ceiling value was selected from an initial pilot MCMC run with as many candidate clusters as individuals, and excessive empty clusters were subsequently omitted to decrease computation time in the final MCMC runs.

The BMM was fitted to the encounter histories for each year separately using WinBUGS software (Bayesian inference using Gibbs sampling; http://www.mrc-bsu.cam.ac.uk/bugs/). A three-chain MCMC run was used to assess convergence of the MCMC routine, and inference was based on 10 000 iterations after convergence was achieved. The length of the burn-in was assessed using the method of Gelman & Rubin (1992), as modified by Brooks & Gelman (1998), which is based on summary statistics comparing the variances within and between the three different simulated sequences.

## RESULTS

### *Annual Trends in the Strength of Intrapod Associations*

One hundred and fifty-seven different killer whales were documented in the photographic database constructed from summer encounters between 1975 and 2003. The size of the southern resident killer whale population has fluctuated considerably throughout the past three decades (Fig. 1). At the start of the study, the population was at an all-time low following the removal of numerous individuals during live-capture operations (Balcomb et al. 1982; Olesiuk et al. 1990). Although the general population trend has been positive, two periods of decline were evident in the longitudinal population count data. Throughout the last 27 years of the study, relative pod sizes remained consistent, with L pod being the largest of the three pods (Fig. 1). In most years, J and K pods were similar in size, and after 1975, K pod was consistently the smallest of the three pods in the southern resident population (Table 1).

The strength of intrapod association, as quantified by the simple-ratio index (SRI), showed considerable interannual variability both within and across pods (Fig. 2). In general, annual intrapod association was higher within J and K pods than within the larger L pod. However, considerable fluctuation was evident across all three pods. We standardized the annual association indexes to the mean for each pod to look for common temporal patterns. The mean-standardized simple-ratio indexes (SRI) showed that, despite interpod variability, some common trends in intrapod association rates occurred over the 29-year period examined (Fig. 3). In general, intrapod associations appeared relatively high and stable throughout the 1980s. This period of social stability was succeeded by a period of declining intrapod affiliation in the early and mid-1990s, culminating in a remarkable low between 1997 and 2000 that was coincident with the most recent decline in population size. Subsequently, social stability (as measured by the strength of associations within pods) and population size increased again post-2000, returning to the levels experienced during the 1980s (Fig. 3). Despite these apparent trends, population size was not significantly correlated with the overall simple-ratio index ($R = -0.125$, $t_{28} = 0.653$, $P = 0.519$) or the average intrapod simple-ratio index ($R = -0.201$, $t_{28} = 1.067$, $P = 0.295$), and only for J pod was there a significant correlation between annual pod size and intrapod SRI (J pod: $R = -0.430$, $t_{28} = 2.475$, $P = 0.020$; K pod: $R = -0.002$, $t_{28} = 0.012$, $P = 0.990$; L pod: $R = -0.069$, $t_{28} = 0.359$, $P = 0.723$).

A change-point analysis identified significant changes in the time series of intrapod association rates for all three pods (Table 2). Change-points were detected with ≥95% confidence for both J and L pods. A plot of the change-point model fit to the data from all three pods indicated that the variability in intrapod associations did not exceed the maximum range expected assuming no change

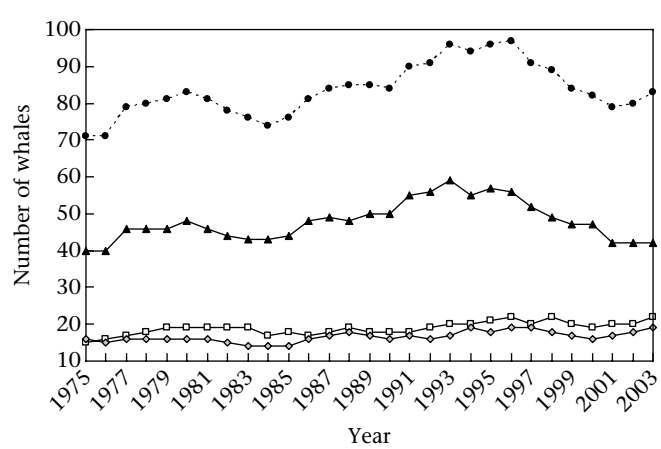


**Figure 1.** Annual size of the southern resident killer whale population and the three primary social pods, based on photographic identification counts of the number of individuals alive in June 1975–2003. ●: population counts; ▲: L pod; □: J pod; ◇: K pod.

