Exploring the mechanisms and functions underpinning the social networks of an endangered population of killer whales, *Orcinus orca*

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April 2012

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ABSTRACT

For the majority of social species, group composition is dynamic, and individuals are interconnected in a heterogeneous social network. In this study I investigate the mechanisms underpinning social structure in the endangered southern resident killer whale (*Orcinus Orca*) population using a long term dataset, and explore the consequences of these.

My results demonstrate that resource availability may be an important determinant of social network structure. A significant relationship between the connectivity of the social network and salmon abundance occurred, with a more interconnected network in years of high salmon abundance.

As networks are non-random, highly connected individuals may play a key role in population processes such as information and disease transmission. While associations occurred both within and between matrilines, females had a significantly higher number of associates than males, as did older individuals of both sexes. Older males played a more important role in interconnecting the network.

The attributes of group leadership were then investigated in matrilines and in individuals. Leadership was not a factor of size or mean age of matriline. However, there was a significant relationship between leadership score and the matriline sex ratio. Individually, females had higher leadership scores than males, and there was a positive correlation between leadership score and age in both sexes. I suggest that the oldest females have the highest
leadership scores due to increased ecological knowledge that comes with a prolonged lifespan.

Using multi-generational records for two populations of killer whales, I show that both reproductive and post-reproductive mothers increase the survival of offspring, particularly in older male offspring. This is consistent with theoretical predictions, and may explain why female killer-whales have evolved the longest post-reproductive lifespan of all non-human animals.

Given the role that individuals of high network centrality can play in population processes, understanding the driving forces behind social network structure is vital when designing effective conservation and management plans.
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ACKNOWLEDGEMENTS

Firstly, I would like to thank my supervisor Darren Croft, whose continual guidance, support and patience have been invaluable to me. I would like to thank Dan Franks his helpful co-supervision and for advice and support with data analysis. I am also exceptionally grateful to Jens Krause and Lesley Morrell for getting me started with my Ph.D.. In addition I would like to thank Safi Darden for acting as my mentor throughout my Ph.D..

Without the long term collection of photographs and video footage by the staff at the Center for Whale Research, San Juan, this project would not have been possible. I have been lucky to work with some fantastic people on San Juan, and special thanks goes to the director, Ken Balcomb, his passion and dedication to research and conservation have been truly inspirational. I also thank the permanent staff Dave Ellifrit, Erin Heydenrich, Lisa Moorby and Astrid Van Ginneken, and a series of long term volunteers; Barbara Todd, Kathy Babak, Kim Marlor, Candice Emmons, Adam Ü, Stewart Macintyre, Stefan Jacobs, and Earthwatch volunteers. I particularly thank Erin Heydenrich and Timmy Morris for their continual friendship and support during fieldwork over the last eight years. I would also like to thank Isis, the whale watch dog, for taking me for plenty of walks.

My thesis has benefited from insightful discussions with Kim Parsons, Dick James and Kevin Simmonds. I would also like to thank all the members of the CRAB group at the University of Exeter for their help and advice particularly Natasha Boyland, Mat Edenbrow, Jess Isden, Dave Jacoby, Kim Jayne, Christina Meier, Alessandro Macario, Beth Nicholls, Xarini
Pacheco-Pacheco, Paul Rose, Lou Styles and Mark Whiteside. I would also like to thank Caroline Dingle, Paul Foster, Jess Isden and Emma McKinnley for help with proof reading.

Special thanks to Katie Foster, Beth Nicholls, Jess Isden, Lou Styles, Simon Schnetler, Pete Spence, Dean Ferris, Rachel Coombes and Dylan for encouraging regular breaks (usually coinciding with warm days and clean waves).

Finally, I extend my thanks to my parents, Paul and Lyn, who have supported me from the first day I announced I was going to be a marine biologist (at the age of 5) right through to today.

This work was funded by a BBSRC studentship.
DECLARATION

The work contained in this thesis has involved collaborations with Safi Darden (SD), John Ford (JF), Sonia Mazzi (SM), Lesley Morrell (LM), Kim Parsons (KP) and Astrid van Ginneken (AG). Their contributions are listed below. As my principal supervisor, Darren Croft was involved in all chapters. Dan Franks (DF) was responsible for constructing null models for all analysis, and was also hugely helpful in advising me about analytical techniques. Ken Balcomb, the director of the Center of Whale Research, was responsible for the photograph and video collection from 1976-2011, along with a team of volunteers and staff (I was on staff from 2004-2011, and developed the association databases independently, from previously collected photographs and video footage).

Chapter II. AG assisted with database work, the chapter also benefited from insightful discussions with LM and KP. Salmon abundance data were provided by the Pacific Salmon Commission.

Chapter III. DF constructed network diagram (figure 3.1), and provided null model data for figure 3.3.

Chapter V. JF provided multi-generation demographic data for the northern resident killer whales. DF and SM constructed the Cox proportional hazards model. The chapter also benefited from insightful discussions with SD.
In addition, some of the work in this thesis has been published, or submitted for publication:


All photographs and video footage were collected under whale watch guidelines or under MMPA research permit #532-1822 and/or DFO license #2006-08/SARA-34.
Chapter I.

General Introduction:

Exploring the social networks of an endangered population of killer whales (*Orcinus orca*)
1.1. LIVING IN GROUPS

In the animal kingdom many species, both vertebrates and invertebrates, live in groups (Ebensperger 2001; Krause & Ruxton 2002). Group living occurs across a wide range of taxonomic groups, examples include (but are by no means limited to): colonies of ants (Giraud et al. 2002), shoals of fish (Godin et al. 1988), flocks of birds (Powel 1974), and herds of ungulates (Fryxell et al. 1988). For the majority of social species group composition is dynamic and individuals are interconnected in a heterogeneous social network (Krause & Ruxton 2002). Such population social structure is a central concept in sociological analysis (Cook & Whitmeyer 1992). In addition, social structure is a key aspect of a population’s ecology and biology (Lusseau et al. 2006) and the social groups of both terrestrial and marine animals can vary considerably in size and structure. Hence, gaining knowledge of the mechanisms and functions underpinning this is important for both applied and fundamental purposes. The social groups of terrestrial and marine animals can vary considerably in their size and structure. In this first section I begin by reviewing the costs and benefits of group living and sociality.

1.1.1. Costs and benefits of group living and sociality

There are both costs and benefits associated with group living and sociality (Krause & Ruxton 2002). These are considered separately in the next two sections.

1.1.1.1. Benefits of group living

Group living may occur passively when animals happen to clump around a particular resource, such as food or water. Alternatively animals may actively choose to be part of a
group. One of the major benefits of group living is predator avoidance which can occur in several ways. Firstly there is the “many eyes theory” (Lima & Bednekoff 1999), which shows a negative relationship between the groups size and the level of individual vigilance. This is based on the fact that more individuals are scanning for predators as group size increases, hence individuals can afford to reduce their personal vigilance and devote more time to foraging (Lima 1995). The “many eyes theory” can be seen in many socially feeding vertebrates including mammals [e.g. bighorn sheep (Ovis Canadensis) (Berger 1978; Rieucau & Martin 2008), pronghorn (Antilocapra americana) (Lipetz & Bekoff 1982), feral goats (Capra hircus) (Shi et al. 2010) and hoary marmot (Marmota caligata) (Holmes 1984)], birds [e.g. the lesser rhea (Rhea pennata pennata) (Barri et al. 2012), red-crowned cranes (Grus japonensis) (Wang et al. 2011), starlings (Sturnus vulgaris) (Powel 1974), house sparrows (Passer domesticus) (Elgar & Catterall 1981) and willow tits (Poecile montanus) (Ekman 1987)] and even some species of fish [e.g. Minnows (Phoxinus phoxinus) (Magurran et al. 1985) and glowlight tetra (Hemigrammus erythrozonus) (Godin et al. 1988)]. Secondly, another benefit of group living is the dilution effect which can lead to safety in numbers, where the probability of a specific individual being captured decreases with increasing group size (Hamilton 1971). One study exploring this investigated ocean skaters (Halobates robustus) predated on by juvenile South American pilchard (Sardinops sagax), they showed that as group size increased capture probability decreased (Foster & Treherne 1981). Living in a group reduces individual predation risk in other species, including redshanks (Tringa totanus) (Cresswell 1994) and monarch butterflies (Danaus plexippus) (Calvert et al. 1979). Like with ocean skaters (Foster & Treherne 1981), as group size increases the risk to each individual of being selected by a predator decreases (Krause & Ruxton 2002). Finally individuals can benefit from group living by simply huddling together for warmth (Robin et al. 1998; Wan 2003).
1.1.1.2. Benefits of sociality

Sociality implies a number of individuals interacting together which can lead to complex social relationships and structure (Wey et al. 2008). Sociality may or may not occur alongside group living where it does occur benefits can include: transferring information between individuals (Sernland et al. 2003; Vickery et al. 1991), cooperative foraging (Caraco & Wolf 1975; Stenberg & Persson 2005), pooling skills (Giraldeau 1984) or cooperative defence of young or territories (Packer et al. 1990). Each of these points will be considered in turn.

Various types of information can be shared between group members. For example, individuals may share information about the quality of a foraging area. Where food is patchily distributed each group member can more accurately assess the quality of the patch if knowledge is pooled (Sernland et al. 2003). Animals may also increase their own food intake by learning to eat new foods or by learning of new foraging areas from conspecifics (Giraldeau 1984). For a number of species sociality can also provide adaptive benefits during cooperative foraging, whereby individuals can work together to hunt prey that would be too large or difficult to catch for a single animal. Examples can be seen in large carnivores such as lions (*Panthera leo*) (Stander 1992) and some populations of killer whales (*Orcinus orca*) (Pitman & Durban 2012). In such coordinated attacks different individuals may take on different roles within the group hence pooling the skills of the group to maximize success (Giraldeau 1984).

Sociality also has the benefit of allowing information to be passed quickly from one individual to the next. Such information may include warning against predator attacks
Pre-flight movements in pigeons (*Columba livia*) have been shown to signal to the rest of the group whether the individual is leaving due to predator detection or for some other reason (Davis 1975). Comparable work on pelicans (various *Pelecanus* species), northern gannets (*Morus bassanus*), red-footed boobies (*Sula sula*) and cormorants (various *Phalacrocorax* species) have also shown similar pre-flight behaviour (van Tets 1965). In mammals, including Belding’s ground squirrels (*Spermophilus beldingi*) (Sherman 1977), vervet monkeys (*Cercopithecus aethiops*) (Seyfarth et al. 1980), Diana monkeys (*C. Diana*) (Zuberbuehler et al. 1997), ring tailed lemurs (*Lemur catta*) (Macedonia 1990), Barbary macaques (*Macaca sylvanus*) (Fischer et al. 1995) and mongoose (*Suricata suricatta*) (Manser 2001) alarm calls are used to warn other group members of danger. Alarm calls will vary depending on the predator type and the extent of the danger (Manser 2001). Alternatively, individuals can signal to one another when it is time to move to a new area (Bousquet et al. 2011). For example, in white-faced capuchins (*Cebus capucinus*) movement is usually initiated by an individual emitting a trill (Boinski & Campbell 1995). Likewise, group movement in green woodhoopoes (*Phoeniculus purpureus*) is often coordinated by the use of vocal signals (Radford 2004).

Aside from information transfer social animals can also benefit from cooperative rearing and protection of young. Meerkats (*Suricata suricatta*) provide a key example of this where an alpha pair will be the main animals producing pups but other females that have never reproduced will lactate, hunt for the pups and provide protection for them (Clutton-Brock et al. 2001). In birds azure-winged magpies (*Cynopica cyanus*) also cooperatively breed and work by Valencia et al (2006) has shown that offspring’s cell mediated immune response was positively correlated with an increase in the number of helpers at the nest site. Similarly female sperm whales (*Physeter macrocephalus*) from stable social groups called “units”
In these groups females will cooperate and provide care for each other’s young while the mother performs deep foraging dives (Gero et al. 2008). In addition, when under attack from killer whales all individual sperm whales will form a Marguerite formation. This is where adults will surround a young animal with their tail flukes facing out to protect the young from attack (Pitman et al. 2001).

1.1.1.3. Costs of group living and sociality

The decision to live in a group represents a dynamic trade off between the benefits (discussed above) and the costs associated with such group living and sociality. Costs may include increased competition for food (Beauchamp 1998), food stealing (Suraci & Dill 2011), more competition for space or mates (Emlen & Oring 1977), increased probability of detection by predators or an increased exposure to pathogens (Woodroffe et al. 2009). Examples of these costs can be seen across a range of taxa. For example, larger flocks of redshanks will incur more attacks from sparrow hawks (*Accipiter nisus*) than smaller ones (Cresswell 1994). However, as previously discussed, the dilution effect will mean that the probability of an individual being captured is actually smaller. Several studies show a higher predator success rate when the prey group is smaller (Trail 1987; Treherne & Foster 1982). Larger groups also have a higher probability of being detected by their predators; however encounter rate is often smaller (Ioannou & Krause 2008; van Schaik et al. 1983). In addition to this, where groups are larger there will be an inevitable increase in competition for food, as there are only a finite number of resources. Where animals exceed the optimal number that the food can support there will, on average, be a reduced food intake by individuals (Krause & Ruxton 2002). Group foraging also increases the probability of kleptoparasitism, where procured food is stolen by intraspecific individuals. Intraspecific kleptoparasitism has been widely
documented in birds [examples include kelp gulls (Larus dominicanus) (Steele & Hockey 1995), ring-billed gulls (L. delawarensis) (Elston et al. 1978), bald eagles (Haliaeetus leucocephalus) (Jorde & Lingle 1988), oystercatchers (Haematopus palliatus) (Tuckwell & Nol 1997)] but is also seen in arachnids (Whitehouse 1997), fish (Nilsson & Brönmark 1999) and mammals (Donald & Boutin 2011). In a similar manner to increased competition for food there will also be increased competition for space and mates (Emlen & Oring 1977). In addition, individuals living in close physical proximity have a greater opportunity to transfer disease or parasites (Lindsey et al. 2009) between one another through frequent contact. However, this may not always be the case, for example Godfrey at al. (2009) found no relationship between the group size in the group living gidgee skink (Egernia stokesii) lizards and the prevalence of blood parasite infections within the groups.

Within a social group individuals may hold different positions (see section 1.2 for explanation) and these will come with their own costs and benefits. For example in figure 1.1 individual A is on the periphery of the social group, this position might be at higher risk from predatory attacks (Morrell et al. 2010) additionally individual A may have less opportunities for interacting with other individuals (for mating or information transfer reasons). However, a benefit of being on the periphery may also limit the chance of infection. More central individuals in the group (e.g. individuals B or D, figure 1.1) might benefit from lower chance of being predated upon (Foster & Treherne 1981; Hamilton 1971; Morrell et al. 2010), and greater access to mates (Godfrey et al. 2009; Sih et al. 2009). There are examples across a range of taxa where males with more social bonds with conspecifics have higher reproductive success [long-tailed manakins (Chiroxiphia linearis) (McDonald 2007), wire-tailed manakins (Pipra filicauda) (Ryder et al. 2009), Assamese maqaque (Macaca assamensis) (Schülke et al. 2010) and forked fungus beetles (Bolitotherus cornutus) (Formica et al. 2012)]. However,
the number of associates an individual has may also be important in understanding the costs associated with holding a central position in the social network. For example where disease transmission is concerned the strength of relationships may be important in the probability of contracting an infection, particularly with weaker pathogens (Wey et al. 2008).

Figure 1.1. Diagrammatic representation of the different positions animals might hold within a social group (see section 1.2 for full explanation of social networks). Individuals are represented by coloured circles (blue males and pink females), and interactions between individuals are represented by lines.

1.1.2. Group structure and composition

Assortative mixing is defined as the extent in which individuals in a network are connected to others that are similar to themselves (Whitehead 1997). Group composition can be dynamic and individuals may assort due to different behavioural or phenotypic traits. Assortment can be passive where individuals of similar phenotype occupy a similar habitat for example (Croft et al. 2005). However, it need not be a passive consequence of animal population structure and habitat choice but can be actively attained (Eshel & Cavalli-Sforza 1982). A classic example of assortative mixing is seen in human populations, where individuals will usually preferentially choose partners of their own race (Newman 2003b). Assortment can have a significant impact on group structure and composition, individuals may choose to
group with others of similar phenotype (Croft et al. 2005; Fowler et al. 2011) or with kin (Couzin 2006). Assortative interactions occurring between individuals may illustrate important adaptive benefits (Croft et al. 2005). Such benefits may include a reduced risk of predation (Chivers et al. 1995), increased foraging efficiency (Krause 1994) and reduced competition for resources (Utne-Palm & Hart 2000).

Evidence for active sorting according to phenotypic characteristics has been shown in humans (Homo sapiens), who will often associate with others that have similar characteristics (Fowler et al. 2011). Trinidadian guppies (Poecilia reticulata) have also been shown to assort with others of similar body length (Croft et al. 2005). In addition, sex is known to impact social structure, for example female guppies often form non-random associations with other females whereas no persistent pairs are found between males (Croft et al. 2006). Individuals can make active social decisions with regard to who they wish to associate with. For example, kin selection can be an important predictor of who associates with whom (Couzin 2006). There are advantages for animals to group with familiar individuals or kin. Such advantages include reduction of competition due to established hierarchies or the evolution of altruistic behaviour (Frommen & Bakker 2004). Additionally, associating with kin can provide inclusive fitness benefits which may include cooperation (e.g. alloparental care or the transmission of socially learned behaviours), communal defence and access to resources and mates (Beck et al. 2011; Cornwallis et al. 2009).

Group living can only be achieved if animals synchronise their activities. Activity synchronisation is costly to individuals, as they must stop what they are doing which may be more profitable to them to achieve this (Conradt & Roper 2000). In addition, such
synchronous behaviour may be problematic in mixed sex groups, where the requirements of males and females are different (Conradt & Roper 2000). Conradt and Roper (2000) suggest that activity synchronisation explains about 35% of the sexual segregation observed in red deer (*Cervus elaphus*). They further suggest that such social segregation may also be due to differences in environmental requirements or competitive or aggressive interactions between the sexes. External factors can also impact the way individuals assort within a group. For example, female Trinidadian guppies have been shown to develop social recognition and demonstrate female-female assortment preferences in the presence of sexual harassment from males (Darden et al. 2009). They will even take this one stage further and actively group with females more “attractive” than themselves to avoid harassment (Brask et al. 2011).

At the level of the group there is a large amount of variation in group stability from species to species. For example, mantled howler monkeys (*Alouatta palliate*) are the only species from the genus *Alouatta* to consistently form large stable groups which contain both adult males and adult females (Bezanson et al. 2008). In contrast, chimpanzees (*Pan troglodytes*) live in fission-fusion societies where animals associate in small groups which may change dramatically several times a day. Individuals form temporary foraging associations of varying sizes dependent on the reliance of patchily distributed fruit trees (Bearzi & Stanford 2007). Like the chimpanzee, bottlenose dolphins (*Tursiops truncates*) are described as living in fission-fusion societies (Lusseau et al. 2003). However, not all populations of bottlenose dolphins have the same fission-fusion lifestyle. Lusseau and Newman (2004) and Lusseau et al. (2003) investigated the social networks of a wild population of bottlenose dolphins in Doubtful Sound, New Zealand. They established that the population was dissimilar to others in that they live in large mixed-sex groups.
The way in which animals choose or avoid other individuals can also lead to heterogeneity in group membership. For example, some individuals may group according to a phenotypic or behavioural particular trait. Such assorting has been documented in the Trinidadian guppy, where individuals will preferentially shoal with others of similar body length (Croft et al. 2005). Healthy animals will also avoid individuals with parasite loads. Both three-spined sticklebacks (*Gasterosteus aculeatus*) (Barber et al. 1998) and banded killifish (*Fundulus diaphanous*) (Krause & Godin 1996) have been shown to avoid conspecifics carrying parasites. This is thought to be a consequence of some learned factor perhaps because the majority of visual predators will choose an individual that is different from a group. Predators may choose a smaller or weaker looking animal that would be easier to capture. To avoid being the “odd one out” fish actively choose to assort with others that look similar to themselves hence maximising the dilution effect (Barber et al. 1998).

1.1.3. *Group position and survival*

The costs and benefits associated with group living are often highly dependent on the spatial position of individuals within a group. The position an animal takes within a group can also have consequences for the survival probability of the individual (Hamilton 1971; Hirsch & Morrell 2011; Krause 1994), the role they play in transmitting information (Krützen et al. 2005; Whitehead 1998a; Whitehead 2010; Whitehead et al. 2004; Wolf et al. 2007) or disease (Cross et al. 2004; Watts & Strogatz 1998) through the group, mating opportunities (Matocq & Lacey 2004; Piertney et al. 1999; Wolf & Trillmich 2008) and the influence they have over collective decisions or movements (Bonanni et al. 2010; Flack et al. 2012). The position an animal takes within a group may impact survival probability because peripheral individuals are more often attacked than individuals towards the centre of the group (Hamilton 1971;
Hirsch & Morrell 2011; Krause 1994). This is known as “the selfish herd” and animals will position themselves relative to other individuals to minimise their own risk of predation (Hamilton 1971). Predation is known to drive sociality through group living however, within a selfish herd social structure can also be affected (Ebensperger 1998). For example, in black-tailed prairie dogs and yellow-bellied marmots (Marmota flaviventris) individuals located on the periphery of the group spend more time scanning for predators than those in the middle (Armitage 1962; Hoogland 1979; Hoogland 1981). Selfish herds have also been identified in ring-tailed coatis (Nasua nasua) and individuals travelling in groups showed varied levels of vigilance depending on where they are situated within the group. Animals on the periphery, particularly nearer the front, have increased vigilance than those near the centre of the group (Di Blanco & Hirsch 2006). Likewise, elk preyed on by wolves (Canis lupus) in Yellowstone National Park show increased vigilance when on the periphery of the group, due to an increased chance of predation (Liley & Creel 2008). It has been suggested that in some species selfish herding has influenced group structure. For example, in red-winged blackbirds (Agelaius phoeniceus) Weatherhead (1983) proposes that superior foraging ability correlates with dominance which in turn allows individuals to gain central roosting positions. In central roosting positions individuals are protected from predation by subordinate individuals. These subordinate individuals are willing to incur increased predation risks as the benefits of following dominant individuals to foraging areas outweigh the costs (Weatherhead 1983).

With regard to information and disease transmission individuals who are highly connected within the group or who act as links between communities will have a disproportionately large effect on social dynamics and population processes (Godfrey et al. 2009; Keeling & Eames 2005; Lusseau & Newman 2004; Pautasso & Jeger 2008; Sih et al. 2009). This has long been established in primates (Berenstain & Sharpe 1966) and more recent work on
bottlenose dolphins has shown that specific individuals within a population take on a “broker” role and act as links between communities (Lusseau & Newman 2004). There are both costs and benefits of holding a central position in the social group. For example, individuals may have increased opportunities for mating due to access to a larger number of potential mates (Godfrey et al. 2009; Sih et al. 2009). However, as contact with other individuals increases so does the probability of contracting and transmitting disease (Wey et al. 2008). Finally, the position of individuals in a group can also impact the influence they have over collective movements. For example, shoals of three-spined sticklebacks and juvenile roach (*Rutilus rutilus*) have been shown to be led by individuals at the front of the group (Bumann & Krause 1993a).

Given the dynamic trade-off individuals face when making social decisions they frequently adjust their social environment in response to this trade-off. The decisions at the level of the individual have implications for population social structure. For the majority of social species individuals live in dynamic societies that are characterised by regular fission-fusion dynamics (i.e. individuals regularly moving between groups). Previous work focusing on group composition does not capture these dynamics and the interconnected nature of the majority of animal societies. One approach that has tremendous potential is to consider the population social structure as a social network. A social network approach models a system which is composed of individuals and their connections (Wey et al. 2008). Dyadic interactions between pairs of individuals are the basic components of social structure (Whitehead 1997) and a social network is a valuable tool for quantifying this social structure in populations. It is highly versatile and allows both the local and global properties of many interconnected individuals to be described (Croft et al. 2004). Exploring human social networks has long been of interest; however, the study of social networks in other animals lags a great deal
behind. In non-human animals network analysis was initially used in the 1940s by Lindenman to describe ecological food webs (Bascompte 2007). More recently networks have been used as a tool to gain understanding of the social organisation and structure underpinning animal societies (examples include work by: Beyer et al. 2010; Bhadra et al. 2009; Böhm et al. 2008; Croft et al. 2006; Croft et al. 2005; Croft et al. 2009; Croft et al. 2004; Drewe 2010; Drewe et al. 2009; Formica et al. 2012; Griffin & Nunn 2011; Guimarães et al. 2007; Hamede et al. 2009; Henzi et al. 2009; Jacoby et al. 2010; Kasper & Voelki 2009; Koyama 2003; Lusseau 2003; Lusseau 2007; Madden et al. 2009; Naug 2008; Patriquin et al. 2010; Williams & Lusseau 2006; Wolf et al. 2007). Such factors can influence the evolution of a species as well as an individual’s biology and ecology (Croft et al. 2006). For example population social structure is central to the way animals exploit their environment (Baird & Dill 1996; Hoelzel 1993), gene flow (Matocq & Lacey 2004; Piertney et al. 1999; Wolf & Trillmich 2008), frequency dependent selection (Lieberman et al. 2005; Nowak & May 1992) and information transfer and disease transmission (Cross et al. 2004; Watts & Strogatz 1998). Many animals live in groups which may differ in composition according to these aspects of life (Bräger et al. 1994; Cross et al. 2004). Describing the social structure of populations and unravelling the mechanisms and ecological factors underpinning this is therefore a key research focus in ecology and evolution.

The rest of this introductory chapter will focus on the application of social network analysis to animal societies. First I will introduce the analytical methods required to explore patterns of relationships occurring between individuals. I will introduce the usefulness of a networks approach to quantify social structure in animal populations and highlight both the limitations and solutions for this technique. I will then examine the practical applications of using a networks approach in the animal kingdom particularly for exploring the internal and external
factors affecting population social structure. Then I will look at social networks in cetaceans, introduce my study species and highlight the current gaps in the research. Finally, I introduce each of my four data chapters which explore in greater detail the mechanisms and resultant functions that form the foundations of social structure in a large brained social mammal.

1.2. NETWORK TECHNIQUES

A networks approach is widely used by the social sciences to describe patterns of interactions between people (Croft et al. 2008). However, more recently it has been used to describe non-human animal association patterns (Croft et al. 2006; Croft et al. 2005; Croft et al. 2004; Drewe 2010; Drewe et al. 2009; Formica et al. 2012; Griffin & Nunn 2011; Guimarães et al. 2007; Henzi et al. 2009; Jacoby et al. 2010; Lusseau 2007; Manno 2008; Miller et al. 2008; Naug 2008; Tanner & Jackson 2011). A prerequisite of applying a networks approach is reliable individual recognition (Croft et al. 2008). Individuals can either be artificially marked (plate 1.1), for example with elastomer tags, flipper or ear tags, or hot or freeze branding. However, this is not necessary in individuals with distinct natural markings on their bodies (plate 1.2) that remain constant over time. These may include distinct fin shapes, pigmentation patterns or pelage patterns.
Plate 1.1. Artificial individual recognition techniques (a) elastomer tags in fish (b) flipper tags in seals (c) freeze or hot branding in marine mammals and cattle

Plate 1.2. Natural markings in animals (a) differences in killer whale dorsal fin and saddle patch shape (b) underside of humpback whale (*Megaptera novaeangliae*) tail flukes (c) pelage patterns on giraffes (*Giraffa camelopardalis*).

Once individuals have been identified (either through artificial or natural markings) and seen with other animals on several occasions their pairwise (or dyadic) interactions can be
recorded. These pairwise interactions are the principal components of a social network (Whitehead 1997). Until recently, these dyadic interactions were considered in isolation, however, rarely do they occur alone (Croft et al. 2005). This highlights the importance of considering them in terms of a network (Croft et al. 2005; Guimarães et al. 2007). This approach has only been used to describe non-human animal associations in recent years (Krause et al. 2007).

