Determinants of group splitting: an examination of environmental, demographic, genealogical and state-dependent factors of matrilineal fission in a threatened population of fish-eating killer whales (*Orcinus orca*)

By

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B.Sc., University of Victoria, 2010

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ABSTRACT

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Group living is a social strategy adopted by many species, where individuals can exhibit long-term social affiliation with others, strengthened through cooperative behaviour and often kinship. For highly social mammals, changes in group membership may have significant consequences for the long-term viability and functioning of a population. Detecting significant social events is essential for monitoring the social dynamics of such populations and is crucial to determining the factors underlying these events. Detecting when changes in social organization occur, especially with incomplete data, poses significant analytical challenges. To resolve this issue, I developed and assessed a straightforward, multi-stage and generalizable method with broad utility for ecologists interested in detecting and subsequently investigating causes of changes in social organization. My approach illustrates the frequency and ecological relevance of binary group fission and fusion events in a population of fish-eating ‘Resident’ killer whales (*Orcinus orca*). Group fission is a process commonly found in social mammals, yet is poorly described in many taxa, and has never been formally described in killer whales. To address this gap, I provided the first description of matrilineal fission in killer whales, from a threatened but growing Northern Resident killer whale population in which matrilineal fission has been observed for the past three decades. I also undertook the first comprehensive assessment of how killer whale intragroup cohesion is influenced by group structure, demography and resource abundance. Fission in

Northern Resident killer whales occurred both along and across maternal lines, where animals dispersed in parallel with their closest maternal kin. I show that fission in this population is driven primarily by population growth and the demographic conditions of groups, particularly those dictating the nutritional requirements of the group. I posit that intragroup food competition is the most likely explanation for group fission in this population, where prey abundance also has ancillary effects. As group fission can have a direct impact on the fitness of group members and the long-term viability of a population, this analysis underscores the importance of incorporating studies of sociality into the management of threatened populations of social mammals.

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Danke

DEDICATION

For my mother, Uli

and to all the matriarchs who bind us together

AUTHORSHIP & PUBLICATION STATEMENT

This thesis is composed of two scientific manuscripts of which I am the lead author. Dr. John Ford provided the initial concept for this project and provided the killer whale data. I performed all data analysis, initial interpretation of results and final manuscript presentations. Dr. Chris Darimont, Dr. John Ford, Dr. Lance Barrett-Lennard and Graeme Ellis provided assistance with interpretation of results and also supplied editorial comments and suggestions incorporated into the final manuscripts.

Both manuscripts were written for submission to *Behavioural Ecology and Sociobiology*. The two chapters are therefore formatted according to the guidelines of that journal.

INTRODUCTION

Research context

What makes a society?

> *Sociality means group-living. The formulation of any general theory of social behaviour begins, therefore, with a description of the selective forces causing and maintaining group living.*
>
> —Richard Alexander (1974)

Groups are the fundamental unit of a society. It is often assumed that living in complex social groups is superior to living solitarily, however, there are advantages and disadvantages to both. Group living, like any survival strategy, will continue to be effective and exist only so long as its benefits outweigh the costs to individuals that comprise groups.

Group living can manifest itself in two ways. First, groups may take form in *aggregations*, which are typically established due to short-term benefits to individuals and the longevity of which is dependent on the balance of immediate advantages and disadvantages (e.g. Riipi et al. 2000). Insect swarms and ungulates herding for protection from a nearby predator provide examples. Second, *congregations* arise from benefits to individuals resulting from long-term associations (e.g. Moss 1988; Parsons et al. 2009; Gero et al. 2015). The persistence of congregations is contingent on the balance between short- and long-term benefits and costs (Dunbar and Shultz 2010). This congregational sociality is often referred to as 'higher' sociality and is likely achieved as a function of a species' cognitive capacity; it has been posited that larger brain sizes are thought to be associated with the need to deal with increased complexity of social relationships (Byrne and Whiten 1988) or with the capacity to endure long-term relationships (Shultz and Dunbar 2007). It may be for this reason that most animals exhibiting congregational sociality, such as humans, elephants, lions, primates, and cetaceans, tend to have large brains (Connor et al. 1998).

Most benefits of group living involve mutualistic, cooperative, or altruistic acts. These benefits generally fall into two ecological categories, predation pressure and resource distribution, and include: increased vigilance and predator detection (e.g. Smith 1965; Delm 1990), group defence (e.g. Packet et al. 1990; Gursky 2005), increased foraging efficiency (e.g. Bronikowski and Altmann 1996; Sharpe 2001), division of labour (e.g. Lidgard et al. 2012), greater care for young (e.g. Grimes 1976; Lusseau and Newman 2004), easier access to mates (e.g. Connor et al. 2001; Porschmann et al. 2010), shelter (e.g. Gilbert et al. 2006), an enriched learning environment (e.g. King 1991; McComb et al. 2001; Rendell and Whitehead 2001), and more effective defence of resources (e.g. Mech 1970; Dubois et al., 2002).

Costs of group living are also important factors in the evolution of sociality, often informed by intragroup competition. Like the benefits of group living, costs are most often associated with predation and resource availability. Perhaps the most apparent disadvantage to group living is that it increases the conspicuousness of animals to a predator – though, it allows an individual animal to be inconspicuous in a large group, which can be advantageous. Another disadvantage of group living may be increased competition for space and resources (e.g. Koenig 1981; Janson and Goldsmith 1995; Fritz and de Garine-Wichatitsky 1996). This often results in increased exposure to pathogens and faster dissemination of disease (e.g. Hoogland 1979; Corner et al. 2003). Space competition can also result in physical conflict, which is energetically costly (and potentially fatal) to the individuals involved. Group living can also have reproductive costs to individuals, that may include: competition for mates (particularly for species that mate outside of their group; e.g. Connor et al. 2001; Beise and Voland 2008), as well as suppression of individual reproduction (e.g. Creel and MacDonald 1995; Faulkes and Bennett 2001; VanderWaal et al. 2009), and interference with reproduction (e.g. infanticide: Hardy 1979; Pusey and Packer 1987).

The costs and benefits of group living are functions of group size; as group size increases, the advantages and disadvantages to individuals in groups do so as well, the rate of which is specific to the ecology and social organization of each species and the individual variation found in a given group. The cognitive costs and limitations of species have also been argued to limit group size (Shultz and Dunbar 2007; Dávid-Barrett and Dunbar 2013). It is ultimately the costs of group living that limit group size; when their effects become detrimental to the individuals involved, the group will fragment (e.g. Devore and Hall 1965). For example, group size may be limited by costs of rank competition, as seen in hierarchical systems where the availability of positions within ranks is limited (Ang and Manica 2010; Wong 2011).

It is the differential rate at which advantages and disadvantages increase with group size that provides a theoretical ‘optimal’ size – where the difference between benefits and costs to individuals is greatest. Through management of one’s group size, an individual may theoretically balance the benefits and costs by maintaining membership of an optimal group size (e.g. Creel and Creel 1995; Baird and Dill 1996). This differential rate also indicates a theoretical threshold for when to expect group fragmentation, as costs of group living begin to exceed the benefits to individuals that comprise groups (Lehmann and Boesch 2004).

Group splitting

For socially philopatric animals, those that tend to remain with their group rather than disperse as individuals, large group sizes can produce unfavourable living conditions, under which one’s individual fitness may be compromised. In such cases, the splitting of groups presents the primary means of dispersal for philopatric animals, allowing individuals to disperse without sacrificing all important familiar relationships (e.g. Archie et al. 2006). This phenomenon is found in many mammalian populations, though it occurs relatively rarely within them. Generally poorly understood across taxa, group fission is most well-described in primates (e.g. *Ateles geoffroyi yucatenensis*: Schaffner et al. 2012; *Lemur catta*: Hood and Jolly 1995; Gould et al. 2003; *Macaca fuscata*: Yamagiwa 1985; Oi 1988; *M. maura*: Okamoto and Matsumura 2001; *M. mulatta*: Missakian 1973; Chepko-Sade and Olivier 1979; Chepko-Sade and Sade 1979; Melnick and Kidd 1983; Widdig et al. 2006; *M. sinica*: Dittus 1988; *M. sylvanus*: Prud'Homme 1991; Ménard and Vallet 1993; Kuester and Paul 1997; *Papio cynocephalus*: Van Horn et al. 2007; *Rhinopithecus bieti*: Ren et al. 2012).

Matrilineal society and natal group philopatry

Matrilineal societies are found frequently among gregarious species. In fact, most social mammals are matrilineal to some extent, revolving around the grouping of related females (Armitage 1987). For example, the matriline-based social system can be found in populations of baboons (e.g. *Papio anubis*: Packer 1979), bats (e.g. *Plecotus auritus*: Burland et al. 2001, *Miniopterus shreibersii*: Rodrigues et al. 2010), elephants (e.g. *Loxodonta africana*: Buss 1961), humans (*Homo sapiens*; Allen et al. 2008), hyenas (e.g. *Crocuta crocuta*: Holekamp et al. 1997), killer whales (*Orcinus orca*; Bigg et al. 1990), macaques (e.g. *Macaca fuscata*: Fooden and Aimi 2005), prairie dogs (*Cynomys ludovicianus*; Hoogland 1986), squirrels (e.g. *Sciurus carolinensis*: Koprowski 1996), sperm whales (*Physeter macrocephalus*; Whitehead et al. 1991), and voles (e.g. *Microtus californicus*: Boonstra et al. 1987). The matrilineal social system is considered a highly stable social strategy where both male and female offspring are members of their mother's matrilineal descent group, but only daughters pass on the family line to their offspring. The evolution of matrilineality has been attributed to various factors, including: (1) inclusive benefits gained from kin cooperation in species with paternal uncertainty (e.g., those with polygynous or promiscuous mating systems; Greenwood 1980), as the system provides maternal kin with certainty that they are providing care for animals with whom they share genes (Danielsbacka et al. 2011); (2) individual reproductive success gained by females from the familiarity of local resources, in species whose food resources occur predictably (Lawson Handley & Perrin 2007) and; (3) the tendency for dispersal to be more beneficial to the individual reproductive success of males (through increased mating opportunities; e.g. Pusey and Packer 1987).

Research focus

Killer Whales of the eastern North Pacific

The killer whale (*O. orca*) is an apex predator known to exist in all the world's major oceans, with a minimum estimated total global abundance of 60,000 animals (Forney and Wade 2006). Though widely distributed, the killer whale is found most often in temperate waters and is composed of many discrete regional populations (Leatherwood and Dahlheim 1978; Forney and Wade 2006). Three killer whale *ecotypes* (groupings of killer whales defined by distinct cultural characteristics and ecological specializations; Ford et al. 2000) occur in Canadian Pacific waters. *Residents* are fish-eating killer whales that preferentially forage for salmon, tend to travel in large, cohesive family groups and have a large acoustic repertoire (Bigg et al. 1990; Ford 1991). *Bigg's* (*transients*) are mammal-eating killer whales that usually eat seals, sea lions, dolphins and porpoises (Baird and Dill 1995; Ford et al. 1998). Socially, Bigg's killer whale family units tend to be less cohesive than Residents (Baird and Dill 1996; Baird and Whitehead 2000) and they are known to produce only a small variety of calls (Deecke et al. 2005). *Offshores*, like Residents, are fish eaters with a large variety of acoustic calls, however they often are encountered in extremely large groups and are thought to be shark specialists (Dalheim et al. 2008; Ford et al. 2011; Ford et al. 2014). Only one population of each of the latter two ecotypes is known to regularly occur in British Columbian (BC) waters, while two separate populations of Resident killer whales are found in BC. Despite their overlapping geographic ranges, these four populations of killer whales are acoustically and genetically distinct, as well as socially and reproductively isolated from one another (Bigg 1982; Ford 1991; Barrett-Lennard et al. 1996; Hoelzel et al. 1998; Barrett-Lennard and Ellis 2001; Morin et al. 2010).

As a result of a live-capture fishery (for aquarium displays) that took place in Southern British Columbia and Washington waters in the 1960s and early 1970s (Bigg and Wolman 1975), as well as the naturally small population sizes of killer whale populations, all four populations of killer whales in British Columbia are legally listed under Canada’s Species At Risk Act (SARA) as either Endangered or Threatened. The Southern Resident population, the population hardest hit by the live captures, currently is composed of 83 animals (Balcomb et al. 2016) and is considered Endangered under SARA, while the West Coast Bigg’s and Offshore populations are listed as Threatened under SARA and both number roughly 300 animals (Towers et al. 2012; Ford et al. 2013; Ford et al. 2014).

The Northern Resident Killer Whale (NRKW) population, the focus of this thesis, ranges from southern Washington State to Glacier Bay, Alaska, and is frequently encountered in Canadian Pacific waters. Having been censused regularly since the early 1970s, this population is one of the best-studied killer whale populations in the world; all animals – and the recent genealogy of most – in this closed population are known. This population is considered Threatened and is legally listed under SARA. Though still considered vulnerable to endangerment, this population has been showing signs of recovery, growing in size since the 1970s, and is currently composed of almost 300 animals (Towers et al. 2015).

Killer whales have a mating system in which both sexes mate with multiple partners outside of their natal group and the mother provides care to the offspring (Barrett-Lennard 2000; Ford et al. 2011). All killer whale populations (with known, described social organization) exhibit matrilineal organization, with varying patterns of dispersal. The social organization in Resident killer whales is extremely rare among animal societies. While all mammalian matrilineal systems invest in rearing offspring, male subadults tend to disperse from their family unit once they reach sexual maturation (Greenwood 1980). In Resident killer whales, however, natal philopatry is extremely strong; the bonds between a mother and her offspring persist throughout the whale’s lifetime, with animals of both sexes staying with their mothers for their entire lives (Ford et al. 2000). Even more rare, is that Resident male offspring seem to retain the strongest bonds with their mother throughout their life (Foster et al., 2012a; Wright et al. 2016). A typical Resident family unit will consist of a matriarch, her male and female offspring, as well as the offspring of her female descendants, spanning up to five generations (Bigg et al. 1990).

Because of this strong fidelity to their natal groups, it was thought that as Resident killer whale populations grew, the only opportunity for these philopatric animals to disperse was through the process of matrilineal fission (Bigg et al. 1990). This process involves the splitting of groups along lines of maternal relatedness, such that new groups are predicted to arise after the death of a group’s matriarch (the most recent common maternal ancestor of group members).

Gaps in research

Group fission is a complex, relatively rare, and thus little-understood phenomenon that has yet to be described in detail in killer whales. The long-term study associated with Resident killer whales of the eastern North Pacific provides a unique opportunity to examine matrilineal fission in this species.

Though NRKWs have been studied for over 40 years, their study is hampered by their highly mobility and unpredictable movement patterns. Like most cetacean species with large, often remote geographic ranges, these animals are infrequently and inconsistently encountered and behaviours can only be inferred from observations made at the surface of the water (Mann 1999; Whitehead 2001). Observations of killer whale social dynamics depend on relatively rare and discrete opportunistic encounters with this wide-ranging and sparsely distributed species. Inconsistent and low resight rates often yield imprecise parameter estimates and data gaps in time series, making an assessment of their social history quite difficult.

Despite this, matrilineal splitting has been observed in the growing NRKW population since the mid-1980s (Ford and Ellis 2002). Of significant concern is that high rates of group splitting in the population seemed to coincide with years of low abundance of Chinook salmon (*Oncorhynchus tshawytscha*), the preferred prey of Resident killer whales (Ford et al. 1998; Ford and Ellis 2006). At present, the correlation between NRKW social fission events and Chinook salmon abundance is anecdotal and has yet to be confirmed or thoroughly examined – nor have other potential causes of these fission events (e.g. demographic composition and structure of groups) been studied.

Thesis objectives

1) Detect and locate significant changes in the social organization of the NRKW population, preferably through rule-based, objective and automated methods.
2) Describe the social history and the process of matrilineal fission in NRKWs.

3) Undertake a comprehensive assessment of how fission events (or group cohesion in general) in the NRKW population are affected by population growth, group structure, demography and environmental conditions.

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CHAPTER 1. Using change-point analysis to detect and locate changes in social organization

Abstract

Detecting and locating changes in social organization, especially with incomplete data, poses significant analytical challenges. Here I develop and assess a straightforward, multi-stage and generalizable method with broad utility for ecologists interested in detecting and subsequently investigating causes of changes in social organization. I challenge the procedure by testing it on a 'messy' dataset consisting of scarce, irregularly sampled data, typical of ecological datasets collected on rarely- or opportunistically-encountered animals. I analyzed 803 time series of estimates of association strength between and within social units of a killer whale (*Orcinus orca*) population to detect significant, sustained shifts in mean association strength. Each data series first underwent a non-parametric change-point analysis, using cumulative sums, bootstrapping and binary segmentation. I then subjected data to a quality control charting process, which ultimately produced a mean-shift model. Finally, I scrutinized the detected statistical changes for their biological relevance. Of 231 detected changes, 78 changes were deemed biologically relevant (n=52 fission events; n=26 fusion events). With this approach, I detected 79% of shifts in social association predicted from field observations and cursory visual inspections of time series. Undetected changes were either of distributions not suited to mean-shift models or had too few data points to allow for any detectability. This approach illustrates the frequency and ecological relevance of binary fission and fusion events in animal societies, and the importance of monitoring the social stability of populations for insight into theory and management.

Introduction

The rapid evolution of analytical approaches can yield new insight into fundamental processes related to social animals. Traditionally, sociality, social processes and social structure of animal populations have been described through qualitative methods, based on observations of behaviour, social interactions and group membership (e.g. Missakian 1973; Würsig 1978; Chepko-Sade and Sade 1979; Goodall 1986; Koyama et al. 2002; Bartlett 2003). Over the last two decades, quantitative methods have been developed to define these features of sociality, thereby allowing the detection of changes within them (e.g. Whitehead 1995, 1997; Wittemyer et al. 2005; Archie et al. 2006; Croft et al. 2011). These techniques have provided much improved understanding of the causes of structural changes in social organization, especially for populations where consistent and complete behavioural observations prove difficult (e.g. Whitehead and Christal 2001).

To investigate why changes occur in a process, one must first establish a method to reliably detect them. Manually detecting and determining the location of such changes can often prove difficult due to confounding variation in data series, imprecision of values, data gaps in time series, subjective bias of visual inspection, reliance on arbitrary thresholds, or simply due to the sheer volume of data (e.g. Guralnik and Srivastava 1999). In these cases, rule-based, objective – and ideally automated – quantitative approaches are preferred.

The challenge of quantitatively detecting changes of unknown location in a time series and estimating the location of those changes is referred to as *the change-point problem*, a change-point being a point in time where the statistical properties before and after the point differ. Variously described as *break, turning, or tipping points*, *regime shifting*, *structural breaks*, *detecting disorder* and *segmentation*, the change-point problem has long been discussed in statistical literature (e.g. Shewhart 1926, 1927, 1931; Page 1955; Pettitt 1979) and change-point approaches are widely applied among diverse fields (e.g. Christensen and Rudemo 1996; Talih and Hengartner 2005; Reeves et al. 2007; Kim et al. 2009; Mampaey and Vreeken 2011; Muggeo and Adelfio 2011; Beaulieu et al. 2012). However, they have yet to be commonly applied in ecology.

