Territoriality of cooperative breeding pūkeko (*Porphyrio melanotus melanotus*) under low and high population density conditions

TERRITORIALITY OF COOPERATIVE BREEDING PŪKEKO (*Porphyrio melanotus melanotus*) UNDER LOW AND HIGH POPULATION DENSITY CONDITIONS

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A Thesis Submitted to the School of Graduate Studies in the Partial Fulfillment of the Requirements for the Degree Master of Science

McMaster University

McMaster University

Master of Science (2017)

Hamilton, Ontario (Department of Biology)

TITLE: Territoriality of cooperative breeding pūkeko (*Porphyrio melanotus melanotus*) under low and high population density conditions

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NUMBER OF PAGES: xvi, 97

Lay Abstract

Ecological constraints have been shown to influence the formation of social groups. The decimation of a population of cooperatively breeding pūkeko on the North Island of New Zealand provided us with a unique opportunity to compare two populations under different density conditions. I explored the effect of population density on group composition, parentage, and territory size as a means to understand the costs and benefits of cooperative breeding and joint-nesting. Territory sizes were significantly larger under low density conditions. I was unable to determine whether or not population density influenced offspring dispersal or relatedness amongst group members.

Abstract

Habitat saturation, due to high population density, and predation pressure have both demonstrated to influence the formation of some social systems. For example, helper-at-the-nest systems are formed when offspring delay dispersal due to a lack of suitable territory availability or high cost of dispersal. In one cooperative avian species, the pūkeko (*Porphyrio melanotus melanotus*), a previous comparison between high density (North Island) and low density (South Island) populations found that at high density, there were fewer dispersal opportunities due to habitat saturation resulting in increased relatedness amongst group members. Climatic variations between the North Island and the South Island could explain many of the results previously found. The recent decimation of a large pūkeko population at a North Island site provided us with a unique opportunity to compare group structure between two populations under similar climatic conditions to determine whether or not individuals bred independently in a low density population. For my thesis I aimed to answer three questions. First, how does population density affect the dispersal of offspring from their natal territory? Second, how does population density affect relatedness of adult group members? Third, how does density affect territory size? In this thesis I was unable to determine whether or not dispersal events were occurring or if there was high or low relatedness amongst group members. Territory sizes were significantly smaller at Tawharanui over Shakespear but they were not significantly correlated with group size. Harrier presence was significantly different between paddocks.

Acknowledgements

Firstly, I would like to thank my supervisor, Dr. Jim Quinn, for providing me the opportunity to further my education and foster an already established passion for ornithology. Thank you so very much for taking the risk and shipping me to Middle Earth to chase pūkeko. I am very grateful for the bird handling skills you bestowed on me as well as the wealth of knowledge I gained over these last 2.5 years while under your supervision. Also, it was a pleasure getting to know you and Diane and to be fortunate enough to try your cooking. You make a mean curry and the best hashbrowns. Also, thank you both for your help in data collection. It was very much appreciated.

I would also like to extend a tremendous thank you to my committee member, Dr. Ben Bolker, for all his help in the statistical realm. I honestly could not have made it through without his endless patience and help. His ability to break things down to a level where I could understand made a huge difference in improving my grasp on "R". So thank you. I hope to take the skills I've learned and continue to apply them.

I must also extend a huge thank you to all the wonderful people I had the pleasure of interacting with during my 2 field seasons in New Zealand. I would specifically like to thank Colin Wards and his partner Cheri, Maurice "Mo" Puckett, Matt Maitland, and Ditch Keeling. Colin and Cheri, I honestly cannot tell you how much the both of you mean to me and how much I appreciate all the niceties you bestowed on me my very first field season. I could not have made it through until December without the two of you. It was truly a pleasure to spend my 23^{rd} birthday with the both of you and I cannot wait for the opportunity to see the both of you again. And thank you to Colin for giving me the opportunity to wrangle sheep during my first field season. That was such a memorable day and I loved every second of it. I will never forget handling the brand new lambs that were born in the woolshed because no one knew that those ewes were pregnant. Mo, you are such a fantastic human being and you were such a tremendous help during my time in New Zealand. I enjoyed all our talks and that you were always willing to lend a hand when I needed it. Thank you to Matt Maitland for bestowing upon me knowledge about the parks and the various flora and fauna that inhabit them. I truly learned a lot talking to you and I'm glad that you were supportive of the work that we were doing there. Ditch, I would like to say thank you for lending a sympathetic ear during my last field season and keeping me company during my countless nights of insomnia. I cannot put into words how much it meant to me for you to be there when I broke down. You definitely kept me going through that last month and I cannot thank you enough for that. Also, thank you to all the rangers at both Tawharanui and Shakespear for all the help you all provided during the last two years.

Also, I honestly could not have gotten through these last couple of years without the love and support of my friends and lab mates. I would first like to thank Josh Robertson for all his help in the lab and his unlimited optimism. Even though sometimes your cheerful attitude drove me up the bloody walls and some days you smelt so horrendous I couldn't even stomach being in the lab, I cannot thank you enough for lending me an ear when I needed it and pointing me in the right direction when I had no idea what I was doing. I have to admit you were such an entertainment these last couple of years. You are a fabulous human being and will go so far. I look forward to seeing where you end up. Next, I would like to thank Sheng Hing for his endless support and always being there when I needed it. You were my unofficial cheerleader. I enjoyed all our hangout sessions and all the patience you had to listen to me when I needed someone to rant to about anything. And all those times you talked me off the ledge and helped me find my way when I couldn't see the light. I cannot thank you enough Sheng. Seriously, you are the best and I love you very much. I am also very thankful that you tolerated all my singing in the office. I also need to thank Courtney Young for being the best field partner and roommate ever. We may have had a bit of a slow start but you've been an incredible support since. That last field season was extraordinary and being your roomie has been a pleasure. I don't even know how to thank you for everything you've done for me. Firstly, thank you for introducing me to homemade fudge and chicken tacos. Delicious. Secondly, thank you for having my back and keeping me sane when I needed it. Also, for giving me the confidence to feel beautiful in my own skin and helping me to realise that it's not always about what you wear but how you wear it. And I should thank you for kicking my ass when I needed it and never being afraid to speak your mind. Seriously, some of my best memories are with you. All those times you serenaded me with Enrique Iglesias', "Hero" and when we couldn't stop ourselves from singing along to One Direction's "Perfect". Or all those times we got stuck in South Punchbowl and had to push the car out. Or better yet, when I forgot that the e-brake was on. Or all the times we spent talking to each other on messenger during lab meeting and struggled to not giggle. Getting me hooked on "Rock of ages" and the time I fell asleep during "Moulin Rouge" and started snoring. I love you, Courtney.

You're fantastic and I will miss you so much. Lastly, I would like to thank my friend, Jenn Rebchuk for her academic and moral support as well as all her help with my anxiety attacks, depressive episodes, and boy drama. You've been such a tremendous friend to me since we met 5 years ago and I hope to be there for you in the same capacity anytime you need me.

Lastly, thank you to my Grandparents, Mum, Dad, and Stepdad for all the financial and moral support that you have provided to me throughout my life. Encouraging me to follow my dreams and making me believe that I can accomplish anything. There are not enough words in any language to describe how much I appreciate every single thing that you've all done for me. I know I don't always say it but you guys are amazing. I love you all so very much and I don't think that I would have made it this far without your love and support. Also, shout out to my sisters for being the best sisters this girl could ever ask for. I love you Laura and Kate.

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Declaration of Authorship

I, Meghan R. Healey, declare that this thesis titled, “Territoriality of cooperative breeding pūkeko (*Porphyrio melanotus melanotus*) under low and high population density conditions” and the work presented in it are my own. I confirm that:

- **Chapter 1: General Introduction**
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- **Chapter 2: Kinship and territoriality of cooperative breeding pūkeko (*Porphyrio melanotus melanotus*) under low and high population density conditions**
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  Author Contributions: MRH wrote the manuscript and conducted all statistical analyses. Statistical guidance provided by Dr. Ben Bolker. James Quinn provided comments and revised the manuscript. Field data collected by MRH, JSQ, Diane Fields, and Courtney Young.

- **Chapter 3: General Conclusion**
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Chapter 1

General Introduction

1.1 Introduction

Ecological constraints limit individuals in a manner that forces a change in their behaviour (Bergmüller et al. 2005; Creel et al. 2005; Baglione et al. 2006; Fontaine and Martin, 2006; Lehmann et al. 2007; Valeix et al. 2009). Constraints, such as territory limitation due to population density, can influence the behavioural strategies of an individual towards conspecifics. For example, Bearded vultures (*Gypaetus barbatus*) have been noted to change from a monogamous mating system under low density conditions to a polyandrous trio in response to habitat saturation (Carrete et al. 2006). Prairie Voles (*Microtus ochrogaster*) exhibit increased delayed dispersal by offspring under high density conditions (Lucia et al. 2008). To understand the mechanisms that maintain cooperative and social living, it is important to explore the features that appear to lead to sociality. In this thesis, I aimed to examine the effect of a sudden availability of excess habitat on territoriality and group composition in pūkeko (*Porphyrio melanotus melanotus*), a polygynandrous joint-nesting rail that typically lives in groups with multiple male and female breeders sharing a single nest.

1.2 Dispersal, relatedness, and territoriality

Cooperative breeding is a system in which some adults care for young that are not their own direct offspring (Emlen and Vehrencamp, 1983; Stacey and Koenig, 1990). In avian systems, cooperation can vary from cooperative polygamy or plural breeding, whereby more than a single male or female shares reproductive rights within a social group, that may or may not have helpers, (e.g. Superb starlings *Lamprotonis superbus* (Rubenstein, 2016)) to helper-at-the-nest due to delayed dispersal (e.g. Seychelles warblers *Acrocephalus sechellensis* (Komdeur, 1992)) (Brown, 1987; Koenig et al. 1992; Hatchwell and Komdeur, 2000). Helpers aid the breeders through the feeding of nestlings and fledglings, as well as the incubation and defense of nest and territory (Brown, 1987; Hatchwell and Komdeur, 2000). The retention or addition of helpers has been shown to increase survival of offspring (Lennartz et al. 1987; Blackmore and Heinsohn, 2007) and help in maintaining territorial boundaries through increased defense (Port et al. 2011).

In cooperative groups, helpers are usually kin of the focal breeding pair (Brown, 1987). Hamilton's Rule (1964 a,b) suggests that social behaviour that is a detriment to an individual's fitness (i.e. altruism) occurs only when it increases the inclusive fitness of the performer. Inclusive fitness is comprised of both direct (i.e. the amount of relative fitness an individual gains through personal reproduction) and indirect fitness (i.e. the fitness that an individual achieves through the reproduction of non-descendant relatives) (Hamilton 1964 a,b; Eberhard, 1975). Fitness is measured by the proportion of genes like one's own that an individual promotes to the succeeding generation throughout their lifetime (Eberhard, 1975). The likelihood of helping is highly influenced by the closeness of genetic relatedness between the performer and receiver, the magnitude of the benefit, and the cost to the performer (Eberhard, 1975). Helping raise genetic relatives increases the magnitude of fitness benefits a performer receives because they share a portion of identical genes; thus, kin selection is typically considered to be a factor behind the altruistic behaviour displayed in some cooperative breeding species (Hamilton, 1964 a,b; Maynard Smith, 1964; Eberhard, 1975).

One of the major pre-requisites to cooperative breeding, specifically helper-at-the-nest systems, is the delayed dispersal of offspring (Koenig et al., 1992; Hatchwell and Komdeur, 2000; Hatchwell, 2009). Dispersal is defined as the relocation of an individual irrespective of whether or not they are successful at reproducing after dispersal (Gross dispersal; Greenwood, 1980). The act of dispersing can be voluntary (e.g. Cockburn et al. 1985; Wahlstrom and Kjellander, 1995) or forced (e.g. Cant et al. 2001), environmental (eg. Baglione et al. 2006), or innate (e.g. Howard, 1960; Greenwood and Harvey, 1982). Dispersal is important for both population regulation, spatial distribution, and the genetic structure of a population (Howard, 1960; Greenwood and Harvey, 1982; Bowler and Benton, 2005). The factors that inhibit dispersal must be significantly costly or the benefits of natal philopatry must be substantially beneficial to persuade an individual from pursuing solitary reproduction, otherwise, 'Why stay?'.

Two main hypotheses have been proposed to explain why offspring may choose not to disperse (Koenig et al. 1992). In the ecological constraints hypothesis, a shortage of vacant territories (Emlen, 1982, 1984; Woolfenden and Fitzpatrick, 1984; Pasinelli and Walters, 2002), a high cost of dispersal (Ligon and Ligon, 1990; DuPlessis, 1992), a lack of available breeding partners (Rowley 1965, 1981; Maynard Smith and Ridpath, 1972; Reyer, 1984; Clarke, 1989; Marzluff and Balda, 1990; Walters et al. 1992), and a low likelihood of breeding successfully once obtaining a territory (Reyer 1980; Emlen, 1982; Stacey and Ligon, 1987; Curry 1988) have been identified as the main critical constraints that restrict independent breeding (Hatchwell and Komdeur, 2000). The benefits of philopatry hypothesis proposes that delayed dispersal is not only influenced by external constraints but by the benefits gained by remaining within the natal territory (Stacey and Ligon, 1987, 1991; Hatchwell and Komdeur, 2000). This hypothesis suggests that under varying habitat quality, the benefit of philopatry increases, thus, providing an explanation for the presence of cooperative breeding even in the absence of habitat saturation (Hatchwell and Komdeur, 2000). Although biologists have argued over the precise distinctions between the ecological constraints hypothesis and the benefits of philopatry hypothesis, the latter has become integrated with the former as both assume a cost-benefit analysis of leaving versus staying, with a preference for staying (Hatchwell and Komdeur, 2000).

