The role of social structure and kin associations in the mating system of the polygynous New Zealand sea lion (*Phocarctos hookeri*)

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Gem, granddaughter of 'Mum' (the first female sea lion to begin breeding again on the NZ mainland after 200 years), and her 2016 pup, Walter, at Allan's Beach on the Otago Peninsula. Photography by Imogen Foote, 2016.

Abstract

Mating structure describes the number of mates individuals of each sex are able to acquire, as well as the variance in reproductive success between individuals of the same sex. Such structure has important evolutionary implications for populations. The social structure of a population can have large influences on the mating structure, by determining who interacts with whom in the population and consequently each individual's reproductive success. Kin clustering is a type of social structure that allows the interaction of related individuals in such a way as to increase both direct and indirect fitness, but can also have negative consequences on the population such as the negative effects of inbreeding. Accordingly, ecologists are becoming increasingly interested in how the molecular composition of populations, that is the distribution of genetically related individuals, influences a mating system.

The New Zealand (NZ) sea lion (*Phocarctos hookeri*) is an otariid (eared seal) that displays a polygynous mating system. Females are highly gregarious and aggregate into dense clusters in the breeding colony, allowing males access to many females at once and faciliating the polygynous breeding system. This highly structured breeding system makes NZ sea lions an interesting species for studying social interactions and kin clustering within breeding systems. The overall aim of this research was to assess the role of social structure, in particular association between kin, in NZ sea lions, in order to increase our understanding of the fine-scale structure of polygynous otariid mating systems. Specifically, this research aimed to determine whether interactions between male relatives influence male reproductive success, as well as the role of female mate choice in determining the genetic relatedness of mating pairs, an important factor for subsequent offspring fitness.

Genotypes at 17 pinniped microsatellites were used to assess genetic relatedness of individuals within two populations, the Sandy Bay breeding colony on Enderby Island in NZ's subantarctic islands, and the recently founded Otago Peninsula population on NZ's mainland. Social network analysis was used to determine social interactions between males in the Sandy Bay breeding colony and look for a correlation between genetic relatedness of associates and harem tenure (a proxy for reproductive success). Estimates of genetic relatedness were also used to assess how female mate choice influences the genetic relatedness of mating pairs. This information was used to compare the mating system between the two populations.

Genetic relatedness of male associates did not appear to influence length of harem tenure. However, males that attained high harem tenure displayed increased relatedness compared to males of low harem tenure, suggesting increased reproductive success of certain genetic lineages. Comparison between the two populations (Enderby Island and Otago Peninsula) suggested a difference in the relative importance of male competition and female mate choice. Females in the Otago Peninsula population were observed to choose genetically unrelated mates, while females in the Enderby Island population were mating with males that were more related to themselves than expected by chance. This difference in female mate choice may explain how the colonising population on the Otago Peninsula is maintaining genetic diversity despite its small size.

The present study provides an increased understanding of the fine-scale structure of an otariid breeding colony, including a deeper understanding of the social interactions between kin, and the mechanisms of sexual selection that influence the breeding system of NZ sea lions.

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Chapter 1

General Introduction

1.1 Introduction to mating system structure

In theoretical panmictic populations individuals interact and mate at random, without restrictions from genetic, behavioural or geographical factors (Nagylaki, 1992; Allaby, 2014). In practice, however, a number of constraining factors lead to a mating structure within most populations that has important evolutionary implications (Krause et al., 2015). The mating structure of a population describes the number of individuals of each sex that contribute to breeding, as well as the degree of fitness variation (variation in reproductive success) between individuals (Clutton-Brock, 1989). A range of factors determine the mating structure of a population by influencing reproductive success of individuals within the population. These factors include social structure, which describes the number and types of interactions between individuals of the same and opposite sex, as well as variation in individual traits, such as size, strength or dominance status (McElligott et al., 2001; Lappin and Husak, 2005; Chung and Kim, 2010; Frère et al., 2010a).

Ecologists are increasingly becoming interested in the molecular composition of populations and the interplay between genetic structure and other factors that influence fine-scale breeding structure (Chesser, 1991a,b; Ansmann et al., 2012; Mourier et al., 2012; Nichols et al., 2012; Botero-Delgadillo et al., 2017). For example, several studies examine the relationship between dispersal patterns and genetic relatedness of individuals in a population (Cockburn et al., 1985; Chesser, 1991b; Fabiani et al., 2006; Höner et al., 2007; Costello et al., 2008; Hoffman and Forcada, 2012; Nichols et al., 2012; Botero-Delgadillo et al., 2017; Wang and Yao, 2017; Zhang et al., 2017). Consequently, genetic relatedness, both within and between sexes, and its implications for population dynamics and evolution, has been well studied in many species (Wilmer et al., 2000; Möller et al., 2001; Ortega et al., 2003; Parsons et al., 2003; Fabiani et al., 2006; Hoffman et al., 2007; Cameron et al., 2009; Frère et al., 2010a; Briga et al., 2012; Best et al., 2014; Godfrey et al., 2014; Franco-Trecu et al., 2015; Lopes et al., 2015; Bérénos et al., 2016). Understanding the fine-scale structure and dynamics of species mating systems is central in our understanding of the evolution and biology of the species.

1.2 Mating systems and the evolution of polygyny

A key factor in defining mating systems is the number of mates that individuals of each sex are able to acquire (Emlen and Oring, 1977). This measure is largely dependent on the distribution of resources, such as feeding or breeding sites, and an individual's ability to monopolise said resources (Emlen and Oring, 1977; Travis and Slobodchikoff, 1993). In most cases, individuals of one sex (usually males in mammals) compete for access to resources required by the opposite sex (Trivers, 1972). Members of the opposite sex (usually females) then exercise mate choice in order to acquire access to these resources (Trivers, 1972). Therefore, in situations in which individuals are only able to defend the resources required by one mate, monogamy arises (Emlen and Oring, 1977). This state usually occurs when resources are spread evenly and stably within the population range (Travis and Slobodchikoff, 1993). Because many individuals in the population are successfully able to defend territories and breed under these circumstances, levels of competition may be lower and sexual selection may be weak (Andersson, 1994; Webster et al., 1995).

In contrast to monogamy, polygyny may evolve when males are able to effectively monopolise multiple breeding females (Emlen and Oring, 1977). Polygyny may be either resource-defence, where males defend access to resources that females use (Downhower and Armitage, 1971; Wells et al., 1999; Bohórquez-Herrera et al., 2014), or female-defence, where males directly defend the females in order to mate (Emlen and Oring, 1977; Clutton-Brock, 1989; Wells et al., 1999). In order for polygyny to be energetically beneficial, resources or females must be easily defendable, such as when females display gregariousness and gather in dense groups (Bartholemew, 1970; Emlen and Oring, 1977). In addition to this tendency of females to aggregate, male quality must vary sufficiently so that the benefits to a female of sharing a high quality male with other females outweighs the benefits of breeding monogomously with a lower quality male (Lightbody and Weatherhead, 1988).

The level of parental investment also influences the evolution of mating strategies (Trivers, 1972; Clutton-Brock and Harvey, 1978). In populations where sexual selection for traits that enhance a males reproductive success is weak (as mentioned above), levels of competition between males are low, and fitness may be maximised in both sexes by investing more in care of offspring (Webster et al., 1995). However, in species where one sex is more heavily investing, the opposite sex is free to invest more energy in gaining multiple matings, leading to a polygamous system (Emlen and Oring, 1977). The investing sex (females in polygynous systems) is the choosy sex, while high levels of competition for access to breeding exist within the opposite sex (males) (Trivers, 1972; Clutton-Brock and Harvey, 1978; Clutton-Brock and Vincent, 1991). Competition between males is often intense, and usually leads to a large reproductive skew, where only the most successful males in the population are able to breed. Such competition leads to stronger levels of sexual selection and the evolution of sexually dimorphic traits, such as size dimorphism, elaborate ornamentation, or weaponry (Bartholemew, 1970; Emlen and Oring, 1977; McElligott et al., 2001; Bro-Jørgensen, 2007; Cullen et al., 2014).

1.2.1 Male-male competition in polygynous species

Competition between males for access to mates has led to the widespread evolution of size dimorphism and weaponry in polygynous mammals (Le Boeuf, 1974; Campagna and Le Boeuf, 1988; Lundrigan, 1996; Weckerly, 1998; McElligott et al., 2001). Features such as large size or weaponry will be selected for in males when they confer increased reproductive success to the bearer (Lindenfors et al., 2002). For example, both large size and weaponry are thought to increase a male's reproductive success by conferring advantages in physical disputes (Lundrigan, 1996; Zedrosser et al., 2007). Additionally, in species with defined breeding seasons, larger size in males is believed to help males fast throughout the breeding season in order to increase reproductive effort (Bartholemew, 1970; Wells et al., 1999; Zedrosser et al., 2007). Males can use sexually selected traits such as larger size to constrain female choice through sexual coercion and as a result male breeding behaviour is often thought to mostly control polygynous breeding systems (Clutton-Brock and Parker, 1995). Sexual coercion involves males using force to increase the chances a female will breed with him, and levels are expected to be higher in polygynous populations due to the high levels of competition between males (Clutton-Brock and Parker, 1995; Slater et al., 1997).

1.2.2 Female mate choice in polygynous species

The importance of female mate choice in polygynous mammals is not well understood. However, due to a female's larger investment in offspring in these taxa, female mate choice is hypothesised to be important (Trivers, 1972; Clutton-Brock and McAuliffe, 2009). In general, females benefit from mate choice when it increases the fitness of subsequent offspring, through either increased chance of survival or mating, and has been demonstrated across a range of mammalian taxa (Clutton-Brock and McAuliffe, 2009). For example, where social status is heritable, females that choose to mate with dominant or high ranking males are more likely to have offspring of high reproductive success (Dewsbury, 1982). Such female choice of dominant or high ranking males is observed in species such as the crab-eating macaque (*Macaca fascicularis*) and the bank vole (*Clethrionomys glareolus*) (Noordwijk, 1985; Horne and Ylönen, 1996). Similarly, the choice of males with desirable heritable traits, such as colouration or displaying ability, will increase subsequent offspring reproductive success. This type of choice is observed in species such as the rhesus macaque (*Macaca mulatta*), where females prefer males with increased red facial colouration, and red deer (*Cervus elaphus*), where females display a preference for high roaring rates in males (McComb, 1991; Waitt et al., 2003)

Females may also display mate choice of unfamiliar or genetically unrelated males, which is beneficial as it increases the chances of producing more heterozygous offspring (Kempenaers, 2007). Heterozygosity is generally associated with increased fitness, for example reduced susceptibility to disease and parasites (Acevedo-Whitehouse et al., 2003, 2006). Species such as Cape ground squirrels (*Xerus inauris*), red-backed squirrel monkeys (*Saimiri oerstedii*) and the blue monkey (*Cercophithecus mitis*) show mate choice for unfamiliar males, while species such as Antarctic fur seals (*Arctocephalus gazella*) and the greater sac-winged bat (*Saccopteryx bilineata*) display female choice of genetically unrelated males (Boinski, 1987; Hoffman et al., 2007; Shave and Waterman, 2017). This type of mate choice can have important consequences, such as resulting in sex-biased dispersal of males to groups with unrelated females (Greenwood, 1980; Cockburn et al., 1985; Pusey, 1987). These findings demonstrate that although more constraints may be imposed upon females in polygynous populations, female choice still plays an important role in polygynous mating systems (Clutton-Brock and McAuliffe, 2009).

1.3 Social structure in polygynous species

In sexually reproducing species, social interactions between individuals (i.e. the social structure of the population) play a large role in defining mating systems (Janson, 1986; Parreira and Chikhi, 2015). These include interactions between members of the same sex, such as competition for resources or cooperative behaviours, and interactions between members of the opposite sex, usually involving mate choice and the formation of mating pairs (Janson, 1986; Parreira and Chikhi, 2015). For example, in polygynous species, the level of competitive interactions between males is high (Le Boeuf, 1974; Dubuc et al., 2014). As a result, the number of males interacting with females in sexual encounters will be skewed to only those males who are successful in competitive interactions, giving rise to the polygynous system (Le Boeuf, 1974; Dubuc et al., 2014). These interactions can also influence the social structure in other ways, such as the formation of cooperative behaviours to increase fitness. For example, social interactions may form between females in order to enhance offspring survival, such as in otariids, where female interaction protects offspring from the negative effects of male competition (i.e. harrassment) (Campagna et al., 1992; Chilvers et al., 2005). These examples demonstrate the ways that social interactions can influence fitness of individuals. Therefore, variation in the number and type of interactions can lead to varying levels of fitness and reproductive success between individuals (Silk et al., 2003; Cameron et al., 2009; Frère et al., 2010b).

In the past, studies of evolutionary processes such as sexual selection did not assume any social structure to populations (Campagna and Le Boeuf, 1988; Cockburn et al., 2008). Such assumptions can compromise the outcome of studies because it assumes a well mixed (panmictic) population where any given individual is equally likely to encounter any other individual in the population, suggesting selection pressures are equal for all individuals (Mcdonald et al., 2013; Krause et al., 2015). With increasing knowledge about heterogeneity of social structure in most populations it is now understood that these processes are often more complex, with large variation in selection pressures from individual to individual (Gudelj and White, 2004; Kasumovic et al., 2008). Consequently, it is now becoming clear that the inclusion of social structure is key for an accurate understanding of evolutionary processes (Mcdonald et al., 2013; Krause et al., 2015).

1.3.1 Kin clustering and kin selection

Kin clustering is a type of social structure that occurs when related individuals associate at high levels in a population. Such clustering can occur as a result of mechanisms such as natal philopatry, where individuals return to their birth site to breed (Storz, 1999). In mammals, females are usually the philopatric sex, with males dispersing, leading to high levels of matrilineal structuring in many mammal populations (Greenwood, 1980; Chesser, 1991a; Chilvers and Wilkinson, 2008; Hoffman and Forcada, 2012; Lopes et al., 2015). Kin clustering is often also displayed in species with cooperative breeding, but is common in non-cooperative breeders, indicating benefits beyond cooperative breeding alone. The benefits of kin clustering occur when related individuals interact in such a way as to increase not only direct fitness (individual reproductive success), but also inclusive fitness (reproductive success taking into account reproduction of related individuals) (Hamilton, 1963, 1964; Silk, 2002; West et al., 2002; Gorrell et al., 2010; Briga et al., 2012).

The benefits of kin clustering have been observed across multiple mammalian groups. In populations of African elephants (*Loxodonta africana*), family groups benefit from the sharing of social knowledge from the older, experienced matriarchs, and this knowledge sharing can lead to increased reproductive success for the group (McComb et al., 2001). Alternatively, individuals may help care for the young of relatives, as seen in red squirrels where adoption between kin are observed (Gorrell et al., 2010). This behaviour increases the chance of survival of young and thus increases the helper's inclusive fitness (Hamilton, 1963; Gorrell et al., 2010). Finally, related individuals may form coalitions in order to increase mating opportunities, as seen in lions (*Panthera leo*), chimpanzees (*Pan troglodytes*), and bottlenose dolphins (*Tursiops truncatus*) (Packer et al., 1991; Mitani et al., 2000; Parsons et al., 2003). Specifically, male lions in groups are more succesful than single males in attaining tenure of a group of females, and coalitions often form with related males to increase inclusive fitness (Packer et al., 1991). Coalition formation with relatives can be beneficial because levels of aggression may be lower between related individuals, reducing energy expended in agonistic interactions and allowing increased reproductive effort of both individuals (Franco-Trecu et al., 2015). On the other hand, where mating opportunities are limited, acting as a non-reproductive 'helper' for relatives increases inclusive fitness (Packer et al., 1991).

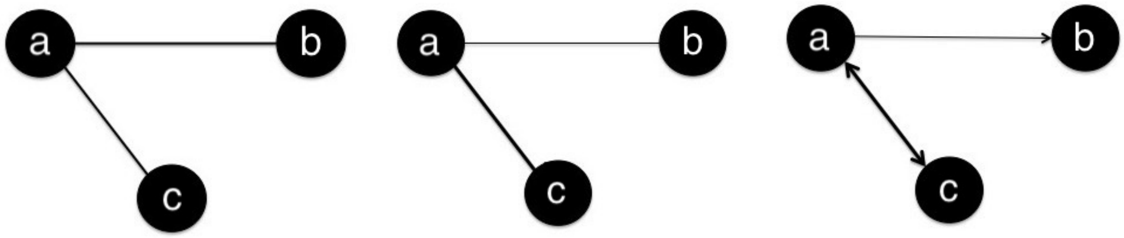
However, kin clustering can have negative consequences for a population. Clustering of related individuals can lead to higher levels of mating between relatives, which can result in increased homozygosity (Garcia-Navas et al., 2016). This increased homozygosity can have negative effects on fitness such as exposure of deleterious recessive alleles, or reduced fitness at heterozygosity-fitness correlated loci (Charlesworth and Charlesworth, 1987; Lynch et al., 1995; Hedrick and Kalinowski, 2000; Hansson and Westerberg, 2002; Acevedo-Whitehouse et al., 2003; Ekblom et al., 2005). Increased homozygosity reduces a population's ability to respond to environmental change, leading to reduced evolutionary potential and increased extinction risk (Frankham, 2005). Therefore, kin clustering represents a trade-off between the benefits of increasing inclusive fitness and the potential risk of inbreeding.

1.4 Social network analysis for studying mating systems

Social network analysis (SNA) has recently emerged as an effective method for studying the complex social relationships in animal populations. As outlined above, incorporating social structure in the study of evolutionary processes is important, and SNA provides a robust method to do this (Croft et al., 2008; Wey et al., 2008; Krause et al., 2015). SNA has been used across a number of taxa in order to determine the factors influencing social interactions. In black bears (*Ursus americanus*), SNA has shown that formation of mating pairs is associated with spatial proximity and age, where mating pairs are likely to form between nearby individuals, and include older males (Moore et al., 2015). SNA analysis in spider monkeys (*Ateles geoffoyi*) revealed social interactions between individuals of the same sex are stronger than interactions between sexes (Ramos-Fernández et al., 2009). In Australian sleepy lizards (*Tiliqua rugosa*), males were more likely to associate with related males, but male and female interactions were more likely to be between unrelated individuals (Godfrey et al., 2009).

SNA allows us to look at how and why social associations form at the individual level and how this influences population or global processes (Croft et al., 2008). The study of social networks is not a new concept; sociologists have been studying social interactions in human populations for decades, while animal scientists have adopted some methods of looking at social interactions in animal populations. The novelty of SNA is that it provides a formal framework with quantitative statistical methods that allow us to take objective measures of the population (Croft et al., 2008; Krause et al., 2015). Importantly, due to the statistical methods available, whole network analysis provides us with more information than simply looking at individual behaviours or individual pairwise associations in isolation (Croft et al., 2008).

Networks are constructed by defining associations between individuals in the population, with nodes (individuals in the population) and edges (associations between individuals) (Figure 1.1a). Networks can be weighted, where edge weights represent the strength of association between individuals (Figure 1.1b), or directed, where edges show the direction of association from actor to receiver (Figure 1.1c). Analyses can then be performed with the population data. Interactions between individuals in the population can be graphically visualized (Figure 1.1). This graphical representation enables the formulation of questions and hypotheses about what factors might be causing any structure observed (Croft et al., 2008; Krause et al., 2015). The network can also be displayed mathematically using an adjacency matrix (Figures 1.1d, 1.1e and 1.1f). Simple descriptive statistics of network properties can be calculated using matrices, such as network size, connectedness and centrality (Croft et al., 2008). The combination of this visualization and the descriptive statistics allows us to identify patterns and communities within the population. From here, we can relate the position of an individual in a network to its individual attributes (such as phenotype or genotype). Network analysis allows us to look at both the influence of the network structure on individual behaviour and vice versa, and how these factors influence population level processes (Croft et al., 2008; Krause et al., 2015).



(a) (b) (c)

	a	b	c
a	-	1	1
b	1	-	0
c	1	0	-

(d)

	a	b	c
a	-	0.2	0.8
b	0.2	-	0
c	0.8	0	-

(e)

	a	b	c
a	-	0.2	0.8
b	0	-	0
c	0.8	0	-

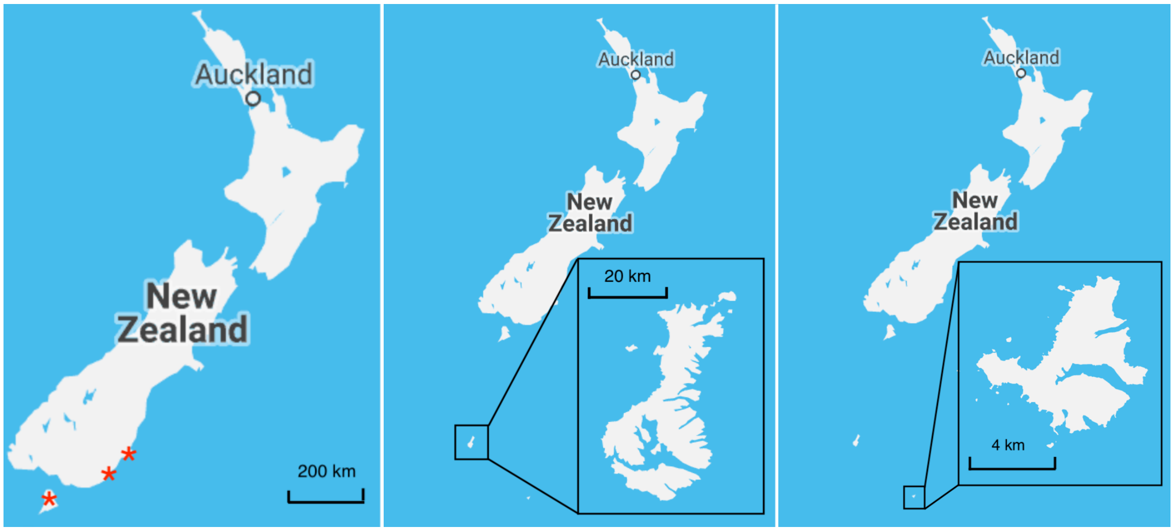
(f)

Figure 1.1: An example of a social network with three individuals (nodes) a, b and c in the population: a) shows unweighted, undirected network with black lines (edges) showing associations between individuals; b) shows a weighted network with edge weight indicating association strength and; c) shows a directed network with arrows showing the direction of association; d), e) and f) are association matrices for the unweighted, undirected network, weighted network and directed network, respectively

Social associations can be defined in any number of ways depending on what is known of the species biology. These associations are often defined in terms of spatial proximity (group membership or space use) (Chaverri et al., 2007; Best et al., 2013, 2014; Armansin et al., 2016) but can also be defined by behavioural interactions (cooperation, competition, sexual interactions) (Archie et al., 2006; Manno, 2008; Madden et al., 2009). One of the strengths of using network analysis over simple observations is the use of association indices. Association indices take simple association counts (the number of times two individuals were seen together or interacting) and adjusts them to reduce bias that may be present in the data due to limitations in data collection (Cairns and Schwager, 1987; Croft et al., 2008). Such bias may arise in species where individuals vary in their probability of being detected during surveys (Cairns and Schwager, 1987; Armansin et al., 2016), or when individuals vary in gregariousness, meaning certain individual's chances of being observed associating with other individuals are lower (Best et al., 2014). Thus, social network analysis provides a robust analytical technique to look at population data and study the causes and consequences of social networks.