Most change-point techniques described in existing change-point literature are not particularly well-suited to the properties of behavioural data. These tend to have small sample sizes, have irregular sampling intervals and are frequently not direct measures, but rather, estimates of behavioural parameters, often associated with high imprecision (e.g. Whitehead 2001). Also, due to cryptic behaviour or large or remote geographic ranges, many wildlife populations (or portions thereof) are infrequently encountered. These realities of ecological research often result in ‘messy’ datasets with missing and imprecise values, making detailed social analyses challenging. Accordingly, shift detection methods specific to ecological analyses should be robust to missing and imprecise data. Though some such methods exist (e.g. Beckage et al. 2007; Gurarie et al. 2009), they rarely function with the scarcity of data (e.g. <50 data points) typical of social analysis datasets. As the ability to detect a change depends on the amount of data before and after the change, detecting change-points in small data series can be difficult.

To confront these challenges, I present a multi-stage and generalizable method suitable for broad use by ecologists that detects and locates statistically and biologically significant sustained shifts in social organization. I illustrate this method with the specific objective of detecting significant sustained shifts in social association strength between dyads of groups and individuals using a combination of change-point analysis (CPA) and quality control charting (QCC).

Killer whale (*Orcinus orca*) social systems provide an opportunity to showcase the value of this approach. As a wide-ranging and sparsely distributed marine mammal, observations of killer whale social dynamics depend on relatively rare and discrete opportunistic encounters. Inconsistent and low resight rates often yield imprecise parameter estimates and data gaps in time series. Here I use data from the long-term study of a fish-eating killer whale population in Canadian Pacific waters (e.g. Bigg et al. 1990; Olesiuk et al. 2005; Towers et al. 2015). Studied since the early 1970s, the Northern Resident killer whale (NRKW) population has grown steadily since the study's inception (in 1973; λ = 2.26% from 1973-2015) and is currently composed of approximately 296 individuals. Resident killer whale society is organized in highly stable matrilineal groups, where family groups (matrilines) are composed of a female and her offspring, and the descendants of her female offspring. Therefore a matriline may contain multiple matrilineal subunits nested within it, which I will refer to as submatrilines. Both sexes exhibit life-long philopatry to their natal group, from which no individual dispersal has been observed (Bigg et al. 1990). Using a novel application and combination of existing analytical techniques, I assess the temporal stability of this population's social organization, providing the first step to investigating causes of its organizational changes.

Methods

Test datasets

Datasets were derived from a long-term photo-identification study of NRKWs off the coast of British Columbia, Canada, where individuals were uniquely identified by their dorsal fin shape and distinct natural markings on their 'saddle patch', the light pigmentation posterior of their dorsal fin (Bigg 1982). Spanning from 1973 to 2012, data consist of records of encounters with individuals and groups of Northern Residents, where at least one individual was positively identified. Encounters were considered to have begun when a group of killer whales was spotted by an observer and to have ended when all the whales seen by the observer had been photographed or were otherwise visually confirmed for identification and/or when the observer left the scene. I restricted the analysis to encounters that occurred between the months of June and October to reduce seasonal influence and ensure comparable survey effort among years. I restricted all intramatriline analysis to association between mothers in a given matriline. This restriction is reasonable as no individual dispersal from the matriline has occurred in this population and all group dispersal has occurred at the submatriline level. Therefore, males and females without offspring never disperse from their mothers and their intramatrilineal associations can be considered equivalent to those of their mothers.

Using these encounter data, I estimated annual pairwise association strengths among all matrilines and among all mothers within matrilines. Association among matrilines was estimated by a Simple Ratio Index (SRI; Ginsberg and Young 1992) and association among mothers was estimated by a Half-Weight Index (HWI; Cairns and Schwager 1987). These association indices (AI) were calculated as follows:

$$SRI = \frac{x}{x + y_A + y_B} \tag{1}$$

$$HWI = \frac{x}{x + \frac{1}{2}(y_A + y_B)} \tag{2}$$

where x is the number of encounters in which both mothers/matrilines A and B were identified, y_A is the number of encounters in which mother/matriline A was identified and mother/matriline

B was not, and y_B is the number of encounters in which mother/matriline *B* was identified and mother/matriline *A* was not.

I then estimated the precision of all AI values, where precision was indicated by the coefficient of variation (CV; Whitehead 2008):

$$CV = \sqrt{}((1 - AI)/x \qquad (3)$$

where AI is the association index value and *x* is the number of encounters in which both mothers/matrilines *A* and *B* were identified.

I considered AI values with CVs greater than 0.5 to be of low precision and omitted all such values from the data series. Also, if one or both members of a dyad were encountered fewer than five times in a year, I omitted the AI value for that year. Data series containing fewer than five high-precision AI values over the study period were considered inadequate representations of the given relationships and insufficient for method testing, and were thus discarded from the analysis. After these deletions, 803 test data series remained. All data manipulations, figure generations and statistical analyses were conducted in the R programming environment (version 3.1.2; R Core Team 2014).

Change-point analysis

The change-point analysis (CPA) I detail here is an iterative, distribution-free approach that combines a cumulative sum algorithm, bootstrapping techniques and binary segmentation (Taylor 2000). Its purpose is to detect and locate multiple significant shifts in mean values, yielding a mean-shift model. As it assumes independence of errors, this approach is unsuitable for autoregressive data series.

I used the following CPA procedure. First, all data gaps in time series were omitted to generate continuous, ‘collapsed’ data series. For each AI value in a given data series (Figure

1.1a), I calculated the cumulative sum (CUSUM) of the difference from the overall mean of the data series. A change in the directionality CUSUM values indicated that a change in the mean had likely taken place (Figure 1.1c). The collapsed data series then underwent bootstrap resampling (1000 replicates, without replacement) to generate bootstrap CUSUMs (Figure 1.1d). If the magnitude of change in CUSUM values in a data series, estimated by the maximum range of the CUSUMs, exceeded the magnitude of change of at least 95% of the bootstrap CUSUMs, a significant change was considered to have occurred. The confidence level of a change was calculated as follows:

$$CL = X/N \tag{4}$$

where X is the number of bootstraps whose CUSUM magnitude of change was exceeded by the original data series' CUSUM magnitude of change, and N is the number of bootstrap samples generated.

If a change was detected, its location was determined by mean square error (MSE) estimation. MSE was calculated for all points in the data series and the year that minimized MSE was considered the best estimate of the year preceding the significant change (Figure 1.1e). The significant shift was said to take place between that year and the subsequent one for which data existed. I then determined the confidence interval (95% CI) for the location of each change by the minimum and maximum values of points contiguous to the change-point for which CLs exceeded 0.95. Once the location of the shift was determined, the data series was bifurcated at the location of the shift and the CPA procedure was repeated for each segment, until no more significant change-points were detected.

Quality control charting

For the second step of this approach, I used quality control charting (QCC) to further increase detection sensitivity at the tail ends of data series. In the first step of the QCC process, the stability of a data series is bounded by parameters called sigma limits, which are generated for Individual and Moving Range (ImR) charts (Figure 1.2; Wheeler and Chambers 1992).

I calculated sigma limits and other pertinent values for ImR charts for each data series according to the following:

$$CL_X = \bar{X} \tag{5}$$

where CL_X is the Central Line for the Individual Chart and $\bar{X}$ is the mean AI.

$$NPL_X = \bar{X} \pm \frac{3\,\overline{mR}}{d_2} \tag{6}$$

where NPL_X is the Upper and Lower Natural Process Limit for the Individual Chart (or "three-sigma limit"), $\overline{mR}$ is the mean Moving Range of all pairs of consecutive AI values, and d_2 = 1.128, the bias correction factor for ranges based on subgroups of size $n = 2$ (Harter 1960). I computed the one- and two-sigma limits using the NPL_X formula, substituting the multiplier in the numerator with 1 or 2, respectively.

$$CL_R = \overline{mR} \tag{7}$$

where CL_R is the Central Line for the Moving Range chart

$$UCL_R = D_4 * \overline{mR} \tag{8}$$

where UCL_R is the Upper Control Limit for the Moving Range chart and D_4 = 3.268 (bias correction factor; Wheeler and Chambers 1992).

If significant outliers were present in the data series, the Central Line was defined by the median AI and median Moving Range for the Individual and Moving Range charts, respectively (Wheeler 2010). Sigma limits were then adjusted accordingly:

$$CL_X = \tilde{X} \tag{9}$$

$$NPL_X = \tilde{X} \pm \frac{3\,\widetilde{mR}}{d_4} \tag{10}$$

where $\tilde{X}$ is the AI median, $\widetilde{mR}$ is the median moving range and $d_4 = 0.954$ (bias correction factor; Harter 1960).

$$CL_R = \widetilde{mR} \tag{11}$$

$$UCL_R = D_6 * \widetilde{mR} \tag{12}$$

where $D_6 = 3.865$ (bias correction factor; Wheeler and Chambers 1992).

I detected significant changes in the Individual Chart (Figure 1.2a) using four criteria sensitive to sustained shifts, defined by the *Western Electric Zone Tests* (Wheeler and Chambers 1992). Changes were considered to have occurred whenever:

1) A single value exceeded either the upper or lower three-sigma limit.
2) At least two out of three successive values exceeded the same two-sigma limit.
3) At least four out of five successive values exceeded the same one-sigma limit.
4) At least eight successive values fell on the same side of the Central Line.

Significant changes in the Moving Range Chart were considered to have occurred whenever a single value exceeded the Upper Control Limit (Figure 1.2b).

Assessment of biological relevance of results

As most data series in the test dataset showed consistent AI values over time (i.e. no expected shifts), ‘typical’ AI ranges could be defined for distinct classes of relationships. I estimated typical ranges for each relationship class using the interquartile range (IQR) of all AI values for the given class. Relationships among sister matrilines were bounded between SRI values of 0.6 and 1.0 and those among distantly and non-related matrilines were bounded between SRI values of zero and 0.3. Intramatriline associations were bounded by HWI values of 0.7 and 1.0.

For the purposes of this study, I aimed to detect the splitting of cohesive social groups (‘fission’), as well as the formation of such groups (‘fusion’). In order to be considered a biologically relevant change, representative of a fission or fusion event, a detected shift had to pass two conditions: 1) the magnitude of the shift had to exceed the average CV of adjacent data points (to overcome possible measurement error), and; 2) the location of the mean had to exit or enter a typical relationship class.

Results

Using the CPA procedure, I detected 166 statistically significant shifts in 141 of the 803 data series. I detected an additional 65 shifts in 44 data series with the QCC procedure. The biological validation process found 153 of these combined 231 shifts to be biologically irrelevant, resulting in 78 statistically and biologically significant shifts detected across 55 data series. All of the biologically relevant shifts were expected (Table 1.1)—expected shifts being determined through visual inspection of AI running averages, as well as through field observations from NRKW researchers.

There were 26 expected shifts in 21 data series that went undetected (Table 1.1). Of these, four were data series that underwent gradual changes, six were data series with extremely high interannual variability and eleven were data series with large data gaps, most with fewer than 10 total data points.

The detectability of fission and fusion events in the test dataset did not differ. Most data series (n = 604 of 803; 75%) could not undergo fission, as the dyads were already associating at the lowest possible level of association (SRI = 0-0.3). There were fewer series that were unable to undergo fusion (n = 107 of 803; 13%). Despite this large difference in sample size, the success rates for detecting fission and fusion events were comparable (76% vs 79%; Tables 1.2 and Table 1.3).

Discussion

CPA-QCC approach

This CPA-QCC procedure offers a promising quantitative approach that mitigates the need for arbitrary thresholds or manual inspection of data series to detect changes in social systems. It does, however, require appropriate data contexts. First, it is designed for stable processes with stochastic shifts—those for which probable cause may be assigned. More variable (or unstable) relationships may be better served by smoothed average methods (e.g. Farley and Hinich 1970), whereas generalized linear modeling may provide a better fit to time series marked by gradual changes (e.g. Chamber et al. 2011). Second, the CPA technique used in this approach is designed to detect abrupt changes (i.e. change occurs between two consecutive periods), and therefore cannot take into account protracted transition periods, when the change from one stable mean to the next occurs gradually. However, large confidence intervals for a change-point's location produced by this CPA technique are often a good indicator of an prolonged transition period.

Under appropriate contexts, and when combined with subsequent steps, the CPA technique used offers a robust method. As illustrated in the first step of the approach, Taylor's (2000) CPA technique is attractive because it is distribution-free and produces confidence levels and intervals for change-points and their locations. However, this non-parametric nature also presents a limitation: it can be less sensitive to changes at the tail ends of data series (Robbins et al. 2011). This issue is effectively resolved, however, when CPA is coupled with QCC, in the second step of the approach. Though it is a parametric procedure, the QCC technique is considered robust to non-normality. Nonetheless, this violation tends to produce Type I errors (Dubois 1991). This tendency was corroborated by this analysis, but was rectified through the assessment of the biological relevance of results in the third step of my approach.

Detecting changes in association strength was difficult when data series had high variation. To mitigate this problem, the CPA technique could be applied differently for data series with or without outliers, as I did in the QCC step of the approach. For any data series with outliers, the CPA technique can simply be conducted using ranks of association values, rather than the values themselves (Taylor 2000).

Most missed changes were from data series containing too few data points, but I identified how these failures of detection can be avoided. In this analysis, I attempted to strike a balance between precision and power by removing data series with too few precise data points to be considered adequate representations of the given relationships. Despite this effort, several data series containing expected shifts eluded the detection procedure because they still contained too few values; when data series contained fewer than ten data points, change-point detection was often unsuccessful. Given that autocorrelation tests are additionally constrained, if not impossible, with such small sample sizes (DeCarlo and Tryon 1993), I recommend restricting analysis to data series containing no fewer than ten data points.

Treatment of missing data

Common in ecological datasets, data gaps present many challenges during analysis. Researchers often confront this problem by removing all data series with missing data from the analysis, filling in data gaps through imputation or interpolation, or excluding missing values by closing data gaps.

In the context of CPA, it is unclear the extent to which these treatments affect the detectability of change-points. Removal of incomplete data series would not affect the CPA procedure itself, but extensive data exclusion may result in too few cases, severely weakening the explanatory power of results. For example, in the test dataset used in this analysis, was I to eliminate all data series with incomplete time series, only seven time series—less than one per cent of the original dataset—would remain. Imputation, as well, is not always a suitable treatment for missing data (Rubin 1976; Little and Rubin 2002; Nakagawa and Freckleton 2008, 2011). Imputation and interpolation can not only artificially inflate the precision of a change-point's location, but can also lead to non-independence of errors and an underestimation of overall variance, thereby increasing the probability of Type I errors (Rosenfield et al. 2010). Excluding missing values may also cause Type I errors, as closing data gaps can lead to discontinuities in the data series that can be mistaken for change-points (Pekarik and Weseloh 1998).

In this analysis, I chose to close data gaps for the CPA procedure and then restored them to be taken into account in the definition of a change-point's location. I was acutely aware of the problems that could arise from this treatment and therefore looked for any undue influence my treatment of data gaps had on the results. Additionally, I preferred this treatment of data gaps because I considered uncertainty in the change-point's location (due to data gaps) important to take into account, rather than something to be disregarded and replaced with an artificially precise value.

Determining biological relevance

Determining biological relevance needs to be tailored to the characteristics of the study system and the specific question being asked of it (see Martínez-Abraín 2007, 2008). Thus, the specific steps I took in this study to determine biological relevance are not necessarily widely applicable. In this case, the stable social structure of Resident killer whales allowed typical ranges of association values to be defined. For animal societies with more dynamic social organization, other frameworks for biological relevancy would likely be required. Moreover, because fission and fusion were important processes to quantify for this population, I took pronounced measures to ensure the biological magnitude of shifts.

Conclusion

As interactions between individuals and higher-level groupings may be used to define a population's social structure (Hinde 1976; Whitehead and Dufault 1999), it stands that significant binary changes in the association between individuals and groups may signify an important change in group membership and social organization of a population. Accordingly, new tools to describe such social dynamics of populations are valuable. The fission and fusion events detected in this study population using the CPA-QCC approach described here are dramatic and sudden shifts in long-term associations that may have significant population-level consequences for the health and functioning of a population (Parsons et al. 2009). Detecting and determining the temporal locations of events like these are key steps in monitoring the social dynamics of populations and are essential to determining the factors that underlie them. This general approach is not restricted to dyadic analyses such as those presented here, and could be readily applied to many data series with gaps and small sample sizes.

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Tables

Table 1.1 Detection success of CPA-QCC approach, after biological validation, for all test data series (n = 803). Predictive values indicate the probability that the model's prediction is true. Success indicates the sensitivity (proportion of true positives) and specificity (proportion of true negatives) of the detection procedure. The two values present in the Expected and Detected Changes cell correspond to the number of data series where all expected changes were detected and the number of data series where at least one (but not all) expected changes were detected, respectively.

		Expected		Predictive value
		Change	No change	
Detected	Change	50 | 5	0	1.00
	No change	16	732	0.98
	Success	0.77	1.00	

Table 1.2 Detection success for fission events using CPA-QCC approach, after biological validation, for test data series in which fission events were possible (n = 199).

		Expected		Predictive value
		Fission	No fission	
Detected	Fission	41	0	1.00
	No fission	13	145	0.92
	Success	0.76	1.00	

Table 1.3 Detection success for fusion events using CPA-QCC approach, after biological validation, for test data series in which fusion events were possible (n = 696).

