The social organisation and mating system of the Brown Kiwi (*Apteryx mantelli*)

A thesis presented in partial fulfilment of the requirements for the degree of
Doctor of Philosophy in Ecology
at Massey University, Albany, New Zealand

Birgit Ziesemann

2011

‘The bird represented on the present plate constitutes a perfectly new genus, which it is not easy to refer to any of the established ornithological orders. It seems however to approach more nearly to the Struthious and the Gallinaceous tribes than to any other, though the very different form of the beak implies a different manner of life.....The head is rather small, and the neck of moderate length; the legs which are situated as in the Penguins, are short and strong.....There is no appearance of a tail, and in place of wings can only be perceived a small single joint on each side.....The colour of the whole bird is ferruginous.....The curious bird is a native of New Zealand.....’

Extract of the first formal description of a kiwi by
G. Shaw and F. Nodder, vol. 24,
The Naturalist’s Miscellany (London, 1813)

ABSTRACT

Mating systems are shaped by the strength and direction of sexual selection, the evolution of differential sex roles, and by the sexual conflict over mating rates and parental duties. Ecological factors and the behaviour of the entire population will then determine whether a certain mating strategy will be adopted by individuals, leading to variable mating systems between populations of the same species. The five kiwi species (*Apteryx* spp.), endemic to New Zealand, have experienced dramatic population declines due to habitat destruction and predation from introduced mammals, resulting in fragmentary low-density populations. Despite that the Brown Kiwi (*A. mantelli*) is still the most numerous among the kiwi species, little is known about aspects of their social organisation and mating system. The Brown Kiwi exhibits male-only parental care for precocial chicks and a sexual size dimorphism with larger females. While such characteristics are typical for polyandrous species, the only reported mating system for Brown Kiwi is monogamy. However, due to their nocturnal and secretive nature, in addition to the scarcity of this species, field observations on their social and mating behaviour are particularly challenging to obtain. Here, I chose one of the few remaining high-density and easily accessible populations of Brown Kiwi on Ponui Island. The exceptional density of this population should increase the potential for interactions between birds and reveal insights into their social organisation and mating system that are difficult to obtain in declining and/or low-density populations. Radio-telemetry was employed to investigate the formation and stability of pairs and groups, intersexual spacing behaviour in relation to the reproductive period of Kiwi, and the breeding behaviour and nesting success of radio-tagged birds. Genetic analysis was used to confirm paternity of incubating males, and to assess genetic relationships between group members. Nocturnal and diurnal spacing and roosting behaviours indicated long-term stable bonds between female-male pairs. Home range sizes of females were only slightly larger than those of males, most likely because of their larger body size. Stable monogamous pairs had largely overlapping ranges in the breeding and the non-breeding season. While such aspects of spacing behaviour are typical for a monogamous mating system, high degrees of nightly interactions between radio-tagged birds were detected, and range overlap was likely to be underestimated given the high number of tagged birds detected within focal birds' ranges and the inability to account for untagged birds. Additionally, some birds formed stable polyandrous trios with largely overlapping ranges and frequent roost site sharing of all trio members. Two males of a polyandrous trio were found cooperatively attending an active nest. Genetic kinship analysis revealed that such groups consisted of unrelated individuals rather than family groups as found in the Tokoeka (*A. australis*). Furthermore, one intra-group offspring of another polyandrous trio was genetically identified. Such findings lead to the assumption that birds may engage in cooperative polyandry. In closed habitats such as on Ponui Island, birds are unable to disperse and leave. Hence, population density may affect the social behaviour and mating system of individuals because of a potential shortage of resources that are important for reproduction. Thus, unpaired and/or floater Kiwi males may have joined existing breeding pairs due the unlike opportunity of independent breeding in a possibly saturated environment. While females may benefit from exhibiting cooperative polyandry at the expense of the caring males, males may have reduced reproductive success due to shared paternity. Nevertheless, the majority of breeding birds consisted of seemingly monogamous pairs and nesting success was high compared with other studied Brown Kiwi populations. In addition, levels of extra-pair paternity were low, indicating that most socially monogamous pairs were also genetically monogamous, despite the potential for social interactions and the freedom of females from parental care. My results confirm previous findings that Brown Kiwi maintain long-term monogamous pairs, most likely because of energetic demands of females during production of disproportionally large, energy-rich eggs, but also because of the high costs of reduced reproductive success for both sexes when a cuckolded male deserts a clutch. Nonetheless, although sample size was small, Brown Kiwi may potentially engage in cooperative polyandry in a high-density population, which demonstrates more flexibility in their reproductive ecology than previously known. The understanding of a species' social and mating system is crucial as reproductive behaviours directly influence the dynamics of a population. This study provides valuable information on kiwi life histories and demonstrates the key paradoxes between Brown Kiwi

reproductive characteristics and their mating system and may highlight the conflicts between the sexes over aspects of reproduction.

ACKNOWLEDGEMENTS

I would like to thank everyone who has supported, assisted and encouraged me in many different ways throughout my PhD candidacy.

Firstly, I would like to thank my supervisors for their support, guidance and encouragement they have provided me personally and professionally. I am indebted to Dianne Brunton for her advice, enthusiasm, for believing in my ideas, for the continuous support in so many different ways, and for making me feel its Christmas in the middle of summer. I also thank Dianne’s family, especially Gaven and Amy, for their hospitality and for enduring me in their home during my stressful write-up period. I thank Isabel Castro for bringing critical ideas into my mind, for sharing all the kiwi gossip, and for our little competitions on who would catch more birds. I am grateful to Weihong Ji for her invaluable help with tracking kiwi at night, for her advice on radio-telemetry, for establishing the collaboration with Landcare Research and for the best dumplings. At this point I would also like to thank Dianne Gleeson who took me under her wings as an ecology-student left without a genetics-lab.

I am extremely grateful to the Chamberlin family; David, Ros, Peter, Pat, Louise, Megan and Michelle, without whom this study would have never been possible. Thank you for opening your home and allowing me to conduct my research on Ponui Island. Thank you for making me feel at home on Ponui, for always having an open ear and open door for me, for teaching me how to shear a sheep and ride a motorbike! Very special thanks to Ros for spending so many hours monitoring Kiwi nests in the middle of winter. Thanks for sharing my enthusiasm when detecting an egg or chick inside the nest! I thank the Clime Group Ltd. for allowing me to catch and sample Kiwi on North Ponui and a special thanks to the local farm manager on North Ponui for their great hospitality.

For enduring help with my field work I would like to thank all volunteers who ever came out with me, but especially Sander Holthuijsen, Merel Boer, Esther

Bloemen, Markus Tischler, Patrick Schultheiss, Sabine Nooten, Julia Latham, Marleen Baling, Manuela Barry, John Cope, Weihong Ji and Dianne Brunton. Thank you for your help with tracking and/or catching Kiwi during the day and night, checking nests, setting up the grid and the solar panel, and for carrying the monstrous 25kg batteries. A big thank you goes to James Fraser with Percy and Marleen Baling for the fantastic record in the Kiwi catch rate on North Ponui.

I am grateful to Dianne Gleeson for the most valuable help and constant support with my Kiwi genetics. I thank Robyn Howitt for being the best lab mentor, and for her patience and trust. I also thank the entire Ecological Genetics laboratory group at Landcare Research for their support, and for being wonderful colleagues.

A special thank you to Hugh Robertson for providing DNA and feather samples of the WKS Kiwi population and for the very helpful and critical comments on the genetics manuscript. For statistical advice I would like to thank Daniel Walsh, Matt Pawley and Dianne Brunton. I thank Fidi Jordan and Frenchy for the map of Ponui Island. Swen Carlin made all the kiwi drawings that appear in this thesis.

I am happy that I had the opportunity to be part of the Ecology and Conservation Group at Albany. Thanks to all of you for the support and for all the fun we had. Especially I would like to thank Mike Anderson, Shauna Baillie, Marleen Baling, Manuela Barry, Taneal Cope, Mark Delaney, Anna Gsell, Monique Jansen van Rensburg, Emmanuelle Martinez-Smagghe, Luis Ortiz Catedral, Kevin Parker, Jo Peace, Mark Seabrook-Davison, Idan Shapira, Karen Stockin, Chris Wedding and Sarah Withwell.

And a very special thanks to all my friends, in New Zealand and on the other side of the world. I thank my family for their continuous support and encouragement, especially my mom Renate, my dad Bernd, my sister Kathrin and my aunt Gitte. Last, but not least a huge thank you to Swen for being my substitute of a whole family in New Zealand.

Funding for this project was provided by an Institute of Natural Sciences Doctoral Scholarship, Massey University, a Grant-in-Aid of Research from Sigma Xi the Scientific Research Society, and a grant from the Australia and Pacific Science Foundation (APSF 07/9). This research was conducted under the full permissions of the New Zealand Department of Conservation (AK/14969/RES and AK-21619-FAU) and the Massey University Animal Ethics Committee (MUAE06/05 and MUAEC07/144).

TABLE OF CONTENTS

Nesting success and breeding ecology in a high-density population of Brown Kiwi (*Apteryx mantelli*)

The genetic mating system and kinship of the Brown Kiwi (*Apteryx mantelli*) in two high-density populations

The social organisation and mating system of the Brown Kiwi (*Apteryx mantelli)*; a general discussion

CHAPTER 1

The evolution and variation of mating systems; implications for the social and the mating system of kiwi (*Apteryx* spp.)

Sexual selection, sexual conflicts, and the evolution of sex roles

The fitness of an individual lies not only in its ability to survive but also to successfully compete for mates and reproduce (Darwin 1871). Darwin (1871) first postulated the theory of sexual selection as the scenario where one sex (usually males) evolves secondary sexual characteristics through competition for mates (usually females) that are choosy. Traits considered to have evolved through sexual selection range from song in birds, visual ornamentation such as plumage colouration in birds, body size, behavioural displays as well as holding territories or other resources (Andersson 1994). Despite mate choice being possible by either sex, the emphasis in sexual selection theory has been on female mate choice as females usually provide greater parental effort including energetic investments in egg production. Thus, theory predicts that females choose among males based on traits that either signal direct benefits (e.g. territory, performance in parental duties) or indirect benefits (e.g. genetic compatibility) (Andersson 1994). Nonetheless, debate on drivers of the intensity of competition and which sex ‘competes’ and ‘chooses’ is ongoing and has led to sexual selection being one of the most intensively studied area in the field of evolutionary biology (reviewed by e.g. Birkhead and Møller 1992b; Andersson 1994; Andersson and Iwasa 1996; Cunningham and Birkhead 1998; Andersson and Simmons 2006; Clutton-Brock 2007; Kokko and Jennions 2008).

Bateman (1948) first proposed that the strength and direction of sexual selection on either sex depends on the relationship between mating success (the number of copulations) and reproductive success (the number of produced offspring). Later, two main concepts were put forward that expanded Bateman’s theory: the parental investment theory by Trivers (1972) and the operational sex ratio (OSR) by Emlen and Oring (1977). Parental investment benefits the survival of the offspring, but it is costly for the parents, as it requires time and energy and reduces the ability to invest in other offspring (Trivers 1972). Further, if parental care is unequally provided by the sexes, the sex that provides less care competes for the sex that provides more care, which leads towards a bias in the OSR, the ratio of receptive females to sexually active males (Emlen and Oring 1977). This in turn drives a disparity of the strength and direction of sexual selection, where selection acts more strongly upon the competing sex, while the opposite sex can afford to be choosy (Trivers 1972). In addition, males usually benefit more from additional mating opportunities and male reproductive success can be much more variable than female reproductive success with some males being significantly more successful than others (Bateman 1948; Arnold 1994; Webster *et al.* 2007).

According to sexual selection theory, mate choice has been the driver in the evolution of the preference for one or multiple traits. However, it has been suggested that the driving mechanism for such preference can better be described as resistance, because males and females have evolutionary divergent interest in reproduction that can lead to distinct sex roles where traits are favoured by one sex but are costly to the other (Parker 1979; Chapman *et al.* 2003; Chapman 2006; Lessells 2006; Parker 2006). Sexual conflict can arise over e.g. mating rates, parental investment, and desertion (e.g. Székely *et al.* 1996; Houston *et al.* 2005; Parker 2006; Székely *et al.* 2007; Thomas *et al.* 2007; Pogány *et al.* 2008). For example, both parents benefit from successful reproduction, but the costs are paid by the parent that cares for the young, whereas the deserting sex can gain by breeding with additional mates at the expense of the caring sex (Parker 2006; Székely *et al.* 2007).

Sexual conflict is not sexual selection, but it is an evolutionary conflict (Parker 2006) that can impose sexual selection (Chapman *et al.* 2003). Because the optimal outcomes over aspects of reproduction differ for males and females, each sex is expected to evolve adaptive sexual traits that bias the outcome to their own interest (Rice 1998). This can even result in sexually antagonistic co-evolution of interacting traits of males and females (as found e.g. in some insects; Arnqvist and Rowe 2002). Additionally, social interactions between and within the sexes, and the behaviour of the entire population (Houston *et al.* 2005; Alonzo 2010), will affect both the expression of, and the selection on, mating and parental investment patterns in both sexes (Thomas *et al.* 2007; Alonzo 2010). Thus sexual selection, sexual conflict over mating and/or parental care, and social interactions within a population are complex and tightly intertwined and shape the variation of mating systems.

Parental care and sex role reversal

In most vertebrates females provide the majority of parental care, while males compete over mating (Emlen and Oring 1977). The difference in the sex roles provides a situation in which sexual selection acts differently on males and females, often leading to morphological differences in sexual secondary traits, for example body size or ornamentation (Fairbairn *et al.* 2007; Van Dijk *et al.* 2010). In approximately 90% of mammalian species, females care alone for their offspring (Rutberg 1983; Clutton-Brock 1989b). Biparental care is the most common form in birds, with about 81% of species in which both sexes share parental duties (Cockburn 2006). Nevertheless, even in bird species with biparental care, the relative investment made by the sexes differs, with females investing more heavily than males (e.g. Møller and Birkhead 1993a; Schwagmeyer *et al.* 1999). However, in some cases such ‘conventional sex roles’ (Kokko and Jennions 2008) are reversed and males provide the majority or even the sole care for the offspring (e.g. Brunton 1988). Male-only care occurs in only 1% (about 90 species) of bird species from 12 different families (Owens 2002; Cockburn 2006). It is predominantly found in four clades of the Charadrii, the shorebirds, and in the ratites, the large flightless paleognathous birds (Cockburn 2006). It also occurs in at least one species of coucal (Andersson 1995; Goymann *et al.* 2004). Common correlates that explain the pattern of male-only parental care shared by these groups have been particularly difficult to identify (Andersson 1995; Ligon 1999; Bennett and Owens 2002; Andersson 2005). Precociality of the young is most often associated with male-only care (Lack 1968), but at least one exception to this rule exists (Andersson 1995). The African Black Coucal (*Centropus grillii*) exhibits male-only parental care for altricial chicks (Andersson 1995; Goymann *et al.* 2004).

In species with male-only care, the opportunities for additional mating by males should be constrained by the care they provide, and females should have more opportunities for remating. Hence sexual selection can be reversed and act more strongly on females (Bennett and Owens 2002; Andersson 2004). Under these circumstances females will compete more intensively over mates and develop sexually secondary characteristics such as e.g. body size. Indeed, most bird species with male-only parental care show a sexual size dimorphism with larger females. For example, seven of the eight species of the family of the *Jacanidae* exhibit sex-role reversal in parental care and females are substantially larger in body size than males (Jenni and Collier 1972; Tarboton 1995; Butchart 2000; Mace 2000). This pattern is found in kiwi (*Apteryx* spp.), where males provide either the sole parental care (Brown Kiwi, *A. mantelli*; Little Spotted Kiwi, *A. owenii*), or the majority of parental care (Rowi, *A. rowii*; Great Spotted Kiwi, *A. lawryi*, Tokoeka, *A. australis*) (reviewed by Sales 2005). Females are also larger in body sizes than males in all five kiwi species (reviewed by Sales 2005).

Social mating system

The social mating system is one component of a series of characteristics (e.g. fertilization, parental care, differential investment of parental care) that are under sexual selection (Møller 1994, 2003) and/or generate a sexual conflict. Social mating systems can be defined based on the observable type and duration of social bonds between males and females (Reynolds 1996), and the number of social partners varies with social mating systems (Bennett and Owens 2002). The type and amount of parental care required to successfully raise young is linked to the type of social mating system that will be exhibited by a species (Emlen and Oring 1977).

The most common mating system in birds is monogamy (Lack 1968; Møller 1986), where one adult female and one adult male establish a social relationship for the purpose of reproduction (Møller 2003). Such bonds can last for a minimum of one breeding event (serial monogamy), for the entire breeding season, or even for life. While biparental care may be one of the strongest correlates of social monogamy, it is not an essential prerequisite (Wittenberger and Tilson 1980). Remaining or reuniting with the same partner may be beneficial for both males and females. For instance, pairs of the Barnacle Geese (*Branta leucopsis)* that exhibited long-term mate retention (sometimes throughout life) had a higher lifetime reproductive success compared with individuals that paired for shorter periods (Black 2001). Divorce, the separation of pair members with the re-mating of at least one member is regarded to be an adaptive strategy of individuals to increase reproductive success (Ens *et al.* 1993; Choudhury 1995). Despite the possible benefits of mate switching, divorce can also be costly; e.g. experience of pair mates may prove greater breeding success, one pair member might be left without a new mate and territory, and other resources can be lost due to divorce (Coulson 1966; Ens *et al.* 1993; Choudhury 1995). In the Barnacle Geese, the length of the pair bond appears to be more important than the number of mates in reproductive success (Black 2001). Mate retention may improve breeding experience and coordination between pair members over a long life span. Long-term pair bonds are most often found in long-lived bird species, where the annual and the life time reproductive success have been found to be closely related to the duration of the pair bond (Ens *et al.* 1996; Black 2001). However, such reproductive benefits of long-term pair bonds have also been found in at least one species of passerine, the short-lived, socially monogamous House Finch (*Carpodacus mexicanus*) (McGraw and Hill 2004). Benefits of long-term pair bonding may also apply to kiwi as they have been found to show strong mate fidelity, and are long lived (> 20 years) (McLennan 1988; Taborsky and Taborsky 1991, 1999; McLennan *et al.* 2004).

Whilst monogamy can be in the interest of both sexes, most often their interests are in conflict and monogamy can be forced upon one sex by the other. To ascertain parentage one sex may restrict the opposite sex from mating with others through mate guarding (Birkhead *et al.* 1987; but see Robertson *et al.* 2001; Wallander *et al.* 2001), multiple mating (Birkhead *et al.* 1987), or through certain mechanisms e.g. applied by some male insects that switch off female receptivity (reviewed by Hosken *et al.* 2009).

Other types of mating systems can broadly be summarised as polygamy. When males form social bonds with more than one female, but each female forms a bond with only one male, it is a form of polygyny (Ligon 1999). Vice versa, if a female pairs up with several males, but each male pairs with only one female, it is polyandry (Oring and Lank 1982; Oring 1986; Ligon 1999). If both sexes mate with several mates without forming actual social bonds it is a promiscuous mating system (Ligon 1999).

The least understood and most puzzling mating system is social polyandry, also termed classical polyandry (Lack 1968; Ligon 1999; Owens 2002). Emphasising the importance of a favourable food situation, Andersson (2005) suggests three steps to the evolution of classical polyandry. The first step is the evolution of male-only parental care (Andersson 2005). Although this is not necessarily a precondition for the evolution of polyandry, it frees females from parental duties and enables them to engage in re-mating opportunities (Jenni 1974; Emlen and Oring 1977; Clutton-Brock 1991; Andersson 1995; Owens 2002). Secondly, female fecundity increases either through sex-specific life history traits such as larger body size, or because of improved nutritional conditions for females (Andersson 2005). Consequently, females can produce larger clutches than males can provide care for, either through an increased number of eggs per clutch or a decrease in clutch sizes but an increase in egg size (Erckmann 1983). The third and last step predicts that females compete over access to additional males while the previous male is caring for their brood, because the more competitive females will produce more offspring (Andersson 2005). Sexual selection pressure might then be stronger on females which may drive a disparity between male and female reproductive traits and interests (Andersson 1994, 2004). In addition, precociality of young often, but not always (Andersson 2004; Goymann *et al.* 2004), favours uniparental care (Emlen and Oring 1977; Oring and Lank 1982; Erckmann 1983; Oring 1986).

Social polyandry appears to be common in species with male-only parental care, for example in some species of pipefish Syngnathidae (e.g. Berglund *et al.* 1988; Jones *et al.* 2001; Wilson *et al.* 2003), in some species of shorebirds (Jenni and Collier 1972; Reynolds 1987; Tarboton 1995; Butchart *et al.* 1999), and in some ratites (Handford and Mares 1985; Fernandez and Reboreda 1998; Ligon 1999). The jacanas (*Jacanidae*) have adopted the most extreme form of polyandry, where females compete more strongly over mating and successful female territories include multiple male territories (Reynolds 1987; Tarboton 1995; Butchart *et al.* 1999; Emlen and Wrege 2004). These females mate with each male within her territory and sequentially produce clutches for each male, who then care for the young with little of no help from the female (Reynolds 1987; Tarboton 1995; Butchart *et al.* 1999; Emlen and Wrege 2004). Polyandry in ratites is mostly found in combination with other mating strategies (Handford and Mares 1985), and females often share in parental care. The only exception appears to be the kiwi, where the only mating system described to date is social monogamy (McLennan 1988; Taborsky and Taborsky 1991, 1999), despite the reversal of the sex roles and the sexual size dimorphism. The Brown Kiwi, especially, fulfils all three steps proposed in the evolution of polyandry; males are the sole providers of parental care of precocial chicks, females produce extremely large eggs using both functional ovaries within a timeframe that is shorter than the necessary incubation period of the male, and females are up to 20% larger then males suggesting that they are under strong selection pressure due to competition over males.

Genetic mating system

While the majority of bird species are indeed socially monogamous, the use of molecular techniques to assess genetic relatedness has revolutionised our view about mating systems (Bennett and Owens 2002). Social observable behaviours do not always correspond to the underlying genetic mating systems and basing the category of mating system on social observations alone can be misleading (Griffith *et al.* 2002). This insight has led to the important distinction between social and genetic mating system. Genetic mating systems depend on the patterns of actual genetic paternity and maternity and is therefore defined based on the number of sexual partners (Bennett and Owens 2002).

In fact, the majority of socially monogamous bird species do engage in extra-pair copulations (EPC) that may or may not result in extra-pair fertilization (EPF) (reviewed by Griffith *et al.* 2002; Westneat and Stewart 2003). In more than 70% of avian species, some offspring are sired by a male other than the social father (reviewed by Griffith *et al.* 2002). True genetic monogamy occurs in less than 25% of the socially monogamous bird species (Griffith *et al.* 2002). One of the most promiscuous socially monogamous bird investigated to date is the

Reed Bunting (*Emberiza schoeniclus*), with about 55% of offspring sired by extra-pair males (Dixon *et al.* 1994). Extra-pair paternity (EPP) can also occur in other mating systems, such as cooperative polyandry, when offspring is sired by males outside the social group (Owens and Hartley 1998). In the cooperatively breeding Superb Fairy Wren (*Malurus cyaneus*) up to 72% of offspring are the result of EPC (Mulder *et al.* 1994). Thus regardless of the social mating system and the type of parental care, males and females may engage in EPC, however, the frequency of EPP varies widely within and among species (reviewed by Westneat *et al.* 1990; Birkhead and Møller 1992a; Birkhead and Møller 1995; Petrie and Kempenaers 1998; Westneat and Stewart 2003). The high prevalence of EPP in socially monogamous species may be because the most suited social mate may not be the most compatible genetic mate, or because all preferred mates are already paired and unavailable. Through mating that occur outside the pair bond, females may be able to choose the most preferred male through cryptic female choice (e.g. sperm competition) (Parker 1984; Birkhead 1998).

The drivers and the adaptive function of engaging in extra-pair copulation are still not fully understood (reviewed by Birkhead and Møller 1992a; Birkhead and Møller 1995; Petrie and Kempenaers 1998; Westneat and Stewart 2003); while social mates may be chosen based on direct benefits such as preferred breeding habitat, territory, or effort in parental care, the benefits gained from EPP have been attempted to be explained based on indirect genetic benefits. In most socially monogamous bird species EPC are often initiated by the female (e.g. Currie *et al.* 1998; Stutchbury 1998). It is still controversial what genetic benefits might be gained through multiple mating but two concepts haven been proposed (reviewed by Jennions and Petrie 2000). Firstly, females prefer to mate with males bearing traits indicating high genetic fitness due to the inheritance of ‘good genes’ to their offspring providing enhanced offspring viability ('good genes' hypothesis; e.g. Kempenaers *et al.* 1992; Gowaty 1996; Hasselquist *et al.* 1996). The second hypothesis states that females prefer some male traits because they indicate that such males possess genes that may increase the sexual attractiveness of the female’s offspring leading to increased mating success ('sexy son' hypothesis; Weatherhead and Robertson

1979). Both hypotheses assume the evolution of a female preference through indirect benefits; however for the good genes hypothesis such indirect effects arise from the production of offspring with higher viability in contrast to in the sexy son hypothesis where effects arise through the production of sons (possibly daughters) that have higher mating success.

In species with male-only parental care, it is generally expected that the rate of EPP is low, because the consequences of retaliation of the cuckolded social male would have an immense negative effect on the reproductive success of the female (e.g. Cezilly and Nager 1995; Møller and Cuervo 2000). Therefore, it is predicted that in such species genetic paternity is high (e.g. Møller 2000; Møller and Cuervo 2000; Sheldon 2002). However, it is controversial whether a simple positive relationship between paternity and the extent of paternal care exists (commented by Kempenaers and Sheldon 1997). One of the most extreme examples is the Ocellated Wrasse (*Symphodus ocellatus*), where all nesting males (100%) solely cared for a large proportion of extra-pair young (Alonzo and Heckman 2010). Also, the African Black Coucal (*Centropus grillii*) exhibits, with 14.2% illegitimate offspring, one of the highest rates of EPP of a socially polyandrous species with male-only parental care (Muck *et al.* 2009). The types of mating strategies exhibited by a species will be related to a combination of ecological and behavioural factors and the associated costs and benefits of certain mating strategies for each individual.

Ecological determinants of social organisation and mating system

The social organisation (i.e. social system) of a species describes the type, the quality and the temporal pattern of relationships between conspecifics (Hinde 1976), including spacing system, grouping behaviour and group size, and mating system. While social organisation has long been thought to be a fixed characteristic of each species, it is now accepted that social organisation can vary widely within the same species and even within populations of the same species (Lott 1991) due to behavioural responses to environmental variations (Emlen and Oring 1977; Lott 1984, 1991). For example, social systems may vary in response to changes in food and mate availability, population density and habitat saturation, predation and hunting pressure as well as many other factors.