A network approach essentially uses a mathematical graph where individuals are represented by (points) and associations are represented by edges (lines) (Croft et al. 2008; Girvan & Newman 2002; Krause et al. 2007) (figure 1.2). By quantifying patterns of contact between individuals networks can be used to assess different aspects of animal society. For example, the way information (Krützen et al. 2005) or disease spreads through a population (Böhm et al. 2008; Drewe 2010; Guimarães et al. 2007), the role individuals play in the social network (Lusseau 2007; Lusseau & Newman 2004), how kin selection and familiarity impacts social structure (Chiyo et al. 2011; Koyama 2003; Wolf & Trillmich 2008), cooperation (Croft et al. 2006), fitness consequences of social network position and structure (Formica et al. 2012) and personality in the context of social networks (Krause et al. 2010). Each of these aspects is discussed fully later.
The social structure of a population is not only defined by positive interactions and relationships including care of offspring (Gowans et al. 2001) and cooperation (Mitani et al. 2000). It also includes other aspects, for example, competition (Barton 2006), dominance (in the acquisition of mates or resources) (Drews 1993) and cannibalism (Fox 1975). Therefore, the social organisation of a population is based upon the nature and quality of interactions between individuals (Gowans et al. 2001) and a trade-off between costly and beneficial associative interactions (Croft et al. 2008). To begin to explore social networks the ways in which animals interact within a group must be considered. Simply counting the number of times two or more animals are seen together will create sampling bias because ultimately some individuals are more likely to be sampled than others. To overcome this association indices can be used (Franks et al. 2010). An association index quantifies the strength of associations occurring between two individuals. The choice of association index depends on the nature of the observations and biases in sampling techniques. Here I present three of the more commonly used association indices used in behavioural ecology.
Table 1.1. Association indices presented are calculated as follows; where a and b represent two individuals, and x is the number of days a and b were observed on the same day. $Y_{ab}$ represents the number of days a and b were both observed but in different groups; $Y_a$ represents the days individual a was seen without individual b and $Y_b$ is the number of days individual b was seen but not individual a (table adapted from Cairns & Schwager 1987).

<table>
<thead>
<tr>
<th>Index</th>
<th>Formula</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Half-weight</td>
<td>$\frac{x}{x + y_{ab} + \frac{1}{2}(y_a + y_b)}$</td>
</tr>
<tr>
<td>(b) Twice-weight</td>
<td>$\frac{x}{x + 2y_{ab} + y_a + y_b}$</td>
</tr>
<tr>
<td>(c) Simple ratio</td>
<td>$\frac{x}{x + y_{ab} + y_a + y_b}$</td>
</tr>
</tbody>
</table>

Initially, association indices were developed to describe the co-occurrence of plant species (Dice 1945). However, over the past 40 years those studying animal behaviour have adopted this method particularly for exploring association strengths in social vertebrates (Bejder et al. 1998). Each index (table 1.1) provides a value from 0 to 1 for each pair of animals where 0 means that the animals are never seen together and 1 indicates they are always seen together. Different indices control for different bias that may arise due to limitations of sampling techniques. The half-weight index (table 1.1a) is the most commonly used index by behavioural ecologists (Cairns & Schwager 1987; Whitehead & Dufault 1999). Therefore, it is often used to increase comparability with other studies. The half-weight index is most appropriate when individuals would be expected to be seen apart more often than together (Whitehead et al. 2005). The converse is true for the twice-weight index (table 1.1b) and this is more commonly used when pairs of individuals are more likely to be seen together than apart (Whitehead 2008). Finally, the simple ratio index (table 1.1c) gives us an exact answer to the question of how often pairs associate. It is assumed that the population of interest is
also the sample (Cairns & Schwager 1987). However, this association index is often used to estimate the frequency of associations over a period of time that was only occasionally sampled. The simple ratio index is usually only appropriate in captive situations where all individuals and associations can be observed (see Gilby & Wrangham 2008; Rossbach & Herzing 1999; Slooten et al. 1993). Throughout my thesis I use the half-weight index as a measure of association as it controls for the bias that individuals are more likely to be seen apart than together. Also the half-weight index is used to increase comparability with other cetacean studies (Beck et al. 2011; Bräger et al. 1994; Gero et al. 2008; Lusseau 2003; Lusseau et al. 2006; Möller et al. 2006; Williams & Lusseau 2006).

Once the strength of interactions occurring between individuals has been established, using an association index, they are combined using a networks approach to explore the social structure of a whole population. The strength of associations obtained from indices can be incorporated to carry out weighted analysis (Lusseau et al. 2008) (figure 1.3).

Figure 1.3. Diagrammatic representation of a weighted network. The nodes represent individuals and the edges represent associations, with the strength of association indicated by the thickness of the line.
Social networks are rarely homogeneous and this non-random structure, or heterogeneity, arises from different individuals occupying different positions within the social network (Godfrey et al. 2009; Keeling & Eames 2005). Both global and local aspects of social network structure can be quantified by exploring different measures within the network. Global network measures describe properties of the whole network. For example, path length ($L$) is a global network measure. To quantify the global population structure, $L$ is used to define the shortest distance from an individual to the rest of the group; a shorter path length may result in faster information or disease transfer between individuals. Local network measures are derived entirely from local considerations of the network structure around each node (Croft et al. 2008). The measures include; clustering coefficient ($C$), degree centrality ($k$) and betweenness ($B$) (Croft et al. 2008). $C$ is defined as the connectivity between an individual’s neighbours, for example, if an individual has two neighbours $C$ tells us whether the neighbours are also connected. A high clustering means that the social network is highly interconnected with a large number of links between individuals. Next, $k$ is the sum of the strength of the associations that an individual has. Together these two measures ($C$ and $k$) give us an estimate of the social structure on a local scale. To explore the position that individuals occupy and their importance in connecting the social network betweenness is used. This essentially tells us how well connected an individual is and how important it is in connecting others in the network. One of two types of network can be constructed. Firstly a symmetric network can be used where all interactions between individuals are equal (Franks et al. 2010). The second type is an asymmetric, or directional, network where associations occur with directionality (Wey et al. 2008). For example, this may be appropriate for grooming or aggression networks (Lehmann et al. 2007; Wittig et al. 2008).
There are two main problems associated with using social networks analysis to describe and quantify animal social structure:

1. The way in which social relationships are inferred.

2. The lack of independence in the data.

Rarely are small groups encountered where every interaction and association can be observed, particularly in wild populations (Croft et al. 2008). For most wild social species a large number of interactions occur out of sight. This is particularly problematic in some species of cetaceans who spend in excess of 95% of their time below water (Wiles 2004). To overcome this problem the “gambit of the group” is used which assumes all animals in the same group are associating (plate 1.3) (Franks et al. 2010). The way in which a group is defined depends on the study species and their environment. Groups can be defined in one of two ways. Firstly physical proximity to another individual can be considered, for example individuals seen within a certain number of body lengths (Croft et al. 2004) are assumed to be part of the same group. Alternatively, individuals sighted in a particular area over a given time (known as the sampling period) can be assumed to be part of the same group (Parsons et al. 2009). The ways in which data are collected affect both the number of groups observed and the frequencies that individuals are observed within the groups.
Plate 1.3. A selection of images illustrating examples of grouping behaviour that can be used to infer social interactions: (a) Killer whales (credit Astrid van Ginneken), (c) African elephants (*Loxodonta africana*) (credit Tracy Cooper), (c) Humpback whales (*Megaptera novaeangliae*).

Next, there is an inherent lack of independence in all network data because every individual’s relationships will be affected by the relationships of those around them and therefore, normal statistical techniques for analysis cannot be used (Croft et al. 2011). The most robust technique to overcome this problem and the group definition issues previously mentioned is the use of null models. Null models use a series of random networks which maintain the characteristics of the population (e.g. age distribution, sex ratios and group size) (see figure 1.4 for further explanation). The observed network can be compared to the null models to then determine whether the observed social structure is likely to result by chance. However, it is important to understand that there are still limitations with creating null models in such a
way particularly in the approach used to randomise the data (for example, whether the nodes or the edges are randomised) is vital in overcoming these limitations (Croft et al. 2008). Combined with the correct use of null models networks are proving to be an invaluable tool for analysing the social structure of complex animal populations. By quantifying social structure the mechanisms and functions underpinning animal social networks can be explored. These are central to many areas of conservation, evolutionary biology and behavioural ecology (Croft et al. 2011).

Figure 1.4. Diagrammatic representation of the randomisation process to construct null models. Each circle represents an individual (pink female, blue male). Individuals are “swapped” between groups a set number of times (n). Sex ratios, group size and age distribution can be maintained by only swapping with other individuals that share such characteristics. After n swaps a network is drawn from the random data and network statistics taken. This is repeated a certain number of times to give a random distribution of the network statistics. The real data can then be compared to this random network data.

1.3. NETWORKS IN ECOLOGY

Increasingly, behavioural ecologists are using social network analysis as a tool to test hypotheses regarding the social organisation of animal groups (Croft et al. 2011). The local and global population structures resulting from who interacts with whom have implications for gene flow, disease transmission, frequency dependent selection, the maintenance of cooperation and cultural continuity through information transfer (Croft et al. 2011). Research
over the last few years has shown that some animal populations are characterised by non-random interactions, or preferred associates, within the social network (Croft et al. 2005; Croft et al. 2004; Krause et al. 2007; Lusseau 2003; Morrell et al. 2008; Pike et al. 2008). Within such a network individuals may play different roles in the social organisation and stability of the population (Manno 2008). Such roles are likely to play a large part in the gene-flow and transfer of disease or information through the group (Pike et al. 2008).

In this section I look at the practical applications of a network approach and the finer scale interactions occurring between individuals. I include a discussion of the fitness costs and benefits of network position, disease transmission and information transfer in relation to different social networks.

1.3.1. Fitness costs and benefits of social network position

Once the nature of the network has been established it is possible to explore specific roles of individuals within the social network, particularly in relation to fitness and cooperation. One technique is to observe whether behaviour is reciprocated (Croft et al. 2008). Grooming in female Tibetan macaques (Macaca thibetana huangshanensis) in Huangshan, China, in large family groups will groom only their closest kin. In contrast individuals in smaller matrilines may spread their grooming more widely among kin perhaps even including non-kin, the authors suggest that this is shaped in part by time constraints (Berman et al. 2008). There are fitness benefits associated with social network position. For example individuals that have high centrality and therefore have frequent social contact with many individuals may have increased opportunities for mating (Godfrey et al. 2009; Sih et al. 2009). There are a variety
of species where males who have more social bonds with conspecifics have higher reproductive success. Examples include, long-tailed manakins (*Chiroxiphia linearis*) (McDonald 2007), wire-tailed manakins (*Pipra filicauda*) (Ryder et al. 2009), assamese macaques (*M. assamensis*) (Schülke et al. 2010) and forked fungus beetles (*Bolitotherus cornutus*) (Formica et al. 2012). These studies all show how the network position can be used as a predictor of individual fitness, through mating success.

**1.3.2. Disease transmission**

Where a central position in a social network can predict fitness through mating success there are also associated costs. For example, with disease transmission the strength of relationships may be important in the probability of contracting an infection, particularly in weaker pathogens (Wey et al. 2008). The way in which individuals interact with one another has a large effect on the spread and dynamics of a disease (Cross et al. 2004). A network approach is an effective and powerful way of investigating the vulnerability of social animals (Guimarães et al. 2007; Lusseau et al. 2008). This in turn can lead to effective management plans where specific individuals can be vaccinated or removed from the population in the event of an outbreak. Infectious diseases are one of the main threats facing the conservation of biodiversity (Guimarães et al. 2007). Initially investigating disease dynamics relied on the principle of mass-action mixing, where all associations between individuals are assumed to be random. The earliest studies of animal social network structure have revealed remarkable similarities to human social networks (e.g. Lusseau & Newman 2004). In particular individuals differ in their centrality and may take on different positions within a social network (Lusseau & Newman 2004; Williams & Lusseau 2006). This has long been known for primates (Berenstain & Sharpe 1966) but more recently has been demonstrated in a
bottlenose dolphin (*Tursiops* sp.) population in Doubtful Sound, New Zealand, where specific individuals appeared to have a central role in acting as links between communities (Lusseau & Newman 2004). Individuals with high network centrality may have a disproportionately large effect on the way information, or disease, flow through a population (Perkins et al. 2009). Such individuals have been termed keystone individuals (Sih et al. 2009), super-spreaders (Keeling & Eames 2005; Pautasso & Jeger 2008), floaters (Godfrey et al. 2009) or brokers (Lusseau & Newman 2004). Identifying these individuals can provide knowledge of how an epidemic develops and the main individuals responsible for the spread of disease (Pautasso & Jeger 2008; Perkins et al. 2009). One of the most well documented examples of such individuals is human movements during the 2003 severe acute respiratory syndrome (SARS) epidemic. The disease first appeared in the Guangdong province of southern China, it then passed to Hong Kong, before spreading to Europe, Africa, Asia, Australia and America, a total of 8,422 people were infected (Small et al. 2006). This spreading was facilitated by a few individuals infecting a large number of people. Super spreading events are not a result of highly contagious individuals but more likely highly connected ones (Li et al. 2004; Peiris et al. 2003; Small & Tse 2005; Small et al. 2006; Wang et al. 2006).

Like in human social structure non-human animal social structure is rarely homogeneous. A network approach is an appropriate technique to identify which individuals play the largest role in the transmission of disease (Naug 2008). The influence of social networks on disease transmission dynamics in honeybee (*Apis* sp.) colonies was analysed by Naug (2008), who showed that organisational structure of a colony could provide some immunisation to young individuals, keeping them separate from infectious individuals. Additionally, Böhm et al. (2008) investigated interactions of Eurasian badgers (*Meles meles*) in the field using radio-trackers to look at how infectious disease may be transmitted through a social network. They
showed that different badger subgroups vary in their importance in disease transmission and that specific individuals were responsible for the spread of disease within their group. The authors also highlight the importance of understanding the interaction between social structure, habitat and population density to gain further insight into accurately predicting the spread and persistence of disease in group living animals. In addition to this, the importance of understanding seasonal variability has been shown in red foxes (*Vulpes vulpes*) where overall subordinates are key in intergroup disease transmission, as they act as a link between both dominant and other subordinate individuals year round (Baker & Harris 2000). Whereas during the winter months males are a greater transmission risk as they move into neighbouring territories looking for mating opportunities (White & Harris 1994). In transient type killer whales individuals with strong associations with a large number of individuals are the ones most likely to facilitate the spread of disease through a population (Guimarães et al. 2007). The authors suggest that special monitoring of the health of the older females (who have the most associates) would be beneficial to detect epidemics at early stages. However, they do not suggest how such an epidemic would be managed.

Croft et al (2006) have shown that a population of Trinidadian guppies (*Poecilia reticulate*) subdivide into small stable communities and they suggest that disease may spread within each community before it transfers between them. Quantifying contact patterns and association rates between individuals in this way is important when trying to assess the dynamics of directly transmitted diseases within populations (Böhm et al. 2008). Contact patterns between individuals can be particularly complex (Loveridge & MacDonald 2001). Members of a group may not all interact with other group members at the same degree and as a result direct contact between members may vary (Böhm et al. 2008). Failure to account for
such complexity of contact patterns and social network structure can result in failure of
disease control patterns (Böhm et al. 2009).

By improving our knowledge of behaviours processes and contact patterns underlying disease
transmission we can gain a valuable insight into the nature of real-life contact networks. This
in turn will help improve disease management strategies (Böhm et al. 2009). Using this
knowledge to predict the vulnerability of populations of animals to disease can help to
prevent the local extinction of endangered populations (Daszak et al. 2000; Guimarães et al.
2007). To the best of my knowledge a social networks approach is yet to be used practically
to isolate, remove or vaccinate specific individuals who facilitate epidemics. However, this
would be a very useful management tool for future conservation and disease control efforts.

1.3.3. Information transfer

Transmission events, other than disease, can occur within a social network. The social
structure of an animal population can also impact how information flows through a social
network. Networks are a valuable tool to track how information is transferred within and
between groups and the evolution and transmission of behaviours. Such information may
include novel foraging techniques (Ford et al. 1998) or public information regarding danger
or resources (Thornton & Malapert 2009). The social structure of a group is likely to affect
the nature of learning, such as the way information is passed from one individual to the next.
For example individuals may learn by imitation (Call et al. 2005) or by direct teaching from
conspecifics (Thornton & Raihani 2008). This in turn can impact the learning and maturation
of young. Some mammals occasionally maintain kin associations after weaning as this reduces the likeliness of costly ecological and social mistakes (Gibson & Mann 2008).

An example of social learning within a population is observed in the vocalisations from different populations of the same species (Riesch et al. 2006). Although, this has not been explored in the context of a social network to date. Such vocalisation can be considered as culture. However the presence of culture in animals, other than humans, is an area of some debate. It has been defined in different ways (see Rendell & Whitehead 2001 for a summary of definitions) overall, it seems to be agreed that culture is the social learning of a specific behaviour. Krutzen et al. (2005) state that “a behavioural trait is considered to vary culturally if it is acquired through social learning from conspecifics and is transmitted repeatedly within or between generations”. Learned social traditions, which remain stable over several generations are known as cultural lineages (Yurk et al. 2002). An example of this is seen in different dialects which are learned either from parent to offspring or from other members of a group (Deecke et al. 2000). Cetaceans are capable of demonstrating vocal learning (Janik & Slater 1997). Both sperm whales (*Physeter macrocephalus*) and killer whales use distinctive culturally acquired vocal dialects (Whitehead 1998a). Male humpback whales (*Megaptera novaeangliae*) use vocal repertoires which are learned socially as forms of sexual displays. All males sing the same phrases within a song. However, these phrases change over time and changes quickly spread through the population. This implies some sort of transmission of information or social learning through imitation among individuals (Janik & Slater 1997; Noad et al. 2000). Similar vocal learning has been shown in some bird songs (Mundinger 1980).
Gregarious animals with long lifespans, such as primates (King 2005) and cetaceans (Rendell & Whitehead 2001), rely on information transfer to take full advantage of their habitat. Other animals learn how to use tools from one another, usually to fully exploit food sources and there are several examples of this across a range of taxa. Such examples include tool use in primates including chimpanzees (Whiten et al. 2005) and orang-utans (*Pongo pygmaeus*) (Call & Tomasello 1994) to obtain food in novel ways. Social learning has also been shown in New Caledonian crows (*Corvus moneduloides*) where individuals exposed to tool use for food retrieval by foster parents had higher levels of twig handling and insertion than their naive counterparts (Kenward et al. 2006). Tools can also be used by marine mammals. Bottlenose dolphins in Shark Bay, Western Australia, use marine sponges as foraging tools, they break them off the sea floor and wear them over their rostrum to forage in the substrate for fish. This behaviour is sex biased and is socially learned from mothers to daughters (Krützen et al. 2005).

At present the quantification of information transfer and social learning using a networks approach is somewhat limited. There has been speculation that individuals holding a central network position act as information brokers for the group. In human society network models have been used to describe the process by which ideas, opinions, information and innovations spread through a group (Valente 1996). Within these models there is a great deal of emphasis on identifying key individuals who may influence the transmission of information through the group (Krause et al. 2007). In animal populations animals differ in their ability to learn from one another and to transmit information (Brown et al. 2006). By applying network theory it becomes possible to predict the way in which socially learnt information flows through a group and how quickly this happens (Krause et al. 2007). In addition to this, it is possible to link different individual attributes to their role in transferring information through a group.
Such attributes may include age, sex, experience or network position (i.e. whether they are central or peripheral). In animal society individuals with specific roles in the social networks have been highlighted in relation to information transfer. For example in a population of bottlenose dolphins “social brokers” were identified (figure 1.5). These individuals act as links between the sub-communities and appear to be crucial to the social cohesion of the population (Lusseau & Newman 2004). Lusseau and Newman (2004) also suggest that these individuals control the flow of information through the population.

Figure 1.5. Bottlenose dolphin social network from Lusseau and Newman (2004). Females are represented as circles and males as squares. The size of the node directly relates to the betweenness of the individual. Nodes shaded in black are “broker animals” with particularly high betweenness.

This information transfer is another key benefit of sociality (full costs and benefits of network position and sociality discussed in section 1.1.1.3.) and by sharing knowledge individuals can
increase their fitness and survival potential through, for example improved foraging efficiency (Thornton & Malapert 2009). The use of association indices to explore information transfer in the context of a social network has begun to prove a valuable approach in elusive species, especially where not every interaction or association can be observed. This is particularly true in cetaceans that spend the majority of their time below the water (Wiles 2004). However work needs to be done to accurately infer the link between network position and role of an individual in transmitting information through a group.

1.4. CETACEAN SOCIAL NETWORKS

In popular human belief the mammalian order Cetacea is thought to contain some of the most intelligent animals. It includes over 80 known species of whales, dolphins and porpoises. In terms of research on social systems it lags some three decades behind primatology (Barton 2006; Simmonds 2006) due to the logistical limitations of conducting fieldwork in the marine environment (Bearzi & Stanford 2007). The introduction of photo-identification has facilitated the study of cetacean social systems (Würsig & Jefferson 1990). However, even with photo identification studying cetaceans in the wild is challenging as they spend most of their time underwater, are free-ranging, fast moving and in some cases very deep diving (Wiles 2004). Using appropriate association indices and a social networks approach can help to overcome this problem and begin to answer interesting questions regarding marine cetacean social systems (e.g. Guimarães et al. 2007; Lusseau 2003; Lusseau 2007; Lusseau & Newman 2004; Stanton et al. 2011; Williams & Lusseau 2006).
As a group cetaceans show a great deal of interspecific variation in group stability from species to species. This group stability ranges from the highly stable matrilineal structure of resident type killer whales (Whitehead 1998b) and long-finned pilot whales (*Globicephala melas*) (Amos et al. 1993b) to the fluid fission-fusion society of spinner dolphins (*Stenella longirostris*) (Bräger et al. 1994) and northern bottlenose whales (*Hyperoodon ampullatus*) (Gowans et al. 2001). Fission-fusion behaviour may be learnt by young individuals and the pre-weaned calves of bottlenose dolphins are exposed to a large number of other associates from a young age to allow them to adapt to this lifestyle (Gibson & Mann 2008). In contrast, for large mammals, that are slow to reproduce, protection of young is vital and likely had a major influence on the development of social systems (Gowans et al. 2001). Evolution of sociality in sperm whales is probably due to the fact that they principally feed on deep water squid (*Architeuthis* sp.). Calves are not capable of diving to the same depths as adults (about 400m) and this has led to alloparental care while the mothers forage at depth. This deep foraging behaviour has resulted in the formation of long-term social bonds between female sperm whales (Gowans et al. 2001).

Social network analysis is proving to be a valuable tool in the study of marine mammal social structure. Lusseau and his colleagues provide several studies which look at social networks in bottlenose dolphins. They explore the properties of the social network and describe different communities within dolphin populations (Lusseau et al. 2006). He also explores the effect of removal of an individual from the group (Lusseau 2003) and looks at the roles of different dolphins in the network and identify individuals who act as links between groups (Lusseau & Newman 2004). The strength of associations between individuals can have huge implications of the vulnerability of a population to disease outbreak. For example, transient type killer whales, that feed predominantly on marine mammals, have very strong social ties between
small groups of individuals this makes groups vulnerable to disease outbreak (Guimarães et al. 2007). Williams and Lusseau (2006) used simulations to show that a resident type killer whale population, that feed on fish, is sensitive to targeted removals highlighting the detrimental effects of removing individuals from matrilineal societies. These studies show the potential of using a networks approach to develop our understanding of killer whale ecology. This will improve our knowledge of matrineal whales which in turn will aid in designing effective conservation and management plans.

1.5. STUDY SPECIES: KILLER WHALES

Killer whales are a cosmopolitan species, they are found in all major oceans from the polar to the temperate regions and their social groups show remarkable stability (Hoelzel et al. 2002). Killer whales are described by Ford and Ellis (2006) as the ”apex (non-human) marine predator” and as a species, they feed on over 120 different types of fish, cephalopod, sea turtles, sea birds, mustelids, pinnipeds and cetaceans (referenced in Ford & Ellis 2006). However, different populations specialise on a particular prey species (Bigg et al. 1990).

Two sympatric forms of killer whale occur regularly in the coasts of British Columbia (Canada), Alaska and Washington State (USA). The two different types, known as transients and residents, differ in morphology, behaviour, habitat use, group dynamics and prey choice. They are also thought to be reproductively isolated (Baird et al. 1992; Ford & Ellis 2006). Group sizes vary considerably between transients and residents which is likely to be due to the degree and nature of cooperative hunting for their main prey type (Baird et al. 1992). Transient whales spend 88.5-94.5% of their time travelling and foraging whereas residents
spend 58-72% of their time engaging in these activities. The rest of their time is spent socialising and resting (Bearzi & Stanford 2007). Extensive observations of transients and residents have shown that they do not travel together (Bigg et al. 1990; Ford et al. 1998), they very rarely associate (either aggressively or otherwise) (Bearzi & Stanford 2007) and are genetically distinct (Baird et al. 1992; Heimlich & Boran 2001). This lack of association is thought to be due to extreme differences in diet (Bearzi & Stanford 2007). Despite the fact that it may be mutually beneficial for resident and transient type killer whales to associate with one another, effectively pooling their skills and increasing the prey availability to the group (Giraldeau 1984), no discernible cooperation occurs between residents and transients. As incorporating an individual into a hunting group, who is unfamiliar with the techniques, would be detrimental to the efficiency of the group (Baird et al. 1992).

Figure 1.6. Diagrammatic representation of the series of progressively smaller units of social organisation used to classify the social structure of the resident type killer whales.
Among types of social groups found in cetaceans the killer whale pod is unique (Bigg 1982). They have the most stable social structure of any cetacean species yet studied (Bräger et al. 1994; Connor & Whitehead 2005; Deecke et al. 2000) and the social organisation of these animals can be classified into a series of progressively smaller units (Bigg 1982) (figure 1.6). Long term matrilineal associations within pods are highly consistent (Bigg 1982) and neither the males nor females disperse and even as adults continue to travel with their mothers. This forms the fundamental social unit of the resident type killer whale society (Ford & Ellis 2002), the highly stable hierarchical matriline. A matriline consists of a female, her sons and daughters and the offspring of her daughters (figure 1.7). A matriline can span one to five (mean 3) generations (Wiles 2004). Members of a matriline have very strong social bonds and will seldom disperse from the matriline for more than a few hours (Bigg et al. 1990; Deecke et al. 2000; Wiles 2004). No individual has been observed permanently dispersing from the matriline (Bigg 1982), with the exception of L98 (southern resident) and A73 (northern resident) in the winter of 2001-2002. Both of these were considered isolated incidents (Killer Whale Recovery Team, 2005). Two or more matrilines travelling, resting, foraging and socialising together at least 50% of the time are known as pods (Wiles 2004). A typical pod contains between 5-20 individual whales (Bigg 1982). Occasionally a pod can number as many as 50 individuals (Wiles 2004). Solitary killer whales are extremely rare and can be either male or female (Bigg 1982). Usually a pod will consist of adult females, adult males, juveniles and sometimes a new calf (Bigg 1982). Over time new pods may form and the most likely explanation for this is the gradual splitting of established pods over several decades (Bigg 1982). Splitting is usually caused by the birth and death of individuals. An especially significant factor prompting such a split may be the loss of a matriarch (Wiles 2004). Several pods may come together intermittently for varying periods of time during which there will usually be a large amount of social interactions between the groups and
when the aggregation divides it does so according to the respective matrilineal components of each pod (Bigg 1982). Several pods seen together intermittently are known as a clan, this is also defined by the acoustic behaviour of pods and is comprised of pods that have similar vocal dialects (Ford 1991). Temporary large aggregations of whales do occur which can consist of up to several hundred individuals. These tend to occur seasonally, coinciding with large concentrations of prey and for social interaction and breeding (Wiles 2004). These aggregations occur between individuals belonging to the same community. Where a community is defined as an assemblage of individuals that reside in the same area and periodically associate with one another (Bigg et al. 1990).
Figure 1.7. An example of one of the matrilines from J-pod. The alpha numeric code represents the individual identification code; the number below represents the date of birth (in italics if estimated) and date of death, if applicable. A solid line indicates a definite relationship, a large dotted line indicates a probable relationship and a small dotted line indicates a likely relationship (courtesy of the Center for Whale Research).

1.5.1. Southern Resident Killer Whales

Around the west coast of North America four distinct communities of resident type killer whales occur. These are known as the northern residents, southern residents (figure 1.8), the southern Alaskan residents and Western Alaskan residents (Wiles 2004). The southern resident killer whales have been intensively studied since 1974. Throughout each year a
photographic census is conducted to provide an absolute abundance of killer whales in the southern resident community. In addition to this during every encounter every individual seen is photographed and recorded (Ford et al. 2000).

Figure 1.8. Summer range of the northern resident killer whales (blue) and southern resident killer whales (red), around Vancouver Island, British Columbia, Canada and Washington State, U.S.A..

The southern resident killer whales are a population of fish eating killer whales occurring in the inshore waters of Washington State, USA and British Columbia, Canada during the summer months (figure 1.8 and figure 1.9) (Hauser et al. 2007a). Ford (1989; 1991) has shown that distinctively different vocal signals are used by the southern residents to the other killer whale communities. Related pods often use structurally similar versions of specific call types, these calls increase in similarity as the genetic relatedness between individuals’
increases. For example, individuals from the same matriline have more similarity in their call structure than those from different matrilines and individuals from different pods have even more distinct call structure (Deecke et al. 1998).