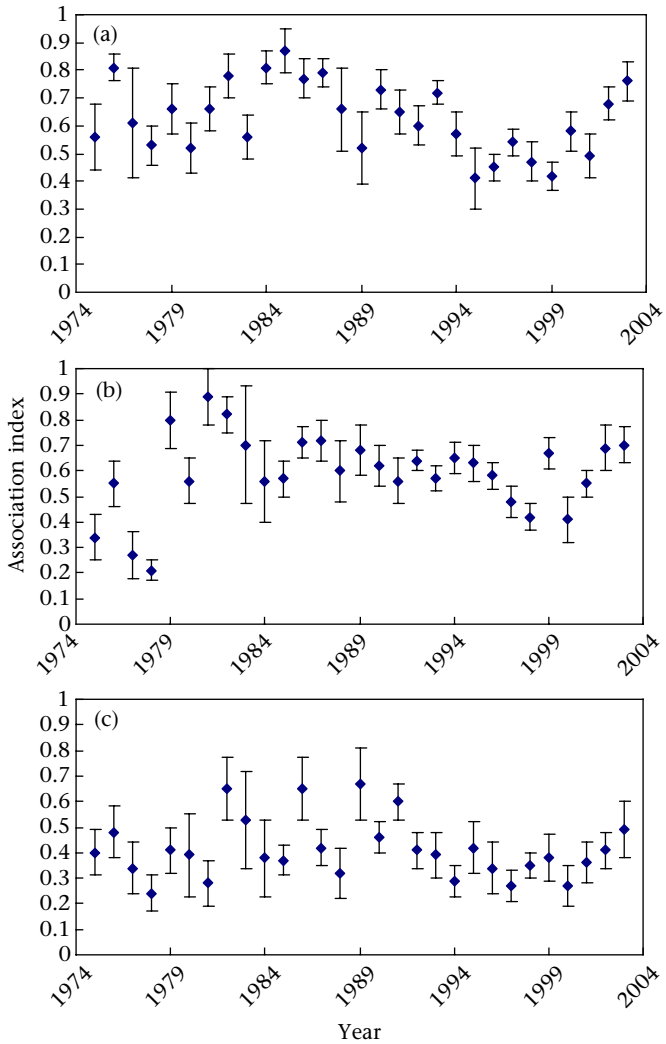


**Figure 2.** Annual mean ± SD intrapod association indexes for (a) J pod, (b) K pod and (c) L pod.

occurred (Fig. 4). However, two periods of significant change were identified (Table 2). The first change detected with 96% confidence was in 1979 when the average intrapod index of association increased from 0.445 to 0.605. The second change, identified with 100% confidence, occurred around 1994 (95% CI = 1992, 1998) when the average intrapod index of association decreased from 0.605 to 0.491.

*The Significance and Persistence of Social Units*

The frame-by-frame photographic records maintained by the CWR were examined to evaluate the probability of whales related by either matriline and/or pod occurring in frames containing multiple identifiable whales. The vast majority (84.38%; $N = 60\,400$) of photographic frames contained only a single identifiable whale. Of the 5012 unique photographic frames containing more than one whale, 1908 (38.1%) contained individuals from only one matriline (as defined in Methods) and 4789 (95.6%) contained whales from a single pod. If we assume spatial proximity is an indicator of social affiliation, the analysis of photographic frames containing multiple whales suggests that whales tend to cluster in space with individuals that they are more closely related to. These patterns clearly support the findings of Bigg et al. (1990), and

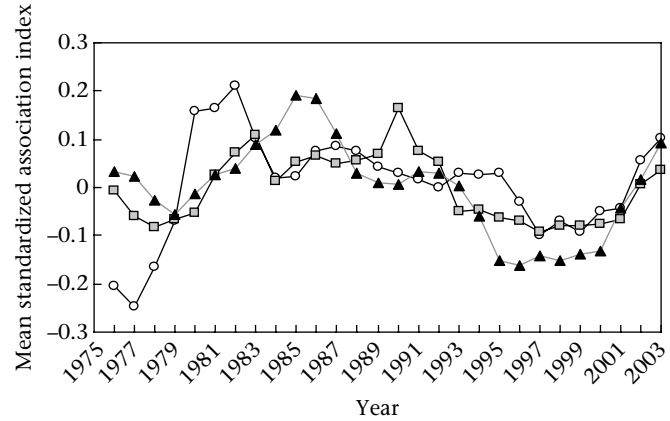


**Figure 3.** Annual intrapod rate of association for each of the three southern resident killer whale pods. ○: K pod; □: L pod; ▲: J pod. Three-year running means were standardized by average annual intrapod association for each pod to facilitate interpod comparison.

highlight the importance of social cohesion and the long-term persistence of kinship-based intrapod affiliations.

Assigning both matriline and pod identity to each of the photographically identified killer whales, we used Mantel tests to assess whether membership to these two hierarchical social units affected the strength of association among southern resident killer whales as measured by the simple-ratio index; do whales preferentially associate within their matrilines and pods? The data were randomly permuted 10 000 times to generate an expectation under the null hypothesis of random associations, and independent Mantel tests were performed assigning either pod or matriline as class variables in SOCPROG. Evidently, both matriline ($t = 18.05$, $P > 0.99$, matrix correlation = 0.165) and pod identity ($t = 15.50$, $P > 0.99$, matrix correlation = 0.381) significantly affected associations among killer whales. However, interannual variability was evident in the significance of matriline membership when we looked at annual grouping patterns within each pod. Within L pod, the largest of the three pods, associations were significantly greater within matrilines than between matrilines in all 29 years (Table 1). The average rate of association was also higher among whales within each of the three currently recognized L subpods ($\bar{X} \pm \text{SD} = 0.589 \pm 0.146$) than among all L pod whales ($\bar{X} \pm \text{SD} = 0.413 \pm 0.094$). The significance of annual intramatriline affiliations was more variable for J and K pods (Table 1). The average rate of association among podmates (intrapod) was greater than that among whales of different pods (interpod) in all years for which data were examined, illustrating the persistence of these large social groups over multiple decades. Not only did these results identify persistent, strong associations among whales within pods, but also a preference for associating with close genetic relatives (matrilines) within these pods.