1.5 New Zealand sea lion mating system

The New Zealand (NZ) sea lion (*Phocarctos hookeri*) is an otariid (eared seal) species endemic to New Zealand (Childerhouse and Gales, 1998). It is the rarest sea lion in the world, and is listed as endangered by the International Union for the Conservation of Nature (IUCN) (Chilvers, 2015), and nationally critical under the NZ threat classification system (Baker et al., 2010). Historically, the NZ sea lion's range extended around the entire NZ South Island coast, and into the North Island. However, Maori subsistence hunting and European sealing caused local extirpation following human settlement in NZ (Childerhouse and Gales, 1998). Now, the majority of breeding occurs on two groups of NZ's subantarctic islands - Campbell Island and the Auckland Islands (Figures 1.2b & 1.2c) (Chilvers et al., 2007). In recent years a small amount of breeding activity has re-established on the NZ mainland around the Otago and South coasts (Figure 1.2a) (Childerhouse and Gales, 1998; Gales, 2009; Chilvers, 2018). In 1994, one female from the subantarctic lineage dispersed to pup on the Otago Peninsula of the South Island (Childerhouse and Gales, 1998). Pup production is steadily increasing in this population, with 13 pups born during the 2017 breeding season alone. More recently, breeding has also established on Stewart Island, with pup production exceeding 35 pups a year between 2014 and 2017 (Chilvers, 2018). Recent research has shown that the subantarctic lineage is genetically divergent from the historic NZ mainland lineage, indicating that breeding on the NZ mainland today represents a recent colonisation by the genetically distinct subantarctic lineage and extinction of the historic NZ mainland lineage (Collins et al., 2014).



(a) (b) (c)

Figure 1.2: Map of a) New Zealand mainland with red asterisks indicating current NZ sea lion breeding sites, b) Auckland Islands location in comparison with NZ mainland and c) Campbell Island location in comparison with NZ mainland

1.5.1 Breeding behaviour

Characteristic of an otariid species, the NZ sea lion displays a polygynous mating system and is a highly gregarious mammal, forming dense breeding colonies on land (Bartholemew, 1970; Wells et al., 1999). The NZ sea lion breeding season usually begins in late November and lasts until mid to late January (Ridgway and Harrison, 1981; Augé et al., 2009; Gales, 2009). Breeding begins when males come ashore and compete to establish breeding territories, with females arriving later, in early December (Gales, 2009). Female NZ sea lions experience high levels of harassment, usually from non-territorial males (males not in the harem), which can result in female death or injury (Chilvers et al., 2005). Approximately five in every 1000 female New Zealand sea lions are killed every breeding season and 84% possess scars from harassment by subordinate males (Chilvers et al., 2005). Consequently, females aggregate in dense groups surrounded by territorial males (males in the harem), with ratios of up to 25 breeding females to one male observed within the breeding harem (Figure 1.3) (Augé et al., 2009; Gales, 2009). This aggregation reduces harassment from subordinate, non-territorial males, resulting in increased female and pup survival (Campagna et al., 1992; Gales, 2009).

The dense aggregation of females allows males access to multiple females at once, and facilitates the polygynous breeding system. Males undergo intense, continuous competition for tenure within the breeding harem (Robertson et al., 2006). Unlike other otariid species where males are believed to remain in the breeding harem for extended, uninterrupted periods (McCann, 1980; Ridgway and Harrison, 1981; Campagna and Le Boeuf, 1988), harem tenure for NZ sea lions is often short and more than half of territorial males will break harem attendance for at least one day during their tenure (Robertson et al., 2006). In otariids, for the most part, only those males that are successful in establishing territory tenure will be successful in reproduction, leading to a high variance in reproductive success among males in the population (Figure 1.3) (Bartholemew, 1970). Such intense competition between males has led to the evolution of sexual size dimorphism, where male otariids are on average three times heavier than females (Weckerly, 1998). Body size in mammals is positively correlated with reproductive success and is thought to aid in physical competitive ability of males (McElligott et al., 2001; Zedrosser et al., 2007). As well as increased competitive ability, size dimorphism in otariids is though to provide large blubber reserves which allow males to fast and remain in the breeding colony for extended periods (Bartholemew, 1970; Wells et al., 1999).

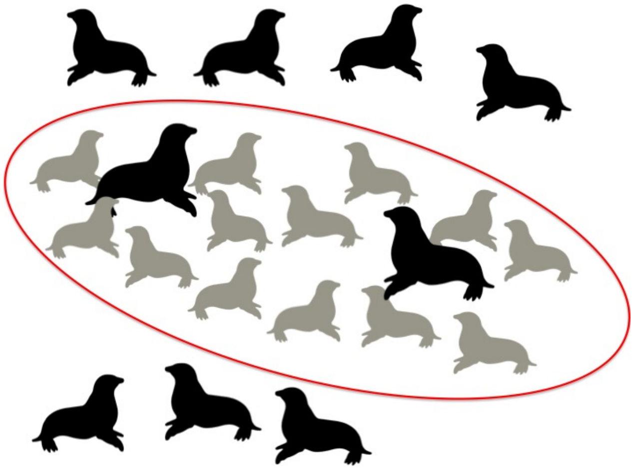


Figure 1.3: Diagram of a NZ sea lion breeding colony where males are represented in black and females in grey. The red circle outlines the breeding harem, with territorial (reproductive) males associating with females inside, and non-territorial (reproductively unsuccessful) outside the harem

NZ sea lions display dispersal patterns characteristic of otariids, with high levels of philopatry (returning to breed at natal site) and site fidelity (repeat sightings at natal or non-natal sites) (Chilvers and Wilkinson, 2008). Levels of philopatry in females are estimated at up to 64%, however philopatry in males is much lower, at an estimated 6.8-12% (Chilvers and Wilkinson, 2008). Females also display significantly higher site fidelity to natal sites than males, who are more likely to be resighted at non-natal sites (Chilvers and Wilkinson, 2008). As a result, males tend to be the more widely dispersing sex, with resightings of males from the subantarctic populations not uncommon on the NZ mainland (Robertson et al., 2006). On the other hand, on the rare occasion that females have been observed breeding at non-natal sites, these sites were usually relatively close to natal sites (Chilvers and Wilkinson, 2008). These dispersal patterns have implications for fine-scale structuring of breeding colonies, such as matrilineal structuring and kin clustering (Lopes et al., 2015). As well as influencing fine-scale genetic structuring, limited dispersal of females can impact the range expansion and recolonisation potential of the species. With the declining numbers observed in the NZ sea lion population, density-dependent factors are not impacting female breeding success (Chilvers and Wilkinson, 2008; Chilvers, 2015; Meyer et al., 2015). As a result, female dispersal to new breeding sites is unlikely and has thus far rarely been observed (McConkey et al., 2002; Chilvers and Wilkinson, 2008).

1.6 Thesis aims

The highly structured, polygynous breeding system of otariid species such as NZ sea lions makes them of interest in studying the influence of social interactions on mating systems (Bartholemew, 1970; Robertson et al., 2006; Gales, 2009). Understanding the dynamics and social structure of mating systems is key in our understanding of the processes that shape the evolution of species. The overall aim of my research is to assess the role of social structure, particularly associations between kin, in influencing the reproductive success of individuals in NZ sea lions. This will increase our understanding of the fine-scale structure of otariid mating systems. In order to address these aims, I will:

- Identify whether a relationship exists between genetic relatedness and male social interactions (defined by space use), and whether associations between kin can act to increase male reproductive success. If kin coalitions increase the reproductive success of male NZ sea lions, a high level of association between male relatives in the breeding harem would be expected.

- Identify the role of female mate choice in a polygynous mating system and whether mate choice of unrelated individuals may help to retain adequate genetic diversity in a small population. Given that the Otago Peninsula population displays an unexpectedly high level of nuclear genetic diversity despite being recently founded by one female, female mate choice of unrelated males would help to explain the maintenance of genetic diversity in this population.

- Increase our understanding of how the above factors influence fine-scale structure of an otariid mating system.

1.7 Thesis structure

The main research outputs of this thesis are contained within two chapters (Chapters Two and Three). Chapter Four discusses the wider relevance of these results in relation to the existing literature.

Chapter Two analyses the role of genetic relatedness in the formation of social interactions between male NZ sea lions, and how this influences male reproductive success. This chapter uses genetic samples collected and genotyped by Osborne et al. (2016) to see if kin association may act to increase male reproductive success. This analysis is done using social network analysis to define social interactions between males of varying reproductive success, and relating this to variation in genetic relatedness.

Chapter Three assesses female mate choice and its role in the maintenance of genetic diversity in the small, colonising Otago Peninsula population. This chapter describes how differences in mating systems between the large Enderby Island breeding colony and the small, newly-founded Otago Peninsula population may alter the strength of female mate choice, as well as the role of female mate choice in choosing genetically unrelated mates and how such mate choice may help to explain the unexpectedly high levels of nuclear genetic variation observed in the Otago Peninsula population. Genetic data for the Enderby Island population was collected and genotyped by Osborne et al. (2016), while genetic data for the Otago Peninsula population was collected by D.O.C. and genotyped in the present study.

Chapter Four places the results from chapters two and three into context of the wider literature, in order to highlight their relevance. I compare my results to similar studies addressing the different forms of sexual selection (male competition and female mate choice) and discuss the implications of my findings for future research and management of NZ sea lions.

Chapter 2

Kin clustering in a NZ sea lion breeding harem

2.1 Introduction

The spatial distribution of individuals in a population and the resulting social interactions are influential on a range of fitness parameters. In polygynous breeding systems, male reproductive success is directly related to access to females which allows an increased number of matings (Bartholemew, 1970; Pörschmann et al., 2010). Males physically compete for access to females directly (female-defence polygyny) or to resources required by females (resource-defence polygyny) or both, in order to exclude rivals (Campagna and Le Boeuf, 1988; Wells et al., 1999; Franco-Trecu et al., 2015). Such competition involves agonistic interactions between males and can be energetically costly (Clutton-Brock et al., 1979; Preston et al., 2011). This competition also causes a high reproductive skew where only a small percentage of males are successful in gaining access to the harem and therefore breeding (Bartholemew, 1970). As a result, there is a wide variance in male reproductive success within a population (Le Boeuf, 1974; Pemberton et al., 1992; Coltman et al., 2002; Dubuc et al., 2014). Consequently, the spatial distribution of males in a polygynous population influences inter-individual competition, with important effects on individual reproductive success.

A range of factors influence social interactions between males, including home range overlap as well as demographic factors such as sex, size and age class (Chaverri et al., 2007; Frère et al., 2010b; Mourier et al., 2012; Best et al., 2014; Godfrey et al., 2014). Genetic relatedness is also an important determinant of social interactions in mammalian societies, influencing dispersal and reproductive behaviours and ultimately individual fitness (Greenwood, 1980; Chesser, 1998). In some populations, individuals will actively avoid highly related members of the opposite sex. Such avoidance behaviour can occur through sex-biased dispersal, where members of one sex (usually males in mammals) leave the natal group thereby preventing breeding with close relatives (Greenwood, 1980; Cockburn et al., 1985; Pusey, 1987; Höner et al., 2007). In other species, female mate choice leads to females actively seeking out unrelated males within the population. This type of choice is demonstrated in species such as Antarctic fur seals (*Arctocephalus gazella*), where females have been observed to move across crowded breeding colonies in order to breed with unrelated males (Hoffman et al., 2007). Such mechanisms of inbreeding avoidance are beneficial for fitness, as mating between related individuals can have negative consequences, such as increased levels of homozygosity (Charlesworth and Charlesworth, 1987; Hedrick and Kalinowski, 2000; Hansson and Westerberg, 2002). Increased homozygosity can lead to inbreeding depression through exposure of deleterious recessive alleles or reduced fitness at heterozygosity-fitness related loci (Charlesworth and Charlesworth, 1987; Lynch et al., 1995; Hansson and Westerberg, 2002; Acevedo-Whitehouse et al., 2003; Ekblom et al., 2005).

In some instances however, related individuals will associate more often than expected, leading to kin clustering within the population. This clustering can result from behaviours such as natal philopatry, which involves individuals returning to their birth site to breed and hence clustering of family lineages (Greenwood, 1980; Chesser, 1991a). Kin clustering can increase fitness in a number of ways. This increased fitness can result from individuals showing higher tolerance of relatives as well as increased helping behaviours such as allomaternal care, knowledge sharing and coalitionary support (Silk, 2002; Gorrell et al., 2010; Briga et al., 2012). Although kin clustering is most widely studied in cooperative breeding systems (Garza et al., 1997; Woxvold et al., 2006; Hatchwell, 2009, 2010; McDonald et al., 2016), it has been found in non-cooperative breeders (Shorey et al., 2000; Coltman et al., 2003; Foerster et al., 2006). These findings suggest that the fitness benefits of interacting with kin extend beyond cooperative breeding.

The formation of male coalitions based on genetic relatedness has been studied in a range of mammal species. Coalitions of males have high levels of association in order to defend territories or gain access to females leading to increased reproductive success (Packer et al., 1991; Grinnel et al., 1995; Mitani et al., 2000; Möller et al., 2001; Parsons et al., 2003). Kin selection predicts individuals will benefit from coalitions with related individuals both directly, through increased reproductive success, and indirectly, through inclusive fitness from increased reproductive success of kin (Hamilton, 1963, 1964). Kinship has been found to play a role in the formation of male coalitions in various mammal species including lions (*Panthera leo*), chimpanzees (*Pan troglodytes*), golden snub-nosed monkeys (*Rhinopithecus roxellana*) and bottlenose dolphins (*Tursiops truncatus*) (Packer et al., 1991; Mitani et al., 2000; Parsons et al., 2003; Qi et al., 2017). However, kin associations have not been consistently demonstrated across or within taxa and appears context dependent. For example, kinship appears important for male coalition formation in some bottlenose dolphin populations (Parsons et al., 2003), but not others (Möller et al., 2001). In lions, the size of the coalition determines whether kinship is important. Small coalitions may be composed of related or unrelated males, but as group size increases, the coalition is likely to be composed of only related males, where some males will act as non-reproductive 'helpers' (Packer et al., 1991). For this reason, the presence of kin coalitions can not be generalised and must be assessed on a case by case basis.

New Zealand (NZ) sea lions (*Phocarctos hookeri*) are an interesting model species to study kin clustering due to their highly structured breeding system. The breeding behaviour of NZ sea lions is characteristic of polygynous otariids. During the austral summer (November to January or early February), NZ sea lions form temporary breeding colonies on remote beaches in NZ's subantarctic islands (Ridgway and Harrison, 1981; Robertson et al., 2006; Augé et al., 2009). Males arrive first and compete through vocal threat displays and physical challenges to establish territories (Marlow, 1975; Gales and Fletcher, 1999; Robertson et al., 2006). Females are highly gregarious and aggregate in dense groups or harems which allows territorial males access to many females at once (McNally et al., 2001; Chilvers et al., 2005), a necessary requirement for polygyny (Bartholemew, 1970; Emlen and Oring, 1977). As observed in other otariids, it is assumed that male NZ sea lion reproductive success is related to the ability to obtain and maintain territory tenure (Bartholemew, 1970; Pörschmann et al., 2010). Under these circumstances, only males who can establish territories within the harem are successful in breeding, leading to a high reproductive skew (Bartholemew, 1970; Pörschmann et al., 2010). As well as this reproductive skew, of those otariid males that are successful, the degree of reproductive success appears related to the length of time a male can maintain his territory (i.e. territory tenure) (Bartholemew, 1970; McCann, 1980). Consequently, challenges between territorial and non-territorial male NZ sea lions are frequent and intense (Robertson et al., 2006). Unlike most other otariid species where males defend territories for long, continuous periods (McCann, 1980; Ridgway and

Harrison, 1981; Campagna and Le Boeuf, 1988), NZ sea lion harem tenure has been shown to be much shorter and often interrupted (Robertson et al., 2006). The displays involved in male-male competition are costly and thus males who can minimise energy expended and maximise territory tenure, such as those in peaceful coalitions with neighbours, should be more reproductively successful (Campagna, 2009).

Research on fine-scale otariid breeding colony structure is limited to a few species. Kin clustering leading to increased fitness has been observed in South American sea lions (*Otaria flavescens*) where related males aggregate near the tide-line of the breeding colony (Franco-Trecu et al., 2015). These males display higher reproductive success than males at other positions within the colony. This pattern suggests some fitness advantage of associating with relatives; presumed to be reduced energy spent in agonistic interactions (Franco-Trecu et al., 2015). Furthermore, most otariid species display site fidelity and philopatry where they return to previous breeding sites or birth sites to breed (Chesser, 1991a; Hoffman et al., 2006; Chilvers and Wilkinson, 2008; Hoffman and Forcada, 2012; Lopes et al., 2015). In extreme cases, such as Antarctic fur seals (*Arctocephalus gazella*), females and males return to within a body length of birth sites (natal philopatry), or their previous breeding site (site fidelity) respectively (Hoffman et al., 2006; Hoffman and Forcada, 2012). Philopatry has important implications for fine-scale genetic structuring, such as in the Galapagos fur seal (*Arctocephalus galapagoensis*) where strong matrilineal structuring within colonies is observed as a result of female philopatry (Lopes et al., 2015). In NZ sea lions, females display higher levels of philopatry, while males show higher site fidelity (Chilvers and Wilkinson, 2008), however the population genetic structuring as a consequence of these behaviours has not yet been studied.

Social network analysis is an emerging tool to study social interactions in animal populations (see Chapter 1) (Armansin et al., 2016; Godfrey et al., 2014). As such, it is an ideal method for studying the mating system and fine-scale genetic structure in NZ sea lion populations. Social network analysis allows the quantification and interpretation of interactions between individuals in a population, and the factors influencing choices of interactions, thus defining fine-scale structure. Networks are constructed by defining associations between individuals, which can be defined in a number of ways (e.g. spatial proximity or behavioural interactions) depending on the research question and what is known of the species' biology (Croft et al., 2008; Farine and Whitehead, 2015). These networks can then be represented graphically and quantitative statistical analyses can be performed. This type of analysis helps in addressing a range of questions regarding relationships and the subsequent fine-scale structure observed within the population (Croft et al., 2008).

2.1.1 Research aims

This research examined the fine-scale breeding behaviour of male NZ sea lions to assess the influence of genetic relatedness on social interactions and consequently individual fitness. I hypothesized that males show a preference for association with related individuals as seen in South American sea lions (*Otaria flavescens*) (Franco-Trecu et al., 2014), and that there is a correlation between genetic relatedness and male association (defined by space use) for males in the harem. Furthermore, under the assumptions that kin associations confer increased fitness (Packer et al., 1991; Mitani et al., 2000; Parsons et al., 2003), and that harem tenure is a suitable proxy for reproductive success (Bartholemew, 1970; Pörschmann et al., 2010), I hypothesized that genetic relatedness should be greater between males of high harem tenure than low harem tenure. This research will reveal whether genetic relationships play a role in NZ sea lion breeding systems, and further our knowledge of fine-scale structure of breeding aggregations of the polygynous otariids.

2.2 Materials and methods

2.2.1 Data collection

Behavioural data were collected during the 2003 breeding season (NZ sea lion breeding seasons follow the austral summer and thus are referred to by the year in January of the season) from 202 males at Sandy Bay breeding colony on Enderby Island, within New Zealand's Auckland Islands archipelago (Figure 2.1) (Robertson et al., 2006). For ease of individual identification, males were marked with a unique alpha-numeric symbol using an ammonia/hydrogen peroxide bleach solution. Skin biopsies for DNA analysis were taken using a cross-bow biopsy system. During the breeding season (early December to mid January), daily beach surveys were undertaken and the location of males recorded using a Garmin GPS 12 (Garmin International Inc., Olathe, KS66062) (Robertson et al., 2006). Harem status of males was recorded at each sighting as a proxy for male reproductive success; 'territorial' males being in the harem, 'peripheral' males within 10 metres of the harem and 'non-territorial' males more than 10 metres from the harem. On 12 December 2002, three beach surveys were conducted (between 9.00-11.00am, 1.00pm-2.30pm and 5.00pm-6.00pm) allowing assessment of the level of male movement within a day to determine if one survey is sufficient to accurately identify male associations.