A high cost of dispersal due to increased predation pressure increases the likelihood offspring and helpers will remain with their social group (Heg et al. 2004; Tanaka et al. 2016). Population density affects the amount/quality of geographic space available for individuals to occupy (Pasinelli and Walters, 2002; Mattheysen, 2005) impacting the emigration of individuals from their natal location (Crespi and Taylor, 1990; Herzig, 1995; Lena et al. 1998; Roland et al. 2000; Albrectsen and Nachman, 2001). Higher population densities result in increased relatedness amongst groups (Jamieson et al. 1994) and reduced chances of dispersal (Komdeur et al. 1995). It can also affect the reproductive success of small groups and breeding pairs due to increased chances of displacement by larger groups (Slobodchikoff, 1984). Year-round territorial permanency may also contribute to habitat saturation because it makes acquiring a territory more difficult for dispersing offspring, thus, making cooperation more valuable (Dillard and Westneat, 2016).

Definitions of "territory" vary: they may be based on proximity to the focal individual, time of year (i.e. breeding vs. non-breeding), the guarded resource (i.e. nesting area, mates, food), or lifespan of the focal individual (Howard, 1920; Noble, 1939; Brown, 1975; Wilson, 1975). The most common definition used in the literature for territory is "any defended area" (Noble, 1939). A more specific definition sometimes used is: a "fixed area from which intruders are excluded by some combination of advertisement (e.g. scent, song), threat and attack" (Brown, 1975). This has been expanded further to incorporate that territory need not be fixed in geographical space but could be spatiotemporal in nature (Wilson, 1975; Kauffman, 1984). For this study, I elaborate slightly on Brown's (1975) definition and describe territory as a fixed geographical space that can vary in size based on the external pressures from bordering territories and is defended to exclude intruders by an individual or group of individuals through advertisement, threat, and attack. Territory is different from home range which is defined as an undefended area which an animal traverses while engaging in fundamental behaviours such as foraging, mating, and raising offspring (Burt, 1943).

Territoriality may perpetuate group living and sociality (Axelrod and Hamilton, 1981). In game theory models, the "prisoner's dilemma" provides a possible explanation for communal breeding in some species (Axelrod and Hamilton, 1981; Craig, 1984) as territory-holders may take on additional individuals in an attempt to maintain their boundaries from adjoining territories. In short, two individuals have a choice between cooperating or "defecting" during any one interaction (Axelrod and Hamilton, 1981). Hypothetically, if two monogamous pairs (Group A and Group B) had neighbouring territories, either group has the choice to remain as a pair or take on an additional member to assist in boundary maintenance. If Group A chooses to defect against Group B by adding another group member, then Group A receives a more advantageous pay-off (i.e. larger territorial area or higher quality resources) in comparison to Group B because they are minimizing the loss that will occur if Group B defects and Group A chooses to cooperate. Furthermore, if both groups choose to mutually defect, then the hypothetical pay-off is less than if they mutually cooperate. Although logically the decision for both groups to remain cooperative offers the greatest long term reward, the decision to defect first best aligns with the self-interest of the group; therefore, providing incentive for each group to defect against the other. Hence, the dilemma in choosing between cooperating and hoping that the other group does as well or each defecting and receiving a less substantial reward (Axelrod and Hamilton, 1981). In Green Woodhoopoes (*Phoeniculus purpureus*), territory size is significantly correlated with group size and larger groups dominate over smaller groups. Breeding pairs are rarely as reproductively successful as groups with helpers unless food is abundant or the external pressure from neighbouring groups is low due to low population density or territorial isolation (Ligon and Ligon, 1990).

In the Resource Dispersion Hypothesis (RDH), groups are thought to develop when required resources are dispersed in such a heterogenous manner that the most economically feasible territory for a monogamous pair (called primary occupants) can accommodate other individuals (called secondary occupants) at no additional cost (Macdonald, 1983; Carr and Macdonald, 1986; Macdonald and Johnson, 2015). It is believed that RDH influences sociality by providing a crutch for groups to develop and that this grouping behaviour may become entrenched and continue, despite changes in the distribution of resources which may no longer require individuals to live in groups (Macdonald and Johnson, 2015). Nevertheless, resource distribution may be an important component of the social framework regardless of the functionality of group living (Macdonald and Johnson, 2015). RDH does not necessarily predict that there be a relationship between territory size and group size as each is independently influenced by the abundance and distribution of available resources (Carr and Macdonald, 1986; Macdonald and Johnson, 2015). Territories are generally thought not to be larger than what is minimally required to satisfy the current occupants. Further enlargement beyond what can feasibly be protected is considered more costly than beneficial. That does not invalidate that there will be groups and territories that are larger than the minimum, as the costs of defending a larger territory may be outweighed by the benefits (i.e. increased reproductive success) (Macdonald and Johnson, 2015). Furthermore, if the secondary occupants are somehow related to the primary occupants than the costs of border defense are mitigated by the coefficient of relatedness. Overall, costs to the secondary occupants must be less than other available options (i.e. stay or disperse) (Macdonald and Carr, 1989; Macdonald and Johnson, 2015). Group living can lead to competition between members over available resources and may influence membership as well as the rewards needed for tolerance (Macdonald and Carr, 1989; Kokko and Rankin, 2006; Macdonald and Johnson, 2015).

In social groups, the opportunity to reproduce is used to keep individuals cooperative (Shen and Reeve, 2010). However, the partitioning of reproductive shares can be unevenly distributed amongst group members, leading to reproductive skew (Keller and Reeve, 1994). There are several models of reproductive skew that aim to explain the general framework for complex societies (Shen and Reeve, 2010; Nonacs and Hager, 2011). Models typically fall in to one of two categories: transactional (concession and restraint) models (where leverage of reproductive payments is used in exchange for cooperation) and tug-of-war models (where individuals have a tug-of-war over their reproductive shares) (Shen and Reeve, 2010). The reproductive skew of a group must lie between the proportion of group reproduction that a subordinate needs to be allocated to stay, and the proportion of group reproduction that the dominant is willing to yield or also needs to have to stay. Overall, the inclusive fitness gains need to be equivalent, or exceed what an individual would achieve from non-cooperation (Reeve and Shen, 2006; Nonacs and Hager, 2011). In concession models, dominants concede reproductive shares to the subordinate in exchange for assistance (Vehrencamp, 1983a, b). In restraint models, the subordinates restrain themselves from over-exceeding their reproductive shares in order to remain in the group and avoid potential eviction by the dominant (Johnstone and Cant, 2001). In either model, the subordinate's inclusive fitness gains need to either be equivalent or exceed the amount they would gain by breeding independently and it is assumed that individuals are able to monitor their relative amount of reproduction and pursue alternative options (ie. Solidarity or join another group) if the amount falls below the minimum level needed (Vehrencamp, 1983a, 2000; Reeve and Shen, 2006; Nonacs and Hager, 2011). However, the probability of successful dispersal, and the coefficient of relatedness can affect the degree of reproductive skew (Vehrencamp, 1983a, b, 2000). Concession models predict that the incentives needed for a subordinate to stay in a group decrease as the ecological constraints on solitary breeding increase, and incentives decrease in magnitude as relatedness increases, because individuals gain indirect benefits through helping (Keller and Reeve, 1994).

1.3 Pūkeko Natural History

The pūkeko (*Porphyrio melanotus melanotus*; Fig. 1.1) is an excellent candidate for understanding the effect of population density on cooperative breeding. A New Zealand native, the pūkeko is a cooperative, joint-nesting species (Jamieson 1997; Vehrencamp and Quinn 2004) with a polygynandrous mating system comprised of groups of 3-12 individuals. Groups normally contain 2-3 breeding males, 1-2 breeding females, and a number of non-breeding individuals of either sex who defend a shared territory and provide alloparental care (Craig, 1980; Craig and Jamieson, 1988). The conversion of native forests into pastureland has allowed population numbers to skyrocket, increasing the amount of land pūkeko can exploit (Bunin and Jamieson, 1985).

Comparisons between the North Island (high density) and South Island (low density) pūkeko groups in New Zealand have suggested that at high density, offspring of both sexes have reduced chances of dispersal due to habitat saturation,

FIGURE 1.1: Adult male pūkeko (*Porphyrio melanotus melanotus*)

resulting in increased relatedness among group members (Craig and Jamieson, 1988; Jamieson et al. 1994; Jamieson, 1997). It has been argued that such increases in relatedness have lead to high reproductive skew and an increase in dominance-related aggression (Jamieson, 1997). Another notable ramification of a high density population was observed by Craig and Jamieson (1988), where 75% of all copulations were between first degree relatives (r=0.5). In contrast, adult group members in the low density South Island population are often genetically unrelated, have more opportunity for independent breeding (lower skew), and lower dominance-related aggression, in comparison to the high density, North Island population (Jamieson et al, 1994; Jamieson, 1997). The variation in density between North Island and South Island sites was thought to be due to varying climatic conditions, where the colder and more severe conditions on the South Island resulted in a higher mortality rate (Jamieson, 1997). It has since been suggested that a lack of year-round territoriality due to harsh weather conditions, contributes to an ambiguous dominance hierarchy leading to a low reproductive skew and unrestrained reproduction (Pers. Comm. J.S. Quinn). Communal clutches at low density sites were found to be 1.4 times larger than those between related females at the high-density site (Jamieson, 1997).

1.4 Thesis Aims

The purpose of this thesis was to explore the social behaviour of pūkeko under two differing levels of population density to determine whether group living and/or kinship within groups is caused by habitat saturation, and what impact such restrictions have on dispersal and territorial holdings. The recent decimation of a large pūkeko population at a North Island site provided us with a unique opportunity to compare group structure under similar climatic conditions; thus, allowing us to see whether individuals bred independently when granted the opportunity or continued to live cooperative kin groups. Helping behaviour is inherited either from genetics and/or culture and could explain why cooperation persists even without ecological barriers (MacColl and Hatchwell, 2003; Charmantier et al. 2007). Investigating the effects of population density on group composition, parentage, and territory quality is vital for understanding the costs and benefits of cooperative breeding and joint-nesting.

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Chapter 2

Territoriality of cooperative breeding pūkeko (*Porphyrio melanotus melanotus*) under low and high population density conditions

2.1 Abstract

Ecological constraints have shown to influence sociality. Under the ecological constraints hypothesis, a lack of alternative territories and predation pressure can affect the dispersal of an offspring, causing them to remain on their natal territory as a non-breeder and gain indirect fitness through providing allo-parental care to subsequent offspring. This can result in an individual later inheriting a breeding position on a good quality territory. In the cooperative breeding pūkeko, a comparison between high density (North Island) and low density (South Island) groups found reduced dispersal due to habitat saturation and increased relatedness amongst group members under high density. The 2011 decimation of one North Island pūkeko population allowed us with a unique opportunity to compare various aspects of sociality between two populations under similar climatic conditions. Here I attempted to answer three questions. First, how does population density affect the dispersal of offspring from their natal territory? Second, how does population density affect relatedness of adult group members? Third, how does density affect territory size? I was unable to confirm or refute whether or not dispersal events were occurring or if there was any relatedness amongst group members. Territory sizes were significantly different between Tawharanui and Shakespear and they were significantly correlated with group size. Harrier presence was significantly different across paddocks but not parks. I recommend that to gain better perspective into the maintenance of the cooperative breeding system exhibited by the pūkeko, a longer term study between these sites should be conducted.

2.2 Introduction

A shortage of vacant territories (e.g. Emlen, 1984; Woolfenden and Fitzpatrick, 1984) is one of the constraints that limit independent breeding according to the Ecological constraints hypothesis (Emlen, 1984; Hatchwell and Komdeur, 2000). Population density, or the number of individuals per unit area (Russell et al. 2010), affects the movement patterns or dispersal of individuals from one geographic space to another (Matthysen, 2005) as well as the amount and quality of geographic space available for individuals to occupy (Pasinelli and Walters, 2002; Mattheysen, 2005). High population density has been shown to influence mating strategies (eg. Monogamy to polyandrous trios in Bearded Vultures *Gypaetus barbatus*; Carrete et al. 2006) as well as the dispersal patterns of offspring (eg. Great tits *Parus major* van Balen and Page, 1989; Prairie Voles *Microtus ochrogaster* Lucia et al. 2008; House sparrow *Passer domesticus* Pärn et al. 2012). Year-round territorial permanency can also cause habitat saturation by reducing territory availability for dispersing offspring (Arnold and Owens, 1998; Arnolds and Owens, 1999; Hatchwell and Komdeur, 2000; Dillard and Westneat, 2016). Additionally, a high cost of dispersal due to increased predation pressure reduces the likelihood offspring and helpers will stray far from their natal location (Heg et al. 2004; Tanaka et al. 2016).