*Modelling Social Clusters Using the Bayesian Mixture Model*

Between 1975 and 2003, the average ± SD annual number of matrilines represented in the photographic identification data was 38.48 ± 3.15, photographed during an average ± SD of 38.21 ± 16.95 encounters per year. The number of distinct clusters represented by the data was estimated by the BMM, and each matriline was assigned a probability of belonging to a cluster based on their resighting pattern across the annual encounter data set. The median number of social clusters that best fit the data ranged from two to six across all years, with an average of 4.03 ± 1.02 over all years. The number of clusters assigned to each of the three pods

ARTICLE IN PRESS



**Table 2**
Summary statistics for change-point analysis of annual association index estimates for the three southern resident killer whale pods, and all three combined (overall)

| Pod | Change-point year | Confidence level | 95% Confidence interval | Average±SD intrapod SRI before change | Average±SD intrapod SRI after change |
|---|---|---|---|---|---|
| J | 1994 | 98% | (1989, 1996) | 0.674±0.110 | 0.491±0.071 |
| J | 2002 | 99% | (2002, 2002) | 0.491±0.071 | 0.720±0.057 |
| K | 1979 | 94% | (1978, 1980) | 0.343±0.148 | 0.754±0.128 |
| K | 1984 | 93% | (1981, 1991) | 0.754±0.128 | 0.601±0.089 |
| L | 1993 | 95% | (1976, 1998) | 0.440±0.129 | 0.361±0.068 |
| Overall | 1979 | 96% | (1977, 1980) | 0.445 | 0.605 |
| Overall | 1994 | 100% | (1992, 1998) | 0.605 | 0.491 |

varied both across years and among pods: J pod had the lowest variance ($\overline{X} \pm \mathrm{SD} = 1.17 \pm 0.38$), L pod had the greatest variance ($\overline{X} \pm \mathrm{SD} = 2.00 \pm 0.85$), and K pod was intermediate between J and L pods ($\overline{X} \pm \mathrm{SD} = 1.34 \pm 0.55$). Shared clusters, where matrilines from more than one pod were assigned to a single cluster, were identified in only 9 of the 29 study years. In 2 of these 9 years (1977 and 1981), shared clusters comprised at least one matriline from each of the three pods. In the other 7 years, shared clusters involved less than 9% of possible available matrilines from pods outside the cluster's dominant pod ($\overline{X} \pm \mathrm{SD} = 8.76 \pm 8.49$). The matrilines within J and K pods were typically assigned to a single cluster for each pod, whereas L pod matrilines were typically divided among at least two clusters. Comparing the number of clusters assigned to each of the three pods, it is evident that most of the interannual variability in the number of social clusters can be attributed to L pod (Fig. 5).

A 3-year running mean of the median number of social clusters estimated by the BMM illustrated dynamic periods of change in the clustering of the southern resident killer whales and declining social stability in the late 1990s (Fig. 5). Furthermore, the median number of social clusters was positively correlated with population size ($R = 0.426$, $t_{28} = 2.44$, $P = 0.021$). The influence of L pod on the clustering dynamics was evident. Direct comparison between these data and the rates of association quantified by the simple-ratio index indicated a high degree of congruence between the two methods of assessing social stability (3-year running means: $R = -0.496$, $t_{26} = -2.91$, $P = 0.007$), where the number of clusters identified by the BMM decreased as the annual simple-ratio index increased.

## DISCUSSION

Assessment of the long-term social affiliations of the southern resident killer whales revealed many significant and persistent associations within a dynamic framework. Analysis of this 29-year photo-identification database indicated that not only do whales of a common pod and matriline tend to cluster together in space and consequently are often photographed simultaneously, but they also tend to associate more frequently than would be expected by random patterns of association. Both the application of a traditional pairwise association index and the Bayesian mixture model identified significant social clusters within the southern resident killer whale population that persisted over the 29-year study. However, both analytical approaches suggested marked temporal changes in the strength of affiliation within social units over the past three decades that may be associated with environmental or demographic changes.

The social structure identified in this study supports the long-held beliefs of a stable matrifocal society composed of a hierarchy of social units within the southern resident killer whale population. The recognition of three higher level social pods maintained through natal philopatry was adopted from direct field observations, and the alphanumeric numbering of the whales as they were identified at the outset of the study shows the nonrandom cohesiveness of these groups (Bigg 1982; Bigg et al. 1990). The current study further illustrates the persistence of the pod structure that was characterized after the first 15 years of photo-identification studies (Bigg et al. 1990). The significance of these social units in resident killer whale populations is corroborated by behavioural studies documenting correlations between social affiliation and acoustic similarity (Deecke et al. 1999, 2000; Miller & Bain 2000; Nousek et al. 2006) and the prevalence of group-specific vocalizations (Ford 1991; Riesch et al. 2005).

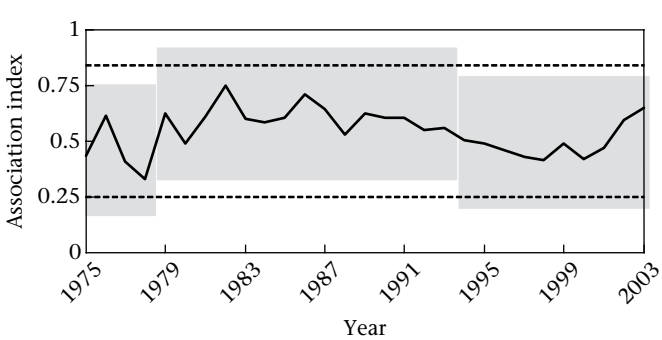


**Figure 4.** Change-point analysis of southern resident killer whale strength of intrapod associations between 1975 and 2003. Solid line represents the average annual intrapod simple-ratio index. Dashed lines are upper and lower control limits. Grey boxes indicate results of the change-point analysis.