The southern resident killer whale population consists of three pods named J, K and L (Wiles 2004). Within these pods there are further matrilineal divisions that are usually observed travelling, resting, socialising and foraging together (Hoelzel 1993). The three pods will come together intermittently and overall they have very similar summer distribution around the southern end of Vancouver Island and the west coast of San Juan Island (figure 1.7) (Hauser 2006; Hauser et al. 2007a).

![Kernel density distributions of southern resident killer whales during the summer months (reproduced from Hauser et al. 2007a).](image)

Prior to the twentieth century the southern resident killer whale population was unexploited (Olesiuk et al. 1990). From 1962-1977 at least 48 whales were removed from the southern resident community for display in public aquaria and for research purposes (Balcomb et al.
1982; Bigg 1982). This prompted a high level of concern regarding the status of the southern resident killer whales and a long term monitoring program was set up in 1973 (Balcomb et al. 1982; Hoelzel 1993). Every individual in the population has been monitored throughout the year through photographic and video surveying. Each individual has also been documented and sexed (figure 1.10) in an annual photographic inventory since 1974 (Olesiuk et al. 1990). These data have been used to produce an absolute abundance for the last three and a half decades. During this time the population has fluctuated from 70 whales in 1976 to a maximum population size of 99 individuals in 1995 (figure 1.11).

Figure 1.10. (a) Female and (b) male killer whale pigmentation patterns around the genital slits, visible when the whale breaches or rolls on its back (courtesy of the Center for Whale Research).

This information, together with behavioural and environmental data, has provided detailed knowledge of population status, movements and social structure of the southern resident killer whale community (Balcomb et al. 1982; Olesiuk et al. 1990).
Salmon is the main food item of the southern resident killer whales particularly in the summer months. They appear to selectively forage chinook salmon (*Oncorhynchus tshawtscha*) (Ford & Ellis 2006; Olesiuk et al. 1990) which comprises the largest proportion of their diet during this time. This is supplemented with chum salmon (*O. keta*), sockeye salmon (*O. nerka*), pink salmon (*O. gorbuscha*), ling cod (*Ophiodon elongatus*) and Pacific halibut (*Hippoglossus stenolepis*) (Ford & Ellis 2006). Recent work by Ford and Ellis (2006) and Hanson et al. (2010) show that from June to September chinook salmon makes up more than 90% of the southern resident killer whales’ diet. The summer distribution of the southern
resident killer whales follows the movement of the migrating chinook salmon (Ford & Ellis 2006).

Conserving a population, such as the southern resident killer whales, poses a particular challenge as both the population and their main prey source, chinook salmon, are classified as endangered (Williams et al. 2011). Due to the recent decline of the southern resident killer whales they have been classified as an endangered population. This classification has been assigned in both America by the US Federal Endangered Species Act and in Canada by the Canadian Federal Species at Risk Act (Hauser et al. 2007a). Each group of whales may be exposed to different levels of risk due to their summer movements. Risk factors could include; prey quality and quantity, toxins, vessel impacts, random small population fluctuations, climate variability, ocean processes or the cumulative effects of some or all of these risks (Hauser et al. 2007a). It is important to begin to make inferences about the impacts of these risks as they are currently unknown. To do this effectively analysis of long term data is vital (e.g. Domenici et al. 2000; Gibson & Mann 2008).

Since 1974 during encounters with the whales every attempt is made, by trained staff from Center for Whale Research, San Juan, USA, to photograph and/or video every individual present on a given day. In addition to this, video footage has been routinely collected since 1996. This provides a huge resource. I intend to use this to explore three levels of association in the southern resident killer whales. Firstly, I will assume individuals photographed on a given day are part of the same group of associating animals. This is facilitated by the fact that killer whales travel in close physical proximity (Bigg et al. 1990; Ford et al. 2000; Parsons et al. 2009), within acoustic range (Miller 2006) and animals travelling together will usually
occupy the same channels of water (i.e. will not take different routes around an island). These data will be used to explore social interactions at the level of the population. Secondly, I will use finer scale interactions occurring between individuals within the population, based on surfacing patterns and who surfaces next to whom, to observe the positions individuals take within the network. Finally, I will construct a directional database, recording who follows whom in the group, from the video footage and begin to make inferences about leadership and following. Specifically I want to explore whether specific individuals or matrilines lead others more frequently and the characteristics of these individuals. Such characteristics may include age, sex or energetic requirements.

Using a social networks approach to describe social structure in animal populations is an emerging trend in behavioural ecology (Croft et al. 2011). Network theory attracts the attention of mathematicians, sociologists and physicists alike. It is a versatile tool which can be used to describe large and small scale properties of many interconnected individuals (Croft et al. 2004). Exploring animal networks provides a tool to link an individual’s behaviour with population biology (Krause et al. 2007). By quantifying social structure the mechanisms and functions underpinning animal social structure which are central to many areas of conservation, evolutionary biology and behavioural ecology can be explored (Croft et al. 2011). Social structure can be shaped by both internal and external factors. Whilst most studies have focused at the level of the group and explored internal factors, such as the presence of kin (Berman et al. 2008) or sorting by a particular phenotype (e.g., body size) (Croft et al. 2005), there is very little knowledge about how ecological variables effect social structure (see Henzi et al. 2009; Tanner & Jackson 2011 for exceptions). Social structure is an essential ecological component of group living species. Therefore it is important to gain understanding of its development and how animals organise themselves into groups (Tanner
& Jackson 2011). Many species which lead rich social lives are threatened by anthropogenic impacts on their environment. Understanding the social behaviour of these may prove critical for future conservation efforts (Couzin 2006). This is particularly important for the southern resident killer whales with their recent classification as an endangered population (Killer Whale Recovery Team, 2005).

1.6. CHAPTER OVERVIEW

The four data chapters presented in this thesis explore the different aspects of killer whale social structure. They address questions concerning both population and individual level structure. The main question underlying this project is “what are the mechanisms and functions underpinning social structure in a large social mammal”. I aim to explore this in the following chapters:

Firstly I explore the social structure of the population as a whole and particularly look at the social network correlates of food availability. Currently there is little understanding of how ecological variables shape population social structure (see Henzi et al. 2009; Tanner & Jackson 2011 for exceptions). Having an understanding of this is important when designing effective conservation and management plans. Organisms in the marine environment are faced with problems related to the dynamic conditions of the oceans, such as patchy resources that vary across spatial and temporal scales. When confronted with such variability in the ecosystem marine predators respond by modifying their distribution to increase survivability (Hauser et al. 2007a). It is possible that southern resident killer whales are experiencing lowered prey densities (Hauser et al. 2007a). As marine mammals have much
lower locomotive costs than terrestrial animals they are able to use migration to avoid unfavourable conditions (Rendell & Whitehead 2001). The aim of Chapter II is to examine the impact that changes in food availability have on both the local and global social structure of the southern resident killer whales. To do this I combine different social network measures using a principal components analysis and explore these on an annual basis in relation to food availability. I use randomisations to ensure that the observed results were not a factor of group size. Resident killer whales feed mainly on salmon (Ford et al. 2010) which they rarely share (Baird et al. 1992) and this results in a high degree of site fidelity. Animals return to the same area coinciding with migrating salmon (Ford & Ellis 2006; Olesiuk et al. 1990). However, as cooperative hunting is not necessary, I would predict in times of low salmon abundance the group will become socially fragmented. This is because individuals will have to invest more time in foraging over a wider area thus limiting the opportunity for social interactions.

Once I have explored the whole population structure and an external factor affecting this I aim to look at the finer scale associations. Social networks are rarely homogenous and different individuals will occupy different positions within a network. The main aim of chapter III is to identify the position individuals hold within the social network and explore the attributes of individuals in different positions. Specifically, I look at the differences in network position and number of associates between animals of different ages and sex. Social networks were based on data collected from surfacing patterns. These networks were compared to random networks to overcome problems related with pseudoreplication and sampling issues. Network measures were also correlated with age and sex to investigate whether individuals network position changes with age. This is important because individuals that hold a central position in the network may be important in the overall connectivity of the
population. They may also play a key role in population processes such as information and disease transmission.

Next I investigate leadership in groups of killer whales. Coordinated movement of animals is one of the most illustrative examples of collective decision making and getting this right is vital to the survival of the group. A key question in population social biology is determining which individuals make decisions within a group and when these occur. The main aim for Chapter IV is to determine whether specific individuals act as leaders and the attributes of such individuals. I explored this in several stages. Firstly, I derived a leadership score (based on earlier work by Bonanni et al. 2010) to look at the role of different matriline in leading the group and the distribution of leadership scores within a group. Leaders were identified when they were at the forefront of collective movements. Then I explore individual age and sex in relation to leadership score. I predict that older females will have superior ecological knowledge and will hence have a more active role in leading the group. Finally I examine how energetic requirements influence an individual’s motivation to act as a leader by comparing the leadership scores of females when they are lactating and when they are not. This chapter serves to provide understanding behind the role of individuals in coordinated group movements and to some extent decision making in an animal population.

Finally, I explore the finest scale associations occurring between a mother and her offspring in Chapter V. Killer whales are unique as they possess the longest post-reproductive lifespan in any non-human animal. Two mechanisms have been proposed to underpin prolonged post-reproductive lifespan. i) An epiphenomenon of increased longevity, in which the evolutionary benefits accrue only during the reproductive phase with no additional fitness benefits after the
last reproductive event. ii) An evolved adaptation in which post-reproductive lifespan increases the survival of an individual’s genes thus increasing its inclusive fitness. To date there is very little evidence that a prolonged post-reproductive lifespan is adaptive in non-human animals. However, resident type killer whales may provide evidence for this. Females stop reproducing in their thirties and forties but can survive well into their nineties. To begin with, I explore the differences in strength of association between sons and daughters with their mothers using the fine scale association dataset and the half-weight index. Secondly, I look at the effect of a mother’s death on the survival of her offspring using a Cox proportional hazards model. In the absence of dispersal local relatedness increases with female age and theory predicts that mothers can maximise their fitness by ensuring their offspring’s survival and reproductive success (Johnstone & Cant 2010). Mothers however should not direct their care equally towards adult sons and adult daughters. As mating occurs outside the matriline a sons offspring will be raised by another group whereas a daughters offspring will be raised within the matriline thus increasing resource competition (Johnstone & Cant 2010). As a result of this I predict that mothers may have stronger associations with sons than with daughters. In addition to this there is a huge degree of sexual dimorphism in killer whales, with males growing considerably larger than females. Therefore it may be beneficial for mothers to invest more in sons to ensure the matriline contains a strong male both for reproductive success and support during antagonistic encounters.

The four data chapters presented in my thesis provide an insight into killer whale social structure on both a large and fine scale. In my final chapter I provide a general discussion of my results. I consider the implications of these findings and finally I explore the future directions I feel I can take this research.
Chapter II.

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

For the vast majority of social species group composition is dynamic and individuals move between social groups leading to a highly interconnected social network. Who interacts with whom and the local and global population social structures have implications for central issues in ecology and evolution (Croft et al. 2008; Krause & Ruxton 2002). Population social structure is central to the way animals exploit their environment. For example animals that live in groups may benefit from cooperative foraging. This is seen in several species and examples include mammal eating killer whales (*Orcinus orca*) who will work together to capture and handle large prey (Baird & Dill 1996; Pitman & Durban 2012). Likewise a pride of lions (*Panthera leo*) may work together to obtain prey that would be too large or dangerous for one individual to handle (Stander 1992). Population genetics can also be impacted by social structure of a population. In some species which are highly kin structured this is expected to significantly impact the population genetic structure (Dobson et al. 1998; Sugg et al. 1996). This has been documented in several species including red howler monkeys (*Alouatta seniculus*) (Pope 1992; Pope 1998), naked mole-rats (*Heterocephalus glaber*) (Faulkes et al. 1997) and black-tailed prairie dogs (*Cynomys ludovicianus*) (Dobson et al. 1998). The size of a social group may also influence gene flow where larger groups will allow increased opportunities for access to potential mates (Krause & Ruxton 2002). Also individuals that are more connected within a network may have increased reproductive success, as has been documented in the forked fungus beetle (*Bolitotherus cornutus*) (Formica et al. 2012). Finally, the flow of information or disease may be impacted by social structure. Where a more densely connected social group will provide increased chances for information or disease to transmit through a group (Cross et al. 2004; Watts & Strogatz 1998). The spread of disease has been documented and it has been shown to vary seasonally depending on contact networks in Tasmanian devils (*Sarcophilus harrisii*) with higher rates
of facial tumour transfer in times when the network is more densely connected (Hamede et al. 2009). Describing the social structure of populations and unravelling the mechanisms and ecological factors underpinning this is therefore a key research focus in ecology and evolution.

Group living and social interactions that occur within a group are important in the ecology and evolution of species. Where food is more abundant groups are generally larger (Jarman 1974 (many antelope species); Chapman et al. 1995 (spider monkeys (Ateles geoffroyi) and chimpanzees (Pan troglodytes)); Janson & Coldsmith 1995 (various primates); Kruuk & Parish 1982 (badgers (Meles meles); Bernstein 1975 (ants (Veromessor pergandei, Pogonomyrmex rugosus, P. californicus)). Understanding this gregariousness may further provide insights into the evolution of sociality. This can be attained by analysing social structure based on group size and composition and particularly by comparing traits among populations (or species) living under different ecological conditions (Crook 1965; Jarman 1974; Seghers 1974). An important determinant of population social structure is the distribution and availability of resources (Tanner and Jackson 2011). At present most studies have focused at the level of the group. Therefore we know very little about how the social dynamics (e.g. the stability of social relationships) are influenced by the ecological environment and the implications of this for the social connectivity of the population.

The social organisation of a population is based upon the nature and strength of interactions between individuals (Croft et al. 2008). Using a network approach to investigate such social connectivity in populations provides us with quantitative metrics to describe the social structure at different levels of organisation, from the individual up to the whole population (Croft et al. 2008; Croft et al. 2006; Lusseau 2003; Lusseau 2007; Lusseau & Newman 2004;
Madden et al. 2009). Social network analysis of animal populations has been applied in many ways. For example disease and parasite transmission has been shown to transmit faster through a densely connected population in a range of different species including badgers (*Meles meles*) (Böhm et al. 2008), brushtail possums (*Trichosurus vulpecula*) (Corner et al. 2003), meerkats (*Suricata suricatta*) (Drewe 2010) and gidgee skinks (*Egernia stokesii*) (Godfrey et al. 2009). Individuals have been shown to have cooperative and behavioural assortative interactions in guppies (*Poecilia reticulata*). Individuals will cooperate with stable partners in predator inspection and shy fish will more often form strong bonds with bolder fish (Croft et al. 2006; Croft et al. 2009). We can also use a network approach to further gain understanding of information transfer (Hoppitt et al. 2010; Krützen et al. 2005). Theoretical work by Hoppitt et al. (2010) has shown that it is possible to model the spread of an innovative behaviour through a population. Whilst Krützen et al. (2005) suggest that tool use in bottlenose dolphins is limited to a social network of frequently interacting individuals (although this was not empirically tested using a network approach). Within a social network individuals can also influence others behaviour and this has been highlighted in several fish species (Darden et al. 2009; Jacoby et al. 2010). Finally, the role individuals play within the network can be quantified, as has been shown in bottlenose dolphins (*Tursiops truncates*) (Lusseau 2007; Lusseau & Newman 2004). At present the relationship between the social network structure of a population and food availability is poorly understood. The little work that has been done suggests that food availability may play an important role in shaping social network structure. For example, in a study on female chacma baboons (*Papio hamadryas ursinus*) Henzi et al. (2009) found that when food was scarce strong associations remained whilst more casual associations became weaker and in some instances were lost. In experiments on European shore crabs (*Carcinus maenas*) Tanner and Jackson (2011) found that when resources were clumped individuals aggregated into cohesive stable subgroups. In
contrast when resources were abundant no stable subgroups occurred. Moreover, recent work on Atlantic killer whales by Beck et al. (2011) showed that the strength of associations among matrilines differed between populations that had different foraging specialisations. Specifically, those individuals that fed on large schools of Icelandic herring showed larger, more stable groups than killer whales feeding on seals off Scotland. Similarly, groups of mammal eating killer whales in the Pacific are usually smaller than those that preferentially feed on salmon (Zerbini et al. 2007).

Figure 2.1. An example of the densely connected social network structure showing all HWI associations during the high salmon periods (15<sup>th</sup> June to 15<sup>th</sup> August) for 2007, (J pod (○), K pod (□) and L pod(∆). Figure drawn using network visualisation software, UCInet (Borgatti et al. 2002).

Here I explore how food availability may impact population social network structure of the southern resident killer whales. They exhibit strong social bonds (Mesnick et al. 1999; Williams & Lusseau 2006) and are organised into highly stable matrilineal social units (Bigg
et al. 1990). The southern resident killer whale community is a highly interconnected, closed population (figure 2.1), with no dispersal by males or females from the maternal group. Southern resident killer whales occur in the coastal waters of British Columbia and Washington State throughout the year. However, they are seen most frequently from June to September (figure 2.2) when they feed on the migrating salmonids (Ford & Ellis 2006; Olesiuk et al. 1990). Chinook salmon (*Oncorhynchus tshawytscha*) comprise the largest proportion of their diet during this time. Their diet is also supplemented with chum salmon (*O. keta*), sockeye salmon (*O. nerka*), pink salmon (*O. gorbuscha*), ling cod (*Ophiodon elongatus*) and Pacific halibut (*Hippoglossus stenolepis*) (Ford & Ellis 2006). Recent work by Ford and Ellis (2006) and Hanson et al. (2010) show that from June to September chinook salmon makes up more than 90% of the southern resident killer whales’ diet. There is well documented temporal variation in the abundance of chinook salmon (figure 2.3). These fluctuations may be due to a combination of anthropogenic impacts and El Niño conditions affecting the survival of juvenile salmon (Beacham et al. 2008; Lackey 2003; Slaney et al. 1996). Previous research proposes that declines in chinook salmon abundance are correlated with reduced killer whale reproductive success (Ward et al. 2009a) and higher mortality rates (Ford et al. 2010). Here I examine the impact that a change in food availability may have on a populations’ social dynamics. I predict that in times of low salmon abundance the population will be socially fragmented as individuals will have to spend more time foraging over a wider area thus limiting the opportunity for social interactions.
2.2. METHODS

2.2.1. Data collection

From 1984 until 2007 sightings of southern resident killer whales were documented by photographic census throughout the year by the Center for Whale Research, San Juan Island, WA, USA (48.551130N, -123.075633W). All observations were carried out from boats (9m trimaran and 5.5m Boston Whaler). During each sampling day every individual killer whale encountered was photographed by trained staff using Canon or Nikon SLR cameras with 300mm fixed lenses (1984-2004) or with Canon or Nikon DSLR cameras with fixed 300mm
or 80-200mm lenses (2003-2007). Sampling was limited to conditions suitable for photo identification, e.g. no rain, and relatively calm sea state (less than Beaufort 4). Individuals were identified by their unique fin shapes, saddle patches and the presence of any nicks or scratches and sexed using the distinctive pigmentation patterns around the genital slits (Ford et al. 2000). I used data from the 15th June until the 15th August each year. This is during the time when the chinook salmon are most abundant and form the major part of the southern resident killer whales’ diet (Hanson et al. 2010). During this time observations were made on a total of 536 sampling days (mean±SD 22.33±9.13 days per year) and a total of 10208 unique photographs were taken which were of sufficient quality for accurate identification. Every individual encountered was identified and included in subsequent analysis regardless of age or gender.

To define social associations I follow the methods presented in Parsons et al. (2009) which recognises that individuals within acoustic proximity have the opportunity to interact (Miller 2006). Every attempt was made to photograph all individuals present which was facilitated by the fact that killer whales travel in close physical proximity (Bigg et al. 1990; Ford et al. 2000; Parsons et al. 2009). Individuals photographed on a given day were assumed to be part of the same group.

To estimate chinook salmon abundance I used data provided by the Pacific Salmon Commission (PSC) (2008). During the study period (15th June - 15th August) the southern resident killer whales often occur from the upper Georgia Strait to the Oregon Coast (figure 2.2) as they follow the migrating salmon. I quantified the abundance of chinook salmon in this region using catch data provided by the PSC (figure 2.3). The PSC undertake test
fisheries during June to August to provide an estimate of chinook salmon abundance based on the number of fish caught which is compared to a reference period (1979-1982) (see PSC (2008) for full details).

Figure 2.3. Chinook salmon abundance index, 1984-2006, calculated as the number of fish caught in specific areas in the Pacific North West divided by the total catch for the reference period from 1979-1982 (See PSC website for full details http://www.psc.org/info.htm). Figure redrawn from data courtesy of the Pacific Salmon Commission (2008).

2.2.2. Social network analysis

To minimise bias due to sampling techniques (Croft et al. 2008; Lusseau et al. 2006) and to maximise the comparability with other cetacean association studies (Beck et al. 2011; Bräger et al. 1994; Gero et al. 2008; Lusseau 2003; Lusseau et al. 2006; Möller et al. 2006; Williams & Lusseau 2006) I used the half weight index (HWI) as a measure of strength of associations
between individuals (see Croft et al. 2008 for further details). Association patterns were calculated within each year from 1984-2007 using the HWI. Association matrices based on the HWI were calculated using SOCPROG 2.4 (Whitehead 2009).

For each annual configuration I quantified both global and local population structure using weighted network measures (Lusseau et al. 2008). The global connectivity describes the connectedness of the entire population whereas the local connectivity describes the finer scale associations between individuals. To quantify the global connectivity of the population I used the average weighted path length \((L)\), which is defined as the shortest distance from an individual to the rest. A shorter path length may result in faster information or disease transfer between individuals. To quantify the local population structure I used the weighted clustering coefficient \((C)\), which is defined as the connectivity between an individual’s neighbours. A high clustering means that the social network is highly interconnected on a local scale. I also calculated average weighted degree centrality \((k)\), which is defined as sum of the strength of the associations that an individual has. Finally, the mean HWI was calculated for the network which provides a measure of the average strength of association. All network measures were calculated in R using the tnet library (Opsahl 2009).

The social network measures that describe the global and local population structure are not independent (Croft et al. 2008) therefore I combined the measures using a principal components analysis (PCA). To determine which component(s) to use in the analysis I use the Kaiser-Guttman criterion where the eigenvalues were calculated for each component of the PCA. I only included components with an eigenvalue greater than one (Jackson 1993). I first explore the effect of salmon abundance on population and group size and population and
group size on social network PCA score using a Spearman’s rank correlation. I then use a Spearman’s rank correlation to examine the relationship between the PCA of the network measures and chinook salmon abundance. To account for autocorrelations in the network data and to control for group-size distributions, demographic effects and sampling, a randomisation test was used to calculate significance (Bräger et al. 1994; Croft et al. 2011; Whitehead 1999). This was performed on the group-based data using swaps of individuals between groups within each sampling year before calculating a Spearman’s rank correlation for that data for each randomisation. 5000 randomisations were generated with 100 swaps per randomisation. Randomisations were programmed in c++.

2.2.3. Ethical note

From 1984-2004 the data were collected under whale watch guidelines that are endorsed by the governments of the USA and Canada in lieu of a regulatory scheme. It is not considered invasive or illegal to watch whales in either country. From 2005 onwards data were collected under federal permits (MMPA permit number 532-1822 and/or DFO license number 2006-08/SARA-34) in both the USA and Canada that allowed approaches closer than the whale watch guidelines (100m approach distance) on a specified number of occasions for research purposes. Data collection complied with the approach guidelines and the requirements (including reporting) of the scientific permits issued.
2.3. RESULTS

There were 167 individuals (80 females, 69 males and 18 individuals of unknown sex) documented during the 24 year period. The population size in any given year ranged from 71 to 98 (mean $\pm$ SD: 85 $\pm$ 6.6).

Component 1 of the PCA was the only component with an eigenvalue greater than 1 (3.72). Therefore I retained this component which described 93.1% of the variance and was used for all subsequent analysis. Clustering coefficient, degree centrality and mean HWI all loaded positively onto the PCA (0.491, 0.500, 0.511 respectively) while path length loaded negatively (-0.498). Thus a high PCA score indicates a high clustering coefficient, degree centrality and mean HWI and a low path length.

I found no significant relationship between salmon abundance and population size ($r_s$=-0.307, $N$=24, $P=0.154$) or between population size and social network PCA score ($r_s$=0.074, $N$=24, $P=0.738$). However, there was a significant positive relationship between salmon abundance and group size ($r_s$=0.457, $N$=24, $P=0.025$) and group size and social network PCA score ($r_s$=0.686, $N$=24, $P<0.001$). In times of high salmon abundance groups tended to be larger which is reflected in the social network as higher clustering coefficient, degree centrality and mean HWI and a lower path length. These relationships were controlled for with the randomisations, where swaps of individuals were constrained by group size based on the real data.
Group-based randomisations (controlling for group size effects, demographics and sampling effort) showed a significant relationship between the social network structure and chinook salmon abundance during the study period ($r_s=0.412$, $N=24$, $P=0.020$, figure 2.4). In years of high chinook salmon abundance the social network exhibited a high clustering coefficient (figure 2.5a), degree centrality (figure 2.5b) and mean HWI (figure 2.5c) and a low path length (figure 2.5d).

![Figure 2.4. Relationship between PCA score of network measures and chinook salmon abundance from 1984-2007.](image)

Figure 2.4. Relationship between PCA score of network measures and chinook salmon abundance from 1984-2007.
2.4. DISCUSSION

Based on the analysis of association data over a 24 year period my results demonstrate a significant relationship between social network structure and food availability. In times of high chinook salmon abundance the southern resident killer whale population is characterised by a highly interconnected social network with a high clustering coefficient, degree centrality and mean HWI and a low path length. This relationship is not simply an effect of population demography, group size or sampling effort all of which were controlled for in my analysis with null models. To the best of my knowledge this study is the first to examine the
relationship between resource availability and both the local and global connectivity of the social network structure in a free ranging population.

It is well documented that resource availability can lead to changes in group size (Baird & Dill 1996; Bernstein 1975; Caraco & Wolf 1975; Chapman et al. 1995; Clark & Mangel 1984; Janson & Goldsmith 1995; Jarman 1974; Kruuk & Parish 1982). I found a significant relationship between salmon abundance and group size, with larger groups forming in years of high salmon abundance. I would expect to see this as more abundant food resources can support larger groups with reduced competition (Chapman et al. 1995; Krause & Ruxton 2002). Group size also had a significant effect on the population social network structure and when the mean group size was small the social network had low clustering coefficient, degree centrality, mean HWI and a high path length.

I found an effect of salmon abundance on the social network structure over and above the effects that could be explained by variation in group size. In times of low salmon abundance the population was characterised by a less connected social network than in times of high salmon abundance. Killer whales benefit from cooperative food searching although they are not thought to hunt cooperatively (Baird 2000). Beck et al. (2011) demonstrate that killer whale family groups remain stable over time regardless of their prey choice. However the results suggest that the social connectivity both within and among groups is affected by prey availability. I suggest that these results are influenced in part by a trade-off between foraging effort and social activity. Thus in periods of low salmon abundance increased time spent searching for prey may reduce the opportunity for social interactions within the group. Reduced time for social interactions is also indicated by a significant decline in the rate of
association among whales during years of low salmon abundance (Parsons et al. 2009). In support of this previous work has demonstrated that when prey are scarce or patchily distributed killer whales not only have to invest more time in locating prey they also spend larger amounts of time spread out away from the rest of the group (Felleman et al. 1991). In addition, killer whales have been observed travelling much further distances during times of low food availability (Nichol & Shackleton 1996). This behavioural adaptation has also been observed in long and short finned pilot whales (*Globicephala melas* and *G. macrorhynchus*), sperm whales (*Physeter macrocephalus*) (Whitehead 1989), common dolphins (*Delphinus* sp.), spotted dolphins (*Stenella frontalis*) and spinner dolphins (*S. longirostris*) (Norris & Dohl 1980). Similar patterns have also been observed in terrestrial animals such as insectivorous primates (Janson & Goldsmith 1995) and elephants (*Loxodonta africana*) (Wittemyer et al. 2005). My results suggest that low food abundance limits the opportunity for social interactions. However, this is not the case for all animals. For example, in a study on female chacma baboons Henzi et al. (2009) observed cyclic changes in the patterns of interaction. There was an increase in the strength of social bonds during times of low food availability. As I looked at the broad scale networks data finer scale interactions between individuals, such as those reported by Henzi et al. (2009), may have been missed.