2.2.2 DNA analysis

Genotypes at 17 pinniped microsatellites were obtained from Osborne et al. (2016) for 104 males present on the breeding beach in the 2003 breeding season. The loci have been demonstrated to be in Hardy-Weinberg proportions and informative in various analyses of otariids (Collins et al., 2014, 2016; Osborne et al., 2016; Collins et al., 2017). Basic statistics for each locus, such as observed heterozygosity (*Ho*), expected heterozygosity (*He*), number of alleles (*k*), and sample size (*N)* were calculated using the Excel add-in GenAlex (version 6.5) (Table 2.1) (Peakall and Smouse, 2012).

Simulations were run using the software package COANCESTRY (Wang, 2011) to identify the best relatedness estimator and to assess the performance of this estimator using the empirical allele frequencies across the 17 pinniped microsatelite loci as described in Taylor (2015). Briefly, the population used in the simulations comprised 100 dyads from each one of the six categories parent-offspring (r_{xy} = 0.5), full siblings (r_{xy} = 0.5), half siblings (r_{xy} = 0.25), first cousins (r_{xy} = 0.125), second cousins (r_{xy} = 0.03125), and unrelated (r_{xy} = 0). Genotypes were simulated using empirical allele frequencies from the dataset of true male NZ sea lions genotypes from the Sandy Bay breeding colony. Estimates produced using the triadic likelihood method (TrioML) were the most closely correlated with the simulated true relatedness (correlation coefficient = 0.87) (see Appendix 1). COANCESTRY was used to calculate TrioML relatedness coefficients for 104 males for which microsatellite genotypes at these 17 loci were available (Osborne et al., 2016).

All analyses were also performed using the Wang relatedness estimator (Wang, 2002), in order to compare results between two relatedness estimators. The Wang estimator was the second best performing estimator with a correlation of 0.83 between true and estimated relatedness values (see Appendix 1).

(a) (b)

Figure 2.1: The Sandy Bay NZ sea lion breeding colony; a) the Auckland Islands with the location of Sandy Bay indicated by an asterisk and b) the breeding beach, with the main breeding harem outlined in red. Brindle coloured individuals are adult females and dark brown individuals are adult males. Males observed outside the red line are considered 'peripheral' (within 10 metres of harem) or 'non-territorial' (more than 10 metres from harem).

Table 2.1: Variation at 17 microsatellite loci in 104 male NZ sea lions from Sandy Bay breeding colony in the 2003 breeding season.

Microsatellite Locus	***GenBank Accession***	***N***	***k***	***Ho***	***He***
PvcA	–	104	8	0.808	0.757
G1A	–	104	6	0.654	0.627
ZcwE03	AM039821	104	4	0.510	0.553
Hg8.10	G02096	104	3	0.471	0.437
OrrFcB7	G34928	103	7	0.660	0.764
Hg6.1	G02091	104	6	0.663	0.625
Hg6.3	G02092	84	6	0.786	0.764
Lc28	AF140584	104	5	0.673	0.705
Pv9	G02096	104	5	0.413	0.513
HI16	AF140588	104	9	0.702	0.724
OrrFCB1	G34933	97	10	0.691	0.803
Lc5	AF417694	104	4	0.500	0.501
Pv11	U65444	104	7	0.894	0.744
Hg4.2	G02090	103	11	0.883	0.837
ZcCgDh5.16	AY676477	103	16	0.796	0.868
M11A	–	104	4	0.510	0.616
ZcwC03	AM039819	82	8	0.793	0.767

N, number of NZ sea lions genotyped at each locus; *k*, number of alleles; *Ho*, observed heterozygosity; *He*, expected heterozygosity.

2.2.3 Assessing genetic relatedness and reproductive success

Unlike other otariid species where males maintain harem tenure for extended periods throughout the breeding season (Ridgway and Harrison, 1981), the turnover rate of male NZ sea lions within the harem is high, and a large number of males break their tenure for at least one day during the season (Robertson et al., 2006). Consequently, reproductive success might vary widely amongst territorial males (if harem tenure is assumed to be a reliable proxy for reproductive success; Bartholemew (1970); Pörschmann et al. (2010)). Male dyads of high, as well as low, harem tenure were assessed to determine if they were more related than expected by chance, and to examine if differences in mean relatedness exist between males in these two categories. This analysis was done by permuting relatedness coefficients across all male dyads in R (version 3.4.0) (R Core Team, 2017). Only 18% of males were recorded as in the harem for more than 40% of their time on the breeding beach, therefore 40% of time spent in harem was chosen as the threshold for males to be considered ’high harem tenure’.

Males with fewer than 10 sightings on the breeding beach across the whole breeding season were removed from the dataset prior to analysis to ensure undersampled individuals did not introduce bias. The number of days each male was recorded as territorial, peripheral and non-territorial were counted and the percentage of time each male spent in the harem was calculated. Male dyads were then assigned as either ‘high harem tenure’, if both males were in the harem for more than 40% of days they were both recorded as present on the breeding beach, or ‘low harem tenure’, if both males were in the harem less than 40% of the days they were both recorded as present on the breeding beach. The ’sample’ function in R was used to construct 1,000 permuted datasets, where relatedness coefficients of dyads were permuted without replacement (R Core Team, 2017). Mean relatedness of each of these two categories (high vs. low harem tenure) was considered to be significantly greater than expected by chance if the observed mean relatedness of that category was greater than the mean relatedness in more than 95% of the permuted datasets. Mean relatedness was considered to be significantly different between the two categories when the observed difference in mean relatedness between categories was greater than the difference in mean relatedness between categories in more than 95% of the permuted datasets.

2.2.4 Social network analysis

A social network of territorial, peripheral and non-territorial males was developed based on spatial proximity of males to determine individual space use and how genetic relatedness shapes interactions. Males were considered to have associated if they had been sighted within 15 metres of each other on the same day, determined using the *geosphere* package (Hijmans, 2016) in R (R Core Team, 2017). Analyses with associations defined as within 5 metres and 10 metres were also run, however the significance of results did not change, so only those for 15m are reported. Analyses were performed with a subset of data excluding males with fewer than

10 sightings, as well as with the full dataset. Significance of results did not change when individuals observed fewer than 10 times were added to the dataset so analysis was carried out with the full dataset.

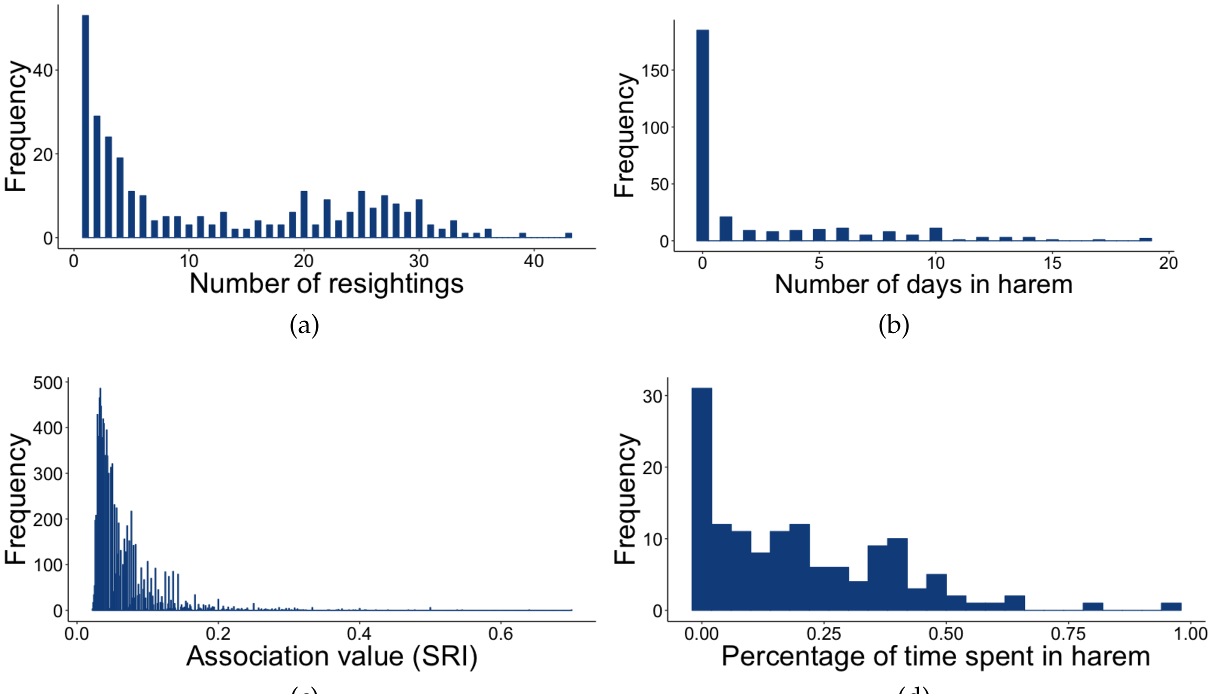
As a measure of association strength, a simple ratio index (SRI) (Croft et al., 2008) was calculated for each male dyad, which is the number of days individuals were seen associating (within 15 metres) divided by the total number of days each individual was seen (associating or not associating). The SRI was chosen as a measure of association strength as it is suitable when observations of individuals are likely to be made if the individual is present (Croft et al., 2008). As daily surveys of the whole beach were made, this assumption is likely to be true. The package *igraph* (Csardi and Nepusz, 2006) was used to construct and visualise a network using the SRI values. The package *asnipe* (Farine, 2017) was used to perform Multiple Regression Quadratic Assignment Procedure (MRQAP) analysis with 10,000 randomisations, to determine the correlation between SRI and relatedness coefficient of dyads.

The modularity coefficient (Q), which identifies communities (dense clusters) within the network, was also calculated using *igraph* for the full network, as well as networks of territorial males only and high harem tenure males only. Q was optimised using the fast greedy optimisation algorithm (Clauset et al., 2004). Networks with Q values > 0.3 are considered to display community structure (Csardi and Nepusz, 2006).

To determine whether associations were random, or whether individuals were associating more or less often than would be expected by chance, observed SRI values were compared to 1,000 permuted data sets. Permutations were performed using the 'sample' function in R to permute sighting dates of individual data points without replacement and SRI values were calculated for each permuted dataset (R Core Team, 2017). The number of sightings, as well as the home range of each individual was kept constant by retaining male locations for all data points and shuffling the sighting dates within the set of observed sighting dates for each particular male. Dyads were considered to be associating less often than expected by chance when 95% of permuted SRI values were greater than the observed SRI value, and associating more often than expected by chance when 95% of permuted SRI values were less than the observed SRI value. Values outside these cutoffs were designated as random association. Dyads associating more, less or the same as expected by chance were coded within an adjacency matrix as 1, -1 and 0 respectively. Further MRQAP analysis using the *asnipe* package (Farine, 2017) was performed in order to determine the correlation between genetic relatedness and dyad association type (associating more, less or the same as would be expected by chance).

2.3 Results

Of the 295 males present on the breeding beach in the 2003 breeding season, 133 had a resighting frequency greater than 10. The mean resighting frequency was 12 days, with the minimum one and maximum 43 days (Figure 2.2a). Of the total males, 110 spent at least one day in the harem. The mean number of days spent in the harem by a territorial male was 6, with the minimum one and maximum 19 days (Figure 2.2b). Of male dyads that were seen associating, the average SRI value was 0.06, with the minimum 0.02 and maximum 0.70 (Figure 2.2c). Out of the 110 territorial males that spent at least one day in the harem, 18% were considered ’high harem tenure’ (in the harem more than 40% of the days they were sighted on the breeding beach).

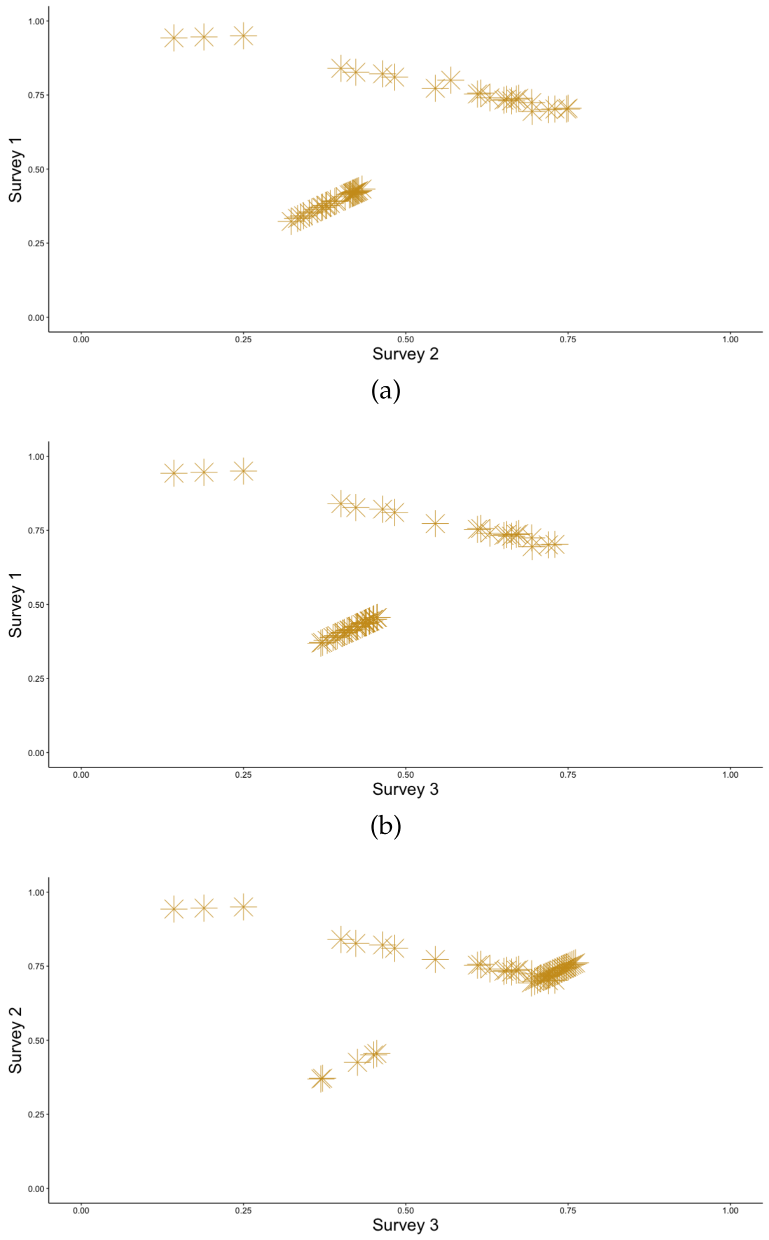


(a) (b)

(c) (d)

Figure 2.2: For the 2003 NZ sea lion breeding season, frequency of a) the number of resightings of males on the breeding beach, b) the number of days territorial males spent in the harem, c) occurrences of association strength (SRI) values for male dyads and d) percentage of time spent in the harem by territorial males.

Analysis of male association patterns across three beach surveys performed on the same day (12 December 2002) showed significant positive correlation (Figure 2.3). This correlation indicates movement of males within the harem within one day is minimal and thus one beach survey per day is sufficient to capture data of male status within the harem.



(a)

(b)

(c)

Figure 2.3: Proportion of total associates remaining the same for each male from each survey conducted on 12 December 2002 (the number of associates from each survey that were present in both surveys out of the total number of associates from both surveys) for a) survey 1 vs. survey 2 (coefficient = 0.49, p < 0.001, n = 50), b) survey 1 vs survey 3 (coefficient = 0.54, p < 0.001, n = 50) and c) survey 2 vs survey 3 (coefficient = 0.64, p < 0.001, n = 50)

2.3.1 Relatedness of high and low harem tenure males

The mean relatedness (TrioML relatedness coefficient) for dyads of high and low harem tenure was 0.11 and 0.09 respectively (Figure 2.4). The mean relatedness for dyads of high harem tenure was significantly higher than expected by chance (randomised mean = 0.088 (0.070 — 0.107, 95% CI), p = 0.031). The mean relatedness for dyads of low harem tenure was not significantly higher than expected by chance (randomised mean = 0.087 (0.087 — 0.088, 95% CI), p = 0.969). The mean difference in relatedness observed between high and low harem tenure males was significantly larger than expected by chance (observed mean difference = 0.023, randomised mean difference = 0.009 (0.001 — 0.022, 95% CI), p = 0.041).

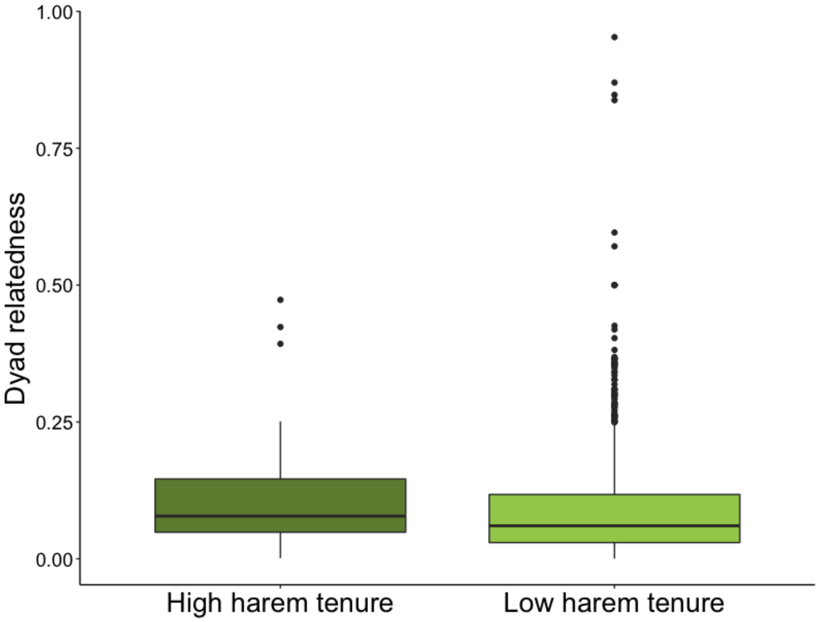


Figure 2.4: Spread of relatedness (TrioML relatedness coefficient) of NZ sea lion male breeding dyads with high harem tenure (more than 40% time spent in harem) (n=63 dyads) and low harem tenure (less than 40% time spent in harem) (n=1,403 dyads).

2.3.2 Male genetic relatedness and social association

No dense subgroupings (modularity), which would be indicative of communities, were identified in the network of all males (Q = 0.19; Figure 2.5), and high harem tenure males only (Q = 0.16; Figure 2.6). A low level of modularity was detected in the network of territorial males only (Q = 0.34). Four communities were identified within this dataset, with each including between 19 and 45 males (Figure 2.7). No overall correlation between male association (SRI) and genetic relatedness was observed when looking across the whole population of males on the breeding beach, indicating no consistent clustering of related males (coefficient = -0.002, p = 0.563, Figure 2.8). This outcome held when looking at subsets of males, including territorial and peripheral males only (coefficient = 0.0037, p = 0.401), as well as males of high harem tenure (coefficient = -0.21, p = 0.887, Figure 2.9), and territorial males only (coefficient = 0.031, p = 0.137, Figure 2.10).

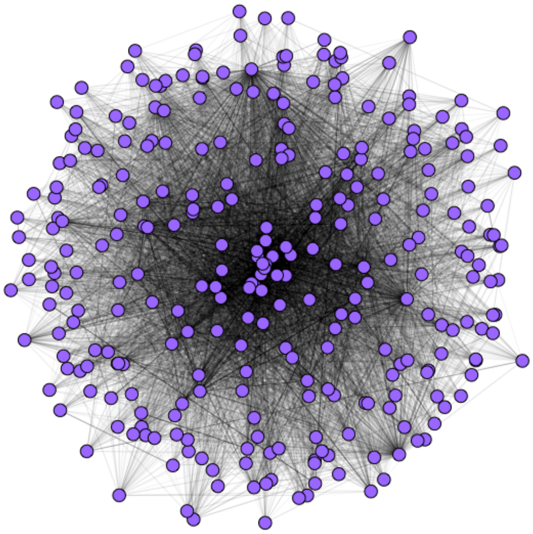


Figure 2.5: Social network of all male NZ sea lions present on Sandy Bay beach during the 2003 breeding season. Nodes (circles) represent individual animals and edges (black lines) represent social associations, where line thickness indicates strength of associations (SRI) (n = 295)

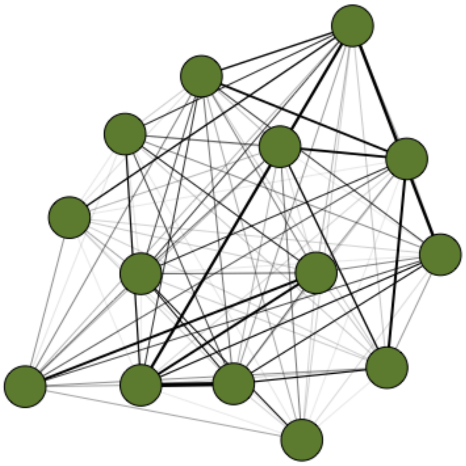


Figure 2.6: Social network of male NZ sea lions with high harem tenure (more than 40% of time on breeding beach spent in harem) present on Sandy Bay beach during the 2003 breeding season. Nodes (circles) represent individual animals and edges (black lines) represent social associations, where line thickness indicates strength of associations (SRI) (n = 14)

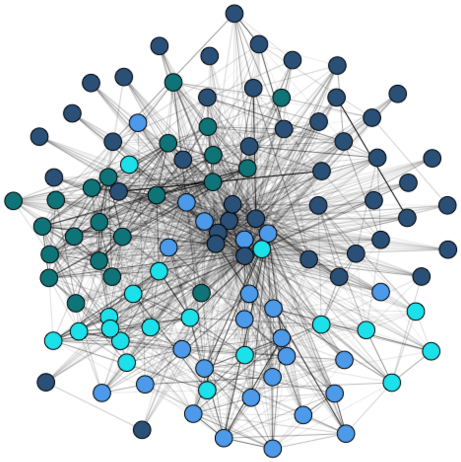


Figure 2.7: Social network of territorial (within harem) male NZ sea lions present on Sandy Bay beach during the 2003 breeding season. Nodes (circles) represent individual animals and edges (black lines) represent social associations, where line thickness indicates strength of associations (SRI). (n = 111). Different shades of blue indicate membership of the four communities identified in modularity analysis (n = 45, 19, 25 and 22).