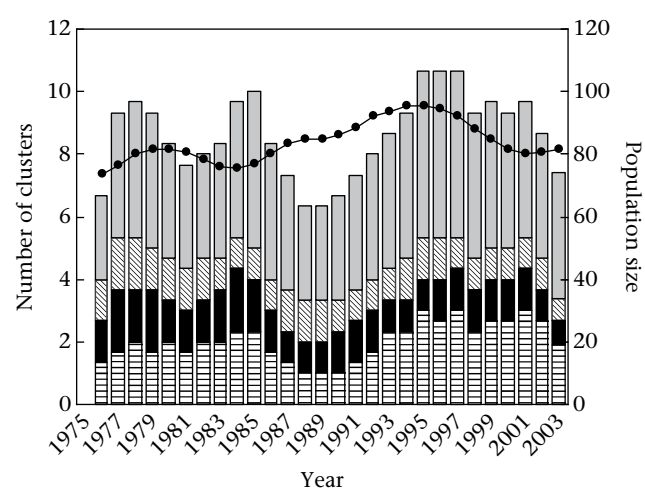


**Figure 5.** Three-year running mean of the median number of social clusters estimated by the Bayesian mixture model fit to the photo-identification resighting of southern resident killer whale matrilines. Results are presented as the number of matrilineal clusters within the population and the number of clusters within each of the three pods. ▭: matrilineal clusters; ▨: J pod; ■: K pod; ▭: L pod; —●—: population size. Note: the number of matriline clusters was less than the sum of the number of clusters for each pod in some years because of shared clusters (see text). The number of clusters on the *Y* axis is additive.

Please cite this article in press as: Parsons, K. M., et al., The social dynamics of southern resident killer whales and conservation implications for this endangered population, Animal Behaviour (2009), doi:10.1016/j.anbehav.2009.01.018

The cohesion of the three commonly recognized pods within the study population (J, K and L pods) was assessed both at the level of the individual and the matriline. The use of an association index allowed us to examine the relative strength of affiliation among individuals both within and between the pods and test the null hypothesis that the southern resident killer whales associate randomly with one another. The results clearly showed nonrandom patterns of association and a significant preference for associating within the larger social units, pods. In all 29 study years, not only were associations significantly greater among whales belonging to the same pod during summer months, but also, the overall average rate of intrapod association was consistently higher than interpod associations. These results are in direct agreement with the findings of Bigg et al. (1990) and suggest that their description of the social hierarchy within the southern resident killer whale population has remained valid over several decades. Despite the unequivocal significance of these social units, interannual variability was evident both across the population as a whole and within each of the three primary pods.

Field studies have also recognized a level of social structure that is intermediate between kin-based matrilines and pods, these intermediary units have been referred to as subpods (Bigg et al. 1987, 1990). Subpods are generally composed of one to several matrilineal units that associate with a high degree of regularity. Some authors have promoted these subpods to the level of pods within the social hierarchy in response to putative pod splitting within L pod in more recent years (Hoelzel 1993; Baird et al. 2005). L pod, the largest of the three pods, showed both the greatest variability in pod size and the lowest rate of intrapod association (Table 1). Furthermore, the Bayesian mixture model reflected the subdivisions within L pod by assigning matrilines within the pod to multiple clusters in most years (Fig. 5). However, the significance of the pod as the largest social unit within the population remained high in every year despite fluctuations in the rate of association among podmates. These patterns reinforce the higher level of fluidity found within L pod, relative to J and K pods, identified through analysis of photographic and observational data 1973–1987 (Bigg et al. 1990), and may indicate that while the currently recognized L pod is a significant social unit, the smaller subunits may be more equivalent to the level of affiliation shown by J and K pods. The current study clearly supports the long-term persistence of this large pod and the social subunits identified by Bigg et al. (1990), and cluster membership estimated by the BMM generally reflected the currently accepted assignment of matrilines to subpods within L pod in most years. However, the decreased level of intrapod cohesion within L pod as a whole may warrant revision of the social unit hierarchy.

Interestingly, L pod was the only pod with significantly greater associations within matrilines than between matrilines in all 29 study years. This result may suggest that matrilineal kin-based units become the social units of greatest importance when pods grow to such an extent that association among all pod members becomes difficult or costly in terms of resource procurement. It is recognized that within social species, optimal group sizes are affected by demographic parameters and environmental constraints, and group fissioning can occur when groups reach a maximal or optimal size (Alexander 1974; Aviles 1999; Lefebvre et al. 2003). However, a high degree of genetic relatedness within social groups can play an important role in the maintenance of large groups where direct fitness costs are offset by the indirect benefits accrued through such behaviours as cooperative care and altruism, and group foraging among genetic relatives (Hamilton 1964; Maynard Smith 1964; Giraldeau & Caraco 1993; Ross 2001). Temporary splitting of pods along genealogical lines may reflect a mode through which the population is able to respond to changing environmental or demographic conditions that favour smaller groups, whilst maintaining and benefiting from strong familial ties. Interannual fluctuations in the number of clusters and the strength of intrapod associations suggest that rather than true fissioning, intermatrilineal divisions within L pod may occur on a temporary basis analogous to the fission–fusion structuring described for other delphinid populations (Wursig & Wursig 1977; Shane et al. 1986; Wells et al. 1987). Fission–fusion dynamics may reflect a behavioural response of this much larger pod to the changing abundance and distribution of resources such as prey patches. However, such group fluidity may also reflect the lower degree of genetic relatedness (as indicated by a greater number of matrilines) within this pod compared to that within J or K pods.