		Expected		Predictive value
		Fusion	No fusion	
Detected	Fusion	30	0	1.00
	No fusion	8	658	0.99
	Success	0.79	1.00	

Figures

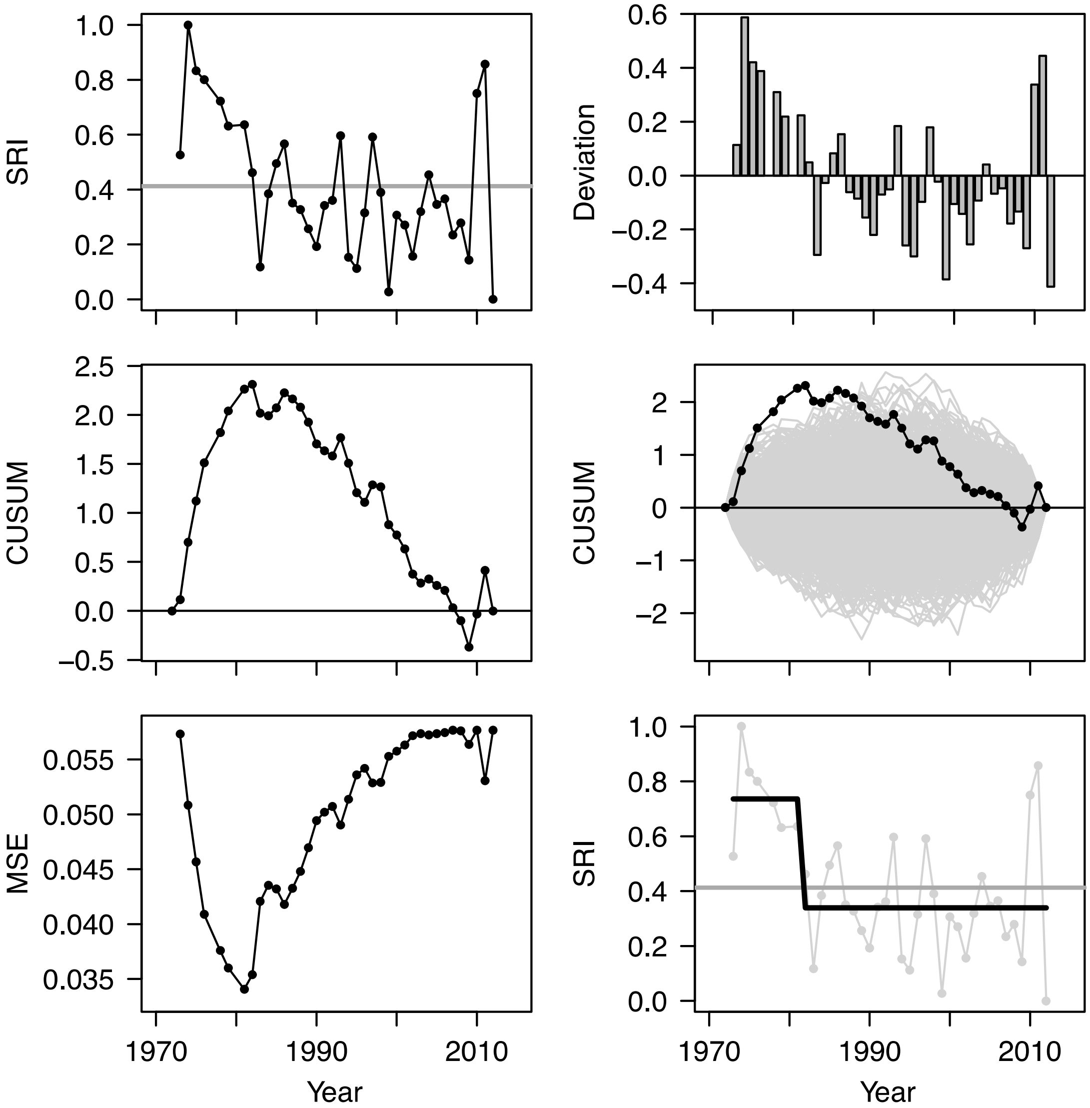

Figure 1.1 Example of the CPA procedure used to detect and locate shifts in **(a)** association strength between two matrilines over time (grey line indicates overall mean). The AI differences from overall mean **(b)** and the cumulative sums (CUSUMs) of these differences **(c)** were computed. **(d)** Bootstrap CUSUMs (grey lines) were then compared to the CUSUM of the data series. **(e)** The location of the shift was estimated by the point in the data series that minimized mean square error. **(f)** In this example, this procedure resulted in a shift detected between 1981 and 1982, when the mean shifted from 0.74 to 0.34 (CL = 98.9%), where grey line indicates the overall mean and black line represents the mean shift model. Data series displayed in Figure 1.1 and 1.2 refer to the same dyadic association.

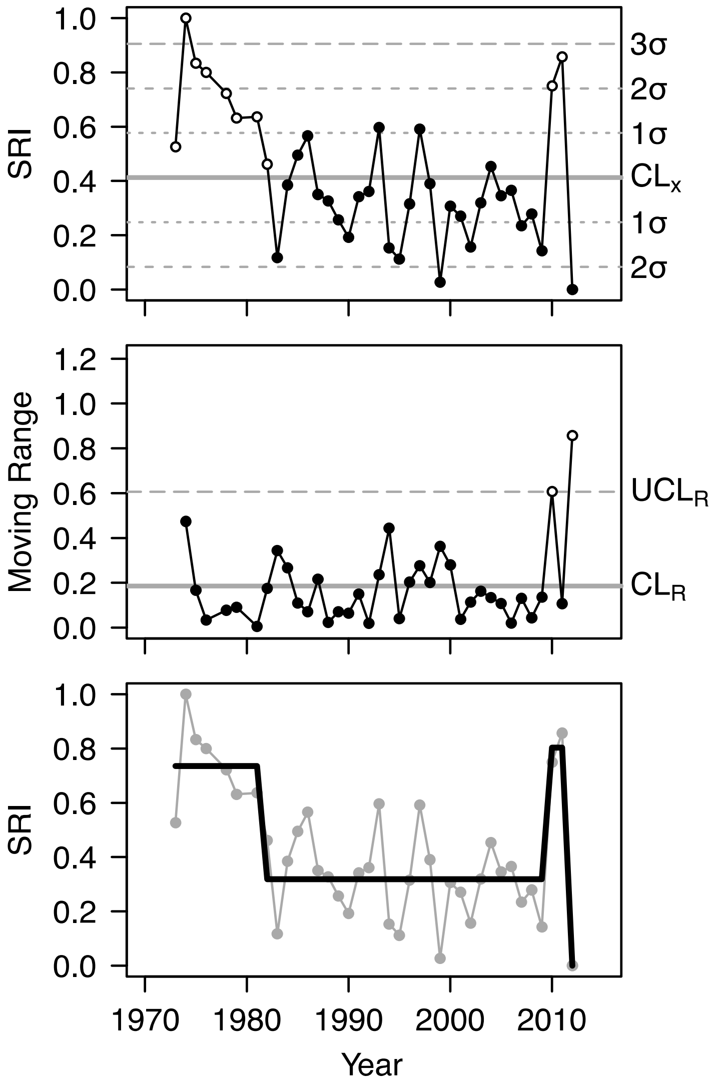

Figure 1.2 Example of **(a)** Individual and **(b)** Moving Range charts of estimated association strength between two family groups. Data series displayed in Figure 1.1 and 1.2 refer to the same dyadic association. Black points indicate regions of statistical stability in the overall process. White points are considered 'unstable' periods during which the source of variation is likely due to an external, assignable cause. In this case, ImR charting detected three distinct shifts during this time series **(c)**; the first reflects the shift found by the CPA process between 1981-82 (Figure 1.1f); the second and third went undetected by CPA, but are clearly detected by the QCC process, between 2009-10 and 2011-12, respectively.

CHAPTER 2. Intragroup competition for food predicts matrilineal fission in a highly philopatric mammal

Abstract

For socially philopatric animals, those that tend to remain with their group rather than disperse as individuals, large group sizes can produce unfavourable living conditions, under which one's individual fitness may be compromised. In such cases, the splitting of groups presents the primary means of dispersal for philopatric animals, allowing animals to disperse without sacrificing all important familial relationships (e.g. Archie et al. 2006). This phenomenon is found in many matrilineal mammalian populations, though it occurs relatively rarely within them. Here I provide the first description of matrilineal fission in killer whales (*Orcinus orca*), from a threatened population where matrilineal fission has been observed for the past three decades but never formally documented. I also undertake the first comprehensive assessment of how killer whale intragroup cohesion is influenced by group structure, demography and resource abundance. Fission was observed to occur both along and across maternal lines, where animals dispersed in parallel with their closest maternal kin. I show that group cohesion in this population is driven primarily by population growth and demographic conditions of groups, particularly those dictating the nutritional requirements of the group. I posit that intragroup food competition is the most likely explanation for group fission in this population, where prey abundance also has ancillary effects. As group fission can have a direct impact on the fitness of group members and the long-term viability of a population, this study underscores the importance of incorporating studies of sociality into the management of threatened populations of social mammals.

Introduction

The matrilineal society is a stable social strategy adopted by many gregarious mammals, revolving around cooperative groups of related females. Most matrilineal societies exhibit sex-biased dispersal, where females are philopatric (remain with their natal group) and males typically disperse, often around the age of maturity (Greenwood 1980; Johnson 1986; Clutton-Brock and Lukas 2012). Under unfavourable group conditions, often due to a group's growth in size or change in composition, group fission is the primary process by which philopatric females may disperse (e.g. Dittus 1988; Henzi et al. 1997; Holekamp et al. 1997; Lefebvre et al. 2003; Van Horn et al. 2007). Group fission in matrilineal societies often occurs along lines of maternal relatedness, allowing animals to disperse without sacrificing all familiar social relationships (Chepko-Sade and Olivier 1979; Archie et al. 2006; Widdig et al. 2006; VanderWaal et al. 2009; Sueur et al. 2011).

Matrilineal fission has yet to be described in killer whales (*Orcinus orca*), despite the matrilineal and philopatric nature of their societies. Piscivorous 'Resident' killer whales of the eastern North Pacific, in particular, provide a compelling study of matrilineal splitting; they are the longest studied killer whales in the world and are known to live in highly stable matrilineal groups where family groups are composed of a female, her offspring, and her descendants through maternal lines, for up to five generations (Bigg et al. 1990). These groups are closed to immigration and both sexes exhibit life-long philopatry to their natal group (Ford et al. 2000; Parsons et al. 2009).

The genealogy and social organization of Resident killer whales has been described through a 43 year-long study which uses photo-identification of individually distinct natural markings to conduct annual censuses of individuals (Bigg 1982; Ford et al. 2000; Towers et al.

2015; Balcomb et al. 2016). This study has also described hierarchical acoustical organization in Resident society: groups of matrilines sharing similar vocal repertoires are called ‘pods’ and are thought to share a common maternal ancestor (Ford 1989; Bigg et al. 1990; Deecke et al. 2010). At their highest level of organization, Resident killer whale populations are composed of acoustic clans, the vocal repertoires of which share none of the same calls (Ford 1991).

In Canadian Pacific waters, the Resident killer whale ecotype is found in two discrete populations that are socially and genetically isolated from one another, despite having overlapping geographic ranges (Bigg et al. 1990; Ford et al. 2000). The Southern Resident killer whale population is an endangered population numbering 83 animals that has shown minimal growth over the period of its study, while the Northern Resident killer whale (NRKW) population has been growing steadily since the beginning of its study in 1973 and currently is composed of 296 animals (Towers et al. 2015; Balcomb et al. 2016). It is due to this long-term growth and strong natal philopatry that new groups were expected to form in the NRKW population through matrilineal fission (Bigg et al. 1990). And it is through the lens of the NRKW population that I provide the first description of matrilineal fission in killer whales.

For the first decade of the NRKW study, pods were socially cohesive units, matrilines within them associating more regularly with one another than with matrilines from different pods (Bigg et al. 1990). In the mid-1980s, researchers first observed matrilines from the same pods associating less frequently with one another, some almost disassociating completely. This phenomenon was so widespread in the population that the term ‘pod’ quickly became an irrelevant construct of Northern Resident social organization (Ford and Ellis 2002). Of the sixteen pods originally described by Bigg et al. (1990), only half met the social definition of ‘pod’ by the year 2000 and only three met the definition in 2014. Today, the term ‘pod’ is restricted to its acoustic definition or, otherwise, is used in an ephemeral sense to describe a group of animals that are encountered together. Here, I use the term ‘social group’ to describe a group of animals that associate frequently with one another over long periods of time (see Box 1).

Box 1: Social and genealogical terminology used to describe Resident killer whale organization in this study

Genealogy: all descendants that can be traced back to a common maternal ancestor known to researchers. This is a completely asocial term, limited in this study to genetically-validated genealogies. I consider ‘known’ maternal genealogies to be those established through maternal associations observed since birth and ‘assumed’ maternal genealogies to be those inferred from consistent behavioural observations amongst animals born prior to the study (*see* Bigg et al. 1990; Towers et al. 2015).

Lineage: a living female with no living maternal ancestors, and all her matrilineal descendants. Like *genealogy*, this term is completely independent of sociality and is limited to relatives known to researchers. This term is used interchangeably with ‘matriline’ so long as no intralineage splitting has occurred within the group (i.e. ‘lineage’ is equivalent to ‘matriline’ so long as all lineage members are socially cohesive).

Matriline: a group composed of a living female who is either socially independent from her maternal ancestors and/or has no living maternal ancestors, plus all her matrilineal descendants with which she is socially cohesive. This term is used interchangeably with ‘lineage’ so long as no intralineage splitting has occurred within the group.

Submatriline: a functional matrifocal unit (at minimum, mother and offspring) that is still socially cohesive with its matriline. All submatrilines are candidates for group dispersal.

Social group: an assemblage of maternally-related individuals frequently and consistently encountered with one another. Social groups may be composed of a single or several matrilines. This long-term affiliation of animals may or may not be equivalent to an acoustical ‘pod’, a genealogy, a lineage or a matriline, depending on one’s location in the study’s time series.

At the start of the study, genealogies, lineages and matrilines all represented equivalent units – it is through the deaths of matriarchs and group fission that these three terms have come to represent different groupings of animals.

Note that when I refer to genealogies and lineages I am only speaking to maternal genealogies and maternal lineages, as paternal genealogies are unknown in this population.

By these definitions, this NRKW study has tracked 90 lineages and 96 matrilines from 51 known (31 assumed) genealogies over a 43-year period (1973-2015). Currently, the NRKW population is composed of 296 animals from 46 known (26 assumed) genealogies. As of 2015, the population contained 40 lineages and 45 matrilines.

Splitting was observed within pods composed of both multiple and single known maternal genealogies. In the former case, it was assumed that the multiple genealogies originated from a common maternal ancestor (Ford 1989, 1991; Barrett-Lennard 2000; Deecke et al. 2010). In the latter, the matriarch of the group was alive at the beginning of the study but, upon her death, her lineage gave rise to multiple lineages that in turn separated socially. This process of lineages splitting apart, termed *intragenealogical fission* (also referred to as 'vertical' fission; Widdig et al. 2006), can be generally described as splitting along maternal lines among lineages that share a common maternal ancestor (Lefebvre et al. 2003).

In the late 1990s, a second process of group splitting began to be observed in the NRKW population: that of daughters dispersing (along with their submatriline) from their natal group while their mothers were still alive. This group dispersal was quite unexpected as, up to that time, all animals in Resident populations were known to stay with their mothers' groups for their entire lives – the only NRKW exceptions being three orphans that became separated from their matrilines following the deaths of their mothers. This process of *intralineage* (or 'horizontal') *fission*—splitting across lines of maternal relatedness (Lefebvre et al. 2003; Widdig et al. 2006)—followed consistent rules: dispersing groups were always matrifocal, always a mother with her descendants. As of 2014, the only group observed to permanently disperse from a living matriarch in the NRKW population was the oldest daughter of the matriarch, along with her submatriline. There was one exceptional case in which the second oldest daughter and her submatriline dispersed from her mother and natal group, though this was only after the oldest daughter (her older sister) and her submatriline had already split from the group. It is worth noting that in all cases, the dispersing daughter was the head of the group's largest submatriline.

The intralineage splitting process was observed throughout the population but only occurred in single-matriline groups, some the products of previous intragenealogical splitting.

In both intragenealogical and intralineage NRKW fission events, product groups became their own discrete social groups, rather than migrating to join others (e.g. Chepko-Sade and Sade 1979; Van Horn et al. 2007). Intragenealogical splits occurred more frequently than did intralineage splits, though the former process began to be observed at an earlier stage of the study than was the latter. While the process of intragenealogical splitting could be quite drawn out, sometimes taking over a decade, the process of intralineage splitting was often relatively quick, on the scale of months to only one or two years.

In addition to describing matrilineal fission in Northern Resident killer whales, I also wished to address concerns that environmental pressures were driving these fission events. High rates of matrilineal splitting in the Northern Resident population were anecdotally observed to coincide with years of low abundance of Chinook salmon (*Oncorhynchus tshawytscha*), the preferred prey of Resident killer whales. Thus, there existed concern that salmon abundance, and consequently fishery competition, may be affecting the integrity of this population's social organization. Here, I present the first comprehensive assessment of how Resident group cohesion is influenced by group structure, demography and resource abundance.

Methods

Population dynamics and group structure

To investigate the effects of NRKW population dynamics on its genealogical and social organization, I examined the relationship between NRKW population growth and various descriptors of group genealogy and structure. First, I studied how genealogically-fixed groupings (acoustical pods and lineages) were affected by population growth by running correlations between population parameters (size and interannual growth rate) and three group characteristics: group size, intragroup maternal relatedness and intragroup cohesion. Second, to examine the effect of population growth on the rate of matrilineal fission and the structure of social groups, I examined the social groups present in the population each year in relation to the population size and interannual growth rate. Social group characteristics that were examined were: the number of social groups in the population, the mean number of lineages per social group and the mean number of individuals per lineage.

To assess intragroup maternal relatedness I estimated the average pairwise coefficient of maternal relatedness (assuming a non-inbreeding population) amongst all individuals within each group. Matrilineal kinship in NRKWs is inferred by tracing individuals from birth and observing close, long-term associations between females and young animals (Ford et al. 2000; Towers et al. 2015). My estimates of intragroup maternal relatedness account for known maternal relationships (animals observed since birth), as well as relationships amongst animals born prior to the study whose maternal genealogical connections have been inferred from consistent behavioural observations. These association-based maternal assignments have been genetically validated, with only two of 73 tested putative maternal relationships (<3%) found to be incorrect (Barrett-Lennard 2000).

Intragroup cohesion was approximated using the Half Weight Index association measure (HWI; Cairns and Schwager 1987):

$$HWI = \frac{successes}{N} = \frac{successes}{successes + \frac{1}{2}(failures)} \qquad (1)$$

where ‘successes’ were encounters in which all lineages or submatrilines of a given group were present, for multilineage and single-lineage groups respectively. ‘Failures’ were any encounters where at least one lineage/submatriline within the social group was present and at least one lineage/submatriline within the social group was absent. To account for the possibility of incomplete encounters, wherein not all individuals present were documented by observers, the count of failures was divided in half. A group was considered cohesive if it exhibited strong intragroup association (HWI >0.6) in the given year.

Longevity of fission

To assess the permanence of group fission events, I estimated the probability that a once-cohesive social group would reform again following fission. Time-sensitive probability of cohesion after fission was derived through Kaplen-Meier non-parametric survival analysis, using the number of years since social groups had split and whether or not they were cohesive in the given year. Survival analysis was conducted using the *survfit* function in the R package 'survival' (Therneau 2014).

Determinants of group fission

Hypotheses

My hypotheses of the mechanism of NRKW group splitting were primarily generated according to first principles of mammalian dispersal and group living (Dieckmann et al. 1999; Lawson Handley and Perrin 2007), and are as follows:

1) *Food competition:* Lack of prey availability increases intragroup competition for food resources, thus promoting fission in order to reduce competition. Alternatively, greater food availability may promote dispersal, as it reduces dispersal costs.

2) *Kinship:* Relatedness drives kin-directed behaviours that promote philopatry (e.g. food sharing: Wright et al. 2016); therefore fission is promoted when a group's average relatedness

decreases, in order to reduce intragroup competition and optimize potential inclusive fitness benefits of within-group cooperation.

3) *Leadership:* The capability of a female to lead her own group and ensure its survival and reproductive success hinges on her accumulated social and ecological knowledge. Fission is inhibited unless a group contains at least two females with sufficient experience to lead their respective groups.

4) *Harassment* of reproductive females by local male kin promotes fission in order to mitigate the energetic costs incurred by females attempting to avoid harassment.

5) *Sexual competition for mates:* Sexual competition for mates among local females in oestrus promotes fission in order to increase mating opportunities. Sexual competition among local males may also promote fission so that males can improve or maintain their rank (e.g. established male breeder challenged by younger, recently matured males).

6) *Sexual competition for food:* Calving synchrony increases intragroup competition for food resources (through increased metabolic costs due to lactation), thus promoting fission in order to reduce intragroup competition. Alternatively, calving synchrony may promote philopatry by increasing a group's capacity for specialized alloparental care (e.g. allonursing). Here, I consider calving to be synchronous when multiple local females birthed calves within such a time interval that their estimated lactation periods overlapped[1].