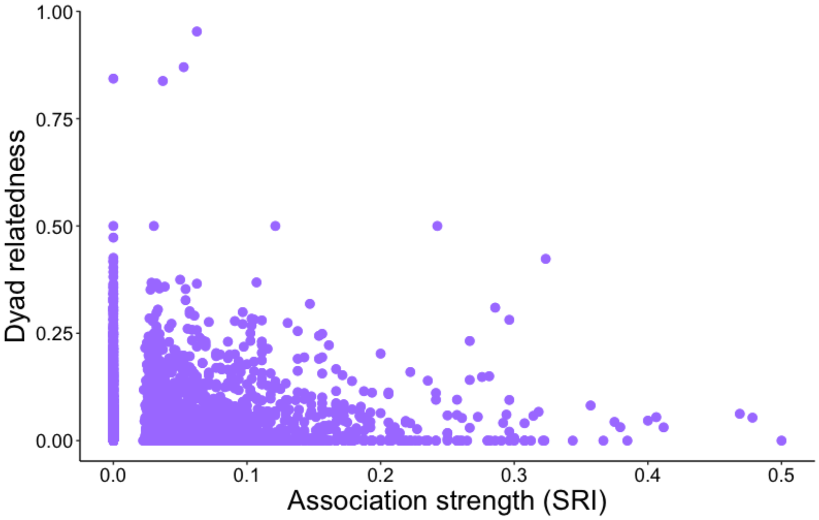


Figure 2.8: Relationship between dyad relatedness (TrioML relatedness coefficient) and association strength (SRI) for all NZ sea lion males present on Sandy Bay beach during the 2003 breeding season (n = 295 males) .

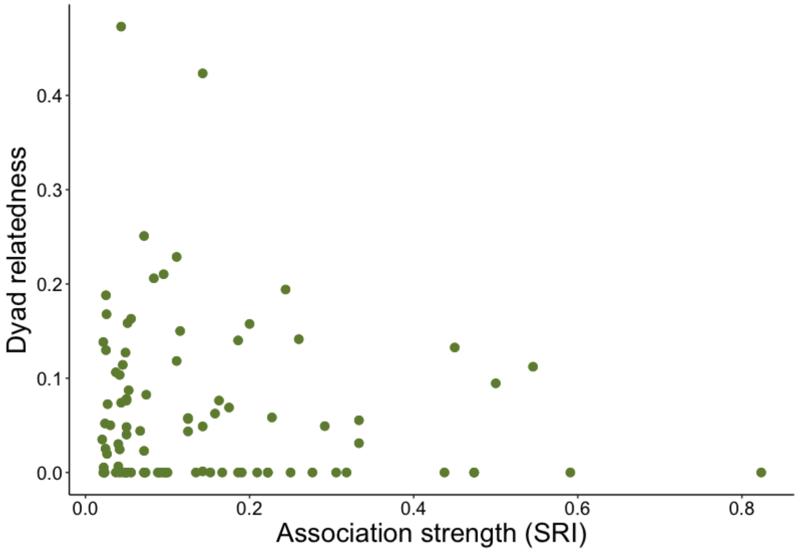


Figure 2.9: Relationship between dyad relatedness (TrioML relatedness coefficient) and association strength (SRI) for NZ sea lion males with high harem tenure (in harem more than 40% of the time on breeding beach) present on Sandy Bay beach during the 2003 breeding season (n = 14).

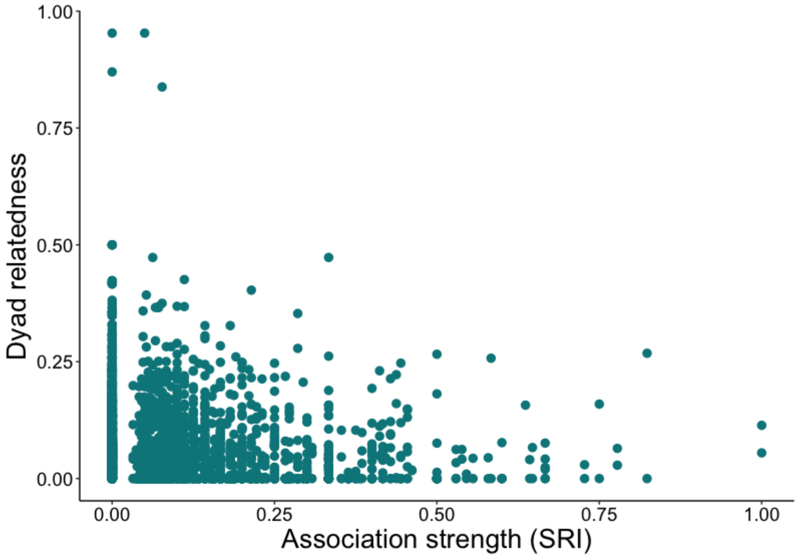


Figure 2.10: Relationship between dyad relatedness (TrioML relatedness coefficient) and association strength (SRI) for NZ sea lion males of territorial (within harem) present on Sandy Bay beach during the 2003 breeding season (n = 111).

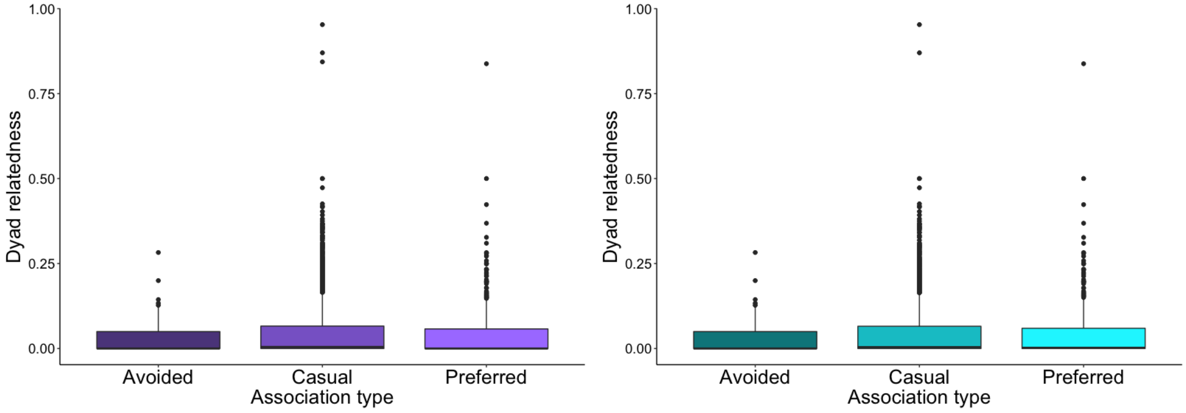
The dataset was also analysed in six one-week time periods, in order to identify trends that might exist for short periods during the breeding season. No correlations between male association (SRI) and genetic relatedness were observed during any one-week periods for all groups of males (all males, territorial and peripheral males only and territorial males only) (Table 2.2).

Table 2.2: Correlations between NZ sea lion male association (SRI) and genetic relatedness (TrioML) during different time periods of the breeding season

	All males			**Territorial & peripheral males only**			**Territorial males only**		
	Correlation coefficient	*p-value*	*N*	*Correlation coefficient*	*p-value*	*N*	*Correlation coefficient*	*p-value*	*N*
4 Dec - 10 Dec 2002	0.032	0.240	146	0.053	0.777	30	*NA*[2]	*NA*[2]	2
11 Dec - 17 Dec 2002	0.036	0.120	174	-0.030	0.587	56	0.035	0.396	22
18 Dec - 24 Dec 2002	0.009	0.341	187	0.050	0.216	88	0.056	0.383	42
25 Dec - 31 Dec 2002 [1]	-0.002	0.527	180	-0.034	0.090	122	0.050	0.297	74
1 Jan - 7 Jan 2003	0.008	0.378	149	0.042	0.065	97	-0.022	0.609	50
8 Jan - 15 Jan 2003	-0.022	0.784	127	-0.044	0.224	65	-0.106	0.543	37

[1] *Mean pupping period*
[2] *Sample size too small to calculate*

Analysis of the full dataset revealed males did not associate with relatives more or less often than expected by chance (coefficient = -0.041 , p = 0.212) (Figure 2.11a). This relationship held when looking at territorial males only (coefficient = 0.059, p = 0.451) (Figure 2.11b)



(a) (b)

Figure 2.11: Mean relatedness (TrioML relatedness estimator) of dyads associating less often than expected by chance (avoided), as expected by chance (casual) and more often than expected by chance (preferred) of a) all males (preferred; n = 1120 dyads, casual; n = 7706 dyads, avoided; n = 104 dyads) and b) territorial males only (preferred; n = 958 dyads, casual; n = 6594 dyads, avoided; n = 104)

2.3.3 Results from Wang relatedness estimator

Similarly to the results from the TrioML estimator, when looking across the whole population of males on the breeding beach, no correlation was observed between male association (SRI) and genetic relatedness using the Wang relatedness estimator, indicating no clustering of related males. This outcome held when looking at subsets of males, including only territorial and peripheral males, as well as only territorial males (see Appendix 1).

Upon analysis of the full dataset, related males were not shown to be associating more or less often than expected by chance (coefficient = -0.041, p = 0.215). However, analysis of territorial males only revealed related males in the harem were associating less often than we would expect by chance (coefficient = 0.051, p = 0.023) (Figure 2.12), suggesting avoidance behaviours between related males.

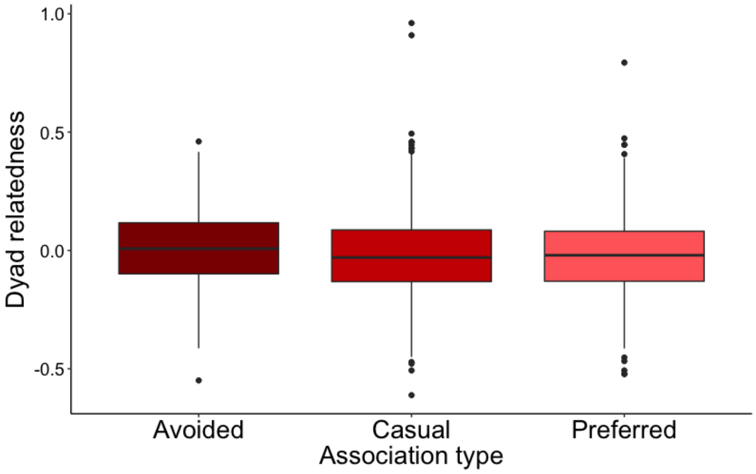


Figure 2.12: Mean relatedness, using Wang relatedness estimator, of dyads associating less often than expected by chance (preferred; n = 1,284 dyads), as we would expect by chance (casual; n = 4,912) and more often than expected by chance (avoided; n = 284)

2.4 Discussion

This study did not identify any relationships between genetic relatedness and social association of males within the breeding harem, indicating genetic relatedness is likely not influencing male spatial interactions that affect male reproductive success in the NZ sea lion. However, differences in relatedness were observed between males of high and low harem tenure, indicating genetic relatedness and grouping of related individuals may still play some role in male NZ sea lion reproductive success.

2.4.1 Harem tenure and genetic relatedness in New Zealand sea lions

A relationship was detected between genetic relatedness and harem tenure, where males of high harem tenure had higher average relatedness than males of low harem tenure. While the difference in mean relatedness of the high harem tenure and low harem tenure groups was small, the significance of the difference renders it worthy of consideration. Although no data directly correlating harem tenure with reproductive success is available for NZ sea lions, this correlation has been demonstrated in other mammal species, including other otariid species, due to increased opportunities for matings (Sommer and Rajpurohit, 1989; Pörschmann et al., 2010; Nagy et al., 2012). Under the assumption that harem tenure is correlated with reproductive success in NZ sea lions, males with high harem tenure should also have higher reproductive success. Therefore, the finding that males of high harem tenure had higher average relatedness suggest some genetic variants may be associated with increased reproductive success in NZ sea lions.

While relatedness is higher between males of high harem tenure, this is not reflected in male association patterns, as there was no correlation between genetic relatedness and spatial association for these males. The observed increased relatedness of males of high harem tenure may therefore be explained by the inheritance of genetic variants that influence reproductive success, rather than the direct association of close kin (Hatchwell, 2010). This concept of an underlying genetic basis to fitness variation has been documented in various wild populations (Ellegren and Sheldon, 2008) and has been identified both at the genome-wide level (Bonin et al., 2005; Beraldi et al., 2007), as well as at individual loci known to affect fitness. An example of genetic variation associated with fitness at a specific locus is the melanocortin-1 receptor (*Mc1r*), which has been linked to the colour variation that influences fitness in birds, mammals and reptiles (Nachman et al., 2003; Mundy et al., 2004; Rosenblum et al., 2004).

In NZ sea lion males, intense competition for access to the harem results in a reproductive skew (Bartholemew, 1970; Robertson et al., 2006), and consequently there should be strong selection for traits that increase a male's reproductive success (Lindenfors et al., 2002). If these traits influencing reproductive success have an underlying genetic basis, this may result in differentiation of the distribution of haplotypes between high harem tenure and low harem tenure males (Fariello et al., 2013), potentially explaining the observed increased relatedness of high harem tenure males. For example, in polygynous populations male reproductive success often increases with dominance status (Cowlishaw and Dunbar, 1991; Dixson et al., 1993; Ortega et al., 2003; Spong et al., 2008). Certain gene associations have been linked to traits related to dominance status such as novelty-seeking and risk-taking, for instance the animal personality-related gene, the dopamine receptor D4 (DRD4) (Okuyama et al., 2000; Momozawa et al., 2005; Korsten et al., 2010; Holtmann et al., 2016). In domestic horses (*Equus caballus*), two single nucleotide polymorphisms (SNPs) in DRD4 were identified and found to be associated with the personality traits 'curiosity' and 'vigilance' (Momozawa et al., 2005). Additionally, in dunnocks (*Prunella modularis*), two DRD4 SNPs were discovered to be associated with another measure of explorative behaviour and risk-taking; flight initiation distance (the time it takes a bird to take flight upon approach by a human) (Holtmann et al., 2016).

Another trait with an underlying genetic basis is mammalian body size (Trumpp et al., 2001). Larger males of various species are often better able to attain higher dominance rank (McElligott et al., 2001; Zedrosser et al., 2007). The extreme sexual size dimorphism displayed by otariids is thought to be a product of sexual selection from male competition for breeding access, suggesting large size confers some fitness benefit in male otariids (Ridgway and Harrison, 1981; Weckerly, 1998; Lindenfors et al., 2002). Identification of genes such as DRD4, or loci involved in determining male size, and their association with male reproductive success, would provide an improved understanding of the genetic basis of fitness in NZ sea lions, and may further reveal why high harem tenure males display increased relatedness.

2.4.2 Kin selection in otariids

Analysis of all NZ sea lion males present on the breeding beach across the whole breeding season indicated no overall genetic structure related to social association based on spatial proximity. This pattern suggests males are not directly associating with relatives in order to increase reproductive success. The study of kin recognition behaviour in otariids has mostly focussed on mother-pup recognition (Trillmich, 1981; Insley, 2000; Insley et al., 2003; Charrier and Harcourt, 2006; Aubin et al., 2015), so the ability of males to recognise relatives is thus far unknown. Studies of males in some otariid species have shown recognition of neighbours (familiar individuals, rather than kin specifically) based on vocal calls (Peterson and Bartholomew, 1969; Roux and Jouventin, 1987), and it has been suggested that males may display reduced agonistic behaviour to these familiar males (Gentry, 1975). Kin recognition through mechanisms such as scent, which has been well studied in other mammalian species (Hepper, 1986; Winn and Vestal, 1986; Brown and Eklund, 1994; Porter, 1998; Green et al., 2015), is yet to be addressed in NZ sea lions (see Chapter 4 for further discussion on knowledge of kin recognition). If male NZ sea lions do not have the ability to discriminate kin, this may explain why associations between kin are not observed in breeding males.

Alternatively, limitations of the present study may have prevented observation of such kin selection. A study of South American sea lions (*Otaria byronia*) also found no correlation between pairwise kinship and geographical distance of territorial males, however territories where males displayed higher overall reproductive success (measured by estimating paternities with multi-locus genotype information) also had increased relatedness (Franco-Trecu et al., 2015). Reduced energy expended in agonistic interactions leading to increased inclusive fitness, was suggested as the mechanism for these patterns of increased relatedness within male South American sea lions of higher reproductive success. However this theory could not be supported with the results of the study, due to the lack of correlation between kinship and geographical distances (Franco-Trecu et al., 2015). It is possible that a similar mechanism exists in NZ sea lions, as suggested by the increased relatedness of high harem tenure males, but that such a relationship could not be demonstrated due to limitations of the study, such as power of the microsatellite set used to resolve relatedness (see Chapter 4 for a full discussion on the limitations of microsatellite datasets).

Kin selection theory predicts related individuals will benefit from association with kin by helping them reproduce, however the benefits of such kin selection may be negated if competition between related individuals is frequent. Hamilton (1964) stated that selection for a gene is a balance between increased fitness of the bearer, and negative effects on kin. Therefore if a gene increases the fitness of the bearer, but has a large negative effect on kin, selection for the gene will be weak (Hamilton, 1964). This reduced selection for kin association may occur when resources are limited, such as breeding territories in otariid populations (Bartholemew, 1970). The benefits of kin selection, for the purposes of increasing each others reproductive success, may be negated if related males are directly competing for breeding access (Hamilton, 1964; Pollock, 1996; West et al., 2002; Platt and Bever, 2009). This scenario may also explain why male NZ sea lions do not appear to associate with relatives, as male relatives may benefit more from competing with non-relatives in order to increase overall familial reproductive success.

2.4.3 Estimates of male reproductive success

The results presented in this chapter rely on the assumption that males who spend more time in the harem have increased reproductive success. This correlation is well supported in mammals, with male territoriality accurately reflecting paternity in species such as lions (*Panthera leo*) (Gilbert et al., 1991), red deer (*Cervus elephus*) (Pemberton et al., 1992), mandrills (*Mandrillus sphinx*) (Dixson et al., 1993) and baboons (*Papio cynocephalus*) (Altmann et al., 1996). However, a number of molecular studies over recent decades have revealed multiple instances of polygynous populations where the observed mating system does not accurately predict male mating success (Pemberton et al., 1992; Coltman et al., 1999; Wilmer et al., 2000; Corlatti et al., 2015). In these cases the reproductive skew characteristic of polygynous populations is usually still supported by genetic data, but with an additional small number of non-territorial males assigned genetic paternity (Coltman et al., 1999; Corlatti et al., 2015).

Successful paternities by non-territorial males are usually thought to be due to alternative mating strategies, or the inability of territorial males to effectively monopolise breeding females (Pemberton et al., 1992; Coltman et al., 1999; Caudron et al., 2010; Corlatti et al., 2015). One instance of this includes a study by Coltman et al. (1999), which uses multi-locus genotypes to infer paternity, and identified multiple Soay rams (*Ovis aries*) with a high number of paternities despite the fact they had rarely been observed consorting with females during behavioural surveys. This finding suggests an alternative mating strategy by some males that does not involve forming consorts with females (Coltman et al., 1999). While no observations have been made of alternative mating tactics in NZ sea lions, studies using genetic estimates of paternity would confirm the strength of the correlation between harem tenure and reproductive success. This would remove the need for assumptions and increase confidence in the present findings.

2.4.4 Importance of assessing relatedness estimators

The differences noted in results for analyses performed with the two relatedness estimators (TrioML and Wang) indicate the importance of a priori assessment of genetic relatedness estimators for accuracy with each new dataset (Taylor, 2015). Although the difference in correlation between true and estimated relatedness values was small (correlations of 0.87 and 0.83 for TrioML and Wang respectively), the significance of some analyses was altered depending on which relatedness estimator was used. Analyses using the Wang estimator, that suggested avoidance of relatives by males, were not replicated with analyses using the more accurate estimator TrioML. While there has been a recent push for this testing of the accuracy of different relatedness estimators to become standard practise (Taylor, 2015), there has been little uptake within the field. The results shown here support the importance of the test, as they reveal the possibility of type I errors (finding significant results when none exist), with type II errors (not finding significant results that do exist) also being likely. This uncertainty makes it difficult to draw firm conclusions on results where such tests have not been carried out (Taylor, 2015).

2.5 Conclusions

This study revealed that patterns of male spatial interactions are not based on genetic relatedness in NZ sea lion breeding colonies. No correlations were observed between genetic relatedness and social associations in males, indicating kin selection apparently does not play an important role in increasing reproductive success in male NZ sea lions. It is possible that male NZ sea lions do not possess sufficient discriminatory ability to recognise close kin, or that fitness benefits accrued from association with relatives are negated by the costs of direct competition with relatives for breeding access. Males who spent a high proportion of time in the harem, and consequently presumably had higher reproductive success, were more related on average than less reproductively successful males. These findings suggest a genetic basis to fitness variation in males NZ sea lions, which provides an interesting avenue for future research.