The most studied form of dispersal is natal dispersal; defined as the permanent relocation of an individual from its birth place to a secondary location where, if it survives and finds a mate, it will reproduce (Howard, 1960; Greenwood and Harvey, 1982). Dispersal is important for both population regulation and the genetic structure of a population (Howard, 1960; Greenwood and Harvey, 1982; Bowler and Benton, 2005). Often, in cooperatively breeding species, offspring that remain on the natal territory will assist their parents in raising subsequent broods (Koenig et al. 1992). This retention of offspring by a breeding pair is believed to be an important element in the evolutionary roots of cooperative breeding (Brown 1987; Ligon and Burt 2004), a system whereby individuals in a social group show care to offspring that are not their own (Koenig and Dickinson, 2004). The retention or addition of auxiliaries/helpers has been shown to increase survival of offspring (Lennartz et al. 1987; Blackmore and Heinsohn, 2007) and help in the maintenance of territorial boundaries (Port et al. 2011). Both the "prisoner's dilemma" and Resource Dispersion Hypothesis provide possible explanations for communal breeding due to increased territoriality in some species (Craig, 1984; Carr and Macdonald, 1986, Macdonald and Johnson, 2015). For this study, I elaborate on Brown's (1975) definition of territory and describe it as a fixed geographical space, containing critical resources, that can vary in size and shape based on the external pressures from bordering territories and that are monopolised and defended to exclude intruders by an individual or group of individuals.

To maintain cohesion in some social groups, reproductive shares are often used or taken as incentive (Shen and Reeve, 2010). Transactional models are instances where leverage of reproductive payments is used in exchange for cooperation. They are comprised of both concession and restraint models. In concession models, dominants concede reproductive shares to the subordinate in exchange for assistance (Vehrencamp, 1983a,b); whereas, in restraint models, the subordinates exercise restraint over unsanctioned reproductive shares in order to avoid eviction (Johnstone and Cant, 2001). In either case, the subordinate's inclusive fitness gains need to either be equivalent or exceed the amount they would gain by breeding independently (Reeve and Shen, 2006; Nonacs and Hager, 2011) otherwise it is more beneficial to pursue alternative options (ie. Solidarity or join another group) (Vehrencamp, 1983a,b, 2000; Reeve and Shen, 2006; Nonacs and Hager, 2011). However, a high cost of dispersal and the degree of kinship can affect reproductive skew (Vehrencamp, 2000). Reproductive skew models, specifically concession models, predict that the amount of incentives needed decrease as the ecological constraints on solitary breeding increase and the magnitude as relatedness increases (because individuals gain indirect benefits through helping) (Keller and Reeve, 1994).

The pūkeko (*Porphyrio melanotus melanotus*), is a large cooperative breeding rail found in open terrestrial or shallow fresh water habitats across New Zealand. pūkeko have been a subject of interest because of their polygamous mating system (multiple breeding males, one to two breeding females, and non-breeding adults of both sexes that act as helpers) and joint-nesting framework (Jamieson et al. 1994; Vehrencamp and Quinn 2004). Joint-nesting is used in reference to a clutch laid by more than one female (Verehencamp, 2000).

Research was conducted at Tawharanui Regional Park (36° 22' 10"S, 174° 49' 58"E) and the Shakespear Regional Park (36° 36' 28"S, 174° 49' 23"E). Both of which are located on the North Island of New Zealand just north of Auckland and hold pūkeko populations. Tawharanui Regional Park was acquired by ARC in 1973. A terrestrial predator-proof fence was installed in 2004 followed closely by an aerial poison drop to eliminate exotic terrestrial mammalian predators. Since 2004, the population has been steadily increasing (Maitland, 2011). Shakespear Regional Park was acquired by ARC in 1967 and construction of a predator-proof fence began in October 2010. After completion of the fence in 2011, the pūkeko at Shakespear Park were decimated as by-kill during an aerial eradication, similar to that of Tawharanui, of exotic terrestrial mammalian predators. This event is estimated to have caused a 96% decline in the pūkeko population (population estimation pre-poison drop (2011)= 5427; estimated population post-poison drop (2012)= 195; Maitland, 2012). Shakespear park had been the focus of previous research as a high-density population site (see Jamieson, 1997).

Previous comparisons between high (North Island) and low density (South Island) pūkeko populations have shown that at high density, offspring of both sexes reduce dispersal, which can lead to increased relatedness among group members (Craig and Jamieson, 1988; Jamieson et al. 1994; Jamieson, 1997). "Concession models" of reproductive skew predict that under increased levels of relatedness there is high reproductive skew and an increase in dominance-related aggression (Vehrencamp 1983; Keller and Reeve 1994; Nonacs and Hager, 2011). Craig and Jamieson (1988) found 75% of all pūkeko copulations at Shakespear park were between first degree relatives (r=0.5). In the South Island population, adult group members were genetically unrelated, had more even reproduction (lower skew), and lower dominance-related aggression, in comparison to the high density, North Island population (Jamieson et al. 1994). Previously, the variation in group composition between North Island and South Island sites was thought to be due to varying climatic conditions, where the colder and more severe conditions on the

South Island resulted in a higher mortality rate (Jamieson, 1997). It has since been suggested that a lack of year-round territoriality due to harsh weather conditions, contributes to an ambiguous dominance hierarchy leading to a low reproductive skew and unrestrained reproduction (Pers. Comm. J.S. Quinn).

This chapter explores the social behaviour of pūkeko under two differing population densities to determine whether group living and/or kinship within groups requires habitat saturation, and what impact that may have on dispersal and territorial holdings. The recent decimation of a large pūkeko population at a North Island site provided us with a unique opportunity to compare group structure at low density with another nearby high-density study site under similar climatic conditions to determine if individuals would breed independently or continue to live in cooperative kin groups. Three main questions were posed. First, how does density affect the dispersal of offspring from their natal territory? Second, how does density affect relatedness of adult group members? Lastly, how does density affect territory size? I predicted: 1) a higher prevalence of offspring dispersal at Shakespear regional park (low density) in comparison to Tawharanui regional park (high density); 2) as a result of higher dispersal of offspring, a lower coefficient of relatedness at Shakespear over Tawharanui; and 3) larger territories in the low density site in comparison with the high density site due to reduced pressure on boundaries. Investigating the possible effects of population density on group composition, and territory quality is vital for understanding the evolution or maintenance of cooperative breeding and joint-nesting.

2.3 Methods

Research Sites

The research sites were the Tawharanui Regional Park (36° 22’ 10”S, 174° 49’ 58”E) and the Shakespear Regional Park (36° 36’ 28”S, 174° 49’ 23”E), both of which are run by the Auckland Regional Council (ARC) and located on the North Island of New Zealand (Auckland Council Regional Parks, 2017). Since the installation of a predator-proof fence in 2004, the population at Tawharanui has been steadily increasing (Maitland, 2011). The pūkeko population at this park has been monitored by our lab since 2008 and was estimated in 2013 to be just above 1300 individuals (Unpublished data). After completion of a predator proof fence in 2011 at Shakespear, the pūkeko there were decimated as by-kill during an aerial eradication of exotic terrestrial mammalian predators. The significant reduction in population density at Shakespear allowed for an exploration into the social behaviour and group composition of pūkeko at low (Shakespear) versus high (Tawharanui) population densities during the pūkeko breeding season (typically from August to January; Haselmeyer and Jamieson, 2001).

Cull information

From May to August 2014, 600 Pūkeko were eliminated from the Tawharanui Regional Park site. The number of Pūkeko at the park had been steadily increasing since the eradication of exotic terrestrial predators in 2004 (Maitland, 2011). Being an open sanctuary, Tawharanui Regional Park operates as a working farm while implementing ecological restoration projects and maintaining full public access.

Many of the restoration projects involve re-vegetation, reforestation, as well as the reintroduction of native and endemic species that had been greatly impacted by predation and foraging from exotic terrestrial mammalian predators. Pūkeko are mostly herbivorous but can be considered opportunistically omnivorous (Carroll, 1966). Pūkeko sometimes eat recently planted flora as well as young of various native fauna (Dey and Jamieson, 2013). Therefore, ARC was granted a permit to reduce the number of pūkeko in specific areas of Tawharanui to reduce their impact on re-vegetation efforts as well as reduce their effect on the planned re-introduction of Takahe (*Porphyrio hochstetteri*) to a North Island mainland site.

Nest checking and chick handling

Nests were located by searching suitable nesting habitat (typically Juncus *spp.*, Carex *spp.*, *Typha orientalis*, and *Pennisetum clandestinum*) (Dey et al. 2014) and by observing behaviour. Nest contents were photographed (females produce individually distinctive eggs), and each egg was measured and individually marked with non-toxic permanent marker as found. GPS coordinates were taken for each nest. Nests were checked every 1-3 days depending on weather and monitored through to hatching, when, chicks were sampled for blood (approximately 200 µl) by basilic veinipuncture and capillary tube collection. Blood was then stored in 2 ml approximately 1.5 ml of Queen's Lysis Buffer (Seutin et. al, 1991) for molecular genotyping. Each chick was marked by cutting a particular toenail for future identification. Later, chicks were banded (with compressible foam lining in the band to prevent it from falling off) to allow examination of survival, dispersal, and within-territory movements.

Adult trapping and handling

Adults were attracted to a trapping area using dried maize 2-4 times per week at each park to prime birds on 15 to 20 territories in each of the two parks. Once the birds were primed, we set walk-in traps (either baited box traps, or corral traps that are set initially in a “U”-shape and then modified with curved inwards ends towards the center of the “U”; once set in final configuration, the trap can be approached from the opening and birds will flush to the back, kept from flying out by a roof of bird-netting). Captured birds were measured, blood sampled (200 µl of blood stored in 1 ml of Queen’s lysis buffer), uniquely colour-banded, and then released. There were 6 different colours upon which unique 4 band combinations were created. Colour bands were secured above the knee while a uniquely coded aluminum band (size: M) was secured below the knee. Morphological measurements of the shield width, bill depth, shield-to-tip, nares-to-tip, tarsus length, and wing chord as well as mass were taken. Any banded birds spotted during observation bouts as well as nest hunting and checks were recorded to determine whether or not dispersal had occurred.

Predator pressure

To determine whether predation pressure could influence dispersal at the two sites, Australasian Harrier (*Circus approximans*) sightings were recorded. The time spent in an individual paddock was recorded and a tally was kept for how many harriers were spotted during the time spent in the paddock.

Territory Size

Groups for territory analysis were chosen based on 3 major criteria: at least one individual adult from the group needed to be identifiable (at least one colour band but preferably a full a complement), they had to be located where they could be monitored without being influenced by my presence or the presence of an observer, and they needed to appear to have the majority of their territory in a paddock as we could not be certain how deep into the bush they went which could possibly influence the results. Groups at both field sites were monitored for a minimum of half an hour (up to two hours) 2-3 times per week and territorial fights were noted and the locations recorded in to the GPS or on a diagram using paddock landmarks to get an approximate location of territorial boundaries. Landmarks nearby were noted and then walked from landmark to landmark to outline approximate boundary lines (minimum polygon) with GPS readings.

Census data collection

Park population counts were conducted almost every month while in the field (September – December) for both the 2014 (n=4) and 2015 (n=3) field seasons. At Tawharanui, population counts occurred over two days beginning in either the early morning (7:00am) and ending early afternoon (12:00pm) or late afternoon (5:00pm) and continuing until dusk (8:00pm). Everything above the blue line was counted on day 1 and everything below the blue line was counted on day 2 (See: Fig. 2.6). At Shakespear, population counts occurred in one day either beginning in the early morning (7:00am-9:00am) or late evening (6:30pm-8:30pm). These time periods were chosen because individuals are believed to be more present and active during early morning and late evening (Bibby et al. 1998; Gregory et al. 2004). Counts at both parks were carried out by surveying from various high points around each park (indicated in Fig. 2.1; Fig. 2.6) using a scope (Bausch and Lomb 60X) or binoculars (Eagle Optics 10X) and from walking transects through paddocks that could not been seen from those points, to ensure maximum visibility. Only birds contained within the boundaries of the pest-proof fence were counted at both parks. For more information see Fig. 2.1 and Fig. 2.6. To get an approximation of the total possible number of birds occupying each park in 2014, a ratio was calculated by counting specific paddocks with known totals on census day and dividing their known total by their count totals. For example, if Paddock A had a total of 26 birds (based on our close observations over the season) but on census day only 22 were counted, we would then take the known total and divide it by the counted total (i.e. 26÷22) which would give us a ratio of 1.18. Multiple ratios were calculated per census and a mean ratio calculated from them. The census total was then multiplied by the mean ratio to give an approximation as to the probable total number of birds in the park. For 2015 estimations, group sizes were used instead of paddocks as paddock counts were determined to be unreliable in estimating populations at Shakespear and to keep consistency between parks.