The changes I observed in social network structure in the current study are only partly explained as a function of food availability. Interestingly I found no relationship between salmon abundance and population size or population size and social network structure. Previous work suggests that there may be a lagged impact of food availability on population size. This has been shown for the northern and southern resident killer whale populations both in terms of survival (Ford et al. 2010) and fecundity (Ward et al. 2009a). A number of other ecological factors that were not measured may have had an impact on the structuring of
the population social network. In particular the distribution of resources may have had a strong influence on the opportunities for social interactions (Tanner & Jackson 2011). In addition the results I present here may be impacted by the way in which I define a group. The present definition of a group was chosen to look at the broad scale social structure. However, future work should look at the impact of food availability on finer scale interactions occurring within the group.

Changes in social structure may have significant implications for population processes such as information and disease transmission (Croft et al. 2008; Krause & Ruxton 2002). Non-random networks with high clustering and short path length have been shown to be susceptible to disease outbreaks (Guimarães et al. 2007). For the southern resident killer whales in times of low chinook salmon abundance the population is less interconnected therefore it may be less vulnerable to an epidemic outbreak. This may be particularly important as in times of low food availability individuals metabolise fat which releases pollutants such as polychlorinated biphenyls resulting in increased susceptibility to disease (Ford et al. 2010). When food is abundant, the southern resident killer whale social network is highly connected which may provide a number of benefits including increased opportunities for mating and information transfer (Croft et al. 2008). The cost of increased exposure to pathogens in times when the social network is highly connected may be less of a problem as the whales will have decreased susceptibility to disease due to plentiful salmon.

The predominant application of social network analysis to non-human animals has been to investigate the internal factors affecting social dynamics (e.g. Croft et al. 2005; Parsons et al. 2003; Williams & Lusseau 2006). My investigation demonstrates the potential of using a
network approach to investigate the relationship between the ecological environment and population social dynamics. This approach is applicable to other species and such understanding is invaluable when designing effective conservation and management plans. This becomes particularly important when both the population and its prey are endangered (Williams et al. 2011). Different populations of killer whales are specialist foragers to a point where it is a limiting factor in their survival (Ford et al. 2010). Despite being endangered chinook salmon are still a targeted species by commercial fisheries and it is important to fully understand the implications of removing large quantities of this species.

Here I have quantified the overall population structure of the southern resident killer whales and explored an external factor that significantly impacts social network structure. In the next chapters I look in more detail at the finer scale internal factors that may affect a population social network. As social networks are rarely homogenous I first begin by exploring the different positions individuals occupy within a social network.
Chapter III.

The role of individuals in a social network: The effect of age and sex on network position
ABSTRACT

Animal social structure is usually heterogeneous and within populations individuals occupy different social network positions. Of particular interest are individuals that have high network centrality as these individuals may play a key role in population processes such as information and disease transmission. Resident killer whales (*Orcinus orca*) are notable for their highly stable population structure, which is extreme even among social mammals. There is no dispersal by males or females from the maternal group. I used association data based on surfacing patterns observed between 1996 and 2010 to quantify the social network and explore the relationship between social network centrality and age and sex. I found the social network to be highly connected with associations occurring both within and between matrilines. Females had a significantly higher number of associates (degree) than males; however, there was no significant difference in network position (betweenness). Age had a significant effect on network position in both male and females. Older individuals of both sexes having a higher network degree and in males older individuals had higher betweenness centrality. Understanding the central role that individuals of high network centrality can play in population processes can provide an insight into gene flow and disease transmission. Hence, identifying the position that individuals occupy in the social network is vital when designing conservation and management plans. My results suggest that an individual’s age and sex are key factors in determining network centrality.
3.1. INTRODUCTION

Population social structure is typically non-random and individuals are interconnected into heterogeneous social networks (Godfrey et al. 2009; Keeling & Eames 2005). Individuals may sort spontaneously according to certain motivational or behavioural traits. Such traits may include associating with animals of similar morphology such as body size and this is known as passive assortment (Ward & Krause 2001). In addition to passive assortment individuals may make active decisions regarding with whom they associate with (Couzin 2006). Such decisions may be based on familiarity (Lusseau et al. 2003; Morrell et al. 2008; Swaney et al. 2001; Ward & Hart 2003) and/or kinship (Frommen & Bakker 2004; Silk et al. 2006; Ward & Hart 2003). Understanding the mechanisms underpinning population social structure is of high importance given the fundamental role that this plays in ecology and evolution. For example, understanding patterns of social organisation in a population provides information regarding opportunities for gene flow (Matocq & Lacey 2004; Piertney et al. 1999; Wolf & Trillmich 2008), disease transmission (Cross et al. 2004; Watts & Strogatz 1998) and cultural continuity through information transfer (Krützen et al. 2005; Whitehead 1998a; Whitehead 2010; Whitehead et al. 2004; Wolf et al. 2007).

Early studies of non-human animal social network structure have revealed remarkable similarities to human social networks (e.g. Lusseau & Newman 2004). In particular, within a social network individuals differ in their centrality and may take on different roles (Lusseau & Newman 2004; Williams & Lusseau 2006). This has long been known for primates (Berenstain & Sharpe 1966) but more recently has been demonstrated in a bottlenose dolphin (Tursiops sp.) population in Doubtful Sound, New Zealand. Specific individuals appeared to have a central role in maintaining the cohesiveness of the population by acting as links.
between communities (Lusseau & Newman 2004). Individuals with high network centrality may have a disproportionately large effect on social dynamics and population processes. Such individuals have been termed keystone individuals (Sih et al. 2009), super-spreaders (Keeling & Eames 2005; Pautasso & Jeger 2008), floaters (Godfrey et al. 2009) or brokers (Lusseau & Newman 2004). For example, individuals with high network centrality may have a huge impact on the spread of disease through a population (Perkins et al. 2009). This makes it easier for an epidemic to develop than in homogenous networks (Pautasso & Jeger 2008; Perkins et al. 2009). In addition to this, the number of associates an individual has may also be important in understanding the costs associated with holding a central position in the social network. For example, with disease transmission, the strength of relationships may be important in the probability of contracting an infection, particularly with weaker pathogens (Wey et al. 2008). A highly publicised example of individuals with high centrality influencing the spread of disease was observed during the 2003 severe acute respiratory syndrome (SARS) epidemic in humans. Spreading of the disease was facilitated by a few individuals infecting a large number of people. Such events are not a result of highly contagious individuals but more likely highly connected ones (Li et al. 2004; Peiris et al. 2003; Small & Tse 2005; Small et al. 2006; Wang et al. 2006). Similar effects may be observed with the transmission of information and various types of information may be shared. For example, individuals may share information about the quality of a foraging area and where food is patchily distributed each group member can more accurately assess the quality of the patch if knowledge is pooled (Sernland et al. 2003). Animals may also increase their own food intake by learning to eat new foods or by learning of new foraging areas from conspecifics (Giraldeau 1984). For a number of species sociality can also provide adaptive benefits during cooperative foraging whereby individuals can work together to hunt prey that would be too large or difficult to catch for a single animal. Examples can be seen in large
carnivores such as lions (*Panthera leo*) (Stander 1992) and some populations of killer whales (*Orcinus orca*) (Pitman & Durban 2012). In such coordinated attacks different individuals may take on different roles within the group, hence pooling the skills of the group to maximize success (Giraldeau 1984). Similarly, sociality allows information to be passed quickly from one individual to the next. This is useful when warning against predator attacks (Proctor et al. 2001). For example, Davis (1975) showed that the pre-flight movements in pigeons (*Columba livia*) act as a signal to the rest of the group informing them whether the individual is leaving due to predator detection or for some other reason. Similar pre-flight behaviour has been shown in pelicans (various *Pelecanus* species), northern gannets (*Morus bassanus*), red-footed boobies (*Sula sula*) and cormorants (various *Phalacrocorax* species) (van Tets 1965). As discussed in Chapter I mammals including Belding’s ground squirrels (*Spermophilus beldingi*) (Sherman 1977), vervet monkeys (*Cercopithecus aethiops*) (Seyfarth et al. 1980), Diana monkeys (*C. Diana*) (Zuberbuehler et al. 1997), ring tailed lemurs (*Lemur catta*) (Macedonia 1990), Barbary macaques (*Macaca sylvanus*) (Fischer et al. 1995) and mongoose (*Suricata suricatta*) (Manser 2001) use alarm calls to warn other group members of danger and calls will vary depending on the predator type and the extent of the danger (Manser 2001).

There may be fitness costs and benefits associated with social network position. For example, individuals that have frequent social contact with many individuals may have increased mating opportunities (Godfrey et al. 2009; Sih et al. 2009). There are examples across a range of taxa where males with more social bonds with conspecifics have higher reproductive success [long-tailed manakins (*Chiroxiphia linearis*) (McDonald 2007), wire-tailed manakins (*Pipra filicauda*) (Ryder et al. 2009), Assamese maqaque (*Macaca assamensis*) (Schülke et al. 2010) and forked fungus beetles (*Bolitotherus cornutus*) (Formica et al. 2012)]. These
studies show the potential of quantifying network centrality to use as a predictor of individual fitness. However, the number of associates an individual has may also be important in understanding the costs associated with holding a central position in the social network. For example, with disease transmission, the strength of relationships may be important in the probability of contracting an infection particularly with weaker pathogens (Wey et al. 2008).

Whilst the role that individuals in different social network positions plays in the context of the transmission of information and disease has received considerable interest (Böhm et al. 2009; Lusseau & Newman 2004; Pautasso & Jeger 2008) the mechanisms driving these differences remains poorly understood. Recent research suggests that an individual’s behavioural phenotype may be a key factor in determining its social network position (Krause et al. 2010). For example, a laboratory based experiment on three-spined sticklebacks (Gasterosteus aculeatus) showed that shy individuals have stronger associations with fewer fish in comparison to bold individuals (Pike et al. 2008). Another example is seen in the Trinidadian guppy which has been shown to take account of phenotype when shoaling. Non-random networks show that fish will preferentially shoal with other individuals of similar body length and shoaling tendency (Croft et al. 2005). As with phenotypic characteristics, personality can also affect animal social structure. Croft et al (2009) have shown that bold Trinidadian guppies (boldness measured on predator inspection tendency and shoaling) had fewer network connections than shy fish and the connections that bold fish did have were on average weaker. This shows that the finer scale social structure is strongly influenced by an individual’s personality and the authors suggest that this may act as an amplifier of selection contributing to the maintenance of cooperation during a task such as predator inspection. More recent experimental work on European shore crabs (Carcinus maenas) found that highly exploratory individuals play a key role in connecting cohesive subgroups of low
exploratory crabs (Tanner & Jackson 2011). The synchronous movements of crabs with low exploratory rates could allow greater effectiveness when finding food than those crabs with higher exploratory rates. The authors further suggest that social structure is sensitive to the interaction between ecological and behavioural differences between individuals.

Mating dynamics could also influence network position. Male killer whales will preferentially mate with females from other matrilines (Amos et al. 1993a; Ford et al. 2011; Pilot et al. 2010). Further work has shown that older males have the greatest reproductive success (Ford et al. 2011). I speculate that this increase in mating success in older males may in turn influence their social network structure by facilitating contact with more females from different matrilines. In addition to behavioural traits physical attributes, such as age and/or sex, may play an important role in influencing patterns of association and thus network centrality. For example matriarchs in elephant (Loxodonta Africana) society are fundamental to the group (McComb et al. 2001) and will often act as leaders (McComb et al. 2011). This has been shown in playback experiments where older females will respond more appropriately to predatory threats. In contrast in northern resident killer whale society higher betweenness scores are usually seen in younger animals, specifically juveniles and sexually immature females. However this relationship is non-significant (Williams & Lusseau 2006).

Individuals that hold a central network position will face a cost/benefit trade off that determines the optimal number and type of social interactions an individual has. This is likely to vary among individuals depending on their current situation. By viewing social decisions using a networks approach allows predictions to be made regarding the way that actors such as age and sex are likely to influence centrality. In the current investigation I explore the
effect of age and sex on social network position in the endangered southern resident killer whale (*Orcinus orca*) population. Killer whales are remarkable for their highly structured matriarchal social systems (Bigg et al. 1990). Much of our understanding of killer whale social structure comes from long-term studies from the coasts of Northwest North America. Where photo-identification surveys have provided detailed co-occurrence records of killer whale groupings since the early 1970s (Ford et al. 2000). These killer whales are listed as endangered under the Endangered Species Act in the U.S.A. and Species at Risk Act in Canada (Hauser et al. 2007a) and are found consistently around the southern end of Vancouver Island during summer months coinciding with chinook salmon (*Oncorhynchus tshawtscha*) runs (Ford & Ellis 2006; Hanson et al. 2010).

To quantify the social structure of the southern resident killer whales I use a network approach. This allows me to explore the roles that individuals may play within the network. I look at general differences between males and females in network position and the effect of age on these patterns. Sociality is particularly significant in resident type killer whale populations and older females play a central role within the matrilines (Parsons et al. 2009). These matriarchs are thought to be important in the cohesion of a social group (Williams & Lusseau 2006). In light of this I predict that older females will have higher measures of network centrality.

3.2. METHODS

Population surveys for the southern resident killer whales were conducted in the coastal waters around the southern end of Vancouver Island. Specifically in the transboundary waters
of the U.S.A. and Canada between Washington State and British Columbia, west of San Juan Island by the Center for Whale Research. In Chapter II photographic data were used, however in 1996 the introduction of the collection of digital video footage facilitated the acquisition of much finer scale association data. From 1996 until 2010 digital videos and high definition videos were collected from boats (9m trimaran and a 5.5m Boston Whaler) and from shore along the west side of San Juan Island, WA, U.S.A. (48.551130N, -123.075633W).

Boat based sampling was limited to conditions suitable for photo identification, i.e. flat sea state and no rain. Individuals were identified by their unique fin shapes, saddle patches and the presence of any nicks or scratches (Ford et al. 2000). Associations between individuals were recorded from the video footage. As I was interested in looking at fine scale associations occurring between individuals I define an association as two or more animals surfacing synchronously (plate 3.1a) or successively (plate 3.1b) within one body length. To control for the sampling bias that pairs of individuals are more likely to be observed apart than together (Cairns & Schwager 1987; Croft et al. 2008) and to increase comparability with other cetacean association studies (examples include Beck et al. 2011; Bräger et al. 1994; Gero et al. 2008; Lusseau 2003; Lusseau et al. 2006; Möller et al. 2006; Williams & Lusseau 2006) I use the half-weight index (HWI) as a measure of association between individuals (see Croft et al. 2008 for further details). An association matrix using the HWI was generated using SOCPROG 2.3 (Whitehead 2009). I used tnet (Opsahl 2009) in R (R development core team 2010) to calculate specific network measures (described below). These were weighted to take into account the strength of associations occurring between individuals (see Chapter I). Specifically, I calculated Freeman’s betweenness and degree (Freeman 1979). Degree is the number of associates to which an individual is linked. Betweenness assesses the importance of an individuals’ position in brokering between the different sub-communities of
the network. I used a weighted analysis to incorporate the strength of these associations (e.g. weighted degree is the sum of the weights of the connections from an individual).

Plate 3.1. (a) K20 and K25 surfacing synchronously within one body length. (b) K12 and K38 surfacing successively within one body length.

Differences in the betweenness and mean weighted degree of males and females were calculated using randomisations of the raw data. The statistical significance was calculated using randomisations which account for the autocorrelations in the data and to control for sampling and demographic effects (See chapter I). To do this the group-based data was permuted by swapping individuals between groups observed within the same month of observation. 5000 null statistics (centrality measures and differences between sexes) were generated with 100 swaps per permutation. P-values were calculated by comparing the observed test statistic to the distribution generated by the randomisations.
Next I explored the relationship between age and centrality. Firstly, ages of the whales born prior 1974 were estimated in several ways (see Ford & Ellis 2002 for full details). Calves in 1974 were aged relative to their size. For juvenile whales in 1974, their age was estimated in reference to the year they became sexually mature. Indirect methods were employed for mature animals in 1974. For females year of birth was estimated from the ages of their offspring and the average age of reproductive cessation. Age of mature males without living mothers was estimated as the latest year the whale could have been born. To explore the relationship between age of the whale and their centrality measures over the study period I recorded their maximum age, which was their age at death or age in 2010. This was compared with degree and age. A Spearman’s correlation was used with P values calculated using the randomisation test procedure outlined above. Randomisations were programmed in c++ and R. Network visualisation was created using Tulip visualisation software with custom python scripts.

3.3. RESULTS

From 1996 until 2010 the survey effort totalled 4677.5 hours, of which 2776.2 hours (59.4%) was spent in the presence of southern resident killer whales. During this time 142 individuals (69 females, 57 males, 16 of unknown sex) were documented.
Figure 3.1. An unfiltered association matrix generated using Tulip visualisation software with custom python scripts illustrating the highly connected social network of southern resident killer whales from 1996 until 2010. Females are shown as red nodes, males blue nodes and animals of unknown sex yellow nodes. Node size relates to individual age at death or in 2010. All connections between individuals are included, those with HWI<0.2 shown as thin lines and associations HWI>0.2 have a thickness proportional to their weights.

The network analysis describes a highly connected social network where all individuals associated with others both within and outside their matriline (figure 3.1). The average number of associates for an individual was 47±22.4. The maximum number of associates was 95 and the minimum was 3. All individuals were recorded in the analysis regardless of the number of associates they had. Those with an exceptionally low number of associates were
not present for the entire study due to either being born late in the study or dying early. There was no significant sex differences in betweeness ($P=0.992$, figure 2a). However, weighted degree differed significantly between the sexes, with females having a higher degree than males ($P<0.001$, figure 2b). Therefore females have a greater number of strong relationships with other individuals than males.

![Figure 3.2. (a) male and female mean (+SD) betweenness. (b) male and female mean (+SD) weighted degree.](image)

I found no significant correlation between female betweeness and age ($r_s=-0.04$, $N=69$, $P=0.93$, figure 3.3a). There was a statistically significant negative correlation between female degree and age ($r_s=-0.05$, $N=69$, $P<0.001$, figure 3.3b). Whilst this negative correlation is statistically significant the effect size was extremely small ($r_s=-0.05$). This shows that neither older nor younger females have more associates or hold a more central position in the social network. In males both betweeness ($r_s=0.52$, $N=57$, $P<0.001$) and degree ($r_s=0.19$, $N=57$, $P<0.001$) were significantly positively correlated with age (figure 3.3c and 3.3d respectively). Therefore older males have both more associates and hold a more central social network.
position than younger ones. The relationship between age and weighted betweenness in males remained significant when the outlier in figure 3.3c (highlighted with a red circle) was removed from the analysis ($r_s=0.28$, $N=56$, $P<0.001$). This illustrates that older males hold a more important position in linking the social network.

Figure 3.3. Centrality measures (weighted betweeness and degree) for males and females in relation to maximum age in 2010. (a) Female weighted betweeness, (b) female weighted degree, (c) male weighted betweeness (outlier highlight in red circle), (d) male weighted degree. Grey circles show the expected distribution of centrality measures produced by the null model and black circles show the observed values.


3.4. DISCUSSION

By gaining an insight into the social structure of animal populations it is possible to explore the roles that different animals fulfil. In this study, I describe the social structure of a highly connected population of killer whales. Most individuals are connected to many others both within their matrilines and among different matrilines. Females had higher weighted degree than males (i.e. females had more associates). However betweenness (or importance of an individual in connecting the social network) did not differ between the sexes. I found a significant effect of age on social network position in both males and females. Older individuals had a greater number of associates in both males and females (the effect size however was very small in females). Moreover male’s age was significantly correlated with network betweenness with older males having a higher network betweenness, meaning they hold a more central position in the social network.

Previous work has documented strong matrilineal social structuring of resident type killer whales in the Pacific Northwest (e.g. Balcomb et al. 1982; Bigg et al. 1990; Deecke et al. 2010; Ford et al. 2000; Parsons et al. 2009). Such stable social systems in which both sexes remain with their mother for life are extremely unusual and have only been described in one other mammalian species, the pilot whale (*Globicephala* sp.) (Amos et al. 1993a). Despite this strong matrilineal structure I find that the population can be interconnected into a single social network with strong associations occurring both within and among matrilines. This result supports the existing evidence of a densely connected social population (Bigg et al. 1990; Olesiuk et al. 1990) which is similar in structure to the northern resident killer whale population in British Columbia (Williams & Lusseau 2006). The northern resident killer
whales also show a densely connected social network with associations within and between family groups (Williams & Lusseau 2006).

When I explored the number of associates an individual has within this densely connected network I found striking similarities to human social networks. In humans the sex of an individual is known to have a strong effect on the size of their social network, with females having larger social networks than males (Tonge 2010). I find similar patterns in the current study, where females also have a larger number of associates than males. I suggest this may occur as a result of the lack of dispersal seen by both sons and daughters. Females will maintain strong associations with all their offspring throughout their lives (Deecke et al. 2010), whereas the strongest bond a male has is with his mother (Ford et al. 2000). This lack of dispersal from the maternal group leads to females having a greater number of strong associates than males. However, weaker bonds are formed outside the group by both males and females as they will not mate within their own matriline (Baird 2000; Whitehead & Mann 2000). This lack of dispersal from the maternal group is extremely rare in animals and the only other species’ with a comparable dispersal pattern are the short-finned pilot whale (Amos et al. 1993a; Amos et al. 1993b). Further genetic work suggests a comparable dispersal system in the long-finned pilot whale (Amos 1998). This may result in females having a greater number of very strong bonds with her offspring, resulting in a higher weighted degree. Whereas males may have weak bonds with more individuals as they seek mating opportunities resulting in a lower weighted degree. Teasing this apart would be a hugely interesting avenue for future research.
In addition to the lack of dispersal in resident type killer whales leading to group living in this population, sociality is particularly significant in resident type killer whale. By the nature of matrifocal societies the oldest females play a particularly important role in group cohesion and hence take a central role within the matrilines (Parsons et al. 2009). The death of a matriarch has been shown to impact the degree of affiliation between and within matrilines (Parsons et al. 2009). Similarly, in elephant society the loss of a matriarch, due to illegal poaching, has also been linked to social breakdown. This has led to the fragmentation of the patterns of social attachment by eliminating the supportive stratum of the matriarchs (Bradshaw et al. 2005). In Chapter III I find a statistically significant relationship between age and weighted degree in females. Surprisingly, the effect size for this relationship was very small suggesting that it has little biological significance. Older females in both killer whale (Foote 2008) and elephant (McComb et al. 2001) societies are thought to possess superior ecological knowledge. This knowledge will have be acquired over time and may been seen as more appropriate behaviour towards predatory threat (McComb et al. 2001; McComb et al. 2011). Such knowledge only becomes useful in changing circumstances; such as the introduction of a predator or the need to move to a new food source (Greve et al. 2009). Older female elephants have been shown to respond appropriately to playback experiments using lion roars than younger ones, probably due to their increased experience of predation events (McComb et al. 2011). By sharing this knowledge older females may need to have more contact with more individuals. In matrilineal animals this will increase the survival and fitness of related individuals. In addition, female relatedness to individuals in the population (both within and outside of their own matriline) increases with age which could drive the weak relationship between degree and age seen in females. I found no correlation between female age and betweeness, hence I suggest that they do not play a key role in the connectivity of the population. I suggest that this may represent a trade-off between the costs
and benefits of individuals holding a central network position. There are costs and benefits of interacting with lots of individuals (see Chapter I for full discussion of this). However, the relative costs and benefits are not likely to be uniform and they will differ among individuals (often in predictable ways). For example, individuals in good physiological condition may be less concerned about increased disease risk than those in poor condition. Alternatively, males might have a greater need to associate with more females to increase their reproductive potential. The age of an individual might also impact the number of others it needs to associate with. For example, a dependant calf will rarely be observed away from it’s mother, however, older individuals will spend more time in the presence of others from different matrilines (Olesiuk et al. 1990). Exploring the adaptive explanations of differences in association patterns for different age or sex classes would provide important insight into the social systems of resident type killer whales.

In contrast to human social networks, where a quadratic relationship between age and degree has been found (Hill & Dunbar 2003), the relationship between age and network centrality in male killer whales appears to be linear. Male killer whales show a strong effect of age on both network degree and network betweenness. Both measures of centrality (degree and betweenness) show an increase with age. I suggest that this can be explained by the fact that inbreeding is often avoided by dispersal by one sex, usually males (Amos et al. 1993a). However, in the absence of dispersal male killer whales have been shown to avoid inbreeding by primarily mating with females from other social groups (Amos et al. 1993a; Ford et al. 2011; Pilot et al. 2010). Hence, individuals with greater reproductive success must have contact with more females from different matrilines. Ford et al. (2011) use microsatellite loci to infer paternal relationships. They show that oldest males have the greatest reproductive success they also highlight that no male fathers offspring within his own matriline. My results
suggest that this increase in reproductive success in older males is facilitated by increased access to mates through higher connectivity in the network. Further research to explore the mechanisms that underpin this relationship would be beneficial to understanding of the link between social systems and mating dynamics in large matrilineal mammals.

In contrast to the results presented here Williams and Lusseau (2006) suggest that there is a non-significant trend towards younger animals (specifically juveniles and sexually immature females) having higher betweenness scores in the northern resident killer whales. The differences in results between this work and my study may be due to population differences. Whales from the northern and southern resident communities have never been seen to interact despite having overlapping home ranges (Ford et al. 2000). They also have distinctly different dialects (Deecke et al. 2000). Differences in vocalisations have been attributed to social relationships between individuals and thus can provide information regarding association patterns (Deecke et al. 2010; Miller & Bain 2000; Rendell & Whitehead 2003). The differences could also be in part due to the way the data were analysed. Williams and Lusseau (2006) state that further work needs to be done to remove issues of independence and sampling bias towards specific individuals in their study, as they do not randomise their data (see Chapter I for explanation). In the current investigation this problem has been overcome with the use of permutation tests and thus controlling for the non-independence of the data and sampling bias.

Earlier work on human social networks has shown that differences in degree and network structure vary with a range of factors (summarised by Hill & Dunbar 2003). Such factors include sex (Dunbar & Spoors 1995), age (Dickens & Perlman 1981), marital status (Rands
1988), physical attractiveness (Reis et al. 1982), personality (Roberts et al. 2008) and levels of education, occupation, or income (Belle 1982). Like in human social networks my results show that both age and sex has a significant effect on network centrality in an endangered population of resident killer whales. Often population management plans assume all animals play an equal part and this can have consequences for the population (Williams & Lusseau 2006). Williams and Lusseau (2006) highlight the need for exploring the role that different age and sex classes play in killer whale society. Removal of specific individuals could have severe consequences for endangered populations of highly social mammals such as elephants and whales (McComb et al. 2001). I present evidence that highlights the importance of a thorough understanding of the social structure and particularly the role of individuals within the population when designing effective conservation and management plans. Conservation and management strategies should take into account that different age and sex classes are exposed to different risks through their number of associates and network position. For example, it would be beneficial to take into account the importance of the older males in the connectivity of the group, particularly when assessing the threats of disease spread through the population. However, in addition, animals can respond to changing environmental conditions through modifying their behaviour and as key links in the social network older males may be important in facilitating this information transfer.

In chapter III I determined that individuals have different network positions dependent on their age and sex. In the next chapter I further explore the role of individuals by specifically looking at leadership. I investigate whether particular matrilines or individuals more often lead others and the attributes and energetic requirements of these leaders.
Chapter IV.