It should be noted that although inbreeding avoidance is often cited as an important factor in the dispersal patterns of social mammals (e.g. Greenwood 1980; Pusey 1987; Kuester et al. 1994), it is omitted in this assessment of group splitting. I have ignored this process as a potential driver of fission as it is considered irrelevant for Resident killer whales. Resident killer whales

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[1] See Table 2.1 for details about the designation of lactation periods

have been shown to be extremely effective at outbreeding, using a mating system known as natal group exogamy; using acoustic cues, males consistently mate with unrelated females, not simply with those outside of their respective matrilines, but with those outside of their acoustical pod and most often with those outside of their acoustical clan (Barrett-Lennard 2000).

Statistical analysis

All statistical analyses were conducted in R (version 3.1.2; R Development Core Team, 2015). To test the six biological hypotheses of the drivers of group fission, I compared a set of generalized linear mixed models (GLMMs) and selected the best-fit model(s) using Bayesian information criterion (Schwarz 1978) score comparisons. I used score differences and model weights for inference. Models with BIC score differences less than four were considered the 'best' models (Burnham and Anderson 2002). If there was any ambiguity in the criterion score comparisons (i.e., weight of the 'best' model < 0.9; Grueber et al. 2011), I model averaged over all candidate models for prediction, using the R package 'MuMIn' (Bartoń 2012).

All candidate models were fit with a binomial error distribution (binary response variable, logit link function) using the *glmer* function in the R package 'lme4', which fits models using maximum likelihood (Laplace approximation) (Bates et al. 2015). GLMMs accounted for variation in group behaviour and repeated measures by including Group ID (N = 56) as a random effect (random intercept term).

Candidate models

I included both multilineage and single-lineage social groups in this analysis, with intragenealogical and intralineage splitting being distinguished by the presence of a common maternal ancestor. The working dataset contained 564 records (group-years restricted to those where there was potential for group fission; i.e., group contained at least two females with living offspring), involving 13 social groups composed of multiple lineages and 43 social groups composed of only one lineage. The 13 multilineage social groups include seven groups where the genealogical connection amongst lineages was unknown and six groups where the genealogical connection amongst lineages was either assumed or sometimes known.

Counts of encounter successes and failures for each social group in each year (sampling period: June-October[2]) were used as the binary response variable in the GLMMs to predict social group cohesion (see Equation 1). The binomial GLMMs thus produced a continuous predictor of social group cohesion equivalent to HWI. The regression is effectively the ratio of successes and failures, weighted by the number of encounters (N). To ensure a minimum threshold of precision for the response variable, each group-year record required a minimum of three cumulative encounters with its lineages/submatrilines to be kept in the analysis.

Candidate models were generated from combinations of demographic, genealogical and environmental explanatory variables (N=25) that were deemed biologically relevant to the six hypotheses, including a null model without any fixed effects (Bolker et al. 2008; Grueber et al. 2011). Each variable was sampled from the year in which the response variable was calculated. Data exploration of explanatory variables followed the protocol described by Zuur et al. (2010). All non-binary predictor variables were centered (mean-subtracted) and scaled (divided by 2 SD) to facilitate the interpretation of effect sizes (Gelman 2008; Schielzeth 2010). Highly collinear variables (variance inflation factor, VIF > 3) were removed from models; this occurred either through the removal of the more derived collinear variable or by correcting the collinear variable by its correlated counterpart.

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[2] I restricted the analysis to encounters that occurred between the months of June and October to reduce seasonal influence and ensure comparable survey effort among years.

Demographic data

I chose nine demographic variables that were relevant to my hypotheses. These variables were derived from annual censuses of the NRKW population conducted since 1973, which detail the condition, age and reproductive status of each animal in each year (DFO 2016a). All demographic variables were computed at the social group level and some were also computed at the level of the subgroup, matriline and population (Table 2.1). The ‘subgroup’ was assumed to be the most likely candidate for dispersal and refers to the largest matriline or submatriline in the social group, for multi- and single-matriline social groups respectively. For groups with living matriarchs (i.e. single-matriline social groups), this usually was the submatriline led by the eldest reproductive daughter of the matriarch. This definition of subgroup did not allow for splitting along maternal lines where no submatriarch existed (e.g. two orphaned adult males separating from their aunt’s matriline); as of 2014, this type of group dispersal had not been observed in Northern Resident killer whales and so I feel confident that this omission is appropriate.

Maternal relatedness

Preferential relationships in many social species are dictated by maternal relatedness (Gouzoules 1984; Walters 1987; Wittemyer et al. 2005; Berman et al. 2008), which is often a good indicator of familiarity amongst individuals (Chapais 2001; Majolo et al. 2008) and has been found to be a good predictor of group fission in various species (Chepko-Sade and Olivier 1979; Archie et al. 2006; Widdig et al. 2006; Van Horn et al. 2007). For Resident killer whales, maternal relatedness has been shown to be a driver of differential prey sharing (Wright et al. 2016), a behaviour which has been proposed as a means for parental control of dispersal in other species (Ekman and Rosander 1992).

For kinship models, I used two measures of the genealogically-based estimate of maternal relatedness (previously described). First, I estimated the average pairwise coefficient of maternal relatedness amongst all individuals within each social group. Second, I estimated the average degree of maternal relatedness between the subgroup's matriarch and her descendants relative to that between her and the rest of her social group. This second measure has been found to be a stronger predictor of group fission than the average pairwise maternal relatedness of the group in other species (Archie et al. 2006).

The reproductive value of individuals was not accounted for in my kinship models, as: 1) it makes interpretation exceedingly difficult; 2) there is no indication that individuals can assess the reproductive value of others, and; 3) reproductive value has been shown in other studies to have no apparent effect on the role of kinship in group choice and dispersal (e.g. Van Horn et al. 2007).

Energetic requirements

In species with philopatric females, dispersing females have been posited to be those whose nutritional requirements are not being satisfied (Isbell and Van Vuren 1996). While group size may offer a coarse proxy for a group's nutritional requirements, such requirements have been shown to vary immensely according to a killer whale's sex, age and reproductive status (Barrett-Lennard et al. 1995; Kriete 1995; Osborne 1999; Williams et al. 2004; Williams and Noren 2009; Noren 2011; Williams et al. 2011). As such, I felt it prudent to derive a variable more reflective of this than group size alone.

To assess intragroup competition for prey resources, I estimated the daily prey energetic requirement (DPER) of each group and its subgroup. This variable was computed by summing the DPER value of each individual in the group, according to their age-sex class. DPER values were calculated using mass-to-calorie equations described by Noren (2011) and estimated average body masses for age-sex classes noted in Ford et al. (2010a). Because of uncertainty in the energetic costs of growth and lactation and the effects of these factors on DPER values, I followed a conservative protocol similar to that proposed by Noren (2011): all animals' DPERs, with the exception of young juveniles (ages 3-6), adolescent males (ages 7-12) and lactating females, were calculated using Noren's lower bound equation (Equation 2). To take into account additional energetic costs of rapid growth, young juveniles' and adolescent males' DPERs were derived using Noren's upper bound equation (Equation 3).

$$\text{Lower bound DPER} = 413.2M_b^{0.75} \tag{2}$$

$$\text{Upper bound DPER} = 495.9M_b^{0.75} \tag{3}$$

where DPER is the daily prey energy requirement in kilocalories per day and M_b is body mass in kilograms.

Any animals of unknown sex were presumed to have the same requirements as a female their age, assuming that the sexually dimorphic increase in body size seen in males co-occurs with 'sprouting'—the onset of sexual maturation of males, physically manifested by the rapid growth of their dorsal fin.

Any animals less than two years of age were assumed to have their caloric requirements satisfied through consumption of their mothers' milk. I therefore took into account lactating females' caloric needs by inflating their estimated caloric requirement by 50% (Kriete 1995; Kastelein et al. 2003). For details about the assignment of lactating status, see Table 2.1.

To contextualize DPER values, I conducted a conversion of kilocalories to number of fish (Appendix 1). Assuming a summer and early fall diet composed entirely of Chinook salmon, a twenty-year old lactating female would require roughly 15 fish each day to satisfy her energetic requirements, whereas her non-lactating and male counterparts would require approximately 10 and 13 fish, respectively, to satisfy theirs.

Salmon abundance data

Chinook salmon dominates the Resident killer whale diet from June to September (Ford and Ellis 2006; Ford et al. 2010b; Hanson et al. 2010), and has been shown to be a significant correlate of Resident killer whale survival and fecundity (Ward et al. 2009; Ford et al. 2010a; Vélez-Espino et al. 2014). Chinook abundance has also previously been identified as a correlate of social behaviours in Resident killer whales, with years of low Chinook abundance associated with smaller group sizes and weaker social network connectivity (Lusseau et al. 2004; Foster et al. 2012).

Chinook stocks from Washington State (USA) to southeast Alaska (USA) were included in this analysis (Appendix 2) and abundance data were composed of two aggregate indices: (1) terminal run reconstruction estimates for southeast Alaska (SEAK), northern British Columbia (NBC), central British Columbia (CBC), west coast Vancouver Island (WCVI), upper Georgia Strait (UGS) and lower Georgia Strait (LGS) (Kope and Parken 2011; Vélez-Espino et al. 2014), and (2) ocean abundance estimates for the Fraser River (early run; FE), Puget Sound (PS) and the upper Columbia river (UC) (PSC 2015). The terminal run reconstruction estimates used are stock-specific population indices for individual stocks known to be present in NRKW diet (Ford et al. 2010b; Vélez-Espino et al. 2014), whereas ocean abundance estimates are approximations of cohort sizes from various stocks vulnerable to particular fisheries (PSC 2015). The indices used were previously found to be relevant indicators of Northern Resident killer whale mortality and fecundity (Vélez-Espino et al. 2014).

Chum salmon (*Oncorhynchus keta*) is an important component of NRKW autumn diet, surpassing Chinook salmon frequency in NRKW diet in early fall (September-October) (Ford and Ellis 2006; Ford et al. 2010b). Chum has been shown to be a useful predictor of RKW vital rates (Vélez-Espino et al. 2013), but has never been studied as a predictor of RKW social behaviour.

Chum stocks from Washington State to northern British Columbia were included in this analysis (Appendix 2) and abundance data consisted of an annual aggregate from three sources: (1) terminal run reconstruction estimates of southern British Columbia (SBC) and CBC fall runs (Canadian fishery areas 11-29; DFO 2016b; Vélez-Espino et al. 2013), (2) terminal run reconstruction estimates for fall runs in NBC (Canadian fishery areas 1-10; English et al. 2016), and (3) terminal run reconstruction run reconstruction estimates for Washington State (including Puget Sound and outer Washington coast) (PSC, 1987-2015). All Canadian terminal run estimates included only 'normal'-timed Chum runs (in fall). Washington run estimates included early, normal and late run estimates, which peak in October, November-December and January, respectively.

Results

Population dynamics and group structure

The NRKW population has grown steadily at an average growth rate of 2.26% since 1973. In eleven different years the population exceeded 4% growth ($R_{\max}$ typical of cetaceans; Wade 1998), with maximum interannual growth reaching 7.8% in one of those years. The population declined in only five of the 43 years of the study, with a maximum loss of 3.85% in one year (Figure 2.1). This overall population growth was reflected in the growth of acoustical pod and lineage sizes, the mean sizes of which were significantly correlated with NRKW population size

($\rho=1.00$, $p<0.01$; and $\rho=0.97$, $p<0.01$, respectively; Figure 2.2a). While the number of acoustical pods in the population remained unchanged, the number of lineages in the population increased with the growing population size ($\rho=0.89$, $p<0.01$). It is interesting to note that the number of matrilines in the population was more tightly coupled to NRKW population size than was the number of lineages ($\rho=0.94$, $p<0.01$). While NRKW population size was highly correlated with both the number and average size of pods and lineages, none of those characteristics were significantly correlated with the population's interannual growth rate.

Intragroup relatedness tends to be inversely related to group size, and so, unsurprisingly, the average maternal relatedness within pods and within lineages were found to be highly negatively correlated to NRKW population size ($\rho=-0.92$, $p<0.01$; and $\rho=-0.90$, $p<0.01$, respectively). As with pod and lineage counts and sizes, the interannual growth rate of the population had no significant relationship to the intragroup relatedness of pods and lineages ($\rho=0.12$, $p=0.47$; and $\rho=-0.012$, $p=0.90$, respectively; Figure 2.2b).

Over the length of the study, average intrapod cohesion steadily decreased, while average intralineage cohesion remained relatively constant (Figure 2.2c). Intrapod cohesion was found to be significantly negatively correlated to NRKW population size ($\rho=-0.83$, $p<0.01$) while intralineage cohesion was found to have a less significant, positive relationship to NRKW population size ($\rho=0.37$, $p=0.017$).

The number of social groups present within the population each year was highly linked to the population's size ($\rho=0.70$, $p<0.01$; Figure 2.3e). The number of groups was also significantly correlated with the population's interannual growth, decreasing as interannual growth increased ($\rho=-0.41$, $p=0.023$; Figure 2.3f). The size and structure of social groups was closely coupled with population size, with the mean number of matrilines per social group decreasing as the population increased (ρ=-0.66, p<0.01; Figure 2.3c) and the number of individuals per matriline increasing as population size increased (ρ=0.96, p<0.01; Figure 2.3a). However, neither the size nor the structure of social groups was found to have any significant link to the interannual growth of the population (ρ=0.018, p=0.92; and ρ=0.25, p=0.18, respectively; Figure 2.3b and 2.3d).

Longevity of fission

The probability that split groups would re-form dropped precipitously within the first three years after splitting, with probability of fusion falling below 50% by year one (Figure 2.4). On average, groups that re-formed did so within the first three years after splitting (mean=2.8 years; median=1 year). In only 5% of cases did fusion occur more than 10 years after splitting. The longest duration between splitting and re-fusing was 15 years (N=2). In both of those cases, the strong re-association of social group members lasted only one sampling period (June-October) before splitting occurred again, along the same lines as the original split.

Determinants of group fission

The three top models selected by BIC scoring combined to have a cumulative conditional probability of 100%. Because the top model had a conditional probability below 0.90 (Table 2.2), model averaging was applied across the candidate models. Of the nine variables found in models of weight, six were considered significant and were associated with food competition, sexual competition for food and kinship hypotheses (Table 2.3; Figure 2.5).

Food competition variables (group size, proportion of physically mature males, Chinook salmon ocean abundance and Chum salmon terminal run abundance) were significant predictors in all candidate models that held any weight; therefore, I am confident that these are important predictors of group cohesion. Of the six food competition variables, only median group age and Chinook salmon terminal run abundance were not found to be useful predictors of group cohesion (Table 2.3; Figure 2.5). According to the model-averaged results, group size had the greatest effect on group cohesion, predicting lower group cohesion with increasing group size, while higher proportions of physically mature males in the group had a significant negative effect on group cohesion as well (Table 2.3; Figure 2.6a and 2.6b). Of the salmon predictors, only the ocean abundance index for Chinook salmon and the terminal run index for Chum salmon were found to have any significant effects on group cohesion. Increases in Chinook ocean abundance and Chum terminal run abundance predicted a slight positive effect on group cohesion (Table 2.3; Figure 2.6d and 2.6e). Sexual competition for food, represented by the proportion of lactating females in the subgroup, was found to be a significant predictor of group cohesion and was found in all models that held any weight. Higher proportions of lactating subgroup females predicted lower group cohesion (Table 2.3; Figure 2.6c).

All remaining predictors identified by the averaged models were associated with the kinship hypothesis, but were accompanied by considerable uncertainty. Average maternal relatedness (adjusted for group size) predicted greater group cohesion as it increased (Table 2.3; Figure 2.6f). However, although it was a significant predictor, average maternal relatedness was found in only one of the top candidate models with 45% model weight (Table 2.2; Figure 2.5). The presence of a matriarch was found to be an insignificant predictor of group cohesion and was only found in one of the top candidate models with 8% model weight. In this case, it predicted greater group cohesion if a group’s matriarch was alive (Table 2.3).

In an independent assessment of predictors that used machine-learning techniques, food competition variables were similarly determined to be the best predictors of group cohesion (Appendix 3).

Discussion

Patterns of group fission in the NRKW population

The NRKW population is currently 2.5 times larger than it was at the beginning of the study in 1973, and has steadily increased with growth rates often nearing and sometimes exceeding the maximum theoretical rate of increase typical of cetaceans (Figure 2.1). With this impressive population growth and the strong natal philopatry exhibited by both sexes in this population, it was expected that new social groups would arise through the process of matrilineal fission (Bigg et al. 1990). The number of social groups present within the population each year was highly linked to the population's size; roughly, for every twenty additional animals in the population a new social group formed.

As acoustical pods and maternal lineages grew in size, their average maternal relatedness decreased, creating favourable conditions for group fission. This process was prevalent in acoustical pods, with average intrapod cohesion declining over time (Figure 2.2). Surprisingly, average intralineage cohesion in the population was found to marginally increase over the time series. I believe this to be an artifact of sampling effort becoming more consistent, intense and regimented over the more recent years of the study, rather than any actual change in the interactions among individuals within the same lineage. Most importantly, these findings show the pervasiveness of intragenealogical fission within the population and the relative infrequency of intralineage splitting.

While both intragenealogical and intralineage fission occurred in the NRKW population, intragenealogical splitting was more frequently observed. Intragenealogical splitting occurred at least once in all pods that were capable of undergoing this type of fission, and proceeded to take place within some of the subsequent social groups that resulted from previous intragenealogical splits. Conversely, intralineage fission was comparatively rare, with less than 5% of daughters permanently dispersing from their mothers over the course of the study. This differential relative frequency between the two processes was expected, and is commonly seen in other social species (Lefebvre et al. 2003), as groups preferentially split along maternal lines rather than across them, maximizing the maternal relatedness of the resulting groups (Widdig et al. 2006; Lawson Handley and Perrin 2007). It is likely for this reason that intralineage splitting was not observed in NRKW groups composed of more than one lineage.

The presence of a matriarch has been shown to promote group cohesion in many mammalian species (e.g. Chepko-Sade and Sade 1979; Wittemyer et al. 2005; Archie et al. 2006; Berry and Bercovitch 2014). Although matriarch presence was not a significant predictor in our top models, the differing rates of intragenealogical and intralineage fission, as well as the strict ‘preference’ towards intragenealogical splitting in cases where the potential for both processes existed, suggest that matriarchs do play a significant role in reducing the likelihood of fission. As the most recent common ancestor of all group members, a matriarch increases the average maternal relatedness of her group and likely promotes familiarity among group members through their association with her (Holmes and Sherman 1983; Chapais 2001). Acoustically, Resident killer whale matriarchs may maintain a high level of group call structure stereotypy and thus likely play a large role in the maintenance of a group’s identity (J. Ford and J. Pilkington, *pers. comm.*). This rigid acoustical identity allows groups and individuals to reliably recognize kin and thus benefit from cooperative, kin-directed social behaviour (e.g. Wright et al. 2016), which ultimately has implications for social group cohesion (Ford 1989, 1991; Deecke et al. 2010). Perhaps most importantly, as the oldest member of the group, a matriarch is her group's richest source of ecological and social knowledge and, through social transmission, can enhance her group's collective knowledge (McComb et al. 2001; McAuliffe and Whitehead 2005). Her leadership undoubtedly has the ability to affect her group's wellbeing (Foley et al. 2008; McComb et al. 2011; Berry and Bercovitch 2014; Brent et al. 2015) and may influence group members' dispersal decisions. The fitness costs of reduced social contact with the matriarch could potentially inhibit a submatriline's dispersal, which might be delayed until submatriline members (especially the submatriarch) have acquired sufficient knowledge from the matriarch (e.g. Lutermann et al. 2006).