Within populations the conflicting interests between the sexes over mating opportunities and parental care can generate variable mating systems (Davies 1989, 1992); however, between populations, ecological conditions certainly play a major part in determining the outcome (Emlen and Oring 1977). For instance, Emlen and Oring (1977) aimed to explain the variation of mating systems within an ecological framework. They propose that the potential of an individual to exhibit polygamy is constrained by the degree to which the environment allows individuals to acquire mates (environmental polygamy potential hypothesis), either directly (e.g. herding) or indirectly through the control of resources important for reproduction (Emlen and Oring 1977). This hypothesis asserts that when critical resources such as food, breeding habitat and receptive mates are spatially clumped within the environment, some individuals will be able to defend resource patches economically (Brown 1964), being able to monopolize several mates (Verner and Willson 1966; Orians 1969). Hence, heterogeneously distributed resources generally lead to polygamous mating systems and group formation (Emlen and Oring 1977). On the other hand, the potential for polygamy is lowest when resources are uniformly distributed, because resources can not be economically defended and individuals tend to disperse evenly within the environment and rarely encounter multiple mates (Emlen and Oring 1977). Thus, homogenously distributed resources are likely to lead to monogamy and solitary living (Emlen and Oring 1977). For example, Dunnocks (*Prunella modularis*) have a highly variable mating system, ranging from monogamy, polyandry, polygyny and polygynandry (Davies and Lundberg 1984). These different mating strategies are related to the male Dunnocks' ability to control access to females which in turn depends on female spacing patterns that are directly correlated to the distribution and availability of food resources (Davies and Lundberg 1984).

As indicated above, spacing systems are strongly influenced by the distribution of food and mates and are therefore tightly linked to a population's mating system. Food has been suggested to have a strong effect on the degree of range overlap and territoriality (Carpenter and MacMillen 1976; e.g. Armstrong 1991; Maher and Lott 2000). If food becomes scarce, the costs of defending such resources might exceed the benefits derived from them and consequently an increase in range size and overlap can be expected (Brown 1964; Carpenter and MacMillen 1976; Maher and Lott 2000; McLoughlin *et al.* 2000). On the other hand, with increasing food resources, a reduction in range size and overlap and a shift towards territoriality can be expected. However, if food resources are overabundant, the likelihood of territoriality again decreases as the costs of defending intruders into the territory begin to exceed the benefits (Brown 1964; Carpenter and MacMillen 1976; Maher and Lott 2000; McLoughlin *et al.* 2000). Territoriality and non-overlapping ranges are often associated with monogamous mating systems, while largely overlapping ranges are associated with polygynous mating systems (Orians 1969; Emlen and Oring 1977).

To realise this potential of polygamy, potential mating partners have to be available within the population. In polyandrous bird species, for instance, the degree of polyandry is related to the degree of breeding asynchrony, the lengths of the breeding season and the population sex ratio, because this enables females to mate and produce sequential clutches with several males (Schamel and Tracy 1977; Colwell 1986; Andersson 2004). In addition, population density may play an important role in mate availability. In populations that are fragmented and/or isolated and at low densities, individuals may not have the opportunities to monopolise mates for engaging in additional mating. On the other hand, high population density will ultimately lead to an increase in social interactions such as competition or cooperation for acquiring resources (e.g. food, habitat) and/or mating partners, copulations, and parental care (e.g. Møller 1991; Westneat and Sherman 1997; Stewart *et al.* 2010), because resources have to be shared by more individuals. Thus, population density is expected to influence many demographic factors of a population, including dispersal, space use, group size, and mating system. In fact, impacts of population density on social organisation and mating system have been observed in several species. For example, in Bitterlings (*Rhodeus sericeus*), high male density led to a collapse of territoriality as an adaptive behaviour because defending against intruders became too costly (Reichard *et al.* 2004).

Similarly, female Root Voles (*Microtus oeconomus*) decreased the exclusiveness of their home ranges with increasing density of resident females in a controlled experiment on the effects of population density on female space use (Hoset *et al.* 2008). In a high density population of the Brown Kiwi, evidence for exclusive territories was not found and range overlap between neighbouring birds was enormous (Potter 1989). In contrast, this species maintains and defends well-defined territories with no or minimal range overlap in low-density populations (McLennan 1988). Travis *et al.* (1995) observed an increase of group size with an increase in population density in Gunnison's prairie dogs (*Cynomys gunnisoni*) and a consequent shift from a social system suggestive of monogamy to one suggestive of polygyny. Such changes in the spacing system of animals in response to increasing population density can also be supported by the fact that animals have been observed to expand their ranges when neighbouring animals were experimentally removed (e.g. Norman and Jones 1984; Boutin and Schweiger 1988), or when neighbours dispersed and left (e.g. Lovallo and Anderson 1995). However, in closed and/or isolated habitats such as islands, animals cannot disperse and thus the effect of population density on the social organisation and mating system may be more prominent. This scenario was observed in a population of the Bearded Vulture (*Gypaetus barbatus*) inhabiting a restricted geographical area (the Pyrenees, Spain), where habitat saturation lead to a shift from a monogamous to a polyandrous social system (Carrete *et al.* 2006). With an increase in population density, the number of polyandrous trios increased with subordinate males joining existing breeding pairs due to habitat shortage and inability of independent breeding (Carrete *et al.* 2006).

It is likely that a combination of several ecological factors rather than just a single factor promotes changes in the social organisation of animal populations, but it has been particularly difficult to identify ecological correlates that can explain the underlying genetic mating system. Breeding synchrony and breeding density have been put forward as the traditional factors influencing the genetic mating system in birds (Stutchbury and Morton 1995; Westneat and Sherman 1997; Møller and Cuervo 2000; Owens 2002). For example, families of the Clay Coloured Robin (*Turdus grayi*) that bred synchronously had higher rates of EPP compared with families of the same population that bred asynchronously (Stutchbury *et al.* 1998). Stutchbury and Morton (1995) hypothesised that the rate of EPP in a number of passerine species is correlated with the degree of breeding synchrony of females (the proportion of females that are reproductively active at the same time). Stutchbury and Morton (1995) suggest that breeding synchrony increases the benefits for males and females of seeking extra-pair mating, because breeding synchrony enables females to compare male quality and choose an extra-pair mate and it enables males to seek extra pair copulations when the OSR should be relatively equal and thus the male-male competition at its lowest. However, empirical results have been controversial of the breeding synchrony hypothesis. Most studies have found it difficult to find a positive relationship between breeding synchrony and the rate of EPP in comparison between species and between populations of the same species (e.g. in Yellow Warbler *Dendroica petechia* (Yezerinac and Weatherhead 1997); Blue Tit *Parus caeruleus* (Kempenaers 1997); Golden Whistlers *Pachycephala pectoralis* (Van Dongen and Mulder 2009)). Indeed, it has been suggested that breeding asynchrony instead of synchrony promotes EPP (Birkhead and Biggins 1987), because this enables mate guarding during the fertile period of the social mate and the opportunity to seek EPP when the social mate is no longer fertile (Birkhead and Biggins 1987; Birkhead and Møller 1992b). Hence, breeding synchrony may lead to the inability of seeking extra pair copulations during mate guarding duties of the fertile mate.

Breeding density has been proposed as another correlate that positively influences the rate of EPP (e.g. Morton *et al.* 1990; Møller 1991; Birkhead and Møller 1992b). This hypothesis predicts that females and males of species that nest at high densities, such as colonial nesting birds, have increased opportunities to seek EPC, because of the close proximity of neighbours and the availability of extra-pair mates (Møller 1991; Møller and Birkhead 1993b; Petrie and Kempenaers 1998). In addition, at high population densities, suitable breeding habitat is often limited leading to an increased number of unmated floaters (non-breeding individuals that did not acquire a territory for breeding) (Brown 1964; Stutchbury and Robertson 1985; Kokko and Sutherland 1998), potentially providing an even larger pool of extra-pair mates. While some studies indeed have reported a positive relationship between breeding density and EPP (e.g. Eastern Bluebirds *Sialis sialis* (Stewart *et al.* 2010); Bearded tits *Panurus biarmicus* (Hoi and Hoi-Leitner 1997a); Barn Swallows *Hirundo rustica* (Møller 1991)), others have not found a relationship between these two variables (e.g. Tree Swallows *Tachycineta bicolor* (Dunn *et al.* 1994; Conrad *et al.* 2001)). In a comparative study, Westneat and Sherman (1997) did not find any evidence that EPP is correlated with breeding density or breeding synchrony among 72 different bird species. However, they found that within species, the rate of EPP increased with increasing breeding density (Westneat and Sherman 1997). Therefore, breeding density may in fact influence the rate of EPP within populations of some species, but the occurrence and frequency of EPP may depend on multiple social and ecological factors (Westneat and Sherman 1997; Stewart *et al.* 2010).

Research on Kiwi (Apteryx spp.) with emphasis on the Brown Kiwi (A. mantelli)

Kiwi (*Apteryx* spp.) are particularly interesting candidates for the study of social and mating systems, given the theoretical predictions and empirical findings concerning the evolution of avian mating systems.

The five recognised species of kiwi (Burbidge *et al.* 2003) are the smallest members of the ratites, a taxonomic group of large flightless birds in the Southern Hemisphere. Kiwi are endemic to New Zealand and have been instated as the unofficial national emblem of the country. They have evolved largely in the absence of terrestrial mammalian predators, uniquely occupying a nocturnal, ground- and forest-dwelling niche more typical of small mammals than birds, and today co-exist with alien mammals introduced by Polynesian and European settlers (Wodzicki 1950; McLennan *et al.* 1996; Sales 2005). Despite some interspecific differences in their social system, all species of kiwi exhibit sexual size dimorphism with females being larger than males, have precocial young and males provide the majority, and in some case all, parental care. Although such characteristics are often found in bird species that exhibit social polyandry, the reported mating system for all five kiwi species is monogamy. In the Great Spotted Kiwi (*A. lawryi*) (McLennan 1990; Colbourne 2002; Sales 2005) and the Rowi (*A. rowii*) (Colbourne 2002; Sales 2005), both members of a pair share in parental duties, whereas in the Brown Kiwi (McLennan 1988; Taborsky and Taborsky 1999; Colbourne 2002), and in the Little Spotted Kiwi (*A. owenii*) (Jolly 1989, 1990) only the males incubate and provide brood care. The Tokoeka (*A. australis*) lives in family groups and groups members help in incubation (Sturmer and Grant 1988; Colbourne 1991, 2002).

Even though I will focus on research that has been conducted on the Brown Kiwi, there is relatively little known about the social organisation and the mating system of all kiwi species. One explanation may be that today, most kiwi species are scarce and not easily accessible for studying their behaviour. All kiwi species are threatened to different degrees and at risk of extinction (Holzapfel *et al.* 2008). Historical, archaeological as well as genetic data have shown that most (possibly all) kiwi species were once more abundant and widespread than today (Butler and McLennan 1991; Hitchmough 2002; Holzapfel *et al.* 2008; Shepherd and Lambert 2008). Since human arrival in New Zealand, kiwi populations have drastically declined, mainly due to habitat loss and predation from introduced mammals, but this went virtually unnoticed until only the early 1990s (McLennan and Potter 1992).

The Brown Kiwi

The Brown Kiwi is still the most abundant and widespread kiwi species, but most Brown Kiwi populations are still in decline, are at low-densities, and require intensive conservation management to sustain their survival or to increase their numbers (Hitchmough 2002; Holzapfel *et al.* 2008). In contrast to records suggesting historical Brown Kiwi densities of 40-100 birds/km^2 (Buller 1888), present densities in many mainland populations rarely exceed 4 adult birds/km^2 (McLennan and Potter 1992). The recognition of this decline has prompted extensive research efforts focussing on examining the causes of population decline. Human-induced habitat destruction, the competition with, and the predation by, introduced mammals have been identified as the main causes of decline of most populations (McLennan *et al.* 1996; McLennan *et al.* 2004). Kiwi chicks are an especially vulnerable life stage and suffer severe predation, mostly by stoats (*Mustela erminea*) and other mustelids (*Mustela* spp.) (McLennan *et al.* 1996; Basse *et al.* 1999; McLennan *et al.* 2004). The predation of young birds has resulted in significant recruitment failures into breeding populations, leading to rapid and drastic declines of populations (McLennan *et al.* 1996; Hitchmough 2002; McLennan *et al.* 2004).Due to the low-densities of most remaining Brown Kiwi populations on the New Zealand mainland, little is known about the species, which is further complicated by the secretive and nocturnal habits of Brown Kiwi.

Brown Kiwi possess some unique characteristics of reproduction and parental care. In particular, Brown Kiwi females are larger than males and produce extremely energy-rich (c. 61% yolk), and disproportionally large eggs in relation to body weight (Reid 1971b, 1971a; Calder *et al.* 1978). The males are solely responsible for incubation and the incubation stage is one of the longest known among birds (c. 74-84 days; Calder *et al.* 1978). Males also provide post-hatch parental care (brooding) for the precocial chicks. However, only a few previous studies have addressed aspects of the social organisation and mating system of Brown Kiwi populations (McLennan 1988; Potter 1989; Taborsky and Taborsky 1991, 1992, 1999). Behavioural data suggest that Brown Kiwi form long-term monogamous pair bonds and that the spatial system is defined by territorial males and females, sharing of territories by pair members and little overlap between ranges of neighbouring birds (McLennan 1988; Taborsky and Taborsky 1991, 1992). In addition Taborsky and Taborsky (1991) report the occurrence of unmated floater males and unmated but territorial males. Conversely, Potter (1989) was not able to detect defined territories and range overlap between neighbours of either sex was enormous. He also observed a divorce rate between pair members of approximately 50% (Potter 1989) and at least one case of nest usurpation; observations not reported in any other Brown Kiwi population. Despite that all such study populations occurred at different population densities, with the highest density found in Potter’s (1989) study population, all studies have concluded that Brown Kiwi are monogamous (McLennan 1988; Potter 1989; Taborsky and Taborsky 1999). However, all of the authors acknowledge that Brown Kiwi have a high potential for polyandry due to their reproductive and parental care characteristics (McLennan 1988; Potter 1989; Taborsky and Taborsky 1999). Past results from studies of Brown Kiwi social and mating behaviours acknowledge the need for further detailed research on the effects of population density and the potential constraints on increased sociality and polyandry. Increased sociality is found in the Tokoeka (Sturmer and Grant 1988; Colbourne 1991, 2002), and biparental care is found in the Great Spotted Kiwi (McLennan 1990; Colbourne 2002; Sales 2005) and the Okarito Brown Kiwi (Colbourne 2002; Sales 2005).

The Ponui Island Brown Kiwi population

To investigate Brown Kiwi social organisation and mating system, as well as to improve our knowledge on general kiwi reproductive ecology, I chose a model population of Brown Kiwi which is still of exceptional high density. The study population on Ponui Island is easily accessible and is one of the highest densities in the wild which makes it more feasible to study their social behaviour. The high population density also provides an excellent scenario for assessing whether Brown Kiwi exhibit their potential for increased sociality, alternative mating strategies or polyandry. In such settings, social interactions such as competition and cooperation are expected to be increased and mate availability should not constrain mating tactics, mating system and sociality.

The Brown Kiwi population on Ponui Island originated from only 13 founders that were introduced from three different source populations in 1964 at the request of the landowners (Miles and Castro 2000). Six birds came from Little Barrier Island, seven from Waipoua Forest (Northland). Further demographic details such as sex ratio and age of the founder population are unknown. Despite the presence of a high density of ship rats (*Rattus rattus*), Norway rats (*Rattus norwegicus*), and a population of feral cats (*Felis catus*), the Ponui Kiwi population has experienced rapid population growth since its introduction and is now thought to be one of the few high-density kiwi populations in New Zealand with estimates of 100 birds per km^2 (Cunningham *et al.* 2007). Stoats have previously been sighted on Ponui by the landowners, but their status on the island is unknown. Due to founding birds being sourced from geographically and genetically distinct populations (Baker *et al.* 1995; Burbidge *et al.* 2003; Shepherd and Lambert 2008), the Department of Conservation considers the Ponui Island population of ‘low conservation concern’. However, their low conservation status combined with the high population density provides a unique opportunity to study this endangered species that would not be possible in declining, intensively managed and conservation-sensitive populations.

Research objectives and thesis layout

The overall aim of this thesis was to gain detailed information on the social organisation and mating system of the Brown Kiwi that can only be gained where birds are abundant (high population densities), and to compare findings with previous studies on Brown Kiwi. Additionally I aimed to discuss findings in the light of the effects of population density on social and mating behaviours. I addressed the overall aim by establishing four main objectives:

Objective 1: Investigate the type and duration of social associations between identified individual birds, to identify social grouping and pairing behaviour, to gain insights into the social system of the population.

Objective 2: Investigate the spacing system of neighbouring and/or socially associated and identified male and female Brown Kiwi, and to assess how their spatial behaviour differs between the breeding and the non-breeding season, in order to gain insights into the social organisation of the population.

Objective 3: Investigate the nesting behaviour and the nesting success of the population and to identify incubating males and the offspring they raise.

Objective 4: Investigate the genetic relationships between potential parents and their offspring as well as between members of pairs and groups, to reveal the underlying genetic mating system of the study population and another high density population of Brown Kiwi for comparisons.

Thesis outline

The main chapters (2-5) of this thesis are presented as a series of interrelated manuscripts that have been prepared (chapter 2, 3), published (chapter 5) or accepted (chapter 4) for publication in scientific journals. Since each chapter was written as an independent piece of research, some repetitions between chapters, especially in the introduction- and method sections, were inevitable. The four main chapters (2-5) examine general aspects of social organisation and mating system of Brown Kiwi on Ponui Island, including behavioural, spatial and genetic analyses.

Chapter one provides a detailed literature review on how sexual selection, parental care and sexual conflict shape avian social mating systems. It further elaborates on the underlying mechanism that lead to the broad variation in social mating systems and how different the underlying genetic mating system can be. Ecological factors that are likely to influence the outcome of a certain social organisation and mating system are discussed in detail. I introduce the study species of this research in the light of previous research findings and introduce the study population investigated here. Finally, I provide the overall aim and research objectives of this research.

Chapter two aims to address ***Objective 1***. Observing direct social interactions between individuals of nocturnal, cryptic and wide-ranging animals is difficult, but these individual-based social interactions form the basis of the social organisation within a population. However, Kiwi shelter during the day and their roosting behaviour is an important element of social associations between individuals. Therefore, in chapter three I examine the frequency and duration of direct social associations between radio-tagged Kiwi during their diurnal roosting, to gain information on the formation and stability of social groups and pairs relative to their social and mating system.

Chapter three addresses ***Objective 2***. Investigating spatial behaviour of members of a population reveals information about their social organisation and can provide insights into the mating system. Thus, chapter two examines intersexual space use patterns of radio-tagged neighbouring Brown Kiwi during their active nocturnal phase. Employing radio-telemetry I examine seasonal variations in female and male home ranges, range overlap, direct nightly interactions between individuals, to assess the social organisation and gain information on the mating system of the Ponui population.

Chapter four deals with ***Objective 3***. Knowledge about nesting success and general breeding ecology is often difficult to obtain or unknown from threatened, low-density populations. Nonetheless, this is crucial knowledge to understand a species' life history and its influences on their mating system. In chapter four I assess the nesting success and the breeding ecology of the Ponui Kiwi population and compare my findings to other Kiwi populations of different densities on the New Zealand mainland. At the same time monitoring breeding males and their nests, enabled me to assess the identity of incubating males and the offspring they raised. Chapter four has been published as:

> Ziesemann, B., Brunton, D.H., and Castro, I.C. 2011. Nesting success and breeding ecology in a high-density population of Brown Kiwi (*Apteryx mantelli*). *Emu* 111, 148-154.

Data for this chapter/publication were collected in the field and in the laboratory (necropsies) by me. I conducted all data analyses and wrote the manuscript with valuable input and edits by my supervisors D.H. Brunton and I.C. Castro. Advice for statistical analyses was provided by D.H. Brunton.

Chapter five investigates ***Objective 4***. The social mating system does not always correspond to the underlying genetic mating system. In this chapter, I conduct genetic parentage analyses to assess alternative mating strategies and genetic kinship relationships of social breeding groups, to draw a conclusion on the underlying mating system of the Ponui population and an additional high-density Brown Kiwi population on the New Zealand mainland. Chapter five is currently under review for publication as:

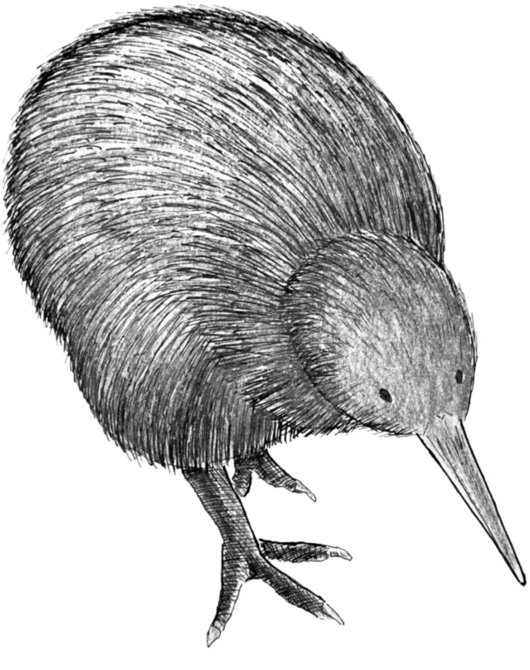
> Ziesemann, B., Gleeson, D., Castro, I.C., Robertson, H.A., Ji, W., Brunton, D.H. In review. Flexibility in the mating system of two high-density Brown Kiwi (*Apteryx mantelli*) populations.

I collected all behavioural data and blood samples of the Ponui population. H. Robertson provided behavioural data, DNA and feather samples of the WKS population. I conducted all laboratory and statistical analyses and interpreted the results with support and input by D. Gleeson. D. Gleeson provided laboratory space and equipment as well as laboratory assistance. W. Ji established the collaboration with Landcare Research (D. Gleeson) where laboratory analyses were conducted. I. C. Castro provided funding for radio-telemetry equipment and radio-transmitters of the Ponui population. The remaining costs of this research were funded with a grant from the Australia and Pacific Sciences Foundation of D. H. Brunton. I wrote the manuscript with improving comments and edits by all co-authors, D. Gleeson, I.C. Castro, H. Robertson, W. Ji and D.H. Brunton.

Chapter six provides a summary of the key findings of my research as well as a detailed discussion on how such findings on Brown Kiwi social organisation and mating system fit into the broader context of avian mating systems. I further identify limitations to this research study and discuss directions for future research.

CHAPTER 2

Roosting behaviour, roost sharing and long-term social groups in a high-density population of Brown Kiwi (*Apteryx mantelli*)



Abstract

Interactions between individuals shape the social organisation of a population and thereby influence the mating system. However, interactions are difficult to observe in threatened and nocturnal animals, such as the Brown Kiwi (*Apteryx mantelli*), a ratite species endemic to New Zealand. I examined diurnal roosting behaviour of radio-tagged Brown Kiwi on Ponui Island to assess social behaviour of individuals in one of the species' remaining high-density populations. Males and females moved to a different roost site often, but showed loyalty to some roost sites that were used sequentially over time. Up to eight different birds were recorded to use the same roost site in sequence indicating overlap of ranges and the potential for social interactions between these birds. Roost-switching frequency was positively correlated with the stability and permanency of the roost site. I calculated a pair-wise sharing index (PSI) to quantify the frequency and seasonality of roost sharing. The majority of birds (90%; 27/30) roosted with at least one other bird at least once during the course of this study (2005-2008). Female-male pairs and female-male-male trios constituted the majority of observed roost sharing. However, only a small number of birds were strongly associated (4%; 18/415 dyads), and these were categorised as pairs and trios based on the frequency and duration of their social association. Pairs and trios roosted together over several breeding and non-breeding seasons, indicative of stable arrangements. This is the first reported case of stable polyandrous trios for this species. Roost sharing may facilitate the maintenance of long-term social relationships between individuals. I conclude that the social organisation of this population is characterised by stable socially monogamous pairs and a lower number of socially polyandrous trios, and that the population’s high density may have led to the variation of social group formation for a species that is elsewhere solitary or in female-male pairs.

Introduction

Interactions between individuals that result as a response to surrounding ecological conditions are the key determinants of the social organisation (i.e.

social system) of a population (Hinde 1976; Lott 1984, 1991). These interactions may include competition, dominance or cooperation for acquiring resources and mating partners, as well as competitive or cooperative parental care (Whitehead 1997). Thus the social organisation of a species describes the type, the quality and the temporal pattern of relationships between conspecifics (Hinde 1976). An understanding of the social organisation is important as it shapes the mating system exhibited by individuals and therefore contributes to the knowledge of the reproductive biology of a population and life history characteristics of the respective species.

However, studying social interactions of nocturnal, cryptic and threatened animals can be challenging, as such behaviours are difficult to observe in the wild. Such is the case for the Brown Kiwi (*Apteryx mantelli*), one of the five kiwi species endemic to New Zealand (Burbidge *et al.* 2003; Heather and Robertson 2005). The Brown Kiwi is still the most abundant kiwi species, but has experienced dramatic population declines and range contractions (McLennan *et al.* 1996; McLennan *et al.* 2004; Holzapfel *et al.* 2008). Determining social associations between birds such as pairing status of breeding birds can be particularly difficult as Brown Kiwi females do not participate in incubation and parental care and are rarely seen egg-laying.

Brown Kiwi spend a large proportion of their time roosting in day-time shelters and consequently roosting behaviour may play an important role in their social life. For example, in the Tent-making Bat (*Artibeus watsoni*), the majority of social behaviours such as mating and rearing young occur at the roost (Chaverri and Kunz 2006). Thus, roosting behaviours and roosting associations have been suggested to have a considerable influence on social tactics of tent-making bats (Chaverri *et al.* 2007). Diurnal roosting behaviour of Brown Kiwi can provide a direct measure of social associations between individuals that are difficult to establish during their active period at night or solely based on their breeding status.

Previous radio-telemetry studies have investigated roost site selection and habitat use of Brown Kiwi and have found that there are multiple roost sites available to Kiwi throughout their home ranges (McLennan *et al.* 1987). The types of roost sites used by Brown Kiwi have been described by a number of authors (Colbourne and Kleinpaste 1983; McLennan *et al.* 1987; Potter 1989; Taborsky and Taborsky 1995), and include hollow logs, natural cavities, surface roosts, thick marsh plantings, excavated burrows as well as anthropogenic habitat structures (Taborsky and Taborsky 1995). Further, this species has been described to be territorial, socially monogamous and to maintain long-term male-female pair bonds (McLennan *et al.* 1987; McLennan 1988; Taborsky and Taborsky 1992, 1999). Pairs frequently, but not always, share roost sites (McLennan *et al.* 1987; Potter 1989). In high-density populations, space use patterns of Brown Kiwi appear to differ; overlapping home ranges replace territoriality and sequential roost sharing is common (Potter 1989). In fact, population density may impact the spatial distribution of individuals within a population as resources have to be shared by more individuals. Population density has been proposed as the driving factor for increased numbers of polyandrous trios in Bearded Vultures (*Gypaetus barbatus*) (Carrete *et al.* 2006), and for the increased sociality in Tent-making Bats (Chaverri *et al.* 2007). Indeed, more complex social structures such as group formation and an increased degree of roost sharing may be more prevalent at high population densities. Hence, in this study I took the opportunity to investigate the roosting behaviour of identified, radio-tagged individuals within a high-density Brown Kiwi population on a New Zealand offshore island in order to determine the social associations between birds and to gain an understanding of their social organisation.

Methods

Study site and study population

This study was conducted on Ponui Island (Ponui; 36°50’S, 175°10’E) located approximately 16km southeast of Auckland in the Hauraki Gulf, New Zealand (Figure 2.1). About two thirds of Ponui is in pasture and one third consists of mixed broadleaf forest, Kanuka (*Kunzea ericoides*), and Kauri (*Agathis australis*), interspersed with wetlands (Miles and Castro 2000; Castro 2006).

The Ponui population was established from 13 Brown Kiwi introduced to the island in 1964 (Miles and Castro 2000), and is now estimated at a density of 100 birds per km^2 (Cunningham *et al.* 2007). This is in contrast to some mainland Brown Kiwi populations that occur at densities of approximately one bird per km^2 (McLennan *et al.* 1987; McLennan 1988). The study site on Ponui covered approximately 200ha and incorporated three forested catchments, wetland and pasture.