DNA extraction

DNA was extracted following a standard phenol–chloroform–isoamyl alcohol (25:24:1) protocol (Sambrook et al. 1989). Briefly, a 100 µl of blood-lysis buffer mixture was placed in 500 µl of Queen's Lysis Buffer with 10 to 15 µl of proteinase K (20 ng/µl; Thermo Scientific) and were either left rotating at 37 °C overnight or incubated for 2 hours at 55 °C. Approximately 600 µl of phenol–chloroform–isoamyl alcohol mixture was added to each sample, vortexed for 1 minute and centrifuged for 5 minutes at maximum speed (14,000 rpm). The supernatant was then removed and placed in a separate tube. This extraction was repeated once more and followed by the addition of 600 µl of pure chloroform. Samples were then also vortexed for 1 minute and centrifuged for 5 minutes at maximum speed and supernatant removed. To precipitate the DNA, 50 µl of 3M sodium acetate was added to each sample and 500 µl of 95% ethanol added. Samples were then inverted until DNA precipitate was visible. Samples were centrifuged for 10 minutes and supernatant removed. 200 µl of 70% ethanol was then added and samples centrifuged for 5 minutes to clean the DNA pellet. Ethanol was then removed using a p200 and any remaining ethanol allowed to evaporate from tubes for 15-25 minutes. 30 to 100 µl of TE buffer was then added to each sample, depending on the size of the pellet, and samples left at 37 °C overnight. Samples were then stored at -20 °C until ready for use.

Post-extraction, DNA quantity and quality were assessed by NanoDrop spectrophotometry (NanoDrop Technologies). In preparation for genotyping, a polymerase chain reaction (PCR) amplification was carried out at a total volume of 10 µl per sample: 1 µl of 10 X Taq buffer, 0.2 µl of BSA (5 mg/µl), 0.3 µl of 10mM dNTP, 0.2 µl of 25 mM MgCl2+, 0.2 µl of each primer (10 µM) (Table 2.1), 6.2 µl of ddH20, 0.2 µl of Taq polymerase (5000 units/ml; New England Biolabs), and 1.5 µl of genomic DNA. Larger DNA concentrations (>80 ng/µl) were diluted to about 50 ng/µl to reduce the potential impact of inhibitors when PCR amplified (with fluorescently labeled primers). PCR was performed in a PTC-200 Peltier Thermal Cycler (MJ Research). Protocols were as followed: denaturation at 94 °C for 4 min, followed by 30 cycles of 94 °C for 30 s, Ta (as determined for each primer set) for 30 s, and 72 °C for 60 s with a final extension at 72 °C for 10 min then set to 4 °C until sample removal. PCR products were ethanol precipitated and submitted to the Natural Resource DNA Profiling and Forensic Centre (NRDPFC; Trent University, Peterborough, ON) where they were run on an ABI 3730 DNA analyzer with GS-500 size standards. Microsatellite fragment lengths were scored by eye in GeneMarker 1.91 (SoftGenetics, LLC).

Sexing and Genetic Analyses

Sexing of Pūkeko was done by inspecting amplicons from PCR with intron 16 in the NIPBL-i16 gene (Suh et al. 2011), and run on a 2 or 3% electrophoretic agarose gel (Healey et al. in review; Hing et al. 2017).

For genetic analyses, 22 primer sets (Table. 2.1) were tested to see if they would be able to determine relatedness within groups at both Tawharanui and Shakespear. Ten of these primers were previously developed by our lab through 454-sequencing of pūkeko and smooth-billed ani samples. The remaining twelve were primers that had been developed for Takahe. These primers were chosen because they had demonstrated high variability either based on studies using South Island pūkeko (Grueber and Jamieson, 2011) or a sub-species of purple swamphen (*Porphyrio porphyrio*) from the Java Islands (Subrata and Storch, 2012). Each primer set was tested in a temperature gradient PCR amplification and imaged on agarose gel (2%) to determine an effective annealing temperature (T_a). Once T_a was established, a small number of individuals (n=2-5) from different families were imaged on agarose gels to look for variability before considering them for genotyping. Ten of the 22 primer sets (Table. 2.1) appeared promising and were sent off for genotyping at NRDPFC. Each primer to be genotyped was tested against a number of individuals (n=4-19) from different families and locations at both parks to see whether they would be viable for parentage analysis. Five birds from 2 different families on the South Island were also tested against four primers which had demonstrated the highest variability on agarose and from genotyped samples. As the South Island population is not as inbred as the North Island populations they allowed us to screen for alleles not seen when testing them on the North Island birds.

Statistical Analyses

All analyses were conducted in R version 3.1.2 (R Core Team 2015) using the lme4 (Bates et al. 2014), glmmTMB (Magnusson et al. 2016), and car (Fox and Weisberg 2011). A Welch's t-test was used to determine whether there were statistical differences between population density and density per hectare at Tawharanui and Shakespear. A generalised linear mixed model was used to examine variation in territory area between parks. Park was a fixed effect with territory area as the response variable and group size as a random effect. A generalised linear mixed model was also used to examine the effect of group size on territory area. Group size was a fixed effect with territory area as the response variable and park as a random effect. A linear model was used to examine differences in group sizes between parks. Park was a fixed effect with group size as the response variable.

For predation pressure, time in and time out of each paddock were converted to a decimal representing the time of day as if each day was scaled from 0 to 1. Time elapsed was then calculated by subtracting time in from time out. Two generalized linear models were created to determine among paddock variance. In both cases, proportion of harriers present per minute was the response variable with park (Tawharanui or Shakespear) as a fixed effect. One model had paddock as a random effect (alternative model) while the other did not (null model) to compare the goodness of fit of the data. A likelihood ratio test was done comparing the two models to see the effect of paddock on the proportion on harriers present per minute. A similar comparison was used to see if there was a difference between parks. To determine if time of day had an effect on the density of harriers a generalized additive mixed model with time of day as a smooth term (a cubic spline with 5 degrees of freedom); park as a fixed effect; paddock as a random effect; and an offset accounting for the length of the observation period. Predicted number of harriers was treated as a Poisson response.

There was not enough data to statistically test whether dispersal was occurring at either of the two field sites. Therefore, qualitative examples at both parks were presented. All plots were created in ggplot2 (Wickham, 2009).

2.4 Results

Population density comparison

In 2015, Tawharanui Regional Park had an overall larger estimated population than Shakespear Regional Park (Tawharanui= 1035.74 ± 171.15 SE; Shakespear= 323.39 ± 78.46 SE; $t_{2.8}$ = -3.78; p=0.036; Fig. 2.3). Estimated adult population density per hectare was also larger at Tawharanui over Shakespear (Tawharanui=275ha; Shakespear=220ha; Tawharanui= 3.77 ± 0.62 SE adults per hectare; Shakespear=1.47 ± 0.36 SE adults per hectare; $t_{3.2}$ = -3.20; p=0.045; Fig. 2.4).

Dispersal

Data collected were insufficient to statistically determine whether dispersal from the natal territory was occurring, thus, qualitative examples are provided. Table 2.2 lists fully banded chicks that were spotted in the 2015 field season in their natal territory at Tawharanui. Across both field seasons (2014/2015) there were no instances of fully banded young found outside their natal territory at Tawharanui in the 2015 field season. Only 6 offspring of the 13 captured and fully banded during the 2014 season were spotted in the 2015 field season. Nine of the 12 fully banded adults in the 2014 field season were seen in 2015 (Table 2.3). These birds were spotted in locations very near where they were originally trapped, suggesting that no dispersal events took place. However, re-sight data of birds banded prior to 2014 demonstrates that some movement has taken place (See Table 2.4).

At Shakespear, only a few (n=6) of the banded chicks from the 2014 field season (n=30) were spotted or re-captured in 2015. Five of six individuals were spotted in their natal/original capture location (Table 2.5). One individual was spotted in its natal territory at the beginning of the 2015 field season but was spotted approximately 1.4km away in a different paddock in January 5, 2016, suggesting that dispersal may have occurred late in the 2015 breeding season. At Shakespear, 11 (5 offspring, 5 adults) of the 22 birds fully banded during the 2014 field season were re-sighted during the 2015 season. Of those adults caught and banded during the 2014 season, none were spotted very far from their original trapping location, typically in paddocks adjacent to their trapping location, suggesting that no dispersal occurred (Table 2.6).

Predation pressure

There was significant variation in harrier presence across paddocks ($X^2 = 35.52$; $\mathrm{SD}_{paddocks} = 0.8329$; 95% CI = 0.5082048, 1.3097572; $p = 2.52 \times 10^{-9}$) but not parks ($X^2 = 0.0575$; $p = 0.8105$). Time of day had a significant effect on the number of harriers present (p=0.001341; Fig. 2.5).

Intra-group relatedness

To determine relatedness 22 potential primers were tested for variability. Of those original 22, ten were considered very promising and sent off to be genotyped (See: Table 2.7). Genotyping results indicated that despite finding an adequate number of alleles, none could be used to determine differences within groups as most (and in some cases all) members within a group had identical alleles for all primers tested.

Territory size

A generalised linear mixed model comparison between territories at both Tawharanui (n=5) and Shakespear (n=5) with group size as a random effect found a significant difference in the size of territories between parks with smaller territories at Tawharanui (Tawharanui= 11 497.8 ± 1989.7 m^2 standard error; Shakespear= 18 076.2 ± 2989.5 m^2 standard error; p=0.011; estimate= -0.4921; Fig. 2.6; Table. 2.8). There is not a significant effect of group size on territory area (Group size (estimate=1601; 95% CI = -1816.998, 5018.875); ParkTAWH (estimate= -10670; 95% CI = -22430.358, 1091.403); p= 0.169; Fig. 2.7; Table. 2.9). A linear model comparison between group sizes at Tawharanui (n=15) and Shakespear (n=14) found group sizes were larger at Tawharanui, although the difference fell above the alpha level of 0.05 (Tawharanui= 6.93 ± 0.60 standard error; Shakespear= 5.43 ± 0.45 standard error; p=0.0595; estimate= 1.5048; Table. 2.10).

Behavioural Observations

Some evidence suggests that despite ample available space (given the pre-poison drop density), individuals continued to live in groups (See Table 2.11; Table 2.12).Twenty-two of 23 groups recorded at Shakespear over both field seasons consisted of 3 or more individuals. Additionally, a single pair was identified at Shakespear to have successfully nested and laid 4 eggs in a relatively empty paddock. By our next nest check the nest was abandoned and the eggs cold and wet. Upon sampling the eggs for DNA, I found that they consisted of near term embryos. It is unusual for individuals to abandon after clearly investing a considerable amount, thus, suggesting that some external pressure had caused them to abandon before hatching. A return trip to look for a possible re-nest revealed a group of 3 adults inhabiting the vicinity around the original nest.

At Tawharanui in 2014, three known groups, residing in paddocks which had been targeted by the cull, were recorded to have nests with 10 or more eggs present

(See Table 2.13). Only 1 of 3 groups managed to hatch young, but only 1 of the 10 offspring hatched in that group survived to 2 weeks post-hatch. Overall, these groups appeared to have limited success at bringing a nest to hatching, most likely due to uncontrolled laying resulting in an inability to incubate properly. This lack of success suggests there may have been a disruption to the female social dominance hierarchy.

2.5 Discussion

Population density and the resultant degree of habitat saturation has been demonstrated to have tremendous influence on sociality and reproductive strategies of territorial species (Komdeur et al. 1995). The estimated population was significantly lower at Shakespear due to the decimation of the population in 2011.

While I did not see enough dispersal to establish to what extent density may influence dispersal differences between the parks, the only natal dispersal event was seen at Shakespear. While anecdotal, this demonstrates that natal dispersal occurred at Shakespear as predicted under low density conditions by the literature (Jamieson et al. 1994; Jamieson, 1997). One shortcoming of my re-sighting effort is that I limited re-sighting to the parks (Shakespear and Tawharanui) and some birds could have dispersed outside this area. The one confirmed dispersal event at Shakespear was near the end of the 2015 breeding season (January 5, 2016; Pers. Comm. J. Quinn.). As our field season only covers 1/3 of the year, there is a chance that other young may have dispersed after our departure (typically late December) but perished prior to our arrival (typically early September) for the subsequent breeding season. Most young disperse prior to the laying of the first egg or the onset of hatching (Craig, 1979; Jamieson et al. 1994).