Patterns of intralineage fission in NRKWs were very similar to those observed in a population of Rhesus macaques (*Macaca mulatta*; Chepko-Sade and Sade 1979) in that only the eldest daughters of matriarchs dispersed with their submatrilines. However, while Chepko-Sade attributed this to 'peripheralization' of the eldest daughter's group—her low dominance rank relative to her sisters due to their closer social proximity to their mother—, I do not believe this to be the case in NRKWs. First, a dominance structure among sisters has never been noted in Resident killer whales. While subgroups often travelled distantly from the rest of their social group prior to splitting, antagonistic behaviour was never observed between dispersed killer whale groups and their former group at any point during the fission process, as has been seen in primates (e.g. Missakian 1973). Second, dispersing groups in intralineage splitting events were always the largest submatrilines in their respective groups, and so I suspect that the dispersing submatriline was not delineated via dominance rankings among sisters, but rather was likely delineated according to its size. By this rationale, it might be expected that the second or third oldest daughter of a matriarch disperse in the future, should she be the head of the largest submatriline in her group.

Influence of group structure

Behaviours that strengthen and maintain social bonds among individuals but are costly to the individual have the potential to delineate substructures within groups. Since animals can be limited as to the number of individuals with which they can conduct a key behaviour, they may be unable to maintain strong bonds with all individuals within their group, beyond a certain group size. This limitation may be cognitive (Shultz and Dunbar 2007; Dávid-Barrett and Dunbar 2013), physiological (Pollard and Blumstein 2008; Bergmüller et al. 2010), or behaviourally adaptive (e.g. used as a means of reducing intragroup conflict or competition, Kudo and Dunbar 2001; Lehmann and Dunbar 2009). It follows that more substructured groups are thus less cohesive and have a higher probability of undergoing fission. As a rule, larger groups tend to be more substructured than smaller ones (Lefebvre et al. 2003).

It has been proposed that group size, in addition to substructuring behaviour, influences group cohesion (Sueur et al. 2011). This may also be the case in Resident killer whales: if one assumes that kin-directed prey-sharing behaviour reinforces social bonds among Resident killer whales (Wright et al. 2016), it also has the potential to delineate substructures within a group, between which social bonds are weaker. Group structure, as defined by the number and mean size of matrilines within a group, was not shown to have any effect on the prediction of NRKW group cohesion in our models. This may be because, if prey sharing is the prevalent substructuring mechanism for NRKW groups, the matriline may not be the most appropriate structural unit. Maternal prey sharing with daughters in NRKWs ceases after daughters begin producing offspring (Wright et al. 2016), which means that the structural units of NRKW groups may be better represented by submatrilines, as opposed to matrilines.

It has been proposed that population growth may influence group structure, where significant growth results in a small number of large matrilines per social group and negative or slow growth results in a large number of small matrilines per social group (Melnick and Kidd 1983). This is because, in the former case, high fecundity within matrilines (as a consequence of low mortality) results in large matrilines. These large matrilines exhibit cohesion due to the minimal range among ages of group members (Lefebvre et al. 2003). In the latter case, social groups are composed of smaller, less related (and thus less cohesive) matrilines as a result of high mortality and low fecundity (Lefebvre et al. 2003). The NRKW population has exhibited three phases of population growth: the population grew steadily from the beginning of the study in 1973 until 1992 (λ=2.95%), at which point it began experiencing high rates of mortality and almost no overall growth until 2004 (λ=0.35%). From 2004 onwards, the population once again showed significant growth (λ=3.13%) (Figure 2.1a and 2.1b). The frequency of fission within the population increased in the late stages of the first phase of population growth and into the early stages of the second phase of no overall growth (Figure 2.1c). This resulted in an apparent increase in the number of social groups in the NRKW population during that time, the number of which has remained relatively consistent since (Figure 2.3e and 2.3f). Like Melnick and Kidd's (1983) hypothesis, after the first phase of significant growth in the NRKW population, social groups tended to be composed of fewer, larger matrilines (Figure 2.3). At present, most social groups are only composed of a single matriline. Those that are not are composed of small matrilines that have shown little growth due to low fecundity, resulting from either high female mortality or a natural lack of females in the group (i.e. dead-end matrilines soon to become extinct).

Group cohesion as predicted by intragroup competition for food

Of the six hypotheses, intragroup competition for food was found to be the best predictor of group fission, primarily driven by demographic rather than environmental factors. Intragroup competition for food was able to predict both intragenealogical and intralineage fission with similar success, indicating that there is no apparent difference in the drivers of these two processes.

A group's nutritional requirements can be represented by the number of animals in the group, the age structure of the group, and the proportion of animals that require disproportionate amounts of food due to costly metabolic processes (e.g. physically mature males and lactating females). I predicted that increases in those group features would increase metabolic requirements and thus would adversely affect group cohesion. This predicted effect was thought to occur through: a) a change in the group's daily activity budget, where time spent socializing would be sacrificed in favour of foraging to satisfy nutritional needs, thus weakening social bonds within the group, and/or; b) through decreased foraging efficiency (as more fish are required to be caught per prey patch) forcing groups to separate to improve their foraging success.

By far the predictor with the greatest effect on group cohesion was a group's size. Increasing group size predicts a continuous decrease in the probability of group cohesion, with the predicted probability of group cohesion dropping below 50% when a group's size reached 20 individuals (under average conditions for all other predictors) (Figure 2.6a). Group splitting occurring at a relatively predictable group size implies that intrinsic, rather than environmental, factors are primarily responsible for fission (Thierry et al. 2004; Sueur and Maire 2014). Despite this, it must be noted that extrinsic pressures can have direct impact on a population's dynamics and on group characteristics (Sueur et al. 2011; e.g. food availability influences mortality and fecundity) and may affect the favourability of a group's demographic conditions (e.g. Eckman and Rosander 1992), and therefore may still be important auxiliary factors in group fission.

Group size was highly correlated with a group's estimated caloric requirement and a group's average maternal relatedness (RA*g*). In all comparable models, when included along with the group's median age (A*g*) and proportion of physically mature males (PM*g*), group size out-competed the caloric estimation for the group (DPER*g*). This may be because: a) DPER*g* does not adequately estimate the true caloric needs of particular demographic classes of animals, and/or b) the accompanying variables, A*g* and PM*g*, may take into account additional processes affecting intragroup food competition other than individuals' caloric needs (e.g. foraging independence, nutritional contributions to the group via prey sharing). The lower average relatedness among members of a growing group results in decreased benefit to be gained from cooperation amongst individuals (Frank 2013) and therefore may lead to lower group cohesion (e.g. Chepko-Sade and Olivier 1979). Though there was uncertainty as to whether relatedness (adjusted for group size) was an important predictor of group cohesion in NRKWs, maternal kinship is known to be associated with important cooperative foraging behaviours (Wright et al. 2016) and so, if food competition is the primary driver of group cohesion, kinship likely plays a role as well.

Intragroup food competition also explains why the presence of physically mature males in the social group predicts a decrease in group cohesion (Figure 2.6b). Physically mature males have a disproportionate impact on their group's nutritional stress, as they require substantially more caloric input than the average animal (Noren 2011) and they contribute little to intragroup prey sharing (Wright et al. 2016). A fully-grown male can require approximately 2-3 times the amount of calories required by a young animal, roughly 13-16 Chinook salmon per day (Appendix 1).

Although the proportion of physically mature males in the group could also be representative of sexual competition among local males, I do not believe this is the underlying driver for several reasons. First, rankings amongst males are likely established as they come into maturity (G. Ellis and J. Ford, *pers. comm.*), so the proportion of sexually mature (but not yet physically mature) males (M*g*) is expected to be more representative of intragroup male-male competition than is the proportion of physically mature males. Of the two predictors, the proportion of physically mature males was found to be the stronger predictor of cohesion, in both the GLMMs and random forest analyses (Appendix 3). Second, if group dispersal occurred because physically mature males were looking to improve their mating opportunities, one would expect to see a moderate frequency of individual male dispersal throughout the population (e.g. Bigg's killer whales: Baird and Whitehead 2000), which is not observed in Residents. Third, in intralineage splits, dispersing submatrilines tend to be composed of younger animals—many do not contain any physically mature males—so their dispersal often does little to mitigate sexual competition among physically mature males in the overall group.

Sexual competition for food also helped to predict group cohesion, with higher proportions of lactating subgroup females predicting lower group cohesion. High proportions of lactating females indicate synchronous calving is occurring within the group, which means greater energetic compensation (i.e. greater food intake) is required of the group to produce enough milk to feed their calves. A female's food intake can increase by 1.5-2 times when lactating, especially in her first few months of producing milk (Kriete 1995; Kastelein et al. 2003; Noren 2011); she may be required to catch roughly five more fish per day than her non-lactating counterparts (Appendix 1). It should be noted that the strong negative effect of lactating females on group cohesion does not preclude the possibility that allonursing within the group occurs (e.g. Gero et al. 2009; Leung et al. 2010; Gero et al. 2014) but rather suggests that the metabolic costs of lactation on the group outweigh the potential benefits of synchronous calving at the group level.

While the proportion of lactating females in the group (FL*g*) and those in the subgroup (FL*s*) were notably correlated with one another, FL*s* directly out-competed FL*g* in all comparable models. This may indicate that dispersal may only be initiated when per capita sexual competition within the subgroup reaches a particular threshold. The same threshold among the whole group may be exceeded, perhaps in favour of the social and learning needs of new mothers (e.g. Lutermann et al. 2006), until the point when per capita food competition amongst lactating subgroup members is exceeded – at which point fission is initiated. VanderWaal et al. (2009) describe a similar process in their findings, where the number of females in lion prides often exceeded group sizes optimal for foraging; it was only until groups exceeded sizes that negatively affected per capita reproductive success of subgroups that prides underwent splitting. Alternatively, FL*s* may be indicative of the subgroup's caretaking capacity, and fission may be inhibited until an adequate number of subgroup females have accrued sufficient calf-rearing experience to disperse. This is unlikely as one would expect the number of reproductive females in the subgroup (FR*s*) to be a better indicator of this than FL*s*, and FR*s* was directly out-competed by FL*s* in all comparable models.

Although I expected that higher median group ages would predict lower group cohesion as a result of increased food requirements of older individuals, median group age was not a significant predictor of cohesion in any model. This may be because of multiple processes associated with animals' ages that affect group cohesion in conflicting ways. A higher median age suggests more mature individuals in the group and, from an energetic standpoint, this would likely mean that the group as a whole requires more calories to satisfy its energetic needs, which might promote fission. Alternatively, mature individuals (particularly adult females) typically contribute the most to 'bonding' behaviours like caretaking, foraging, and prey sharing—behaviours that are thought to promote social cohesion (Waite 1988; Wright et al. 2016).

While our models indicated that intrinsic group characteristics had a greater influence on NRKW group cohesion than environmental pressures, two of the salmon abundance predictors remained important explanatory variables in the top models. Higher abundances of both Chinook and Chum salmon predicted higher group cohesion (Figure 2.6e and 2.6f). Of interest is that the effect of Chum and Chinook salmon abundances on group cohesion were of similar strength (Figure 2.5). This may indicate that though Chum salmon is often considered less important of a prey item for RKWs than Chinook salmon, due to its lower frequency in RKW diet and its lower caloric content, it may in fact have just as significant an impact on RKW sociality as Chinook salmon, particularly on a seasonal basis.

It is worth mentioning that both of these important salmon species are subject to commercial and recreational fisheries and so their management will undoubtedly play a large role in the recovery of Resident killer whale populations. This fisheries competition is not insignificant; the annual number of Chinook salmon required by the two Resident populations is estimated to be roughly half of the total combined commercial and recreational marine harvest of

Chinook salmon between Southeast Alaska and Oregon in 2014 (Appendix 1; PSC 2015). In addition to concerns about the general abundance of Resident killer whale prey, dramatic decreases in the body size of Chinook and Chum salmon in the North Pacific have also been observed over the past four decades (Ricker 1981; Bigler et al. 1996; Groot et al. 2010; Lewis et al. 2015). It is likely that these changes in the quantity and quality of prey have indirectly impacted group cohesion of NRKWs, through their effects on killer whale mortality and fecundity (Ford et al. 2010a; Vélez-Espino et al. 2013, 2014). My findings also support the growing body of evidence (e.g. Lusseau et al. 2004; Parsons et al. 2009; Foster et al. 2012) suggesting that prey availability has impacts reaching beyond the vital rates of Resident populations, and can also directly affect the social dynamics of these populations.

Conclusion

I have argued here that population growth and demography drive matrilineal fission in Northern Resident killer whales. Group cohesion is primarily determined by intrinsic characteristics of groups that dictate food competition, though significant ancillary effects of food abundance were also observed. Kinship may have further effects on group cohesion, especially through food-related processes like kin-directed prey sharing. As group fission has a direct impact on the fitness of group members (Silk et al. 2003) and can have important genetic consequences for a population (Melnick and Kidd 1983), my findings underscore the importance of incorporating studies of sociality into the management of threatened populations of social mammals.

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Tables

Table 2.1 Descriptions of demographic variables found in the model set as fixed explanatory factors. ‘Level’ denotes the levels at which the given variable was sampled: *g* = within social group; *s* = within subgroup; *l* = within lineages; *p* = across population; *m* = from matriarch; *sm* = from subgroup matriarch. ‘Rationale’ describes why I chose to include the variable in the models. ‘Confidence’ speaks to the quality of data for the given variable.

Variable	Description	Level	Rationale	Confidence
N	• **Number of individuals** in the group	*g*	• The greater the number of animals in a group, the higher the intragroup competition for resources (e.g., Dittus 1988; Majolo et al. 2008; Sueur et al. 2011) • Group size is relevant to many density-dependent drivers that may be influencing group fission (e.g., food competition, per capita reproductive success)	• In cases of uncertain birth and death years and animals missed in a given census year, this estimate is a best estimate rather than an exact count
		s	• The dispersing group may be the submatriline putting most strain on the group (i.e., largest submatriline) • Akin to “potential group size”, seen to be a stronger factor than total group size in fission of lion prides (VanderWaal et al. 2009)	
		l	• The average number of individuals per lineage in the social group • This is paired with the count of lineages within the social group (S*g*) to describe the group’s matrilineal structure (see S*g* rationale for details)	
S	• **Number of lineages** in the group	*g*	• Group substructuring, delineated by relatedness, weakens social links in large groups and has been proposed as an intrinsic driver of group fission (Lefebvre et al. 2003; Sueur et al. 2011) • In species where fission occurs at a constant group size, it is suggested that fission is driven by an intrinsic factor like structuring (as opposed to some external, environmental pressure) (Melnick and Kidd 1983)	

Variable	Description	Level	Rationale	Confidence
L	• L*m* indicates whether a **maternal ancestor common to all group members is alive** in the given year (1=yes, 0=no)	*m*	• This distinguishes intralineage from intragenealogical splits as the matriarch of the group is alive for intralineage splits but not alive for intragenealogical splits • Matriarchs are thought to play a vital role in the health, survival, and success of their group, as repositories of social and ecological knowledge (e.g. Brent et al. 2015). The knowledge of the group's leader can influence the social and ecological knowledge of the group as a whole • The presence of a common maternal ancestor may mitigate some costs of group living, promoting philopatry (e.g., group foraging efficiency likely increased by matriarch's experience, by her ability to lead group to areas of sufficient prey availability)	• See N confidence
A	• A*sm* denotes the **age of the subgroup matriarch** • Age used as a proxy for knowledge and experience, qualities accumulated over an animal's lifespan	*sm*	• A female may delay dispersal until she's gained enough knowledge of foraging areas, timing of salmon runs, etc. (e.g. Lutermann et al. 2006) • Age has been found to be a strong predictor of dispersal in other species (e.g., Mares et al. 2014) • In elephants, a group's trust in its matriarch's leadership abilities and social knowledge has been shown to increase with her age (McComb et al. 2001; McComb et al. 2011) • Once females have gained sufficient knowledge to lead a group themselves, the benefits of remaining with their mothers/sisters may cease, thus promoting dispersal (Wright et al. 2016)	• Ages are estimated for animals alive at the beginning of the study; confidence in ageing becomes significantly higher as the study goes on
	• A*g* and A*s* denote the **median age** of all extant members of the social group and subgroup, respectively	*g & s*	• Higher median age indicates a group formed mainly of independent adults, whereas a lower median age indicates a group with many dependent juveniles ((in)dependence here is with respect to foraging) • This variable efficiently describes the balance between caretakers/providers and dependents in a group • Higher median age also suggests that the caloric requirement of the group as a whole is greater • In cases where the distribution of ages within a group is highly skewed, median age is better suited to describing a group's age structure than is mean age	

Variable	Description	Level	Rationale	Confidence
M	• Count of **sexually mature males** who are not yet physically mature, as a proportion of group size • Males are considered to attain sexual maturity when the growth of their dorsal fin attains a height-to-width ratio (HWR) greater than 1.4 (see Olesiuk et al. 2005)	*g*	• This will be paired with FR to assess the intensity of potential harassment by local males • High proportions of newly mature and established mature adult males have been found to be a cause of fission in primates (Furuya 1969), where fission stabilizes male dominance hierarchy among males by lowering their numbers in groups (Carpenter 1942). This will be paired with PM to assess the intensity of male-male competition amongst sexually mature and physically mature males	
PM	• Number of **physically mature males**, as a proportion of group size • Physically mature males are considered to be those whose dorsal fins are fully developed (i.e. have reached asymptotic growth) (see Olesiuk et al. 2005)	*g & s*	• As the estimated caloric requirement of groups (DPER), when corrected for group size, is highly correlated with PM*g* and A*g*, this variable will be paired with A*g* and N*g* to approximate the caloric requirement of a social group. • This will also be paired with M to assess the intensity of male-male competition amongst sexually mature and physically mature males (e.g., Carpenter 1942; Furuya 1969; Dittus 1988)	
		p	• Specifically this variable is an approximation of ‘desirable’ males across the population: those outside of the given group’s acoustic clan or subclan (see below) • Older RKW males tend to be the sires of calves (Barrett-Lennard 2000; Ford et al. 2011), which is why I am selecting for physically mature males as desirable mates • NRKW matings are almost always extra-clan pairings, and always extra-subclan pairings (Barrett-Lennard 2000); if the given group is in G or R clan, desirable mates must be outside of the given clan, and if the given group is in A clan, desirable mates must be outside of the given group’s subclan • This will be paired with FE to assess the intensity of potential mate competition among local females (i.e. number of desirable mates for every female in oestrus in the group)	• This will be a maximum value (likely an overestimate) as not all groups will meet each other in a given sampling period. To combat this, Mares et al. (2014) divided this count by the number of groups in the population (i.e., average number of potential mates per group) and looked at the number of intergroup encounters; however, the dataset used in this analysis does not have the type of resolution required to be able to do this effectively.