Birds were caught with the help of trained kiwi-tracker dogs. Two-stage radio transmitters (Kiwitrack Ltd., New Zealand) were attached to the tibia of the birds' legs following the technique of Robertson and Colbourne (2003). Each transmitter had a unique radio frequency which allowed individual identification. Radio transmitters were also programmed to change their pulse rate indicating a bird's activity (moving, resting, or dead). Given the nocturnal, forest-dwelling and cryptic habits of kiwi, radio telemetry offered the best methodology available to study their natural spacing behaviour. Sexes of radio-tagged birds were assessed based on morphological differences between males and females (Heather and Robertson 2005) and confirmed by genetic analyses from feather samples (Huynen *et al.* 2002; Equine Parentage and Animal Genetics Services, Palmerston North, NZ).

Radio tracking

Radio-telemetry was applied to study kiwi roosting behaviour from October 2005 until December 2007. I monitored a total 36 adult tagged Kiwi, including 15 females and 21 males. The number of monitored tagged adult birds fluctuated between the study years due to transmitter failures, deaths and newly caught and tagged birds. Birds without transmitters were occasionally sighted but could not be monitored regularly.

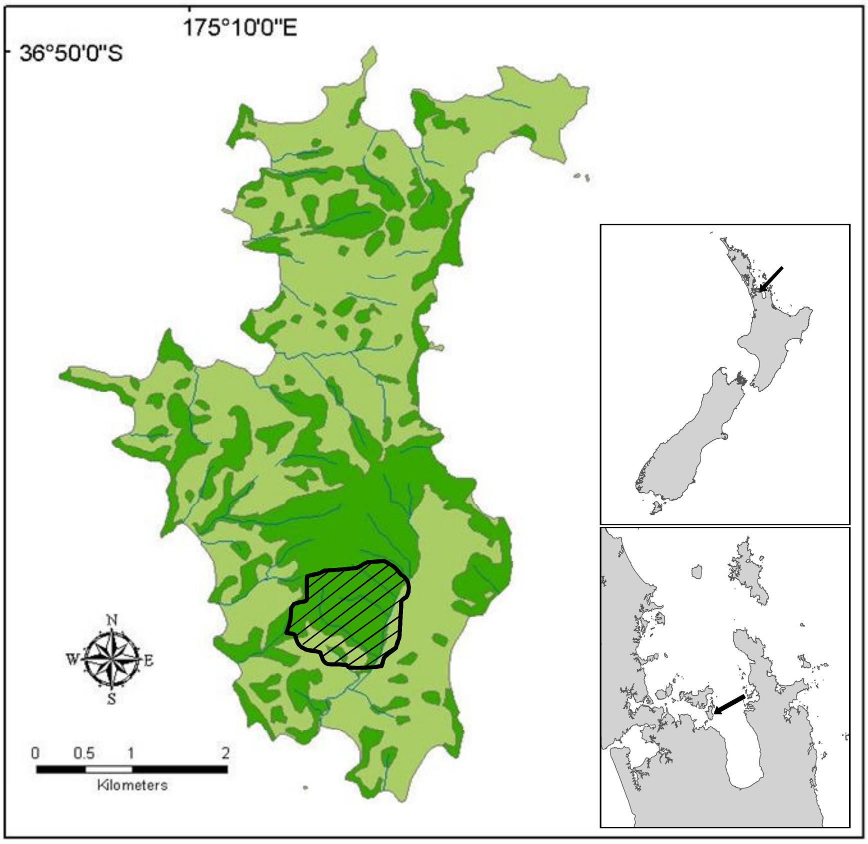


Figure 2.1: Location of the study site Ponui Island in relation to the New Zealand mainland. The 200ha core area of the study site is located at the southern part of the island (encircled).

Birds were tracked on foot using Telonics TR4 radio receivers and hand-held three-element Yagi antennae (Kiwitrack Ltd., New Zealand). Diurnal locations of inactive radio-tagged birds were obtained by homing in on the animals (White and Garrott 1990) and recording locations directly as grid coordinates using global positioning units (GPS; Garmin International, Inc., GPSmap 60C). Whenever the global positioning unit was unable to obtain a location fix (due to poor satellite reception under dense canopies), the bearing and the distance from the nearest fixed reference point with known grid coordinates (chapter 3) were recorded. Bearings and distances recorded in the field were converted into grid coordinates. Each radio-tagged adult Kiwi was located once a day, approximately three to four times each month throughout the study period. Once a bird was located I recorded the location and type of roost site used and determined whether they were alone or with other tagged Kiwi by scanning through all active Kiwi radio frequencies. In the cases that birds were not sighted, I was unable to determine the presence of untagged birds. Types of roost sites were broadly categorised as 1) surface roosts: roost sites that were non-stable structures, e.g. roosts under dead plant material, shrubs, marsh planting, and 2) burrow roosts: roost sites that consisted of stable permanent structures, e.g. hollow logs or tree trunks, earth cavities.

Roosting behaviour of tagged birds was investigated over the entire study period and compared between the breeding and the non-breeding season. I used the standard definition of breeding season, defined as ‘the length of time during the year when a particular species can potentially breed’ (Winkler 2001) for the study population; the period covering the mating and the nesting (egg incubation and chick brooding) season, including the inter-clutch period as some birds laid second or replacement clutches (chapter 4). The non-breeding season was the remainder of the time where no breeding activities occurred. In 2005, monitoring commenced during the breeding season (October) and lasted until the last week of December when the last chick permanently left the nest. However, one male initiated a nest in January 2006 and the chick died at point of hatch in March 2006. Since this was the only male found actively nesting late in the season I did not take this nest into consideration for defining the breeding season in 2005. Breeding activities in 2006 started in the second week of May and lasted until the last week of November. In 2007, breeding activities occurred from the first week in June until the last week in January 2008. Since females have not been found to participate in incubation and brood care for the chicks, but males are bound to the nest location during parental duties I only counted the number of roost sites used by males when they were not engaged in parental activities.

Roost switching

To investigate roost switching behaviour for each radio-tagged individual, I divided the total number of tracking days for each bird by the total number of tracking days a bird spent in a particular roost location (tracking days were not necessarily consecutive). Roost switching was calculated only for those birds that were located at least five times in each season. I only included roost locations for which I was able to obtain GPS coordinates to avoid double counting locations. The proportion of observations (location fixes) each bird was found using the two roost types (surface-, burrow roosts) was calculated by dividing the total number of tracking days each bird was located in each roost type by the total number of tracking days for each bird.

Roost sharing

Pair-wise sharing indices (PSI; Willis and Brigham 2004, 2005) between birds that were located simultaneously (same day) were calculated to assess patterns of social associations between individuals. The PSI compares the observed proportion of roost sharing of two individuals (‘dyad’) to an expected proportion of roost sharing of a dyad. The calculation of the expected value takes into account the roost switching behaviour of each Kiwi in the dyad and the number of simultaneous days both individuals were located. PSI scores range from -1 indicating that birds share roost sites less often than expected, increasing to +1 indicating that birds share roost sites more often than expected by chance. PSI scores were calculated for each dyad yielding a symmetrical matrix. PSI scores were derived for the entire study period (overall) and in the case of positive PSI scores of dyads, the PSI was calculated separately for the breeding and the non-breeding season. PSI scores were only calculated when both individuals of a dyad were located simultaneously at least five times in each season (breeding-, non-breeding season).

Further, I examined the total number of individuals using the same roost site, simultaneously and/or sequentially. For this I assessed how many different roost locations each radio-tagged bird used over the entire study period, counting observations of birds in the same location only once. I then counted the total number of males and females that were located at these roost sites. Only roost sites with accurate grid coordinates were considered.

Statistical analysis

All statistical analyses were performed in PASW Statistics 18 (SPSS Inc., Chicago, Illinois, USA) and results were considered significant at $\alpha = 0.05$. Non-parametric tests were used, because variables were not normally distributed (Shapiro-Wilks tests). The frequency of roost switching between males and females in the breeding season and in the non-breeding season was compared using Mann-Whitney *U* tests. To test the difference in the frequency of roost switching in the breeding season compared to the non-breeding season for each sex, Wilcoxon signed-ranks tests were used. Spearman rank correlation was used to assess the relationship of roost switching frequency and the proportion of observations each bird spend in each roost type (burrow roosts vs. surface roosts).

To investigate whether the rate of roost sharing is influenced by the reproductive period of Brown Kiwi, PSI scores of dyads with overall positive PSI scores were compared between the breeding and the non-breeding season using the Wilcoxon signed-rank test. Each PSI score was considered an independent data point as each dyad involved a different combination of individuals and thus represented a unique combination. Proportion and PSI index data are presented as median values with interquartile range (IQR) and count data are given as median values with range (minimum-maximum), unless otherwise stated.

Results

Thirty-six tagged individuals were located 1337 times with an average of 37 (± 19 SD) location counts per individual. The types of roost sites used by Kiwi on Ponui were similar to those of kiwi at other locations (McLennan *et al.* 1987; McLennan 1988; Potter 1989; Taborsky and Taborsky 1995). These ranged from hollow logs, hollow tree trunks, earth cavities and hollows under tree roots and these were categorised as ‘burrow roosts’. ‘Surface roosts’ ranged from roosts under dead plant material, under shrubs or other dense vegetation and under thick marsh plantings.

Roost switching

The rate of roost switching was calculated for 30 of the 36 study birds, including 14 females and 16 males. Six birds were located less than five times and thus roost switching could not be calculated. The number of roost sites used did not differ significantly between the sexes (Mann-Whitney *U*-test: $U = 103$, $P = 0.708$, $n = 30$), with females using a median of 10 (range: 2-19) roost sites and males using a median of 7.5 (range: 2-16) roost sites. Roost switching of females occurred after a median of 2.3 days (range: 1.2-5.7), not significantly different from the median of 1.8 days (range: 1-7.7) by males (Mann-Whitney *U*-test: $U = 111$, $P = 0.967$, $n = 30$). In the breeding season, females switched roosts after a median of 2 days (range: 1.2-4), similar to males who switched roost sites after a median of 1.8 days (range: 1.4-6) (Mann-Whitney *U*-test: $U = 110$, $P = 0.934$, $n = 30$). Likewise, in the non-breeding season, there was no significant difference in the frequency of roost switching between the sexes (females: 1.7 days (range: 1-8), males: 1.9 days (range: 1.1-8.3); Mann-Whitney *U*-test: $U = 106$, $P = 0.803$, $n = 30$). There were also no significant differences in the rate of roost switching between the seasons for females (Wilcoxon signed-ranks test: $Z = -0.031$, $P = 0.988$, $n = 14$) or for males (Wilcoxon signed-ranks test: $Z = -1.25$, $P = 0.229$, $n = 16$).

Birds spent a median proportion of 0.25 (IQR: 0.75) using surface roosts and a median proportion of 0.75 (IQR: 0.72) using burrow roosts. Birds that spent more time using burrow roosts stayed in them for more days before they switched to another roost site compared to birds that used surface roosts which switched roost sites more frequently (Spearman rank correlation: $r_s = 0.908$, $P < 0.001$, $n = 30$, reciprocal relationship to proportion of observations using surface roosts) (Figure 2.2).

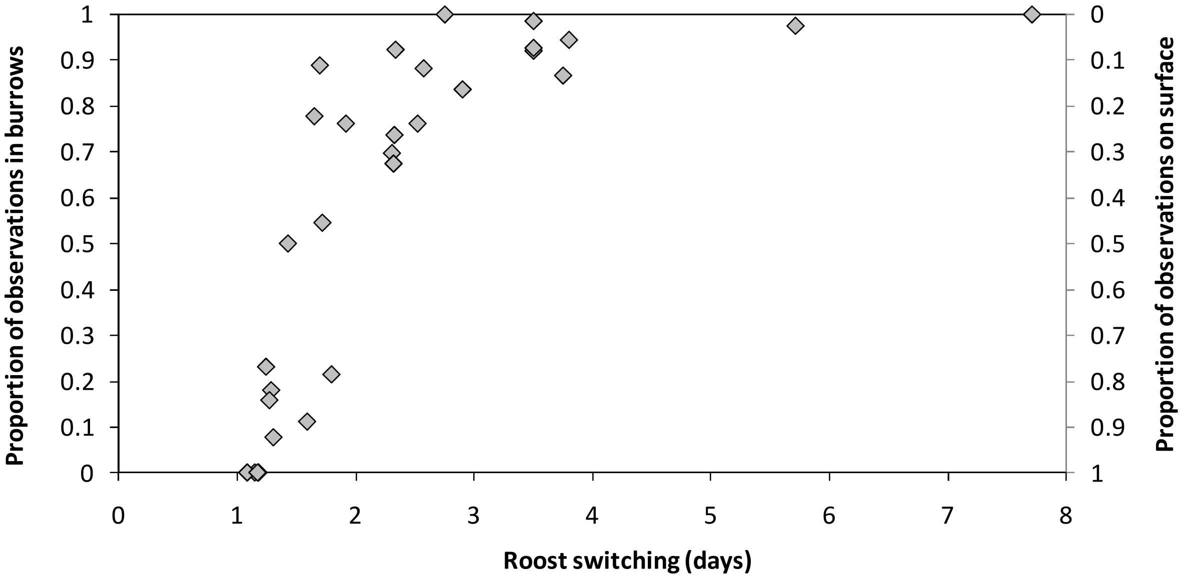


Figure 2.2: Spearman rank correlation presenting the relationship between the rate of roost switching (days) and the proportion of observations birds used burrow roosts or surface roosts for 30 radio-tagged Brown Kiwi on Ponui Island.

Roost sharing

Of a possible 435 dyads (symmetrical PSI matrix), PSI scores could only be calculated for 415 dyads, because the individuals of members of the remaining dyads were not located simultaneously on a minimum of five days. The 415 dyads involved 30 tagged birds, including 14 females and 16 males. Scores varied from -0.91 to 0.73 (median: -0.1, IQR: 0.11).

In only 22 dyads (5%; 22/415) did the two individuals of each dyad roost together at least once during the course of this study. However, this involved 90% (27/30) of all birds, 13 females and 14 males. Nevertheless, only eighteen of all PSI scores (4%; 4/415) were positive, involving 80% (24/30) of birds, 79% (11/14) females and 81% (13/16) males (Table 2.1). Positive PSI scores indicated that these individuals roosted together more often than expected by chance and at least twice during the study period. Median value for positive PSI scores of the 18 dyads was 0.51 (range: 0.02-0.73, IQR: 0.53).

Table 2.1: Categorisation of dyads of radio-tagged Brown Kiwi males (M) and females (F) on Ponui that showed positive pair-wise sharing indices (PSI). STD = number of simultaneous tracking days, TD = number of tracking days members of a dyad were found roosting together.

Dyad no.	Sex ID1	Sex ID2	STD	TD Together	PSI	Roost sharing
1	F1	M1	21	16	0.66	Frequent, Pair1
2	F2	M2	35	20	0.54	Frequent, Pair2
3	F3	M3	19	16	0.73	Frequent, Pair3
4	F4	M4	22	9	0.35	Frequent, Pair4
5	F5	M5	54	35	0.58	Frequent, Pair5
6	F6	M5	14	11	0.53	Frequent, Pair6
7	F7	M6	56	34	0.49	Frequent, Pair7
8	M7	M8	50	29	0.53	Frequent, Trio1
9	F8	M7	62	44	0.67	Frequent, Trio1
10	F8	M8	49	29	0.54	Frequent, Trio1
11	M9	M10	19	8	0.29	Frequent, Trio2
12	F9	M9	15	13	0.65	Frequent, Trio2
13	F9	M10	12	7	0.34	Frequent, Trio2
14	F4	M11	28	2	0.02	Occasional, Pair
15	F10	M12	32	3	0.06	Occasional, Pair
16	F8	F11	38	5	0.08	Occasional, Trio with M7
17	F11	M7	42	4	0.05	Occasional, Trio with F8
18	F10	M13	24	2	0.04	Occasional, Pair

Dyads with positive PSI scores involved combinations of female-male, but also female-female and male-male pairs. Two females had each very high PSI scores with two males. In fact, these individuals were found roosting as a trio on 45% (trio1) and 64% (trio2) of simultaneous tracking days of all three individuals of a trio, respectively. Dyad 14 to 18 showed lower PSI scores compared to dyads 1 to 13, indicating that these individuals did not roost together as frequently as individuals from dyads with high PSI scores (Table 2.1).

PSI scores were then calculated separately for the breeding- and the non-breeding season for dyads that showed positive PSI scores to assess the impact of the reproductive period on the frequency of roost sharing. PSI scores were obtained for 16 of the 18 dyads; one female had less than five simultaneous tracking locations with two males and PSI scores could consequently not be calculated for the two dyads (Figure 2.2). The reproductive period of brown kiwi did not significantly affect the frequency of roost sharing (Wilcoxon signed-ranks test: Z = -0.414, P = 0.679, n = 16) with a median PSI score of 0.4 (range: -0.27-0.71, IQR: 0.59) in the breeding season and a median PSI of 0.2 (range: -0.12-0.71, IQR: 0.5) in the non-breeding season.

While roost switching did not necessarily lead to roost sharing, several tagged birds sequentially used the same roost sites. A minimum of 579 different roost site locations of a total of 36 tagged birds were identified. The median number of birds that used a particular roost site was 1, but at least one roost site was used by a maximum of eight (3 females, 5 males) different kiwi sequentially and another by up to seven (3 females, 4 males). Both of these sequentially used roost sites were spacious, hollow, but solid tree logs.

Individuals of dyads 1-13 were frequently found roosting as pairs or trios over extended periods of time, often covering several kiwi breeding and non-breeding seasons. Some of the first tagged birds were roosting together at the very start of the study (April 2005). These birds appeared to maintain stable social bonds. For several pairs the bond continued during the entire course of the study (2 years 10 months) (Figure 2.3).

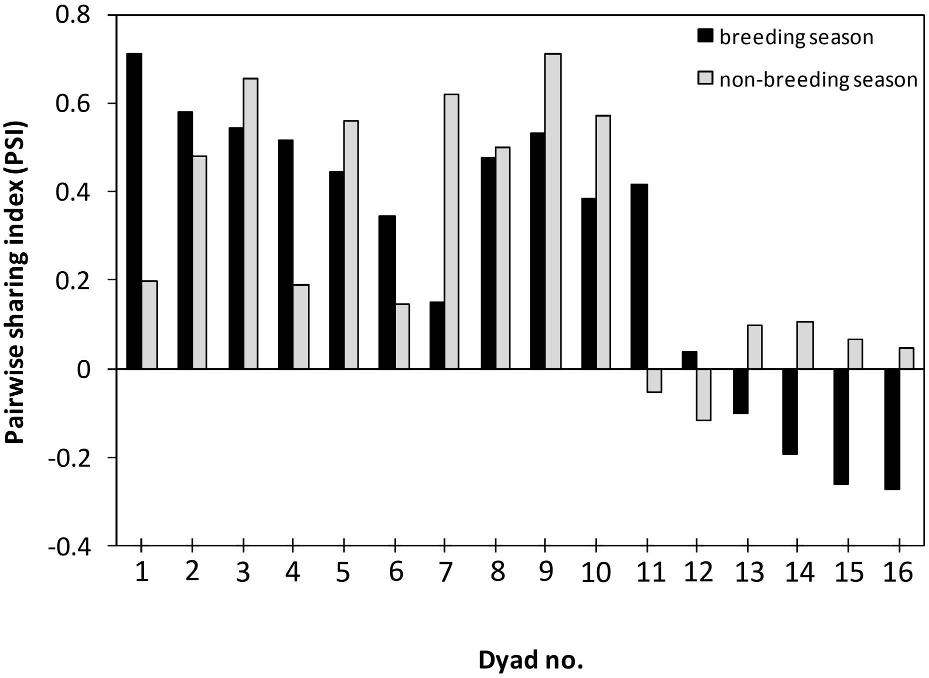


Figure 2.2: Pair-wise sharing indices (PSI) for radio-tagged Brown Kiwi dyads on Ponui with overall positive PSI in the breeding season (black bars) and in the non-breeding season (grey bars).

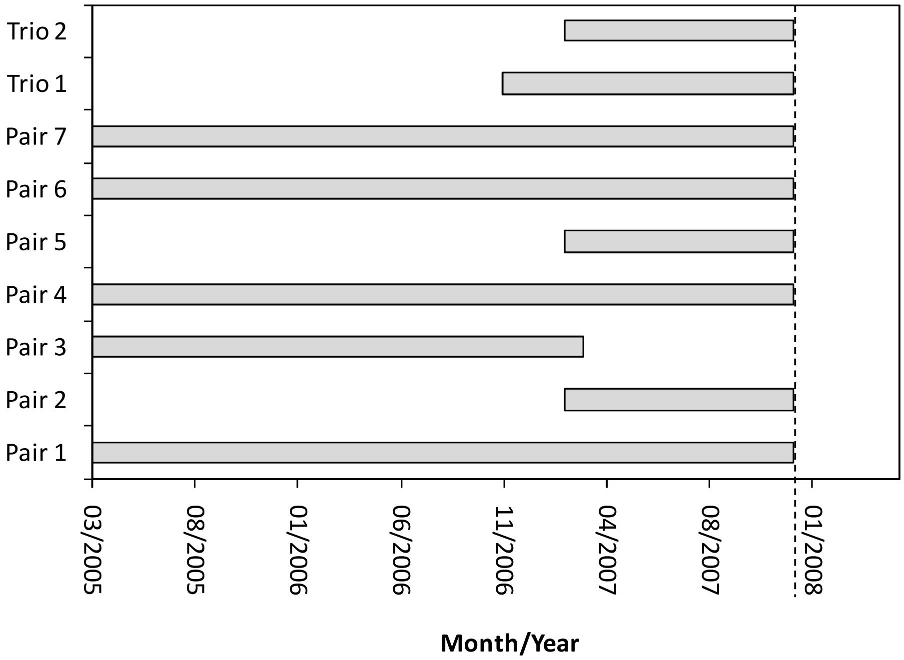


Figure 2.3: Duration of social bonds of radio-tagged Brown Kiwi pairs and trios on Ponui Island based on the long-term frequency of roost sharing; starting from the first time they were found roosting as a group. Dashed line indicates the end of the present study.

Discussion

Roost switching

The majority of tagged Brown Kiwi on Ponui switched roost sites often, moving to a different site about every two days. However, many birds showed loyalty to a number of roost sites that they sequentially used over time. Determining the minimum number of locations (≥ 5 tracking days) per bird can influence the rate of roost switching by restricting the maximum number of roost sites per birds to the minimum number of tracking days of that bird, if the bird switches roosts every day. Nonetheless, there was no evidence that this was the case in this study, because the number of roost sites used by each individual was always lower than the number of tracking days obtained for each individual. In addition, if birds were located on consecutive days using the same roost site, they were ranked with higher roost site fidelity (lower roost switching frequency) compared to birds that used the same roost site, but were intermittently located over the same number of tracking days. But yet, the rate of roost switching calculated here represents a temporal pattern of a sample of radio-tracked birds (Whitehead 1995), because the longer birds are monitored the more novel roost sites they will eventually use as new potential roost sites will emerge (e.g. ground holes through uprooted trees etc., *pers. obs.*) and old roost sites may become unusable (e.g. collapse of ground cavities, flooding of cavities etc., *pers. obs.*).

Studies of roost selection by bats have suggested that roost site fidelity is higher when roost structures are more permanent or rare (e.g. Brigham 1991; Lewis 1995; Weller and Zabel 2001). In fact, most individuals on Ponui that switched roost sites after short periods were roosting more often on the surface, under shrubs, under dead vegetation material or in the swamp (surface roosts). In contrast, birds that used roost sites for longer periods were generally using hollow logs or trunks and natural cavities (burrow roosts). Brown Kiwi are flexible in their use of roost sites (Potter 1989; Taborsky and Taborsky 1995), and on Ponui birds could use the majority of habitats that provide some degree of shelter. However, stable permanent roost structures, such as hollow logs and tree trunks and earth cavities, may provide a preferred microclimate and better protection from harsh weather conditions and daylight. Similarly, Potter (1989) found that intensively used roost sites had common features, such as providing shelter from daylight, weather and from predators, whereas roosts that were not used for extended periods generally provided sparse cover often on the surface. On Ponui, such preferred permanent roost structures may be in short supply as the remaining mature forest is limited to gullies in the forested areas. Large areas of Ponui have been heavily modified for farming and are covered in pasture and/or regenerating forest or shrub.

Frequent roost site switching has also been suggested as a strategy for reducing ectoparasite load in many mammalian species, because such movements can break up the life cycle of ectoparasites (Butler and Roper 1996; Roper *et al.* 2002; Reckardt and Kerth 2007). Ectoparasites can cause severe fitness reduction of their hosts (e.g. Lehmann 1993; Brown *et al.* 1995) and parasite populations can build up quickly inside a roost site. Brown Kiwi on Ponui have been observed to carry heavy loads of ectoparasites, such as ticks, fleas and mites (Castro 2006; *pers. obs.*). Since tagged individuals had multiple roost sites, leaving sites for longer periods of time before returning to the same site might be enough to reduce ectoparasite populations inside the roost site. On the other hand, some roost sites were sequentially used by a minimum of eight different individuals, potentially inhibiting a decrease in ectoparasite numbers inside the roost. The relationship between the degree of roost occupancy and ectoparasite load is a topic that should be explored further in this population.

Roost sharing

Spatial proximity and/or association between individuals are generally considered prerequisites of interactions between such individuals, which over time, can evolve into social relationships or they are important for the maintenance of existent relationships (Smolker *et al.* 1992). Only a few dyads of Brown Kiwi on Ponui showed strong social associations (high positive PSI scores) and the majority of dyads never associated with one another during the course of this study. This indicates that Brown Kiwi selectively chose their roost mates and maintained social bonds with only a small number of conspecifics. Nonetheless, most of the males and females for which PSI scores were obtained, roosted with one or more birds at least once during the study period and some roost sites were used by up to eight different Kiwi sequentially, suggesting overlap of their ranges and a high likelihood of social interactions between these individuals. The majority of roost sharing occurred between female-male pairs, which maintained their bond beyond the breeding season and were found roosting together over extended periods of time. For some pairs the bond lasted the entire duration of this study, nearly three years. This behaviour is typical for a socially monogamous mating system and supports other studies that found that Brown Kiwi live in long-term female-male pair bonds (McLennan 1988; Taborsky and Taborsky 1991). However, I also detected strong social associations between trios (2 males, 1 female). These polyandrous groups maintained long-term associations. Roost site sharing may be crucial for the maintenance of social bonds between individuals and shelters may provide sites for information exchange between pair mates e.g. in terms of the reproductive status of the members of the pair mediated through direct contact or even scent.

Despite some group members occasionally roosting with extra-group individuals, pairs and polyandrous trios exhibited long-term mate retention (long-term social association). Only one potential case of divorce of a pair was detected where the male paired with another female while the first female remained unmated. This is in contrast to Potter's (1989) findings of a pair divorce rate of over 50% in another high-density Brown Kiwi population on the New Zealand mainland. Long-term mate retention can be beneficial especially in long-lived species where the annual and the life time reproductive success are often found to be positively related to the duration of the pair bond (Ens *et al.* 1996; Black 2001). In Brown Kiwi, both sexes can live at least 20 years (McLennan *et al.* 2004). Mate retention may improve breeding success and coordination between pair/group members over a long life span (Mock and Fujioka 1990).