Chapter 3

The role of female mate choice in maintaining genetic diversity of a small, colonising population

3.1 Introduction

In animals such as birds and fish, knowledge of female mate choice, where females select mates based on genetic quality in order to increase offspring fitness, is extensive (Pruett-Jones and Pruett-Jones, 1990; Alatalo et al., 1992; Ekblom et al., 2005; Schaedelin and Taborsky, 2010; Beausoleil et al., 2012; Ding et al., 2014; Sardell et al., 2014; Whittingham and Dunn, 2016). In contrast, female mate choice is less understood in mammals, particularly those with a polygynous breeding strategy where female choice is thought to be largely constrained (Clutton-Brock and McAuliffe, 2009). The classical example of a mammalian polygynous mating system involves males competing for access to females or the resources that females use, with only the most superior males being successful (Campagna and Le Boeuf, 1988; Le Boeuf, 1974; Pemberton et al., 1992; Wade, 1979; Arnold and Duvall, 1994). This observation suggests males play a large role in controlling the mating system. However, the importance of female mate choice in such populations has been documented. For example, female mate choice can allow females to choose unrelated mates, which drives dispersal of male relatives, thus limiting inbreeding (Cockburn et al., 1985; Höner et al., 2007; Costello et al., 2008). Furthermore, female mammals are usually solely responsible for care of offspring, including gestation, suckling and care for many months, or in some cases years (Mann, 2009). Due to this much larger investment in reproduction, female mate choice is hypothesised to be advantageous when it allows a female to choose between mates of varying quality (Trivers, 1972). Consequently, female mate choice may play a more important role than previously realised in mammalian populations, with subsequent evolutionary implications for the species (Clutton-Brock and McAuliffe, 2009).

In general, females may choose males based on either material benefits or ’good’ genes (Tregenza and Wedell, 2000; Mays Jr and Hill, 2004). Material benefits may be provided by males when they are able to monopolise resources, such as feeding or birthing sites, and hence these benefits are conferred on the female upon breeding with the male (Dechmann et al., 2007). ’Good’ genes refers to females choosing males that display desirable traits that are indicative of genetic health or subsequent offspring fitness (Jaquiéry et al., 2010). In some populations, there is no ’best’ male for all females, but instead females choose males in order to increase heterozygosity of offspring (Tregenza and Wedell, 2000; Mays Jr and Hill, 2004; Hoffman et al., 2007).

Otariid mating systems are widely recognised to display extreme polygyny with a high level of reproductive skew (i.e. overrepresentation of a few dominant males in the gene pool). This reproductive skew leads to high levels of male-male competition and results in the evolution of traits such as sexual size dimorphism where males are on average three times heavier than females (Bartholemew, 1970; Weckerly, 1998; Wells et al., 1999). In these classically polygynous species, male behaviour is often considered to largely control the breeding system with territorial males herding females and pups (Campagna and Le Boeuf, 1988; Campagna et al., 1992). However, female mate choice has been observed to be important within the polygynous harem in some otariid species, such as Antarctic fur seals (*Arctocephalus gazella*) where females will move across crowded breeding colonies in order to find heterozygous and unrelated mates (Hoffman et al., 2007). Consequently, otariid populations are interesting models for studying female mate choice.

New Zealand (NZ) sea lions (*Phocarctos hookeri*) are an otariid species that display this polygynous breeding system. The NZ sea lion population is currently in decline and the population is classified as endangered (Chilvers, 2015) with breeding mostly limited to small offshore islands (Chilvers et al., 2007). Following historical extirpation from mainland NZ, NZ sea lion males have returned to haul-out locations around the Otago coast (Robertson et al., 2006; Chilvers and Wilkinson, 2008). However, strong natal philopatry in females meant breeding was limited to the subantarctic breeding colonies (Chilvers and Wilkinson, 2008). That was until 1994 when one female from the subantarctic population, nicknamed 'Mum', dispersed to the mainland to pup on the Otago Peninsula (McConkey et al., 2002). Almost all pups born on the Otago Peninsula since 1994 are descended from this one female (McConkey et al., 2002).

Small, colonising populations, such as the Otago Peninsula NZ sea lion population, are of conservation concern due to the small number of founding individuals (Caughley, 1994; Bodkin et al., 1999; Mock et al., 2004). The fewer individuals that comprise the founding population, the less likely the population is to establish successfully (Caughley, 1994; Veltman et al., 1996; Berggren, 2001; Szucs et al., 2017). This trend can be observed because small founding populations are usually not genetically representative of the original population, and therefore will likely display decreased genetic diversity (Bodkin et al., 1999; Mock et al., 2004; Peacock et al., 2009; Sonsthagen et al., 2012; Szucs et al., 2017). Reduced genetic diversity makes populations more susceptible to local extinction because of reduced reproductive potential and ability to respond to environmental changes (Frankham et al., 2002; Frankham, 2005; Wittmann et al., 2014; White et al., 2015). Because of its small size (one founding female) and relative isolation, we would expect the Otago Peninsula population to suffer from reduced genetic diversity, and this is observed in the low levels of observed mitochondrial genetic diversity (Collins et al., 2017). Unexpectedly however, the Otago Peninsula population shows similar nuclear genetic diversity to the subantarctic population (Collins et al., 2017). This similarity suggests that although the breeding population of females is small, females on the Otago Peninsula have access to the same levels of genetic diversity in mates as females in the subantarctic population.

Due to the relatively small scale of breeding on the Otago Peninsula, the nature of the mating system varies from that displayed in the larger subantarctic colonies of NZ sea lions. In the larger breeding colonies, females aggregate in harems, allowing males access to many females at once and thus a small number of males can dominate breeding (Robertson et al., 2006; Augé et al., 2009; Gales, 2009). Aggregation of females around a dominant male confers benefits by reducing harassment from subordinate males, which increases female and thereby pup survival (Campagna et al., 1992) . However, such groupings also result in aggressive behaviour between territorial males as they compete for females, which can injure or kill females and their pups (Bartholemew, 1970; Ridgway and Harrison, 1981; Campagna and Le Boeuf, 1988; Chilvers et al., 2005). In large breeding colonies, this effect can be diluted as females aggregate in larger harems, and are therefore less likely to come into contact with aggressive males (Cassini, 2000).

On the Otago Peninsula however, with only a small number of females present, females do not obtain the same benefits from aggregation, and remain mostly solitary in order to avoid harrassment from males (Cassini, 2000; Chilvers et al., 2005). This female behaviour means males are less able to monopolise territories and maintain dominance of a group of females (Augé et al., 2009; Gales, 2009). Differences in the mating system between the Otago Peninsula and subantarctic populations, in terms of the influence of male breeding behaviour and female mate choice, could be responsible for the maintenance of genetic diversity in the Otago Peninsula population. Identifying such differences in the mating system between the two populations will deepen our understanding of the aspects of gene flow and population dynamics that enable small, founder populations, such as the Otago Peninsula population, to survive and thrive. As the rarest sea lion in the world, successful population recovery hinges on successful range expansion, making the establishment of new populations such as the Otago Peninsula population significant (Lalas and Bradshaw, 2003; Robertson et al., 2006).

3.1.1 Research aims

This research aimed to investigate and make comparisons between female mate choice in two NZ sea lion populations; the small, recently founded Otago Peninsula population, and the larger breeding colony on Enderby Island in NZ's subantarctic islands. The main objective was to investigate similarities and differences in female mate choice between the two populations in order to help explain how the small, semi-isolated population on the Otago Peninsula is maintaining nuclear genetic diversity following its recent founder event (Collins et al., 2017). I hypothesised that despite its small size, females in the Otago Peninsula population have access to a similar gene pool of males as females in the subantarctic population. I also hypothesised that due to differences in the structure of the breeding system, female mate choice will be less constrained in the Otago Peninsula population, and that it acts as a mechanism to retain heterozygosity of offspring (e.g. Hoffman et al. (2007)). The answers to these questions will further our understanding of female mate choice in polygynous otariid mating systems, and also increase our knowledge of the mechanisms that facilitate population expansion in recovering populations such as the NZ sea lion.

3.2 Methods

3.2.1 Data collection

3.2.1.1 Otago Peninsula

As part of the tagging and monitoring system of the Otago NZ sea lion population undertaken by the Department of Conservation (DOC), small toe clippings have been taken from each pup upon tagging at the end of each breeding season. Unique combinations of clipped toes aid in individual identification, and the removed tissue is used for DNA analysis (J. Fyfe, personal communication). Samples are available for the majority of individuals born on the Otago Peninsula from 1998 onwards (78 out of 93 pups born, see Appendix 2). A small number of individuals were not included in the analysis (n = 17) due to loss of tissue since collection. Breeding occurs for a defined period once a year, so female NZ sea lions give birth to a maximum of one pup per year (Marlow, 1975; Robertson et al., 2006). Where possible, mother-pup relationships are inferred based on proximity and suckling behaviours in the first weeks of the pup's life (Chilvers et al., 2007). Overall, DNA samples were available for 35 known mother-pup pairs (35 pups to 10 different mothers), and a further 5 individuals for which maternities were not known (see Appendix 2).

3.2.1.2 Enderby Island

Skin biopsies for DNA analysis were collected from tagged females with pups in the 2003 breeding season (NZ sea lion breeding seasons follow the austral summer and thus are referred to by the year in January of the season). These females were monitored over subsequent breeding seasons until 2007 and skin biopsies for DNA analysis were collected from each pup born during this time (Collins et al., 2017). The Enderby Island dataset comprised 180 females and 580 pups, therefore in order to have the same chance of detecting effects, and thus being able to make fair comparisons between the two populations, a random subset of individuals was selected to match the sample size of the Otago Peninsula population. In both populations, where mother-pup relationships were known (Chilvers et al., 2007), females were placed into categories of having one to six pups throughout the study period (six was the total number of pups observed to be born from one female in the Otago Peninsula population). Females and their pups were then randomly selected from the Enderby Island categories to match the number of individuals in the same category in the Otago Peninsula population (see Appendix 2). For the remaining pups in the Otago Peninsula population whose maternities were unknown, mother-pup groups were randomly selected from the Enderby Island population to match the total Otago Peninsula sample size (n = 78).

3.2.2 Genetic analysis

Genetic data for the Enderby Island population was taken from Osborne et al. (2016). DNA for the Otago Peninsula population was extracted using a Chelex 100 protocol (Walsh et al., 1991), and amplified at 14 pinniped microsatellite loci using multiplex polymerase chain reactions with M13-tagged primers as described in Collins et al. (2017) (see Table 3.1). The loci have been demonstrated to be in Hardy-Weinberg proportions and useful in various analyses of otariids (Collins et al., 2014, 2016; Osborne et al., 2016; Collins et al., 2017). Genotyping of PCR products was performed using an ABI 3730xl DNA Analyser (Genomic Analysis Service, University of Otago). Microsatellites for the Otago Peninsula population were scored using the software GENEIOUS v. 9.1.6 (http://www.geneious.com, Kearse et al. (2012)). PCR amplification and subsequent genotyping was performed twice at all loci for all individuals to account for failed amplification, as well as for error checking and ensuring reliability of data. Data was analysed in the software Micro-checker v. 2.2 to assess for allelic dropout and null alleles (Van Oosterhout et al., 2004). A small number of individuals (<5%) failed to amplify at more than 30% of loci and so were excluded from the analysis.

The total PCR reaction volume (2 µl) comprised 1 µl dry DNA, 1 µl Type-it Master Mix (Qiagen), 0.1 µM fluorescently labelled M13 primer, 0.016 µl of each forward primer, 0.064 µM of each reverse primer and 0.82 µl PCR water. LIZ500 size standard (GeneScan) was used as a relative measure for determining allele sizes. A touchdown protocol was used for PCR-amplification of the microsatellites. This comprised an initial denaturation step of 95°C for 15 min, eight cycles of 94°C for 30 s, an annealing temperature of 60°C (reduced by 1°C each cycle) for 90 s, and a 72°C extension step for 60 s, then 25 cycles of 94 °C for 30 s, 52°C for 90 s, and 72°C for 60 s, and a final extension of 60°C for 30 min.

Table 3.1: Microsatellite variation of NZ sea lion female and pup samples from Otago Peninsula (N = 78) from 1998 to 2017 and Enderby Island* (N = 78) from 2001 to 2007.

Microsatellite Locus	*GenBank Accession*	*Multiplex run/dye*	*Otago Peninsula*				*Enderby Island*			
			N	*k*	*Ho*	*He*	*N*	*k*	*Ho*	*He*
PvcA	-	1, 6-FAM	70	6	0.66	0.60	78	7	0.42	0.50
G1A	-	1, 6-FAM	70	4	0.50	0.51	78	12	0.49	0.55
OrrFcB7	G34928	1, NED	75	6	0.64	0.64	78	10	0.65	0.75
Hg8.10	G02096	1, NED	75	3	0.41	0.42	77	15	0.70	0.80
Hg6.1	G02091	1, VIC	78	7	0.44	0.46	77	16	0.83	0.85
Hg6.3	G02092	1, VIC	66	6	0.80	0.76	77	9	0.60	0.65
Lc28	AF140584	1, PET	76	4	0.74	0.65	78	7	0.68	0.73
Pv9	G02096	1, PET	76	5	0.41	0.36	78	8	0.71	0.76
HI16	AF140588	2, 6-FAM	76	5	0.62	0.65	77	10	0.65	0.69
OrrFCB1	G34933	2, 6-FAM	76	7	0.66	0.66	78	9	0.62	0.72
Lc5	AF417694	2, VIC	77	4	0.57	0.54	77	10	0.66	0.81
Hg4.2	G02090	2, NED	76	9	0.83	0.83	78	17	0.81	0.81
ZcCgDh1.8	AY676475	2, VIC	77	1	0.00	0.00	75	15	0.83	0.83
ZcCgDh5.16	AY676477	2, PET	76	7	0.74	0.70	78	15	0.64	0.82

N, number of NZ sea lions genotyped at each locus; *k*, number of alleles; *Ho*, observed heterozygosity; *He*, expected heterozygosity.
*Data from Osborne et al. (2016)

3.2.2.1 Estimating parentage

The software COLONY (Jones and Wang, 2010) was used to estimate family relationships within each population. COLONY uses multilocus genotypes and full-pedigree likelihood methods to infer sibship and parentage with a range of flexible parameters including mating system, genotyping error and species type (Jones and Wang, 2010). As no male parent genotypes were available for the Otago population, only female and offspring genotypes were inputted into COLONY to estimate unknown maternities and maternal sibships. COLONY can then infer paternities, paternal sibships and paternal genotypes based on pup genotypes.

Calibration of COLONY was performed to assess its ability to reconstruct known relationships within the population. Individuals with known maternal-offspring relationships (n = 57) were selected from the Otago Peninsula population. Multilocus genotype information for these individuals was entered into COLONY as if the relationships were unknown. Four runs were performed, using different parameters for run length, likelihood probabilities and inbreeding in each run. The results from each run were compared to the known relationships to assess which combination of parameters gave the most accurate results (see Appendix 3).

All data for the Otago Peninsula population and the Enderby Island population were then run separately through COLONY, using the best performing parameters identified in the previous step. Data inputs included genotype information of offspring and potential mothers, as well as known maternal sibships and a list of excluded possible maternities. Female NZ sea lions reach sexual maturity at four years of age and so individuals were excluded as possible mothers if they were younger than four when a pup was born (Chilvers et al., 2010). In order to minimise error, only estimated relationships with a probability of 0.8 or higher were included in subsequent analysis. Relationships with a probability < 0.8 were classified as unrelated.

3.2.3 Assessing mate choice and paternal contribution

To understand the role of female mate choice in the two NZ sea lion populations, three separate analyses were conducted. Firstly, to assess whether females were exerting mate choice based on genetic relatedness, mating pairs were analysed to see if they were more or less related than expected by chance. Secondly, to assess whether females in each population had access to a range of unrelated males as mates, or whether females were consistently choosing males of certain genotypes, genetic relatedness between multiple mates of each female was analysed to see if these males were more or less related to each other than expected by chance. Finally, to assess whether the number of males available for females to mate with was similar between the two populations, the proportion of different males a female had pups with, relative to her total number of pups, was analysed.

Inferred paternal genotypes estimated by COLONY were used to analyse the genetic relatedness between individuals within both populations using two methods; the triadic likelihood (TrioML) relatedness coefficient and Nei and Li's genetic similarity (GS) (Nei and Li, 1979; Wang, 2007). Genotypes at each loci for each individual were only included if they had a probability of 0.8 or higher. The software COANCESTRY (Wang, 2011) was used to calculate the TrioML relatedness coefficient. Simulations run in COANCESTRY (as described in Chapter 2 methods) showed that relatedness estimates produced with TrioML were the most closely correlated with the simulated true relatedness for both populations (Otago - 0.80, Enderby Island - 0.85) (see Appendix 4). Nei and Li's GS was calculated in R (version 3.4.0) (R Core Team, 2017) using the formula $GS_{ij} = 2 \times N_{ij}/(N_i+N_j)$ where N_{ij} is the number of alleles shared by individuals i and j, and N_i and N_j are the total number of alleles of the individuals i and j, respectively Nei and Li (1979); R Core Team (2017).

Genetic relatedness between a female and her mates was analysed to see if females were mating with partners that were more or less related to herself than expected by chance. TrioML and GS values were calculated for all combinations of possible mating pairs in each population. Pairs were then placed into categories of 'true mating pairs' if COLONY had inferred mating between them or 'non-mating pairs' if COLONY inferred no mating. The observed difference in mean TrioML or GS values between 'true mating pairs' and 'non-mating pairs' was compared to 1000 permuted datasets to see if the difference between the two categories was greater or less than expected by chance, indicating mate choice based on genetic relatedness. Permutations were performed using the 'sample' function in R to permute the categorisation of 'true mating pairs' and 'non-mating pairs' without replacement (R Core Team, 2017). The number of matings as well as the number of different mates per individual was kept constant by only permuting the category of 'true mating pair' or 'non-mating pair' within the set of mating pair observations for each female. Mean genetic relatedness was considered to be significantly different between the two categories when the observed difference in mean relatedness between categories was greater than or less than the mean relatedness between categories in more than 95% of the permuted datasets (Bejder et al., 1998).

Where significant differences in relatedness were found between true mating pairs and non-mating pairs, further analysis was performed to identify whether this difference was real, or due to unmatched sample sizes of true mating and non-mating pairs. In order to do this analysis, a random sample of non-mating pairs was selected using the sample function without replacement to match the number of true mating pairs. This random sampling was performed 100 times, and p-values for each randomly sampled dataset were calculated in order to assess whether the significant difference remained stable across all random samples.

In order to assess the genetic diversity of males that females in each population had access to, genetic relatedness between multiple mates of the same female partner was analysed. This analysis was done by calculating TrioML and GS values between all males in the population. Males were then placed into the categories of ′shared a female′ if COLONY inferred that both males in the dyad had mated with the same female or ′did not share a female′ if COLONY inferred that they had never mated with the same female. The observed difference in mean TrioML or GS values of male dyads that ′shared a female′ and dyads that ′did not share a female′ was compared to 1000 permuted datasets to see if the mean difference in relatedness between the two categories was greater or less than expected by chance. Permutations were performed using the ′sample′ function in R to permute the categorisation of ′shared a female′ and ′did not share a female′ without replacement (R Core Team, 2017). The number of matings per individual as well as the number of individuals each male shared a female with was kept constant by only permuting values within the set of observations for each male. Mean genetic relatedness was considered to be significantly different between the two categories when the observed difference in mean relatedness between categories was greater than or less than the difference in mean relatedness between categories in more than 95% of the permuted datasets.

To look at the number of males available to each female for mating, female ′mate diversity′ was analysed to assess the number of different males that females in each population mated with relative to their total number of matings. This analysis was done by counting the number of different males each female mated with as well as the number of pups each female had. The proportion of 'mate diversity' was calculated by dividing the number of different mates by the total number of pups for each female. Mean 'mate diversity' was compared to see if there was a difference between the means of the two populations. The difference between means of the two populations was compared to 1000 permuted datasets to see if the means were significantly different to what would be expected by chance. Permutations were performed using the 'sample' function in R to permute combinations of mating pairs without replacement. The number of matings per individual was kept constant by only permuting male IDs within the list of mating pairs. The mean 'mate diversity' was considered to be significantly different between the two populations when the observed difference in means was greater than the difference in means in more than 95% of the permuted datasets.

3.2.4 Limitations of COLONY

COLONY uses full-pedigree likelihood methods which are generally thought to be more accurate than pairwise methods, as information from multiple individuals is considered when each relationship is being analysed (Wang and Santure, 2009). In the present study COLONY inferred paternities and paternal genotypes, which allowed analysis of male genetic diversity and relatedness. At each locus, multiple possible genotypes are estimated with different degrees of confidence, making it difficult to determine with certainty the true genotype across all loci for all individuals. As a result, error may arise when assigning relationships, where genuine relationships may be excluded or false relationships may be incorrectly inferred (Marshall et al., 1998). This error may be due to genotyping error, or mutations in the microsatellite markers used (Queller et al., 1993; Hoffman and Amos, 2005). Here, only genotypes with probabilities of 0.8 or higher were included in analysis in an attempt to reduce possible error, allowing a high level of confidence in results.