Variable	Description	Level	Rationale	Confidence
FR	• Number of **reproductive-age females** in the group, as a proportion of group size • A female's reproductive lifespan is considered to begin two years before the birth of her first known calf (viable or not). The end of a female's reproductive lifespan is considered the year after the birth of her last calf.	*g*	• Reproductive females are the most frequent provisioners in prey-sharing interactions (Wright et al. 2016) and exhibit many other behaviours that serve the group as a whole, likely promoting group cohesion, such as parental care during foraging bouts (Waite 1988; Packer et al. 1990) • Conversely, reproductive-age females present in a group may cause significant intragroup sexual competition and reproductive conflict (e.g. Cheney et al. 2012). Per capita reproductive success has been found to be inversely correlated to the number of reproductive-age females in other species (Armitage and Schwartz 2000; VanderWaal et al. 2009)	• The start of a female's reproductive lifespan is a somewhat conservative estimate as she may have previously given birth to non-viable offspring that was not observed. • As the end of the study may artificially assign post-reproductive status to still-fecund females, I do not assign post-reproductive status to animals that have given birth within the last 5 years[3] of the study and are younger than 42 years old[4]. The mean age of last calving is 35.5 years, so I am likely being mildly conservative in assigning reproductive-age status.
		s	• Potential female group size in lions was shown to be a stronger indicator of dispersal than overall group size; almost no splitting occurred unless subgroup size exceeded the point where individual reproductive success was reduced (VanderWaal et al. 2009) • In other species, dispersal has been found to be delayed until the subgroup accumulates enough female kin (Armitage and Schwartz 2000; Van Horn et al. 2007)	
FL	• Number of **lactating females** in the group, as a proportion of group size • Lactation is estimated probabilistically from known births of calves; a lactating female is any female who has calved in the given year or any female who gave birth to a viable calf in the previous year	*g & s*	• Lactating females are an estimate of the group's capacity for alloparental care through nursing (e.g. Gero et al. 2009; Leung et al. 2010; Gero et al. 2014), which may promote group cohesion • Alternatively, lactating females' caloric requirements are significantly greater than females of any other reproductive status (Noren 2011); increased metabolic requirements add to intragroup competition for prey resources and thereby may promote fission	• This estimate will be a minimum value, as: 1) females who birth *unobserved* non-viable calves would not be counted as lactating females and; 2) I may be underestimating the longevity of lactation; 3) I assume that female killer whales cannot spontaneously lactate to allonurse kin (whether this occurs in killer whales is currently unknown)

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[3] Based on the average calving interval of 4.88 years (Olesiuk et al. 2005)

[4] This age was determined based on the 95% probability of senescence (Appendix 4)

Variable	Description	Level	Rationale	Confidence
FE	• Number of **females in oestrus** (i.e., fecund females available to reproduce; non-pregnant, non-lactating reproductive-age females), as a proportion of group size • Oestrus is estimated probabilistically from known births of calves; a female is considered in oestrus if she is of reproductive age (see FR*g* description), is not lactating (see FL*g* description) and is not pregnant (i.e., she did not calve in the following year).	*g & s*	• Competition for mates may promote dispersal in order to increase mating opportunities (Dittus 1988; Prud'Homme 1991)	• This estimate will be a maximum value (likely an overestimate), as females who miscarry or birth unobserved non-viable calves will be counted as females in oestrus, and some previously lactating females may, in fact, still be lactating

Table 2.2 Rankings of candidate models according to BIC. Top models, according to BIC score differences under four, are indicated in bolded font. K = number of estimated parameters, LL = log-likelihood; BIC = Bayesian information criterion score; Δ = difference between the candidate model's score and that of the top score; Wt = model weight, the model's conditional probability of being the best model.

Fixed effects	**K**	**LL**	**BIC**	**ΔBIC**	**BIC Wt**
N*g*, A*g*, PM*g*, FL*s*, CK.oa, CK.tr, CM	**9**	**-1203.98**	**2464.98**	**0.00**	**0.47**
N*g*, A*g*, PM*g*, FL*s*, CK.oa, CK.tr, CM, RA*g*†	**10**	**-1200.86**	**2465.07**	**0.09**	**0.45**
N*g*, A*g*, PM*g*, FL*s*, CK.oa, CK.tr, CM, L*m*	**10**	**-1202.56**	**2468.46**	**3.48**	**0.08**
N*g*, A*g*, PM*g*, FL*s*, CK.oa, CK.tr, CM, RA*g*†, A*sm*†, A*s*, FR*s*	13	-1196.52	2475.40	10.41	0.00
N*g*, A*g*, PM*g*, CK.oa, CK.tr, CM, R*xm*	9	-1210.42	2477.86	12.88	0.00
N*g*, A*g*, PM*g*, FR*s*, CK.oa, CK.tr, CM	9	-1211.08	2479.18	14.20	0.00
N*g*, A*g*, PM*g*, FR*s*, CK.oa, CK.tr, CM, R*xm*	10	-1208.01	2479.38	14.39	0.00
N*g*, A*g*, PM*g*, CK.oa, CK.tr, CM, RA*g*†	9	-1212.70	2482.42	17.44	0.00
N*g*, A*g*, PM*g*, CK.oa, CK.tr, CM	8	-1216.06	2482.81	17.82	0.00
N*g*, A*g*, PM*g*, FR*s*, CK.oa, CK.tr, CM, RA*g*†	10	-1209.76	2482.87	17.88	0.00
N*g*, A*g*, PM*g*, FR*s*, CK.oa, CK.tr, CM, L*m*	10	-1210.36	2484.08	19.09	0.00
N*g*, A*g*, PM*g*, FL*g*, CK.oa, CK.tr, CM	9	-1214.58	2486.18	21.20	0.00
N*g*, A*g*, PM*g*, CK.oa, CK.tr, CM, L*m*	9	-1215.35	2487.71	22.73	0.00
N*g*, A*g*, PM*g*, FR*g*, CK.oa, CK.tr, CM	9	-1216.04	2489.10	24.11	0.00
DPER*g*, FL*s*, CK.oa, CK.tr, CM, RA*g*†	8	-1225.58	2501.84	36.86	0.00
DPER*g*, FL*s*, CK.oa, CK.tr, CM	7	-1229.95	2504.24	39.26	0.00
DPER*g*, FL*s*, CK.oa, CK.tr, CM, RA*g*†, A*sm*†, A*s*, FR*s*	11	-1217.41	2504.50	39.52	0.00
N*g*, M*g*, PM*g*	5	-1242.20	2516.08	51.10	0.00
DPER*g*, DPERs†, CK.oa, CK.tr, CM	7	-1244.03	2532.40	67.41	0.00
DPER*g*, FR*s*, CK.oa, CK.tr, CM	7	-1244.86	2534.07	69.09	0.00
DPER*g*, FL*g*, CK.oa, CK.tr, CM	7	-1245.22	2534.78	69.80	0.00
DPER*g*, CK.oa, CK.tr, CM	6	-1249.49	2537.00	72.01	0.00
DPER*g*, FR*s*, CK.oa, CK.tr, CM, RA*g*†	8	-1243.38	2537.44	72.46	0.00
N*g*, N*s*†, CK.oa, CK.tr, CM	7	-1246.93	2538.20	73.22	0.00
DPER*g*, FR*g*, CK.oa, CK.tr, CM	7	-1249.30	2542.94	77.96	0.00
N*g*, N*s*†, A*s*, PM*s*, CK.oa, CK.tr, CM	9	-1246.53	2550.08	85.10	0.00

Fixed effects	**K**	**LL**	**BIC**	**ΔBIC**	**BIC Wt**
N*g*, R*xm*	4	-1274.10	2573.55	108.57	0.00
N*g*, R*xm*, A*sm*†, A*s*, FR*s*	7	-1272.35	2589.05	124.06	0.00
N*g*, FR*g*, M*g*	5	-1280.99	2593.65	128.67	0.00
N*g*, FR*g*, PM*p*	5	-1284.92	2601.51	136.52	0.00
N*g*, RA*g*†	4	-1289.46	2604.26	139.28	0.00
N*g*, FE*s*, PM*p*	5	-1286.73	2605.14	140.16	0.00
N*g*, L*m*	4	-1290.41	2606.15	141.17	0.00
N*g*, FE*g*, PM*p*	5	-1288.17	2608.02	143.04	0.00
N*g*, FR*s*, PM*p*	5	-1288.34	2608.36	143.37	0.00
N*g*, RA*g*†, A*sm*†, A*s*, FR*s*	7	-1287.56	2619.47	154.49	0.00
N*g*, L*m*, A*sm*†, A*s*, FR*s*	7	-1288.77	2621.88	156.90	0.00
N*g*, A*sm*†, A*s*, FR*s*	7	-1288.77	2621.88	156.90	0.00
S*g*, N*l*, R*xm*	5	-1305.76	2643.19	178.21	0.00
Null	2	-1398.25	2809.17	344.19	0.00

† Adjusted for group size

Table 2.3 Factors affecting the probability of social group cohesion, according to model averaged results, with group ID (N=56) as a random intercept term. A*g* = median age of group; CK.oa = Chinook salmon ocean abundance index; CK.tr = Chinook salmon terminal run abundance index; CM.tr = Chum salmon terminal run abundance index; FL*s* = proportion of lactating subgroup females; L$m_{[1]}$ = living matriarch; N*g* = group size; PM*g* = proportion of physically mature males; RA*g* = average maternal relatedness of the group. Significant variables are bolded. SE = unconditional standard error, which adjusts for model selection uncertainty in addition to sampling variance.

Parameter	Estimate*	SE	95% CI	Relative importance
(Intercept)	**1.00**	**0.17**	**(0.67, 1.32)**	
A*g*	-0.07	0.13	(-0.33, 0.18)	1.00
CK.oa	**0.29**	**0.06**	**(0.17, 0.41)**	**1.00**
CK.tr	0.09	0.06	(-0.04, 0.21)	1.00
CM.tr	**0.22**	**0.07**	**(0.08, 0.35)**	**1.00**
FL*s*	**-0.40**	**0.08**	**(-0.56, -0.24)**	**1.00**
L$m_{[1]}$ ‡	0.49	0.29	(-0.07, 1.05)	0.08
N*g*	**-2.17**	**0.23**	**(-2.62, -1.71)**	**1.00**
PM*g*	**-0.73**	**0.12**	**(-0.96, -0.49)**	**1.00**
RA*g* †	**0.27**	**0.11**	**(0.06, 0.47)**	**0.45**

* Standardized effect sizes

† Adjusted for group size

‡ L$m_{[0]}$ (no living matriarch) is the reference category

Figures

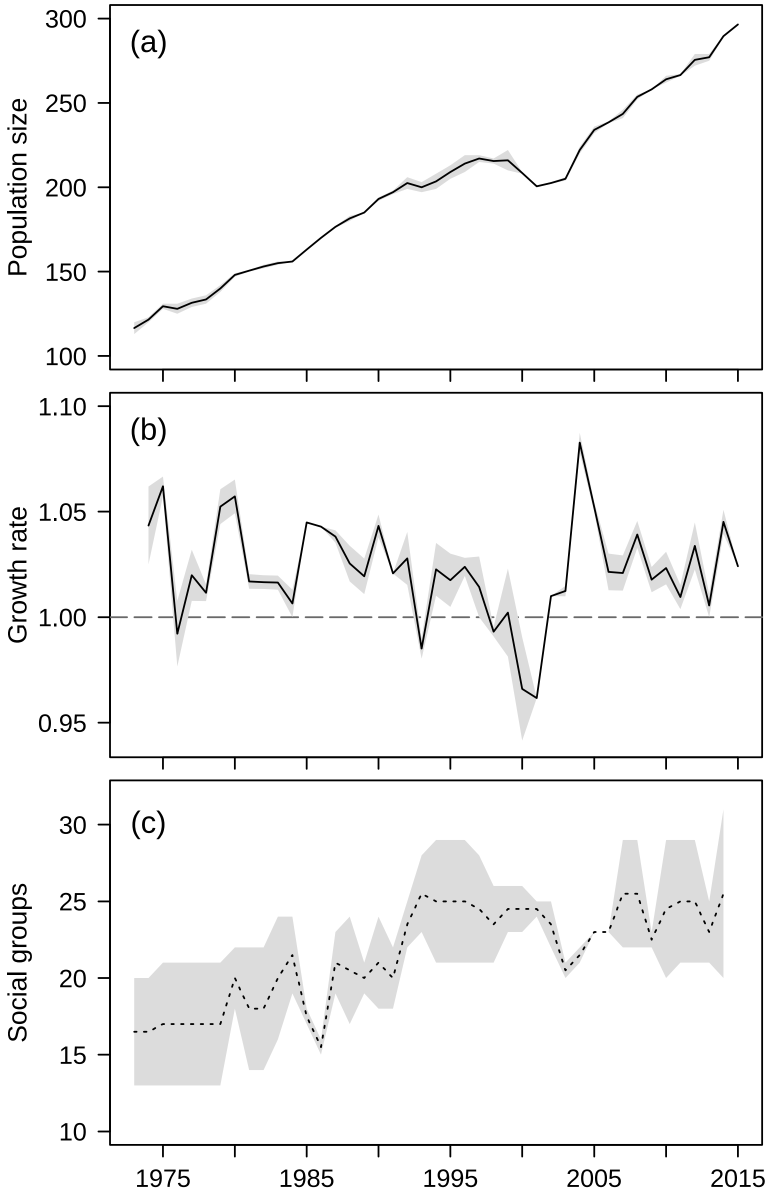

Figure 2.1 Northern Resident killer whale **(a)** population size and **(b)** population annual growth rate, and **(c)** the number of social groups present in the population. Grey shading denotes minimum and maximum values of estimates.

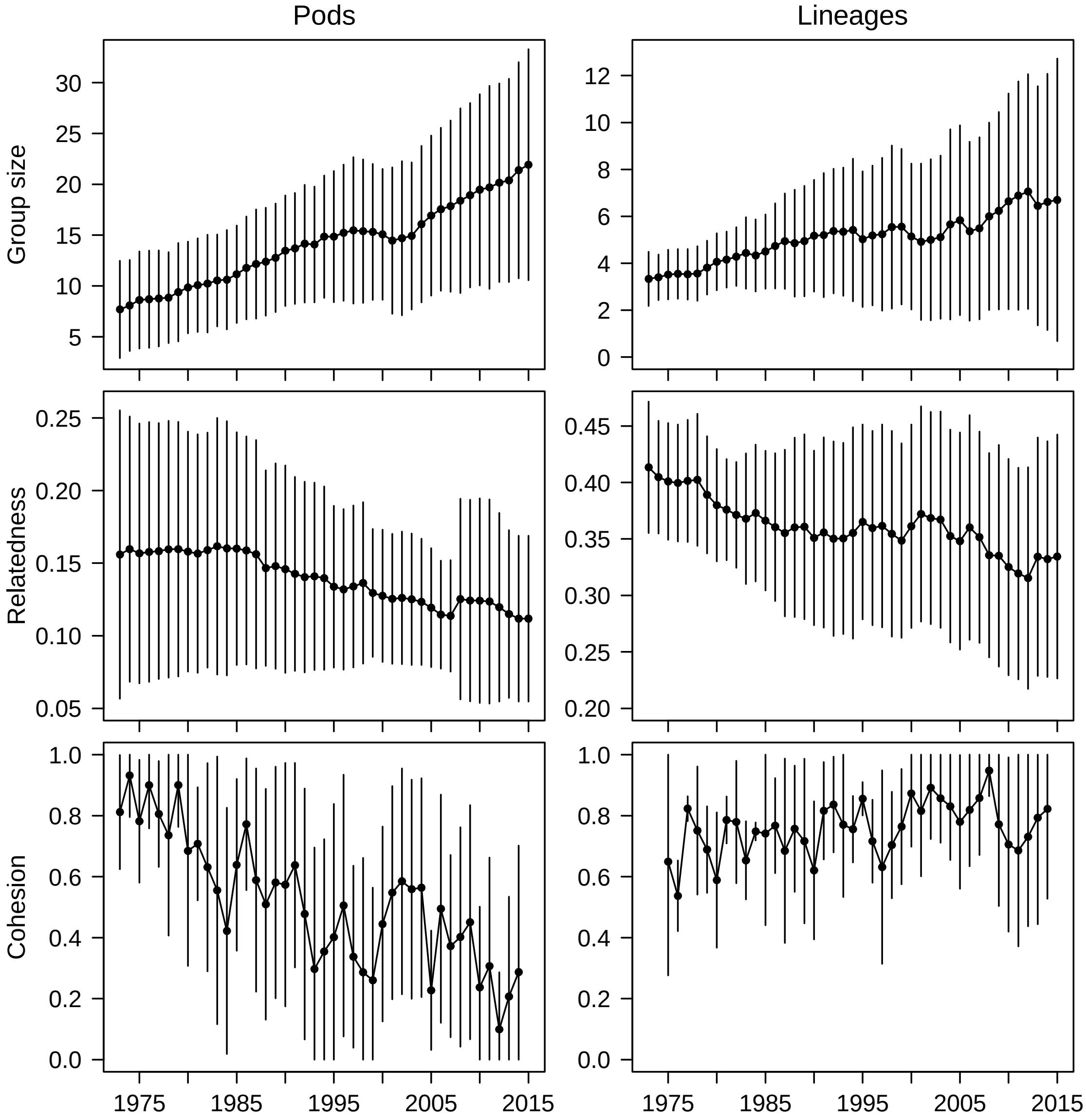

Figure 2.2 Mean number of individuals (group size), average pairwise maternal relatedness and average strength of cohesion (association estimated by HWI) within pods (left) and within lineages (right) over the period of the study. Dots represent mean values while whiskers denote standard deviation of estimate.