The presence of stable polyandrous trios has not been reported in the Brown Kiwi previously. Nonetheless, most other ratite species exhibit high levels of sociality with both, solitary pairs and groups (Bertram 1980; Handford and Mares 1985; Reboreda and Fernandez 1997; Hough *et al.* 1998). To date, the only kiwi species to have been reported as breeding in pairs, as well as groups, is the Stewart Island Tokoeka (*A. australis*) (Sturmer and Grant 1988; Colbourne 1991, 2002). It has been suggested that Tokoeka groups consist of family members that share territories with helpers that assist in incubation and brood care for the chicks (Colbourne 1991, 2002). However, this is based on partially known pedigrees and genetic analysis of relatedness of Tokoeka group members is lacking. I caught one trio on the northern part of Ponui that consisted of two adult females and one seemingly sub-adult male and confirmed using genetic parentage assessment that the male was the son of one of the females (chapter 5). However, the stability of this trio could not be assessed, because the birds were only caught once and were not radio-tagged for continuous monitoring. Long-term trios and same-sex-roosting pairs in the Ponui population were found not to be composed of close relatives (based on kinship assessment using microsatellite markers; chapter 5). Furthermore, all members of trios on Ponui were of breeding age (adults) based on morphological measurements. In addition, two males of a trio were found to share incubation of a clutch (chapter 4). Thus it is highly likely that trios in the Ponui population are breeding rather than family groups.

The high population density of Brown Kiwi on Ponui could have potentially influenced the formation of trios. At high population densities, more individuals have to share resources which may lead to increased competition for independent breeding and a possible shortage of suitable breeding habitat. Females of trios on Ponui were found to roost more often with one of the trio males (based on a higher PSI score). Therefore, the second male of a trio could be a subordinate male that joined an existing breeding pair because of territory or mate shortages in a saturated high-density population. This scenario has been observed in Bearded Vultures (*Gypaetus barbatus*) where a progressive increase in population density of these typically monogamous birds has led to an increased formation of polyandrous trios with subordinate males joining existing breeding pairs due to habitat saturation (Carrete *et al.* 2006). Ongoing monitoring of the Ponui population after completion of the present study has detected two additional polyandrous trios, yielding a total of four stable trios among the radio-tagged birds (I. Castro, *pers. comm.*). Additionally, the two males of trio2 have also been observed roosting with a different female on several occasions. Thus it seems likely that more trios exist than were detected, partly due to the difficulties of detecting social associations with untagged birds.

Conclusions

Investigating the roosting behaviour of identified radio-tagged Brown Kiwi offered the opportunity to assess direct social associations between individuals that are difficult to confirm for night active kiwi. Examining individually tagged birds over an extended period produced valuable information on the structure and temporal scale of the social organisation in the population. This allowed identification of social relationships such as pairs and trios that were long-term and frequently socially associated. Although the majority of social groups consisted of long-term, socially monogamous male-female pairs and the frequency of social polyandry was low, Brown Kiwi on Ponui exhibit variation of group formation not previously documented for a species considered to live solely in female-male pairs or solitarily and to be highly territorial. In addition, it seems likely that more polyandrous trios exist, but that they went undetected due to the difficulties of determining social associations amongst untagged birds, as well as the relatively low number of tagged birds that data were derived from. In conclusion, the social organisation of Brown Kiwi on Ponui is characterised by long-term socially monogamous pairs and a lower number of polyandrous trios. The high population density of Brown Kiwi on Ponui potentially increases social interactions between birds and may lead to many different social arrangements with an increased potential of a socially polyandrous mating system.

CHAPTER 3

Spacing behaviour of the Brown Kiwi (*Apteryx mantelli*) in a high-density population: implications for the Brown Kiwi mating system

Abstract

Space use patterns of individuals can provide insights into the social and mating system of populations. This study examined seasonal variation of range characteristics and interactions of neighbouring, radio-tagged female and male Brown Kiwi, a species endemic to New Zealand, in one of the few remaining high-density populations. Males decreased their range sizes during the breeding season, possibly due to their duties as sole providers of parental care while females maintained larger ranges in both seasons. Females were predicted to require larger ranges than males due to their larger body size and the high energetic costs of egg production. Male-only parental care may also enable females to seek extra-pair copulations. However, high abundance of additional birds within female and male ranges would not necessarily require females to increase their ranges to seek receptive mates. Socially associated birds (SA; pairs, groups) showed substantial range overlap with an increase in overlap during the breeding season, indicating stable social bonds. Moderate overlap between neighbouring individuals that had no social association with each other (NSA) occurred and was influenced by their sex. NSA males overlapped substantially less with each other compared to NSA males and females, whereas NSA females showed the highest degree of overlap with each other. Nevertheless, spatiotemporal interactions between neighbouring birds were extremely high during both breeding and non-breeding seasons regardless of the sexes of the interacting birds and several additional radio-tagged Kiwi were detected within home ranges of focal birds, indicating underestimation of range overlap. The spatial organisation in this population is characterised by the long-term range sharing of SA birds, indicating high mate fidelity, territorial NSA males and of females that maintain home ranges rather than territories. Due to the high population density associated with a potential increase in social interactions between individuals, and the increase in female ranges during the breeding season, females have a high potential for engaging in extra-pair mating. This study reveals intersexual differences in spacing behaviour in relation to the reproductive period of Kiwi and shows that Kiwi exhibit characteristics of social monogamy with high mate fidelity despite high levels of social interaction.

Introduction

Ecological and social factors such as the distribution and abundance of food, habitat resources, sex ratio, population density as well as the availability of potential mating partners are critical components that shape the social organisation and consequently influence the mating system of a population (Orians 1969; Emlen and Oring 1977; Clutton-Brock 1989a). The impacts of these selective forces are likely to be different for males and females with each sex adopting specific behaviours to ensure survival and maximise reproductive success (Orians 1969; Emlen and Oring 1977; Clutton-Brock 1989a; Reynolds 1996). This sex-based differential response is likely to be reflected by the temporal-spatial distribution of individuals in relation to the distribution, defensibility and competition for resources such as food, suitable habitat and mating partners that are crucial for survival and reproduction.

The home range of an animal is defined as an ‘area used by the individual in its normal activities of food gathering, mating and caring for young’ (Burt 1943) and is distinct from a territory, that is defended and provides the holder(s) with exclusive use of resources (Noble 1939; Maher and Lott 1995). Within a species, home range size and the degree of range overlap can vary with sex as a result of temporal and spatial distribution of resources that influence individual fitness (Armstrong 1991; Maher and Lott 2000; McLoughlin *et al.* 2000; Wauters *et al.* 2005). Range overlap between individuals can additionally provide indirect information about the probability of direct social interactions (e.g. Shier and Randall 2004). Consequently, the location of individuals in space and time can provide considerable insights in the identification and understanding of the social organisation and mating strategies of the sexes. Indeed, spacing systems have been studied to assess social and mating systems of many mammalian (e.g. Gaulin and FitzGerald 1988; Eccard *et al.* 2004; Shier and Randall 2004; Edelman and Koprowski 2006; Blondel *et al.* 2009) and some bird species (e.g. Hingrat *et al.* 2004).

Kiwi (Apterygidae) are a family of flightless birds endemic to New Zealand (Heather and Robertson 2005). All five kiwi species (*Apteryx* spp.) (Burbidge *et* *al.* 2003) have experienced dramatic range contraction and reduction in population size due to habitat destruction and predation from introduced mammals that has resulted in a mosaic of fragmented low-density populations (McLennan *et al.* 1996; McLennan *et al.* 2004; Holzapfel *et al.* 2008). The Brown Kiwi (*A. mantelli*) is the most widespread and numerous kiwi species with a remaining total population of c. 25 000 individuals (Holzapfel *et al.* 2008). Due to the patchy distribution and the wide-ranging, nocturnal and secretive nature of kiwi, it is difficult to obtain reliable data on social behaviours in the wild. Nevertheless, most radio-tracking studies of Brown Kiwi suggest a monogamous mating system with a moderate degree of home range overlap between neighbouring birds (except for pair members) and high territoriality (Colbourne and Kleinpaste 1983; McLennan *et al.* 1987; McLennan 1988; Taborsky and Taborsky 1992, 1999). In these studies, territories were rarely defended by aggressive encounters between birds but rather by long distance calls (Colbourne and Kleinpaste 1983; Taborsky and Taborsky 1992). Social non-aggressive encounters occurred almost exclusively between members of a pair, and pairs remained together on their territories throughout the study period (Taborsky and Taborsky 1992). However, a single study has shown enormous home range overlap of radio-tracked Brown Kiwi, a lack of detectable territoriality, and a high degree of mate switching (Potter 1989). Potter’s (1989) study was carried out on a high-density Brown Kiwi population where resources such as food, suitable breeding habitat, and potential mating partners have to be shared by more individuals. Consequently, it is expected that population density influences the spatial distribution of individuals within such a high-density population. Nonetheless, no studies have investigated the differences in the spacing behaviour of males and females in relation to their reproductive and non-reproductive period. Given our current knowledge of Kiwi biology, in particular their male-only parental care and significant sexual size dimorphism, I predict sex-specific differences in spacing behaviour that both reflect and influence their social and mating system.

In this chapter I investigated the intersexual variation in seasonal (breeding vs. non-breeding season) home range characteristics and spatial-temporal interactions of neighbouring adult Brown Kiwi in relation to their social organisation and mating system. This study focuses on an introduced, translocated Brown Kiwi population at densities indicative of pre-human settlement in New Zealand. At these high population densities I predict that the competition for resources and numerous social interactions between individuals is increased (Møller 1991; Westneat and Sherman 1997; Stewart *et al.* 2010) which will consequently influence the spatial distribution of individuals (e.g. Stradiotto *et al.* 2009).

Methods

Study site and study population

This study was conducted on Ponui Island (Ponui; 36°50'S, 175°10'E) located approximately 16km southeast of Auckland in the Hauraki Gulf, New Zealand. About two thirds of Ponui is in pasture and one third consists of mixed broadleaf forest, Kanuka (*Kunzea ericoides*), and Kauri (*Agathis australis*), interspersed with wetlands (Miles and Castro 2000; Castro 2006). The Ponui population was established from 13 Kiwi introduced to the island in 1964 (Miles and Castro 2000) and is now estimated at a density of 100 birds per km^2 (Cunningham *et al.* 2007). This is in contrast to some mainland Brown Kiwi populations that occur at densities of approximately one bird per km^2 (McLennan *et al.* 1987; McLennan 1988). The study site on Ponui covered approximately 200ha and incorporated three forested catchments, wetland and pasture.

Birds were caught with the help of trained kiwi-tracker dogs. Two-stage radio transmitters (Kiwitrack Ltd., New Zealand) were attached to the tibia of the birds' legs following the technique of Robertson and Colbourne (2003). Each transmitter had a unique radio frequency which allowed individual identification. Radio transmitters were also programmed to change their pulse rate indicating a bird's activity (moving, resting, or dead). Given the nocturnal, forest-dwelling and cryptic habits of kiwi, radio telemetry offered the best methodology available to study their natural spacing behaviour. Sexes of radio-tagged birds were assessed based on morphological differences between males and females (Heather and Robertson 2005) and confirmed by genetic analyses from feather samples (Huynen *et al.* 2002; Equine Parentage and Animal Genetics Services, Palmerston North, NZ).

Radio-tracking

Location fixes (fixes) were obtained from a total of 26 radio-tagged adult Kiwi, including 14 males and 12 females, between February 2007 and February 2008, covering the Kiwi breeding and non-breeding season. Among the 26 radio-tagged birds, 12 focal neighbouring animals (six males and six females) were intensively tracked to allow robust estimates of home range and core area characteristics to be calculated. The 26 Kiwi inhabited an area compromising approximately 100ha within the core area of the study site and were chosen, because they occurred in close proximity to one another, the best scenario to assess spatial and direct social interactions.

I used the standard definition of breeding season, defined as ‘the length of time during the year when a particular species can potentially breed’ (Winkler 2001) for the Ponui Kiwi population: the period covering the mating and the nesting (egg incubation and chick brooding) season, including the inter-clutch period as some birds laid second or replacement clutches (chapter 4). The non-breeding season was defined as the period in which no such activities occurred. On Ponui, Kiwi breeding activities occurred from the first week in June 2007 until the last week in January 2008 (chapter 4), resulting in an 8-month long breeding season and 4-month long non-breeding season. Since Kiwi have an extended breeding season and do not breed in synchrony, it is possible that some individual birds did not breed at all, or only for a fraction of time within the overall breeding season. Thus, in addition to quantifying ranges during the breeding and non-breeding seasons, I also looked at ranges of known nesting birds before, after, and during the nesting event but within the breeding season.

Birds were tracked on foot using Telonics TR4 radio receivers and hand-held three-element Yagi antennae (Kiwitrack Ltd., New Zealand). Nocturnal locations of radio-tagged birds were obtained using a modification of the ‘homing in’ technique (White and Garrott 1990) whereby the direction (bearing) and the distance from the observer to the strongest signal of the radio transmitters were estimated. Here, birds were not tracked to their final location but from a distance determined (c. 40-50m) not to disturb their natural spacing behaviour (*pers. obs.*). Prior to my tracking study, I set up a 20m x 20m grid system with a total of 545 grid points covering the area of forest with dense canopy within the study area. Each point was individually labelled with numerals and letter combinations and with reflective tape to make them visible at night. Grid coordinates were taken for each point during the day using hand-held global positioning units (GPS; Garmin International, Inc., GPSmap 60C) with an extended antenna that reached above the canopy. These reference points were crucial for tracking Kiwi at night when it was impossible to obtain accurate locations using hand-held GPS units due to the poor satellite reception in parts of the forest. All GPS locations were recorded with a location accuracy of 3-8m and I considered them as true locations. Nightly observer locations were recorded by their grid coordinates using a hand-held GPS unit and/or known grid coordinates of fixed reference points within the study site. Bearings and distances recorded in the field were converted into grid coordinates based on the known location coordinates of the observers. If signal reflection made the estimation of the direction of the strongest radio signal impossible, then the location point was discarded. I used the modified homing-in method because a pilot study conducted on radio-tagged Kiwi on Ponui using the alternative triangulation method yielded unreliable results (Castro *et al., unpubl. data*). Here, bearings to the strongest signal could not be correctly identified due to signal bounce within the hilly terrain and dense vegetation. Tracking and following Kiwi in closer proximity to the observer combined with extensive knowledge of the topography of the study area by the observers provided more accurate location estimates (Withey *et al.* 2001).

The social associations (social pairs and groups) between the 12 focal individuals were previously assessed based on the frequency and duration of roost sharing (chapter 2). Among these, I identified two pairs, one trio and one group consisting of two males and two females (quartet). However, members of the quartet were most often found roosting as polyandrous trios with the two males and one of the females and as pairs of same-sex members (chapter 2).

During the period of this tracking study, one female could not be assigned a partner but she had previously been paired to one of the focal males until they divorced and the male repaired with a new female but she appeared to remain alone and not re-mated. Radio tracking of focal animals was carried out in continuous 4-7h shifts over the entire nocturnal activity phase of Brown Kiwi with fixes taken at 5-min intervals. Since the aim was to track animals occurring in close proximity to one another simultaneously during the active period of Kiwi, I chose the short time interval between consecutive fixes and intermittently scanned for all 26 tagged individuals while tracking one focal animal. Diurnal locations of focal birds were determined when possible by precisely locating inactive animals in their daytime shelter and recording locations directly as grid coordinates using global positioning units.

The linear location error of my radio-tracking method which presents the mean distance between estimated and actual locations was assessed by conducting a ‘beacon study’. People with radio-transmitters attached to their ankle (approximate height of transmitters attached to Kiwi legs) were tracked through the study area. Tracked people recorded their locations using either a global positioning unit or fixed reference points with known grid coordinates. The observers tracked the radio-tagged people using the modified homing in technique (described above) with fixes taken every five minutes. This method enabled me to simulate the movement of transmitters that occurs when estimating locations of mobile kiwi. Each observer took an average of 19 fixes and a total of 57 fixes was obtained. The mean linear distance error of the total number of fixes taken by three observers was 52.7m (± 31.1 SD; $n = 57$ fixes) and 31 (54%) of these fixes had location errors < 52.7m. There was no significant difference in the location error between the three observers (one-way analysis of variances (ANOVA): $F_{2, 54} = 2.14$, $P = 0.127$, $n = 57$). The linear location error of sighted Kiwi (visually seen and/or inactive sheltering in burrows) was not quantified; however such locations were certainly more accurate than those obtained by the beacon study. Sheltering birds were precisely located at their exact location. Thus, the beacon study provides valuable information about the accuracy of my tracking system and provides a conservative estimate of the true linear error obtained when tracking Brown Kiwi.

Home range and core area size

Annual range sizes and range sizes during the breeding and the non-breeding seasons of the 12 focal Kiwi were estimated using Ranges 8 software (Kenward *et al.* 2008). Home ranges included the 95% isopleths (hereafter referred to ‘home range’) and core areas included the 50% isopleths (hereafter referred to ‘core area’). In addition, ranges of known nesting birds during the nesting event (‘nesting range’) and after and/or before the nesting event (‘non-nesting range’) but within the breeding season were calculated. Female breeding status is difficult to assess because female Brown Kiwi do not appear to participate in incubation and post-hatch parental care. Therefore nesting- and non-nesting ranges were only calculated for females socially associated to nesting males and their ranges were estimated based on the time of nesting of their mate.

Home range and core areas were calculated with the fixed kernel estimate (Worton 1989) using the least-squares cross validation method to obtain the smoothing parameter and a 40m x 40m matrix resolution. To allow comparisons with previous studies I also calculated the home range and core area sizes using the minimum convex polygon (MCP) (Mohr 1947). In spite of the MCP still being the most frequently used estimator for home range sizes, it suffers from several severe shortcomings (Macdonald *et al.* 1980; Harris *et al.* 1990; Kenward *et al.* 2001; Börger *et al.* 2006). The MCP is based merely on the minimum outline border of location points and can consequently overestimate home range size as it is extremely sensitive to outliers as well as small sample sizes (Macdonald *et al.* 1980; Kenward *et al.* 2001; Börger *et al.* 2006). As an alternative, the non-parametric kernel density estimate provides a more realistic estimate of space use as home range boundaries are calculated based on the utilisation distribution (Worton 1989). The utilisation distribution represents the frequency an animal uses each location within its home range (Worton 1989). Therefore, statistical comparisons were only made on range characteristics derived with the fixed kernel method.

To reduce autocorrelation between fixes only those that were taken at least one hour apart were used for estimating range sizes. The assumption underlying the effects of autocorrelated data on home range estimates is that for a given number of autocorrelated locations less information is available compared to the same number of independently measured locations and hence home range size will be underestimated (Swihart and Slade 1985b, 1985a). Fixes taken one hour apart may not yield complete independence but removing autocorrelation completely will result in the loss of important biological features of an animal's home range (Reynolds and Laundre 1990; De Solla *et al.* 1999; Blundell *et al.* 2001). Indeed, Reynolds and Laundre (1990) and De Solla *et al.* (1999) found that autocorrelated data provided a better estimate of the home range size than independent data points and that kernel density estimates do not require serial independence of fixes. Hence, the accurate estimation of a home range should not be constrained by the assumption of statistical independence, but instead it is advisable to increase the number of observations and using constant time intervals to increase accuracy and precision of the estimate (McNay *et al.* 1994; De Solla *et al.* 1999). I correlated numbers of fixes against range size to determine the degree to which range size estimates were influenced by the number of fixes and therefore differences potentially related to sample biases.

Static and dynamic interactions between individuals

Two different measures of space use sharing between individuals have been defined; static and dynamic interactions (Macdonald *et al.* 1980). Static interactions are the spatial overlap of two (or more) home ranges without reference to time, whereas dynamic interactions measure the temporal association between individuals within the spatial overlap area (direct social interactions between individuals) (Macdonald *et al.* 1980).

Static interactions in terms of the degree of range overlap between neighbouring birds were calculated for home ranges and core areas of 12 focal Kiwi during the breeding and non-breeding season using Ranges 8 (Kenward *et al.* 2008). Within each season the overlapping area of neighbouring ranges was expressed as the proportion of overlap of each individual's range with the range of each of the other focal individuals. This yielded an asymmetrical pair-wise matrix (dyadic data). Several problems are associated with the analysis of spatial overlap; if two individuals (dyad) have zero overlap in their home range, then this dyad either expresses mutual avoidance/territorial defense or they just reside in different parts of the study site; both options result in zero probability of overlap. For the purposes of this study I assumed individuals with zero overlap have exclusive home range and core area use, because all of the 12 focal birds were neighbours. In addition, I determined the number and sex of overlapping individuals and additional tagged Kiwi (*n* = 26) that were detected within each of the 12 home ranges and core areas of focal birds.

Dynamic interactions were then assessed for focal birds that exhibited some degree of home range overlap and for which simultaneous fixes during each of the two seasons were obtained. I calculated Jacobs ‘cohesion’ index (Jacobs 1974) and performed this analysis using Ranges 8 (Kenward *et al.* 2008). The index is obtained by comparing the actual mean distance of simultaneous or near simultaneous (‘same time’) locations for a pair of individuals (dyad) with all possible distances between those two individuals based on all known locations of these two individuals (Kenward *et al.* 2008). Jacob’s index values range from -1 indicating no interactions (negative indices; observed distances were large compared to possible distances) to +1 indicating interactions (positive indices; observed distances were small relative to possible distances) between individuals. Thus a single Jacob’s index value was obtained for each dyad (symmetrical matrix). Indices were calculated for each dyad with range overlap in the breeding and in the non-breeding season. Location fixes taken within 10min of each other were considered as simultaneous.

Statistical analysis

Statistical analyses were performed using R version 2.11.1 (R Core Development Team 2010) and tests were deemed significant at α = 0.05. Results are presented as means ± SD unless otherwise stated. All response variables and model residuals were tested for their normal distribution using probability plots and applying the Shapiro-Wilk test; homogeneity of variances was tested using the Bartlett’s test.

An independent sample *t*-test was performed to assess the mean differences in annual home range and core area sizes of males and females. A repeated-measures ANOVA was performed to determine any effects of sex and season on home range and core are sizes. Statistical inferences about home range and core area sizes during the nesting- and the non-nesting periods could not be justified due to the small sample of birds tracked.

Asymmetrical matrices of range overlap (static interaction) between birds resulted in correlated data (dyadic data). Therefore, the lme4 package (Bates and Maechler 2010) was used to build linear mixed models in R, enabling me to control for the effects of random factors and correlated data. Members of a dyad that had a social association with each other (i.e. pair, trio, and quartet) were referred to as ‘socially associated’ (SA), whereas members of a dyad that had no social association with each other were referred to as ‘non-socially associated’ (NSA). Firstly, the effects of social status (SA vs. NSA) and season (breeding vs. non-breeding) on the degree of home range and core area overlap were examined. Dyad-sex was not included as a factor because the majority of SA birds consisted of male-female (MF) pairs and thus male-male (MM) and female-female (FF) combinations had very small sample sizes. Secondly, it was tested whether dyad-sex (FF vs. MF vs. MM) and season (breeding vs. non-breeding) had an influence on the degree of home range and core area overlap between birds that were non-socially associated (NSA) to each other. Social status, season and dyad-sex were determined as fixed factors, dyad-ID was included as a random factor and the proportion of range overlap was the response variable. Parameter estimates were obtained with restricted maximum likelihood (REML). The non-normal distribution of model residuals resulted in the significance of model terms for the most parsimonious model being obtained by Monte Carlo simulations with 999 permutations. Akaike’s Information Criterion (AIC; Burnham and Anderson 2002) was used to select the most parsimonious model that adequately explained the data. All models under consideration were ranked according to their AIC values from ‘best-fit’ (lowest AIC) to ‘worst-fit’ (highest AIC). AIC differences (ΔAIC) between models are reported to compare the strength by the different models for being the most approximate model. Models with >2 AIC units difference can be considered to have substantial strength over the other models under consideration (Burnham and Anderson 2002).

Results

Home range and core area sizes

Fixes of the 12 focal birds were obtained on average on 29 different dates (± 6, range: 21-40) with a mean of 14 (± 4) different dates during each season. On average, 94 (± 23, range: 67-134) fixes were taken per individual with an average of 44 (± 10, range: 28-61) during the breeding and 50 (± 21, range: 21-87) during the non-breeding season. The majority of locations for each individual were obtained during the active nocturnal period of kiwi with an average of 74 locations (± 21, range: 47-111), whereas the average number of locations obtained for each individual during their non-active diurnal period was 20 (± 4, range: 15-29). I found no correlation between the number of location fixes and the sizes of home ranges and core areas for the annual period, the breeding season, the nesting-range or for the non-nesting range (Spearman rank correlation for all tests: $P > 0.05$). This generally indicates that the number of location fixes obtained per individual was sufficient to estimate range sizes. However, during the non-breeding season the number of location fixes taken and the sizes of home ranges were correlated (Spearman rank correlation: $r_s = 0.84$, $P = 0.001$). Therefore home range comparisons between non-breeding and breeding seasons need to be assessed with caution.

The MCP method generally resulted in larger home range size estimates when compared to the fixed kernel method, especially for annual range size and range size during the non-breeding season. In contrast, seasonal core areas during the breeding season were slightly smaller than those derived using the kernel estimate.

The average size of annual home ranges and core areas of females were slightly larger than those of males, but this difference was not statistically significant (home range: t = -0.712, *d.f.* = 10, P = 0.493, n = 12; core area: t = -0.213, *d.f.* = 10, P = 0.836, n = 12). Seasonal home range and core area sizes of males were smaller during the breeding compared to the non-breeding season. In contrast, female home ranges and core areas were larger during the breeding season compared to the non-breeding season, but there were no significant differences in the average seasonal home range and core area sizes between males and females (home range: $F_{1,10}$ = 0.51, P = 0.492; core area: $F_{1,10}$ = 0.436, P = 0.524) (Table 3.1, Figure 3.1, 3.2). Range sizes during nesting and during the periods before and after nesting, but within the breeding season, could only be calculated for four males and for two females that were socially associated to nesting males. I was unable to confirm breeding status of members of a polyandrous trio and one seemingly unpaired female. Nevertheless, some of the birds classified as non-nesters could have participated in breeding that went undetected during the study, particularly nesting attempts that failed early. Non-nesting birds could also have engaged in extra-pair copulations without providing parental care. Finally, female breeding status is difficult to assess because female brown kiwi do not appear to participate in incubation and post-hatch parental care and could have paired with untagged birds. Ranges for the remaining two females that were each socially associated to breeding males had too few location fixes during the period of the nesting event to obtain reliable estimates of range sizes. Nevertheless, home range and core area sizes of breeding males and females during the nesting period were generally smaller compared to the non-nesting period (Table 3.2). However, this could be biased by the small numbers of location fixes that were obtained for either sex during the nesting-period.

Table 3.1: Home range (95% isopleths) and core area (50% isopleths) sizes (ha) of radio-tagged Brown Kiwi males (M) and females (F) on Ponui Island during the breeding and the non-breeding season and annual ranges estimated using the fixed kernel (KE) and the minimum convex polygon (MCP) methods. Means are given ± SD.