The patterns resolved in this study clearly illustrate a dynamic social structure with significant changes in the strength of killer whale affiliations during the summer months between years and decades. The decline in social cohesion experienced through the 1990s was common to all three pods and evidenced by both analytical approaches. Moreover, this period of declining social cohesion coincided with the most recent population decline. Such dramatic changes in the social structure of the population may indicate a response to socioecological shifts, and could have significant demographic consequences. Broad examination of the data for correlations between pod size, or population size, and measures of social affiliation failed to reveal trends consistent across all pods. However, the coincidental declines in both social cohesion and population size, and the positive correlation between population size and number of matriline clusters (estimated by the BMM) may suggest concurrent responses to extrinsic variables (e.g. prey abundance and distribution). Because of the paucity of data outside the summer season, seasonal effects were not examined, so the social dynamics described herein only reflect patterns from summer encounters. Quantifying these trends in social structure is the first step towards understanding the factors shaping such social dynamics and the effects of changing patterns of social structure. Further analyses exploring potential explanatory covariates and seasonal effects are warranted to resolve significant factors shaping killer whale populations.

Both intrinsic and extrinsic factors affect sociality. The distribution and abundance of prey are recognized among the most important extrinsic factors influencing social structure for most medium and large terrestrial carnivores (Kruuk 1966; Bekoff & Wells 1980; Messier 1985; Vucetich et al. 1997). However, while interactions between cetacean grouping behaviour and prey type and availability have been found for killer whales (Baird & Whitehead 2000; Lusseau et al. 2004), the social consequences of such extrinsic factors remain unknown. For the southern resident killer whale population that shows such strong and persistent social ties, resolving this missing link is critical for the conservation of this endangered population. The temporal shifts in social cohesion identified in this study may reflect a response to important changes in prey type or availability and warrant further investigation. Ford et al. (2005) found a significant correlation between chinook salmon, *Oncorhynchus tshawytscha*, abundance and trends in killer whale survival, suggesting that prey limitation may be an important factor in population declines. Understanding the social consequences of population dynamics in response to changes in prey abundance is critical.

Extrinsic variables are known to shape the group structure of many social mammals; however, sociality itself may play an important role in the persistence of this population. By their very nature, matrifocal societies confer particular significance to older females. As such, the death of a matriarch may affect the degree of affiliation both within and between matrilines. Recent studies examining killer whale social networks suggest that particular

Please cite this article in press as: Parsons, K. M., et al., The social dynamics of southern resident killer whales and conservation implications for this endangered population, Animal Behaviour (2009), doi:10.1016/j.anbehav.2009.01.018

ARTICLE IN PRESS



matrilines or individual whales may play central roles in maintaining cohesion within social networks (Williams & Lusseau 2006). The patterns of mating shown by this population will also undoubtedly be affected by shifts in social structure. The best information available to-date indicates that whales within the three southern resident killer whale pods mate outside their natal pod, but within the population (Barrett-Lennard 2000; Barrett-Lennard & Ellis 2001). As such, changes in the degree of social cohesion and the number of social clusters within the population could have marked effects on mating patterns and population growth rates. Considering the longevity of killer whales (females have been estimated to live at least 80 years; Olesiuk et al. 1990), long-term observational studies, such as those on which the current study was based, are important for understanding both the social and population dynamics of killer whales. Despite nearly three decades of data, uncertainty surrounding the implications of the social dynamics described here and the underlying causes still remain.

The inherent grouping patterns described in this study may confer both positive and negative conservation implications. While social interactions provide the opportunity for cultural transmission and social learning (Giraldeau et al. 1994; Deecke et al. 2000; Rendell & Whitehead 2001; Yurk et al. 2002), this structuring also affects population permeability in terms of disease transmission (Altizer et al. 2003; Cross et al. 2004). Mammalian species such as killer whales that live in complex social groups may be particularly vulnerable to infectious diseases for a number of reasons. Most obviously, disease risk is enhanced as a direct result of the close proximity of individuals and the high rates of interindividual contact (Altizer et al. 2003; Caillaud et al. 2006; Guimaraes et al. 2007). Knowledge of association patterns can provide key insight into disease dynamics and, in the case of the African buffalo, *Syncerus caffer*, a critical link between environmental fluctuations and disease dynamics (Cross et al. 2004). Recent studies have emphasized the importance of incorporating data on social structure within epidemiological models (Nunn et al. 2008). highlighting the effect of nonrandom associations of individuals within a population on the spread of infectious disease.

The weight of evidence suggests a strong, yet indirect link between social structure and population dynamics that is probably driven by extrinsic factors. The southern resident killer whale population is a small, demographically closed, endangered population that is characterized by numerous intrinsic characteristics that have the potential to negatively affect its survival. Quantitatively evaluating the social structure and describing the long-term social dynamics of this population provides a first, critical step towards understanding the links between the extrinsic factors shaping social structure and the consequences of past and future changes in social and population dynamics. Real-time responses to extrinsic factors are often reflected by changes in the stability of social units, as such, characterizing past and present social structure provides a benchmark for monitoring the future health of the southern resident killer whale population.