Who follows whom: Identifying leaders in an endangered population of killer whales (*Orcinus orca*)
ABSTRACT

The coordinated movement of animals is one of the most illustrative examples of collective decision making and the success of this will impact the survival of the group. A key question in population social biology is determining which individuals may be important in leading a group. I explore the attributes of group leadership at two levels in an endangered population of killer whales (*Orcinus orca*). I look at both matriline leadership and individual leadership. At the level of the matriline I determine group characteristics that may influence leadership and the degree of variance in leadership within a matriline. At the level of the individual I explore how leadership tendency is influenced by both individual attributes and energetic demands. Specifically I test if leadership tendency changes as a function of lactation state. Association data were obtained from surfacing patterns observed from video footage between August 2001 and July 2009. I found that some matrilines led or followed more than would be expected by chance; but this was not a factor of matriline size or mean age of matriline. However, there was a significant positive correlation between leadership score and the sex ratio of the group, with leadership tendency increasing with the proportion of females in the matriline. At the level of the individual females had significantly higher leadership tendency than males and in both sexes there was a significant positive correlation between leadership and age. There was no significant relationship between centrality and leadership score in neither males nor females. I suggest that the oldest females have the highest leadership scores due to these individuals having a prolonged lifespan, which allows them to acquire superior ecological knowledge. This in turn may result in increased survival and fitness of the matriline. Leadership scores were significantly higher in females during lactation which I suggest is driven by increased energetic demands. I discuss these findings in the context of the evolution of leadership behaviour in animal groups and highlight the importance of
understanding the roles of individuals in coordinated group decisions, particularly when designing effective conservation and management plans.
4.1. INTRODUCTION

Collective travel and group living provide a range of benefits to group members. Such benefits include increased vigilance for predators, predator avoidance, enhanced foraging efficiency and increased navigational accuracy (Krause & Ruxton 2002). The coordinated movement of animals is one of the most illustrative examples of collective decision making (Flack et al. 2012) and is vital to the survival of individuals in the group (King & Cowlishaw 2007). Reaching a consensus about decisions regarding the nature and timing of group activities allows animals to maintain social cohesiveness. This is imperative if individuals in groups are to benefit from sociality (Bonanni et al. 2010). To achieve spatial cohesion during collective movements individuals within a group must be able to coordinate themselves with one another (Bousquet & Manser 2011). Within a group engaging in collective movement there will be leaders and followers. Leaders are defined as those individuals that are more influential with respect to decision outcomes and followers will accept the decisions of leaders (Bonanni et al. 2010). As a few individuals follow a leader others follow the first followers and eventually the group will take a unified direction (Sumpter 2006). Leadership can emerge in different ways. In many cases only a few individuals within the group will have appropriate knowledge to allow them to effectively lead the group, such knowledge may include information regarding food sources (Couzin et al. 2005; Reebs 2000; Swaney et al. 2001) or habitat sites (Franks et al. 2002). An example of sharing information regarding food sources comes from the strongly gregarious golden shiner fish (*Notemigonus crysoleucas*). Individuals were trained on the location of a food source and when these experienced individuals were placed in a shoal of naïve fish they would lead the shoal to food (Reebs 2000). This is thought to occur through social facilitation of foraging movements or by obtaining following behaviour (Reebs 2000). In the context of habitat choice one of the most popular examples of leading a group is the “waggle dance”, which is performed by honey
bees (Franks et al. 2002). Scout honey bees use the waggle dance to inform conspecifics about the distance and direction to a potential new nest site (Franks et al. 2002).

Different types of leadership can occur. Often leadership is shared and some groups rely on “distributed leadership”. Examples are seen in white-faced capuchins (*Cebus capucinus*) (Meunier et al. 2006) and brown lemurs (*Eulemur fulvus fulvus*) (Jacobs et al. 2008), where several individuals are responsible for the movements of the group. Alternatively, important experience may come with age and/or dominance (Able & Bingman 1987; Couzin & Krause 2003; Couzin et al. 2005; Faria et al. 2010; Jacobs et al. 2008; King et al. 2009; Krause & Ruxton 2002) and leadership may belong to the highest ranking or the oldest and most experienced member of a social group (Bonanni et al. 2010). Elephants (*Loxodonta africana*) have matrifocal social structure and in this society the oldest females, or matriarchs, are fundamental to the group (McComb et al. 2001) often acting as leaders (McComb et al. 2011). Likewise, in the dwarf mongoose (*Helogate parvula*) decision making regarding foraging initiation, travelling path taken, travelling duration and the choice of resting sites is dictated by the breeding and dominant female (Rasa 1987). In mountain gorillas (*Gorilla gorilla beringei*) initiation of group movements falls to the alpha male (Schaller 1976). In homing pigeons (*Columba livia*) less experienced individuals will usually follow more experienced ones (Flack et al. 2012). Aside from age or dominance leadership may also be taken by individuals with different physical attributes. For example, in the strongly gregarious golden shiner fish leadership positions are usually occupied by larger fish regardless of whether large or small fish have superior knowledge about food sources (Reebs 2001). In contrast, research on ants (*Camponotusja ponicus*), which assumed that the most active individuals initiating nest building were leaders, showed that the majority of leaders were smaller individuals whilst larger ants tended to occupy follower roles (Chen 1937).
Leadership is often not stable and may be temporarily occupied by the most suitable individual. In meerkats (*Suricata suricatta*), who do not food share, individuals forage cohesively and frequent changes in leadership occur depending on individual knowledge of food resources (Bousquet & Manser 2011).

Leaders may arise if they have one or more of the following traits: 1. if they are in possession of certain information which others do not have (Johnstone & Manica 2011; Sumpter 2006). 2. If they have more confidence in their own knowledge than the knowledge of their conspecifics (Conradt et al. 2009; Flack et al. 2012). 3. If the benefits of moving the group by inflicting their preferences on conspecifics outweigh the costs of staying in one place (Johnstone & Manica 2011). Decision making depends on both social interactions within the group and assessment of environmental opportunities (Amé et al. 2006). Leaders will only emerge when others are willing to follow. Therefore individuals that are too committed to their own cause may increase the risk of fragmentation of the group (Bousquet & Manser 2011; Conradt et al. 2009). Fragmentation of a group is generally disadvantageous to social animals (Krause & Ruxton 2002) as they lose the benefits of group living (see Chapter I). Many animals can remain in cohesive groups even when their needs differ. Theoretical work has shown that individuals will often “lead according to need” (Conradt et al. 2009). Further experimental work using pairs of fish has shown where there is conflict of interest individuals may take it in turns to lead the group. This has been shown in the three-spined sticklebacks (*Gasterosteus aculeatus*), however it is unclear how these conflicts are resolved in groups larger than two (Harcourt et al. 2010). There are trade-offs to consider when initiating group movement. There is a chance that the group might fragment if the followers needs do not match the leaders and fragmentation comes with a loss of the benefits of group living (Conradt et al. 2009; Krause & Ruxton 2002). Animals will often “lead according to need”
where individuals in want of a certain resource will risk fragmentation of the group by taking on the role of a leader. An example of this is seen in shoals of juvenile roach (*Rutilus rutilus*) (Krause et al. 1992) and in mixed shoals of roach and chub (*Leuciscus cephalus*) (Krause 1993b) where individuals deprived of food will position themselves at the front of the group and as a result will have a greater control over the direction of group movement.

The advantage of becoming a group leader is having control over the timing, distance and direction of a moving group, ensuring that the leaders own needs are met (Fischhoff et al. 2007). Where there are leaders there also need to be animals willing to follow. In the three-spined sticklebacks shy fish are more faithful followers than bold fish. Harcourt et al. (2009a; 2009b) suggest that leadership may be reliant on individual personality differences which are reinforced by social feedback. Followers’ behaviour is often determined by the nature of their social bonds to the leader, particularly in species where reaching agreement regarding decisions is not shared equally among members (Bonanni et al. 2010). There are costs associated with becoming a follower particularly if there are conflicts of interest between leaders and followers. However, animals will continue to follow despite any potential costs when the long-term benefits derived from social or genetic associations outweigh the short-term costs of complying with the leaders present decision (King et al. 2008). There are also associated costs of leadership. Spatial positioning within a group is known to significantly impact the probability of attack (Morrell et al. 2010). This has been shown in fish shoals where in 82% of successful predation events it was the lead fish that was attacked (Bumann et al. 1997). Further field studies on baboons have shown that the highest ranking male is most often the one to lead the group to new foraging areas. Where the group encounters a predator it is the highest ranking males that meet it first (Janson 1990a; Janson 1990b; Rhine
& Westlund 1981). As previously discussed there are also considerable benefits of leading a group particularly for increased foraging opportunities (Bumann & Krause 1993b; Conradt et al. 2009; Fischhoff et al. 2007). Therefore both leadership and following are adaptive strategies and the optimal strategy may differ among individuals. Whether or not an individual takes up a lead position is often a trade off between predation risk and food intake, so is likely to be motivated by their current nutritional state (Krause 1994). This has been shown in field studies on fish where starved individuals more often occupy front positions within the shoal, whereas fed individuals will take up more central positions (Krause 1993a; Krause 1993b). Likewise, plains zebras have been shown to lead the group more frequently when they are lactating and their nutritional needs are greater (Fischhoff et al. 2007).

Currently little empirical data are available for characterising the roles individuals play in producing collective behaviours (Bousquet & Manser 2011; Conradt et al. 2009; Flack et al. 2012). In the present study I recorded patterns of leadership based on spatial position in travelling groups (Bonanni et al. 2010) in an endangered resident killer whale (Orcinus orca) population. Killer whale social systems are highly structured and there is no dispersal by males or females from the maternal group resulting in a matrifocal society (Bigg et al. 1990). Males can live into their fifties whereas females can reach 100 years of age (Olesiuk et al. 1990), despite reproductive senescence occurring in their thirties and forties (Bigg et al. 1990). I explore leadership in killer whale society at two levels; firstly I look at the level of the matriline. Secondly I explore leadership at the individual level. At both levels I answer several questions. At the level of the matriline I aim to determine whether attributes of the whole group impact leadership. Specifically I will look at whether matriline size, average age within the matriline or sex ratio impact leadership. I also investigate how leadership is distributed within a matriline by exploring the coefficient of variation of leadership score.
within matrilines. In the second part of this chapter I explore leadership at the individual level. I aim to determine which sex more often leads the group whether there is a correlation between leadership and age and whether an individual’s position within the social network impacts their leadership. I predict that due to the extreme longevity of female killer whales (male maximum lifespan: ~56 years, female maximum lifespan: >90 years) (Olesiuk et al. 1990) they will have opportunities to acquire superior ecological knowledge. Such knowledge may include salmon migration patterns and prime feeding sites. Therefore these older individuals will be the most suitable animals to act as leaders within the group. This has previously been observed in elephants where the oldest females have the greatest knowledge of predation threats and will usually act as leaders (McComb et al. 2011). Finally I look at how leadership differs with energetic requirements, specifically, differences in individual leadership scores when females are lactating and when they are not. I predict that as female killer whales require up to 42% more food when lactating (Williams et al. 2011) they will have greater motivation to lead the group to find new food sources (Conradt et al. 2009).

4.2. METHODS

4.2.1. Data collection

During the summer months, coinciding with the chinook salmon (*Oncorhynchus tshawtscha*) runs (Ford & Ellis 2006; Hanson et al. 2010), the southern resident killer whale population is regularly seen around the southern end of Vancouver Island. From 1976-2010 this population has varied in size from 70 to 99 individuals (Balcomb et al. 1982; Bigg et al. 1990; Ellifrit et al. 2010). Association data were collected from the 26th of August 2001 until the 31st of July 2009. The survey effort totalled 3806 hours, 42% of which was in the presence of southern resident killer whales. During this time approximately 751 hours of video footage was
collected from boats (9m trimaran and 5.5m Boston Whaler) during conditions suitable for photo identification, i.e. not raining and relatively flat sea state (less than Beaufort 4) or from the shore of San Juan Island, USA. When observing killer whales digital video footage was collected by trained staff from the Center for Whale Research. Video footage was edited and cut into separate clips which were sections of footage showing a complete group of whales.

Figure 4.1. A group as defined by the chain rule where individuals with a distance of less than 3 body lengths between them are assumed to be associating. As long as the distance between individuals a and b are less than 3 body lengths apart and the distance between individuals b and c is less than 3 body lengths apart all three animals (a, b and c) are assumed to be part of the same group (figure adapted from Croft et al. 2008).

Groups were defined as two or more animals in close physical proximity within approximately 3 body lengths of any other group member (using the chain rule) (Croft et al. 2008) (figure 4.1) and travelling in the same direction (plate 4.1) at the same speed (Gero et al. 2008). Every attempt was made to capture entire groups of animals. Individuals in the video footage were identified starting from the front and continuing to the back of the group. As killer whales spend the majority of their time below water (Wiles 2004) leadership was established when they came to the surface to breathe. Individuals positioned at the front of a
travelling group were recorded as leaders (Bumann & Krause 1993a; Harcourt et al. 2009a) on one or more surfacing, all other whales were classified as followers. This was chosen as the definition of a leader because previous work on fish shoals has shown that front individuals are most often responsible for leading collective movements (Bumann & Krause 1993b). This assumption is further supported by theoretical models which have shown that front individuals have greater tendencies to lead the group and initiate new movements than rear individuals (Huth & Wissel 1992).

Individual killer whales were identified by differences in fin shapes, saddle patches and the presence of any nicks or scratches. The sex was determined by distinct pigmentation patterns around the genital slits (Ford et al. 2000).

Plate 4.1. Representation of the definition of leaders and followers. The front whale (J28) is considered to be the lead whale in this group the follower whales are J31, L77, L25, L94 and L22. Please note this image is for explanatory purposes only and the actual data were collected from video footage showing complete groups of whales.
4.2.2. Matriline leadership scores and matriline characteristics

To determine the role of different matrilines in leadership I assumed the matriline of the first whale as the lead matriline and all other whales belonging to other matrilines were considered follower matrilines. Only the front whale from each matriline was included in the analysis. I calculated a matriline leadership score based on the similar work on dogs by Bonanni et al. (2010). To ensure matrilines were not over represented as leaders or followers they were only recorded a maximum of once (for each leader and follower) on a given day. If they appeared in more than one clip individuals could still only be recorded once as a leader and once as a follower on a given day. Sampling period was set to day because often limited time was spent in the presence of a particular group and the amount of data collected during smaller sampling periods, e.g. per hour, was too small. When in a travelling group southern resident killer whale matrilines rarely had members from other pods of matrilines joining them. However, over a period of days new group compositions were observed. Therefore I decided recording leadership on a weekly or monthly basis would not give the resolution needed for accurate analysis of the data. For each matriline I divided the total number of days a matriline was in a leader position by the sum of the total number of days it was seen behaving as a leader or a follower. The value for leadership score ranged from 0-1 where 0 indicates that the matrilines were never seen leading and 1 means they were always acting as leaders. This method controlled for sampling bias (i.e. matrilines not seen as frequently in the study).

I then used a chi-squared test to examine whether the matriline leadership scores differed to that which would be predicted by chance, based on the number of days different matrilines were seen. I used a Spearman’s rank correlation to explore whether there was a correlation between matriline leadership score and matriline attributes. Specifically I looked at
correlations between matriline leadership score and average age of the matriline, matriline size and sex ratio in the matriline.

4.2.3. Leadership within the matrilines

To examine how leadership was distributed among individuals within matrilines I calculated the coefficient of variation in leadership score within each matriline. The coefficient of variation is a measure of the ratio of the standard deviation to the mean and it is useful for comparing the degree of variation from one data series to another, even if the means are drastically different from each other. Therefore it was an appropriate technique to investigate variation in leadership scores within matrilines. Specifically I looked at the coefficient of variation in relation to three different matriline attributes; mean age, sex ratio and group size.

4.2.4. Leadership score and individual characteristics

To examine the relationship between leadership and attributes (age and sex) in individuals I identified the leader of each group from video footage (see above). To ensure individuals were not over represented as leaders or followers they were only recorded a maximum of once (for each leader and follower) on a given day. Therefore if they appeared in more than one clip they could only be recorded a maximum of two times (once as a leader and once as a follower) on any given day. I then calculated a leadership score for each individual, using the methods of Bonanni et al. (2010). As with matrilines for each individual whale I divided the total number of days it behaved as a leader by the total number of days it acted as a leader or a follower. This controlled for sampling bias (i.e. individuals not present for the entire study or not seen as frequently).
A one-way ANOVA was used to test for differences in leadership between the sexes. Next, using a Spearman’s correlation I investigated the relationship between individuals’ maximum age at the end of the study (or at death) and leadership for both males and females. I used maximum age at the end of the study (or at death) as the data were compiled over the entire study period. Additionally, as young animals are known to usually follow their mothers (Bigg et al. 1990) all juveniles (classified as pre-reproductive individuals younger than 12 years (Olesiuk et al. 1990)) were removed from the analysis.

4.2.5. Leadership score and energetic requirements

Finally I determined the effect of lactation on leadership in females. Start of lactation was assumed on the first day a female was seen with a new calf and continued for 18 months (or until the death of the calf if it died before it reached 18 months). Calves are known to solely nurse for the first year then will continue to take milk with some solid foods for up to two years (Olesiuk et al. 1990). Outside of this time females were recorded as not lactating. Leadership score was calculated as previously described for the periods when females were lactating and when they were not. Dependent calves (<18 months) were removed from the analysis to ensure that they did not bias the data (Olesiuk et al. 1990). To ensure sufficient data on individuals, individuals had to be observed during lactation a minimum of 7 times to be included in the analysis [all individuals that were observed 7 times whilst in lactation were observed >20times outside of lactation]. I compared leadership scores for the same individuals during periods of lactation and non-lactation using a Wilcoxon signed rank test (due to a small sample size).
4.4.6. *Leadership score and network position*

It is well documented that resident killer whales will preferentially travel in their family groups (Bigg et al. 1990) and as in chapter III I quantified the finest scale associations occurring both within and between these groups. To determine whether there was a relationship between leadership score and network centrality I used surfacing data collected from videos to define fine scale associations. Animals surfacing synchronously or successively, within one body length, were assumed to be associating. I quantified the social structure of the southern resident killer whale community using a network approach. I used tnet (Opsahl 2009) in R to calculate centrality scores and weighted the analysis to take into account the strength of associations. Specifically, I calculated Freeman’s betweenness and degree (Freeman 1979). Betweenness assesses the importance of an individuals’ position in linking the network. Degree is the number of associates an individual is linked to. Data were compiled over the entire study period to ensure a large enough sample size. Although it is likely that centrality does not remain stable over time, by compiling the data I could look at centrality on a broad scale. Finer resolution in the data would be needed to calculate centrality on a daily, weekly or annual basis. I determined the relationship between these centrality measures and leadership score, in both sexes, using a partial correlation which controlled for age.

4.3. *RESULTS*

From the 26th of August 2001 until the 31st of July 2009 105 individuals (55 females, 43 males and 7 gender unknown) were recorded belonging to 19 different matrilines (labelled A-U). Two matrilines (G and L) died out before the 26th of August 2001. Association data
collected during this time was used to explore the leadership within the southern resident killer whale community.

4.3.1. Matriline leadership scores and group characteristics

There was a large amount of variation in the number of days a matriline was observed leading (mean number of observations ± SD: 26 ± 16.02) or following (mean number of observations ± SD: 39 ± 22.34). This was controlled for by calculating proportional leadership scores of the matrilines. There was also variation in matriline leadership scores (0.38 ± 0.07); matriline P had the highest leadership score (0.45), followed by E (0.44), D (0.43) and H (0.43). Matrilines Q (0.17), U (0.24) and I (0.28) had the lowest leadership scores. Observed leadership scores differed significantly from scores expected by chance ($X^2 = 177.615$, d.f. = 18, $P<0.001$ figure 4.2a and 4.2b). This significance was not an artefact of sampling bias as I controlled for the number of times an individual had been observed in the calculation of leadership scores. This shows that leadership score differs between matrilines, with specific matrilines taking up the leading position more often than would be expected by chance.
Figure 4.2. (a) The leadership score defined as the proportion of days matrilines were in leader (blue) or follower (red) positions. (b) the total number of days matrilines were observed as leaders (blue) or followers (red).

There was a slight positive correlation between leadership score and matriline size which was not statistically significant ($R_s=0.329, N=19, P=0.168$) (figure 4.3a). This suggests that larger matrilines are more often at the front of the travelling group, however, it is not statistically
significant. There was also a non significant positive correlation between average age in the matriline and matriline leadership score ($R_s=0.208, N=19, P=0.392$) (figure 4.3c) with older matrilines more often leading. There was a significant positive correlation between the proportion of females in the matriline and leadership score ($R_s=0.530, N=19, P=0.020$) (figure 4.3b). This shows that matrilines with more females are more often at the forefront of collective movements.

Figure 4.3. The relationship between matriline attributes and leadership score (a) The relationship between matriline size and leadership score. (b) The relationship between mean age of matriline and matriline leadership score. The outlying matriline contains only one individual. (c) The relationship between the proportion of females in matriline and matriline leadership score.
4.3.2. Leadership within the matrilines

How leadership was distributed within matrilines was explored using the coefficient of variation of leadership score. This showed a significant relationship between the coefficient of variation of leadership score within the matriline and average age of the matriline ($R_s = -0.739, N=17, P<0.001$) (figure 4.4), the matrilines with an older mean age having a lower coefficient of variation. This could imply that matrilines which contain older individuals may have a more evenly distributed leadership among individuals within the matriline. The correlation between coefficient of variation and group size ($R_s = 0.413, N=17, P=0.099$) and sex ratio ($R_s = -0.064, N=17, P=0.808$) was not statistically significant. However, there was a positive trend for an increase in coefficient of variation in leadership score within groups with an increase in group size.

Figure 4.4. The relationship between coefficient of variation in leadership score within a matriline and average age of the matriline
4.3.3. Leadership score and individual characteristics

I explored leadership between the sexes and showed that male and female leadership scores differed. Females had a significantly higher leadership score than males ($F_{(1,98)}=39.56$, $p<0.001$) (figure 4.5). This result shows that females are more often at the forefront of collective movements than males.

![Figure 4.5. Male and female leadership scores. Graph shows the mean leadership score ± one standard deviation.](image)

In addition to females having higher leadership scores than males there was also a significant positive relationship between leadership score and individual age when all individuals were included, regardless of sex. Older individuals had higher leadership scores than younger ones ($R_s=0.918$, $N=105$, $P<0.001$, figure 4.6). When the analysis was split by sex and individuals
of unknown sex removed from the analysis the relationship between leadership score age was still highly significant in both females ($R_s=0.840$, $N=56$, $P<0.001$) and males ($R_s=0.825$, $N=43$, $P<0.001$). Overall this shows that despite females having a higher leadership score in both males and females older individuals are more likely to act as leaders.

To ensure the significant result was not being driven by a large number of immature individuals with very low leadership scores I removed animals under the age of 12 years from my analysis. In spite of this I still found significant positive results for the relationship between leadership score and age ($R_s=0.831$, $N=71$, $P<0.001$). This remained true for when individuals were categorised by sex. The relationship between male age and leadership score remained significant ($R_s=0.684$, $N=24$, $P<0.001$) and likewise for females ($R_s=0.721$, $N=47$, $P<0.001$).

Figure 4.6. Positive relationship between age and leadership score in southern resident killer whales in both females (x) and males (o).
This shows that leadership is not being driven simply by dependent and immature offspring following their mothers.

4.3.4. Leadership score and energetic requirements

To explore whether energetic requirements impacted an individual’s motivation to lead the group I used leadership data from females both when they were lactating, and when they were not. I determined that energetic requirements can also impact an individuals leadership motivation. All females observed lactating and not lactating during the study period (n = 6) had a higher leadership score whilst lactating (figure 4.7). Further analysis revealed that this result was significant and lactating females had a significantly higher leadership score than non-lactating females (Z=-2.201, N = 6, P=0.028, figure 4.8). I further tested the data using an ANOVA to ensure that this was not a factor of lactating females being older (F(1)=1.214, P=0.271). As females require up to 42% more food when lactating (Williams et al. 2011) and all individuals used in the analysis showed a higher leadership score during this time I suggest that the greater need for food increases a females motivation to lead the group.
Figure 4.7. Paired data showing female leadership score when they are lactating and when they are not.
4.3.5. Leadership score and network position

Finally, I tested leadership score in relation to individual’s network position. I found no significant relationship between leadership score and either betweenness or degree when all individuals of known sex were included in the analysis ($R_s=0.081$, $N=98$, $P=0.428$ and $R_s=0.081$, $N=98$, $P=0.190$ respectively). When I split the analysis by sex the same patterns were found within each sex (males: $R_s=-0.206$, $N=43$, $P=0.196$ and $R_s=-0.021$, $N=43$, $P=0.899$, females: $R_s=0.156$, $N=55$, $P=0.256$ and $R_s=0.094$, $N=55$, $P=0.495$ respectively).

Figure 4.8. Leadership score when females are lactating and not lactating. Graphs show median, upper and lower quartiles and range of data.
(figure 4.9 and figure 4.10). This suggests that the network position an individual holds does not impact their leadership score.

Figure 4.9. The relationship between leadership score and betweenness in females (x) and males (o).

Figure 4.10. The relationship between leadership score and degree in females (x) and males (o).
4.4. DISCUSSION

In Chapter IV I explored the attributes of both leading matrilines and leading individuals in an endangered population of killer whales. The aim was to explore whether specific matrilines or individuals led the group more than would be expected by chance. I also wanted to investigate the attributes of these leaders to observe whether there was a correlation between leadership and a particular attribute. Firstly I looked at matriline leadership. All matrilines occupied both a leading and following position, however the extent to which they held this position varied considerably between matrilines. The results showed that there was a significant positive correlation between matriline leadership score and ratio of females to males within the matriline, with matrilines containing more females having a higher leadership score. However, matriline leadership score did not significantly correlate with matriline size or mean age. Next I investigated the distribution of leadership scores within the matrilines using the coefficient of variance. I found a significant correlation between mean age of the matriline and the coefficients of variance of leadership score suggesting that leadership was more equally distributed in matrilines that had an older mean age.

After determining the attributes of leading matrilines I focused at the level of the individual. Overall females had significantly higher leadership score than males. However, both males and females showed a significant positive correlation between age and leadership score. There was no statistically significant correlation between leadership score and betweenness or leadership score and degree. These results provide evidence that older females take the most active role in leading groups of killer whales. Further to this I showed a difference in individual leadership score when females were lactating and when they were not. I suggest that the greater need for food during lactation motivates these females to lead the group more
frequently. This suggestion concurs with the work of Conradt et al. (2009) who propose that individuals will “lead according to need”. These findings are discussed in more detail in the following sections.

4.4.1. Matriline leadership scores and group characteristics

Previous work has shown that in animal groups consisting of several related subgroups some subgroups may have a disproportionately large impact on the overall movements of the whole group. This may be a direct result of different groups having different needs which may alter their motivation to lead the group. For example, in zebras (*Equus burchelli*), small family groups with a high number of lactating females will more often initiate movement of the whole herd than those without (Fischhoff et al. 2007). This occurs to ensure that groups with lactating females are the first to reach a water supply ensuring they have ample drinking opportunities. Similarly, the southern resident killer whale population forms highly stable matrifocal social groups and several matrilines will often travel together (Bigg et al. 1990). Within these pods I found that different matrilines spent a greater proportion of time leading the group than others. I suggest that where members of different family groups travel together specific matrilines or individuals may have a larger influence on group movement (Deaner et al. 2005; King & Cowlishaw 2009). Where the sex ratio in the group was female biased the group had a higher leadership score. As with zebras (Fischhoff et al. 2007) this may be a result of lactating females in the group having higher energetic requirements. Similar findings have been shown in white-handed gibbons (*Hylobates lar*) where groups with females will more often initiate the movements of the whole troop. As females with long gestation and lactation periods have higher reproductive costs this can translate into an increased motivation to lead the group (Barelli et al. 2008). I propose that a similar mechanism
underpinning matriline leadership in the southern resident killer whales is occurring as females have much higher reproductive costs than males (Bigg et al. 1990). Groups containing more females may have higher energetic requirements than those with fewer and therefore the matriline may have a greater motivation to lead others. Once the matriline leadership had been established I explored how leadership was distributed within a matriline.

### 4.4.2. Leadership within the matrilines

When exploring the relationship between leadership score and mean age of the matriline older matrilines had lower variation in leadership scores. If I assume that older killer whales possess superior ecological knowledge, as occurs in humans (van Vugt 2006) and elephants (McComb et al. 2011), maybe if there are more older individuals within a matriline (resulting in an older mean age) the matriline will have such superior ecological knowledge. In some species such as elephants (McComb et al. 2011), dwarf mongoose (Rasa 1987), mountain gorillas (Schaller 1976) and homing pigeons (Flack et al. 2012) a single dominant individual is responsible for the movements of the group. In contrast, the coefficient of variance I find suggests that killer whales may provide an example of a more distributed leadership occurring within the matriline. In groups with distributed leadership decision making is often shared between several individuals, examples of this are seen in white-faced capuchin monkeys (Leca et al. 2003; Meunier et al. 2006) and brown lemurs (Jacobs et al. 2008). I suggest that in older matrilines leadership becomes distributed amongst several members. However, to understand this further I looked at leadership on an individual basis.
4.4.3. **Leadership and individual characteristics**

In most cases individuals in a group will belong to different age and sex classes and are therefore likely to have different needs at different times yet the group must still remain cohesive (Jacobs et al. 2008). I found a significant relationship between individual attributes (age and sex) and leadership score. In both males and females there was a positive correlation with age and older individuals of both sex had higher leadership scores than younger animals. This could be explained in part by the stability seen in resident killer whale matrilineal groups (Bigg et al. 1990) permitting habitual leader follower relationships to develop (Chase et al. 2002; Fischhoff et al. 2007; Goessmann et al. 2000). Some individuals within the group are likely to possess superior ecological knowledge or specific skills and these individuals have a higher chance of becoming a leader than those without (Flack et al. 2012; King et al. 2009). The positive correlation between age and leadership in both sexes in the killer whales has also been documented in other species including humans (van Vugt 2006) and elephants (McComb et al. 2011) especially in areas that require specific knowledge. Removing immature individuals (pre-reproductive, under 12 years (Olesiuk et al. 1990)) from the analysis did not affect the relationship between leadership score and age.