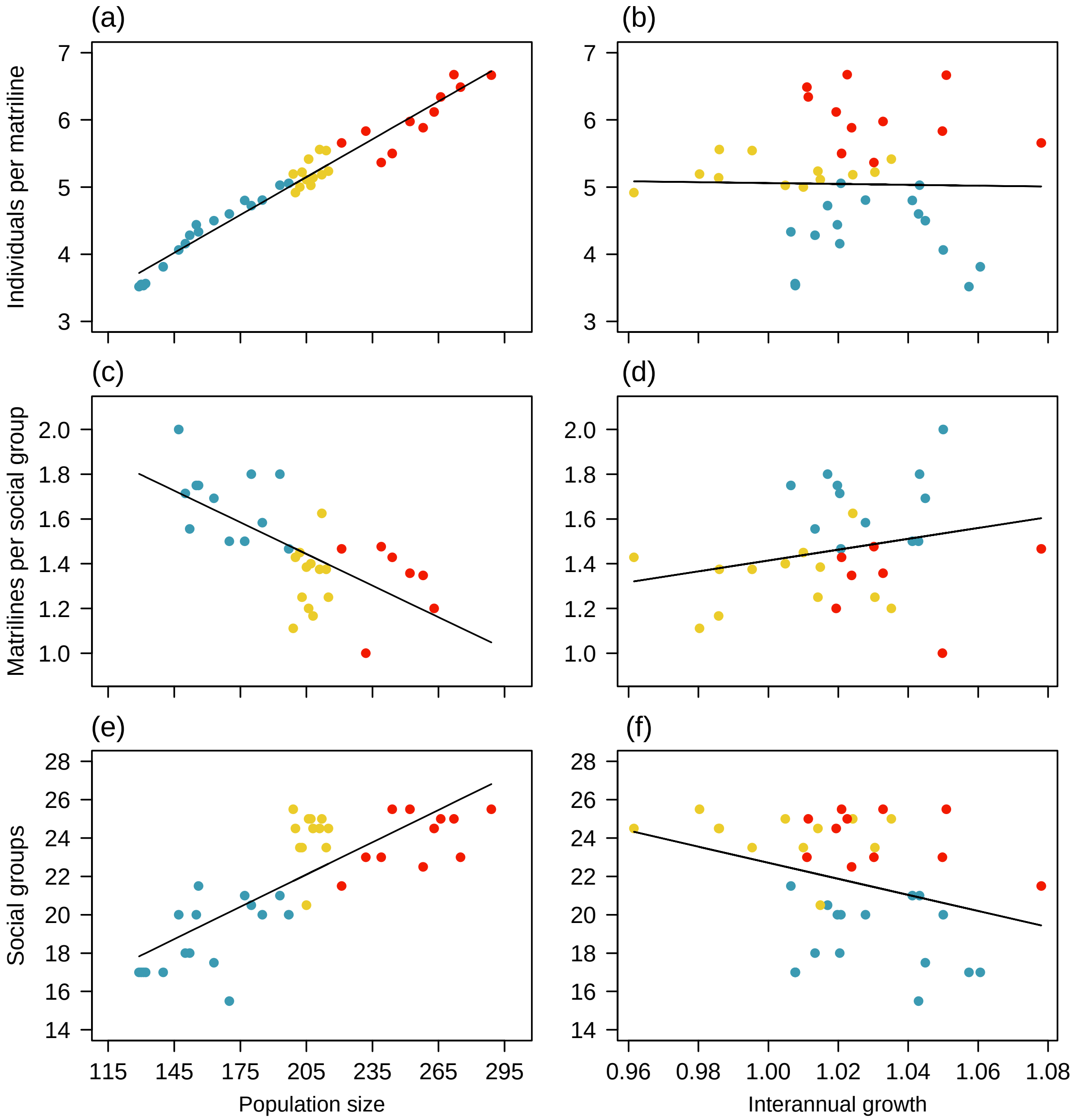

Figure 2.3 (a,b) Mean number of individuals per matriline, **(c,d)** Mean number of matrilines per social group, and **(e,f)** Estimated number of social groups in the NRKW population, in relation to population size and interannual growth rate of the population. Dots coloured according to the time period in which they were found: blue = 1973-1991 where the population exhibited steady growth (λ=2.95%); yellow = 1992-2003 where the population experienced high rates of mortality and almost no overall growth (λ=0.35%); red = 2004-2015 where the population showed significant growth (λ=3.13%). Black line denotes predictions of linear regressions.

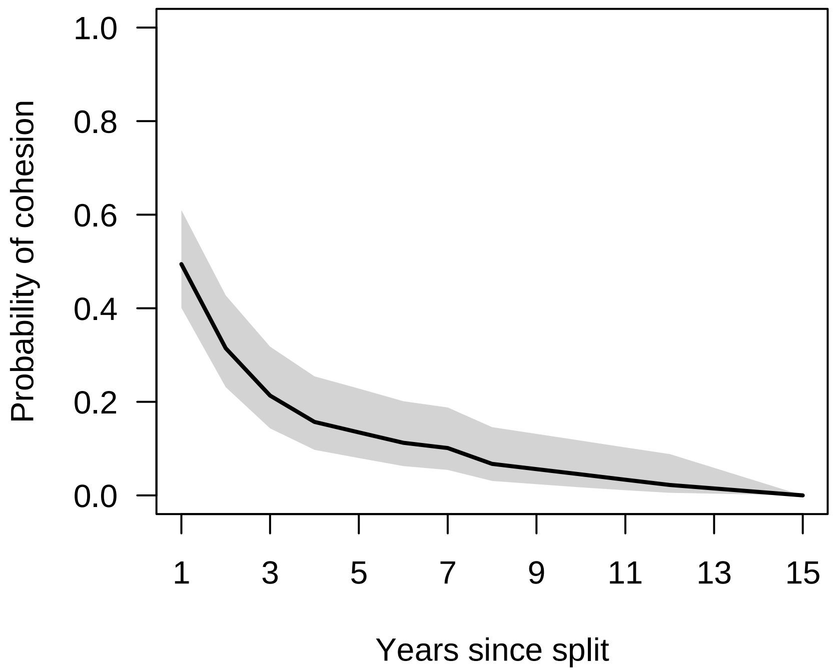

Figure 2.4 Probability that formerly cohesive NRKW social groups will re-form as a function of the time elapsed since the group had split (in years).

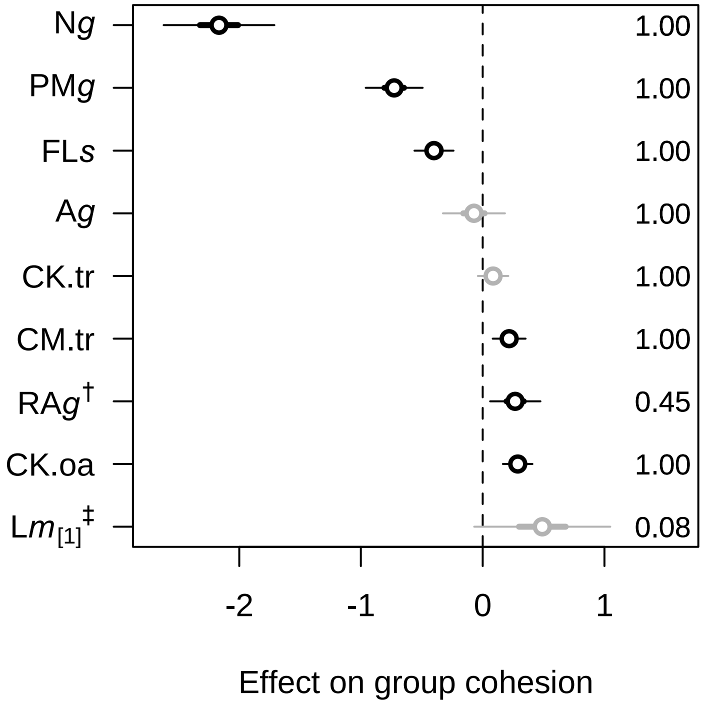

Figure 2.5 Effect of predictor variables on the probability of social group cohesion (per 2 SDs of the predictor), according to the model average of candidate models. A*g* = median age of group; CK.oa = Chinook salmon ocean abundance index; CK.tr = Chinook salmon terminal run abundance index; CM.tr = Chum salmon terminal run abundance index; FL*s* = proportion of lactating subgroup females; $Lm_{[1]}$ = living matriarch (‡ $Lm_{[0]}$, no living matriarch, is the reference category); N*g* = group size; PM*g* = proportion of physically mature males; RA*g* = average maternal relatedness of the group (†adjusted for group size). Relative variable importance shown in right panel of plot. Dots denote centered and scaled parameter estimates and thick and thin bars represent 50% and 95% confidence intervals, respectively. Non-significant variables (i.e., CIs encompassing zero) in grey. Significant variables in black.

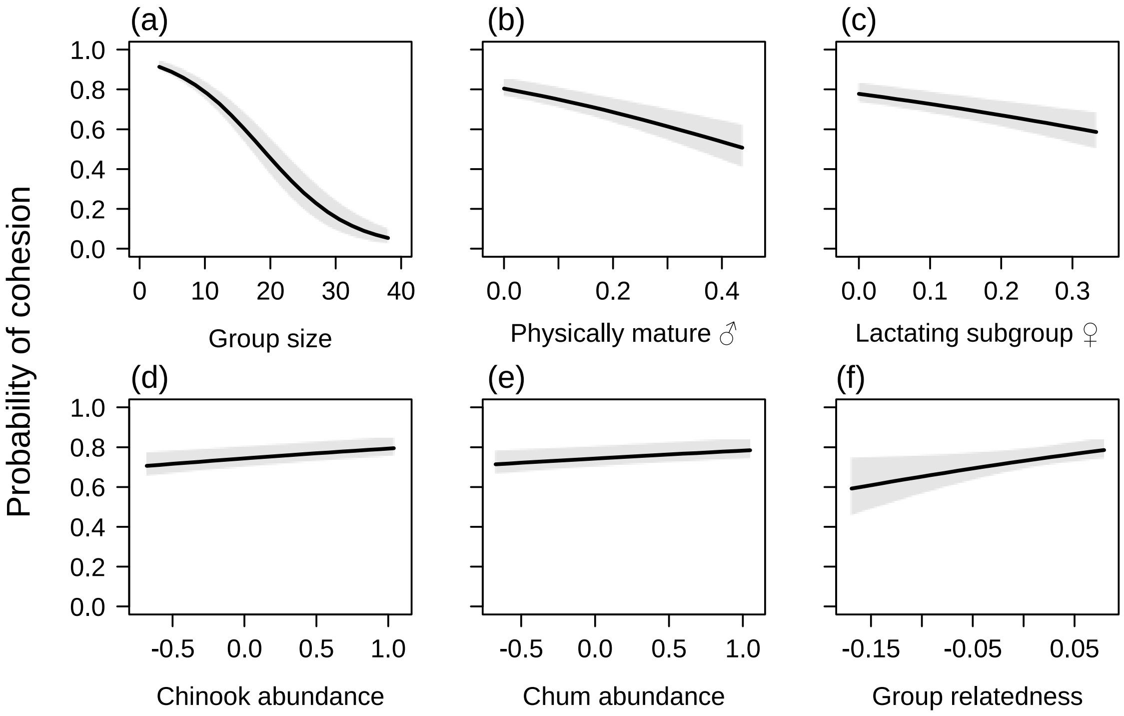

Figure 2.6 Probability of group cohesion as predicted by significant predictors of averaged models: **(a)** group size, **(b)** physically mature males (as a proportion of group size), **(c)** lactating subgroup females (as a proportion of group size), **(d)** centralized Chinook salmon ocean abundance, **(e)** centralized Chum salmon terminal run abundance, and **(f)** average pairwise maternal relatedness of the group (corrected for group size), when setting all other predictor variables to their mean values. 95% confidence bands denoted by shading.

CONCLUSION

> *One encounter with [them] revealed a snippet of their lives. ... [They] had occupied this place for nearly ten thousand years. How many hours are there in ten thousand years? Nearly eighty-eight million. What does it mean, then? Can I see eighty-eight million hours cupped there, in the palm of my hand? It is impossible to view [them]—all that they are—in a handful of sand grains. But if sand grains are all you have, you treat them as precious, each a crystal of knowing, inside which other, unexpected, truths might arise.*
>
> — Eva Saulitus, *Into Great Silence*

Summary of key research findings

As interactions between individuals and higher-level groupings may be used to define a population's social structure (Hinde 1976; Whitehead and Dufault 1999), it stands that significant changes in the association among individuals and groups may signify an important change in group membership and social organization of a population. The fission and fusion events detected in our study population are dramatic shifts in long-term associations that may have significant population-level consequences for the health and functioning of the population (Parsons et al. 2009). Detecting and determining the temporal locations of events like these are key steps in monitoring the social dynamics of populations and are essential to determining the factors that underlie them.

Both intragenealogical and intralineage matrilineal fission have been prevalent in the growing Northern Resident killer whale population. I demonstrate here that population growth and demography drives this matrilineal fission process. Cohesion of Northern Resident groups is primarily determined by internal characteristics of groups dictating intragroup food competition, though I do observe significant auxiliary effects of Chinook and Chum salmon abundance. Kinship may also have an effect on group cohesion, especially through food-related processes like kin-directed prey-sharing behaviour (Wright et al. 2016). Matrilineal fission may hold significant ecological and evolutionary consequences for a population – making social dynamics studies such as this essential to the management of threatened populations of social mammals.

Future studies… or what I would do if this were a PhD

1) Include early (summer) Chum terminal run abundance estimates from Northern British Columbia in the Chum abundance index. I have not been able to attain these estimates but the early Chum runs in Northern BC are relatively sizable and may be an important index to include, as this is one of the first large 'pulses' of prey available to NRKWs after winter.
2) Examine salmon indicator areas as separate predictors to determine if certain areas' abundances are stronger predictors of NRKW group cohesion than the coast-wide aggregates. If this were the case, this could allow for more geographically focused conservation measures. Of note: this was undertaken in the assessment of the effect of Chinook and Chum salmon abundance on RKW mortality and fecundity and was found to be less useful than coast-wide aggregates (Vélez-Espino et al. 2013, 2014).
3) Study the intensity of coastal Chinook and Chum fisheries over the time series to assess whether competition for salmon has changed.
4) Examine possible lagged effects of predictors on group cohesion (i.e., the signal of certain variables may be stronger when sampled from years prior).

5) Undertake a formal comparison between the population and social dynamics of the Northern and Southern Resident populations to more thoroughly describe the influence of population dynamics on the social organization of Resident killer whales.

Research contributions

Social organization is an integral component of the population biology of many species, as it may affect habitat range and use, predation pressure, the diffusion of learned behaviours, spread of disease, kin recognition and opportunities for reproduction (Alexander 1974). Many species that lead social lives are threatened by anthropogenic impacts on their environment (Couzin 2006). The potential for anthropogenic influence on a population's sociality is highly concerning, as it may confer external influence on breeding behaviour and population genetic structure (Pilot et al. 2010) and ultimately on a population's resilience and survival. Understanding the social behaviour of these species is critical, not only to provide context for the impacts that anthropogenic resource use has on animal populations, but also to provide a tool to gauge impacts and inform future conservation efforts.

In this work, I have described tools for detecting and locating changes in social organization in a population where complete, high-resolution data are not always available. I also provide the first description of matrilineal fission in killer whales, as well as the first comprehensive assessment of how intragroup cohesion in Resident killer whales is influenced by group structure, demography and resource abundance. With sociality highly linked to so many integral processes within killer whale populations such as the maintenance of cooperation, the transmission of information, and the preservation of effective outbreeding mechanisms (Barrett-Lennard 2000; Rendell and Whitehead 2001; Riesch et al. 2012), factors highlighted by these analyses may have consequences reaching far beyond the social organization of the population.

The results of these analyses indicate that group fission is predicated on intrinsic group factors directly related to prey. Considering Resident killer whales depend on and have a rigid preference for salmonid prey species of high economic importance, it is clear that Chinook and Chum salmon management must be conscious of the needs of Resident killer whale populations to ensure the whales' recovery. These results will hopefully contribute to the growing body of knowledge that may be used to inform resource management and conservation decisions regarding Resident killer whales and their prey.

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APPENDIX 1. Energy content of salmon prey

To put the daily caloric requirement (DPER) of Resident killer whales into context, I converted this variable into equivalent numbers of fish. This conversion was done under two scenarios: first, assuming NRKW diet during the sampling period (June-October) was composed only of Chinook salmon; and second, assuming NRKW diet during the sampling period was composed of 70% Chinook and 30% Chum salmon. The 70:30 Chinook:Chum ratio was an approximation of the relative composition of NRKW prey samples collected between June and October (Ford et al. 2010, Table 9).

To obtain numbers of fish, I simply divided the estimated daily caloric requirement by the energetic value of the given prey species. As the energetic value of prey items varies greatly with their age, I used the distribution of aged NRKW prey samples to dictate the size composition of fish consumed in the calculations. NRKWs have been found to mainly consume Chinook salmon of 4-5 years of age (83% of diet samples; Ford et al. 2010) as well as Chum salmon of 4-5 years of age (97% of samples; DFO 2016a). Energetic values for each species and age class were derived by converting the average weight for each age class to kilocalories, using formulae developed by O’Neill et al. (2014) (Tables A1.1 and A1.2).

Chinook salmon consumed by NRKWs on average provided three times more calories than Chum salmon; the average Chinook salmon provided approximately 16375 kilocalories, whereas the average Chum salmon provided roughly 5470 kilocalories. If one assumes that NRKWs have a diet consisting only of Chinook salmon, roughly 61 fish would be required each day to satisfy a group’s daily caloric requirement of one million kilocalories. If 70:30 Chinook:Chum diet is assumed, approximately 53 Chinook and 23 Chum would be required each day to satisfy those same daily caloric needs. At the population level, if one assumed a yearround 100% Chinook diet, the NRKW population would require roughly 910,277 Chinook salmon each year and both Resident populations combined would require 1.25 million Chinook salmon.

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Table A1.1 Chinook salmon age distribution in NRKW diet samples, biological characteristics and energy content by age.

Age (years)	Proportion of NRKW diet samples [a] (n=318)	Average fork length (mm) [b]	Average weight (kg) [b]	Energy content (kcal/fish) [c]
2	< 0.01	425	1.1	2099.8
3	0.11	581	3.1	5560.9
4	0.48	808	8.5	14352.3
5	0.35	939	13.3	21861.8
6	0.05	961	13.7	22479.3
7	< 0.01			*22479.3

Source: a) Ford et al. 2010 Table 9; b) Ford and Ellis 2006 Table 9; c) Using formula 7 from O’Neill et al. (2014)

* Average fork length and weight not available for 7 year old Chinook, so weight (and therefore energy content) assumed to be the same as a 6 year old Chinook.

Table A1.2 Chum salmon age distribution in NRKW diet samples, biological characteristics and energy content by age.