Harrier density between parks was not statistically significant but there were significant differences amongst paddocks. This result indicates that some paddocks have a higher density of harriers which might increase predation pressure on those paddocks, influencing offspring survival and movement. Previous work on the pūkeko has indicated that harrier predation rates on nests increase when alternative prey options such as rabbits are not available (Haselmeyer and Jamieson, 2001). As Shakespear had been declared “rabbit free”, it is possible that predation pressure is high enough at Shakespear to influence egg and nestling survival. The presence of helpers has been linked to reduced predation on eggs and nestlings as well as increased fledgling success in other species (Stripe-backed wren *Campylorhynchus nuchalis* Rabenold 1984, 1985; Bi-coloured wren *Campylorhynchus griseus* Austad and Rabenold, 1985; Florida scrub jay *Aphelocoma coerulescens* Schaub et al. 1992; Karoo scrub robin *Erythropygia coryphaeus* Lloyd et al. 2009). This could explain why individuals were appearing to continue to live in groups despite the availability of space. On the other hand, it is presumed that increased predation can make dispersal risky, especially since individuals may be required to sample multiple unfamiliar territories until they find a suitable one (Clobert et al., 2009; Bocedi et al., 2012). Individuals might choose to remain on their natal territory because parents can provide nepotistic benefits (e.g. protection from predators or access to food resources) to offspring that they are unlikely to receive when in a group of unrelated individuals (Siberian Jay *Perisoreus infaustus* Ekman and Griesser, 2002; Griesser, 2003; Griesser and Ekman, 2004, 2005; Griesser et al., 2006; Carrion crow *Corvus corone corone* Chiarati et al. 2011). This may explain as to why at Shakespear Park, two chicks from a paddock with higher perceived dispersal risk due to increased harrier density did not disperse, whereas the individual who did disperse came from a paddock with a lower harrier density.

The benefits-of-philopatry hypothesis suggests that delayed dispersal is influenced by the inclusive benefits gained from remaining on the natal territory and assisting kin (Stacey and Ligon, 1987, 1991; Hatchwell and Komdeur, 2000). A comparison between North Island (high density) and South Island (low density) pūkeko groups in New Zealand found reduced dispersal by offspring due to high density conditions resulted in increased relatedness among group members (Craig and Jamieson, 1988; Jamieson et al. 1994; Jamieson, 1997); whereas group members in the low density South Island population were determined to be genetically unrelated (Jamieson et al, 1994; Jamieson, 1997). Only 10 of the 22 primers (Table. 2.1) were considered suitable for genotyping but none were able to be used for determining group relatedness. Although determination of relatedness and parentage in pūkeko has been attempted previously using mini-satellite probing with some success (Jamieson et al. 1994; Lambert et al. 1994), microsatellites are a more powerful tool for genetic analyses because of their locus specific and multi-allelic nature, co-dominant inheritance, relative abundance, reproducibility, and genomic coverage (Liu and Cordes, 2004). However, as pūkeko are a polygynandrous cooperative species, determining parentage and relatedness is difficult because offspring can have a number of potential parents (Lambert et al. 1994). Also, research conducted at Shakespear by Craig and Jamieson (1988) determined that approximately 75% of copulations were between first degree relatives, resulting in a high amount of inbreeding in situations where young did not disperse. Although it does not affect the overall allelic frequency, inbreeding has been demonstrated to increase the proportion of homozygotes in the population (Keller and Waller, 2002). It can also result in higher levels of band sharing within breeding groups (Lambert et al. 1994).

Group size can determine a group's ability to hold and maintain a territory (Craig, 1979). Thus, in accordance with the "prisoner's dilemma" (Craig, 1984), we may witness smaller groups being pushed out by larger groups. During our first field season at Shakespear, we had one pair that abandoned their nest (with nearly developed embryos) apparently displaced by a larger group. The larger group made it difficult for the pair to maintain their territorial boundaries, causing them to abandon. Craig (1979; 1984) mentioned that to be successful, pairs needed to either bring on another male or be extremely aggressive. In Green Woodhoopoes, breeding pairs are rarely as reproductively successful as groups with helpers unless food is abundant or the external pressure from neighbouring groups is low due to low population density or territorial isolation (Ligon and Ligon, 1990). We did find that 22 of 23 groups with known sizes consisted of 3 or more individuals. Like Craig (1979), we did not find there to be any significant correlation between group size and territory size in pūkeko.

Territories at Shakespear were significantly larger than those at Tawharanui. In pūkeko, territory size appears to either remain constant or slightly decrease with an increase the number of birds or adjoining territories in the immediate area (Craig, 1979). In Great tits (*Parus major*), territory sizes were found to be above average when population densities were experimentally lowered (Wilkin et al. 2006). Group size can determine the ability of a group to hold a territory (Craig, 1979). However, group sizes were not significantly different between Shakespear and Tawharanui despite the availability of space (given the pre-poison drop density) (See Table. 2.11; Table. 2.12). Low statistical power because of small sample sizes could explain a lack of significant results. Previous research between high (North Island) and low (South Island) density pūkeko populations found a significantly higher number of adults per group under high density conditions (Jamieson, 1997; Dey et al. 2012).

I was unable to accurately quantify dispersal rates and whether group relatedness varied between the high density and low density sites. Dispersal has been established under low density conditions, as well as a lower coefficient of relatedness amongst group members which can affect reproductive skew (Jamieson et al. 1994; Jamieson, 1997). Territory size has been linked to breeding success, with larger territories resulting in higher breeding success than smaller ones (Canada Warbler *Cardellina Canadensis*, Flockhart et al. 2016). The ability to hold a territory has also been linked to increased survivability and production of offspring (Craig, 1979; 1984). Future studies should be conducted to look into the degree of relatedness amongst group members and the effect that might have on reproductive skew. Therefore, I recommend that, to gain better perspective into the maintenance of the cooperative breeding system exhibited by the pūkeko, a longer term study between these sites should be conducted to study whether the effects of high and low density are perpetrated without climate as a confounding factor.

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FIGURE 2.1: Shakespear Regional Park as viewed from Google Earth. The thick red line traces the pest-proof fencing and the blue line indicates the nothern border of Shakespear Regional Park. Yellow stars indicate the vantage points. The red star indicates a paddock which could not been seen clearly from any vantage point and was counted by walking a transect through it.

Google earth V 7.1.7.2606. (May 31, 2016). Shakespear Regional Park, Army Bay, New Zealand. 36° 36’ 28.35”S, 174° 49’ 23.12”E, Eye alt 16748 feet. TerraMetrics 2016. http://www.earth.google.com [January 15, 2017].

FIGURE 2.2: Tawharanui Regional Park as viewed from Google Earth. The thick red line traces the pest-proof fencing and the blue line separates which paddocks were counted on separate days. Yellow stars indicate the vantage points.

Google earth V 7.1.7.2606. (March 27, 2016). Tawharanui Regional Park, Tawharanui Peninsula, New Zealand. 36° 22' 10.88"S, 174° 49' 58.09"E, Eye alt 16671 feet. DigitalGlobe 2016. http://www.earth.google.com [January 15, 2017].

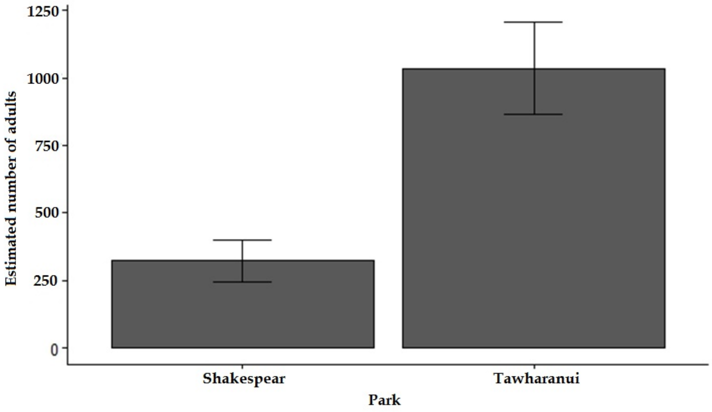

FIGURE 2.3: Bar graph showing mean estimated population size between Tawharanui and Shakespear Regional Parks with standard error bars (Tawharanui=1035.74±171.15; Shakespear= 323.39±78.46; t = -3.20; p=0.036)

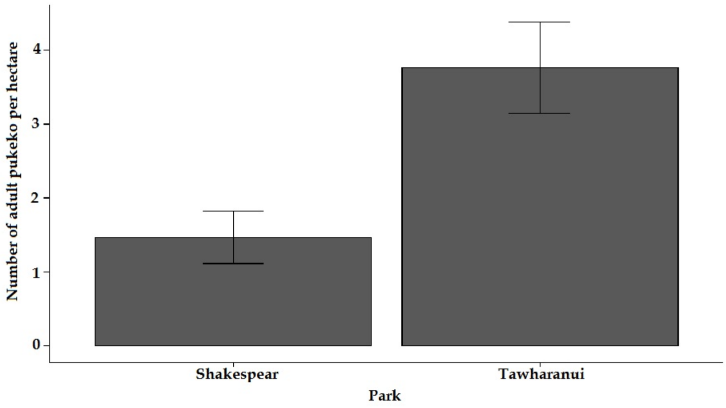

Figure 2.4: Bar graph showing mean number of adult pūkeko per hectare between Tawharanui and Shakespear Regional Parks with standard error bars (Tawharanui=275ha; Shakespear=220ha; Tawharanui= 3.77±0.62; Shakespear=1.47±0.36; p=0.045)

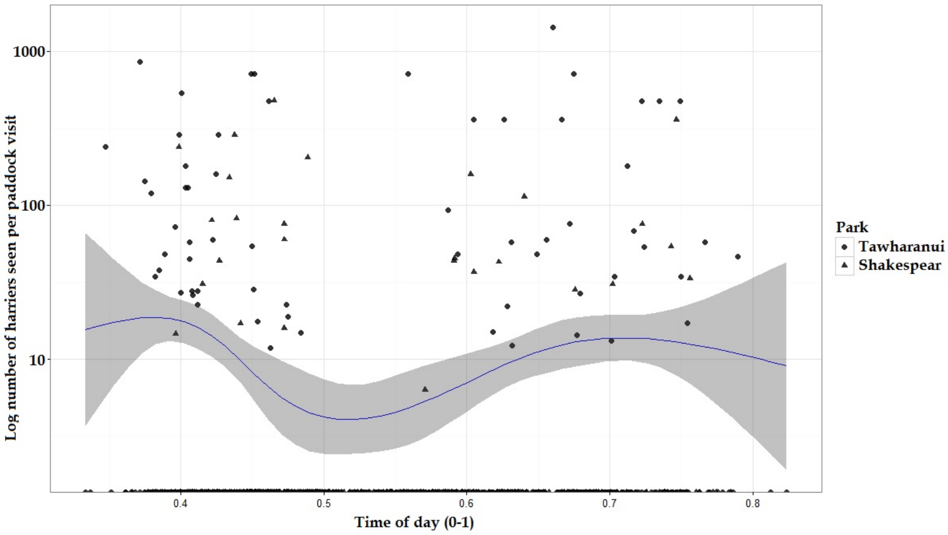

Figure 2.5: Log number of harriers seen throughout the day with significantly fewer seen mid-day (p=0.001341). Line is the baseline average of harriers seen per day with the grey area indicating the amount of variation between Shakespear and Tawharanui with Tawharanui as a baseline. Each point represents a visit to a paddock and the time of day in which it was entered.

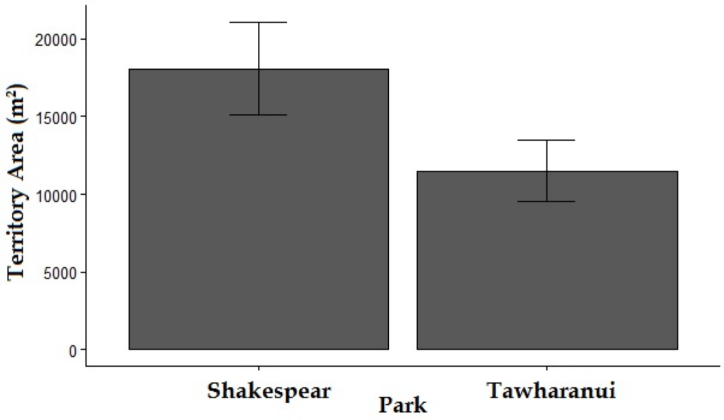

FIGURE 2.6: Mean Territory size (m^2) at Shakespear and Tawharanui Regional Parks with standard error bars (Tawharanui=11497.83±1989.67; Shakespear=18076.17±2989.53; p=0.011; estimate= -0.4921)

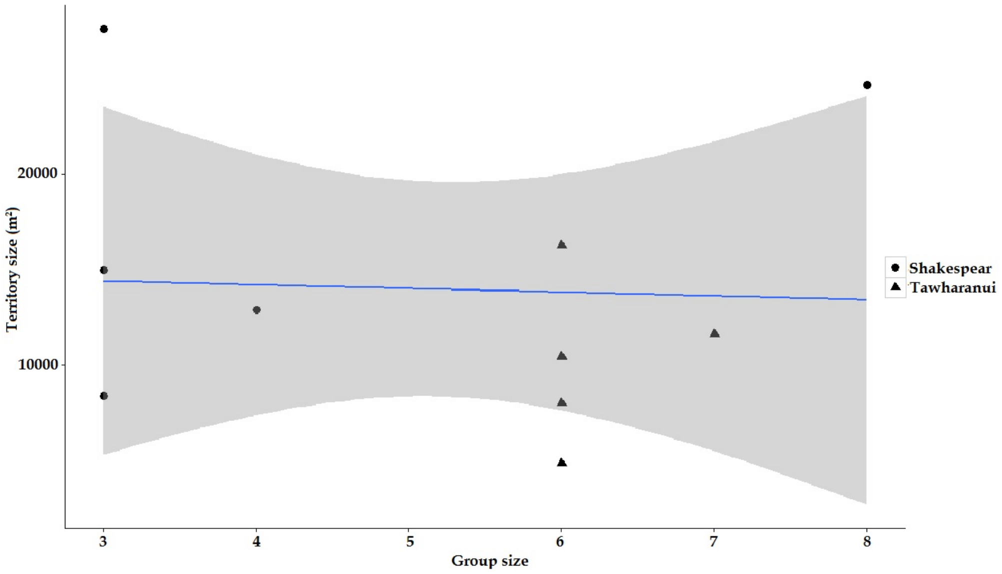

FIGURE 2.7: Scatter plot comparison of group size and territory area (Group size (estimate=1601; 95% CI = -1816.998, 5018.875); ParkTAWH (estimate= -10670; 95% CI = -22430.358, 1091.403); p= 0.169).