Females had significantly higher leadership scores than males this may be as a result of the increased longevity seen in females. However, this result is unlikely to be influenced by the fact that offspring will often travel behind their mothers (Bigg et al. 1990) as removal of these individuals (<12 years old) from the analysis still resulted in a strong positive relationship between age and leadership score in both males and females. In other species the dominant or older females also act as leaders. For example, ruffed lemurs (*Varecia variegata*) that form stable groups are usually led by a dominant female (Overdorff et al. 2005). The
older females in these groups are thought to be motivated to lead the group to ensure they are first to arrive at a food source and hence have a higher food intake (Overdorff et al. 2005). At this stage it is unknown whether killer whales travelling at the forefront of collective movements have a greater food intake, this would be worth exploring in future research. Another explanation for older females more often acting as leaders may be similar to that of elephants. McComb et al. (2011) provide results illustrating how the knowledge acquired by the oldest females over time effects the anti-predator responses of the group as a whole. Although killer whales have no natural predators (Ford et al. 2002), older females may have acquired superior ecological knowledge regarding food sources or migration routes which I suggest makes them better leaders. In contrast to resident killer whale society, males most often emerge as leaders in primate society; again, this occurs in relation to prioritising their food intake. A study with wild baboons supports this where the alpha male arrives first on a food patch and will monopolise it (Hogan et al. 1994; King et al. 2009). Again, in contrast to the resident killer whales, in human society, male leadership is still custom in most societies probably due to the fact that psychological tests have shown that males have higher self confidence and dominance than females (King et al. 2009; van Vugt & Spisak 2008). However, in western human society, leading a group is unlikely to result in monopolisation of food resources, so we cannot rule this out. I explore this in killer whales by investigating the relationship between energetic requirements of females and their motivation to lead the group.

4.4.4. Leadership score and energetic requirements

The results I present support the hypothesis that individuals “lead according to need” (Sueur et al. 2010) with females having a higher leadership score when they are lactating. Lactating
females require up to 42% more food in comparison to when they are not lactating (Williams et al. 2011). Thus the relationship between leadership and lactation may be a result of females having a greater need for resources to ensure the survival of their offspring and to meet their own energetic requirements. As these resident killer whales do not cooperatively forage (Ford et al. 2002) it would not be beneficial for females with greater energetic requirements to rely on those better at finding food. Like killer whales, plains zebras also form two tier social organisation, with several tightly bonded harems forming loosely bonded herds. Their movement is usually initiated by lactating females. This occurs to ensure these females are the first to arrive at a water source which is particularly important when water is scarce (Fischhoff et al. 2007). Similarly lactating African buffalos (*Syncerus caffer*) will often lead the group ensuring they receive enough food (Prins 1989). However, in contrast female chacma baboons (*Papio hamadryas ursinus*) that were lactating were less likely to initiate group movement than females that were not lactating. Leadership decisions seemed to be shared amongst males rather than females (Stueckle & Zinner 2008). This may occur because lead individuals also experience greater predation risk (Janson 1990a; Janson 1990b; Rhine & Westlund 1981) hence lactating females might protect their young by positioning themselves nearer the middle of the group. The position an individual takes within a group will also impact its centrality.

4.4.4. Leadership score and network position

Social network metrics are a powerful tool for analysing social structure to the level of the individual (Prins 1989). Unlike the strong relationships between leadership score and age, sex or energetic requirements (lactation state) I found no significant correlation between an individual’s position in a network and the likelihood that they would emerge as group
leaders, either with the data combined for both sexes or split by sex. This finding is surprising, as recent work on other species suggests that the extent to which individuals act as leaders and followers is closely related to the social network structure. This is seen in a variety of social animals. Such examples include elephants who were well connected, such as matriarchs, most frequently led the herd (McComb et al. 2001). In ravens (Corvus corax) those that occupying the most central position in the roost often act as leaders (Wright et al. 2003). In a population of rhesus macaques (Macaca spp) the older or more dominant males were often the ones at the front during group movement and in addition these individuals also possessed the highest centrality scores (Prins 1989). The results of the current study may differ due to our definition of leadership. In the present study, I define leaders by their relative position and speed in relation to the group (Faria et al. 2010) and individuals at the front of the group were considered to act as leaders (Bumann & Krause 1993a; Kiflawi & Mazeroll 2006). I suggest that being at the front of the group may result in lower centrality scores than those at the centre. Further work needs to be done to explore the ways in which a specific killer whale can lead the group. It would be beneficial to this study to investigate whether individuals situated nearer the centre of the group can also act as leaders by using acoustic cues (which can travel up to 10km (Miller 2006)). However, to date, the there are no such data available on this.

In a social population such as the southern resident killer whales it is important to understand how group cohesion is facilitated as this will give us knowledge of the importance of different individuals to the decision making of the whole group. Social constraint impacts must be acknowledged with regard to their critical roles in group decision making (Prins 1989). Understanding this is vital when designing effective conservation and management.
plans which is particularly important when dealing with an iconic population of animals, such as the southern resident killer whales.

Here, in Chapter IV, I have quantified leadership and shown that older individuals, usually females, will more often occur at the forefront of travelling groups. In the final data chapter (V) I begin to look at how interactions between individuals can impact survival. Particularly I focus on mother offspring relationships.
Chapter V.

An adaptive benefit of a mother’s prolonged lifespan in killer whales (*Orcinus orca*)
ABSTRACT

The evolution of a prolonged post-reproductive lifespan has attracted considerable interdisciplinary attention; primarily because of the long post-menopausal lifespan seen in humans. Across non-human species females rarely have a lifespan that extends beyond their last parturition. Female killer whales (*Orcinus orca*) are an exception to this and although reproduction ceases in their thirties and forties they can survive well into their nineties. Two mechanisms have been proposed to underpin the evolution of such an extended female post-reproductive lifespan: i) an epiphenomenon of increased longevity, in which evolutionary benefits accrue only during the reproductive phase with no additional fitness benefits after the last reproductive event and ii) an evolved adaptation in which post-reproductive lifespan increases the survival of an individual’s genes, increasing its inclusive fitness. There is currently little evidence that prolonged post-reproductive lifespans are adaptive in non-human animals. In this chapter I test the hypothesis that a prolonged lifespan in female killer whales is an adaptive benefit in which they insure the increased survival of their own genes through the mating success of their offspring. I approach this in two ways. Firstly, I examine the pattern of social interactions between mothers and their offspring in the southern resident killer whale population (1996-2010). Interestingly there were sex differences in these patterns with sons attaining significantly stronger bonds with their mothers than daughters. Secondly using multi-generational demographic records (1974-2010) from both the southern and northern resident populations I examine the consequences of the loss of a mother for offspring survival. Regardless of reproductive status mothers increase the survival of their offspring, however this effect was strongest for older sons. For male offspring less than 30 years old the mortality risk increases by 3.1 times in the year following their mother’s death. For males over 30 years of age this risk increases to 8.3 times. In contrast, female offspring under 30 years of age show no increase in mortality risk following the death of their mother.
Whilst daughters over 30 years of age show a small increase in mortality risk (2.7 times) in the year following their mother’s death. Additionally, for offspring over thirty years the death of a post-reproductive mother resulted in a 13.9 fold increase in mortality risk in sons and a 5.4 fold increase in mortality risk in daughters in the year following their mother’s death. Theory based on kinship dynamics predicts that old mothers maximise their fitness by ensuring their offspring’s survival and reproductive success. There is an asymmetry however in the benefits of helping sons and daughters. Mating occurs outside of the matriline thus a son’s offspring are raised by another group (where any rearing costs are incurred). Whereas a daughter’s offspring are raised within the group increasing within-group competition. I suggest that my findings in Chapter 5 provide support for the hypothesis that mothers can therefore maximise inclusive fitness benefits by directing care towards sons.
5.1. INTRODUCTION

The evolution of a post-reproductive lifespan has attracted considerable interest across a range of disciplines, primarily because of the long post-menopausal lifespan seen in humans (Cant & Johnson 2008; Kachel et al. 2011; Lahdenperä et al. 2004). Cohen (2004) provides a review of post-reproductive lifespans in mammals. He reviewed 47 different species from eight orders and found that 83% of these showed some evidence of post-reproductive lifespans. A post-reproductive lifespan is defined as “the time between age at reproductive cessation and age at death living beyond reproductive cessation” (Cohen 2004). To correct for the fact that not all organisms die whilst giving birth to their last offspring Caro et al (1995) consider reproductive cession to have occurred once one inter-birth interval has passed since the last reproductive event. Of the 47 species surveyed by Cohen (2004) 38 had some evidence of a post-reproductive lifespan. The majority of these post-reproductive lifespans were short and extended only as long as the young were dependent on maternal care (Kachel et al. 2011). However, three exceptions to this were; short-finned pilot whales (Globicephalus macrorhyncus), killer whales (Orcinus orca) and humans who all showed an extensive post-reproductive lifespan (mean post reproductive lifespans: pilot whales 14 years (Kasuya & Marsh 1984), killer whales 30+ years (Olesiuk et al. 1990) and humans 21-30 years (Hill & Hurtado 1996)). In human women the post-reproductive lifespan is considered to be an adaptive benefit of ageing, as post-reproductive females can make a large contribution to the fitness of their children and grand children (Hawkes et al. 1998; Shanley & Kirkwood 2001). Reznick et al (2006) state that “evolutionary theory predicts that an extended post-reproductive lifespan should evolve only when the post-reproductive females can contribute significantly to the fitness of their offspring or relatives”. This can only occur when individuals have extended social networks which allows older females to contribute to the fitness of kin (Hamilton 1966). The female post-reproductive lifespan of humans, killer
whales and short-finned pilot whales extends far beyond the time period that offspring are dependent on their mother (Kachel et al. 2011). It has been suggested that females experience such a post-reproductive lifespan to increase their inclusive fitness through helping kin (Hawkes 2004; Hawkes et al. 1998). This has been demonstrated in humans where mothers who received help from post-reproductive females had healthier offspring. As the new mothers spend a lot more time with their new offspring their foraging ability is reduced whereas the grandmother can continue to forage for the mother (Hawkes et al. 1997). This is known as the “grandmother effect” (Hawkes 2004; Hawkes 2010; Lahdenperä et al. 2004). Lahdenperä et al (2004) use data from a Finnish human population to show that both sons and daughters who had a post-reproductive mother living in the same village had children earlier, had shorter inter-birth intervals and more offspring survived to adulthood. They suggest that the family assistance that is provided by grandmothers is a key factor underpinning human longevity.

The decrease of reproductive function as age increases is common in many mammals (vom Saal & Finch 2005) and according to evolutionary theories of senescence there should be no selection for a post-reproductive lifespan (Peccei 2001). However, selection may have occurred for a post-reproductive lifespan if there were fitness benefits. It may have occurred where there was a greater benefit for females to stop reproducing in earlier life and invest in helping grandchildren, hence this would result in a shortened reproductive lifespan (Peccei 2001).

Where prolonged female post-reproductive lifespans do exist two mechanisms have been proposed to underpin such occurrences: i) an evolved adaptation in which post-reproductive
lifespan increases the survival of an individual’s genes, increasing its inclusive fitness and ii) an epiphenomenon of increased longevity, in which evolutionary benefits accrue only during the reproductive phase with no additional fitness benefits after the last reproductive event. A prolonged post-reproductive lifespan can be adaptive if females increase the survival and reproductive success of their offspring (Hawkes 2004; Hawkes 2010; Hill & Hurtado 1991; Lahdenperä et al. 2004; Peccei 1995; Peccei 2001). Where post-reproductive lifespans are an epiphenomenon either as a result of a physiological trade-off favouring efficient reproduction in the early fertile part of life or the by-product of an increase in lifespan or life expectancy (Peccei 2001). Prolonged post-reproductive lifespans could arise in maternally dependent species where mothers have a post-reproductive lifespan equivalent to the time required to raise the last born offspring (Packer et al. 1998). These two mechanisms are not necessarily mutually exclusive and whether reproductive senescence is a result of selection for early reproduction or selection for a post-reproductive lifespan is hugely challenging to decipher.

Currently, there is little understanding of the adaptive benefits of a prolonged post-reproductive lifespan in non-human animals. Whilst some analysis looking at the relationship between inclusive fitness benefits and prolonged post-reproductive lifespan exist in humans few studies have empirically addressed the question of why such post-reproductive lifespans evolve (Reznick et al. 2006) particularly in non-human animals. Selection for such prolonged post-reproductive lifespans should only occur where there is a direct benefit to fitness (Foote 2008; Reznick et al. 2006). Such a benefit to fitness might be the insurance of the reproductive success of children through the survival and wellbeing of grandchildren. As previously mentioned, currently post-reproductive lifespans have only been observed in 3 species; short-finned pilot whales, killer whales and humans. The striking similarity between these three species is that they all exhibit highly stable social structure which can facilitate
post-reproductive helping (Foote 2008). Mounting evidence in humans shows that post-reproductive females contribute to the reproductive success and survival of their adult offspring hence increasing their own inclusive fitness. This is known as the grandmother hypothesis (Cant & Johnson 2008; Kachel et al. 2011; Lahdenperä et al. 2004). In humans, multi-generational demographic records from populations in Canada and Finland during the 18th and 19th centuries showed that the presence of a grandmother living locally was associated with improved reproductive success in their offspring (Lahdenperä et al. 2004). In contrast, in other species with extended family groups, such as lions and baboons, females only live long enough to care for their last offspring (Packer et al. 1998). The evolution of post-reproductive helping is rare in non-human animals and it is usually younger individuals who act as helpers (Clutton-Brock 2002). However, in some primates (chimpanzees and gorillas) and cetaceans (pilot whales and killer whales) the role is switched and older females may take on a helping role (Kachel et al. 2011; Lahdenperä et al. 2004; Ward et al. 2009b).

In spite of help that new mothers may receive from older females when young are dependent on their mother’s milk they provide a vital resource bond for their offspring (Huang et al. 2009). In addition to this anecdotal evidence also suggests that mothers provide an emotional bond for their offspring (Goodall 1990). The gradual shift towards independence from the mother is known as weaning (Cirulli et al. 2003; Huang et al. 2009) and the mother-offspring bond will usually become weaker during this time. Independence from the mother is often associated with independence from the mother’s milk supply and birth of a sibling (Newberry & Swanson 2008). Bottlenose dolphins (Tursiops truncatus) considerably decrease associations with their young at weaning and independence must be achieved relatively early (Gibson & Mann 2008). Occasionally mother-offspring bonds will be maintained (Newberry & Swanson 2008). For example, ewes maintain associations with their lambs for up to 2.5
years after they are weaned (Lawrence 1990) and beef cows will show a social preference towards their own offspring long after weaning (Veissier et al. 1998).

One way females can increase the survival and reproductive success of their offspring is by forming a strong social bond with them throughout their adult life. This can ensure mating opportunities are gained through social status which can be attained through the mothers rank within the group (East & Hofer 2001). In addition to this females can make sure their grandchildren are provisioned for (Hawkes 2004). Another benefit of maintaining a social bond between a mother and her offspring are increased opportunities for the social transmission of information such as food sources or predation risks (Newberry & Swanson 2008). Such prolonged associations have been observed in elephants where females live in matriarchal societies (McComb et al. 2001; McComb et al. 2011). The suggested benefit of adults remaining with their mother is to utilize the matriarch’s superior knowledge to enhance their own survival potential. These oldest females have been shown to respond more cautiously to predatory threat than younger females (McComb et al. 2001). They will make ecologically relevant decisions in an area critical to their survival and that of their offspring (McComb et al. 2011).

In addition to remaining with a mother exploit their superior ecological knowledge animals can also remain with their mother to enhance their own social status. For example, the strongest bond in two species of primate, the chimpanzee (*Pan troglodytes*) and the bonobo (*P. paniscus*), occurs between a mother and her son (Furuichi 1989; Ihobe 1992; Kano 1982; Kuroda 1979; van Hooff & van Schaik 1994). This is a stark contrast to other primate species where males will usually form lasting coalitions with other males (van Hooff & van Schaik
Male bonobos with dominant mothers have been shown to be able to feed freely within a desired feeding site, allowing them access to the best resources (Furuichi 1988; Kano 1982). In addition to this van Hooff and van Schaik (1994) suggest that in chimpanzees the primary reason for a mother to maintain the bond with her son is to increase her inclusive fitness benefits through promoting her son and ensuring is mating success.

The loss of such a strong social bond has been linked to the health and survival of the surviving individuals. However, at present quantitative evidence is limited to human communities. In human society individuals who have consistent social bonds will often have interdependent health (Rostila & Saarela 2011). For example, the “widowhood effect” occurs in humans where the death of a spouse negatively impacts the survival of the partner (Boyle et al. 2011; Elwert & Christakis 2008; Schwarz & Seber 1999; Subramanian et al. 2008). More recently, survivorship in humans in relation to loss of a parent, particularly a mother, has been proven to have a larger effect on young children but little impact on adults (Rostila & Saarela 2011). This may occur because a parent is a primary attachment bond for their children whereas adults are more independent (Barak 2006; Rostila & Saarela 2011).

In non-human animals an exceptionally long post-reproductive lifespan is present in female killer whales. A mother will have her last calf in her thirties or forties (Olesiuk et al. 1990), however the oldest female is currently estimated to be over 90 years of age (Ellifrit et al. 2010). As a species killer whales are the oceans top predator feeding on a range of different animals including teleost fish, sharks and rays, cetaceans, pinnipeds, birds, and turtles (Ford et al. 2010). However, different populations of killer whales are incredibly specialised in their prey choice and foraging techniques to a point where it is a limiting factor in their survival
(Ford et al. 2010). Such differences in foraging techniques have led to variation in group dispersion between different populations; an example is seen in the resident and transient killer whale populations around Vancouver Island (Hoelzel & Dover 1991). Residents feed mainly on salmon (Ford et al. 2010) which they rarely share (Baird et al. 1992). This results in a high degree of site fidelity with animals returning to the same area coinciding with the migrating salmon (Ford & Ellis 2006; Olesiuk et al. 1990). With the exception of two isolated incidents (Chapter I) there is no dispersal by either sex from their maternal group (Bigg et al. 1990) and both resident males and females maintain strong bonds with their mothers throughout their lives (Miller & Bain 2000) (plate 5.1).

Plate 5.1. Adult sons, L88 (i, born 1993) and L78 (ii, born 1989), travelling with their post-reproductive mother L2 (iii, born 1960).

In chapter V I explore the differences in strength of association between males and females with their mothers and the effect of a mother’s death on the survival of her offspring in the resident type killer whales. In the absence of dispersal local relatedness increases with female age. Theory predicts that mothers can maximise their fitness by ensuring their offspring’s survival and reproductive success (Johnstone & Cant 2010). Mothers, however, should not
direct their care equally towards adult sons and adult daughters. As mating occurs outside the family group a son’s offspring will be raised by another matriline whereas a daughter’s offspring will be raised within the matriline, hence increasing resource competition. In addition to this, older and larger males have the greatest reproductive success (Ford et al. 2011) therefore it would be beneficial for the mother to produce a large son. Thus I predict that mothers should preferentially direct their care towards male offspring to maximise their own inclusive fitness (Johnstone & Cant 2010). As a consequence of this I further predict that I will find stronger associations occurring between a mother and her sons than mothers and their daughters. I also suggest that this may impact the survival of male offspring. In addition I expect to see a greater decrease in the survival of sons following the mortality of a mother than I would see in daughters. I chose to explore survival rather than reproductive success in individuals as data on the reproductive success of males is limited at present and only data for the southern resident population is available (see Ford et al. 2011). By exploring survival I can greatly increase the sample size and the accuracy and power of the survival model.

5.2. METHODS

Two resident type killer whale populations are regularly observed around Vancouver Island (figure 5.1). The southern resident killer whales occur from the Oregon Coast to the upper Georgia Strait. The northern resident killer whales are usually found from the midpoint of Vancouver Island to south eastern Alaska (Ford et al. 2000). Both populations can be observed year round but are encountered more frequently during the summer months coinciding with the salmon runs (Ford et al. 2010). Firstly I explored the associations in the southern resident killer whale population.
Figure 5.1. The summer range of the northern (red) and southern (yellow) resident killer whales occurring in the inshore waters of Washington State, USA and British Columbia, Canada.

5.2.1. Associations occurring between mothers and their offspring

Association data were collected for the southern resident killer whales from 1996-2010. Association data were obtained by regular observations throughout the year where every individual killer whale encountered was videoed by trained staff using Hi8, DV and HDV recording equipment. Boat based photographic censuses were conducted throughout each year. Sampling was limited to conditions suitable for photo identification e.g. no rain and relatively flat sea state. Individuals were identified by their unique fin shapes and markings and sexed using the pigmentation patterns around the genital slits (Olesiuk et al. 1990) (figure 5.2). During this time southern resident killer whales were encountered on 60.4 ± 13.5 days per year which totalled 1385hrs 33mins of video footage. This totalled 20,829 unique sections showing associations (plate 5.2) of sufficient quality to ensure accurate individual identification. Every individual was identified and included in subsequent analysis, regardless of age or gender.
Figure 5.2. (a) Female and (b) male killer whale pigmentation patterns around the genital slits, visible when the whale breaches or rolls on its back (courtesy of the Center for Whale Research).

Associations were based on surfacing patterns observed from the video footage. If animals surface simultaneously, or immediately one after another (within one body length) they were assumed to be associating (Plate 5.2).

Plate 5.2. (a) J47 and J17 surfacing successively within one body length. (b) J47 and J14 surfacing synchronously within one body length.
Associations between females and their offspring were calculated from 1996-2010 when both were alive using the half-weight index (HWI) (Whitehead 2008). The HWI was used to reduce bias due to sampling techniques (Croft et al. 2008; Lusseau et al. 2006) and to increase the comparability with other cetacean association studies (Bräger et al. 1994; Gero et al. 2008; Lusseau 2003; Lusseau et al. 2006; Möller et al. 2006; Williams & Lusseau 2006).

Where $a$ and $b$ represent two whales $X$ is the number of days $a$ and $b$ were seen associating. $Y_{ab}$ represents the number of days $a$ and $b$ were both observed but in different groups; $Y_a$ represents the days individual $a$ was seen without individual $b$ and $Y_b$ is the number of days individual $b$ was seen but not individual $a$. To allow visual inspection of the social structure networks were constructed in UCINET and Netdraw (Borgatti et al. 2002) for the unfiltered data showing all associations. Next networks were constructed with the data filtered with HWI>0.5 to highlight the strongest associations.

I explore the differences in strength of maternal associations in sons and daughters. To deal with dependencies in the data and to control for group size distributions, demographic effects and sampling bias and to account for autocorrelations in the network data I used a randomisation test to calculate significance (Bräger et al. 1994; Croft et al. 2011; Whitehead 1999). Autocorrelations arise as each individual's associations are not independent; randomising the data allows alternative models to be constructed which can control for such
biases (Croft et al. 2011). Each randomisation was performed on the group-based data using swaps of individuals between groups within each sampling year before calculating a Spearman’s rank correlation for that data for each randomisation. 5000 randomisations were generated with 100 swaps per randomisation. Randomisations were programmed in c++. A one-tailed t-statistic was conducted to explore the hypothesis that males have stronger associations with their mothers than females. After establishing where the strongest associations lie in the southern resident killer whale social network I looked at the impact of the loss of this bond on the survival of individuals.

5.2.2. Offspring survival following maternal death

From 1974-2010 multi-generational demographic records were collected for both the northern and southern resident killer whale populations from boat based surveys and individuals were identified as previously described. Mothers were identified by association patterns and young calves regularly seen in the presence of reproductive females were assumed to be her offspring (Bigg et al. 1990). Recent molecular work has demonstrated that this method accurately identifies mother – offspring relationships in resident killer whales (Ford et al. 2011). Mortality was assumed if an individual did not return with their matriline for a full year (Olesiuk et al. 1990). The death of a whale’s post-reproductive mother is a rare event and, as a result, to ensure an adequate sample size and to increase the statistical power of the model data from both populations were combined. Despite being reproductively isolated the two populations share the same life history traits (Olesiuk et al. 1990). The northern and southern resident killer whale populations consisted of 210 females, 189 males and 190 whales of unknown sex. Post-reproductive females were defined as those over 45 years of age, this estimate is likely to be conservative as the latest a female has been observed
giving birth to a calf was 48, however, this was considered to be exceptionally late (Olesiuk et al. 1990). Ages of the whales born prior 1974 were estimated in several ways (see Ford & Ellis 2002 for full details). Calves in 1974 were aged relative to their size. For juvenile whales in 1974 their age was estimated in reference to the year they became sexually mature. Indirect methods were employed for mature animals in 1974 for females year of birth was estimated from the ages of their offspring and the average age of reproductive cessation. Age of mature males without living mothers was estimated as the latest year the whale could have been born. During the study period (1974–2010) 37 reproductive mothers died and 40 post-reproductive mothers died. 94 males, 41 females and 85 whales of unknown sex with known mothers died during this time. Whilst 73 males, 114 females and 26 offspring of unknown sex with known mothers are still alive in the two populations (data for northern resident killer whales courtesy of John Ford, Cetacean research program, Nanaimo, Canada, data for southern resident killer whales courtesy of Ken Balcomb, Center for whale research, San Juan Island, USA).

A Cox proportional hazards regression analysis was fitted to the combined multi-generational demographic data for both the northern and southern resident killer whale populations. The hazard function was assumed as:

\[
h(t) = h_0(t) \exp \{ \gamma_1 I_{50} g_1(t) + \gamma_2 I_{50} g_2(t) + \gamma_3 I_{50} g_3(t) + \alpha d_{30+} + \beta I_{30+} I_S + \delta I_{mad_{45}} + \eta I_{mad_{45}} I_S \}
\]

where:

- \( h(t) \) = the hazard function \( (h) \) at a particular time \( (t) \)
- \( I_{30+} = 1 \) if the age of the whale at mother’s death is >30 years, and 0 otherwise;
$I_5$ is 1 if the whale is male and 0 if female;

$g_1(t) = 1$ if the whale's mother is alive at time $t$ and 0 otherwise;

$g_2(t) = 1$ if the whale’s mother has died at time $t$, $t_{md} < t \leq t_{md}+t_0$, and 0 otherwise, $t_{md}$ denotes time of mother's death;

$g_3(t) = 1$ if the whale’s mother has died at time $t$ and $t > t_{md}+t_0$, and 0 otherwise; for fixed $t_0$.

$I_{mad>45} = 1$ if the whale’s mother is dead and the mother was older than 45 years at her death.

The parameter values ($\alpha$, $\beta$ and $\delta$) all remain constant (table 5.1). The model parameters were determined using Akaike information criterion (AIC) (Akaike 1974). This is a model selection method and the fewer parameters included give the best fit for the model. The parameter values given in table 5.1 were also calculated using an AIC optimisation technique. 10000 replications were used and the mean p-values were taken for each parameter, where P<0.05 the parameter was significant to the hazard and was therefore included in subsequent analysis.

Table 5.1. Parameter estimates for the fitted survival model. Parameters $\gamma_1$, $\gamma_2$ and $\gamma_3$ are the effects of different life-stages of the whale’s death (before mother’s death, the year after mother’s death, and the rest of the time until death or the end of the study) on sex difference in survival. Parameter $\alpha$ is the effect of whale age (over 30 or not) on survival, $\beta$ is whether the whale is over 30 and the sex of the whale, and $\delta$ is if whales mother was post-reproductive at death.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean</th>
<th>std. dev.</th>
<th>Average p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\gamma_1$</td>
<td>0.663648</td>
<td>0.107916</td>
<td>0.000031</td>
</tr>
<tr>
<td>$\gamma_2$</td>
<td>1.84999</td>
<td>0.186158</td>
<td>0.000011</td>
</tr>
<tr>
<td>$\gamma_3$</td>
<td>1.145078</td>
<td>0.081895</td>
<td>0.000030</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>1.327899</td>
<td>0.066131</td>
<td>0.000210</td>
</tr>
<tr>
<td>$\beta$</td>
<td>0.129401</td>
<td>0.05048</td>
<td>0.623159</td>
</tr>
<tr>
<td>$\delta$</td>
<td>-0.71908</td>
<td>0.097622</td>
<td>0.219546</td>
</tr>
</tbody>
</table>
$t_0$ was set to 1.5 to capture three key “exposure” times: before mother’s death, the year after mother’s death, and the remaining time until offspring’s death or end of study. These exposure times were considered to be a good representation of the different scenarios where the presence/absence of a mother may impact offspring survival. A stepwise model selection routine using AIC with $\eta = 0$ to choose between models was selected. The AIC provides us with a measure of how good the model fits the data. To account for individuals of unknown sex a simulation was used and individuals of unknown sex were assigned as male/female with probability 0.5 over 10000 replications. A previous version of the model included population and offspring age categories 0-15 and 15-30 (and interaction term $\beta$) all of which were non-significant, as determined by AIC and thus removed from the final model. There was no significant effect of mother’s age at death on the survival of males and females (parameter $\delta = -0.72$, $p = 0.23$). To calculate the hazard ratio for different scenarios, $h(t)$ was calculated for two individuals and one was divided by the other. This model was used to determine the effect of the loss of a post-reproductive mother on the survival of her adult offspring.