3.3 Results

The significance of all results was not affected by the genetic relatedness estimator used (TrioML or Nei and Li's GS), hence for simplicity, only results using TrioML are reported for all analyses.

As noted in previous genetic studies of NZ sea lions (Collins et al., 2014, 2016; Osborne et al., 2016; Collins et al., 2017), no evidence for allelic dropout or null alleles was found in the present study.

3.3.1 Calibrating COLONY

The inclusion of the inbreeding parameter gave the best performing run in COLONY (see Appendix 3). However, including inbreeding for dioecious species is not recommended except for in cases where high levels of inbreeding are well documented for the species (Wang, 2017), which is not the case for NZ sea lions (Collins et al., 2017). Parameters for runs 2 and 3 were the next equally best performing (Table 3.2, 3.3 & see Appendix 3). For simplicity parameters under run 2 only were used for further analysis. The overall accuracy of COLONY in assigning pairs under these parameters was 0.99.

Table 3.2: NZ sea lion mother-offspring relationships assigned by COLONY compared to known relationships in the Otago Peninsula population determined using parameters in calibration run 2

		Known relationship		
		Mother-offspring	Unrelated	Total
COLONY assigned relationship	Mother-offspring	**35**	2	*37*
	Unrelated	6	**613**	*619*
	Total	*41*	*615*	*656*

Table 3.3: Summary statistics describing relationships as determined using parameters in calibration run 2

Summary statistic	Mother-offspring	Unrelated
True positive rate[1]	0.854	0.997
False positive rate[2]	<0.01	0.15
Precision[3]	0.95	0.99

[1] True positive rate is the number of relationships assigned correctly out of the total number of known relationships in that category

[2] False positive rate is the number of known relationships that are incorrectly assigned out of the total number of known relationships in the category they were incorrectly placed into

[3] Precision is the number of relationships assigned correctly out of the total number of COLONY assigned relationships in that category

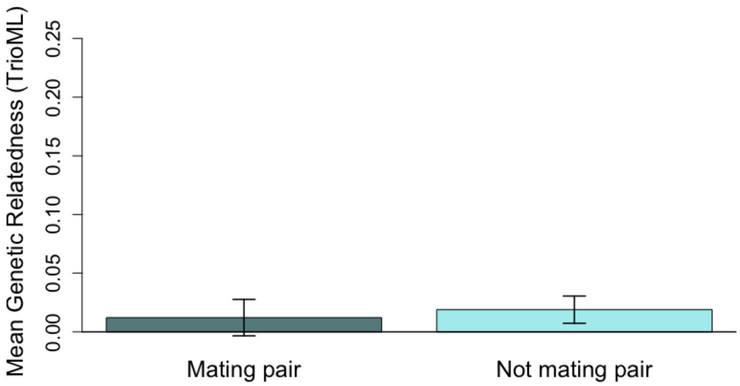
3.3.2 Genetic relatedness of male and female breeding pairs

3.3.2.1 Otago Peninsula

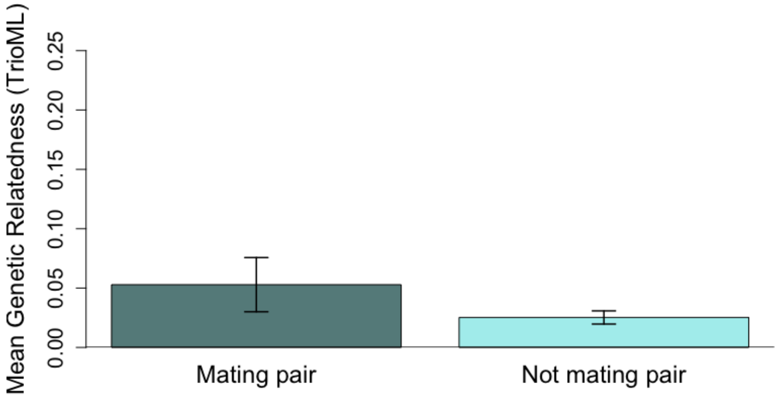
For the 55 pups in the Otago Peninsula population, COLONY inferred 35 different mothers, and 16 different fathers. The mean relatedness (TrioML relatedness estimator) for Otago Peninsula mating pairs and non-mating pairs was 0.012 and 0.019 respectively (Figure 3.1a). Permutation tests revealed that the mean difference in relatedness of true mating pairs and non-mating pairs was not significantly larger than expected by chance (observed mean difference = 0.007, randomised mean difference = -0.003 (-0.029 — 0.017, 95% CI), $p = 0.243$).

3.3.2.2 Enderby Island

For the 53 pups in the Enderby Island population, COLONY inferred 34 different mothers, and 18 different fathers. The mean relatedness (TrioML relatedness estimator) for Enderby mating pairs and non-mating pairs was 0.053 and 0.025 (Figure 3.1b). The mean difference in relatedness of true mating pairs and non-mating pairs was significantly larger than expected by chance (observed mean difference = 0.028, randomised mean difference = 0.005 (-0.006 — 0.018, 95% CI), $p = 0.003$).



(a) Otago Peninsula



(b) Enderby Island

Figure 3.1: Mean genetic relatedness (TrioML) of true NZ sea lion mating pairs and male-female dyads that are not mating pairs: (a) Pairs from Otago Peninsula population from 1998 to 2017 (N mating pairs = 42; N non-mating pairs = 188; N individuals = 30) and (b) Pairs from Enderby Island population from 2001 to 2007 (N mating pairs = 53; N non-mating pairs = 485; N individuals = 47).

When random samples were taken of non-mating pairs to match the number of true matings pairs in the Enderby Island population (n = 53), the significantly higher genetic relatedness of true mating pairs ($p < 0.05$) was observed in 69% of the 100 random samples (Figure 3.2).

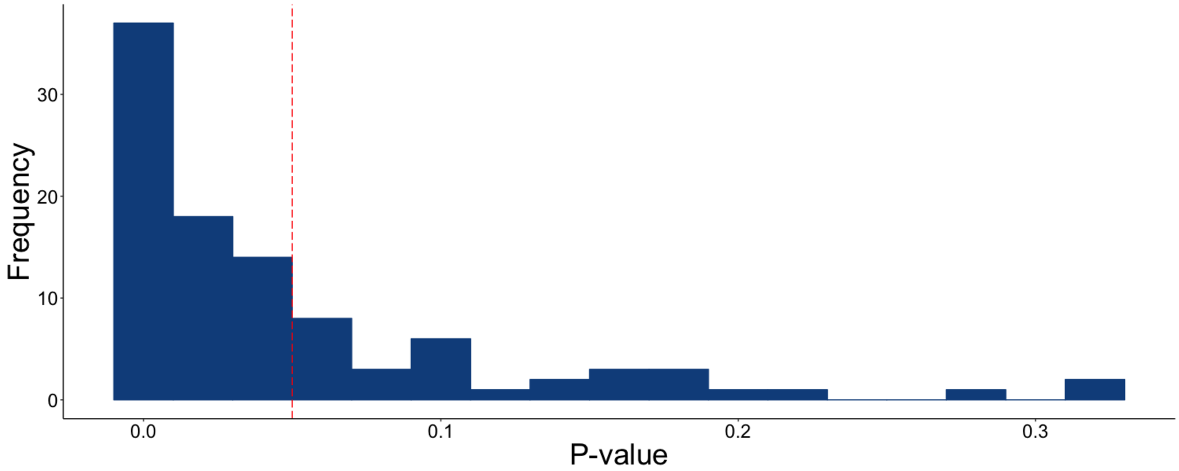


Figure 3.2: Distribution of p-values when 100 random samples of genetic relatedness (TrioML estimator) of 53 non-mating pairs are compared to the genetic relatedness of the 53 true mating pairs in the Enderby Island population. Dashed red line indicates the significance threshold of 0.05, where p-values below this threshold indicate a significantly higher relatedness of true mating pairs compared to non-mating pairs.

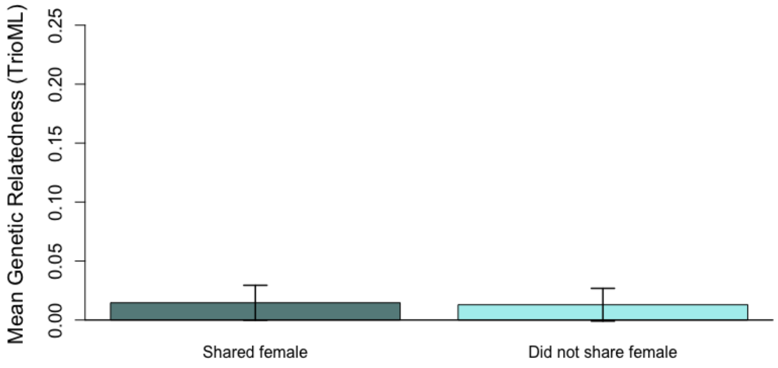
3.3.3 Genetic relatedness of males that share a female partner

3.3.3.1 Otago Peninsula

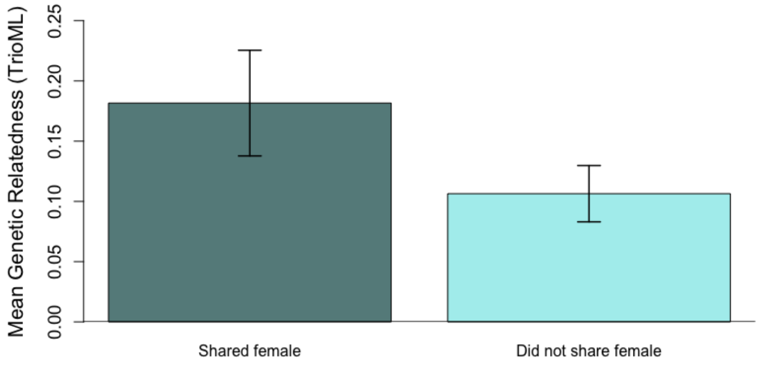
Out of the 16 males identified as fathers by COLONY comprising 123 dyads, 38 dyads were inferred to have shared a female partner, while 85 dyads did not. The mean relatedness of males that shared a female partner and males that did not share a female partner was 0.015 and 0.013 respectively (Figure 3.3a). The mean difference in relatedness of dyads that shared a female and dyads that did not share a female was not significantly larger than expected by chance (observed mean difference = 0.002, randomised mean difference = 0.002 (-0.014 — 0.023, 95% CI), $p = 0.51$).

3.3.3.2 Enderby Island

Out of the 18 males identified as fathers by COLONY comprising 136 dyads, 26 dyads were inferred to have shared a female partner, while 110 dyads did not. The mean relatedness of males that shared a female partner and males that did not share a female partner was 0.18 and 0.11 respectively (Figure 3.3b). The mean difference in relatedness of dyads that shared a female and dyads that did not share a female was significantly larger than expected by chance (observed mean difference = 0.075, randomised mean difference = 0.019 (-0.022 — 0.059, 95% CI), *p* = 0.015).



(a) Otago Peninsula



(b) Enderby Island

Figure 3.3: Mean genetic relatedness (TrioML) of male NZ sea lions who mated with the same female (shared a female) and never mated with the same female (did not share a female): (a) Pairs from Otago Peninsula population from 1998 to 2017 (N dyads shared female = 38; N dyads did not share female = 85; N individuals = 16) and (b) Pairs from Enderby Island population from 2001 to 2007 (N dyads shared female = 26; N dyads did not share female = 110; N individuals = 19).

Comparison of the microsatellite variation of males from COLONY inferred genotypes between the two populations revealed that the pool of males contributing to breeding in the Otago Peninsula population appeared to display relatively fewer alleles per locus as well as lower observed heterozygosity (*Ho*) and expected heterozygosity (*He*) (Table 3.4).

Table 3.4: Microsatellite variation of NZ sea lion males from Otago Peninsula (N = 16) from and Enderby Island (N = 18) from genotypes inferred by COLONY.

Microsatellite Locus	***GenBank Accession***	***Otago Peninsula***				***Enderby Island***			
		N	***k***	***Ho***	***He***	***N***	***k***	***Ho***	***He***
PvcA	-	16	4	0.44	0.61	18	10	1.00	0.84
G1A	-	16	2	0.44	0.40	17	19	1.00	0.92
OrrFcB7	G34928	16	6	0.56	0.65	16	14	0.94	0.89
Hg8.10	G02096	16	2	0.19	0.17	7	11	1.00	0.89
Hg6.1	G02091	16	5	0.44	0.38	12	10	0.92	0.77
Hg6.3	G02092	16	4	0.81	0.71	16	17	1.00	0.90
Lc28	AF140584	16	3	0.44	0.48	6	8	1.00	0.82
Pv9	G02096	16	3	0.25	0.23	17	15	1.00	0.85
HI16	AF140588	16	4	0.56	0.65	11	9	0.82	0.73
OrrFCB1	G34933	16	7	0.69	0.71	18	16	1.00	0.83
Lc5	AF417694	16	4	0.50	0.46	12	7	1.00	0.72
Hg4.2	G02090	16	7	0.75	0.80	11	8	1.00	0.83
ZcCgDh1.8	AY676475	16	1	0.00	0.00	17	16	0.94	0.91
ZcCgDh5.16	AY676477	16	7	0.75	0.80	15	17	1.00	0.92

N, number of NZ sea lions genotyped at each locus; *k*, number of alleles; *Ho*, observed heterozygosity; *He*, expected heterozygosity.

3.3.4 Mate diversity

The number of males a female mated with ranged from 1 to 5, with a mean of 2.2 for the Otago Peninsula population and 1 to 4, with a mean of 1.7 for the Enderby Island population. The number of pups per female ranged from 1 to 6 in the Otago Peninsula population, and 1 to 5 in the Enderby Island population. The mean mate diversity (number of different males that females in each population mated with relative to their total number of matings) for females in the Otago Peninsula population and Enderby Island population that had more than one pup was 0.93

and 0.94 respectively (Figure 3.4). The mate diversity was not significantly different between the two populations (observed mean difference = 0.007, randomised mean difference = -0.019 (-0.050 — 0.018, 95% CI), $p = 0.13$).

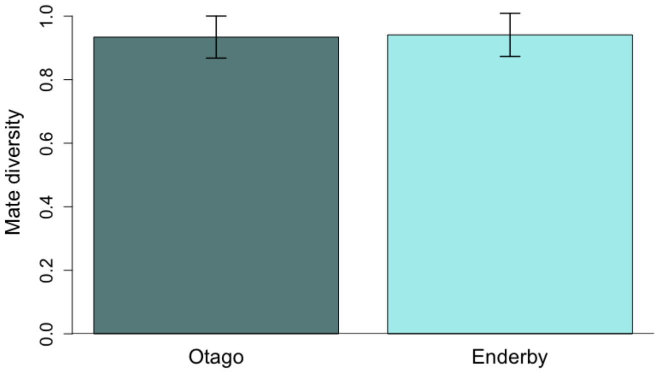


Figure 3.4: Number of mates relative to the total number of matings (mate diversity) for females in the Otago (N = 22) and Enderby (N = 28) population of NZ sea lions that had more than one pup.

3.4 Discussion

This study identified variation in female mate choice between two NZ sea lion populations; a small newly-founded population with solitary breeding, and a larger breeding colony with aggregated breeding harems. Mate choice of genetically similar individuals was observed in the larger Enderby Island source population, whereas females in the newly-founded Otago Peninsula population mated at random with respect to genetic relatedness. This finding suggests that mate choice to increase genetic diversity of offspring may be important in NZ sea lions, but that constraining factors may prevent females from mating with unrelated males under some circumstances.

3.4.1 Genetic relatedness of mating pairs

A difference in female mate choice based on genetic relatedness exists between the two populations, with females from the Enderby Island population mating with males that are more related to themselves than expected by chance, while relatedness of females and their mates in the Otago Peninsula population was random. However, the significantly higher genetic relatedness of Enderby Island mating pairs was not observed in all repeated analyses matching sample sizes of non-mating and true mating pairs, making it difficult to draw firm conclusions about these results. Regardless, the results found here indicate a tentative trend that warrants further investigation. If females in the Enderby Island population truly are choosing mates with increased relatedness to themselves, this finding would be somewhat unexpected. Given the choice, theory would predict that females should choose unrelated mates in order to maximise offspring diversity and avoid the negative consequences of inbreeding depression (Charlesworth and Charlesworth, 1987; Frankham, 2005; Hoffman and Amos, 2005; White et al., 2015). However, there is evidence that in certain cases, inbreeding may be tolerated, and may even increase fitness (Smith, 1979; Waser et al., 1986; Kokko and Ots, 2006). The theory behind this is a form of kin selection, whereby mating with a related individual further spreads genes that are identical by descent, thus increasing inclusive fitness (Smith, 1979;

Kokko and Ots, 2006). In fallow deer (*Dama dama*), females are likely to mate with their fathers (Smith, 1979). This observation is explained as an altrustic behaviour by females, which increases inclusive fitness, and Smith (1979) suggested that this inbreeding would not be selected against until female fitness is reduced by one third. Further research is required to confirm whether this suggested trend of females choosing related males as mates can be confirmed, and if so, what fitness benefits female NZ sea lions may achieve by mating with more related males.

3.4.2 Female mate choice and population dynamics

The mate diversity (number of different mates relative to the total number of matings) was not significantly different for females from the two populations. In both populations the majority of matings resulted from the formation of new mating pairs, meaning most pups from one female had different fathers. However, the genetic relatedness of a female's mates did vary between the two populations. Greater relatedness was observed between males that share a female mate in the Enderby Island population, but not the Otago Peninsula population. This finding suggests the observed differences in genetic relatedness of mates between the Enderby Island and Otago Peninsula populations is not due to constraints imposed by a limited number of mates in either population. Consequently, such differences in mating system may arise from constraints such as male breeding behaviour (e.g. competition for harem tenure) influencing the genetic diversity of available mates (Smuts and Smuts, 1993; Clutton-Brock and McAuliffe, 2009).

Males in large NZ sea lion breeding colonies, such as the Enderby Island population, undergo intense competition for access to the breeding harem (Gales, 2009). Only a small number of males are successful, leading to a large reproductive skew (Robertson et al., 2006; Gales, 2009). In other mammal species, factors such as size, dominance and aggression are correlated with a male's reproductive success (Bartholemew, 1970; McElligott et al., 2001; Ortega et al., 2003; Zedrosser et al., 2007). Therefore sexual selection should favour genetic variants that make males more reproductively successful (Bartholemew, 1970; Clutton-Brock and Harvey, 1978). The reproductive skew favouring certain genetic variants leads to a smaller gene pool of available mates in the breeding harem, which could explain the greater relatedness between males that share a mate in the Enderby Island population (Ellegren and Sheldon, 2008).

This situation is akin to the lek paradox, which describes the evolution of female preference for specific male traits, and is thought to deplete genetic variance in the male gene pool (Kirkpatrick and Ryan, 1991). The paradox lies in that such depleted male genetic variance would negate any benefits for females to remain choosy after several generations (Kirkpatrick and Ryan, 1991). Results from the Otago Peninsula population in the present study support previous claims for the resolution of the lek paradox whereby females show preferences for males that will produce more heterozygous offspring (Hoffman et al., 2007). This preference allows female choice to remain beneficial generation after generation. However, results from the Enderby Island population suggest that male breeding behaviour displayed in larger breeding colonies may be constraining female choice, preventing females from using mate choice to maintain heterozygosity of their offspring.

One interesting finding from this study was the males from the Otago Peninsula population appeared to display fewer alleles per locus as well as lower *Ho* and *He*. This result suggests that although this population displays a similar level of nuclear genetic diversity to the larger Enderby Island population (Collins, 2017), the males contributing to breeding are not fully genetically representative of the whole population. However, these findings highlight how relatively few migrants are required to homogenise allele frequencies, and that this small amount of gene flow is adequate for maintaining a viable population (Spieth, 1974; Mills and Allendorf, 1996).

Unlike the Enderby Island breeding colony, no defined breeding harem is present on the Otago Peninsula, resulting in more infrequent and dispersed matings. When mating opportunities are limited in the main breeding harem, such as seen in behaviourally polygynous otariid populations, males may assume alternative mating strategies (Caudron et al., 2010; de Bruyn et al., 2011; Flatz et al., 2012). Males that disperse to the NZ mainland may do so because they are unable to compete with dominant males in the subantarctic breeding colonies and dispersal improves their chances of breeding (Lawrence, 1987; Robertson et al., 2006; Davidian et al., 2016). Consequently, these males may not be subject to the same levels of intense sexual selection, leading to a reduced reproductive skew and improved breeding opportunities. As a consequence, the gene pool of males contributing to breeding may display a higher level of within-group genetic diversity if it includes a larger proportion of males from the population (as observed when there is a reduced reproductive skew).

Alternatively, certain individuals may be more likely to disperse than others. Behaviours such as migration and dispersal have been associated with certain genetic variants in some species (Dingemanse et al., 2003; Matthews and Butler, 2011), however this association has not yet been studied in otariids. If such a behaviour-genotype correlation exists in otariids, males that disperse to the NZ mainland may differ genetically from the non-dispersing males in the subantarctics. This wider genetic diversity, alongside a decreased ability of males on the Otago Peninsula to control access to females, may allow females more freedom to choose unrelated mates. This mechanism further helps to explain the low level of relatedness between mating pairs in the Otago Peninsula population as well as the high nuclear genetic diversity compared with the observed mtDNA diversity (Smuts and Smuts, 1993; Cassini, 2000; Chilvers et al., 2005; Clutton-Brock and McAuliffe, 2009).