Age (years)	Proportion of NRKW diet samples [a] (n=205)	Average fork length (mm) [b]	Average weight (kg) [c]	Energy content (kcal/fish) [d]
3	0.01	580	3.9	4134.5
4	0.65	722	5.0	5228.8
5	0.32	768	5.8	5968.6
6	0.02	810	6.3	6450.3

Source: a) DFO 2016a; b) DFO 2016b; c) Using Chum length-to-weight conversion from Marr (1943); d) Using formula 9 from O’Neill et al. (2014)

APPENDIX 2. Indices of salmon abundance

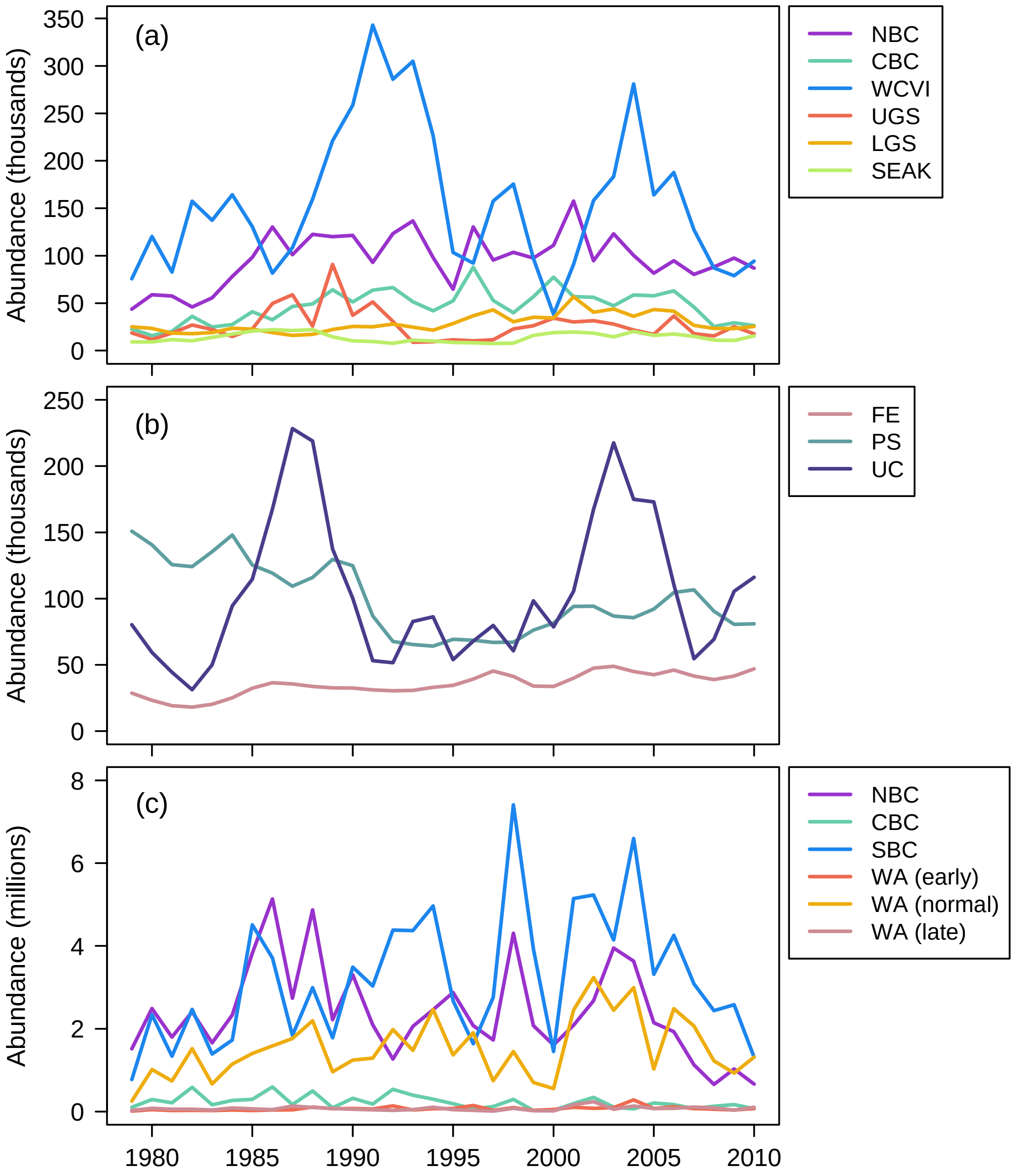

Figure A2.1 Sources of salmon data: **(a)** Chinook salmon terminal run reconstruction estimates for six North Pacific regions in NRKW range: southeast Alaska (SEAK), northern British Columbia (NBC), central British Columbia (CBC), west coast Vancouver Island (WCVI), upper Georgia Strait (UGS) and lower Georgia Strait (LGS); **(b)** Chinook salmon ocean abundance estimates for three areas: Fraser early (FE), Puget Sound (PS) and upper Columbia (UC); **(c)** Chum salmon terminal run reconstruction estimates for four areas in NRKW range: NBC (Canadian fishery areas 1-10), CBC (Canadian fishery areas 11-13), southern British Columbia (SBC) (fishery areas 14-19, 28 and 29) and Washington State (including Puget Sound and outer Washington coast). All Canadian run estimates are for 'normal'-timed (fall) chum runs only. Washington run estimates include early, normal and late estimates, with peaks occurring in October, November-December and January, respectively.

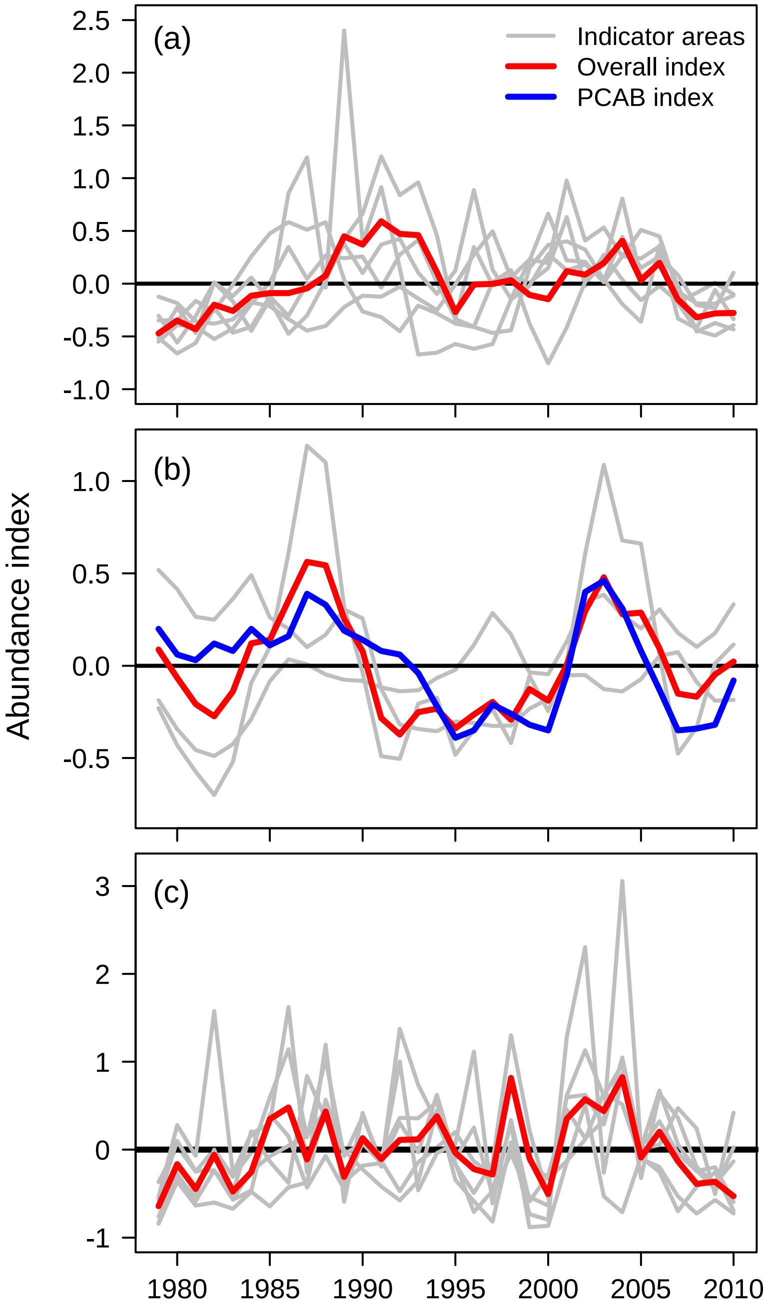

Figure A2.2 Centralized indices of salmon abundance according to **(a)** Chinook salmon terminal run indicators and overall index (CK.tr), **(b)** Chinook salmon ocean abundance indicators and overall index (CK.oa), and **(c)** Chum salmon terminal run indicators and overall index (CM.tr). Overall indices are centered (mean-subtracted) and scaled (divided by 2 SDs) aggregate totals of indicators areas described in Figure A2.1. Chinook PCAB index used in Ford et al. (2010a) and Foster et al. (2012) included for comparison; the PCAB index is a coast-wide aggregate of fish available *and allowable* to particular fisheries, whereas the Chinook ocean abundance index I use indicates stock-specific cohort size available to ocean fisheries.

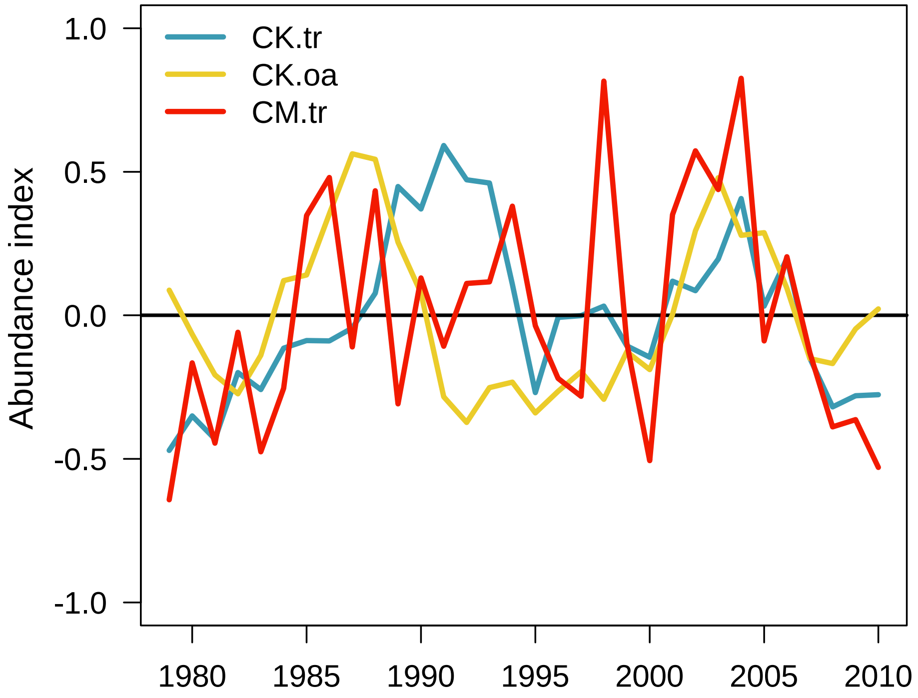

Figure A2.3 Centralized overall indices of salmon abundance used in analysis: Chinook terminal run index (CK.tr), Chinook ocean abundance index (CK.oa), and chum terminal run index (CM.tr).

APPENDIX 3. Random forest analysis of social group cohesion predictors

Methods

As an evaluation of group cohesion independent of the GLMM comparison, I assessed the relative importance and effect of the predictor variables using the machine learning (ML) algorithm, random forest (RF; Breiman 2001). The regression RF is an ensemble of independently constructed decision trees, built through the random selection of predictor variables at each node from which the variable and value that optimizes the split is determined. RF is effectively the mean prediction of the individual trees. Using the R package 'randomForest' (Liaw and Wiener 2015), I ran a regression RF with 500 trees and eight variables tried at each split to predict group cohesion (HWI), with sampling stratified by Group ID. The relative importance of predictors was assessed in two ways: accuracy and node impurity. These measures indicate the extent to which mean square error (MSE) and residual sum of squares (RSS), respectively, increase when the given variable is randomly permuted, with large changes indicating important variables. Partial dependency plots were also generated to illustrate the marginal effect of different predictors on the response variable.

Results

As with the GLMMs, RF suggested that intragroup competition for food was an important predictor of group cohesion. According to both percent increase in MSE and node purity, the top predictor of group cohesion was a group's estimated daily caloric requirement (DPER*g*; Figure A3.1). RF predicted social group cohesion to continuously decrease with increasing DPER*g*, with the predicted probability of group cohesion dropping below 50% as the group's caloric needs reach approximately 2 million kilocalories per day (roughly 122 Chinook salmon; see

Appendix 1) (Figure A3.2a). According to percent increase in node purity, the average maternal relatedness of a group, as well as a group's overall size, may also possibly be important predictors of group cohesion, with the probability of group cohesion dropping dramatically when average group maternal relatedness drops below 0.2 (just below the maternal relatedness of first cousins or grandmother-grandoffspring) and when group size exceeds approximately 12 individuals (Figure A3.2).

It should be noted that RF assesses all candidate predictors independently, ignoring collinearity. This is why all of the top predictors are variables that are highly correlated with one another. The top predictor (DPER*g*) shows the greatest change in the probability of group cohesion at approximately two million kilocalories; such energetic requirements are found in groups of 10-15 NRKW individuals with average group maternal relatedness of 0.1-0.2. This is also why these results are not completely equivalent to those of the GLMMs; while GLMMs look at the cumulative effect of all variables within a given model, RF assesses the singular impact of a given variable.

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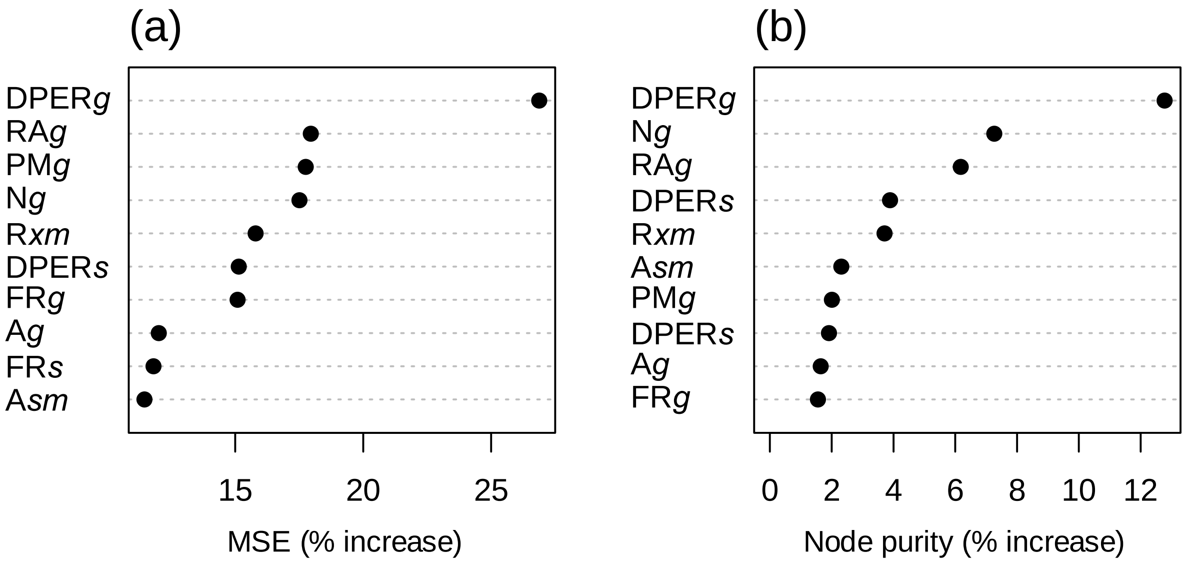

Figure A3.1 Variable importance as ranked by ML algorithm RF, according to the change in **(a)** accuracy (measured by mean square error, MSE) and **(b)** node purity (measured by residual sum of squares), when the given variable is randomly permuted. Plots restricted to the top ten variables according to accuracy and node purity, respectively.

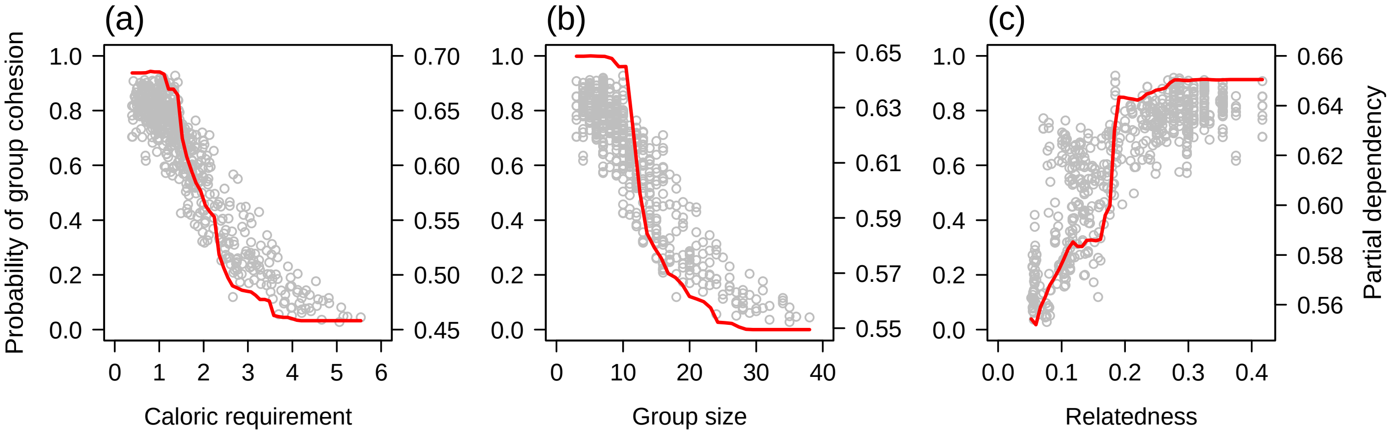

Figure A3.2 Group cohesion (HWI) as predicted by the top-ranked predictors identified by RF: a group’s **(a)** daily estimated caloric requirement (in millions of kilocalories), **(b)** size (number of individuals), and **(c)** average maternal relatedness. Grey open dots denote predictions for the 564 group-years and red line shows the marginal effect of the predictor variable on the prediction of HWI.

APPENDIX 4. Onset of reproductive senescence

Older, mature females that have previously produced calves are considered to be of unknown reproductive status; the female could either still be fecund or she may be post-reproductive. To examine this, I generated age-specific probabilities of fecundity. Here I consider reproductive senescence to be the inverse of fecundity.

Age-specific probability of fecundity was derived through Kaplen-Meier non-parametric survival analysis, using the age at which a given female produced her last known viable calf (Figure A4.1). Survival analysis was conducted using *survfit* function in the R package 'survival' (Therneau 2014). For this analysis, I included females no younger than 30 years of age, who were known to be reproductive and in whose age estimate I was confident (year of birth known within 3 years; n = 42).

The oldest age at which a NRKW has produced a viable calf is 48 years (±3 years). The average age at last calving is 35.3 (sd = 4.3). Of the 40 animals observed, 95% had their last calf by 43 years of age. Given the gestation period of killer whales (~514 days; Duffield et al. 1995), the mean age of last conception is 33.9 years. Due to the possibility of undetected miscarriages and non-viable calves, these estimates provide the minimum estimate of age at last calf and last conception.

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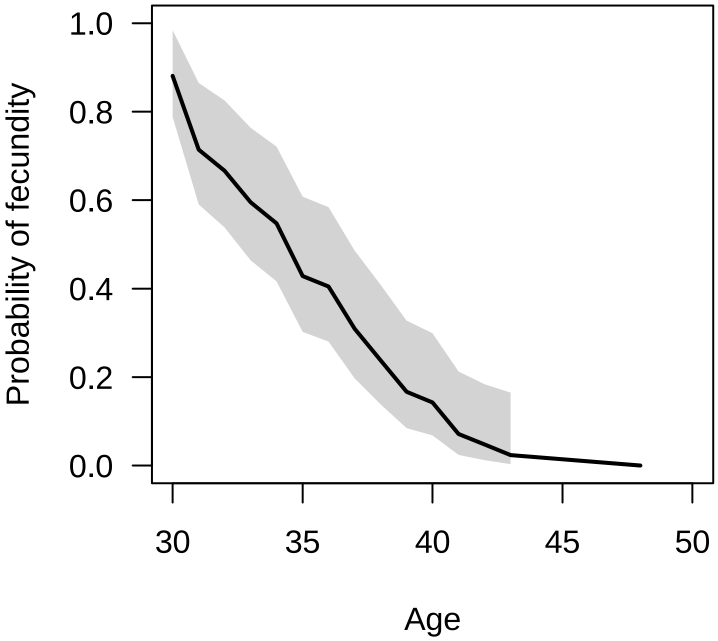

Figure A4.1 Age-specific probability of fecundity. This refers to the probability that a female will birth her last viable calf by a given age. This distribution is assumed to be representative of the inverse probability that an animal is post-reproductive at a given age. Shading represents 95% confidence bounds.