ID	**Sex**	**Total fixes**	**Night fixes**	**Day fixes**	**Annual**				**Breeding season**				**Non-breeding season**			
					KE_95	**KE_50**	**MCP95**	**MCP50**	**KE_95**	**KE_50**	**MCP95**	**MCP50**	**KE_95**	**KE_50**	**MCP95**	**MCP50**
3	M	124	103	21	5.93	2.23	11.88	2.50	4.29	1.50	4.17	1.05	3.98	1.31	12.67	2.27
5	M	72	53	19	2.48	0.75	3.22	1.02	1.75	0.64	2.11	0.66	2.48	0.83	2.71	0.58
12	M	85	69	16	4.43	1.82	4.22	0.94	3.00	1.29	2.44	0.63	3.08	1.18	3.61	1.03
14	M	97	74	23	5.73	1.97	8.87	2.71	3.08	0.85	5.18	0.76	3.96	0.98	9.68	2.77
17	M	67	47	20	5.83	2.36	9.40	1.72	4.36	1.50	3.00	0.48	2.72	0.76	9.55	1.81
26	M	103	83	20	7.50	2.78	20.86	2.02	2.46	0.92	2.79	0.79	5.75	1.39	20.27	6.28
6	F	134	111	23	5.91	2.26	12.48	2.52	3.97	1.67	5.63	0.97	4.71	1.24	12.22	1.15
9	F	75	60	15	3.37	1.25	4.76	1.20	3.01	1.39	3.36	0.82	1.74	0.35	3.88	1.21
15	F	82	64	18	10.40	3.59	13.36	1.79	4.10	1.68	2.78	0.82	3.70	0.95	10.47	1.68
16	F	127	98	29	6.55	1.81	15.26	3.36	10.36	4.08	9.62	2.12	4.46	1.16	17.37	3.24
22	F	92	73	19	6.84	2.31	11.73	2.57	2.38	0.38	7.21	1.12	5.53	1.50	12.78	2.34
25	F	70	50	20	4.06	1.26	20.40	1.49	1.41	0.43	3.28	0.82	2.72	0.78	20.00	2.10
Mean	M	91.33	71.50	19.83	5.32	1.98	9.74	1.82	3.16	1.12	3.28	0.73	3.66	1.08	9.75	2.46
SD	M	21.17	20.39	2.32	1.70	0.69	6.36	0.74	1.02	0.36	1.16	0.19	1.20	0.26	6.42	2.04
Mean	F	96.67	76.00	20.67	6.19	2.08	13.00	2.15	4.20	1.60	5.31	1.11	3.81	1.00	12.79	1.95
SD	F	27.32	23.64	4.84	2.48	0.87	5.09	0.81	3.18	1.35	2.71	0.51	1.39	0.40	5.62	0.79

Table 3.2: Range sizes (ha) of individual radio-tagged Brown Kiwi males (M) and females (M) on Ponui Island during actual nesting event ('nesting range') and non-nesting time ('non-nesting range') within the kiwi breeding season estimated using the fixed kernel (KE) method. Ranges were calculated for the 95% isopleths and the 50% isopleths. Means are given ± SD.

ID	**Sex**	**Social status**	**Period of nesting event**	**Range during nesting event**					**Range during non-nesting event**				
				Total fixes	**Night fixes**	**Day fixes**	**KE95**	**KE50**	**Total fixes**	**Night fixes**	**Day fixes**	**KE95**	**KE50**
5	M	Trio with ID9 (F) and ID26 (M)	07/08/07 – 03/09/07	7	6	1	0.63	0.15	43	35	8	1.79	0.58
12	M	Pair with ID25* (F)	21/11/07-21/01/07	10	9	1	0.32	0.07	31	24	7	3.54	1.59
17	M	Pair with ID15 (F)	18/08/07-31/10/07	10	4	6	2.62	0.97	18	15	3	4.79	1.59
26	M	Trio with ID5 (M) and ID9 (F)	07/08/07 – 03/09/07	11	8	3	0.54	0.25	41	34	7	1.98	0.61
9	F	Trio with ID5 (M) and ID26 (M)	07/08/07 – 03/09/07	6	4	2	0.32	0.1	48	41	7	3.02	1.24
15	F	Pair with ID17 (M)	18/08/07-31/10/07	13	10	3	2.21	0.94	21	18	3	3.26	1.24
Mean	M			9.50	6.75	2.75	1.03	0.36	33.25	27.00	6.25	3.03	1.09
SD	M			1.73	2.22	2.36	1.07	0.41	11.44	9.42	2.22	1.41	0.58
Mean	F			9.50	7.00	2.50	1.27	0.52	34.50	29.50	5.00	3.14	1.24
SD	F			4.95	4.24	0.71	1.34	0.60	19.09	16.26	2.83	0.17	0.00

*not able to calculate range sizes due to small number of location fixes during nesting period

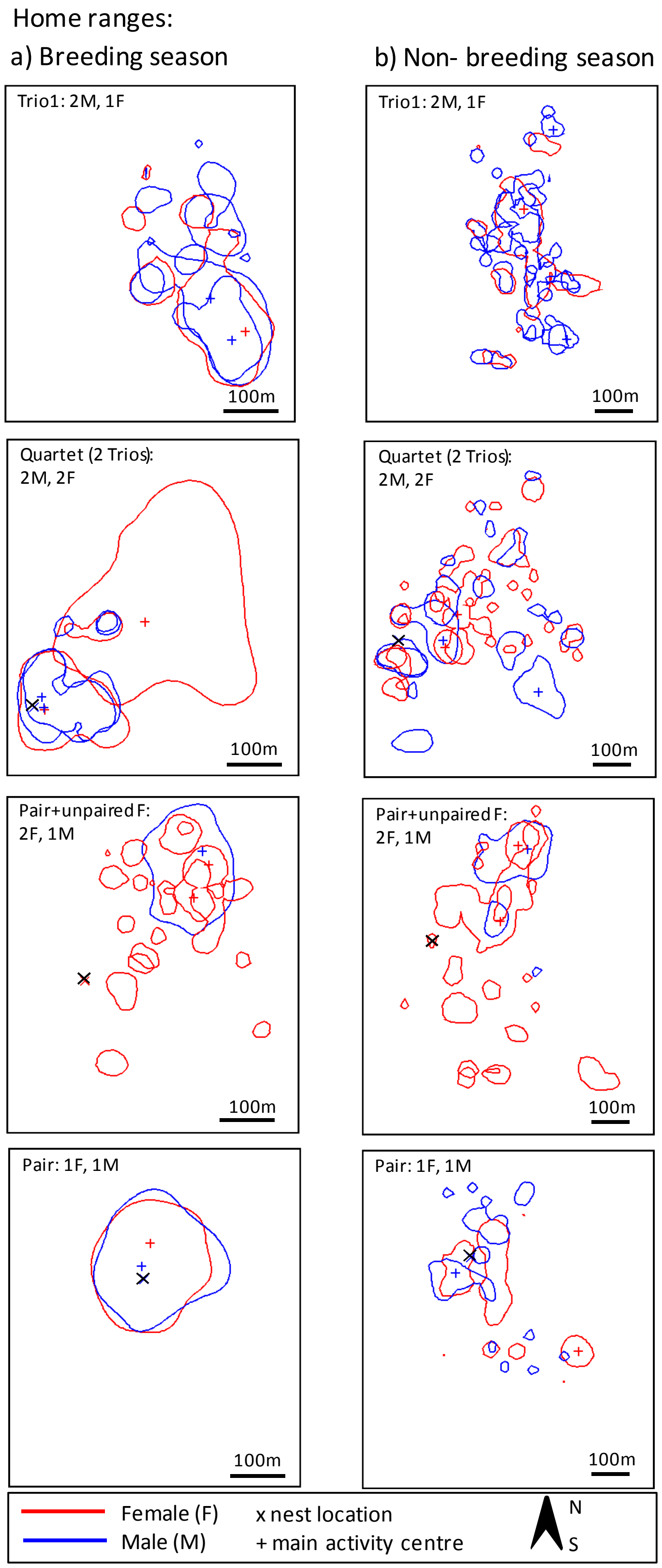


Figure 3.1: Home range (95% isopleths) sizes (ha) and overlap obtained using the fixed kernel methods of radio-tagged brown kiwi males (*n* = 6) and females (*n* = 6) on Ponui Island. a) Home ranges during the breeding season, b) Home ranges during the non-breeding season.

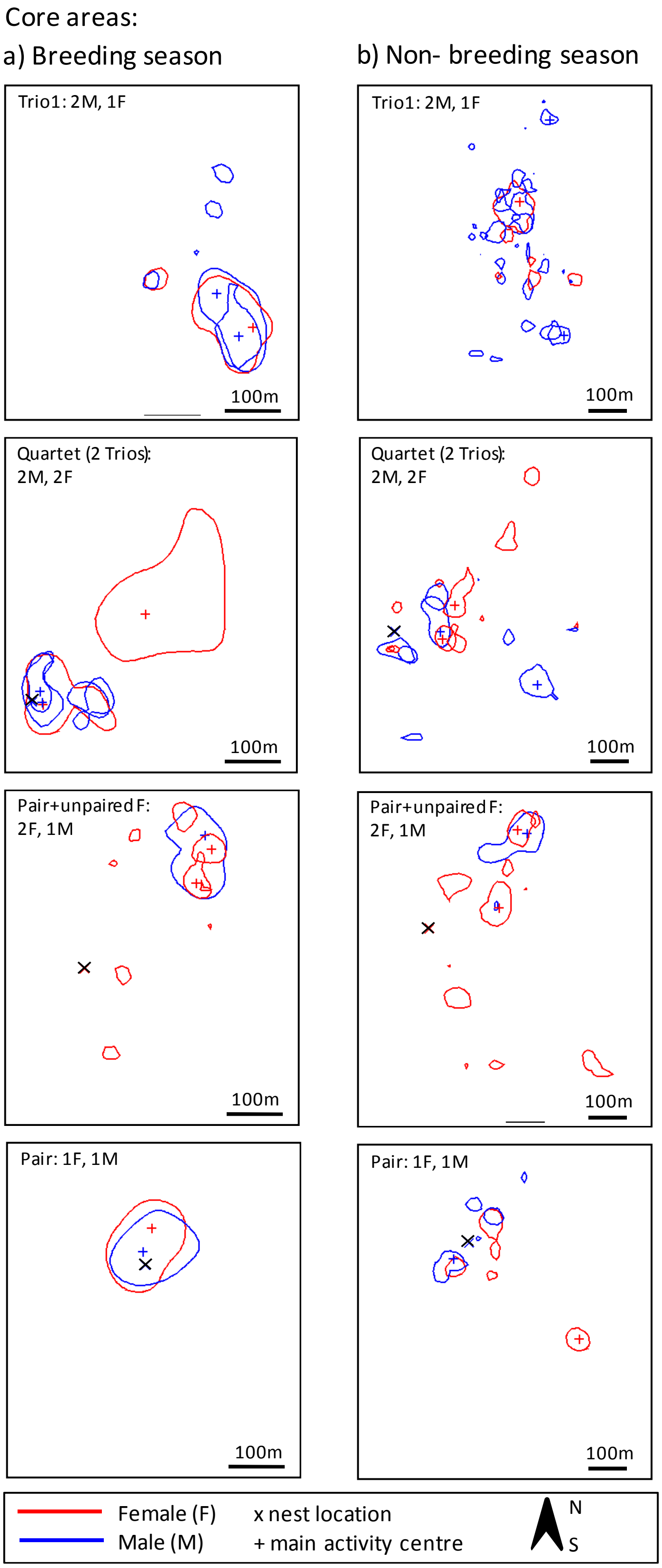


Figure 3.2: Core areas (50% isopleths) sizes (ha) and overlap obtained using the fixed kernel methods of radio-tagged Brown Kiwi males (*n* = 6) and females (*n* = 6) on Ponui Island. a) Core areas during the breeding season, b) Core areas during the non-breeding season.

Static interactions

Asymmetrical matrices of range overlap of neighbouring focal birds for each season resulted in 22 dyads (2 FF, 4 MM, 16 MF) for which members of a dyad were socially associated (SA) and 110 dyads (28 FF, 26 MM and 56 MF) for which members of a dyad were not socially associated (NSA). Results presented here are based on 'best fit' models.

The most parsimonious models for testing the effects of social status and season on home range and core area overlap included the interaction term between these two factors. These models were chosen as they showed lower Akaike's Information Criterion (AIC) values compared to models without the interaction term (core area overlap: ΔAIC = 42.1 units; home range overlap: ΔAIC = 4.7 units). The social status of birds significantly influenced the degree of range overlap. Regardless of season, home ranges and core areas of SA dyads overlapped on average 45.9 ± 26.8% and 35.1 ± 29.8%, respectively. This was substantially more than the average overlap of home ranges (14.8 ± 17.5%) and core areas (3.5 ± 7.6%) of NSA dyads (home range: $t = 8.85$, Monte Carlo $P = 0.002$; core area: $t = 14.87$, Monte Carlo $P = 0.002$). Season did not show a significant effect on the degree of range overlap (home range: $t = -1.21$ Monte Carlo $P = 0.234$; core area: $t = -0.175$ Monte Carlo $P = 0.808$), with an average home range overlap of 13.4 ± 20.9% and core area overlap of 3.1 ± 8.5% during the breeding season, and 11.4 ± 11.6% home range and 2.8 ± 5.2% core area overlap during the non-breeding season. However, season significantly affected the degree of range overlap of SA birds (interaction social status*season); their home ranges overlapped on average 55.3 ± 32.8% during the breeding season and 36.5 ± 14.5% during the non-breeding season ($t = -3.352$, Monte Carlo $P = 0.002$). Core areas of SA birds overlapped on average 48.3 ± 34.6% in the breeding season and 22 ± 15.9% in the non-breeding season ($t = -7.684$, Monte Carlo $P = 0.002$). Season did not have an effect on the degree of range overlap between NSA birds (Figure 3.3).

The majority of SA dyads consisted of male-female combinations and they showed extensive range overlap. However, I further investigated whether range overlap of NSA birds is affected by the sex of the birds (dyad-sex). Here, the most parsimonious model included dyad-sex only as it was already assessed that season did not affect overlap between NSA birds and the best model showed lower AIC values compared to the model including season (core area overlap: ΔAIC = 20.5 units; home range overlap: ΔAIC = 16.5 units). Home ranges of MM dyads overlapped on average 8.8 ± 11.6% which was significantly less compared to the average overlap of MF dyads (14.7 ± 17.4%) and FF dyads (20.6 ± 20.5%) (*t* = -3.017, Monte Carlo *P* = 0.004). Core areas of MM dyads also overlapped on average (1.6 ± 3.2%) significantly less compared to MF (3.2 ± 7.8%) and FF (5.8 ± 9.4%) dyads (*t* = -2.678, Monte Carlo *P* = 0.008) (Figure 3.4).

Home ranges and core areas of individuals, regardless of their social status, were overlapped by at least one other bird during both the breeding and in the non-breeding seasons. It is likely that the estimation of range overlap is an underestimation given that up to 11 radio-tagged individuals were detected within a focal bird's home range. In general, focal female ranges overlapped with more individuals and more individuals were detected within their ranges compared to males (Table 3.3).

Dynamic interactions

Regardless of social status and sex, Jacob's index of dyads of the 12 focal birds that exhibited some degree of range overlap (static interaction) varied from -0.18 to 0.93. During the breeding season 100% of indices were positive and varied from 0.03 to 0.87, indicating that birds were closer together than the expected distances. In the non-breeding season indices ranged from -0.18 to 0.93 with a total of 92.7% of all indices being positive, again indicating close proximity between birds.

Ranges of all SA dyads overlapped extensively and 100% of the Jacob's indices between these birds were positive in both seasons, varying from 0.19 to 0.87 in the breeding season and from 0.41 to 0.93 in the non-breeding season. Likewise, NSA dyads that showed range overlap had 100% positive indices in the breeding season, varying from 0.03 to 0.81 and 90.1% positive indices during the non-breeding season, varying from -0.18 to 0.87.

Table 3.3: Median number and gender of radio-tagged birds with ranges that overlap with other birds (*n* = 12) and the median number and gender of radio-tagged birds (*n* = 26) that were detected within the ranges of the 12 focal birds. N is the number of range owners and median values are given with the range in parenthesis.

Season/sex of range owner	***n***	**Number of overlapping birds (min-max)**				**Number of birds detected (min-max)**			
		Home range		**Core area**		**Home range**		**Core area**	
		M	**F**	**M**	**F**	**M**	**F**	**M**	**F**
Breeding									
Males	6	3 (1-3)	5 (3-5)	1 (1-2)	2 (2-4)	5.5 (1–7)	8 (3–10)	4 (1-5)	4.5 (1 -6)
Females	6	4.5 (2-6)	4 (2-5)	2 (2-4)	1.5 (1-4)	7 (3–10)	7.5 (2–10)	4.5 (2–10)	4.5 (1–10)
Non-breeding									
Males	6	4 (1-5)	5 (4-6)	3 (1-4)	4.5 (3-5)	9 (2–11)	8.5 (4–11)	4 (2–9)	7 (4–8)
Females	6	5.5 (3-6)	4.5 (3-5)	4.5 (2-6)	3 (2-5)	9.5 (2–11)	8 (3–10)	7.5 (2–10)	5.5 (3–7)

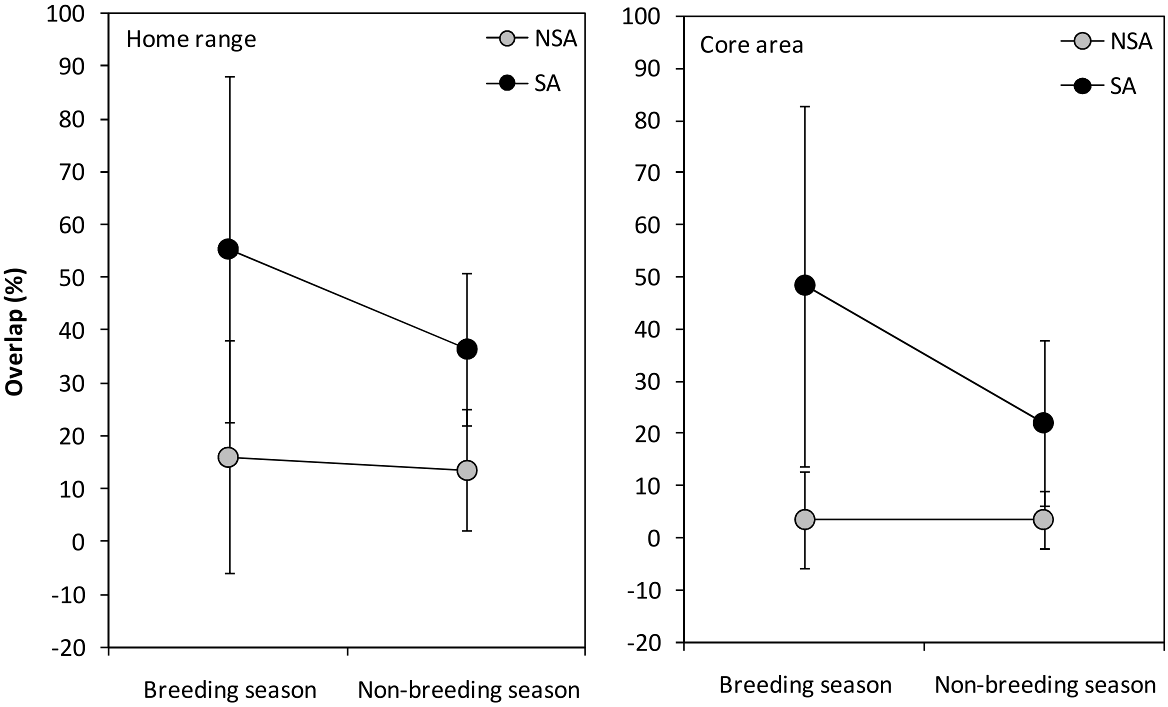


Figure 3.3: Mean percentage of home range and core area overlap of SA dyads (*n* = 22) and NSA dyads (*n* = 110) in the breeding and the non-breeding season. Means are given ± SD.

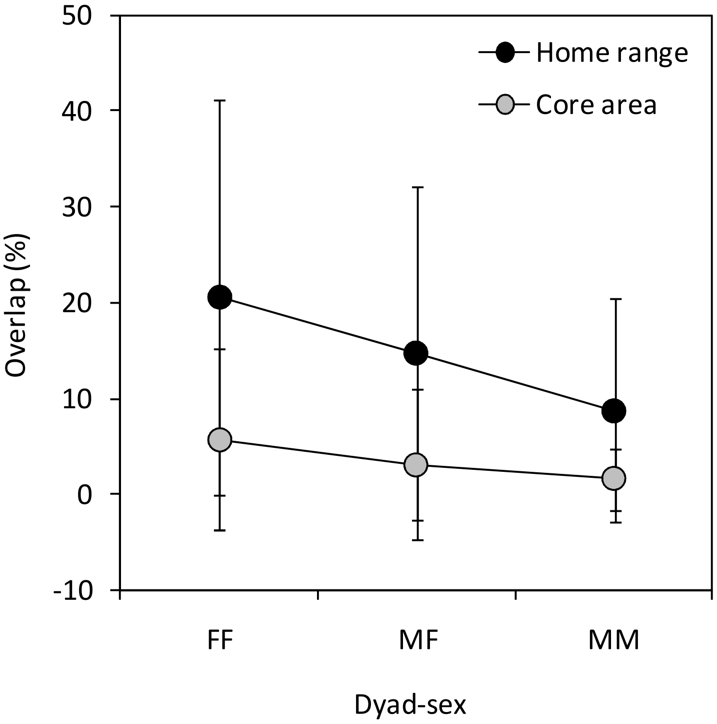


Figure 3.4: Mean percentage of home range and core area overlap of NSA dyads in relation to their sex (FF: *n* = 28, MF: *n* = 56, MM: *n* = 26). Means are given ± SD.

Discussion

The ‘homing in’ technique to track Brown Kiwi on Ponui was preferred to conventional methods such as triangulation to obtain reliable location fixes of radio-tagged birds due to the hilly terrain, dense vegetation in some areas and the narrow gullies in the forest of the study site. However, it also bears the disadvantages of being extremely costly in terms of labour and time due to tracking only one focal bird at any given time. Clearly, this resulted in the small sample sizes of male and female Brown Kiwi for which home ranges and core area characteristics could be estimated. General inferences about female and male Brown Kiwi range characteristics were drawn from a relatively small pool of tracked birds which may represent only a fraction of the birds inhabiting the 100ha area in which the tracking study was carried out. Nonetheless, the home range data presented here are based on large numbers of location fixes per individual (except for nesting- and non-nesting ranges) collected over many different days/nights and thus yield robust estimates of Brown Kiwi range sizes that almost certainly reflect the movement of Kiwi. Kernel estimators were chosen as they are likely to yield a realistic picture of Brown Kiwi space use because they are based on the utilization distribution that describes the frequency an animal uses locations within its home range over time (Worton 1989) and can therefore identify areas of greater use. In addition, kernel density estimators are less sensitive to autocorrelated data than other home range estimators (Swihart and Slade 1997).

Animals that have established home ranges usually move through them in a non-random way (De Solla *et al.* 1999; Powell 2000), most likely due to extensive knowledge of the features within the home range and the repeated use of certain areas (e.g. feeding sites, roost sites) and hence, no location is biologically independent (Blundell *et al.* 2001). Indeed, it has been shown that removing autocorrelation and moving towards independent locations will result in the loss of important biological features of an animal’s home range (De Solla *et al.* 1999) and even in the loss of critical information about reproductive strategies (Blundell *et al.* 2001). Furthermore, De Solla *et al.* (1999) suggest that short total sampling intervals but with independent locations potentially result in the underestimation of home ranges (Swihart and Slade 1985a), because short sampling intervals provide less information about space use. Therefore, I opted to collect locations of individuals that are not completely independent but were collected over many different tracking nights and days as not to miss important information of Kiwi spacing behaviour.

Male and female Kiwi home range size

Although not conclusive, the non-significant differences in range sizes between the sexes could be a result of the small sample size of tracked birds. Nevertheless, on Ponui female Kiwi have slightly larger home ranges and core areas during the breeding season compared to the non-breeding season and compared to males. Previous studies on Brown Kiwi home ranges also conclude that female ranges were larger than those of males (McLennan *et al.* 1987; Potter 1989; Taborsky and Taborsky 1992), although these studies did not distinguish between the breeding and non-breeding season. There are two possible explanations for the relative difference in annual and seasonal range sizes between males and females: the limitation of receptive and suitable mates or food. Female Brown Kiwi do not appear to participate in incubation and brood care (McLennan 1988; Colbourne 2002), enabling them to increase their home ranges during the breeding season to increase social contacts with males and engage in alternative mating strategies and thereby maximise their reproductive output (Emlen and Oring 1977). Breeding males, however, are bound to the nest area for one of the longest incubation periods known among birds (c. 74-84 days; Calder *et al.* 1978) and only leave the nest for a few hours (McLennan 1988, Colbourne 2002), consequently inhabiting smaller ranges during the breeding season and over the entire year. Indeed, home ranges and core areas of nesting males are substantially smaller than their ranges prior to or after the nesting event within the breeding season. Unfortunately this could be biased due to the lower number of location fixes that were obtained from birds during nesting, due to the short and irregular time intervals (*pers. obs.*) that nesting males leave the nest at night, and more data are required to confirm this result. Incubating males may only be available for females that seek extra-pair copulations for very brief periods during the night and such periods when the males are off their nests are likely to be used for foraging to regain energy expenses during the long incubation period. However, Brown Kiwi breed asynchronously, which may allow females to seek non-nesting extra-pair receptive males, entailing that they have to range further. Alternatively, females may benefit from enlarging their ranges to increase encounters with males and to obtain extra-pair copulations. Although the function of extra-pair copulation that results in extra-pair paternity is still unclear, it has been suggested that females may gain genetic benefits when selecting genetically compatible fathers for their offspring (Spottiswoode and Møller 2004; Griffith and Immler 2009). Nonetheless, considering the high population density of Brown Kiwi on Ponui Island and the detection of additional radio-tagged males within female ranges may not necessarily require females to range further to engage in alternative mating strategies. Potential mates may be available to females freed from parental duties even within their core areas.

A second possibility is that female Brown Kiwi require larger areas than males due to their larger body size. Although changes in the productivity of habitats influence body weight, the size of a home range also correlates with body weight (Harestad and Bunnel 1979), i.e. the larger the body size the larger the range, and is most likely due to the increased food requirement of larger body size. Female Brown Kiwi are up to 20% larger than males (Colbourne and Kleinpaste 1983; Taborsky and Taborsky 1991) and have to be in good physical condition for producing the disproportionally large and extremely energy-rich egg (Reid 1971b, 1971a; Calder *et al.* 1978; Calder 1979). In contrast, in the non-breeding season, the energetic demands imposed on females are much lower possibly resulting in slightly smaller ranges during this time. The constraints for breeding males are likely to cause a trade-off between occupying a large home range with better food resources and providing the parental care (nest attendance) necessary for successful reproduction.

It remains inconclusive whether females have larger ranges because of their freedom from parental duties and their ability to engage in alternative mating, or because of higher energetic demands, or a combination of both. Further research on the energetic demands by females and males during the breeding and during non-breeding period, and the seasonal availability and distribution of food resources is thus needed. Further research is also required to assess the availability of suitable receptive mates to females and whether this results in larger female ranges despite the high population density. Even at high population densities the operational sex ratio may be female biased as receptive males may not be readily available due to nesting asynchrony and the demography of the population.