As there was no significant effect of mother’s age at death on the survival of males and females ($\beta$ and $\delta$, table 5.1) the model was revised to remove mother’s age at death:

$$h(t) = h_0(t) \exp\{\gamma_1 I_{s1} g_1(t) + \gamma_2 I_{s2} g_2(t) + \gamma_3 I_{s3} g_3(t) + \alpha d_{30+}\}$$

The survival parameter estimates (table 5.2) were fitted to the survival equation. The survivorship was then derived using the equation with different parameterizations for $I_{s0+}$, $I_s$, $g_1$, $g_2$ and $g_3$. As with the analysis including age of mother’s death, the model was fitted to the same combined multi-generational demographic data for both the southern resident killer
whales and the northern resident killer whales. In the previous model, sex and the presence of a post-reproductive mother did not significantly contribute to \( h(t) \). Therefore, in the same way as previously described, a stepwise model selection routine that uses AIC and the model with \( \eta = 0 \) was used. Essentially this means that the combined value for the mother being post-reproductive and the sex of the offspring was removed for the Cox proportional hazard equation. Then a simulation study was performed on this to account for missing sexes. The sex of 399 whales is known, again for the remaining 190 whales with unknown sex a simulation was performed by assigning them as male/female with probability 0.5 over 10000 replications.

Table 5.2. Parameter estimates for the fitted survival model. Parameters \( \gamma_1, \gamma_2 \) and \( \gamma_3 \) are the effects of different life-stages of the whale’s death (before mother’s death, the year after mother’s death, and the rest of the time until death or the end of the study) on sex difference in survival. Parameter \( \alpha \) is the effect of whale age (over 30 or not) on survival.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean</th>
<th>std. dev.</th>
<th>Average p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \gamma_1 )</td>
<td>0.61416</td>
<td>0.09833</td>
<td>0.00059</td>
</tr>
<tr>
<td>( \gamma_2 )</td>
<td>1.73757</td>
<td>0.16972</td>
<td>0.00031</td>
</tr>
<tr>
<td>( \gamma_3 )</td>
<td>1.04194</td>
<td>0.06899</td>
<td>0.00007</td>
</tr>
<tr>
<td>( \alpha )</td>
<td>1.98353</td>
<td>0.03828</td>
<td>0.00078</td>
</tr>
</tbody>
</table>

5.3. RESULTS

5.3.1. Associations occurring between mothers and their offspring

From the association data collected I show that the southern resident killer whale social network is highly interconnected (figure 5.3a). However, when the network is filtered to show only the strongest bonds with a HWI>0.5 (figure 5.3b.) it becomes apparent that the majority (70%) of the strong associations occur between a mother and her offspring. 21% of
strong bonds occur between siblings and only 9% occur between individuals that are not closely related.

Figure 5.3. (a) The highly interconnected social network of the southern resident killer whales, constructed using video data from 1996-2010. (b) The strong connections remain after the data are filtered to only include strong associations with HWI>0.5. (Red circles indicate mothers, blue sons, and yellow daughters, white are individuals with no HWI over 0.5).

Males have significantly stronger associations with their mothers than females (HWI: 0.44±0.18 and 0.30±0.21 respectively) this means that proportionally males spend more time in the presence of their mothers than females do (figure 5.4.) (t = 1.56, p < 0.001). This is unlikely to be due to females living longer as the HWI is scaled between 0 and 1 over any period of time which eliminates such bias.
Figure 5.4. Sex differences in strength of association of sons and daughters with mother. Median, upper and lower quartiles and range are shown. Data based on fine scale associations occurring from 1996-2010.

5.3.2. Risk of offspring death following maternal death

The results from the Cox proportional hazards model show that if at time $t$ two whales, one male and one female, have not yet experienced the death of their mother then the risk of death of the male is 1.85 times larger than the hazard of the female. The results show that both post-reproductive and reproductive mothers increase offspring survival, particularly in older male offspring (figure 5.5). For male offspring less than 30 years old the mortality risk increases by 3.1 times in the year following their mother’s death (figure 5.5). For males over 30 this risk increases to 8.3 times (figure 5.5). In contrast, female offspring under 30 show no
increase in mortality risk following the death of their mother whilst those over 30 show some increase in risk (2.7 times) in the year following their mother’s death (figure 5.5). Finally, for offspring over thirty years the death of a post-reproductive mother resulted in a 13.9 fold increase in mortality risk in sons and a 5.4 fold increase in mortality risk in daughters in the year following their mothers death. Whales are assumed to have died rather than dispersed following their mothers death because 38 years of evidence shows that the individuals are never again seen with their population (Center for Whale Research and Pacific Biological Station, unpublished data). Secondly, photo identification and genetic studies in the eastern north Pacific Ocean are so comprehensive now that if they were still alive they would have been documented and there is no evidence, either photographic or genetic, of these animals dispersing (Ken Balcomb, pers comms).
Figure 5.5. Illustrative survival curves of male and female offspring who experience their mothers death at different ages. Note that the survival probability after mother’s death continues to decline in males at both age points and in older females.

5.4. DISCUSSION

The evolution of a post-reproductive lifespan is not limited to humans and early reproductive senescence is reported in up to a third of the recorded species’ maximum lifespans (Reznick et al. 2006). However the presence of an extended post-reproductive lifespan is a much rarer event (Cohen 2004). To date there has been little evidence that the evolution of a prolonged post-reproductive lifespan in non-humans is adaptive. Using a long term association dataset (1996-2010) and multi-generational demographic records (1974-2010) I provide support for
the adaptive benefit of a prolonged post-reproductive lifespan in two populations of resident killer whales. Firstly, I show that the strongest associations occurring in resident type killer whale society are those between a mother and her offspring and that sons have significantly stronger associations with their mothers than daughters. Secondly, I show that older sons have a higher mortality risk after the death of their mother than daughters, regardless of the age of the mother. However, risk of mortality for both males and females is considerably higher if the mother who dies is post-reproductive. Although a son’s risk of mortality is still much higher than a daughter’s. In light of this I discuss two options for why such a prolonged post-reproductive lifespan may have occurred in these killer whales.

The findings presented here support previous research that highlights the interconnected nature of the southern resident killer whale population with many connections occurring between individuals (e.g. Ellifrit et al. 2010; Ellis et al. 2007; Ford & Ellis 2002; Ford et al. 2000; Parsons et al. 2009). However, I also show that the strongest bond in killer whale society occurs between a mother and her male offspring. Previous work has suggested that the mother-offspring relationship is the strongest (Deecke et al. 2010) and adult males are more often seen swimming next to their mother than adult females (Bigg et al. 1990). Based on the results of this research I can conclude that males have significantly stronger relationships with their mothers than females. This may occur if mothers assist their sons in foraging and provide support during agonistic encounters (Baird 2000) or these bonds could serve to maintain a son’s social status. Evidence of this can be seen in chimpanzees and bonobos where a male’s rank position in the social group is directly related to the presence and status of his mother (van Hooff & van Schaik 1994). The adult sons of older females have a more central position within the group than males with younger or absent mothers (Furuichi 1989). The social rank of a mother can also greatly affect the reproductive success
of her male offspring in polygamous mammals, such as in red deer (*Cervus elaphus*) (Dusek et al. 2007). However, the influence of a mother’s social status on the social status of her offspring can be influenced through the inheritance of traits such as body size, muscular strength, agility or scent (Barrette 1993; Maestripieri 2003; Yahner 1978). It would be interesting to explore the link between mother and offspring body size and social status in the resident killer whales, however at present this has not been investigated. There is evidence to suggest that post-reproductive mothers have little effect on their daughter’s reproductive success in resident type killer whales (Ward et al. 2009b). I further suggest that mothers may increase their inclusive fitness via their male offspring which results in the stronger associations between mothers and sons that I observe in the current chapter.

The results presented in this chapter provide evidence that the death of a mother has a significant negative impact on the survival of her sons which is seen to a much lesser extent in daughters. I suggest that this may occur for two reasons. Firstly, mothers may provide great support for their male offspring during foraging or antagonistic encounters (Bigg et al. 1990), secondly there may be some physiological immune response associated with the loss of such a strong social bond (Barak 2006). Both points are discussed in further detail later. Males over the age of 30 years have a considerably higher mortality risk than those less than 30 years. In addition, earlier research suggests that older males have the highest reproductive success in this population of killer whales (Ford et al. 2011). This offers compelling evidence that providing maternal support for sons will increase inclusive fitness benefits for mothers particularly as the age of her son increases. As prolonged post-reproductive lifespans are rare there is limited evidence to explore the mechanisms underpinning this. The most convincing research can be found in the human literature where menopausal females will care and provision for younger grandchildren (Cant & Johnson 2008; Hawkes 2004; Hawkes 2010;
Hawkes et al. 1998; Kachel et al. 2011; Sear et al. 2000; Shanley & Kirkwood 2001). Theory predicts that selection for the extension of a lifespan beyond an individual’s reproductive years should only occur where it makes a direct contribution to fitness (Foote 2008; Reznick et al. 2006). Such helping has only been found in three species all of which that possess extended social networks and it is possible to directly influence the survival of kin (Hamilton 1966). Likewise, where post-reproductive females occur in the order Cetacea the presence of females with prolonged post-reproductive lifespans is limited to those with the most stable social structure; short-finned pilot whales and killer whales (Hoelzel 1991).

The findings of this chapter suggest that the loss of a mother is associated with an increased mortality hazard for males. This may be in part due to direct benefits the mother provides to the sons such as support during foraging (Bigg 1982; Bigg et al. 1990). The social status of mothers has been shown to improve the foraging success in primates. The sons of high ranking female bonobos have been allowed access to the best feeding sites when foraging with their mothers (Furuichi 1988; Kano 1982). Mothers can also provide support during antagonistic encounters (Bigg 1982; Bigg et al. 1990). Animals with stable social units will usually avoid encounters with other groups or when they occur these encounters are often characterised by aggression (Christal et al. 1998). Conversely, this inter-group animosity is not universal and killer whales are one of the few species that provide an exception to this (Baird 2000) and matrilines are often seen associating with one another. However, anecdotal evidence during rare encounters between different killer whale ecotypes has reported some aggression (Balcomb, pers comms) although these observations are uncommon.
In addition to the loss of support from the mother, the increase in mortality risk may also be due to the distress caused by the loss of the social bond with their mother. The ability to feel and express emotions is evolutionary (Barak 2006) and these emotions can influence behaviour which in turn can be linked to physiological and immune responses (Spanagel & Weiss 1999). It is assumed that mammals other than ourselves have the ability to experience negative feelings associated with social loss (Newberry & Swanson 2008). Therefore, the death of a mother can cause emotional responses (Bradshaw & Schore 2007; Cirulli et al. 2003; Heim & Nemeroff 1999) which may result in early death of offspring. Traumatic social disruption from a single event, such as the loss of a mother, can create structural vulnerability for psychopathogenesis and perhaps early death by having sustained effects of brain plasticity (Bradshaw & Schore 2007; Cirulli et al. 2003; Heim & Nemeroff 1999). In humans the effect of loss of social bond is well documented, particularly the loss of a spouse (Elwert & Christakis 2008; Espinosa & Evans 2008; Subramanian et al. 2008). Furthermore, human survivorship in relation to loss of a parent, particularly a mother, has been shown to have a large effect on younger children. However, unlike our results, little effect is seen in adults (Rostila & Saarela 2011). It is not clear how such effects operate in non-human animal populations however there is anecdotal evidence to suggest that they do. For example, Goodall (1990) provides an account of the emotional attachment between an adult male chimpanzee and his mother. After maternal death the son appeared to go through bereavement and subsequently he died. This link between loss of a mother and ensuing death of the offspring may not be solely attributed to an emotional response; it may also be the driving force behind the evolution of post-reproductive lifespans in females.

In summary, in this chapter, I show that the key inclusive fitness benefits to post-reproductive females are via male rather than female offspring. My results suggest that the presence of a
mother increases the survival probability of her adult sons to a much greater extent than observed in her daughters. I suggest that two factors promote increased longevity in sons in the presence of a mother. Firstly, older males have greater reproductive success than younger ones (Ford et al. 2011). Ford et al. (2011) show that the probability of parental success increases with the age of the male. This is unusual as in many mammalian species males reproductive success increases with age until they reach their prime condition and then decreases as the male continues to age (Hollister-Smith et al. 2007; Nussey et al. 2009; Wroblewski et al. 2009). In addition to the oldest males having the greatest reproductive success they also have the largest body sizes (Fearnbach et al. 2011) and Ford et al. (2011) suggest that this may also attribute to their mating success. Killer whales are sexually dimorphic and adult males are considerably larger than adult females, with much larger appendages (flippers, dorsal fins and flukes) (plate 5.3). I further suggest that by mothers investing more in sons they can ensure they reach maximum size. This can benefit their reproductive success and hence the have significant inclusive fitness benefits for the mother.

Plate 5.3. Images showing sexual dimorphism differences in (a) male and (b) female adult killer whales.
Secondly as there is no dispersal from the maternal group (Olesiuk et al. 1990) and males do not mate within their matriline (Ford et al. 2011) their offspring will be raised by another matriline hence decreasing competition within the mother’s family group (Johnstone & Cant 2010). In addition to this, a female can only have a few calves whereas males can have many therefore ensuring the son’s reproductive success over daughters improves the inclusive fitness benefits for the mother. Crucially, the fact that selection appears to favour resident killer whale mothers to provide support to male offspring could explain why they have evolved the longest post-reproductive lifespan of all non-human animals.
Chapter VI.

General Discussion:

Implications of findings and future directions
Quantifying the social structure of animal populations and exploring the mechanisms and functions underpinning this are key to many aspects of behavioural ecology (Croft et al. 2011). The aim of my thesis was to investigate the mechanisms and functions of the social network structure of a large brained social mammal, using a population of killer whales (*Orcinus orca*). I used a long-term dataset to look at both external and internal factors affecting and underpinning social network structure. In this discussion chapter I summarise the key findings from my thesis and discuss the implications of these. I then explore the impacts this has on conservation and management plans and suggest future directions for further research.

My main study population was the southern resident killer whales, which occur around the southern end of Vancouver Island, coinciding with migrating salmon (*Oncorhynchus* sp.) (Ford & Ellis 2006). In addition, I use multi-generational demographic records from the northern resident killer whale population in Chapter V. Analysis presented here concurs with existing research which shows that resident type killer whales have a densely connected matrilineal social structure (e.g. Balcomb et al. 1982; Bigg et al. 1990; Deecke et al. 2010; Ford et al. 2000; Parsons et al. 2009). Social systems such as this where there is no dispersal by either males or females from the maternal group are highly unusual and have only been described in one other mammalian species, the pilot whale (*Globicephala melas*) (Amos et al. 1993a). With this in mind, I explored the broad and fine scale social structure of this wild population of killer whales using a long-term association dataset derived from photographs and video footage. Firstly, I quantified the overall population social structure of the southern resident killer whales and determined that an external factor, food availability, significantly impacts the social network structure (Chapter II). In the next chapters, I explored the social structure in more detail using the finer scale association data; I investigated internal factors
that may influence the social network structure at the level of the individual. As social networks are rarely homogenous I looked at the effect of age and sex on individual network position (Chapter III) and the attributes of leaders and followers in a travelling group of killer whales (Chapter IV). Finally, I investigated the finest scale interactions occurring between a mother and her offspring with a particular focus on the impact that the loss of the maternal bond has on the survival of both her sons and daughters (Chapter V). I have taken a two pronged approach to investigate the social network structure of a population of killer whales. I have looked at both the mechanisms and functions underpinning their social structure with the aim of beginning to explain the driving forces behind social structure and stability in a large free ranging mammal.

6.1 Mechanisms: The ecological environment and social structure

A fundamental aspect in the study of any social species is the stability and size of social groupings (Christal et al. 1998). A large amount of variation in social organisation between species can be attributed to ecological and social pressures (Chapman 1990). There are a range of external mechanisms, or ecological variables, which can impact animal social structure. Such factors include resource (e.g. food and/or space) availability (Henzi et al. 2009; Tanner & Jackson 2011) and predation risks (Hill & Lee 1998; Kie 1999). It is well documented that predation risks influence group social structure. However, as the top predator in the ocean killer whales are not at risk from predation by other animals (Hoelzel et al. 2007). On the other hand there is a large amount of literature showing that group size varies according to resource availability and a greater food supply is known to support larger groups of animals (Baird & Dill 1996; Bernstein 1975; Caraco & Wolf 1975; Chapman et al. 1995; Clark & Mangel 1984; Janson & Goldsmith 1995; Jarman 1974; Kruuk & Parish
At present there is limited evidence to suggest a change in resource availability or distribution impacts social network structure (see Henzi et al. 2009; Tanner and Jackson 2011 for exceptions). In chapter II I addressed this gap in the literature by quantifying social network structure in relation to fluctuations in food availability.

Different ecological pressures, particularly distribution of food resources, result in different types of dispersion by females to allow them to optimise their food intake and to ensure access to mates. Males must adopt different dispersal strategies dependent on this. Such ecological factors (i.e. food availability and distribution) may result in constraints on the social organisation and behaviour of a group of individuals (Chapman 1990). In Chapter II I quantified the overall population structure of a large brained social mammal, the southern resident killer whales, and determined that food availability significantly impacts social network structure. Specifically I showed that in times of high chinook salmon abundance the population social structure was more interconnected than in times of low food availability. To date only two other studies have explored the effects of resource availability on social network structure (Henzi et al. 2009; Tanner & Jackson 2011). The first, by Henzi et al. (2009), looked at how changes in food availability impact the social structure of female chacma baboons (Papio hamadryas ursinus). They show that when food is scarce their associations became more polarised into both constant and casual associations with stronger bonds being maintained between individuals (Henzi et al. 2009). The second was conducted under controlled experimental conditions with European shore crabs (Carcinus maenas). Social structure was shown to be sensitive to the interaction between behavioural and ecological differences among individuals. When food was clumped crabs that had low exploratory tendencies become more central to the social network (Tanner & Jackson 2011).

To the best of my knowledge, the findings presented in Chapter II are the first to explore the
social network correlates of food availability in a wild free ranging animal population. I have addressed this gap in the literature using photographic data collected over 24 years for the southern resident killer whales. I found a significant effect of chinook salmon (*O. tshawytscha*) abundance on the social network structure over and above the effects that could be explained by variation in group size. In times of high chinook salmon abundance the population was characterised by a more connected social network than in times of low chinook salmon abundance. Resident type killer whales do not hunt cooperatively (Baird 2000) or food share (Baird et al. 1992) and I suggest that my results are influenced in-part by a trade-off between foraging effort and social activity. When food is scarce a larger amount of time must be allocated for food searching resulting in reduced opportunities for social interactions. This is supported by the fact that there is a significant decline in the rate of associations among whales in years of poor salmon availability (Parsons et al. 2009). Previous work has documented changes in group size with food availability. For example, Chapman (1990) showed that the social groupings of spider monkeys (*Ateles geoffroyi*) in Santa Rosa are very much restricted by food abundance and the amount of food available will set an upper limit on the number of animals that can associate together. Similarly an example of how food availability specifically impacts social structure comes from female chacma baboons as previously discussed. They remain in their natal groups as adults (Henzi & Barrett 2003) forming strong differentiated associations with conspecifics which can influence individual fitness (Silk et al. 2003).

Resource patchiness poses a problem for all species in both terrestrial and marine animals. However in addition to this animals in the marine environment are often faced with problems relating to the dynamic conditions of the ocean that vary across spatial and temporal scales. To overcome these problems presented by the dynamic marine environment marine predators
respond by modifying their distribution (Hauser et al. 2007b). This behavioural adaptation is seen in a range of marine mammals including long-finned pilot whales, short-finned pilot whales (*G. macrorhynchus*), sperm whales (*Physeter macrocephalus*) (Whitehead 1989), common dolphins (*Delphinus* sp.), spotted dolphins (*Stenella frontalis*) and spinner dolphins (*S. longirostris*) (Norris & Dohl 1980) all of which have been shown to adjust their behaviour in relation to moving prey resources. Similar patterns have also been observed in terrestrial animals such as insectivorous primates (Janson & Goldsmith 1995) and elephants (*Loxodonta africana*) (Wittemyer et al. 2005) who will move onto a new feeding patch once their food has become diminished. In addition to this the results of Chapter II suggest that such changes may have a profound effect on a population’s social network structure.

The interaction between the distribution of animals in space and the population social network structure has received little attention. The studies to date clearly demonstrate that the distribution of animals in space and time can have a dramatic effect on the patterning of social interactions. For example, geographic distance between different groups of meerkats (*Suricata suricatta*) plays an important part in dictating the strength and frequency of interactions between groups, with groups further apart interacting less frequently (Drewe et al. 2009). Furthermore, a population of Galapagos sea lions (*Zalophus wollebaeki*) could be separated into five distinct communities which could almost entirely be explained by separation in space (Wolf et al. 2007). Both food availability and space have significant impacts on population processes. Such processes may include the way animals exploit their environment (Baird & Dill 1996; Hoelzel 1993), transfer of information or disease (Cross et al. 2004), population viability and mating opportunities (Matocq & Lacey 2004; Piertney et al. 1999; Wolf & Trillmich 2008).
Investigating the impact of external mechanisms and the ecological environment, specifically food availability, on overall population social structure does not give us information regarding the internal mechanisms, particularly those responsible for driving social structure in a heterogeneous social network. To explore this further, I looked at the age and sex of individuals in relation to their role in the connectivity of a social network (Chapter III) and the decision making in the form of leadership of a social group (Chapter IV).

6.2 Mechanisms: internal mechanisms impacting animal social structure

Animal social networks are rarely non-random and this leads to a heterogeneous social network structure (Godfrey et al. 2009; Keeling & Eames 2005). There are remarkable similarities between human and non-human animal social networks in particular in the way individuals take on different roles. Specific individuals may be peripheral in the social network and have fairly limited impact on, for example, the transfer of information through the group. In contrast others may be more central and have a much larger effect on the connectivity of the social network (Lusseau & Newman 2004). Individuals that play a vital role in the connectivity of the network might have a much larger number of associates than others or may interconnect many others (Croft et al. 2008; Krause et al. 2010; Newman 2003a). The position individuals occupy in a social network has received a great deal of interest in the context of the transmission of disease and information (Böhm et al. 2009; Lusseau & Newman 2004; Pautasso & Jeger 2008). However the mechanisms driving these differences in individual social network position and the attributes of individuals taking specific social roles remains poorly understood. Lusseau and Newman (2004) provide one of the first studies using a networks approach to quantify the role of individuals in the social network in a population of bottlenose dolphins (Tursiops sp.). They showed that there were
“social brokers” within the population who were responsible for linking different subgroups. The temporary removal of the broker animal resulted in fewer associations occurring between the two groups. This provides evidence of the importance of establishing the role of individuals within a social network as animals with high centrality will play an important part in the connectivity of the social network. Hence they will also be key in population processes such as disease transmission (Barthélemy et al. 2005; Böhm et al. 2009; Böhm et al. 2008; Cross et al. 2004; Eames & Keeling 2003; Hamede et al. 2009; Keeling & Eames 2005; Small & Tse 2005; Small et al. 2006; Watts & Strogatz 1998) or information transfer (Krützen et al. 2005; Whitehead 1998a; Whitehead 2010; Whitehead et al. 2004; Wolf et al. 2007). A combination of different attributes may influence the position an individual will take in the social network. Such characteristics could include; age, sex, phenotype, personality and the presence of familiar or related individuals. I discuss each of these characteristics in turn.

6.2.1 Age in relation to social network position

Sociality is particularly significant in resident type killer whale populations with older females playing a central role within the matrilines (Parsons et al. 2009). These matriarchs are thought to be important in the cohesion of a social group (Williams & Lusseau 2006). In contrast to this, I determined that there was no significant correlation between female age and betweenness or degree centrality (Chapter III). However, there was a positive relationship between male age and both betweenness and degree centrality. This suggests that older males are more connected and more central to the social network than younger ones. This was surprising as in elephants, who have similar matriarchal society, it is the older females who are fundamental to the family group and increase social cohesion within the group (McComb
et al. 2001; McComb et al. 2011). I suggest that the results I found in Chapter III may be due to the mating strategy of killer whales, they avoid inbreeding by mating with females from other matrilines (Amos et al. 1993a; Ford et al. 2011; Pilot et al. 2010) and older males have the greatest reproductive success (Ford et al. 2011). This would result in older males being observed with a greater number of individuals from other matrilines hence increasing their betweenness and degree centrality. These highly central individuals will also have implications for the mating dynamics of the population as they have increased access to potential mates (Matocq & Lacey 2004; Piertney et al. 1999; Wolf & Trillmich 2008).

In contrast to my findings in Chapter III, Williams and Lusseau (2006) suggest that higher betweenness scores are usually seen in younger animals, specifically juveniles and sexually immature females, in the northern resident killer whales. I suggest that the differences between this work and my findings may be in part due to differences in the data analysis techniques. I have overcome the issues of non-independence of the data and sampling bias with the use of randomisations and null models. However, Williams and Lusseau (2006) state that their study would benefit from further work to remove issues of independence and sampling bias towards specific individuals in their study (see Chapter I for explanation). Alternatively, the results could be due to female choice, with more females actively seeking older mates. Females of many species will preferentially mate with older males over younger ones as they have demonstrated longevity and it is assumed that they can pass on superior genes to their offspring (Brooks & Kemp 2001). In Chapter III I suggest that the higher betweenness scores seen in older males may be a result of them having higher reproductive success with females outside of their matriline. Other examples where older males are preferred are seen in the female redlip blenny (Ophioblenius atlanticus). Males in this species have been shown to guard their broods longer thereby increasing their reproductive
success (Côté & Hunte 1993). Attaining mates and protection of offspring are important to ensuring an animal’s reproductive success (Chapman 1990).

6.2.2. Sex in relation to social network position

In addition to the age of individuals sex is also known to impact social structure. The gender of an individual is understood to have a strong effect on the size of their social network in humans (Tonge 2010). Likewise, I showed that individual’s sex also impacts social structure in killer whales. I found that female killer whales have a significantly higher number of associates than males (Chapter III) and suggest that this may occur due to the lack of dispersal seen by both sons and daughters. The strongest bond occurs between a mother and her male offspring (Chapter V) and this may occur if mothers preferentially provide sons with support during antagonistic encounters or help during foraging (Baird 2000). They may do this to ensure the fitness of their sons as there is a large degree of sexual dimorphism (Olesiuk et al. 1990) and larger (older) males have greater reproductive success (Ford et al. 2011). Additionally, the presence of a mother could serve to maintain the son’s social status which may facilitate access to females in other matrilines. Evidence of this can be seen in chimpanzees and bonobos where a male’s rank position in the social group is directly related to the presence and status of his mother (van Hooff & van Schaik 1994). In addition to this, once a female killer whale’s daughter has her own calves the daughter will begin to associate more with her own offspring (Bigg et al. 1990), hence giving her a larger number of strong associates. Further to this, mothers may invest more in sons and remain more closely bonded to them as she will have greater opportunities to increase inclusive fitness via their male rather than via their female offspring (Chapter V), as a daughters offspring are raised within the matriline.
The presence of different sex ratios in a group can have implications for the social structure of populations. Although same sex alliances are not thought to occur in resident type killer whales (Rose 1992) they are seen in other species. Male alliances form Kanyawara chimpanzees (Pan troglodytes schweinfurthii) who form stronger alliances with other males than females form with other females. This occurs because males use their alliances with other males to move up the dominance hierarchy. Whereas female association patterns appear to be a consequence of individual ranging behaviour (Gilby & Wrangham 2008). In alliances in another primate species, the spider monkey, males work together for both potential reproductive gains and territorial defence. In contrast, female spider monkeys often form very small groups or are solitary (Chapman 1990). The authors suggest that this occurs as males are attempting to locate females with which they can breed whilst females are avoiding male harassment and are protecting their infants be remaining alone on the territorial boundaries. Similarly male alliances for reproductive gain are observed in bottlenose dolphins (T. truncatus and T. aduncus) where related males form alliances which appear to be used to increase reproductive success (Parsons et al. 2003). Likewise patterns of kinship influence male-male alliances in elephants however the benefits of these associations are not known at present (Chiyo et al. 2011). Unlike males, who often use alliances for reproductive gain, females frequently form single sex groups to avoid male harassment. Single sex aggregations are common in marine predators such as sharks. For example, in the cat shark (Scyliorhinus canicula) a few individual females form strong aggregations with more peripheral animals. The addition of male sharks results in peripheral females becoming more tightly associated with the other females (Jacoby et al. 2010). Another example is seen in Trinidadian guppies (Poecilia reticulata) who take this one stage further and will actively group with females more “attractive” than themselves to avoid harassment (Brask et al. 2011). Female guppies often form non-random associations with other females whereas no persistent pairs were
found between males (Croft et al. 2006). All of these cases provide evidence of active sorting by sex for different reasons which can increase an individual’s fitness through survival and reproductive success.