Primer pairs	Sequences (written 3'->5')	Repeat Motif	Source	Heterozygosity*	Species designed for	Product size*
JSQ0140_Fwd1 JSQ0187_Rvs1	F-TTGCGAATTCATAGCAAAGC R-TTGATTGCCTTTGTCATTGC	ATATT	454-Sequencing	N/A	pūkeko/Ani	N/A
JSQ0535_Fwd2 JSQ0018_Rvs2	F-TTGTGCTGGGGACTTATATGC R-ACATGTCCCCACTAGCTCCC	ATTTT	454-Sequencing	N/A	pūkeko/Ani	N/A
JSQ0150_Fwd3 JSQ1011_Rvs3	F-TGTTCCTAACGCTGTGGTTCC R-ATCTCCACCCCACCTTTTCG	ATGG	454-Sequencing	N/A	pūkeko/Ani	N/A
JSQ0838_Fwd4[a] JSQ0896_Rvs4	F-TGCTGTCCTTGTCCCAAAGC R-GGAAGGTCAGAGAGCATGGC	ATGG	454-Sequencing	N/A	pūkeko/Ani	170-200
JSQ0506_Fwd5 JSQ0078_Rvs5	F-TGCCAGCAGAACTGTATGCC R-GCACGTTTGCTCCTTGAACC	AAAT	454-Sequencing	N/A	pūkeko/Ani	N/A
JSQ0892_Fwd6 JSQ0725_Rvs6	F-TAACATTCTCCCCTCGTCCC R-ACCAGTGTCACTCTCTCGGG	TCC	454-Sequencing	N/A	pūkeko/Ani	200-300
JSQ0099_Fwd7 JSQ0053_Rvs7	F-TTTTCTTGGGAGGTTGGGG RTGTTTTGTTCCAGGTTTTCAGG	ATT	454-Sequencing	N/A	pūkeko/Ani	300-400
JSQ0536_Fwd8[a] JSQ0900_Rvs8	F-TCAGCAGATCTCCCCAGAGC RTCCTCGTTATTTTGGTAAGCACC	ATT	454-Sequencing	N/A	pūkeko/Ani	N/A
JSQ0611_Fwd9 JSQ0992_Rvs9	F-AAACCATGGCAAACCAGAGG R-ATAGAATGGTTTGGGCGTGG	ATC	454-Sequencing	N/A	pūkeko/Ani	N/A
JSQ0590_Fwd10 JSQ0936_Rvs10	F-CTGTGCACCTGAGTATGAGGC RCATGTGAAAGGGCTGAAATGG	AAC	454-Sequencing	N/A	pūkeko/Ani	N/A
PHO12F PHO12R	F-AGCGAGGGAACCTGCGAG R-AGAAAGCGGGTGGGAGGA	$(GA)_{17}$	Grueber et al. 2008	0.4	Takahe	138-148
PHO16BF[a] PHO16BR	F – CCTGGAGCACAGTCCTGCCC R – CCCCCTGTCCCCCACACTTC	$(GA)_9GGAG$	Grueber & Jamieson, 2011	N/A	Takahe	194
PHO20F[a] PHO20R	F – TGTGGTCATAGCCAGCAC R – GAGTACGCAACATCAATGC	$(GA)_{12}GG(GA)_2$	Grueber & Jamieson, 2011	N/A	Takahe	185
PHO28F[a] PHO28R	F-TCAGTGAAACAAAACATC R-AAGTACAATTTGGTATCG	$(GA)_2TA(GA)_7(GT)_4$	Grueber et al. 2008	0.4	Takahe	70-80
PHO41F[a] PHO41R	F – TATTTCTGCAAGCCCACAGG R – ACCCCCAGACCAAGGAGTAT	$(TG)_2TTC(GT)_7G_7$	Grueber & Jamieson, 2011	N/A	Takahe	101
PHO44F[a] PHO44R	F-AGCCTGCCAGTACCTGAAGG R-CATGAACAGTCAGCCAAAGG	$(AC)_{13}(AC)_6$	Grueber et al. 2008	N/A	Takahe	143-145
PHO46F[a] PHO46R	F-TGCCATGGTGGAGGTGTG R-TTTGACCACTGCCCTCTC	$(AC)_{14}$	Grueber et al. 2008	0.48	Takahe	104-116
PHO47F[a] PHO47R	F-AGCTAACAAGGAGTTACCTG R-GAGCATGAGTATCTGAGAAG	$(AC)_9$	Grueber et al. 2008	0.16	Takahe	91-93
PHO60F[a] PHO60R	F-GAAAGCAAGTGTGGCTC R-CACCAGGTATTGCATTAC	$(CA)_{14}(GA)_6(CA)_{12}(GA)_2(CA)_{13}$ $(GA)_3(CA)_{18}(CT)_{12}(CTCA)_2$	Grueber et al. 2008	0.52	Takahe	198-224
PHO62F PHO62R	F-CTGTCTTTTTTATACCATAC R-ATGTGATGGGGCTGTAG	$(CATA)_2TA(TG)_{10}$	Grueber et al. 2008	0.48	Takahe	110-114
PHO84F PHO84R	F-CACACAGAAGAACTCCCACC R-CCCCAGACAATAAGGTTGC	$(CA)_{15}$	Grueber et al. 2008	0.6	Takahe	157-161
PHO107F PHO107R	F-GCTTCCTTCTGCACTGG R-GGAGATGTATGTGTTTGGG	$(GT)_{10}$	Grueber et al. 2008	0.44	Takahe	120-122

TABLE 2.1: The 22 primer sets tested. The 10 sets sent off for genotyping at NRDPFC are marked with [a].

∗valuesarefrompreviouspublications

ID	**Capture Location**	**Date captured**	**Re-sight Location**	**Re-sight Spotted**
RY/BY (M-81222)	North Coast Center	21/09/2014 (FB: 04/11/2014)	North Coast Center	23/10/2015
GB/YB (M-82702)	SPB Trig	05/11/2014	SPB Trig	12/10/2015
NW/WN (M-82741)	NPB E	24/11/2014	NPB E	09/11/2015
BB/GB (M-81228)	NPB E	04/09/2014 (FB: 28/09/2014)	NPB E	22/09/2015
BR/GB (M-83186)	Workshop North	10/09/2014	Workshop North	30/11/2015
GB/YY (M-83187)	Workshop North	10/09/2014	Workshop North	30/11/2015

TABLE 2.2: Offspring at Tawharanui Regional Park that were fully banded during the 2014 field season and re-sighted during the 2015 field season. Natal location is the location in which the individual was fully banded.

ID	Capture Location	Date captured	Re-sight Location	Re-sight Spotted
WW/RW (M-83156)	Stockyard 1 East	30/09/2014	Stockyard 1 East	20/09/2015
BR/YR (M-81191)	Stockyard 1 North Centre	30/09/2014	Stockyard 1 North Centre	10/10/2015
YB/WW (M-81190)	North Punchbowl Southeast	11/10/2014	North Punchbowl Southeast	05/09/2015
GG/RG (M-81182)	North Punchbowl Southeast	11/10/2014	North Punchbowl Southeast	14/09/2015
RY/BB (M-82736)	Stockyard 1 North Centre	27/10/2014	Stockyard 1 North Centre	10/10/2015
WY/RB (M-82730)	South Punchbowl Trig	02/11/2014	South Punchbowl Trig	09/11/2015
RW/WR (M-82729)	South Punchbowl Trig	02/11/2014	South Punchbowl Trig	09/11/2015
YW/WY (M-82728)	South Punchbowl Trig	02/11/2014	South Punchbowl Trig	05/09/2015
RN/GB (M-83269)	Stockyard 2 West Lagoon	21/11/2014	Stockyard 2 West Lagoon	11/09/2015

TABLE 2.3: Adults at Tawharanui Regional Park that were fully banded during the 2014 field season and re-sighted during the 2015 field season. Capture location is the location in which the individual was fully banded. The re-sight day is the first day the individual was re-sighted at the park during the 2015 field season.

Band Combo	**Band #**	**Band Location**	**Band Date**	**Re-sight Location**	**Resight Date**
BB/GG	81237	Stockyard 1	13/5/2013	Stockyard 1	25/10/2015
BB/GN	83166	Lagoon Flats (Centre)	8/3/2012	Hay 2	30/11/2015
BB/GY	66625	Hayter's Stream (SW)	13/10/2008	Stockyard 2	20/9/2015
BB/WN	66914	East Camp (SE)	19/7/2010	Lagoon Road	10/1/2016
BB/WW	83299	North Punchbowl (S)	23/11/2010	North Punchbowl	1/11/2015
BB/YG	83192	Stockyard 1 (NW)	16/1/2012	Stockyard 2	20/9/2015
BG/BB	83197	North Punchbowl (S)	20/1/2012	North Punchbowl	22/9/2015
BG/BR	81240	Stockyard 1 (SE)	9/5/2013	Cactus	12/10/2014
BG/BY	66629	Stockyard (NW)	19/1/2009	Cactus	2/11/2014
BG/GR	81239	Stockyard 2 (NE)	11/5/2013	Stockyard 2 (NE)	11/10/2014
BG/GR	81239	Stockyard 2 (NE)	11/5/2013	Road flats	19/9/2014
BG/GY	66762	Hay	8/1/2009	Stockyard 2	22/11/2014
BG/WR	83158	Stockyard 2 (NE)	22/11/2013	Stockyard 2	12/9/2015
BR/BR	83297	North Punchbowl (S)	23/11/2010	North Punchbowl	31/10/2015
BR/BW	***66835***	***Camp West***	***9/7/2010***	***Stockyard 1***	***28/9/2014***
BR/BY	66630	Stockyard (NW)	12/12/2008	Stockyard 1	28/10/2014
BR/WY	66764	Hay	22/10/2008	Stockyard 1	25/9/2014
BR/YB	83185	Stockyard 2 (NE)	22/11/2013	Stockyard 1	12/10/2014
BR/YB	83185	Stockyard 2 (NE)	22/11/2013	Stockyard 1	28/10/2014

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Band Combo	Band #	Band Location	Band Date	Resight Location	Resight Date
BR/YY	66785	Twin Hills Gate	29/12/2008	Stockyard 1	22/11/2014
BW/BG	81215	Stockyard 2 (S)	15/11/2013	Stockyard 2	28/10/2014
BW/BR	81218	Cactus (SE)	15/11/2013	Road flats	11/10/2014
BW/BR-B	81218	Cactus (SE)	15/11/2013	Road flats	6/10/2014
BW/GW	81214	Stockyard 1 (NC)	10/11/2013	Stockyard 1	29/9/2014
BW/GY	66763	Road flats (CS)	4/12/2008	Stockyard 2	20/9/2015
BY/BY	66765	Hay	22/10/2008	Stockyard 4	12/9/2015
BY/NG	83285	Stockyard 1 (NC)	10/11/2013	Cactus	28/10/2014
BY/RG	83159	Stockyard 1 (NW)	22/10/2013	Stockyard 2	22/11/2014
GB/BY	***66784***	***M16***	***29/11/2008***	***Stockyard 2***	***25/9/2014***
GG/BR	81217	Stockyard 2 (S)	15/11/2013	Stockyard 2	20/9/2015
GG/WW	83348	North Punchbowl (NW)	26/10/2010	North Punchbowl	15/11/2014
GG/WW	***83348***	***North Punchbowl (NW)***	***26/10/2010***	***Cactus Hill***	***21/12/2015***
GG/YY	66960	Hay 3	6/9/2010	Stockyard 1	12/10/2014
GG/YY	***66960***	***Hay 3***	***6/9/2010***	***North Coast***	***21/12/2015***
GR/GY	***66824***	***Hay***	***3/12/2008***	***Cactus***	***2/11/2014***
GR/YR	83294	North Punchbowl (S)	23/11/2010	North Punchbowl	31/10/2015
GR/YR	83294	North Punchbowl (S)	23/11/2010	North Punchbowl	6/1/2016