Interactions between individuals

Neighbouring Kiwi on Ponui that were socially associated (SA) exhibited a substantial degree of home range and core area overlap in both seasons, indicating the long-term stability of pair or group bonds beyond the reproductive period. SA birds overlapped to a greater extend in the breeding season compared to the non-breeding season, possibly due to coordinated breeding activities. Indeed, I found two males of a socially polyandrous trio cooperatively attending a nest (chapter 4), which resulted in a high degree of range overlap between these two males. In addition, females socially paired to breeding males were often located close to the nest before the male emerged from the nest at night (*pers. obs.*). In contrast, neighbouring NSA birds exhibited range overlaps to a much lesser extend compared to SA birds in both seasons regardless of their sex. Core areas of NSA birds only overlapped to a very low degree, potentially indicating avoidance behaviour within this area. Yet, range overlap on Ponui may be largely underestimated because inferences of range overlap are based on only 12 radio-tagged Kiwi and not all birds within the study area were radio-tagged. Some individuals may be floaters, but the shape and expansion of their home range could not be confirmed. Nevertheless, this scenario increases the likelihood of social interactions, the existence of more breeding groups than reported here (formed solely by untagged birds or by untagged birds with tagged birds not detected in this study) and the potential for seeking extra-pair copulations.

Despite range overlap being an indication of space sharing between individuals, it does not necessarily mean that individuals with overlapping ranges directly encounter each other (Kernohan *et al.* 2001). Therefore, incorporating dynamic interactions (temporal) showed that Kiwi on Ponui with range overlap, regardless of their social status or sex, were in close proximity indicating direct interactions (positive Jacob's indices). This suggests that range overlap (static interaction) can be used as a proxy for direct interactions between birds on Ponui. In fact, extensive direct interactions were detected between NSA birds with overlapping home ranges in the breeding season (100% positive indices) as well as in the non-breeding season (92.7% positive indices). Thus, despite some birds overlap with their home range to a small extent, they still appear to interact with each other within the overlap zone.

Previous studies have suggested that Brown Kiwi are highly territorial, unless birds are socially associated (Colbourne and Kleinpaste 1983, McLennan *et al.* 1987, Taborsky and Taborsky 1992). On Ponui, the lowest degree of range overlap was evident between neighbouring NSA Kiwi males during both seasons. In the breeding season, this may be because males have smaller ranges due to their parental duties or because they are the more territorial sex resulting in less overlap in either season. In contrast, ranges of neighbouring NSA females overlapped to a much greater extent and with slightly more individuals in both seasons. Indeed, a higher degree of range overlap between females has been found in other populations (Taborsky and Taborsky 1992, 1999). It appears that female Brown Kiwi are less territorial compared to males and it is possible that males maintain territories while females have home ranges considering the differences in range overlap with other birds.

Such differences in the degree of range overlap of individuals may be in response to environmental factors. For example, food abundance has been suggested to have a strong effect on the degree of range overlap and territoriality and their associated costs and benefits (e.g. Carpenter and MacMillen 1976; Armstrong 1991; Maher and Lott 2000). However, whereas most emphasis has been on food as a governing factor in the spatial behaviour of animals, other additional factors, such as the availability of nest- and/or shelter sites and population density (Newton 1994; Schradin and Pillay 2005; Schradin *et al.* 2010) and the associated dispersion of potential mating partners, can have a strong influence on the spatial organisation of populations (Butchart *et al.* 1999). This is arguably the case in the Ponui Kiwi population. A small founder population of Brown Kiwi (n = 13) were introduced to Ponui in 1964 and they have experienced rapid population growth since then (Miles and Castro 2000). This growth has now levelled off and the population is assumed to be near carrying capacity with estimates of at least 100 birds per km^2 (Cunningham *et al.* 2007). In a closed island ecosystem, largely modified for farming, it is expect that key resources may become limited. An increased pressure of neighbouring birds due to high population density may result in reduced mobility within smaller, less overlapping ranges (Butchart *et al.* 1999) of males and an increase of male territoriality. Males may become increasingly territorial during the reproductive period, possibly to assure paternity through mate guarding and defending intruders. This might be especially important for Brown Kiwi males that provide the sole parental care with an extremely long incubation period (Calder *et al.* 1978). Indeed, at least one socially paired female on Ponui has been shown to engage in extra-pair copulations (chapter 5).

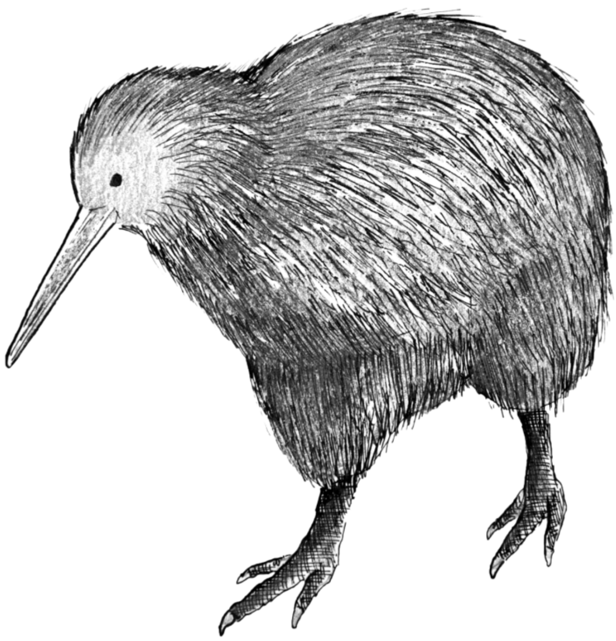
The effects of high population density on space use patterns can be corroborated with findings of previous radio-tracking studies on Kiwi. Although these studies used slightly different methods to estimate home range sizes, the high population size on Ponui is predicted to generally result in smaller, overlapping home ranges compared to other Brown Kiwi populations (McLennan *et al*. 1987). For example, in a low-density Kiwi population (c. four adult Kiwi per km^2), home ranges were fourfold larger than on Ponui with little or no overlap of neighbouring birds and pairs showed high territoriality (McLennan *et al.* 1987, McLennan 1988). In contrast, smaller home ranges, greater degrees of range overlap, and the detection of floaters were found in two high-density populations (Potter 1989; Taborsky and Taborsky 1992).

In summary, female and male Brown Kiwi on Ponui exhibited differences in their ranging patterns, potentially but not conclusively in response to sex-specific requirements in terms of reproduction including parental care and energetic demands. In addition, their spacing behaviour may be influenced by the high population density as density may govern an increase in social interactions and competition for limiting resources.

I suggest that social pairs and groups (trios and quartet) exhibit social monogamy (social polyandry for trios), considering the long-term extensive range sharing and frequent spatiotemporal interactions that are typical for such a mating system. However, given the presence of the sexual size dimorphism, male-only parental care combined with the observed seasonal differences in spacing patterns between the sexes, females have a high potential of engaging in alternative mating strategies, while males appear to be the more territorial sex and are restricted by the amount of parental care required for successful reproduction.

CHAPTER 4

Nesting success and breeding ecology in a high-density population of Brown Kiwi (*Apteryx mantelli*)



Abstract

Brown Kiwi (*Apteryx mantelli*) is a species in serious decline despite immense conservation efforts. Fundamental information on Kiwi breeding is scarce, in part due to their low-density populations and nocturnal habits. Here I report on the nesting success and breeding ecology of one of New Zealand's remaining high-density Brown Kiwi populations present on Ponui Island, over three breeding seasons. Nesting success was high (47%) compared to other Brown Kiwi populations and 85% of all failures occurred during incubation. In contrast, fledging success was very high (89%). The majority of clutches were one-egg clutches (69%) with second and replacement clutches being rare. Male nest site fidelity was high and reused nest burrows hatched significantly more chicks than burrows not previously used. In addition, two cases of nest usurpation and one of cooperative breeding were observed. I conclude that competition for resources associated with high population density result in reduced clutch size, reuse of nests and nest usurpation and that such life history impacts are particularly relevant for species, such as kiwi, with high energetic demands for breeding. Finally, given that the density of Kiwi on Ponui is indicative of pre-human New Zealand, this study provides a significant insight into Brown Kiwi breeding ecology that is not possible in declining low-density populations. Indeed, this study reveals that aspects of Brown Kiwi life history are more flexible than previously assumed and vary significantly with ecological conditions.

Introduction

A detailed understanding of the breeding behaviour and social organisation of threatened species is fundamental to their successful conservation, but such information is often scarce or even unknown prior to their endangerment. Such is the case for the Brown Kiwi (*Apteryx mantelli*), one of five kiwi species endemic to New Zealand that is in serious decline (Holzapfel *et al.* 2008). Most Kiwi populations have suffered significant losses since human arrival in New Zealand, due to human-induced habitat destruction and predation from introduced mammals (Taborsky 1988; McLennan *et al.* 1996; McLennan *et al.*

2004). Whereas the factors responsible for these declines are well understood, the nesting success and breeding behaviour of kiwi are not. This scarcity of knowledge is partially due to kiwi being nocturnal, wide-ranging birds and often in remnant low-density populations.

Only two other published studies (McLennan 1988; Potter 1989) provide detailed information on nesting success and behaviour of wild Brown Kiwi. Potter (1989) investigated a high-density (c. 40 birds per km^2) mainland population (18 pairs) in Paerata Wildlife Management Reserve, Northland, New Zealand. This population persisted in the presence of introduced predators such as ferrets (*Mustela furo*), feral cats (*Felis catus*) and possums (*Trichosurus vulpecula*). In contrast, McLennan (1988) studied a low-density Brown Kiwi population (c. 1 bird per km^2; McLennan *et al.* 1987; McLennan 1988), a mainland site on the East Coast of New Zealand's North Island. Introduced predators (possums, feral cats and stoats (*Mustela erminea*)) were also present at this study site (McLennan *et al.* 1987).

Brown Kiwi usually nest in newly excavated cavities or modify natural burrows, such as hollow logs or holes (Calder 1979; McLennan *et al.* 1987). They generally breed in the austral winter with a peak egg-laying period from mid winter to mid spring (Potter 1989; Potter and Cockrem 1992), and lay one or two clutches per breeding season consisting of one to two eggs. However, Brown Kiwi females are physically capable of laying up to seven eggs within a season (Colbourne 2002). The eggs are amongst the largest in comparison to the females' body mass known for birds (Reid 1971b; Calder *et al.* 1978). The Brown Kiwi males provide all parental care following egg-laying and the incubation period is typically between 74 to 84 days; one of the longest among birds (Reid and Williams 1975; Calder *et al.* 1978). The precocial chick is nourished by the energy-rich yolk for the first few days after hatching (Reid 1971b; Calder *et al.* 1978; Calder 1979) and the male parent leaves soon after (McLennan 1988). It is still not known whether Brown Kiwi chicks are fed by their parents (McLennan 1988).

In this chapter, I present data on the nesting success and breeding ecology of Brown Kiwi in one of the few remaining high-density populations in New Zealand. This population provides an opportunity for comparisons with other Kiwi populations and to understand nesting ecology of a large population of Kiwi at densities indicative of pre-human New Zealand.

Methods

Study site and study population

This study was conducted on Ponui Island (Ponui; 36°50’S, 175°10’E) located approximately 16km southeast of Auckland in the Hauraki Gulf, New Zealand (Figure 2.1 in chapter 2). About two thirds of Ponui is in pasture and one third consists of mixed broadleaf forest, Kanuka (*Kunzea ericoides*), and Kauri (*Agathis australis*), interspersed with wetlands (Miles and Castro 2000; Castro 2006). The Ponui population was established from 13 Brown Kiwi introduced to the island in 1964 (Miles and Castro 2000), and is now estimated at a density of 100 birds per km^2 (Cunningham *et al.* 2007). The study site on Ponui covered approximately 200ha and incorporated three forested catchments, wetland and pasture.

Sampling methods

Birds were caught with the help of trained kiwi-tracker dogs. Two-stage radio transmitters with unique radio frequencies were attached to the tibia of birds following Robertson and Colbourne (2003). Radio transmitters were also programmed to change their pulse rate indicating a bird’s activity (moving, resting, or dead). Fifty-seven Kiwi (25 females, 29 males, 3 chicks) were fitted with radio-transmitters (Kiwi Track Ltd., New Zealand) from April 2005 to March 2008. The number of tagged birds fluctuated between years due to transmitter failures, deaths, births, and newly tagged birds. Breeding data were collected from 14 adult females and 20 adult males. Radio-telemetry offered the best low invasive method for studying their nocturnal and cryptic behaviour (S.J. Cunningham and I.C. Castro, *unpub.data*). Sexes of radio-tagged birds were assessed based on morphological differences between males and females (Heather and Robertson 2005) and confirmed by genetic analyses from feather samples (Huynen *et al.* 2002; Equine Parentage and Animal Genetics Services, Palmerston North, NZ).

All radio-tagged adult Kiwi were located approximately four times a month using a TR4 Telonics radio-receiver and a Yagi aerial (Kiwi Track Ltd., New Zealand). Males were considered to be non-breeding if they were never observed roosting with a mate or inside a nest containing an egg. Breeding status of females could not be confirmed, as they do not incubate or brood. Burrows found during daytime searches were classified as potential nests if they were an established burrow with an entrance concealed with vegetation (McLennan 1988). Additionally, when males were found alone within a suitable burrow it was assumed that they were nesting. To avoid causing nest abandonment by incubating males, such nests were later checked at night when radio-tagged males were detected as absent from the nest. Active nests were confirmed when eggs were confirmed as present. Active nests were checked approximately twice a week for the daytime presence of the incubating tagged male. Nightly nest-checks varied for each male, but nests were generally checked once every two weeks. Total monthly rainfall (mm) and average monthly air temperature (°C) were obtained for the 2006 and 2007 breeding seasons from the National Climate Database (CliFo: the National Institute of Water and Atmospheric Research’s National Climate Database, see http://clifo.niwa.co.nz, accessed 17 February 2009). Weather data were used from the nearest weather station on Waiheke Island (36° 48’ S, 175° 06’ E), c. 12km north-west of the study site on Ponui Island.

The age and development of embryos was quantified by ‘candling’ (Lokemoen and Koford 1996; Bassett 2006). A few nest cavities were too deep to safely remove eggs and the egg-laying dates for those nests were calculated by backdating from observed hatching dates. Dead eggs were retrieved from the nest after male desertion and a necropsy was conducted to determine embryo age.

Statistical Analysis

Nesting success

Stanley's model (2000) was used to calculate, 1) nesting success as the probability of a nest surviving from the onset of incubation to fledging (when Kiwi chicks leave the nest permanently), 2) hatching success as the probability of a nest surviving from incubation to hatching, and 3) fledging success as the probability of a nest surviving from nestling to fledging. Each measure was calculated for the 2006 season, the 2007 season and overall (2005, 2006, 2007 pooled). Partial nesting information for the 2005 breeding season resulted in small sample sizes (*n* = 5 nests) and I did not use Stanley's model for this season. Stanley's model enables estimation of stage-specific daily survival probabilities without making assumptions about the exact transition period between nest stages, and allows for varying intervals between nest checks (Stanley 2000).

Stanley's programme (http://www.esapubs.org/archive/ecol/E081/021/default.htm) was run using the NLIN procedure in SAS 9.1 software (SAS Institute Inc., Cary, NC, USA). All nests were found during the incubation stage so that survival probability during egg-laying was not calculated and the programme was appropriately modified (Armstrong *et al.* 2002). Median durations of 78 days for incubation and 23 days for nestling stage were used in the model and derived from this study. The delta method (Seber 1982) was used to calculate the approximate standard error for the total survival probability of a nest and ninety-five percent confidence intervals were calculated after Burnham *et al.* (1987).

Finally, apparent nesting success was calculated as the proportion of nests that produced at least one fledgling for comparison to other studies (McLennan 1988; Potter 1989). I also calculated breeding parameters derived from the total number of nests found and the total number of eggs laid and refer to these as 'apparent success' estimates. Hatching success was the number of hatchlings per total number of eggs laid, apparent fledging success was the number of fledged chicks per total number of hatchlings, and apparent breeding success was the number of fledglings per total number of eggs laid.

Clutch size

Average clutch sizes were calculated for each breeding season and clutch sizes (1-egg- vs. 2-egg clutches) were compared between seasons using a G-test calculated in Excel (Microsoft Office 2007).

Nest site fidelity

Nest success in relation to nest reuse was compared using a Fisher's exact test performed in SPSS v. 16 (SPSS Inc., Chicago, Illinois, USA). In this analysis, only clutches (first, second, replacement clutches) from males that bred for at least two seasons were included. A clutch was considered successful if it produced at least one offspring.

All statistical analyses were considered significant at $\alpha = 0.05$. Results are presented as means ± SE, unless otherwise stated.

Results

Breeding season

Twenty-six clutches were found between 2005 and 2007. I had no data for the exact laying period in 2005, but egg-laying lasted 157 days in 2006 (from the first week in June) and 252 days in 2007 (from mid June) (Figure 4.1). The longer breeding season in 2007 resulted in the last successful hatching in February 2008. In 2006, the peak egg-laying occurred in June. In contrast, in 2007, egg-laying occurred every month from June to November with most nests found between October and November.

Average annual rainfall was similar during both study years with 95.3 ± 16.5mm in 2006 and 96.7 ± 22.5mm in 2007. However, the monthly rainfall pattern was different between years. Both years had high autumnal rainfall, but 2006 had low rainfall during the Kiwi winter breeding season in contrast to the high breeding season rainfall of 2007 (Figure 4.1). Likewise, the average monthly air temperature was similar in the two years (2006: 14.7°C and 2007: 15.2°C) but temperatures during the winter (June-August) were generally lower in 2006 compared to 2007. In summary, the 2006 breeding season was slightly drier and colder than the 2007 season (Figure 4.1).

Nesting success

The 26 nests produced over three breeding seasons had sufficient information for use in nesting success analysis (Table 4.1). Half of these nests fledged at least one offspring and Stanley's model resulted in an estimate of nesting success that was only slightly more conservative. Eighty-five percent of the 13 unsuccessful nests failed during the incubation period and two nests failed during the nestling stage. Nesting success was lowest in the 2006 breeding season. Incubation continued if one of the eggs of a clutch was viable, but if both eggs died the males abandoned soon after. One egg disappeared from a nest and the male abandoned. Stanley's model yielded slightly lower estimates for hatching and fledging success compared to apparent success (Table 4.1, Table 4.2). Eggs that hatched successfully were incubated on average for 80 ± 2.4 days (*n* = 11), and chicks fledged on average 24 ± 3.3 days after hatching (*n* = 8).

Breeding effort

Seventeen males were monitored for a minimum of two consecutive breeding seasons (2005 and 2006 or 2006 and 2007) and of these, eight (47%) nested twice or more, four (24%) nested once and five (29%) did not nest. Breeding males were either paired to a single female or were associated to a trio consisting of two males and one female (chapter 2). Two males in a trio were found together inside a nest containing one viable egg, but the nest was abandoned by both a few weeks later and a cracked egg was found inside the nest. Females were never found incubating. At least one previously established pair and one trio did not nest annually.

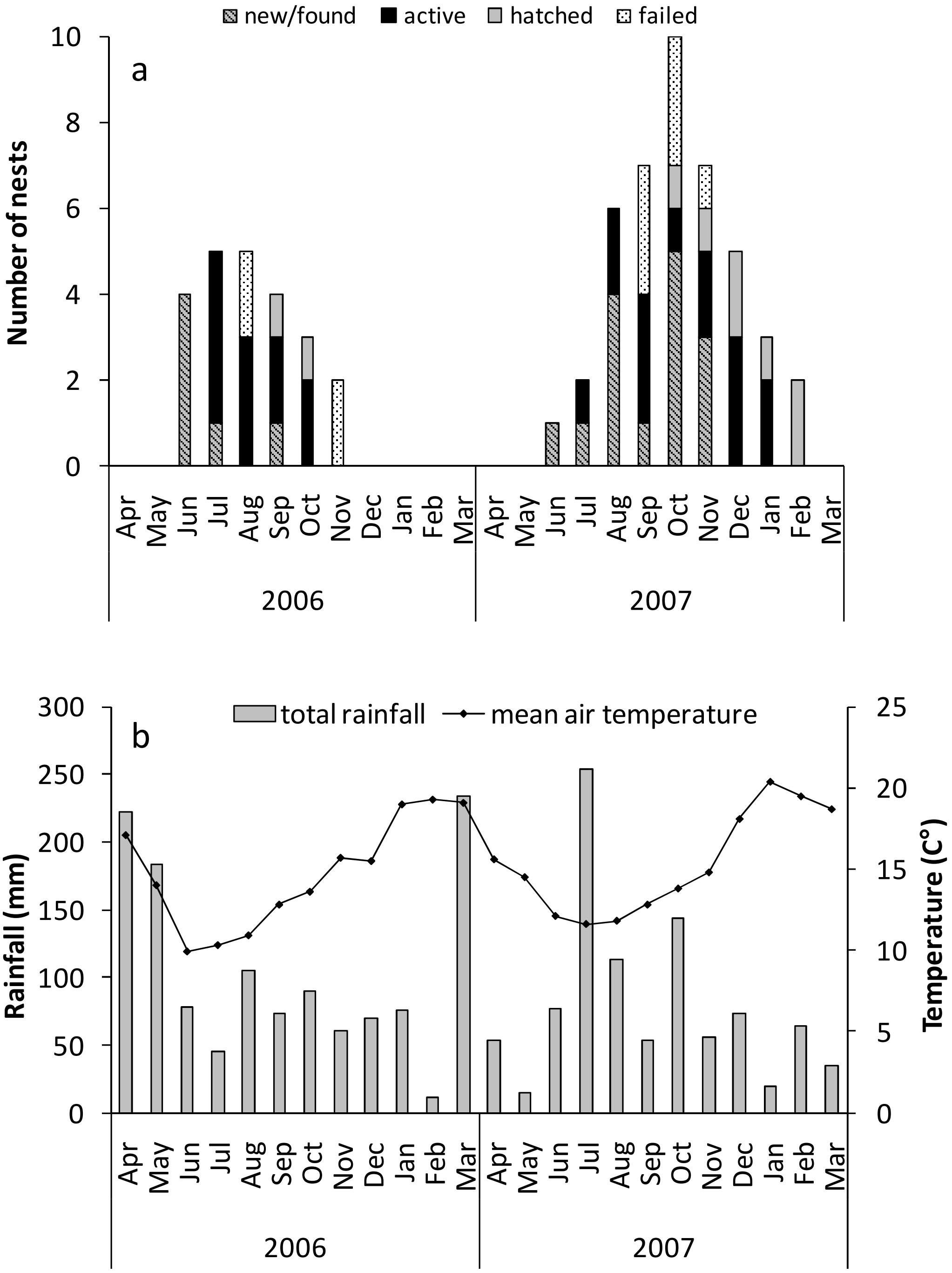


Figure 4.1: (a) Time of breeding of Brown Kiwi on Ponui (2006 and 2007 breeding seasons): found nests become active nests (i.e. nests containing viable egg(s)) in the month following their detection. (b) Total monthly rainfall and monthly average air temperature obtained from nearest weather station (36° 48’ S, 175° 06’ E; Copyright NIWA 2009) (b).

Table 4.1: Percentages of hatching, fledging and nesting success obtained under Stanley's model (2000), apparent nesting success and mean clutch sizes for the breeding seasons of 2006, 2007 and overall (pooled 2005, 2006, 2007), and apparent nesting success and mean clutch size for 2005 of Brown Kiwi on Ponui; *n* indicates sample size.

Breeding season	*n*	Mean clutch size (± SE)	% Hatching success (95%CI)	% Fledging success (95%CI)	% Nesting success (95%CI)	% Apparent nesting success (± SE)
2005	5	1.4 (± 0.2)	n/a	n/a	n/a	60 (± 24.5)
2006	6	1.6 (± 0.3)	53.4 (12.9-82.6)	67.4 (5-95.2)	36 (9.1-75.9)	33.3 (± 21.1)
2007	15	1.2 (± 0.1)	53.4 (23.3-76.4)	90.8 (37.6-99.1)	48.5 (23.5-74.3)	53.3 (± 13.3)
Overall	26	1.3 (± 0.1)	53 (30.4-71.3)	89.3 (58-97.7)	47.4 (28.2-67.4)	50 (± 10)

Clutch size

Twenty-six clutches were incubated by 12 different males, including one incubated by two males. The mean complete clutch size was 1.3 ± 0.1 eggs. More one-egg clutches were laid (69%, 18/26) and no difference in the ratio of 1-egg to 2-egg clutches was found between the three breeding seasons (G = 4.44, d.f. = 2, $P > 0.05$, $n = 26$). One clutch contained three eggs; the third egg was laid while the second egg was viable but the first egg had died. All three eggs were laid with an interval of approximately 27 to 30 days, the duration of egg production after fertilisation (Cockrem *et al.* 1992; Jensen and Durrant 2006). Thus, this appeared to be a rare incidence of a three-egg clutch. Nineteen (73%) of all clutches were first clutches, four (15%) were replacements after failure of the first clutch and three (12%) were second clutches. One of the second clutches followed a replacement clutch, thus this female laid three clutches. I was unable to determine whether the success of first and second clutches was associated due to the small sample size.

Nest reuse

Twenty-five clutches were incubated by males that bred for a minimum of two breeding seasons. Seventeen of these clutches (68%) were laid in burrows previously used by the same males. Clutches laid in reused nests were significantly more successful compared to clutches in previously unused nest burrows (Fisher's exact test; $P = 0.03$, $n = 25$) (Figure 4.2).

Nest usurpation

Two cases of nest usurpation were observed. An untagged male took over incubation of a one-egg clutch of a radio-tagged male who was consequently displaced. A few weeks later, the egg was found dead and a newly laid egg was being incubated by the untagged male. The second egg also died during incubation and the untagged male abandoned the nest. Approximately four days after nest usurpation, the radio-tagged male had moved to a new nest and was incubating an egg containing a 50-day old embryo (determined later by necropsy). The radio-tagged male had been incubating for 11 days before abandoning. Therefore, the egg must have been successfully incubated by another male for at least 39 days prior to the radio-tagged male usurping the nest.

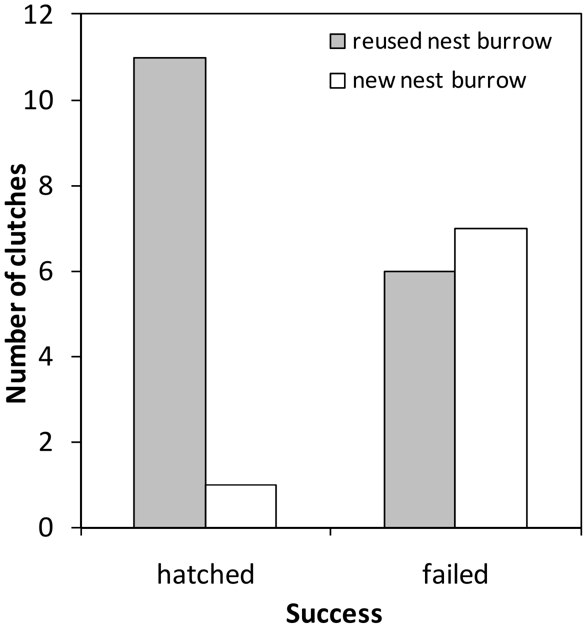


Figure 4.2: Nest success (i.e. if the nest produced at least one hatchling) for reused versus new nest burrows of breeding Brown Kiwi males on Ponui; P = 0.03, Fisher's Exact test.

Table 4.2: Percentages of apparent success estimates of Brown Kiwi on Ponui over three breeding seasons (2005-2007) in comparison to other studied populations. Data for the other Kiwi populations were derived from Potter (1989) and McLennan (1988). Apparent nesting success for McLennan (1988) is given as range as I could not determine whether three fledged chicks came from two (14.3%) or three (21.4%) different nests. Data for the present study are given as means ± SE; *n* indicates sample size.