6.2.3. Other phenotypic characteristics and social structure

Age and sex are not the only attributes that can impact animal social structure. Other phenotypic traits or an individual’s personality can also affect this. I did not explore phenotypic traits or personality of the killer whales in relation to their social structure and social dynamics due to logistical limitations of collecting such data from a wild population of killer whales. However, I cannot rule these out, as evidence in other species suggests that they can play an important role in shaping social dynamics. In addition to grouping by sex, animals will often associate with others that share similar phenotypic characteristics. For example, humans usually associate with others that share similar characteristics (Fowler et al. 2011). Likewise Trinidadian guppies also take account of phenotype when shoaling. Non-random networks show that fish will preferentially shoal with other individuals of similar body length and shoaling tendency (Croft et al. 2005).

Personality can also affect animal social structure in different ways. Personality is used to define differences between individual consistency in behaviour (Krause et al. 2010). Behavioural phenotypes were quantified by Croft et al (2009) in Trinidadian guppies, they explored predator inspection and shoaling tendency as measures of boldness. They showed that bold fish had fewer network connections than shy fish and the connections that bold fish did have were on average weaker. This shows that the finer scale social structure is strongly
influenced by an individual’s personality. The authors suggest that this may act as an amplifier of selection contributing to the maintenance of cooperation during a task such as predator inspection. More recent experimental work on European shore crabs determined that highly exploratory individuals play a key role in connecting cohesive subgroups of low exploratory crabs (Tanner & Jackson 2011). Tanner and Jackson (2011) suggest that synchronous movements of crabs with low exploratory rates mean they are more effective at finding food than those with higher exploratory rates. They further suggest that social structure is sensitive to the interaction between ecological and behavioural differences between individuals.

6.2.4. Active social decisions and social structure

Resident type killer whales do not disperse from their maternal group (see chapter I for details of an isolated incident) and even as adults both males and females remain with their mother (Bigg et al. 1990). Individuals that live in such groups are thought to gain indirect fitness benefits through cooperation with relatives (Trivers 1985).

Understanding how individual traits impact social structure begins to provide an insight into the mechanisms and functions underpinning animal social structure. However, it is also important to understand the effect of active social decisions, such as those in resident killer whales. Associating with kin can strongly influence the evolution of social behaviour through kin selection and can therefore be an important predictor in who associates with whom (Couzin 2006). Frequent interaction promotes social tolerance (Gilby & Wrangham 2008) and kin have been shown to preferentially associate with one another in a number of species.
The evolution of such specialised cooperative societies is thought to be dominated by this kin selection (Clutton-Brock 2002). Theory further predicts that there are advantages for animals to group with familiar individuals or kin. Such advantages include reduction of competition due to established hierarchies or the evolution of altruistic behaviour (Frommen & Bakker 2004). When groups consist of related individuals sociality can increase both individual and inclusive fitness through cooperation, such as allopatrial care or the transmission of socially learned behaviours, communal defence and access to resources and mates (Beck et al. 2011).

Group living and sociality facilitate key aspects of life such as feeding, reproduction, communication, learning, defence and suitable responses to environmental cycles, such as seasonal changes in food supply (Bräger et al. 1994). Like many animals southern resident killer whales group according to kin, however, unlike most other animals, there is no dispersal by either sex from the maternal group (Bigg et al. 1990). I further show that the strongest associations within a population occur between a mother and her offspring (Chapter V). Other examples where animals have preferred associates are seen in many species including sperm whales where females have preferred associates within a group. These preferences correlate positively with the relatedness between individuals, therefore more closely related females associate more frequently (Gero et al. 2008). Kin selection also plays an important role in the evolution of elephant sociality and Archie et al (2006) have shown that genetic relatedness can be used to predict patterns of temporary splitting in a fission-fusion society of African savannah elephants. In these elephants individuals are more likely to associate with those from other groups if the matriarchs are genetically related. They suggest that social bonds between related groups persist for decades after the oldest females die. Further examples can be found in fish such as the three-spined stickle backs
(Gasterosteus aculeatus) (Frommen & Bakker 2004). These fish will preferentially associate with familiar kin and appear to be able to discriminate between kin and non kin. This is important in mate choice decisions as it allows individuals to avoid the costs associated with inbreeding.

6.3. Functions

So far, I have discussed both the external and internal mechanisms underpinning animal social structure in relation to the work presented in this thesis and in a wider context. Heterogeneous networks play an important part in the evolution of communities and the decisions animals make (Ghosh & Lerman 2009). A consequence of an individual’s interactive strategies is the network position it occupies (Krause et al. 2010). However, to understand social structure more comprehensively the functions behind observed social structure in animal populations must be explored.

6.3.1. Functions: Leadership and Hierarchy

In addition to the benefits of group living (as discussed previously and in Chapter I) travelling as a group has a number of additional advantages including; increased navigational accuracy, predator avoidance and enhanced foraging efficiency (Flack et al. 2012; Krause & Ruxton 2002). Coordinated movements vary from small daily foraging or ranging activities to large migrations (Flack et al. 2012). To maintain a cohesive group during collective movements animals must be able to make joint decisions or one individual must have a disproportionally large effect on the group movement with others willing to follow (Flack et al. 2012). Human society cannot function without group decisions and decision making is
part of everyday life (Conradt & List 2009; Conradt & Roper 2005). Reaching consensus about decisions vital to individual and group fitness is essential if the group wants to avoid splitting (Conradt & Roper 2005). Naturalists have been puzzled for centuries by the coordinated movements of animals such as; herds of ungulates, flocks of birds, shoals of fish or swarms of insects (Conradt et al. 2009; Conradt & List 2009). Coordination is a key component of spatial cohesion in moving animal groups (Bousquet & Manser 2011). Leadership can materialize in different ways in many cases appropriate knowledge to lead the group is only possessed by a few individuals. Leaders may possess information regarding food sources (Couzin et al. 2005; Reebs 2000; Swaney et al. 2001) or migration routes (Couzin et al. 2005; Lindauer 1957). Important knowledge and experience may come with age and/or dominance (Able & Bingman 1987; Couzin & Krause 2003; Couzin et al. 2005; Faria et al. 2010; Jacobs et al. 2008; King et al. 2009; Krause & Ruxton 2002). Therefore leadership may belong to the highest ranking, or the oldest and most experienced member of a social group (Bonanni et al. 2010). Elephants (Loxodonta Africana) have matrifocal social structure and in this society the oldest females, or matriarchs, are fundamental to the group (McComb et al. 2001) and will often act as leaders (McComb et al. 2011). Alternatively, leadership can be shared, this is known as “distributed leadership”, and several individuals will be responsible for the movements of the group. Examples of animals reaching a consensus with regard to decision making may include; a flock of birds leaving a foraging patch (Black 1988), a swarm of bees choosing a new nest site (Seeley & Visscher 2004) or a group of primates deciding where to travel after a period of rest (Stewart & Harcourt 1994).

The roles of leaders and followers have been explored for considerable time and there is evidence to suggest that different state or status dependent characteristics influence leadership. These include; level of dominance (King et al. 2008), hunger (Krause et al. 2000),
boldness (Harcourt et al. 2009a; Harcourt et al. 2009b) or lactation state (Fischhoff et al. 2007) in a range of species (King et al. 2009). Leadership is often not stable and may be temporarily occupied by the most suitable individual. In meerkats (Suricata suricatta), who do not food share, individuals forage cohesively and frequent changes in leadership occur depending on individual knowledge of food resources (Bousquet & Manser 2011). Another early example by Chen (1937) describes the nest building ability of different ants (Camponotus japonicus) and suggests that the most active ants instigate nest building and are therefore the leaders of the group. More recently in plains zebras (Equus burchelli), leadership is dictated by reproductive state and energetic requirements of the females. Groups are often led by individuals that are lactating this may have fitness consequences as leaders are often the first to arrive at water sources (Fischhoff et al. 2007). I found similar results in females with lactating individuals leading the group more often than when they were not (Chapter IV). I propose that killer whale females have greater motivation to lead the group as they require up to 42% more food when they are lactating (Williams et al. 2011).

Specific individuals have been highlighted as leaders in many species. McComb et al (2011) stress the importance of leaders in directing the actions of other individuals in a group (King et al. 2008; Lusseau & Conradt 2009; Maransky & Bildstein 2001; Wright et al. 2003). Making the correct decisions is vital in allowing animals to maximise their foraging success and lower predation risk (King & Cowlishaw 2007). In Chapter IV I show the importance of different attributes of individuals leading a group of killer whales. I found a positive correlation in leadership in both males and females with age, however overall females have significantly higher leadership than males. Older individuals have been shown to act as leaders in a range of species. For example, ruffed lemurs (Varecia variegata) form stable groups which are usually led by a dominant female (Overdorff et al. 2005). The authors
suggest that the dominant, and often oldest, female initiates group movements to ensure she is the first to arrive at a food source and gets the highest quantities. Like the work of Overdorff et al (2005), McComb et al (2011) show that oldest female African elephants usually emerge as leaders of their group. They provide results illustrating how the knowledge acquired by the oldest females over time effects the anti-predator responses of the group as a whole. In contrast to both these species, and the findings presented in Chapter IV, males more often emerge as leaders in primate society. A study on wild baboons provides support for this, the alpha male is the first on a food patch and will monopolise it (Hogan et al. 1994; King et al. 2009). Similarly, in humans, male leadership is still custom in most societies probably due to the fact that psychological tests have shown that males have higher self confidence and dominance than females (King et al. 2009; van Vugt & Spisak 2008). Likewise, in dogs (Canis lupus familiaris) the oldest and highest ranking individuals will most often act as leaders (Bonanni et al. 2010). Based on the findings of these previous studies and the results presented in Chapter IV I suggest that the extreme longevity of female killer whales (Olesiuk et al. 1990) facilitates greater opportunities for social learning and acquiring knowledge. In turn this makes them the most appropriate leaders ensuring the fitness and survival of their matriline.

Killer whale social hierarchy is female dominant (Olesiuk et al. 1990). Many other species, across a range of taxa, also have various types of social and dominance hierarchies (Chase et al. 2002). Examples of such animals include Palaearctic ants (Leptothorax gredleri) (Heinze & Lipski 1990) where only the highest ranking queens lay eggs. In baboons (Papio Anubis) rank within the group is maintained by the way that subordinates behave towards high ranking individuals (Rowell 1966). In another primate, the pigtail monkey (Macaca nemestrina), a females rank position within a group is related to her oestrous cycle as
oestrous females are more tolerated by the dominant males in the group (Bernstein 1969). In meerkat society a dominant breeding pair are helped to care for their offspring by non-breeding subordinates (Griffin & West 2003). Likewise in naked mole rats (*Heterocephalus glaber*) the breeding is monopolised by a single female and several males with subordinates taking on helping roles (Holmes et al. 2007). Hierarchies also occur outside of mammals and reef fish (*Paragobiodon xanthosomus*) have been shown to have stable hierarchy which is dictated mainly by body size (Wong et al. 2008).

Collective movements in animal groups occur from individual interactions (Fischhoff et al. 2007) and group members are likely to vary in age and knowledge which results in mixed levels of individual experience regarding navigation, foraging areas or risks. Therefore the most inexperienced individuals will usually follow others, this is fairly general to wide ranging social species (Flack et al. 2012). This behaviour allows inexperienced individuals to benefit from the knowledge of more experienced ones hence increasing their own fitness. Individuals with superior knowledge have been shown to manipulate the movement of the group; trained shoaling fish, golden shiners (*Notemigonus crysoleucas*), can coordinate the direction of the groups travel (Reebs 2000). Cliff swallows (*Petrochelidon pyrrhonota*) will follow their colony neighbours (Brown 1986). Naive homing pigeons will follow those with more knowledge of a route (Flack et al. 2012) and trained meerkats will more often initiate group departure than untrained conspecifics (Bousquet & Manser 2011). I suggest that the findings from Chapter IV show that older females are more often at the forefront of collective movements in a travelling killer whale group which may suggest that they are leading the group. I further speculate that the increased longevity of females allows them to acquire superior ecological knowledge regarding foraging areas, or routes and this allows them to become effective leaders within the group.
6.3.3. Functions: Reproductive success

Social networks can be used as a tool to predict individual fitness through reproductive success. For example, the copulation success of forked fungus beetles (*Bolitotherus cornutus*) is positively correlated with network centrality and negatively co-varied with clustering coefficient (Formica et al. 2012). Frequent social contact, with many individuals will increase mating opportunities available (Godfrey et al. 2009; Sih et al. 2009). Examples occur across a range of taxa where males with more social bonds have higher reproductive success. Examples include: long-tailed manakins (*Chiroxiphia linearis*) (McDonald 2007), wire-tailed manakins (*Pipra filicauda*) (Ryder et al. 2009) and assamese maqaque (*Macaca assamensis*) (Schülke et al. 2010). In resident killer whale society the oldest males have the greatest reproductive success (Ford et al. 2011). In addition to this I show that older males also have more associates and a more central network position than younger ones (Chapter III) and I suggest this may increase their access to mates. There is no evidence to suggest that killer whale males father offspring within their own pod (Ford et al. 2011) and the same is thought to be true for long-finned pilot whales (Amos et al. 1993b). This means that for a killer whale male to be successful he needs access to females from different pods. This may partly explain why the older males who hold a central position within the social network also have the greatest reproductive success. As discussed killer whales have highly stable social structure. This may be explained in part by the fact that when individuals leave their natal group they will lose any affiliative relationships with familiar and related conspecifics in addition to any inclusive fitness benefits they may have incurred from helping relatives (Christal et al. 1998). Whereas by remaining in their natal group individuals can benefit directly from the support of relatives, hence increase the health and reproductive output of the matriline. Unlike killer whales, sperm whales will permanently move away from their maternal group. Christal et al.
were unable to provide a functional explanation for the occurrences of transfers due to the apparent high costs and lack of benefits to new members.

The benefits of group living and sociality can be enhanced by the presence of kin who can improve their own inclusive fitness by increasing the survival probability and reproductive success of offspring and siblings. Mothers in several mammalian species are known to invest more in raising sons than daughters, a pattern that I find in relation to the association strengths between mothers and their offspring in killer whales (Chapter V). Similar results have been reported in elephant seals (*Mirounga angustirostris*) (Reiter et al. 1978) and red deer (*Cervus elaphus*) (Clutton-Brock et al. 1981) where males are weaned later than females and males also tend to be larger (Clutton-Brock et al. 1981). In all species where close bonds between parents and offspring are maintained there are increased opportunities for the social transmission of information such as food sources or predation risks (Newberry & Swanson 2008). In Chapter V, the survival of adult offspring is impacted by the survival of the mother. I show that a mother’s mortality has a significant negative impact on the survival of her sons which is seen to a much lesser extent in daughters. This effect was present regardless of the age of the mother. Males over the age of 30 years have a considerable increase in mortality risk than those less than 30 years. For a killer whale mother to increase her inclusive fitness theory predicts that she should invest more in her sons than daughters. This should occur as a son’s offspring will be raised outside of their matriline so they will not incur an increase in competition for resources within the matriline (Johnstone & Cant 2010). In addition to this, sons are able to produce more offspring than daughters who will usually only give birth to one calf approximately every five years (Olesiuk et al. 1990). In addition to this older males have greater reproductive success than younger ones (Ford et al. 2011). Ford et al (2011) show that the probability of parental success increases with the age of the male. Further to
this, these oldest males also have the largest body sizes (Fearnbach et al. 2011) and Ford et al. (2011) suggest that this may also attribute to their mating success. As killer whales are sexually dimorphic I further suggest that by mothers investing more in sons they can ensure they reach maximum size which can benefit their reproductive success. This in turn will have significant inclusive fitness benefits for the mother. Further to this, and in contrary to the grandmother hypothesis in humans, post-reproductive mothers have little effect on their daughter’s reproductive success in resident killer whales. Ward et al. (2009b) show that post-reproductive females did not have an effect on the inter calf interval of their daughters or the number of calves they can produce. In chapter V I further show a decrease in survival probability to adult sons if their mother is post-reproductive. This risk is also seen in daughters but to a far lesser extent. This provides convincing evidence that mothers increase their inclusive fitness via their sons rather than their daughters.

Post-reproductive lifespans in mammals are not uncommon (see Cohen 2004 for summary table). Although the majority of these post-reproductive lifespans were short and extended only as long as the young were dependent on maternal care (Kachel et al. 2011). However, there are exceptions to this; these are the short-finned pilot whales which have an average post-reproductive lifespan of 14 years (Marsh & Kasuya 1986), the killer whale, who stops reproducing in their forties but can survive well into their nineties (Olesiuk et al. 2005), and humans (Cohen 2004). Most of the current research on the evolution of post-reproductive lifespans is found in the human literature (examples include: Hawkes 2004; Hawkes et al. 1998; Kachel et al. 2011; Norris & Pryor 1991; Sear et al. 2000). The post-reproductive section of human lifespans is thought to be an adaptive feature of aging. This is because post-reproductive females can make contributions to the fitness of their children and grandchildren, hence increasing their own inclusive fitness (Cant & Johnson 2008; Hawkes
The results of Chapter V provide the first evidence that a prolonged post-reproductive lifespan in non-human animals is adaptive. Moreover, the work presented in Chapter V provides evidence that social structure can influence important life history traits, and where such stable social structure influences inclusive fitness for females. This may even be the driving force behind the evolution of a prolonged post-reproductive lifespan in this highly social mammal.

6.4. Conservation

In recent years networks have proven to be a valuable tool in the study of free ranging marine mammal populations (Beck et al. 2011; Bräger et al. 1994; Gero et al. 2008; Lusseau 2003; Lusseau 2007; Lusseau et al. 2006; Möller et al. 2006; Williams & Lusseau 2006). I propose that with the maturation of long-term datasets we can begin to ask more important questions which will improve current conservation and management strategies. Important questions may include those regarding reproductive success, fitness consequences of network position or the impact of the loss of an individual on the overall population. These types of questions cannot be answered with short term datasets therefore highlighting the value of using long term datasets in conservation management and species protection.

The oceans occupy 71% of the earth surface all of the oceans are interconnected and they are currently undergoing substantial changes as a result of human activities. However at present the impact on marine mammal biodiversity remains poorly understood (Davidson et al. 2012). Difficulties associated with studying marine species have slowed our advances in
knowledge (Gero et al. 2008) and understanding which marine mammal species are at risk and require urgent attention is problematic (Davidson et al. 2012). Currently, the International Union for the Conservation of Nature Red List classifies 32 out of 128 species of cetacean as threatened with extinction (Davidson et al. 2012). Surprisingly however, 62 species of cetacean cannot be classified due to deficient data (ICUN red list). This highlights a major gap in our knowledge of marine mammals and particularly the whales and dolphins.

Many toothed whales live complex social lives (Connor et al. 1998) and the inaccessible nature of whales and dolphins means that gaining insight into their social organisation is a challenge. However without this information it is impossible to assess the status or threats of a population (Amos et al. 1993b). Often population management plans assume all animals play a similar role within the group which can have consequences for the population (Williams & Lusseau 2006). It is becoming known that individuals differ in the role that they play within an animal group (see Chapter III for full discussion). Individuals may be removed from a group in one of two ways. Either by targeted removals such as older elephants removed for their superior tusks (Barnes & Kapela 1991) or juvenile individuals removed from killer whale populations for aquaria (Olesiuk et al. 1990). Alternatively natural removals can occur through disease or old age. Either way the loss of different individuals will affect the group in different ways depending on the position that the individual held within the social network (Chapter III). In addition to understanding the importance of the roles of individuals within a social network long-term datasets provide an important resource for the demographic analysis of long lived animals. They provide information regarding survival, without relying on age distribution assumptions (Brault & Caswell 1993). We can gain knowledge of individual reproductive history, and we can begin to explore the social structure and systems of the population (Brault & Caswell 1993). This allows us to design
and implement more effective conservation and management plans. Using a long term association dataset I have shown the conservation value of using a networks approach to explore the mechanisms and resultant functions underpinning social structure in an endangered population of killer whales. I have shown that killer whale social structure is impacted by environmental variables, particularly salmon abundance (Chapter II) and therefore show how the conservation of one target species can be impacted by the conservation strategy (or lack of) of other species. This highlights the importance of taking an eco-system level approach in management strategies particularly to take into account such interactions with other environmental variables. Using finer scale data I showed that killer whales take different positions within the social network which can have conservation implications for the transfer of information or disease, mating dynamics and gene flow (Chapter III). Leadership was assessed in the context of collective group movements (Chapter IV). For beneficial conservation efforts having knowledge of decision making and collective movements allows us to further understand the social dynamics of the group. We can use this information to assess the importance of different individuals in the population and begin to explore the consequences of loss of such and individual (Williams & Lusseau 2006). Finally, the strongest relationships within a killer whale population were established and the consequences of the loss of this bond explored (Chapter V). I believe that networks have proven to be an invaluable tool in assessing the population social structure. However, there are a great many more questions we can ask using a networks approach (see section 6.5).

In addition to describing the social network structure it is also important to have understanding of the natural history of a species or population (Bascompte & Jordano 2007). Once a network has been described we can use it to explore the ecological and evolutionary mechanisms underpinning the association patterns we observe (Bascompte & Jordano 2007).
By gaining knowledge of the nature and duration of social bonds occurring between individuals we can assess the value of sociality for a species (Christal et al. 1998). A networks approach provides us with information regarding the fitness implications of social structures, from the entire population level down to the individual level (Krause et al. 2007).

There is an emerging trend in behavioural ecology to use social network analysis as a powerful tool in describing animal population social structure (Beyer et al. 2010; Böhm et al. 2008; Croft et al. 2006; Croft et al. 2005; Croft et al. 2009; Croft et al. 2004; Drewe 2010; Drewe et al. 2009; Formica et al. 2010; Formica et al. 2012; Griffin & Nunn 2011; Guimarães et al. 2007; Hamede et al. 2009; Henzi et al. 2009; Jacoby et al. 2010; Koyama 2003; Krause et al. 2010; Lusseau 2003; Lusseau 2007; Lusseau & Newman 2004; Madden et al. 2009; Manno 2008; McCowan et al. 2008; Miller et al. 2008; Naug 2008; Naug 2009; Patriquin et al. 2010; Williams & Lusseau 2006). This allows us to quantify social structure at different levels (individual, dyadic, groups, communities) and has great potential to explore future questions in behavioural ecology (Croft et al. 2011). From a conservation point of view we can begin to ask questions regarding disease transmission within a population (Böhm et al. 2009; Böhm et al. 2008; Naug 2008; Perkins et al. 2009). We can also look at cultural continuity within animal populations and particularly how culture arises and how important it is to conserve this (Galef 1992; Krützen et al. 2005; Laland & Hoppitt 2003; Laland & Janik 2006; Mesnick et al. 1999; Rendell & Whitehead 2001; Whitehead 2010). Socially learned behaviours are important in the way that animals interact with their environment and hence conserving this should be a priority, however, at present suitable data on this are scarce (Whitehead 2010). In addition to this there is a considerable need to better integrate behavioural information into wildlife conservation approaches (Ashe et al. 2010). Many species including chimpanzees, cetaceans and elephants have complex social lives which are
threatened by anthropogenic and environmental impacts. Therefore understanding the social
behaviour and systems of these species and how human/environmental interference impacts
these is vital for future conservation efforts (Couzin 2006). The collective movement and
decision making in animals has captured the attention of artists, naturalists, philosophers and
scientists for a long time (Couzin 2009). This wide interest should be used to promote public
awareness and help support future research and conservation actions.

6.5. Limitations and Future Directions

Due to the nature of the marine environment most cetacean behavioural researchers must
overcome the fact that their study species spends the majority of their time below water. In
my thesis the surfacing data I used was only recording a small percentage of their associative
behaviour. To some extent I have overcome this by using the half-weight index as a measure
of association which takes into account that not every association is observed. Moreover the
work presented in this thesis is based on a large amount of data (Chapter II: 24 years,
Chapters III and IV: 15 years, Chapter V: 36 years) which has taken a tremendous effort to
collect.

To ensure that appropriate conservation and management plans are implemented in both the
southern resident killer whales and in other species there is a great deal more we can do to
build on the research presented here. There is a large amount of scope to develop this work
further using such a long term dataset and a networks approach. I showed that the social
network structure of the killer whale is correlated with their food availability; however, this is
only one component in a hugely dynamic environment. As this population has been classified
as endangered it would be important to explore how other natural aspects of their environment impact their social structure. For example, it would be interesting to incorporate information regarding their location, tidal state or the topography of the seabed. In addition, there is a huge whale watch community, and from 1996 to 2010 the average number of boats (both private and commercial) seen with the whales at a given time is $10.5 \pm 9.6$ and the maximum number seen was 120 (Center for Whale Research, unpublished data). The impacts of boats have begun to be assessed in relation to evasive tactics (Williams & Ashe 2006). However, no work has been done to accurately quantify the effects and explore the implications of the disturbance and noise of these boats on the social structure of the whales. The movements of the whales make land based studies possible (Hauser 2006) and I propose that we should investigate the social structure from shore both in the presence and absence of boats. This would allow us to make inferences regarding the way that such anthropogenic impacts affect their social behaviour.

In addition to gaining an understanding of the external factors affecting the social structure of these whales we need to look at the internal dynamics, particularly of individual network position within the social network in more detail. I have begun to explore the roles of individuals within the network and quantify network position in relation to age and sex. I think this could be investigated further by including other information, such as reproductive state or the matriline they belong to. This would provide further insight into the mechanisms underpinning the heterogeneous social network structure. Likewise, there is a large amount of potential to develop the leadership analysis further. Here I assumed the front whale to be the leader of a group. However, due to the acoustic nature of the marine environment they could potentially lead from other positions within the group. Obtaining both acoustic and behavioural data to observe whether a specific cue is given before a change in direction
would allow us to record which animals initiate such changes. To date there are no data of this nature but it would be an exciting avenue to explore. I would also like to explore the fitness of individuals through their reproductive success in relation to their position within a social network. Fitness indices could be calculated using the number of calves a female has which survive beyond weaning in relation to the theoretical maximum number of calves she could have had based on her age (Olesiuk et al. 1990). If we explore this in relation to network position we can get an understanding of her access to potential mates, how group size affects fitness and support from other individuals in the group. It would be particularly interesting to look at the relationships of adult females with their own mothers following the birth of their offspring to investigate to what extent mothers ensure the reproductive success of their daughters.

Finally, the majority of the data collected on the southern resident killer whales is obtained during the summer months and at present we have very limited knowledge regarding their winter movements. There are current proposals by the National Marine Fisheries Service (File # 724-1824-01) to tag the southern resident killer whales. However, as they are an endangered population, tagging is highly invasive (plate 6.1) and tag lifespan is hugely variable (23-29 days average duration, range 2-76 days) (Ken Balcomb, pers comms) there has been great objection to this. Although it would be of interest to know the movement of the whales in greater detail during the winter months I do not feel that this should be done with risk to the animals. If following their winter movements becomes feasible I feel it would be of interest to understand the habitat use for critical habitat assessment. It would also be of interest to explore whether the social structure remains stable during the winter months particularly as the majority of calves are born during this time (Olesiuk et al. 1990).
Plate 6.1. (a) Transient ecotype killer whale T99A thirty-five days after tagging and two days after tag transmission ceased, illustrating fresh exit wounds at barb sites. (b) Close-up view of T99A exit wounds at barb sites, illustrating extent of tissue extrusion. The open wound does not appear to be infected (Photos courtesy of the Center for Whale Research www.whaleresearch.com).

To summarise, the social networks of the southern resident killer whales are affected by both the ecological environment and individual characteristics and relationships within the network can impact the survival of individuals. The nature of the association dataset presented here is unique and every individual has been known and re-sighted regularly since 1974. I suggest that this makes the southern resident killer whales a good candidate population for developing the techniques used here. The techniques presented can be applied to other species and animal populations to give us a greater understanding of the mechanisms and functions underpinning animal social structure and the implications of these. This will greatly aid in the conservation and management of animal groups on a worldwide scale.
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Indeed, the threat of emerging infectious diseases of wildlife poses a significant challenge to biodiversity and human health. Daszak, P., Cunningham, A. A. & Hyatt, A. D. (2000) highlighted this issue in their work published in Science, where they discussed the threat of emerging infectious diseases of wildlife to both biodiversity and human health.


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