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Band Combo	Band #	Band Location	Band Date	Resight Location	Resight Date
GR/YR	83294	North Punchbowl (S)	23/11/2010	North Punchbowl	28/9/2014
GY/BY_M	83212	Stockyard 1	15/2/2012	Stockyard 1	10/10/2015
GY/GG	81211	Stockyard 1 (N)	19/6/2013	Stockyard 1	25/10/2015
M_NN/N_N	83163	Staff (SE)	23/2/2012	Staff	26/9/2015
NB/BY	66813	Hayter's Stream (SW)	29/1/2009	Stockyard 2	18/11/2014
NN/NN	83163	Staff (SE)	23/2/2012	Staff (SE)	30/11/2015
NR/NR	83162	Staff (SE)	23/2/2012	Workshop	30/11/2015
RB/GY	66819	Hayter's Wetland	19/11/2008	Stockyard 1	30/9/2014
RB/G-Y	66819	Hayter's Wetland	19/11/2008	Hay 1	9/1/2016
RB/RG	83194	North Punchbowl (S)	20/1/2012	North Punchbowl	11/10/2015
RB/WN	83196	North Punchbowl (S)	20/1/2012	North Punchbowl	28/10/2015
RG/BY	***66828***	***Hay***	***27/11/2008***	***M16***	***20/12/2015***
RR/GM-Y	66781	Campgroup Road Gate	23/2/2009	Swede	11/9/2014
RR/GY	66781	Campgroup Road Gate	23/2/2009	Stockyard 2	1/10/2014
RR/YB	83302	East Camp (NE)	21/9/2010	Campground	29/8/2014
RY/BR	***81159***	***East Camp (NW)***	***13/5/2013***	***Stockyard 1***	***27/10/2014***
RY/RY	***83301***	***East Camp (NE)***	***21/9/2010***	***South Punchbowl***	***3/11/2015***
RY/WB	***66911***	***East Camp (SE)***	***19/7/2010***	***Stockyard 1***	***28/10/2014***
WB/BY	66820	Hayter's Wetland (N)	29/12/2008	Stockyard 1	2/11/2014

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Band Combo	Band #	Band Location	Band Date	Resight Location	Resight Date
WB/WN	83230	North Punchbowl (NW)	30/1/2012	North Punchbowl	14/10/2014
WG/RW	83222	Hay 1 (N)	29/1/2012	Hay 1	30/11/2015
WW/RR	66959	Hay 1 (N)	17/9/2010	Hay 2	15/9/2014
WW/WY	66829	Camp West (SW)	15/10/2008	M16	20/12/2015
WW/YY	66995	Cactus (S)	11/8/2010	Stockyard 1	10/10/2015
YB/BB	***83346***	***West Camp (E)***	***7/8/2010***	***Staff***	***13/9/2014***
YB/GB	83330	North Punchbowl (S)	23/11/2010	North Punchbowl	30/11/2015
YB/RG	***83321***	***North Punchbowl (S)***	***23/11/2010***	***Stockyard 1***	***12/10/2014***
YB/YY	66964	Stockyard 1 (NW)	23/8/2010	Stockyard 1	12/10/2014
YN/GG	83329	Stockyard 1 (NW)	21/10/2010	Stockyard 2	25/10/2015
YN/GG	83329	Stockyard 1 (NW)	21/10/2010	Stockyard 2	2/11/2014
YN/WN	83320	North Punchbowl (NW)	30/1/2012	North Coast	18/9/2014
YN/WN	83320	North Punchbowl (NW)	30/1/2012	North Punchbowl (W)	21/12/2015
YN/WN	83320	North Punchbowl (NW)	30/1/2012	North Punchbowl	4/11/2015

TABLE 2.4: Tawharanui birds banded prior to 2014 with their band date and location as well as the re-sight location and dates for 2014 and/or 2015. Those individuals bolded and italicised indicate movement. Data courtesy of Courtney Young.

ID	Capture Location	Date captured	Re-sight Location	Re-sight Spotted
RW/RW (M-82716)	Holding	06/11/2014	Yards	23/09/2015
RW/RW (M-82716)	Holding	06/11/2014	Rakino	05/01/2016
Y/-M	Pump	10/10/2014	Pump	04/11/2015
/G	Pump	10/10/2014	Pump	04/11/2015
G/-M (M-83151)(GR/YY)	Bore	03/10/2014	Bore	19/11/2015
RY/RY (M-82748)	Mendip Hills*	13/12/2014	Kaiunga*	08/10/2015
GB/GB (M-82705)	Excluder*	13/10/2014	Pump*	09/09/2015

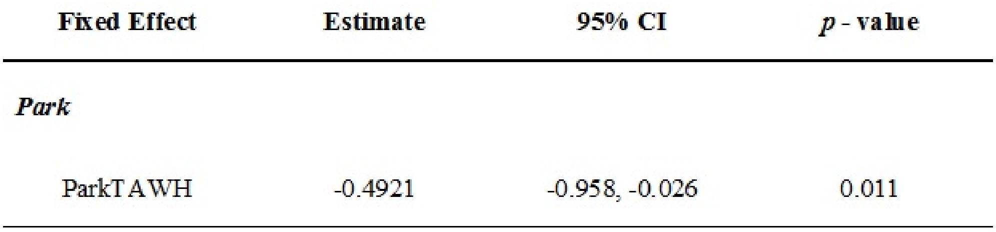
TABLE 2.5: Offspring at Shakespear Regional Park that were fully banded during the 2014 field season and re-sighted during the 2015 field season. Natal location is the location in which the individual was fully banded. Paddocks marked with an asterisk (*) are neighbouring and the territory of the group from which the nestlings hatched encompasses neighbouring parts of both paddocks.

ID	**Capture Location**	**Date captured**	**Re-sight Location**	**Re-sight Spotted**
GG/GG (M-83188)	Annie's	23/09/2014	Annie's	09/09/2015
BB/BB (M-82703)	Annie's*	28/10/2014	Yards*	09/09/2015
GG/YY (M-82725)	Holding*	06/11/2014	Yards*	09/09/2015
WW/YY (M-82714)	Kaiunga*	23/10/2014	Bore*	09/09/2015
RR/YY (M-83189)	Annie's*	23/09/2014	Holding*	23/09/2015

TABLE 2.6: Adults at Shakespear Regional Park that were fully banded during the 2014 field season and re-sighted during the 2015 field season. Capture location is the location in which the individual was fully banded. The re-sight day is the first day the individual was re-sighted at the park during the 2015 field season. Paddocks marked with an asterisk (*) are neighbouring and the territory of the group encompasses neighbouring parts of both paddocks.

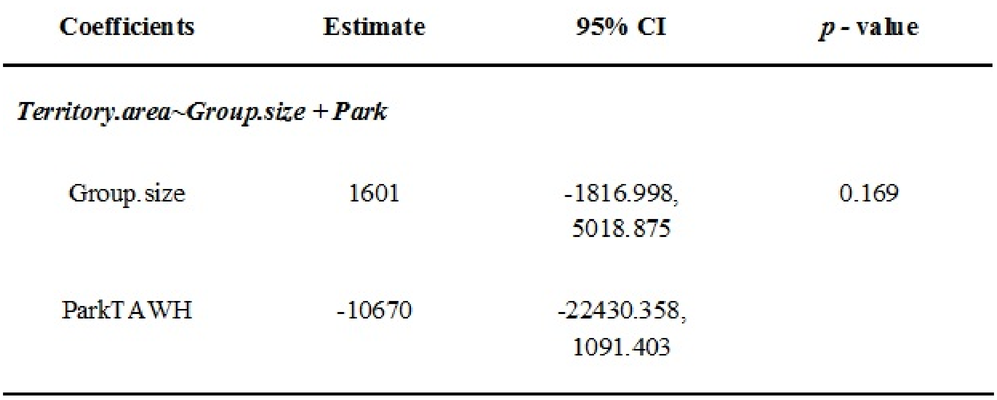
Primer pairs	**Ta**	**Alleles found**	**Number of individuals tested**	**Problems**
JSQ0838_Fwd4 JSQ0896_Rvs4	Undetermined	Undetermined	9	Too much non-specific amplification
JSQ0536_Fwd8 JSQ0900_Rvs8	Undetermined	Undetermined	9	Too much non-specific amplification
PHO16BF PHO16BR	58.5	186, 188, 192	15	Most members within a group had identical alleles and therefore could not tell inheritance; Each individual tested had 4 peaks but 2 were present across all individuals suggesting false alleles present
PHO20F PHO20R	Undetermined	180, 186	7	Same two alleles for every individual tested at every temperature across the gradient
PHO28F PHO28R	44.3	64	7	Only one allele found
PHO41F PHO41R	62.6	91, 101, 114	18	Most members within a group had identical alleles and therefore could not tell inheritance
PHO44F PHO44R	49.5	140	4	Oversaturation
PHO46F PHO46R	51.7	104, 106, 110, 112	18	Most members within a group had identical alleles and therefore could not tell inheritance
PHO47F PHO47R	44.3	86	7	The one allele was found in all individuals tested
PHO60F PHO60R	56	78, 84, 96, 104, 106	19	Most members within a group had identical alleles and therefore could not tell inheritance

TABLE 2.7: The 10 primer sets sent off for genotyping at NRDPFC.



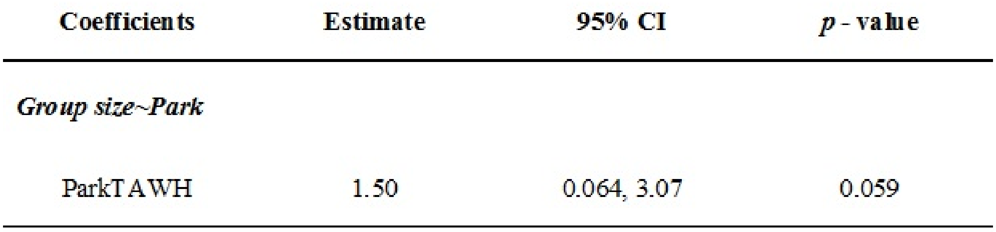
Fixed Effect	**Estimate**	**95% CI**	***p* - value**
Park			
ParkTAWH	-0.4921	-0.958, -0.026	0.011

TABLE 2.8: Generalised linear mixed model with a poisson distribution was used to examine variation in territory area between Tawharanui and Shakespear Regional Parks. Park was a fixed effect with territory area as the response variable and group size as a random effect. Model sample size was 5 social groups at Tawharanui and 5 social groups at Shakespear.



Coefficients	Estimate	95% CI	*p* - value
Territory.area~Group.size + Park			
Group.size	1601	-1816.998, 5018.875	0.169
ParkTAWH	-10670	-22430.358, 1091.403	

TABLE 2.9: Linear model to examine differences in group sizes and territory area between parks. Park and group size were fixed effects with territory area as the response variable. Model sample size was 5 social groups at Tawharanui and 5 social groups at Shakespear.



Coefficients	**Estimate**	**95% CI**	***p*-value**
Group size~Park			
ParkTAWH	1.50	0.064, 3.07	0.059

Table 2.10: Linear model with a poisson distribution was used to examine differences in group sizes between parks. Park was a fixed effect with group size as the response variable. Model sample size was 15 social groups at Tawharanui and 14 social groups at Shakespear.

Nest ID	**Date Found**	**Found as nest? (Y/N)**	**How many eggs?**	**How many chicks known?**	**Group size (Adults only)**	**Number of times re-sighted**	**Last time sighted (2014 season)**	**Spotted in 2015**
Nest C	19/09/2014	N	Unknown	3 (2 alive)	Unknown	0	19/09/2014	N
Nest G	24/09/2014	Y	5	3	7	0	03/10/2014	N
Nest H	24/09/2014	Y	8	4	8	1	08/10/2014	N
Nest I	24/09/2014	Y	7	4	5	2	10/10/2014	N
Nest J	01/10/2014	N	Unknown	7	5	0	01/10/2014	N
Nest K	02/10/2014	N	Unknown	1	Unknown	0	02/10/2014	N
Nest L	03/10/2014	N	Unknown	3	4	0	03/10/2014	Y
Nest M	10/10/2014	N	Unknown	2	5	0	10/10/2014	Y
Nest N	17/10/2014	N	Unknown	2	6	0	17/10/2014	N
Nest O	22/10/2014	N	Unknown	1	2	0	22/10/2014	N
Nest P	23/10/2014	Y	2	2	Unknown	0	05/11/2014	N
Nest R	23/10/2014	N	Unknown	2	3	1	06/11/2014	Y
Nest S	23/10/2014	N	Unknown	7	7	0	23/10/2014	N
Nest T	06/11/2014	Y	5	1	5	0	27/11/2014	N
Nest V	13/11/2014	N	Unknown	2	Unknown	0	13/11/2014	N
Nest X	04/12/2014	N	Unknown	2	Unknown	0	04/12/2014	N
Nest Y	04/12/2014	N	Unknown	2	Unknown	0	04/12/2014	N
Nest Z	13/12/2014	N	Unknown	2	Unknown	0	13/12/2014	N

TABLE 2.11: Compilation of 2014 groups with chicks at Shakespear Regional Park. Data include nest identification, the date of discovery (dd/mm/yyyy), whether it was found as a nest, how many chicks were known, estimated group size, the last time they were spotted in 2014, and whether they were spotted in 2015.