Population	Number of seasons	% Apparent hatching success (± SE)	% Apparent fledging success (± SE)	% Apparent nesting success (± SE)	% Apparent breeding success (± SE)	Reference
Ponui Island	3	54.3 (± 8.5) *n* = 35	89.5 (± 7.2) *n* = 19	50 (± 10) *n* = 26	48.6 (± 8.6) *n* = 35	Present study
Paerata	3	23.1 *n* = 26	83.3 *n* = 6	25 *n* = 20	19.2 *n* = 26	Potter (1989)
Hawke's Bay	2	28.6 *n* = 21	50 *n* = 6	14.3-21.4 *n* = 14	14.3 *n* = 21	McLennan (1988)

Discussion

Breeding season

The winter breeding by Brown Kiwi on Ponui is typical for this species (Cockrem *et al.* 1992; Potter and Cockrem 1992). However, breeding success varied significantly with year, despite the presence of similar numbers of breeding birds. The 2007 season was longer and more clutches were produced compared to 2006. While the 2006 season was drier and colder, the wetter conditions that occurred during the 2007 nesting period were more likely to provide the better invertebrate food supply (Colbourne and Kleinpaste 1983), necessary for chick survival, the production of the energy-rich eggs by females, and for males undertaking the long incubation duties. Consistent with this hypothesis was the finding that nesting success was higher in 2007.

Nesting success and breeding effort

Nesting success rates on Ponui were high compared to other Brown Kiwi populations (McLennan 1988; Potter 1989). Moreover, Potter (1989) and McLennan (1988) only report apparent nesting success, a measure that generally overestimates success, as early failed nests are often not detected (Jehle *et al.* 2004).

On Ponui, some established pairs and one trio did not breed annually, similar to results found in Potter’s (1989) high-density population, but contrasting with McLennan’s (1988) observations where all pairs bred each year. Nevertheless, almost half of all radio-tagged Kiwi males on Ponui attempted to nest at least twice over three seasons; an estimate that seems high compared to other ratite species. Even though breeding data for wild ratite species is scarce and substantial variation in social and mating systems occurs, ratite nesting success and breeding effort tends to be low. Low proportions of Greater Rhea (*Rhea americana*) and Lesser Rhea (*Rhea pennata*) males attempt nesting, and >6% of Greater Rhea males produce chicks (Fernandez and Reboreda 1998; Barri *et al.* 2009). Eighty percent of male Southern Cassowaries (*Casuarius casuarius johnsonii*) breed only once every three years (Moore 2007). Likewise, nesting success is low in ostriches (*Struthio camelus*), despite their large communal clutches (Bertram 1992), and in emus (*Dromaius novaehollandiae*) (Coddington and Cockburn 1995).

Most Kiwi nests on Ponui failed during the incubation period, but once chicks hatched the probability of fledging success was high. Similar high mortality rates during incubation were reported in the other populations (Potter 1989; McLennan 1988). Causes of egg mortality could not be confirmed in my study, but were unlikely to be related to researcher presence as I confirmed, using radio-telemetry, the presence of breeding males inside their nests the day following the nightly nest checks. Additionally, live eggs were never found inside abandoned nests. The disappearance of eggs from a nest has been reported previously (Potter 1989; McLennan 1988). In the case of two males from a trio observed together inside a nest, to the best of my knowledge, this is the first reported case of shared incubation in the Brown Kiwi, it is likely that they damaged the egg within the small nest chamber and caused mortality. It was unknown whether these males were genetically related or paired to the same female (but see chapter 5). Nonetheless this observation suggests that this species may engage in alternative mating strategies under certain ecological circumstances such as high population density.

Clutch size

Breeding frequency and nesting success were high in the study population, but most clutches only contained a single egg, second clutches were rare, and first clutch failures meant that in some seasons several pairs and one trio did not produce any offspring. Similar results were observed by Potter (1989), whereas McLennan (1988) reported only two-egg clutches and replacement clutches. Breeding density can negatively impact reproduction in some bird species (e.g. Both 1998; Brouwer *et al.* 2009), but not in others (e.g. Alatalo and Lundberg 1984; Nicolaus *et al.* 2009). Increased population density ultimately increases the competition for critical resources (Emlen and Oring 1977; Newton 1994). However, density-dependent effects on reproduction are difficult to detect and may only operate when populations near carrying capacity. Such is arguably the case on Ponui as this Kiwi population has experienced rapid growth since its establishment and is possibly near carrying capacity. Where competition is high, birds would benefit from energy savings obtained by reducing the number and size of clutches. The smaller clutch size in the two high-density Kiwi populations (Potter 1989; present study) compared to the low-density population (McLennan 1988) is consistent with this hypothesis.

Nest reuse and nest usurpation

Incubating males demonstrated strong nest site fidelity and some males reused nest burrows over three consecutive seasons. This may be due to nest site limitations (e.g. Newton 1994; Aitken *et al.* 2002), as large areas of Ponui are unsuitable (pastures and shrubs) for excavating new burrows and contain few natural cavities. In fact, cases of nest usurpation have been observed in this study and by Potter (1989), but not by McLennan (1988). The reuse of nests can have negative effects on reproduction through exposure to ectoparasites (e.g. Møller 1990; Wiebe 2009). Nevertheless, Kiwi males that reused burrows hatched significantly more chicks than males using new burrows.

Reusing nests can reduce the time and energy costs of new excavations (Shields 1984; Barclay 1988) and result in earlier breeding attempts (Gauthier and Thomas 1993; Wiebe *et al.* 2007). Nest reuse is expected to be highest in species where energy savings are important. I suggest Brown Kiwi are limited by energy costs due to their breeding activities; the long incubation period by males and the production of the disproportionally large eggs by females.

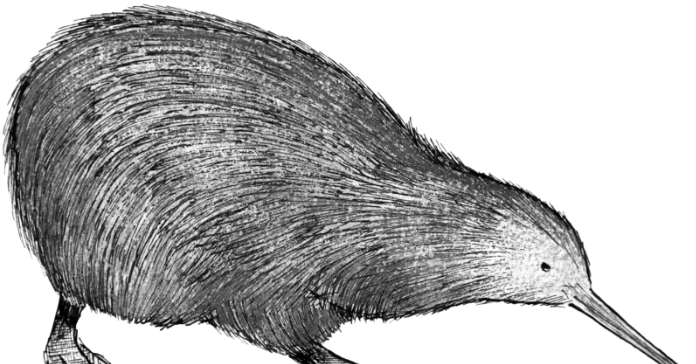
Alternatively, nest sites near good foraging sites, particularly for newly hatched chicks (Taborsky and Taborsky 1995) or with optimal microclimates may be more likely to be reused. To what extent Kiwi in other populations reuse nests is not fully known, but old broken eggshells have been found inside nests (McLennan 1988; Potter 1989; Colbourne 2002). Reuse of nests also appears to be common in other kiwi species (the Rowi, *A. rowii*) (Colbourne 2002).

Conclusions

On Ponui, Kiwi breeding parameters appear to be affected by increased competition for limiting resources due to high population density. Brown Kiwi may benefit from the reduced energy expenditure of smaller and fewer clutches, and the reuse of nest sites and hence maintain a high nesting success in contrast to other populations. The density of the Ponui Kiwi population is likely be representative of Brown Kiwi populations prior to human settlement in New Zealand and can therefore provide significant insights into Brown Kiwi breeding ecology that are not possible in declining low-density populations. This study demonstrates how flexible aspects of Kiwi life history can be in varying ecological settings. A sound understanding of breeding productivity is of particular importance as it provides information on demographic trends of a population. Knowledge on how ecological factors such as population density can influence the breeding ecology and nesting success of species is most important especially as some Brown Kiwi populations introduced to enclosed mainland sites or off-shore islands are increasing in numbers and may reach high density levels within a few generations.

CHAPTER 5

The genetic mating system and kinship of the Brown Kiwi (*Apteryx mantelli*) in two high-density populations



Abstract

The social and the genetic mating systems of a species can differ markedly, thus inferring genetic mating systems from observable social systems can often be misleading. Little is known about the mating system of Brown Kiwi (*Apteryx mantelli*), a species endemic to New Zealand, possibly due to its nocturnal and cryptic habits and its patchy distribution. Here, I report the use of microsatellite markers to determine the genetic mating system of two populations of Brown Kiwi that still occur at high densities. The social mating system of both populations was characterised by long-term monogamous pairs, stable social groups that consist of more than the male and female pair members, and of loose social associations between several birds. Although genetic monogamy appears to be the predominant mating system for Brown Kiwi, at least 5.7% of offspring were found to be genetically unrelated to the incubating male, the putative father. Most members of social groups were not significantly closer related than mated pairs. Shared incubation by males of social groups suggests that Brown Kiwi may occasionally exhibit facultative social cooperative polyandry. However, further investigations and long-term monitoring is needed to assess whether males gain paternity under this mating system. Alternative genetic mating strategies, such as extra-pair copulations, and the formation of social groups of unrelated adults may be facilitated by high population density with the resulting increase in social interactions between individuals. These findings suggest that Kiwi are potentially more flexible in their social and genetic mating system than previously documented.

Introduction

The incorporation of molecular analysis of parentage and kinship in the studies of animal mating systems has revealed that observable social behaviours do not always correspond to genetic mating strategies (reviewed by e.g. Petrie and Møller 1991; Birkhead and Møller 1992c; Petrie and Kempenaers 1998; Griffith *et al.* 2002). In fact, mating systems are substantially more diverse, encompassing a greater variety of mating strategies than previously assumed (reviewed by e.g. Petrie and Møller 1991; Birkhead and Møller 1992c; Petrie and Kempenaers 1998; Griffith *et al.* 2002). This has led to the important distinction between the social mating system (determined from behavioural field observations) and the genetic mating system (determined using genetic assessment of parentage).

Indeed, many bird species are socially monogamous, maintaining a stable pair bond with one partner for at least one breeding season, but engage in extra-pair copulations with others. For example, the predominantly socially monogamous Emu (*Dromaius novaehollandiae*) has high levels of extra-pair paternity (EPP) that result from extra-pair copulations (Taylor *et al.* 2000). Approximately 11% of offspring of socially monogamous bird species are the result of extra-pair copulation, and exclusive genetic monogamy has been found in less than 25% of socially monogamous birds studied to date (reviewed by Griffith *et al.* 2002). In fact, the ratites, the group of paleognathous flightless birds, including the Emu, exhibit a broad variety of social and genetic mating strategies (Handford and Mares 1985). The mating system of the Ostrich (*Struthio camelus*) has been described as polygynandry with multiple paternity and maternity detected within any given nest (Kimwele and Graves 2003). The Lesser Rhea (*Rhea pennata*) and the Greater Rhea (*Rhea americana*) exhibit polygyny with sequential polyandry combined with communal egg laying across several nests (Handford and Mares 1985; Fernandez and Reboreda 1998). Although not yet investigated, it is expected that the highly promiscuous mating system of rheas results in multiple paternity and maternity within nests. Information on the social and genetic mating systems of cassowaries (*Casuarius* spp.) is scarce, but the Southern Cassowaries (*Casuarius casuarius johnsonii*) exhibits polygyny with simultaneous or sequential polyandry (Crome and Moore 1990; Moore 2007).

Kiwi (*Apteryx* spp.) are the smallest members of the ratite family, and are endemic to New Zealand (Heather and Robertson 2005). The Brown Kiwi (*A. mantelli)* is the most numerous and widespread species of kiwi and the only reported mating system for this species is monogamy with long-term pair bonds (McLennan 1988; Taborsky and Taborsky 1999). Speculation that Brown Kiwi may in fact be sequentially polyandrous is based on characteristics of its reproductive behaviour and parental care (McLennan 1988; Potter 1989;

Taborsky and Taborsky 1999). Brown Kiwi exhibit reversed sexual size dimorphism and males are the sole providers of incubation and brood care for the precocial chicks (McLennan 1988, Taborsky and Taborsky 1999). These features are not always indicators of polyandry, but they are strongly associated with this mating system (Jenni 1974; Emlen and Oring 1977; Oring 1986; Owens 2002; Andersson 2005), especially in precocial ground-nesting shorebird species (e.g. Jenni and Collier 1972; Reynolds 1987; Butchart 2000). In species with high nest failure rates, such as many ground-nesting species, females need to be able to re-nest quickly and males often assume greater parental care duties (Brunton 1990). It is hypothesised that freedom from parental duties potentially allows females to produce sequential clutches and subsequently increase their reproductive output (Emlen and Oring 1977; Taborsky and Taborsky 1999). Such a female strategy may lead to sequential polyandry. However, in Kiwi, females need to be in good physical condition to produce their large, energetically expensive eggs, which has an extremely long development (c. 27 to 30 days from fertilisation to egg-laying; Cockrem *et al.* 1992; Jensen and Durrant 2006) and an extraordinarily long incubation period (c. 74-84 days; Calder *et al.* 1978). However, this could theoretically release female Kiwi from parental duties and allow her to go on to produce sequential clutches with a different male while the first male is still incubating (Taborsky and Taborsky 1999).

The uncertainties about the precise nature of the Brown Kiwi mating system stem from the difficulties of studying this species. Given the kiwi's cryptic, wide-ranging and nocturnal behaviour, sexual interactions, such as courtship and copulations, are difficult to observe in the wild. Moreover, most Brown Kiwi populations have drastically declined since human arrival in New Zealand (Holzapfel *et al.* 2008), resulting in a patchy and isolated distribution of populations, generally at low densities of less than four adult birds per km^2 (McLennan 1988) making it difficult to obtain data on their social behaviour.

However, in kiwi populations of high densities (Potter 1989; Colbourne 1991; Taborsky and Taborsky 1999), social interactions between individuals have been found to be more prevalent and a variety of social associations between individuals has been observed (e.g. Potter 1989; Colbourne 1991). For example, family groups of another kiwi species, the Tokoeka (*A. australis*) on Stewart Island, share territories and engage in cooperative breeding (Sturmer and Grant 1988; Colbourne 1991, 2002). Social groups, other than socially monogamous female and male pairs, have been found to form long-term stable bonds among Kiwi of the Ponui Island population (chapter 2). Additionally, Ponui birds, whether they belong to a stable social group or not, have been observed to form temporary loose associations with individuals of either the opposite or the same sex by roosting with each other (chapter 2). These findings demonstrate flexibility in the social system of kiwi. Thus, in high-density populations, I expect an increase in the degree of interactions between individuals, because resources, such as breeding habitat, territories, food, and mating partners have to be shared by a higher number of individuals. This scenario could potentially increase the rate of extra-pair copulations or favour other alternative mating strategies (Møller 1991; Westneat and Sherman 1997; Petrie and Kempenaers 1998; Stewart *et al.* 2010).

The objectives of this study were to determine the genetic mating system and genetic relatedness of Brown Kiwi in two high-density populations for which observational data on their social organisation was available. Specifically, I aimed to (1) determine the frequency of extra-pair paternity (EPP) in each population by testing if the male providing parental care was the genetic father of the egg(s) he incubated, and (2) to determine the genetic relationship between members of social groups.

Methods

Study sites and study populations

The genetic mating system and genetic kinship of two high-density Brown Kiwi populations on Ponui Island (Ponui) and at the Whangarei Kiwi Sanctuary (WKS) was investigated. Ponui is located in the Hauraki Gulf, approximately 16km southeast of Auckland, New Zealand (36°50’S, 175°10’E). The island consists of a patchwork of pasture, mature podocarp-broadleaf and mixed forests, wetlands and regenerating shrubs (Miles and Castro 2000). The study site on Ponui encompassed an area of approximately 200ha. In contrast, WKS is located on the New Zealand mainland in central Northland (35°37'S, 174°08'E) (Robertson and Fraser 2009). The study sites at the WKS consisted of four remnant podocarp-broadleaf and mixed forest fragments of different sizes (Hodges: 35ha, Purua: 110ha, Rarewarewa: 55ha, and Riponui: 45ha) surrounded by small plantations of Radiata Pine (*Pinus radiata*) and pasture (Robertson and Fraser 2009). All four forest fragments were in close vicinity and connected by pasture. Young birds, in particular, were often found to move between different forest patches (H. Robertson, *pers. comm.*).

In both populations, data on the social and pairing status, and the breeding behaviour of individually radio-tagged birds were available from previous telemetry studies (chapters 2, 3, and H. Robertson *pers. comm.*). Radio-tagged birds had been closely monitored using radio telemetry and social groups or other social associations between individuals, and individuals that lived on adjacent home ranges were identified as well as breeding males.

In the Ponui population, blood samples from a total of 88 birds were obtained. This included 30 radio-tagged adult birds (11 females, 19 males). Among these tagged Kiwi, seven pairs (47%, 14/30) and two social groups (23%, 7/30) were identified. I also identified an additional social group (trio), which was only caught once and was not radio-tagged. A total of 19 offspring were incubated and raised by seven radio-tagged males. In the WKS population, blood samples were obtained from a total of 145 birds, including 28 radio-tagged adult males and 10 radio-tagged adult females. Among the radio-tagged birds, a total of 20 birds were in a pair-relationship (53%, 20/38), with all radio-tagged females being paired to breeding males. All 28 radio-tagged males were observed breeding, producing a total of 70 offspring. Allele frequencies that are representative of the entire populations were obtained from all collected samples for both populations, but not all of these samples were tested for paternity or kinship analysis.

Samples consisted of whole blood, muscle tissue and feathers. Up to 200µl of blood was taken from the tarsometatarsal vein of the bird's leg using single-use 25 gauge needles and syringe. Blood samples were stored in either Seutin's buffer (Seutin *et al.* 1991) or 95% ethanol. Tissue samples were obtained from dead embryos during necropsy. A small piece of the leg muscle was cut with a sterile scalpel and placed in 95% ethanol or frozen at -20°C. Feather samples were obtained as shed feathers during capture and stored in sealed paper bags at room temperature. All adult birds were sexed based on morphological measurements (Heather and Robertson 2005) and DNA sexing using feather samples (Huynen *et al.* 2002).

DNA isolation and microsatellite genotyping

Genomic DNA from blood and tissue samples was extracted by proteinase K digestion and a modified protocol of the standard phenol/chloroform extraction method (Maniatis *et al.* 1989). Genomic DNA from feather samples was extracted by using a X-tractor Gene™ (Corbett Robotics, Australia) DNA extraction robot and by using a Chelex 100 resin extraction protocol (Walsh *et al.* 1991).

Individuals were genotyped at 12 polymorphic microsatellite markers previously isolated from Brown Kiwi (Shepherd and Lambert 2006; Jensen *et al.* 2008; Table 5.1). Microsatellite DNA amplification was performed using Polymerase Chain Reaction (PCR) with either the forward or the reverse of each microsatellite primer pair end-labelled with fluorescent dye (Applied Biosystems, Lincoln, USA). Fluorescently labelled primers were multiplexed according to their optimum annealing temperature, the size of amplified DNA fragment and their fluorescent colour label. Multiplex PCR amplifications were carried out for three sets of markers (M47, M54, M56td) in a GeneAmp® PCR System 9700 thermal cycler (Applied Biosystems, Lincoln, USA). I multiplexed primers KMS18 and KMS16B (M47), primers KMS1, KMS7R, KMS14B, KMS30 and KMS37 (M54) and primers Apt29, Apt30, Apt37, Apt59 and Apt68 (M56td). Amplifications were performed in 10µl reactions with FastStartTaq DNA Polymerase PCR buffer (Roche PCR Kit), 10nmol of each primer, 2mM dNTPs, 10nmol BSA, 0.8U FastStartTaq polymerase (Roche PCR Kit) and approximately 20ng of DNA. The PCR profiles for M47 and M54 followed Jensen *et al.* (2008) and M56td was according to Shepherd and Lambert (2006), except that a touchdown profile (58°C-56°C) was also used. To verify amplifications, PCR products were run on a 2% agarose gel along with a 1kb DNA ladder as a molecular weight marker. Gels were stained with ethidium bromide and exposed to UV light for visual checking. PCR products of microsatellite primers were separated using capillary electrophoresis on an Applied Biosystems Genetic Analyser 3130xl (Applied Biosystems, Lincoln, USA) according to the manufacturer's instructions and raw fragment sizes were categorised manually into allele classes ('binning') by carefully scrutinising each raw allele size. In addition, the programme Flexibin (Amos *et al.* 2007), developed for automated binning, was used for comparison with manually inferred binning results. While Flexibin correctly assigned most fragment lengths into the same allele classes as determined manually, it performed poorly in some cases as it falsely classified allele fragments which in fact were artefacts of other markers within the multiplex PCR and Genescan reactions. Such allele classes had to be manually adjusted. Genotypes were entered manually into a spreadsheet.

Errors in microsatellite genotyping may arise in several different ways (see Hoffman and Amos 2005 for summary of genotyping errors), and can lead to false inferences about the genetic relationship between individuals (Hoffman and Amos 2005). Hence, to assess the rate of genotyping error in the dataset of the Ponui and the WKS Kiwi populations, subsamples of individuals from each population were re-genotyped and compared to previously obtained genotypes. Individuals were deliberately re-genotyped between one and three times each when allele scoring was ambiguous, due to faint and/or unclear fragment peaks, presumed contamination, and/or artefacts and interferences with additional microsatellite markers within the multiplex PCR and Genescan reactions. In most cases, microsatellite markers were individually amplified and genotyped to avoid such interferences with additional markers. Error rates per reaction were calculated as the number of incorrect genotypes divided by the total number of reactions (re-genotyped) used for comparison (Hoffman and Amos 2005).

Likewise, error rates per allele were calculated as the number of incorrect alleles divided by the total number of alleles (Hoffman and Amos 2005). The rate of genotyping error was calculated for each locus and across all loci for each population.

Table 5.1: Microsatellite DNA loci used in the present study to assess genetic diversity, parentage and kinship of the Ponui and the WKS Brown Kiwi populations. T_a = microsatellite primer annealing temperature.

Locus name	**Repeat motif**	**Primer sequence**	**T_a (°C)**	**Reference**
Apt29	$(TG)_{12}$	F: AGTAGCTACATGCGTACGTGTC R: TGGCCCACCTGGAGATGTGCA	56	Shepherd and Lambert 2006
Apt35	$(CA)_{14}C_6$	F: CAGCTTGTCTCAGGGAGCATTTGT R:CTATCTCAAGCGGCATCACAAAAG	58	Shepherd and Lambert 2006
Apt37	$(AC)_4T(CA)_3TG(CA)_8$	F: CTGATTTGGCTTACTGCTGAC R: AAGGCTGAATCCAGGCCAA	56	Shepherd and Lambert 2006
Apt59	$(AAAC)_4(AC)_{14}$	F: TCTGTGCCTTGGAAGCAGTC R: GGAAGCTTGGGATCACTGGG	56	Shepherd and Lambert 2006
Apt68	$(TG)_{11}$	F:GGACCAGTGTGTTTATATATTCTGC R: TGCAGATTCAGCCAGTAACG	56	Shepherd and Lambert 2006
KMS1	$(AT)_5GT(AT)_3GT(AT)_3$ ... $(AT)_5GTN_4(AC)_{11}$	F: AAAGCAGCCAAGTTTTTC R: TGAATGGAGTCAAGGAAG	54	Jensen *et al.* 2008
KMS14B	$(AAAT/C)_N$	F: GCTAACATTCACTTGGCATC R: TGAATCCCTTGGATACTGAGA	54	Jensen *et al.* 2008
KMS16B	$(GT)_8$	F: CCCCCCACTAAGTCTG R: AAGTATTCTTGGTAAACAGG	47	Jensen *et al.* 2008
KMS18	$(GT)_{16}$	F: TGCCTTCTCTGCTTGAG R: ATCCTCCAAATGCCC	47	Jensen *et al.* 2008
KMS30	$(GT)_9N_{10}(GT)_4$ $N_6(GT)_6$ ... $(GA)_{20}$	F: CTGTCAAAATCATCTTTACCAC R: TTTCTCTGAGTTTCCGTCC	54	Jensen *et al.* 2008
KMS37	$(AC)_7$	F: TTCCAGAGCACACACTTAG R: GCATAGAACTCACATTTGC	54	Jensen *et al.* 2008
KMS7R	$(GT)_4(CT)_9CC(CT)_{10}$	F: GCTTGTCCCTTTAGATTTAGCGG R: GTTTTCCCTCCTACTCAATGCTC	54	Jensen *et al.* 2008

Microsatellite analysis

Observed and expected heterozygosities and the number of alleles per locus were calculated using the programme ARLEQUIN 3.11. (Excoffier *et al.* 2005). Test for Hardy-Weinberg equilibrium was calculated after Guo and Thompson (1992) and linkage disequilibrium was calculated after Slatkin (1994) and Slatkin and Excoffier (1996) using ARLEQUIN 3.11 (Excoffier *et al.* 2005). Sequential Bonferroni corrections were applied after multiple comparisons to adjust the alpha level to avoid type I errors (Rice 1989). Frequencies of null alleles and large allelic drop-out were estimated using the programme MICRO-CHECKER 2.2.3. (Van Oosterhout *et al.* 2004). These analyses were performed on all genotyped individuals of the Ponui and the WKS populations.

Parentage analysis

Non-exclusion probabilities for each microsatellite locus and combined over all loci were calculated for both populations from the genotypes of potential parents only using the programme CERVUS 3.0 (Kalinowski *et al.* 2007). The non-exclusion probability represents the probability that an unrelated, randomly chosen individual from the population will not be excluded from parentage at one locus or combined over all loci. Probabilities of non-exclusion were calculated separately for the case when neither parent was known (NE-P1) and when one parent was known (NE-P2) (Jamieson and Taylor 1997; Marshall *et al.* 1998). Probabilities of non-exclusion provide a comparative measure of the used loci information content along with the levels of diversity at each locus for the use in parentage analysis (Jones *et al.* 2010).

Parentage was assessed using exclusion analysis by comparing the genotypes of potential fathers, potential mothers and potential offspring using CERVUS 3.0 (Kalinowski *et al.* 2007). Any candidate parents that had allelic mismatches with the offspring at two or more loci were excluded from parentage. Mismatches at only one locus were not counted in order to account for genotyping errors (see Table 5.2) and to avoid overestimation of the level of extra-pair paternity.

First, maternity was verified by testing whether the genotype of females socially associated to breeding males matched that of the offspring raised by her mate. Only offspring incubated/raised by breeding males of which I could identify the socially associated females were included in maternity analysis (Ponui: *n* = 18 offspring, *n* = 6 potential mothers; WKS: *n* = 26 offspring, *n*= 10 potential mothers). I was unable to identify the social bond of some of the breeding males (Ponui: *n* = 1 offspring, *n* = 1 breeding male; WKS: *n* = 44 offspring, *n* = 18 breeding males) and thus the offspring they incubated/raised were not tested for maternity.

Thereafter, paternity analysis was carried out using exclusion analysis (1) without known mothers (mismatch candidate father/offspring) (Ponui: *n* = 19 offspring; WKS: *n* = 70 offspring) and (2) with known mothers (mismatch known mother/candidate father/offspring) (Ponui: *n* = 18 offspring; WKS: *n* = 26 offspring). I was not able to sample the complete breeding population in the two Brown Kiwi populations. Thus, when there was a lack of exclusion I assumed paternity to the breeding male and maternity to his socially paired female.

The average number of candidate fathers differed for each offspring (Ponui: *n* = 8.5 males; WKS: *n* = 8.3 males) based on field observations. In the Ponui population, only tagged males that had reached breeding age and had adjacent home ranges to monitored breeding groups were considered as potential fathers. Likewise, in the WKS population only tagged breeding age males from each forest fragment were considered as candidate fathers of offspring from that forest fragment. While young birds frequently move between forest remnants in the WKS population, adult birds become territorial (H. Robertson, *pers. comm.*).