3.4.3 Genetic viability of founding populations

In recent decades, many species have faced dramatic declines in population sizes due to loss of habitat, hunting and climate change (Doroff et al., 2003; Long et al., 2007; McKinney, 2008; Randi, 2011; Koenig et al., 2017). Although many species are now recovering through human-mediated conservation action (Thomas et al., 2009; Randi, 2011; Gummer et al., 2015; Brown et al., 2017), a main concern in the formation of new populations, whether it is through human intervention (such as translocations) or a species dispersal to inhabit a new breeding site, is that the new population is not genetically representative of the source population (Bodkin et al., 1999; Mock et al., 2004; Peacock et al., 2009; Sonsthagen et al., 2012; Szucs et al., 2017).

As only a small number of individuals contribute alleles to the new population (in the case of the Otago Peninsula NZ sea lion population only one maternal lineage), the diversity of the gene pool is often reduced compared to the original population and can experience reduced heterozygosity (Bodkin et al., 1999; Broders et al., 1999; Mock et al., 2004; Peacock et al., 2009; Sonsthagen et al., 2012; Szucs et al., 2017). Such reduced heterozygosity can have negative fitness effects such as exposure of deleterious recessive alleles (Charlesworth and Charlesworth, 1987). Additionally, reduced heterozygosity can make individuals more susceptible to parasites and disease, as well as negatively affecting reproductive success (Acevedo-Whitehouse et al., 2003; White et al., 2015). Therefore, a key factor in successful establishment of founder populations is maintaining genetic diversity (Zenger et al., 2003).

Although low mitochondrial genetic diversity is observed in the Otago population (Collins et al., 2017), the results from this study reveal an interesting mechanism whereby at low densities, female mate choice may play a more active role allowing mating with unrelated individuals. This finding is important as it allows new, low density populations to maintain adequate nuclear genetic diversity for population survival. In threatened populations such as the NZ sea lion, understanding mechanisms by which new populations can be established is critical information in species protection and management.

3.5 Conclusions

Here I revealed differences in the mating systems between the Otago Peninsula and Enderby Island NZ sea lion populations, which may help to explain how small, colonising populations avoid loss of genetic variation. Females in the smaller Otago Peninsula population chose more unrelated and genetically diverse mates than females in the larger Enderby Island population. Female mate choice may be less constrained by male mating behaviour on the Otago Peninsula, where breeding is more dispersed than in the Enderby Island breeding harem. These results provide important insights into how small founder populations of NZ sea lions minimise loss of genetic variation and avoid the associated negative effects. This information is important in understanding how succesful range expansion can occur, and should be considered when developing management plans for the threatened NZ sea lion.

Chapter 4

General discussion

The aim of this research was to investigate the role of social structure, particularly associations between kin, in the NZ sea lion mating system. The findings presented increase our knowledge of fine-scale structure of mating systems in polygynous otariids such as the NZ sea lion. In this chapter, these findings are summarised and their relevance to wider knowledge on mating systems and NZ sea lion biology is discussed.

In this thesis I have assessed the genetic factors influencing social interactions between males in a breeding colony, and how this relates to male-male competition and thus reproductive success. While genetic relatedness did not appear to influence social interactions of males in the breeding harem, males that spent more time in the harem (high harem tenure males) showed a higher level of relatedness than low harem tenure males. These findings do not support the presence of kin selection in males, whereby related males associate in order to increase reproductive success. In Chapter 2, I discussed the implications of these findings by suggesting that this increased relatedness of high harem tenure males results from a genetic basis of fitness variation, whereby variation in certain loci across the genome influences a males competitive ability and thus reproductive success.

I also assessed female mate choice in two different NZ sea lion populations, to see how density-dependent factors influence the interplay between male competition and female choice, and how female choice may act to retain genetic diversity in a small, colonising population. Females in the small, newly-founded population on Otago Peninsula showed mate choice of genetically unrelated males, and chose consecutive mates that were unrelated to each other. Females in the larger, dense breeding colony on Enderby Island appeared to mate with males that were more genetically related to themselves than expected by chance, and were choosing males that showed higher relatedness to each other for consecutive matings. Assessment of the number of males contributing to breeding, and the number of different mates females in each population were breeding with suggested that females were not constrained by the number of males available in either population. In Chapter 3, I discussed the possible constraints from male behaviour acting upon females in the Enderby Island breeding colony, and how female mate choice in the Otago Peninsula population may be allowing the population to retain a moderate level of genetic diversity despite its small size and the observed newly-founded status.

The results obtained in this study contribute to our understanding of the role of both male and female behaviour in the mating system, mechanisms of female mate choice in polygynous populations, and factors that influence male reproductive success and fine-scale structure in otariid breeding colonies.

4.1 Sexual selection in New Zealand sea lions

Sexual selection occurs through two separate, but related, mechanisms. The first is intrasexual selection where individuals of one sex compete with each other for access to breeding. The second is intersexual selection where individuals of the opposite sex exert selection pressures through choosiness for mates with certain traits (Darwin, 1872). In this research, I have demonstrated the importance of both mechanisms in the NZ sea lion.

4.1.1 Intraspecific selection (male-male competition)

The research in this thesis has revealed that variance in male reproductive success does not depend on genetic relatedness of male associates, unlike species such as lions (*Panthera leo*), chimpanzees (*Pan troglodytes*), golden snub-nosed monkeys (*Rhinopithecus roxellana*) and bottlenose dolphins (*Tursiops truncatus*), where spatial association with kin has been observed as an important factor in determining male reproductive success (Packer et al., 1991; Mitani et al., 2000; Parsons et al., 2003; Qi et al., 2017). However, increased genetic relatedness of high harem tenure males suggests some genetic variants/lineages are associated with increased reproductive success in NZ sea lions. Male-male competition is well known to be important in otariid populations, and the resulting consequences on evolution of traits such as size dimorphism are well understood (see Chapter 1) (Ridgway and Harrison, 1981; Lindenfors et al., 2002; Chilvers et al., 2005; Pörschmann et al., 2010; Cullen et al., 2014; Franco-Trecu et al., 2014, 2015).

The genetic basis of different male traits on a male's ability to compete for breeding access are often not well understood, however, this research suggests that certain genetic variants may be associated with male NZ sea lion reproductive success (as measured by harem tenure). As discussed in Chapter 2, identification of loci correlated with high reproductive success would help to establish the traits that are important for male competition, and the genetic variation associated with these traits. Such research would further our knowledge of the genetic basis of fitness variation and genetic factors that influence reproductive success (Ellegren and Sheldon, 2008).

4.1.2 Interspecific selection (female mate choice)

Behavioural observations suggest NZ sea lion breeding behaviour is dominated by male-male competition. However, my research revealed some female behaviour that can not be explained by male competition (Chapter 3). As discussed above, if male-male competition is the predominant form of sexual selection, we might see an overrepresentation of certain genetic lineages, whereby males that possess certain traits (e.g. size, dominance status) are more reproductively successful. This overrepresentation of genetic lineages is likely observed in the Enderby Island population, where males of higher harem tenure display increased relatedness (Chapter 2), and males that share a female mating partner have increased relatedness (Chapter 3). However, in the Otago Peninsula population, I observed lower genetic relatedness between mating males that shared a female partner, as well as lower relatedness of mating pairs compared to the Enderby Island population. These findings suggest female mate choice may play a larger role in the formation of mating pairs in the Otago Peninsula population, allowing females to choose unrelated mates (Chapter 3).

4.1.3 Contrasting effects of intraspecific and interspecific selection

As discussed in Chapter 3, breeding behaviour varies between the two populations, and hence influences the type of sexual selection displayed. Females in the Otago Peninsula population remain largely solitary in order to avoid harrassment from males, whereas females in the Enderby Island population aggregate into dense harems to reduce the effects of male harrassment (Chilvers et al., 2005). This female behaviour suggests male competition does not play as large a role in the Otago Peninsula population, as females are more free to move around and assess different males before mating.

In contrast, females in the Enderby Island colony may be more constrained in mate choice by male competition, and thus have more limited ability to compare multiple males. These observed differences in breeding behaviour between the two populations may help explain the similar levels of genetic diversity in the two populations; the reduced constraints imposed by male behaviour in the Otago Peninsula population, alongside a selection of males similar to that in the Enderby Island population, may be allowing females to maintain genetic diversity of offspring through mate choice of unrelated males. As a consequence of these factors, we may expect to see weaker sexual selection for traits influencing male competition in the Otago Peninsula population. This is because if females are choosing more genetically diverse mates, traits that increase a male's competitive ability may have no, or little, selective benefit.

Sustained differences in the form of sexual selection displayed by the two populations has the potential for evolutionary consequences, such as reduced selection for traits that increase male's competitive ability. However, as the Otago Peninsula population grows and density increases, a shift towards mating behaviours as observed in the Enderby Island population will likely be observed, with aggregation of females and thus the relative importance of male competition should increase (Chilvers et al., 2005; Augé et al., 2009; Gales, 2009). Therefore, the current differences in the form of sexual selection displayed in either population will likely not have any long term consequences on sexually selected traits, however will allow newly-founded populations to remain genetically viable through increased heterozygosity of offspring.

4.2 Population recovery through range expansion

The current NZ sea lion population size (N_c) estimate is less than 10,000 individuals (Meyer et al., 2017), however recent research has estimated that historical N_c may have reached up to 200,000 individuals (Robertson, 2015; Collins et al., 2016). While it is likely that the carrying capacity (K) may have recently declined due to factors such as increased anthropogenic competition for fish and climate change, these figures suggest that the NZ sea lion population is not currently at K (Robertson, 2015; Collins et al., 2016). As a result, increasing N_c should be a primary focus of population management, allowing density-dependent factors to trigger dispersal to form new breeding sites (Roux, 1987). Unlike many threatened species, NZ sea lions are not facing large-scale habitat loss, and range expansion has been pinpointed as the key to population recovery (Robertson et al., 2006).

4.2.1 Re-colonisation and female dispersal

Historically, a great number of otariid populations have been subject to population and range reduction resulting from human harvest (Hofmeyr et al., 1997; Pitcher et al., 2007; de Oliveira et al., 2009; Dickerson et al., 2010; Collins et al., 2016). The subsequent range expansion and recolonisation process has been documented in some *Arctocephalus* species (Roux, 1987; Bradshaw et al., 2000). This recolonisation process was defined in four distinct stages by Roux (1987). 'Survival' stage describes the survival of individuals in the remnant population before breeding starts again. 'Establishment' details the period following initiation of breeding where breeding only occurs in a limited number of colonies, followed by 're-colonisation' where breeding extends to new breeding colonies. The final stage, 'maturity' occurs when the population reaches carrying capacity of the environment and population growth slows (Roux, 1987). The current stage of the NZ sea lion population should be considered as 're-colonisation', however it is important to remember that the current Otago Peninsula population is a genetically distinct lineage from the historical mainland population founded by one rare migrant (Collins et al., 2014).

Typically the 're-colonisation' phase occurs when high density at a breeding colony (i.e. density dependence) causes a shortage in breeding sites, initiating movement of inexperienced breeders to nearby sites (Roux, 1987; Bradshaw et al., 2000). Male NZ sea lions are the more widely dispersing sex, and males from the subantarctic population are frequently sighted in non-natal sites such as the NZ mainland (Robertson et al., 2006; Chilvers and Wilkinson, 2008). However, due to the high levels of natal philopatry observed in female NZ sea lions, dispersal to new breeding sites is unlikely without pressure from density-dependent factors such as competition for access to food or breeding sites in the established populations (Roux, 1987; Chilvers and Wilkinson, 2008). Therefore, increasing the population of breeding females in existing colonies is a key step in population recovery. This requirement further reinforces the need for effective management of ongoing impacts, such as fisheries bycatch, to allow population growth through female dispersal (Leung et al., 2012; Meyer et al., 2015). However, the results from this study highlight how a new population can successfully establish with only a small number of founding females due to females ability to maintain genetic diversity of offspring through mate choice.

4.2.2 Issues of genetic diversity in new populations

The subantarctic breeding colonies are relatively isolated and there is a large distance between this population and the newly colonising populations on the NZ mainland. Lack of gene flow between the two populations has the potential to cause issues such as loss of genetic diversity and inbreeding in the small mainland population (Charlesworth and Charlesworth, 1987; Lynch et al., 1995; Frankham, 2005). However, this distance appears not to be an issue with a similar level of genetic diversity observed in both populations indicating a reasonable amount of nuclear gene flow (Collins et al., 2017). The results from the present study help to explain this observation, by suggesting that male dispersal from the subantarctic population to the NZ mainland allows females a sufficiently similar selection of males in the both populations to maintain genetic diversity of offspring (see Chapter 3). These findings are reassuring, suggesting that breeding behaviour in new, low density populations will mean subsequent population expansion of NZ sea lions will likely not result in genetic issues such as reduced heterozygosity.

One issue that remains, however, is the low level of mitochondrial DNA (mtDNA) diversity in the Otago Peninsula population, resulting from the the population being founded by only one maternal lineage (Collins et al., 2017). Mitochondria are important organelles involved in energy production for cellular functions, therefore mutations in mtDNA can have serious consequences and lead to a number of diseases (Hatefi, 1985; Linnane et al., 1989; Raha and Robinson, 2000). MtDNA mutations can have detrimental impacts on egg size, fecundity and fertility as well as causing various degenerative diseases and contributing to the aging process (Linnane et al., 1989; Raha and Robinson, 2000; Gemmell et al., 2004; Dowling et al., 2008). MtDNA mutations are reasonably common, owing to the physical conditions within the mitochondria and the fact that mtDNA does not encode any DNA repair mechanisms (Bohr, 2001; Rand, 2001). However, fortunately mtDNA mutations with large, negative effects are reasonably rare (Hill et al., 2014). Due to the small number of breeding females in the Otago Peninsula population, any deleterious mutations that may occur in mtDNA could quickly increase in frequency through genetic drift, and have negative effects on the viability of the population (Gemmell et al., 2004; Dowling et al., 2008). This possibility highlights the importance of increasing the number of female migrants to the Otago Peninsula population important.

4.3 Potential management strategies

The results from this study suggest male dispersal between breeding populations is adequate to ensure a reasonable amount of nuclear genetic diversity in colonising populations on the NZ mainland. Given this finding, female dispersal should be the main focus of management plans to increase population range. One method often used in management of threatened populations is translocation of individuals from one area to another (Armstong and McLean, 1995; Armstrong and Seddon, 2008; Seddon, 2010; Weeks et al., 2011). Translocation is often used to return species to their native range following extirpation, but has also been used to introduce threatened populations to new areas as a method of range expansion (Seddon, 2010). 'Genetic rescue', the translocation of individuals from one population to another, has also proven effective in boosting genetic diversity of small, low diversity populations (Hedrick and Fredrickson, 2010; Weeks et al., 2011). In NZ conservation, translocations have proven an extremely effective tool in protecting a number of highly threatened native bird species. Translocations have successfully prevented extinction in species such as the kakapo (*Strigops habroptilus*), little spotted kiwi (*Apteryx oweni*), South Island saddleback (*Philesturnus c. carunculatus*), takahe (*Porphyrio hochstetteri*) and the black robin (*Petroica traversi*) (Flack, 1978; Atkinson, 1990; Armstong and McLean, 1995; Armstrong and Craig, 1995; Armstrong, 1995; Jamieson and Wilson, 2003).

Very few studies on otariid translocations have been done. A study by Hindell and Pemberton (1997), looking at diving behaviour of Australian fur seals (*Arctocephalus pusillus doriferus*), relocated an individual 450 km from the site of capture and observed this individual returning to its original site within 15 days. It is likely that the long range dispersal capabilities (Hindell and Pemberton, 1997; Collins et al., 2014), combined with strong philopatry and site fidelity of otariids (Hoffman et al., 2006; Chilvers and Wilkinson, 2008; Hoffman and Forcada, 2012), would result in translocated individuals returning to original capture sites in the majority of cases.

Whilst mtDNA diversity in the Otago Peninsula population is low, nuclear diversity is moderate (Collins et al., 2017). Therefore, translocation of individuals to increase genetic diversity would be primarily beneficial by increasing mtDNA diversity. However, movement of a large enough number of females to be of benefit to the Otago Peninsula population (potentially 25 females; Steeves et al. (2017)) would require great effort and cost. Additionally, these individuals would have to be anaesthetised, which comes with high health risks (Meise et al., 2014). Finally, as discussed earlier, the chances of mtDNA mutations with large, negative effects on reproductive potential are likely low (Hill et al., 2014), meaning the cost and effort involved in translocations of female NZ sea lions may outweigh the benefits.

Considering all of the above factors, translocation of females to establish new breeding populations, or to increase mtDNA diversity of existing small populations such as the Otago Peninsula population, are probably not feasible.

A better option for management would be to increase protection of the subantarctic population to allow maximal growth, encouraging higher rates of breeding dispersal in females. The main factor affecting breeding colonies in the subantarctic islands is overlap with fisheries, resulting in resource competition and fisheries-related bycatch (Robertson and Chilvers, 2011). Considering this issue, stricter regulation on fisheries would be required for better population protection. A recent study by Meyer et al. (2015) indicates that growth rates of NZ sea lion populations in the Auckland Islands are most responsive to adult female survival. Coincidentally, NZ sea lion females are most at risk from fisheries related bycatch mortality (Robertson and Chilvers, 2011; Leung et al., 2012; Meyer et al., 2015). The study by Meyer et al. (2015) also suggested that NZ sea lions will continue their current population decline without effective intervention.

One method of range expansion, to overcome the reliance on density dependent factors, would be attempting to attract females to new breeding beaches. Due to the gregariousness of females, decoys have previously been investigated as a method of attracting females to suitable pupping sites (Augé and Chilvers, 2010). While the use of decoys to attract species to certain sites is wide-spread (Sharp and Lokemoen, 1987; Story, 1991; Wild et al., 2017), this was the first study to use decoys to attract a pinniped species (Augé and Chilvers, 2010). Results from Augé and Chilvers (2010) indicate that artificial decoys made of white fabric can be succcessful in attracting both male and female sea lions to new beaches. Therefore, the use of decoys could be further investigated as a means of range expansion, however this method relies on the assumption that females are already making this long-range dispersal from the subantarctics to the NZ mainland.

4.4 Molecular methods for detecting fine scale structure

Microsatellites are useful in elucidating historical population structure as well as current population trends such as genetic diversity and levels of inbreeding in NZ sea lions (Collins et al., 2014, 2016; Osborne et al., 2016; Collins et al., 2017). Microsatellites are short repeat sections of DNA that vary in the number of repeats between individuals. They are highly informative and useful in a variety of research including kinship analysis, genetic linkage analysis and population genetics, as well as practical applications in disease diagnosis and forensics (Nöthen et al., 1999; Tan et al., 2003; Kurushima et al., 2006; Crawford et al., 2008; Wang et al., 2011; Li et al., 2012; Coetzer et al., 2017). More recently, however, advances in molecular technology make it relatively cheap and easy to genotype thousands of single nucleotide polymorphisms (SNPs) across the genome (The International Hapmap Consortium, 2005). The use of SNPs allows coverage of a much wider range of loci across the genome compared to microsatellites, which increases the power to detect the significance of trends (Spinks et al., 2014; Taylor et al., 2015). SNPs have also proven more useful than microsatellites in threatened species research, where genetic diversity is too low to discriminate between closely related individuals using microsatellites (Ibarra et al., 2013; Taniguchi et al., 2013; Spinks et al., 2014; Taylor et al., 2015). The present study used a set of 17 pinniped microsatellites to estimate relatedness between individual NZ sea lions. Although NZ sea lions show a moderate level of genetic diversity, making microsatellites informative (Collins et al., 2017), the use of SNPs may have provided better resolution to reveal trends that were not found in this study using microsatellites. For example, as suggested above, certain lineages may be more successful than others in reproduction, leading to the increased relatedness of high harem tenure males. Detection of these lineages may be possible with SNP analysis, allowing finer-scale study of association patterns with relatedness. To the best of my knowledge, no animal research to date has assessed reproductive success of different genetic lineages using SNP analysis, making this a novel area for future study.

4.5 Future research

Study of kin recognition mechanisms in NZ sea lions may provide a deeper understanding of the presence of kin associations. While no correlation was found between genetic relatedness and social association, it is unclear whether this finding is because of an inability to identify kin, or because there is no selective benefit to kin clustering. Kin recognition mechanisms, such as vocal cues (Trillmich, 1981; Kessler et al., 2012), and genetic markers (Brown and Eklund, 1994; Logan et al., 2008; Green et al., 2015), have been identified in mammals. Genetic markers are usually detected through scent, such as the major histocompatibility complex (MHC) and the major urinary protein (MUP) cluster (Brown and Eklund, 1994; Logan et al., 2008; Green et al., 2015). Previous research has identified kin recognition mechanisms in otariids mostly between mother and pup, indicating recognition via vocal cues, with olfaction sometimes used as a secondary cue (Trillmich, 1981; Insley, 2000; Charrier and Harcourt, 2006; Aubin et al., 2015). However, the existence of kin recognition, or its underlying mechanisms, have not yet been identified in NZ sea lions. Identifying whether kin recognition exists in NZ sea lions, and the mechanisms that underpin it, for example olfaction or vocal cues (Hepper, 1986; Brown and Eklund, 1994; Hurst et al., 2001; Aubin et al., 2015), would be an interesting area for further research, and would enhance our understanding of why kin associations may or may not form.

4.6 Summary of conclusions and recommendations

This research provided a new understanding of the fine scale structure in NZ sea lion breeding harems. Kin associations do not appear to be influencing male reproductive success (measured by time in harem), however certain genetic lineages appear to have increased reproductive success, as evidenced by the increased relatedness of high harem tenure males. Females in the newly-colonising Otago Peninsula population appear to have similar choice of males, with apparent reduced constraints on mate choice from male breeding behaviour, allowing maintenance of a similar level of nuclear genetic diversity in the small, colonising population.