## Acknowledgments

The data used in this study are the result of many years of collaborative fieldwork. We are indebted to the many colleagues and volunteers that participated in both fieldwork and data entry and made this project possible. A special note of credit goes to the late M. A. Bigg, and to G. Ellis, D. Ellifrit, A. van Ginneken. The long-term killer whale studies have been supported by Fisheries and Oceans Canada (DFO) and research grants from Earthwatch Institute. This publication was completed as part of K.M.P.'s National Research Council postdoctoral fellowship hosted by the Northwest Fisheries Science Center (NOAA Fisheries).

## References

**Alexander, R. D.** 1974. The evolution of social behaviour. *Annual Review of Ecology and Systematics*, **5**, 325–383.

**Altizer, S., Nunn, C. L., Thrall, P. H., Gittleman, J. L., Antonovics, J., Cunningham, A. A., Dobson, A. P., Ezenwa, V., Jones, K. E., Pedersen, A. B., Poss, M. & Pulliam, J. R. C.** 2003. Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annual Review of Ecology, Evolution and Systematics*, **34**, 517–547.

**Aviles, L.** 1999. Cooperation and non-linear dynamics: an ecological perspective on the evolution of sociality. *Evolutionary Ecology Research*, **1**, 459–477.

**Baird, R. W. & Whitehead, H.** 2000. Social organisation of mammal-eating killer whales: group stability and dispersal patterns. *Canadian Journal of Zoology*, **78**, 2096–2105.

**Baird, R. W., Hanson, M. B. & Dill, L. M.** 2005. Factors influencing the diving behaviour of fish-eating killer whales: sex differences and diel and interannual variation in diving rates. *Canadian Journal of Zoology*, **83**, 257–267.

**Balcomb, K. C., Boran, J. R. & Heimlich, S. L.** 1982. Killer whales in greater Puget Sound. *Reports of the International Whaling Commission*, **32**, 681–685.

**Barrett-Lennard, L.** 2000. Population structure and mating patterns of killer whales as revealed by DNA analysis. Ph.D. thesis, University of British Columbia.

**Barrett-Lennard, L. & Ellis, G. M.** 2001. *Population Structure and Genetic Variability in the Northeastern Pacific Killer Whales: Towards an Assessment of Population Viability*. Nanaimo, British Columbia: Canadian Science Advisory Secretariat. Fisheries and Oceans Canada Research Document 2001/065.

**Bekoff, M. & Wells, M. C.** 1980. The social ecology of coyotes. *Scientific American*, **242**, 130–148.

**Bertram, B. C.** 1978. Living in groups: predators and prey. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 64–96. Sunderland, Massachusetts: Sinauer.

**Bigg, M. A.** 1982. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. *Reports of the International Whaling Commission*, **32**, 655–666.

**Bigg, M. A., Ellis, G. M., Ford, J. K. B. & Balcomb, K. C.** 1987. *Killer Whales: a Study of Their Identification, Genealogy and Natural History in British Columbia and Washington State*. Nanaimo, BC: Phantom Press.

**Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. K. B. & Balcomb, K. C.** 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington state. In: *Individual Recognition of Cetaceans: Use of Photo-Identification and Other Techniques to Estimate Population Parameters* (Ed. by P. Hammond, S. Mizroch & G. Donovan), pp. 383–405. Cambridge: International Whaling Commission.

**Brooks, S. P.** 1998. Markov chain Monte Carlo method and its application. *Statistician*, **47**, 69–100.

**Brooks, S. P. & Gelman, A.** 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, **7**, 434–455.

**Caillaud, D., Levrero, F., Cristescu, R., Gatti, S., Dewas, M., Douadi, M., Gautier-Hion, A., Raymond, M. & Menard, N.** 2006. Gorilla susceptibility to Ebola virus: the cost of sociality. *Current Biology*, **16**, R489–R491.

**Cairns, S. J. & Schwager, S. J.** 1987. A comparison of association indices. *Animal Behaviour*, **35**, 1454–1469.

**Chapman, C. A., Wrangham, R. & Chapman, L. J.** 1995. Ecological constraints on group size: an analysis of spider monkeys and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, **36**, 59–70.

**Clutton-Brock, T. H. & Harvey, P. H.** 1977. Primate ecology and social organisation. *Journal of Zoology*, **183**, 1–39.

**Connor, R. C., Smolker, R. A. & Richards, A. F.** 1992. Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences, U.S.A.*, **89**, 987–990.

**Crook, J. H.** 1970. Social organisation and environment: aspects of contemporary social ethology. *Animal Behaviour*, **18**, 197–209.

**Crook, J. H. & Gartlan, J. S.** 1966. Evolution of primate societies. *Nature*, **210**, 1200–1203.

**Cross, P. C., Lloyd-Smith, J. O., Bowers, J. A., Hay, C. T., Hofmeyr, M. & Getz, W. M.** 2004. Integrating association data and disease dynamics in a social ungulate: bovine tuberculosis in African buffalo in the Kruger National Park. *Annales Zoologici Fennici*, **41**, 879–892.

**Deecke, V. B., Ford, J. K. B. & Spong, P.** 1999. Quantifying complex patterns of bioacoustic variation: use of a neural network to compare killer whale (*Orcinus orca*) dialects. *Journal of the Acoustical Society of America*, **105**, 2499–2507.