Nest ID	**Date Found**	**Found as nest? (Y/N)**	**How many eggs?**	**How many chicks known?**	**Group size (Adults only)**	**Number of times re-sighted**	**Last time sighted (2015 season)**
Nest A	09/09/2015	N	Unknown	2	Unknown	0	09/09/2015
Nest B	09/09/2015	Y	5	2	Unknown	1	08/10/2015
Nest C	15/09/2015	Y	3	4	9	1	01/10/2015
Nest D	15/09/2015	Y	5	4	5	1	30/09/2015
Nest E	17/09/2015	Y	9	4	6	1	07/10/2015
Nest F	17/09/2015	N	Unknown	3	4	3	21/10/2015
Nest G	23/09/2015	Y	10	3	7	1	06/11/2015
Nest H	30/09/2015	N	Unknown	2	3	1	05/11/2015
Nest J	01/10/2015	Y	6	2	9	0	01/10/2015
Nest K	08/10/2015	N	Unknown	1	4	2	25/11/2015
Nest M	15/11/2015	N	Unknown	3	Unknown	0	15/11/2015
Nest N	15/11/2015	N	Unknown	3	6	1	05/11/2015
Nest O	28/10/2015	N	Unknown	1	Unknown	0	28/10/2015
Nest Q	04/11/2015	N	Unknown	1	Unknown	0	04/11/2015
Nest R	04/11/2015	N	Unknown	1	4	0	04/11/2015
Nest S	09/11/2015	Y	12	9	Unknown	0	13/12/2015
Nest T	18/11/2015	N	Unknown	2	Unknown	0	18/11/2015
Nest U	05/11/2015	N	Unknown	1	6	0	05/11/2015
Nest V	05/11/2015	N	Unknown	1	6	0	05/11/2015
Nest W	05/01/2016	N	Unknown	7	Unknown	0	05/01/2016

TABLE 2.12: Compilation of 2015 groups with chicks at Shakespear Regional Park. Data include nest identification, the date of discovery (dd/mm/yyyy), whether it was found as a nest, how many chicks were known, estimated group size, and the last time they were spotted in the season.

Group ID	**Nest ID**	**# of group members**	**# of eggs laid**	**# of chicks hatched**	**Notes**
Stockyard 1 North	Nest A	12	13	0	Re-nested (See Nest AM 2014)
South Punchbowl South West	Nest AC	9	18	0	Re-nested (See Nest BA 2014)
Stockyard 2/Lagoon	Nest AL	14	21	0	Re-nested (See Nest AY 2014)
Stockyard 1 North	Nest AM	12	17	0	Re-nested (See Nest BF 2014)
Stockyard 2/Lagoon	Nest AY	14	14	10	Only 1 chick left after 2 weeks.
South Punchbowl South West	Nest BA	9	17	0	2 eggs found star-pipping but no chicks ever found.

TABLE 2.13: Groups at Tawharanui Regional Park with abnormally large clutches found in paddocks that had been targeted during the 2014 cull.

Chapter 3

General Conclusion

Over the course of my thesis, I proposed three main questions to determine what effect population density might have on group composition, parentage, and territory as a means to understand the costs and benefits of cooperative breeding and joint-nesting. To test these questions, a comparison between pūkeko populations was needed to determine if Tawharanui Regional Park had a significantly higher density of birds than Shakespear Regional Park. A difference in the densities between parks was established for the 2015 season.

My first question was to determine how population density may affect the dispersal of offspring from their natal territory. The Ecological constraints hypothesis (Emlen, 1984) proposes a shortage of vacant territories due to habitat saturation (e.g. Emlen 1984; Woolfenden and Fitzpatrick 1984) as a reason offspring remain on their natal territory. Additionally, previous work on pūkeko found higher rates of dispersal for offspring of both sexes under low density conditions (Jamieson, 1997; Dey et al. 2012). Thus, I predicted that there would be a higher prevalence of dispersal of offspring at Shakespear regional park (low density) in comparison to Tawharanui regional park (high density). Although I did record one dispersal event at Shakespear, my inability to capture/band/re-sight sufficient numbers of offspring prevented a compelling analysis of dispersal. Also, I limited re-sighting to the areas inside the fenced areas of Tawharanui and Shakespear which prevented me from re-sighting any individuals who may have dispersed outside those locations. Furthermore, I suggest that perhaps the difficulties with trapping, finding nests, and re-locating chicks after hatching at Shakespear was due to the eradication event selectively killing off bold birds and leaving risk averse individuals. Research on both birds and mammals have found individualistic variation in risk-taking behaviour and have shown to be influenced by environmental factors (i.e. hunger, predation risk), sex, size, reproductive state, age, and dominance (Koivula et al. 1994; Candolin 1998; Abrahams and Cartar 2000; Kavaliers and Choleris 2001; Lange and Leimar 2001; Mettler and Shivik, 2007). Risk taking has been associated with increased boldness and exploratory behaviour and that such traits are heritable (Great tits *Parus Major*, Van Oers et al. 2004). Boldness and exploratory behaviour has shown to influence whether or not an individual will disperse (Edelsparre et al. 2013).

The Ecological constraints hypothesis also proposes that a high cost of dispersal due to high predation pressure (Ligon and Ligon 1990; DuPlessis 1992; Heg et al., 2004, Groenewoud et al., 2016; Tanaka et al. 2016) can affect the movement patterns of offspring. Thus, Australasian harrier (*Circus approximans*) density was recorded to determine how it might also affect movement in addition to population density. Results found that harrier density between parks was not statistically significant but there were significant differences amongst paddocks, suggesting increased predation pressure on some paddocks. Since, predation has been thought to make dispersal risky (Clobert et al., 2009; Bocedi et al., 2012), individuals may decide to delay dispersal and remain on their natal territory because parents can provide nepotistic benefits to offspring, such as protection from predators, that may not be provided to an individual if they disperse to a group of unrelated individuals (e.g. Siberian Jay *Perisoreus infaustus* Ekman and Griesser, 2002; Griesser, 2003; Griesser and Ekman, 2004, 2005; Griesser et al., 2006). For example, this could possibly explain why two chicks from a paddock with high harrier density at Shakespear Park did not disperse whereas the individual who did disperse at Shakespear came from a paddock with a low harrier density. Conversely, harrier predation on pūkeko nests has been shown to increase when alternative prey options are not available (Haselmeyer and Jamieson, 2001). Lagomorphs (rabbits) are consumed relatively frequently by harriers (Wong, 2002) and as Shakespear has been declared "rabbit free", it is possible that predation pressure may be higher on eggs and nestlings at Shakespear as they are both consumed by harriers (Wong, 2002). In other cooperative species, helpers have been linked to reduced predation on eggs and nestlings as well as increased fledgling success (Stripe-backed wren *Campylorhynchus nuchalis* Rabenold 1984, 1985; Bicoloured wren *Campylorhynchus griseus* Austad and Rabenold, 1985; Florida scrub jay *Aphelocoma coerulescens* Schaub et al. 1992; Karoo scrub robin *Erythropygia coryphaeus* Lloyd et al. 2009).

My second question aimed to determine whether population density affected the relatedness of group members. As previous work comparing the North Island (high density) and South Island (low density) pūkeko groups found increased relatedness among group members under high density conditions due to reduced dispersal (Craig and Jamieson, 1988; Jamieson et al. 1994; Jamieson, 1997), I predicted that there would be a lower coefficient of relatedness at Shakespear compared with Tawharanui. Monoplexes using primers that had been previously tested on pūkeko with mixed success were found to be of little utility for determining relatedness. Alleles were identical between most or all group members for the 10 primers tested leaving me unable to determine differences between group members, let alone other individuals within the park, or in some cases, from the other park. As pūkeko are a polygynandrous, joint-nesting, cooperative breeding species, offspring can have a number of potential parents. Previous research has demonstrated that approximately 75% of copulations were between first degree relatives in pūkeko, resulting in a high amount of inbreeding in situations where young did not disperse (Craig and Jamieson, 1988). Inbreeding has been demonstrated to increase the proportion of homozygotes in the population (Keller and Waller, 2002) and result in higher levels of band sharing within breeding groups (Lambert et al. 1994).

My final question was to determine what effect density had on territory size. Decreased territory size has been linked to the increase in the number of birds or territories in the immediate area (Craig, 1979; Wilkin et al. 2006); thus, I predicted that larger territories in the low density site in comparison with the high density site. Furthermore, group size has been demonstrated to determine a group's ability to hold a territory (Craig, 1979). Our results show that territories at Shakespear are significantly larger than those at Tawharanui. However, group sizes were found to not be significantly different between Shakespear and Tawharanui despite previous research between high and low density pūkeko populations finding a significantly higher number of adults per group under high density conditions (Jamieson, 1997; Dey et al. 2012). But a low p-value (p=0.0595) suggests that our result may be due to a type II error. We did find a significant correlation between group size and territory size with larger groups having larger territories. Thus, as proposed by Craig (1984), the "prisoner's dilemma" could provide a possible explanation as to why group living and communal breeding in the pūkeko might still be prevalent at Shakespear in the absence of habitat saturation. We did have one instance of a pair that appeared to be displaced by a larger group. The larger group may have made it difficult for the pair to maintain their territorial boundaries, and they were forced to abandon. In accordance with the "prisoner's dilemma", pairs may be required to bring on additional individuals to maintain their territory because territory size has been linked to breeding success (Craig, 1984).

Future Directions

The degree to which the decreased density, as a result of the decimation of the pūkeko population at Shakespear, impacted group composition, parentage, and territory quality still requires some clarification. I predicted that there would be a higher prevalence of dispersal of offspring at Shakespear and as a result there would be a lower coefficient of relatedness at Shakespear compared with Tawharanui. Further work is needed to determine the frequency of dispersal at Shakespear to determine if it's as predicted by previous research under low density conditions (Jamieson et al. 1994; Jamieson, 1997; Dey et al. 2012) or if there are other factors, such as risk aversion or predation, which could be impacting dispersal. Future studies should examine individual personality in relation to dispersal to confirm the effects of large scale eradication events. Although a smaller localised pūkeko culling event at Tawharanui Regional Park found no correlation between social dominance or sex on survival (Hing et al. 2017), studies have shown that bolder individuals tend to be more predominantly eradicated during lethal control programs (Linnell et al. 1999; Treves and Naughton-Treves, 2005) making it possible that a mass removal of select individuals from a population may have resulted in an “unnatural” selection for risk averse individuals.

As our ability to determine relatedness was inhibited due to there being limited allelic variability with the primers chosen, I propose that RADseq (Restricted site associated DNA sequencing) be employed to reveal sequence variation (such as single nucleotide polymorphisms or SNPs) (Wang et al. 2009; Andrews and Luikart, 2014). Sequence variations such as SNPs are becoming increasingly popular for answering genetic questions due to their affordability, low mutation rate (Ellegren 2000; Anderson and Garza, 2006; Gihouix et al. 2011), and, their high frequency per number of base pairs allowing them to provide information equivalent to SSRs (single stranded repeats)(Evans and Cardon 2004; Hauser et al. 2011; Weinman et al. 2015). RADseq is commended for its ability to identify polymorphisms in species with or without a reference genome (Hohenlohe et al. 2011; Jones et al. 2013; Viricel et al. 2014).

In addition, it has been argued that increases in relatedness lead to high reproductive skew (Jamieson, 1997). The cull at Tawharanui that occurred appears to have caused disruption to the female dominance hierarchy resulting in excessively large clutches (>15 eggs; Pers. Obs.) with little to no success at producing offspring. It is possible that the most dominant female was removed and created an uncertain dominance hierarchy resulting in a low reproductive skew and unrestrained reproduction (J.S. Quinn, Pers. Comm.). Previous work indicated that pūkeko follow the "concession model" of reproductive skew, where dominant individuals control reproduction of the group (Jamieson, 1997). Future studies should attempt removal of dominant females to determine if an unstable female hierarchy can explain oversized communal clutches. Communal clutches under low skew conditions have been found to be about 1.4 times larger than those under high skew conditions (Jamieson, 1997).

It would be beneficial to further enquire as to whether there were survival differences between nests at Tawharanui versus Shakespear because larger territories (as seen at Shakespear) have been shown to result in higher breeding success than smaller ones (Canada Warbler *Cardellina Canadensis*, Flockhart et al. 2016). I was unable to do so because many of our groups at Shakespear nested outside the paddocks and did not often bring their young into the paddock to feed until they were larger or sometimes not at all (especially when livestock was present) making it difficult to observe groups. Additionally, because of our difficulties at finding nests prior to the commencement of hatching and because many chicks were too small to be banded allowing for visual identification from a distance or their clipped toenail could grow out before re-acquisition, we could not be certain that the individual was one we had previously captured.

In conclusion, although I was unable to provide quantitative evidence for dispersal and whether the coefficient of relatedness varied between the high density and low density sites, I did find territory size to be significantly different between the two sites. Additionally, harrier density was significantly different between paddocks but not parks. I was also not able to find a significant difference between group sizes at Tawharanui and Shakespear. To gain better perspective into the effects population density might have on the cooperative breeding and joint-nesting system exhibited by the pūkeko, a longer term study between these sites should be conducted. Shakespear Park offers an opportunity to study whether previous differences between high and low density pūkeko populations are perpetrated without climate as a confounding factor.

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