This research provides promising evidence of successful colonisation by expanding NZ sea lion populations, but reveals that female dispersal is the main barrier to the formation of new breeding sites. As such, the following recommendations for management and future research are made:

- Perform SNP analysis for increased accuracy of relatedness estimates, and to allow detection of genetic variants associated with male reproductive success.
- Measure male reproductive success through genetic methods to assess whether harem tenure accurately predicts male reproductive success.
- Investigate kin recognition mechanisms in NZ sea lions to assess whether kin recognition exists, and if so how individuals recognise relatives. This research would provide knowledge of why kin associations may or may not form, and potentially provide avenues for further study.
- Provide better protection of the subantarctic population to increase survival of females, allowing the population to reach a critical density threshold to trigger dispersal of females to new breeding sites.

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Appendix 1

Table A1.1. Correlation coefficient of estimated and true (simulated) values of different relatedness estimators calculated in COANCESTRY for males in the Sandy Bay NZ sea lion population

Relatedness estimator	**Correlation coefficient of estimated relatedness values with true values**
Triadic likelihood (TrioML)	0.87
Wang	0.83
LynchRd	0.83
LynchLi	0.82
Queller-Goodnight	0.82
Ritland	0.67

Table A1.2. TrioML relatedness coefficient estimates and true r_{xy} for simulated dyads in six relationship categories calculated in COANCESTRY. Simulated genotypes of dyads were based on the Sandy Bay NZ sea lion breeding colony microsatellite marker sets.

True relationship	**Actual r_{xy}**	**TrioML mean estimated r_{xy}**	**Wilcoxon V**	**P**	**Coefficient of variation**
Parent-offspring	0.5	0.52	738	***	9%
Full siblings	0.5	0.48	2202	NS	28%
Half siblings	0.25	0.23	2068	NS	61%
First cousins	0.125	0.12	2056	NS	89%
Second cousins	0.03125	0.055	3253	*	120%
Unrelated	0	0.051	1326	***	166%

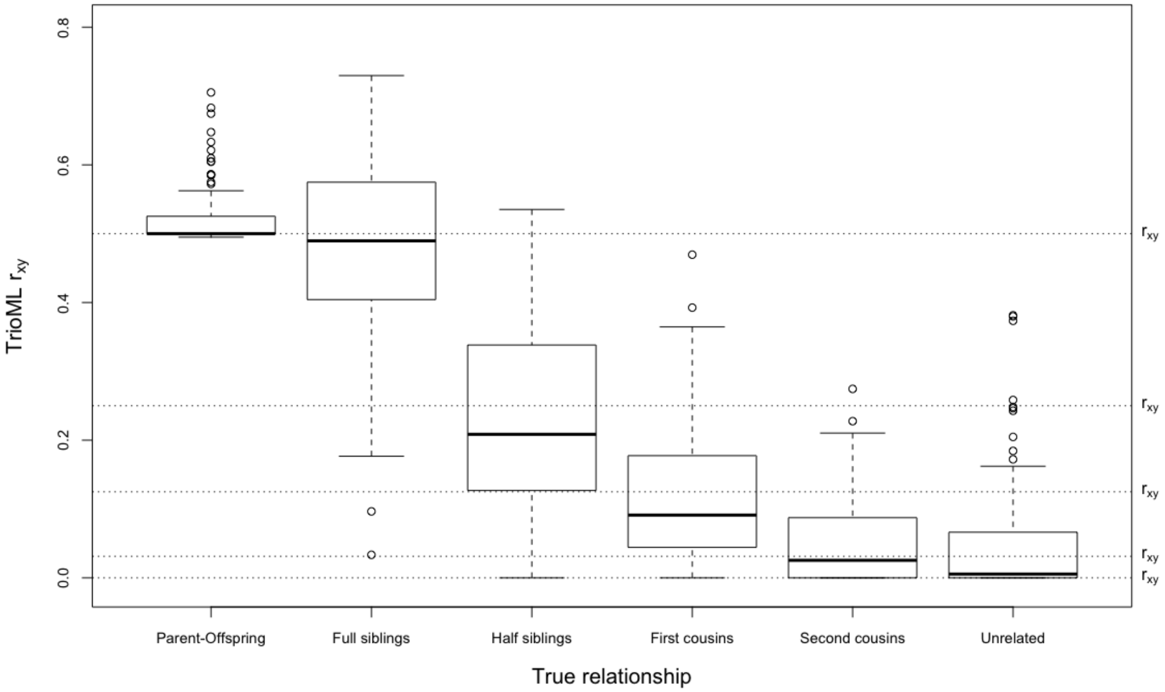

Figure A1.1. Spread of TrioML relatedness coefficient estimates calculated in COANCESTRY for simulated dyads in different relationship categories using simulated genotypes based on the Sandy Bay NZ sea lion breeding colony microsatellite marker sets. Dashed horizontal lines mark true r_{xy} coefficients.

Table A1.3. Correlations between male association (SRI) and genetic relatedness (Wang relatedness coefficient) for different groups of males in the NZ sea lion breeding colony at Sandy Bay, Enderby Island

	Correlation coefficient	**p-value**
All males	0.0068	0.096
Territorial and peripheral males only	0.0039	0.348
Territorial males only	-0.0017	0.559

Appendix 2

Table A2.1. List of individual NZ sea lions from the Otago Peninsula population included in mate choice analysis

Name	Year of birth	Sex	Mother	DNA included in analysis?
Mum	1987	F	unknown	N
Katya	1994	F	Mum	N
Leone	1996	F	Mum	N
Suzie	1998	F	Mum	Y
George	1998	M	Katya	N
Bill	1999	M	Mum	N
Un-named	2000	F	Mum	N
Un-named	2001	M	Mum	N
Victoria	2001	F	Katya	N
Victor	2001	M	Leone	N
Conor	2002	M	Mum	Y
Lorelie	2002	F	Leone	Y
Teyah	2002	F	Suzie	Y
Honey	2003	F	Mum	Y
Paul	2003	M	Katya	Y
Un-named	2003	M	Leone	N
Bruno	2004	M	Mum	Y
Aurora	2004	F	Katya	Y
Waimarie	2004	F	Leone	Y
Nerissa	2005	F	Katya	Y
Zoe	2005	F	Leone	Y
Pani	2005	F	Suzie	Y
Oscar	2005	M	Victoria	Y

Name	Year of birth	Sex	Mother	DNA included in analysis?
Wovoka	2006	M	Mum	Y
Gem	2006	F	Katya	Y
Dylan	2006	M	Leone	Y
Emma	2006	F	Victoria	N
Mia	2006	F	Teyah	Y
Caleb	2006	M	Lorelie	Y
Whetu rere	2007	M	Mum	N
Hine	2007	F	Katya	Y
Madeline	2007	F	Teyah	Y
Jonah	2008	M	Leone	Y
Cockle	2008	F	Aurora	Y
Douce	2008	F	Katya	N
Phil	2008	M	Lorelie	N
Lena	2008	F	Honey	Y
Patti	2009	F	Katya	N
Arnie	2009	M	Teyah	Y
Mana	2009	F	Nerissa	N
Ethan	2009	M	Zoe	Y
Huru	2010	F	Katya	Y
Pippa	2010	F	Teyah	N
Un-named	2010	M	Lorelie	N
Sandy	2010	F	Nerissa	Y
Becky	2010	F	Zoe	Y
Un-named	2011	F	unknown	Y
Joy	2011	F	Leone	Y
BK	2011	M	unknown	Y
Carleigh	2011	F	Teyah	Y
Hiriwa	2011	F	unknown	Y

Name	**Year of birth**	**Sex**	**Mother**	**DNA included in analysis?**
Ngaio	2011	F	unknown	Y
Marama	2012	F	Gem	Y
Seazar	2012	F	Lorelie	Y
Colin	2012	M	Zoe	Y
Moana	2012	F	Teyah	Y
Un-named	2013	F	Mia	Y
Un-named	2013	F	Gem	N
Bella	2013	F	Lorelie	Y
Blake	2013	M	Teyah	Y
Charlie	2013	M	Zoe	Y
Brionie	2014	F	Gem	Y
Nuki	2014	F	Huru	Y
Gail	2014	F	Lena	Y
Vega	2015	F	Hiriwa	Y
Murphy	2015	M	Gem	Y
Un-named	2015	M	Zoe	Y
Ted	2015	M	Lena	Y
June	2015	F	Joy	Y
Morgan	2015	M	Lorelie	Y
Un-named	2015	F	Pippa	N
Un-named	2015	?	unknown	Y
Un-named	2016	M	Mia	Y
Janet	2016	F	Patti	Y
Pebble	2016	F	Moana	Y
Walter	2016	M	Gem	Y
Hannah	2016	F	Zoe	Y
Olive	2016	F	Lena	Y
Mac	2016	M	Pippa	Y

Name	Year of birth	Sex	Mother	DNA included in analysis?
Tektite	2016	F	Hiriwa	Y
Chewy	2016	M	Huru	Y
Un-named	2016	M	Lorelie	Y
Rua	2016	F	Joy	Y
Hope	2017	F	Joy	Y
Ursa	2017	F	Lena	Y
Kahu	2017	F	Lorelie	Y
Kanuka	2017	M	Zoe	Y
Te Hau	2017	M	Hiriwa	Y
Ace	2017	M	Gem	Y
Toka	2017	M	Moana	Y
Rocky	2017	M	untagged female	Y
Thor	2017	M	Patti	Y
Mika	2017	F	Pippa	Y
Carlos	2017	M	Madeline	Y
Hipi	2017	F	Seazar	Y
Awatea	2017	M	unknown	Y

Table A2.2. List of individual NZ sea lions from the Enderby Island population included in mate choice analysis

ID	Year of birth	Mother/pup	Mother ID
C114	unknown	Mother	-
C128	unknown	Mother	-
C155	unknown	Mother	-

ID	Year of birth	Mother/pup	Mother ID
C27	unknown	Mother	-
1414	unknown	Mother	-
b1010	unknown	Mother	-
C117	unknown	Mother	-
C101	unknown	Mother	-
C120	unknown	Mother	-
C145	unknown	Mother	-
C138	unknown	Mother	-
C13	unknown	Mother	-
C33	unknown	Mother	-
C1	unknown	Mother	-
C19	unknown	Mother	-
C43	unknown	Mother	-
C167	unknown	Mother	-
C180	unknown	Mother	-
C15	unknown	Mother	-
C166	unknown	Mother	-
C104	unknown	Mother	-
C113	unknown	Mother	-
C141	unknown	Mother	-
C14	unknown	Mother	-
C175	unknown	Mother	-
P114	2002	Pup	C114
P128	2002	Pup	C128
P155	2002	Pup	C155
0203_pp27	2003	Pup	C27
0304_1414	2004	Pup	1414
2969	2002	Pup	b1010
P117	2002	Pup	C117
0506_117	2006	Pup	C117
1519	2001	Pup	C101

ID	Year of birth	Mother/pup	Mother ID
P101	2002	Pup	C101
P120	2002	Pup	C120
0506_1489	2006	Pup	C145
P138	2002	Pup	C138
0506_1457	2006	Pup	C138
0607_1457	2007	Pup	C138
1758	2001	Pup	C13
P13	2002	Pup	C13
0203_pp13	2003	Pup	C13
0405_13	2005	Pup	C13
1962	2002	Pup	C33
P33	2003	Pup	C33
0203_pp33	2004	Pup	C33
0403_977	2005	Pup	C33
1505	2001	Pup	C1
P1	2002	Pup	C1
0203_pp1	2003	Pup	C1
0304_945	2004	Pup	C1
0405_1	2005	Pup	C1
1988	2001	Pup	C19
P19	2002	Pup	C19
0203_pp19	2003	Pup	C19
0405_19	2005	Pup	C19
0506_19	2006	Pup	C19
1580	2001	Pup	C43
P43	2002	Pup	C43
0203_pp43	2003	Pup	C43
P167	2002	Pup	C167
2939	2004	Pup	C167
P180	2001	Pup	C180
P15	2001	Pup	C15

ID	Year of birth	Mother/pup	Mother ID
0203_pp15	2003	Pup	C15
0405_15	2005	Pup	C15
P166	2002	Pup	C166
P104	2001	Pup	C104
0506_14	2006	Pup	C104
0607_1474	2007	Pup	C104
P113	2002	Pup	C113
P141	2002	Pup	C141
P14	2001	Pup	C14
0203_pp14	2003	Pup	C14
0405_14	2005	Pup	C14
P175	2001	Pup	C175

Appendix 3

Table A3.1. Parameters for COLONY calibration runs

Parameter	**Run 1 (default)**	**Run 2**	**Run 3**	**Run 4**
Mating System I	Female & Male Polygamy	Female & Male Polygamy	Female & Male Polygamy	Female & Male Polygamy
Mating System II	Without Inbreeding	Without Inbreeding	Without Inbreeding	With Inbreeding
Species	Dioecious & Diploid	Dioecious & Diploid	Dioecious & Diploid	Dioecious & Diploid
Run Length	Medium	Medium	Long	Medium
Analysis Method	Full-Likelihood	Full-Likelihood	Full-Likelihood	Full-Likelihood
Likelihood Precision	Medium	High	Medium	Medium
Sibship Size Prior	Without Prior	Without Prior	Without Prior	Without Prior

Table A3.2. COLONY relationship assignments of NZ sea lions (*shown on left) compared to known relationships ([1]shown across top) under different parameters

		Mother-offspring[1]	*Unrelated*	*Total*
Run 1 (default)	*Mother-Offspring**	35	3	38
	Unrelated	6	612	618
	Total	41	615	656
		Mother-offspring	*Unrelated*	*Total*
Run 2	*Mother-Offspring*	35	2	37
	Unrelated	6	613	619
	Total	41	615	656
		Mother-offspring	*Unrelated*	*Total*
Run 3	*Mother-Offspring*	35	2	37
	Unrelated	6	613	619
	Total	41	615	656
		Mother-offspring	*Unrelated*	*Total*
Run 4	*Mother-Offspring*	36	2	38
	Unrelated	5	613	618
	Total	41	615	656

Appendix 4

Table A4.1. Correlation coefficient of estimated and true (simulated) values of different relatedness estimators calculated in COANCESTRY for the Otago Peninsula NZ sea lion population

Relatedness estimator	**Correlation coefficient of estimated relatedness values with true values**
Triadic likelihood (TrioML)	0.80
LynchRd	0.76
Wang	0.75
LynchLi	0.75
Queller-Goodnight	0.75
Ritland	0.68

Table A4.2. TrioML relatedness coefficient estimates and true r_{xy} for simulated dyads in six relationship categories calculated in COANCESTRY. Simulated genotypes of dyads were based on the Otago Peninsula NZ sea lion population microsatellite marker sets.

True relationship	**Actual r_{xy}**	**TrioML mean estimated r_{xy}**	**Wilcoxon V**	**P**	**Coefficient of variation**
Parent-offspring	0.5	0.530	6750	***	16%
Full siblings	0.5	0.526	6300	***	32%
Half siblings	0.25	0.244	4800	NS	73%
First cousins	0.125	0.153	4600	NS	103%
Second cousins	0.03125	0.0838	5000	NS	141%
Unrelated	0	0.0815	8000	***	144%

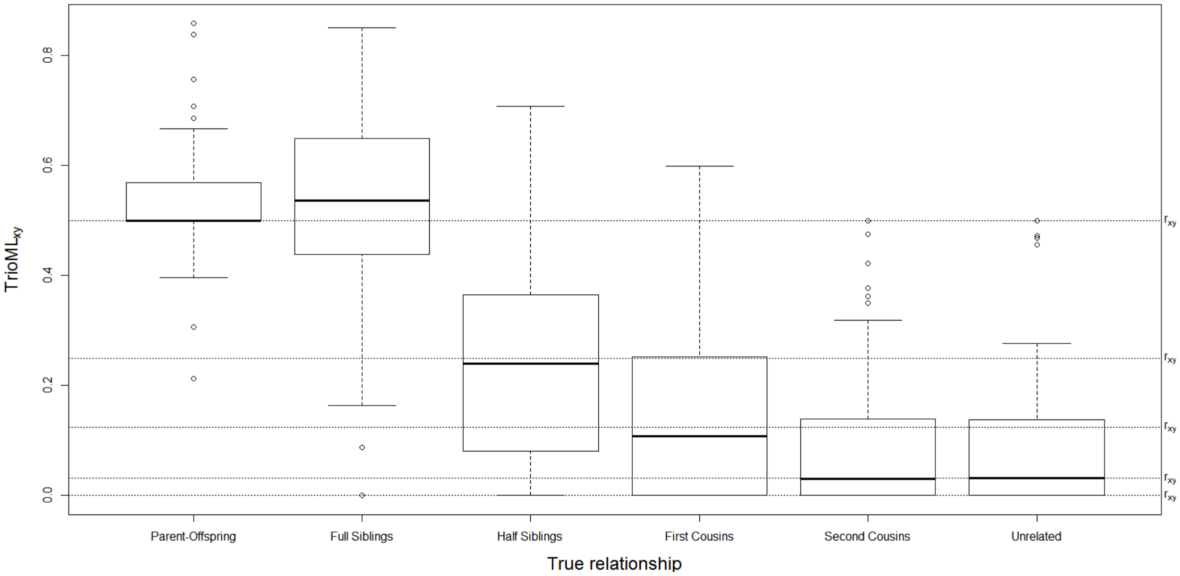

Figure A4.1. Spread of TrioML relatedness coefficient estimates calculated in COANCESTRY for simulated dyads in different relationship categories using simulated genotypes based on the Otago Peninsula population microsatellite marker sets of the Otago Peninsula NZ sea lion population. Dashed horizontal lines mark true r_{xy} coefficients.

Table A4.3. Correlation coefficient of estimated and true (simulated) values of different relatedness estimators calculated in COANCESTRY for the Enderby Island subset NZ sea lion population

Relatedness estimator	**Correlation coefficient of estimated relatedness values with true values**
Triadic likelihood (TrioML)	0.85
Queller-Goodnight	0.84
Wang	0.80
LynchRd	0.79
LynchLi	0.78
Ritland	0.12

Table A4.4. TrioML relatedness coefficient estimates and true r_{xy} for simulated dyads in six relationship categories calculated in COANCESTRY. Simulated genotypes of dyads were based on the Enderby Island NZ sea lion breeding colony subset microsatellite marker sets.

True relationship	**Actual r_{xy}**	**TrioML mean estimated r_{xy}**	**Wilcoxon V**	**P**	**Coefficient of variation**
Parent-offspring	0.5	0.511	6550	***	12%
Full siblings	0.5	0.469	4600	NS	33%
Half siblings	0.25	0.234	4500	NS	60%
First cousins	0.125	0.117	3600	**	106%
Second cousins	0.03125	0.0735	5128	NS	140%
Unrelated	0	0.0559	7600	***	139%

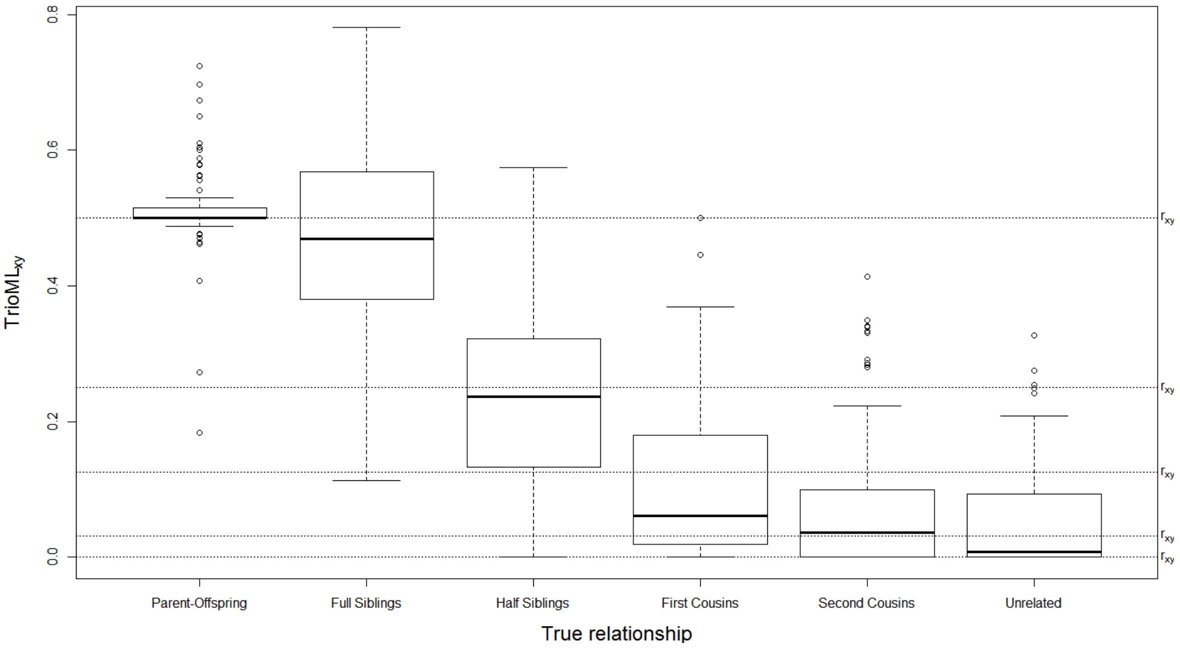

Figure A4.2. Spread of TrioML relatedness coefficient estimates calculated in COANCESTRY for simulated dyads in different relationship categories using simulated genotypes based on the Enderby Island subset microsatellite marker sets of the Enderby Island subset NZ sea lion population. Dashed horizontal lines mark true r_{xy} coefficients.