**Deecke, V. B., Ford, J. K. B. & Spong, P.** 2000. Dialect change in resident killer whales: implications for vocal learning and cultural transmission. *Animal Behaviour*, **60**, 629–638.

**Dey, D., Muller, P. & Sinha, D.** 1999. *Practical Nonparametric and Semiparametric Bayesian Statistics*. New York: Springer.

**Durant, S. M., Kelly, M. & Caro, T. M.** 2004. Factors affecting life and death in Serengeti cheetahs: environment, age and sociality. *Behavioral Ecology*, **15**, 11–22.

**Emlen, S. T. & Oring, L. W.** 1977. Ecology, sexual selection and the evolution of mating systems. *Science*, **197**, 215–223.

**Escobar, M. D. & West, M.** 1995. Bayesian density estimation and inference using mixtures. *Journal of the American Statistical Association*, **90**, 577–588.

Please cite this article in press as: Parsons, K. M., et al., The social dynamics of southern resident killer whales and conservation implications for this endangered population, Animal Behaviour (2009), doi:10.1016/j.anbehav.2009.01.018

**Fernando, P. & Lande, R.** 2000. Molecular genetic and behavioural analysis of social organisation in the Asian elephant (*Elephas maximus*). *Behavioral Ecology and Sociobiology*, **48**, 84–91.

**Ford, J. K. B.** 1991. Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal of Zoology*, **69**, 1454–1483.

**Ford, J. K. B., Ellis, G. M. & Balcomb, K. C.** 1994. *Killer Whales: the Natural History and Genealogy of Orcinus Orca in British Columbia and Washington State*. Vancouver: UBC Press.

**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: UBC Press.

**Ford, J. K. B., Ellis, G. M. & Olesiuk, P. F.** 2005. *Linking Prey and Population Dynamics: Did Food Limitation Cause Recent Declines of 'Resident' Killer Whales (*Orcinus orca*) in British Columbia?* Nanaimo, British Columbia: Canadian Science Advisory Secretariat. Research Document 2005/045.

**Gelman, A. & Rubin, D. B.** 1992. Inference from iterative simulation using multiple sequences (with discussion). *Statistical Science*, **7**, 457–511.

**Ginsberg, J. R. & Young, T. P.** 1992. Measuring association between individuals or groups in behavioural studies. *Animal Behaviour*, **44**, 377–379.

**Giraldeau, L.-A. & Caraco, T.** 1993. Genetic relatedness and group size in an aggregation economy. *Evolutionary Ecology*, **7**, 429–438.

**Giraldeau, L.-A., Caraco, T. & Valone, T. J.** 1994. Social foraging: individual learning and cultural transmission of innovations. *Behavioral Ecology*, **5**, 35–43.

**Gowans, S., Wursig, B. & Karczmarski, L.** 2007. The social structure and strategies of delphinids: predictions based on an ecological framework. *Advances in Marine Biology*, **53**, 195–294.

**Guimaraes Jr., P. R., de Menezes, M. A., Baird, R. W., Lusseau, D., Guimaraes, P. & dos Reis, S. F.** 2007. Vulnerability of a killer whale social network to disease outbreaks. *Physical Review, E*, **76**, 1–4.

**Hamilton, W. D.** 1964. The genetical evolution of social behaviour. I, II. *Journal of Theoretical Biology*, **7**, 1–52.

**Heimlich-Boran, S. L.** 1986. Cohesive relationships among Puget Sound killer whales. In: *Behavioral Biology of Killer Whales* (Ed. by B. C. Kirkevold & J. S. Lockard), pp. 251–284. New York: Alan R. Liss.

**Hinde, R. A.** 1976. Interactions, relationships and social structure. *Man*, **11**, 1–17.

**Hoelzel, A. R.** 1993. Foraging behaviour and social group dynamics in Puget Sound killer whales. *Animal Behaviour*, **45**, 581–591.

**Kappeler, P. & van Schaik, C. P.** 2002. Evolution of primate social systems. *International Journal of Primatology*, **23**, 707–740.

**Keane, B., Waser, P. M., Creel, S. R., Creel, N. M., Elliott, L. F. & Minchella, D. J.** 1994. Subordinate reproduction in the dwarf mongoose. *Animal Behaviour*, **47**, 65–73.

**Keeling, M. J. & Eames, K. T. D.** 2005. Networks and epidemic models. *Journal of the Royal Society Interface*, **2**, 295–307.

**Kruuk, H.** 1966. Clan-system and feeding habits of spotted hyenas (*Crocuta crocuta*). *Nature*, **209**, 1257–1259.

**Lefebvre, D., Menard, N. & Pierre, J. S.** 2003. Modelling the influence of demographic parameters on group structure in social species with dispersal asymmetry and group fission. *Behavioral Ecology and Sociobiology*, **53**, 402–410.

**Lott, D. F.** 1984. Intraspecific variation in the social systems of wild vertebrates. *Behaviour*, **88**, 266–325.

**Lusseau, D., Williams, R., Wilson, B., Grellier, K., Barton, T. R., Hammond, P. S. & Thompson, P. M.** 2004. Parallel influence of climate on the behaviour of Pacific killer whales and Atlantic bottlenose dolphins. *Ecology Letters*, **7**, 1068–1076.

**Maynard Smith, J.** 1964. Group selection and kin selection. *Nature*, **201**, 1145–1147.

**Messier, F.** 1985. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. *Canadian Journal of Zoology*, **63**, 239–245.

**Miller, P. J. O.** 2006. Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. *Journal of Comparative Physiology A*, **192**, 449–459.

**Miller, P. J. O. & Bain, D. E.** 2000. Within-pod variation in the sound production of a pod of killer whales, *Orcinus orca*. *Animal Behaviour*, **60**, 617–628.

**Neal, R. M.** 2000. Markov chain sampling methods for Dirichlet process mixture models. *Journal of Computational and Graphical Statistics*, **9**, 249–265.

**Nousek, A. E., Slater, P. J. B., Wang, C. & Miller, P. J. O.** 2006. The influence of social affiliation on individual vocal signatures of northern resident killer whales (*Orcinus orca*). *Biology Letters*, **2**, 481–484.

**Nunn, C. L., Thrall, P. H., Stewart, K. & Harcourt, A. H.** 2008. Emerging infectious diseases and animal social systems. *Evolutionary Ecology*, **22**, 519–543.

**Olesiuk, P. F., Bigg, M. A. & Ellis, G. M.** 1990. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Reports of the International Whaling Commission, Special Issue*, **12**, 209–244.

**Packer, C., Scheel, D. & Pusey, A. E.** 1990. Why lions form groups: food is not enough. *American Naturalist*, **136**, 1–19.

**Rendell, L. & Whitehead, H.** 2001. Culture in whales and dolphins. *Behavioural and Brain Sciences*, **24**, 309–382.

**Riesch, R., Ford, J. K. B. & Thomsen, F.** 2005. Stability and group specificity of stereotyped whistles in resident killer whales, *Orcinus orca*, off British Columbia. *Animal Behaviour*, **71**, 79–91.

**Ross, K. G.** 2001. Molecular ecology of social behaviour: analyses of breeding systems and genetic structure. *Molecular Ecology*, **10**, 265–284.

**Schnell, G. D., Watt, D. J. & Douglas, M. E.** 1985. Statistical comparison of proximity matrices: applications in animal behaviour. *Animal Behaviour*, **28**, 239–253.

**Shane, S. H., Wells, R. S. & Wursig, B.** 1986. Ecology, behaviour and social organization of the bottlenose dolphin: a review. *Marine Mammal Science*, **2**, 34–63.

**Sinha, A., Mukhopadhyay, K., Datta-Roy, A. & Ram, S.** 2005. Ecology proposes, behaviour disposes: ecological variability in social organization and male behavioural strategies among wild bonnet macaques. *Current Science*, **89**, 1166–1179.

**Sundaresan, S. R., Fischhoff, I. R., Dushoff, J. & Rubenstein, D. I.** 2007. Network metrics reveal differences in social organization between two fission–fusion species, Grevy's zebra and onager. *Oecologia*, **151**, 140–149.

**Symington, M. M.** 1990. Fission-fusion social organization in *Ateles* and *Pan*. *International Journal of Primatology*, **11**, 47–61.

**Vucetich, J. A., Peterson, R. O. & Waite, T. A.** 1997. Effects of social structure and prey dynamics on extinction risk in gray wolves. *Conservation Biology*, **11**, 957–965.

**Wade, P. R.** 2000. Bayesian methods in conservation biology. *Conservation Biology*, **14**, 1308–1316.

**Wells, R. S., Scott, M. D. & Irvine, A. B.** 1987. The social structure of free-ranging bottlenose dolphins. In: *Current Mammalogy* (Ed. by H. H. Genoways), pp. 247–305. New York: Plenum.

**Whitehead, H.** 1997. Analysing animal social structure. *Animal Behaviour*, **53**, 1053–1067.

**Whitehead, H.** 1999. Testing association patterns of social animals. *Animal Behaviour*, **57**, F26–F29.

**Whitehead, H. & Dufault, S.** 1999. Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. *Advances in the Study of Behavior*, **28**, 33–74.

**Whiten, A.** 2000. Primate culture and social learning. *Cognitive Science*, **24**, 477–508.

**Williams, R. & Lusseau, D.** 2006. A killer whale social network is vulnerable to targeted removals. *Biology Letters*, **2**, 497–500.

**Wittemyer, G., Douglas-Hamilton, I. & Getz, W. M.** 2005. The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour*, **69**, 1357–1371.

**Wrangham, R. W.** 1980. An ecological model of female-bonded primate groups. *Behaviour*, **75**, 262–300.

**Wrangham, R. W., Gittleman, J. L. & Chapman, C. A.** 1993. Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behavioral Ecology and Sociobiology*, **32**, 199–209.

**Wronski, T. & Apio, A.** 2006. Home-range overlap, social vicinity and agonistic interactions denoting matrilineal organisation in bushbuck, *Tragelaphus scriptus*. *Behavioral Ecology and Sociobiology*, **59**, 819–828.

**Wursig, B. & Wursig, M.** 1977. The photographic determination of group size, composition and stability of coastal porpoises (*Tursiops truncatus*). *Science*, **198**, 755–756.

**Yurk, H., Barrett-Lennard, L., Ford, J. K. B. & Matkin, C. O.** 2002. Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska. *Animal Behaviour*, **63**, 1103–1119.

Please cite this article in press as: Parsons, K. M., et al., The social dynamics of southern resident killer whales and conservation implications for this endangered population, Animal Behaviour (2009), doi:10.1016/j.anbehav.2009.01.018