Fisher's exact tests were used to test for differences in the proportion of extra-pair offspring between the two populations, (1) without known mothers (mismatch candidate father/offspring), and (2) with known mothers (mismatch known mother/candidate father/offspring. All tests were two-tailed with a significance level of α = 0.05 and performed with PASW Statistics 18 (SPSS Inc., Chicago, Illinois, USA). Means are presented with ± SD.

Relatedness analysis

The relatedness coefficient *R* (Queller and Goodnight 1989) was estimated for all pair-wise combinations of genotypes ('dyads') for each of the two study populations with the programme KINGROUP version 2 (Konovalov *et al.* 2004). The coefficient *R* measures the extent to which two individuals share alleles by direct descent based on the populations' allele frequencies and ranges from -1 to 1. Positive *R* values indicate that two individuals share more alleles by descent than expected by chance with average *R* values approaching 0.5 for full siblings or parent-offspring (first degree relatives). Negative *R* values indicate that two individuals share fewer alleles by descent than expected by chance.

Allele frequencies calculated for all samples from both populations were entered into the programme KINGROUP (Konovalov *et al.* 2004) and used for subsequent relatedness analyses. The distribution of *R* values from each of the entire populations (Ponui: n = 88; WKS: n = 145) were evaluated to determine the overall degree of relatedness within and between the two populations. To test whether members of social groups in the Ponui population were closely related, I compared the average relatedness of the three social groups to the average relatedness of seven mated pairs. Due to pair-wise calculations of *R* and the subsequent non-independence of data points, two-sample randomization tests with 10 000 permutations were applied (Manly 2007). Significance levels were set at $\alpha = 0.05$ and randomization analyses were performed with the programme RT 2.1 (Manly 1997).

KINGROUP was further used to calculate the likelihood that a pair of genotypes of members of social groups fit a user-specified relationship of kinship (null hypothesis H_o versus alternative hypothesis H_a), based on the relatedness coefficient *R*. I tested the alternative hypotheses of full-siblings/parent-offspring (both $H_a = 0.5$), half-sibling ($H_a = 0.25$) and cousin ($H_a = 0.125$) against the null hypothesis of unrelated ($H_o = 0$). The significance of the likelihood was estimated in a simulation routine using 10 000 permutations, based on the populations' allele frequencies and the user-specified hypothesised relationship.

Table 5.2: Locus-specific and overall rates of genotyping errors estimated from concordance of deliberately re-genotyped individual Brown Kiwi (*n* = number re-sampled individuals) from the Ponui and the WKS populations.

Locus name	***n***	**Number of reactions**	**Number of mistyped reactions**	**Number of mistyped alleles**	**Error rate per reaction**	**Error rate per allele**
Ponui						
Apt29	5	13	1	1	0.0769	0.0385
Apt35	3	8	0	0	0	0
Apt37	2	6	0	0	0	0
Apt59	12	28	1	2	0.0357	0.0357
Apt68	4	10	1	2	0.1	0.1
KMS1	4	10	0	0	0	0
KMS14B	5	12	0	0	0	0
KMS16B	6	12	0	0	0	0
KMS18	6	12	2	3	0.1667	0.125
KMS30	6	14	1	2	0.0714	0.0714
KMS37	6	14	0	0	0	0
KMS7R	4	10	0	0	0	0
Overall	63	149	6	10	0.0403	0.0336
WKS						
Apt29	91	203	4	4	0.0197	0.0090
Apt35	19	39	2	3	0.0513	0.0385
Apt37	18	37	0	0	0	0
Apt59	22	48	2	3	0.0417	0.0313
Apt68	20	44	2	2	0.0455	0.0227
KMS1	7	14	0	0	0	0
KMS14B	6	12	0	0	0	0
KMS16B	13	26	0	0	0	0
KMS18	21	44	3	3	0.0682	0.0341
KMS30	10	21	1	1	0.0476	0.0238
KMS37	6	12	0	0	0	0
KMS7R	9	18	2	4	0.1111	0.1111
Overall	242	518	16	20	0.0309	0.0193

Results

Microsatellite diversity

A total of 88 individuals from the Ponui population and 145 individuals from the WKS population were genotyped at all 12 microsatellite loci (Table 5.3.). Locus KMS16B was found to be monomorphic in both populations and was consequently excluded from paternity and relatedness analysis. Mean observed heterozygosity per locus was 0.47 (± 0.26) in the Ponui population, and 0.44 (± 0.29) in the WKS population (Table 5.3). The mean number of alleles per locus was 4.27 (± 2.24) and 4.00 (± 1.55) in the Ponui and the WKS kiwi population, respectively (Table 5.3). Locus Apt35 deviated significantly from Hardy-Weinberg equilibrium in the WKS population after Bonferroni correction (Bonferroni-corrected α value = 0.005; 11 loci) and showed significant linkage disequilibrium after Bonferroni correction (Bonferroni-corrected α value = 0.001; 66 pair-wise comparisons) in both populations and was also excluded from subsequent analyses. The other 10 loci were used for paternity and relatedness analyses which assumed a Hardy-Weinberg equilibrium and independence of data points. Genotypic mismatches of re-genotyped individuals (Table 5.2.) were identified to be due to allele scoring errors due to artefacts and pull-ups of multiplexed markers or faint fragment peaks. Following the correction of such genotyping errors, genotyping errors due to null alleles, large allelic drop-out or false allele scoring due to stutter peaks were not detected in the data set as assessed using the programme MICRO-CHECKER 2.2.3. (Van Oosterhout *et al.* 2004).

Parentage

The combined probability of non-exclusion of paternity of an unrelated individual across 10 microsatellite loci was 0.22 for the Ponui and 0.27 for the WKS population, when the genotype of neither parent was known. However, this value decreased to 0.05 and 0.07 for the Ponui and the WKS population, respectively, when the genotype of at least one parent was known (Table 5.3).

Table 5.3: Data obtained from 11 polymorphic microsatellite markers of two Brown Kiwi populations: Ponui (*n* = 88 individuals) and WKS (*n* = 145 individuals). Locus KMS16B was monomorphic in both populations and was excluded from subsequent analyses. A = number of alleles per locus; H_o = observed heterozygosity; H_e = expected heterozygosity; N-PE1 = non-exclusion probability when no parent is known; N-PE2 = non-exclusion probability when one parent is known; SD = standard deviation of the mean.

Locus name	**Ponui Kiwi**					**WKS Kiwi**				
	A	**H_o**	**H_e**	**N-PE1**	**N-PE2**	**A**	**H_o**	**H_e**	**N-PE1**	**N-PE2**
KMS18	8	0.83	0.83	0.59	0.41	6	0.72	0.71	0.74	0.56
KMS1	2	0.30	0.25	0.97	0.90	3	0.20	0.20	0.99	0.93
KMS7R	2	0.08	0.08	0.99	0.94	2	0.08	0.10	0.99	0.95
KMS14	4	0.33	0.34	0.93	0.81	5	0.48	0.45	0.91	0.78
KMS30	3	0.40	0.38	0.94	0.82	2	0.04	0.04	1	0.99
KMS37	4	0.22	0.22	0.98	0.91	4	0.59	0.55	0.85	0.70
Apt35	8	0.83	0.83	n/a	n/a	5	0.79	0.68	n/a	n/a
Apt29	5	0.65	0.53	0.85	0.74	5	0.68	0.72	0.73	0.56
Apt37	3	0.31	0.34	0.97	0.87	2	0.06	0.07	0.99	0.96
Apt59	6	0.78	0.78	0.63	0.46	6	0.73	0.65	0.76	0.59
Apt68	2	0.41	0.44	0.90	0.83	4	0.44	0.50	0.86	0.77
Mean	4.27	0.47	0.46	0.22*	0.05*	4	0.44	0.42	0.27*	0.07*
SD	2.24	0.26	0.26	n/a	n/a	1.55	0.29	0.27	n/a	n/a

*combined non-exclusion probabilities of all loci (=product of individual non-exclusion probabilities)

In the Ponui population, mothers could be assigned to all 18 offspring tested for maternity. The genotypes of all females paired or otherwise socially associated to breeding males matched with the genotype of the offspring that were incubated by their mates in all 10 loci. Likewise, in the WKS population, all females paired to breeding males matched with the genotype of the offspring incubated by their mates.

When testing for paternity without considering the genotype of known mothers (1), none of the breeding males could be excluded as the genetic father of the offspring they incubated in the Ponui population, resulting in no extra-pair paternity (0% EPP; total *n* = 19 offspring). In the WKS population, in only one case was the breeding male excluded as the genetic father as he had alleles not present in the genotype of the offspring at two loci. This offspring was considered to be the result of extra-pair fertilisation, which yielded an overall rate of extra-pair paternity of 1.4 % (total *n* = 70 offspring).

However, when the genotype of the mother of the offspring was known and included in the exclusion analysis (2), the rate of extra-pair paternity increased in both populations with one (6 % EPP; total *n* = 18 offspring) and three (11.5 % EPP; total *n* = 26 offspring) extra-pair offspring in the Ponui and the WKS populations respectively. In one polyandrous trio of the Ponui population, I detected one case of intra-group paternity with the genotype of one of the males in the trio matching that of the offspring in all 10 loci. This offspring was not sired by the male that incubated, but because both males maintained a stable bond with each other and with the female, I did not consider this a case of extra-pair paternity. One female of the Ponui population had a stable pair bond to her mate while maintaining a loose bond with another male, possibly a floater male, a non-territorial but sexually mature bird. Her mate was excluded as the genetic father of one of her offspring incubated by him. Interestingly, the genotype of the floater male matched with the genotype of the offspring in all 10 loci making him the potential genetic father of this offspring. One case of extra-pair paternity in the WKS population involved a female that was associated with two separate males. One of the males initiated incubation, but was usurped by the other male who then completed incubation. Although no genetic information from the first male was available, the male that completed incubation was not the genetic father of the offspring tested, and so it is possible that the first male was the actual father. This successive incubation by the two males of the WKS population has already been observed in two breeding seasons and therefore appears to be a stable arrangement (H. Robertson, *pers. comm.*).

In total, of all 70 offspring of the WKS population, four were the result of extra-pair fertilisation (5.7%) as allelic mismatches were detected between breeding male and offspring or between breeding male, known mother and offspring at two or more loci. Of the 19 offspring of the Ponui population, one offspring was an extra-pair offspring considering allelic mismatches between breeding male and offspring and between breeding male, known mother and offspring (5%).

The rate of extra-pair paternity appeared to be low in both populations and there was no significant difference in the proportion of extra-pair paternity between the Ponui population and the WKS population, regardless of whether the mother's genotype was included (Fisher's exact P = 0.634) or excluded (Fisher's exact P = 1). All cases of extra-pair paternity occurred independently in different pairs/social groups in both populations.

The lack of polymorphism of microsatellite markers in both populations resulted in a lack of exclusion and the inability to assign each offspring to a particular male, but rather to assess the frequency of extra-pair paternity. However, in the Ponui population I was able to assign 16 offspring (84%, total n = 19 offspring) to particular fathers as they showed no allelic mismatches in their genotypes, including offspring with and without known maternity. In the WKS 31 offspring (44%, total n = 70 offspring) could be assigned as they showed no mismatches with the respective male, including offspring with and without known maternity.

Relatedness of social groups

Overall relatedness (R) in the Ponui population was -0.015 (± 0.3) and -0.007 (± 0.3) in the WKS population (Figure 5.1). Three different social groups were previously identified among the Ponui Kiwi.

Social group 1 consisted of two adult males and one adult female. The average relatedness coefficient in this group, as well as the degree of relatedness between the two males, could potentially indicate first- or second degree relatives (Figure 5.1, Table 5.4). None of the user-specified hypothesis of kinship yielded significant results and I failed to reject the null hypothesis that members of social group 1 are unrelated (Table 5.4). One offspring was produced by this group, which was solely incubated by male M2. However, M2 was excluded as the father of this offspring and only male M1 matched the genotype of this offspring in all 10 loci. Although M1 did not participate in incubation, I considered this case as intra-group paternity rather than extra-pair paternity since both males (M1 and M2) maintained a stable bond with F1 and with each other. Additionally, both males were found together inside a potential nest in the breeding season following the completion of the present study (I. Castro, *pers. obs.*). I was not able to confirm an egg in the nest, but retrieved broken eggshells and a dead chick from the nest after the males abandoned (*pers. obs.*), possibly indicating shared incubation.

Group 2 consisted of two adult males and two adult females. Relatedness between the two females was low, but relatedness between the females and males and between the two males was high, potentially indicating first- or second degree relatives (Figure 5.1, Table 5.4). Nevertheless, I failed to reject the null hypothesis that individuals from social group 2 were unrelated (Table 5.4). This group was involved in breeding with both males simultaneously sharing incubation in a nest burrow. However, this egg was damaged and I was not able to retrieve any DNA to test for genetic parentage.

Group 3 consisted of two adult females and one apparent sub-adult male. This trio was only caught once on Ponui, therefore it could not be establish whether it was a stable group over time. Only the male M1 and female F1 showed high levels of relatedness indicative of first-degree relatives (Figure 5.1, Table 5.4). I accepted the alternative hypothesis that this dyad was in a parent/offspring relationship (Table 5.4). While full-siblings and parent/offspring relationships cannot be distinguished based on the *R* value alone, the latter is more likely considering the difference in ages of the two individuals.

Despite the fact that relatedness between some individuals belonging to social groups could be indicative of first- or second-degree relationships, average group relatedness (n = 12 dyads) was not significantly higher than that of mated pairs (n = 7 dyads) (two-sample randomization test: $P > 0.05$) (Figure 5.1).

Table 5.4: Coefficients of relatedness (*R*) between members of social groups in the Ponui Kiwi population and user-specified hypothesis (H_0 vs. H_a) of relationship with significance values (NS = non-significant; ** = $P < 0.01$) when H_0 ($R = 0$) could be rejected. H_0 tested against H_a for full sibling/parent-offspring (PO) ($R = 0.5$), half-sibling ($R = 0.25$), and cousins ($R = 0.125$). F = female, M = male.

Social Group	ID	Compared ID	Social relationship	*R*	H_0 vs. H_a
Group 1	F1	M2	Trio with M1	0.2381	NS
	M1	F1	Trio with M2	0.2589	NS
	M2	M1	Trio with F1	0.3194	NS
Group 2	F1	F2	Roosted together	-0.2482	NS
	F1	M2	Trio with M1	0.2397	NS
	M1	F1	Trio with M2	0.2532	NS
	F2	M2	Trio with M1	0.1685	NS
	F2	M1	Trio with M2	0.3205	NS
	M2	M1	Trio with F1 Trio with F2 Roosted together	0.3781	NS
Group 3	F1	M1^	Trio with F2	0.385	**** PO**
	F2	F1	Trio with M1	-0.0817	NS
	M1^	F2	Trio with F1	-0.2194	NS

^Individual classified as sub-adult based on morphological measurements; all other birds are adults

Discussion

The results of this study show that the predominant genetic mating system of Brown Kiwi is monogamy, but that Brown Kiwi also exhibit additional social and mating strategies that were previously undescribed. Socially monogamous pairs engaged in extra-pair copulations. In the Ponui population, social groups consisting of more than the female and male pair were involved in breeding, and in the WKS population at least one female was simultaneously paired to two separate males who sequentially shared incubation.

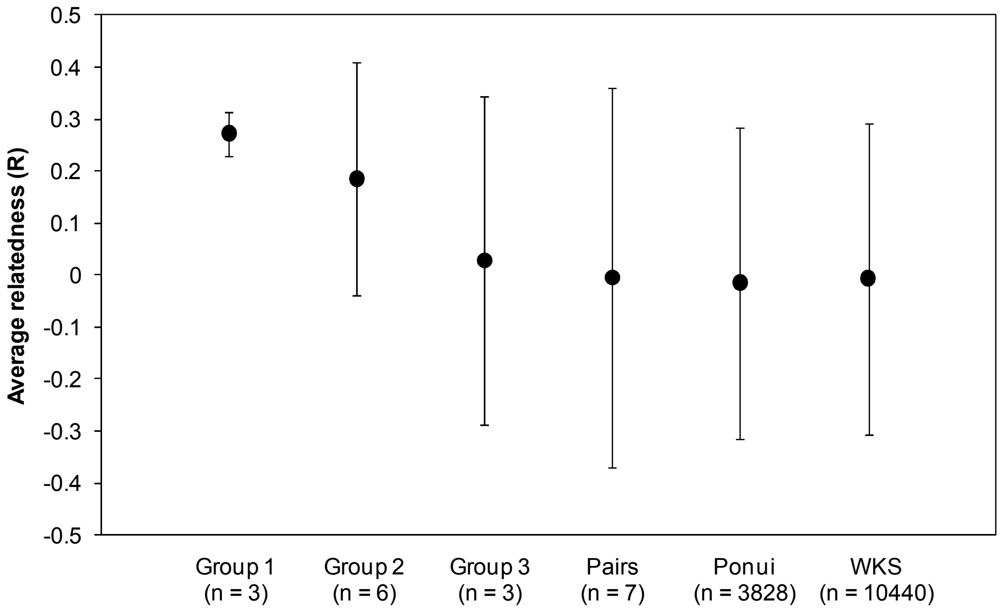


Figure 5.1: Average relatedness (mean *R* ± SD) of social groups and mated pairs of Brown Kiwi of the Ponui population and of the entire Ponui and WKS population. Numbers in parenthesis are number of dyads. Error bars represent standard deviation.

The majority of known pairs in the Ponui and the WKS populations were socially and genetically monogamous with the breeding male being the father of the offspring he incubated and his social mate being the mother. Likewise, most breeding males for which I did not know the social mate, could not be excluded as the genetic father of the offspring they raised, indicating genetic monogamy. However, despite the low polymorphism and the subsequent lower power to exclude candidate fathers for some offspring, the occurrence of extra-pair paternity in both study populations was detected. I conservatively chose to exclude paternity based on allelic mismatches at two or more loci, but given the low polymorphism, offspring that showed even single mismatches could in fact be extra-pair offspring. Therefore the level of extra-pair paternity could potentially be higher than detected here. The occurrence of extra-pair paternity is not surprising and has been found in many socially monogamous species (reviewed by Griffith *et al.* 2002). Indeed levels of extra-pair paternities below 5% have been suggested to deserve explanations (Petrie and Kempenaers 1998). All detected cases of extra-pair paternity in the Ponui and the WKS population occurred independently in different pairs and breeding males. Hence, the rate of extra-pair paternity might be representative of the entire populations as it was not biased towards particular individuals.

Including the genotype of known mothers in paternity analysis significantly improved the ability to detect extra-pair offspring in both populations. These findings stress the importance of determining and genotyping at least one known parent especially when dealing with endangered species, which may have undergone a genetic bottleneck resulting in lowered genetic diversity. The level of polymorphism and average relatedness within each population was similar in the Ponui and the WKS populations, indicating that the proportion of extra-pair offspring might be a realistic estimate for Brown Kiwi populations at high densities.

It is possible that the occurrence of extra-pair paternity is likely to be influenced by population density. High population density changes the spatial distribution of a population, consequently increasing the level of social interactions between individuals, as resources have to be shared by a greater number of individuals. Such a scenario could then increase the potential for extra-pair copulations, because of the close spatial proximity of neighbours and the availability of extra-pair mates (e.g. Møller 1991; Møller and Birkhead 1993b; Westneat and Sherman 1997; Stewart *et al.* 2010). A positive relationship between population density and the rate of extra-pair paternity has been found in some bird species (e.g. Eastern Bluebirds *Sialis sialis* (Stewart *et al.* 2010); Bearded Tits *Panurus biarmicus* (Hoi and Hoi-Leitner 1997b), but not in others (e.g. Tree Swallows *Tachycineta bicolor* (Conrad *et al.* 2001)).

Most kiwi populations have drastically declined since human arrival in New Zealand due to human induced habitat destruction and predation from introduced mammals (McLennan *et al.* 1996; Holzapfel *et al.* 2008). Fortunately, due to an immense national conservation effort for kiwi, some populations are now increasing in numbers (Holzapfel *et al.* 2008). In Brown Kiwi populations of low densities encounters between individuals are expected to be infrequent, with fewer opportunities for re-mating. Additionally, investigating kiwi social and mating behaviours requires very close monitoring of individuals to observe social associations. A previous study on a Brown Kiwi population in Waitangi State Forest (Northland, New Zealand; density of 17.1 birds per km^2) found, using DNA fingerprinting and allozyme analysis, that one out of 14 offspring had been sired by an extra-pair male (Taborsky and Taborsky 1999). The present study is consistent with these previous findings and demonstrates that social monogamy does not always correspond to genetic mating strategies. Nonetheless, the rate of extra-pair paternity remains to be investigated in other kiwi populations and to assess whether population density influences levels of extra-pair paternity.

In the WKS population four breeding males raised the genetic offspring of other males. Two of these cuckolded males were in apparently stable pair-relationships, one had an unidentified mate and one cuckolded male's female appeared to be paired to a second male. This female maintained a stable bond separately with each of the two males who sequentially participated in incubation of the same clutch. However, it is possible that these individuals also formed a polyandrous trio that was undetected. While the genetic fathers of the four illegitimate offspring in the WKS population could not be identified, I was able to identify the genetic father of one offspring incubated by a cuckolded paired male in the Ponui population. His paired female was occasionally found roosting with a floater male, the identified genetic father of the offspring. It has previously been reported that unpaired floater males frequently gain reproductive success through extra-pair copulations (Castro *et al.* 2004; Ewen *et al.* 2004).

Besides exhibiting mating strategies alternative to genetic monogamy, there also was variability in group formation in the Brown Kiwi populations under investigation. Social groups consisting of more than a female and a male occurred in the Ponui population. Most social groups were found to be roosting as polyandrous trios, but even individuals of the same sex that belonged to a social group were observed roosting together (Table 5.4). Although no first- and second degree relatives within social groups were detected (except for group 3), and members of social groups were not more closely related than mated pairs, some individuals within these groups showed high levels of relatedness. Nevertheless, it cannot be assumed that these individuals were necessarily related by direct descent. Due to the complexity of relatedness composition of natural populations, kinship relationships can potentially be overestimated without the knowledge of the population's pedigree (Csillery *et al.* 2006; Van Horn *et al.* 2008). Additionally, due to the lack of known pedigree I have no reference data to determine at what *R* value threshold individuals can be categorised as e.g. full siblings. It is possible that the young male in group 3 assessed as the son of one of the females was such an example. However, this male was clearly sub-adult based on morphological measurements and could in fact be the offspring of the female, indicating close social behaviours among relatives. Such family groups have been observed in the Tokoeka (*A. australis*) on Stewart Island (Colbourne 1991), but genetic assessment of the relatedness of group members has not been investigated. Potentially related helpers of either sex assist with incubation and brood care of the chicks in this kiwi species (Colbourne 1991).

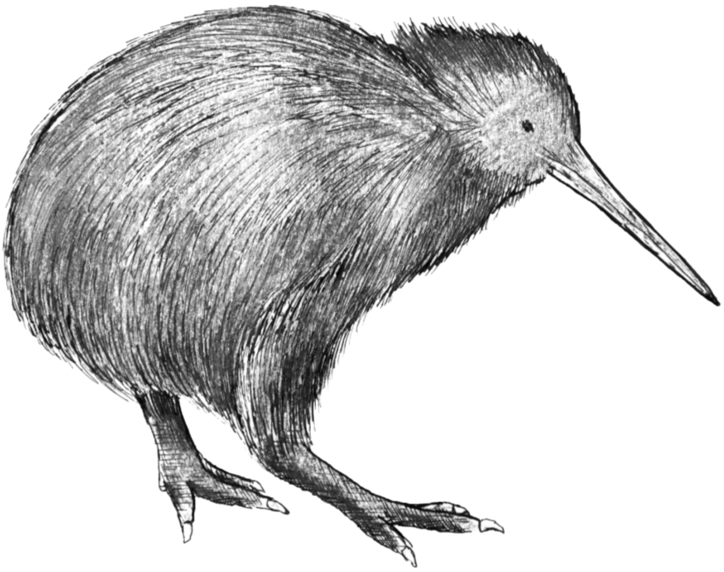
In both study populations, some Brown Kiwi females were socially associated with more than one male (also see chapter 2). Group 1, the polyandrous trio in the Ponui population, was a stable long-term arrangement and they produced one intra-group-offspring. I only found one of the males incubating the nest, however it is possible that I failed to detect that the genetic father also participated in incubation. Members of social group 2 were also most often found to roost as polyandrous trios of different member combinations (Table 5.4, chapter 2). Additionally, in both populations at least two females were associated and/or paired with two separate males. Such simultaneous or sequential pairings are typical for polyandrous mating systems, which are exhibited by several other ratite species where polyandry is often combined with other mating strategies (Handford and Mares 1985). Brown Kiwi exhibit characteristics that are most often associated with a polyandrous mating system: Brown Kiwi females may be socially associated with more than one male, Kiwi exhibit sex-role reversal with male-only parental care and precocial young. In addition, Brown Kiwi females are capable of producing up to seven eggs within one breeding season (Colbourne 2002); a fact that would allow them to produce clutches for additional males while the first male is still incubating the first clutch (Taborsky and Taborsky 1999). However, classical polyandry, where a female sequentially produces clutches with different males, was not detected in the study populations of Brown Kiwi, despite the occurrence of socially polyandrous trios. Also, the female in the WKS population that was independently paired to two males did not lay an additional clutch for the second male, as would be predicted for a classical polyandrous mating system. Instead both males sequentially participated in incubation of the same clutch.

The observation that two unrelated males of a trio from the Ponui population may have shared incubation of one egg raises the possibility that social groups exhibit facultative cooperative polyandry. Cooperative polyandry is a mating strategy where a female forms simultaneous pair bonds and copulates with several males who then care for the clutch cooperatively (Faaborg and Patterson 1981). This is supported by the observation of the two males of group 1 sharing a nest found after the completion of this study, and the detection of an intra-group offspring. It may also be supported by the sequential incubation of one female's clutch by the two males from the WKS population in two successive seasons. The small clutch sizes of kiwi (one to two eggs per clutch with usually one or two clutches per breeding season) mean that both males of trios or other social groups are unlikely to be genetic parents every year. In other long-lived species with small clutches, such as the *Eclectus* parrot (*Eclectus roratus*), it has been found that males of a cooperative polyandrous group father offspring with the same female sporadically over several years (Heinsohn *et al.* 2007). Long-term monitoring and genetic paternity analysis is therefore needed to determine whether Brown Kiwi males in polyandrous trios actually gain paternity under this mating strategy.

In conclusion, the Brown Kiwi mating system described in this study incorporates mating strategies that were not previously documented. Nonetheless, even at high densities, the majority of Brown Kiwi formed true monogamous pairs but, like many other monogamous bird species, some extra-pair paternities were detected. Some birds also formed stable social groups of different structures including possible family groups as well as breeding groups of unrelated individuals, but genetic polyandry could not be detected in the two study populations. However, it remains to be investigated whether Brown Kiwi males of social groups or trios gain paternity under a cooperatively polyandrous mating system. Intensive long-term monitoring of Brown Kiwi populations of low and high densities is necessary to determine the variables associated with extra-pair paternity and the stability and formation of polyandrous trios and other social groups.

CHAPTER 6

The social organisation and mating system of the Brown Kiwi (*Apteryx mantelli)*; a general discussion



Introduction

Mating systems are shaped by the strength and direction of sexual selection, the evolution of differential sex roles, and the competing interests of males and females over mating rates and desertion of parental duties (e.g. Darwin 1871; Trivers 1972; Emlen and Oring 1977; Parker 1979; Houston *et al.* 2005; Parker 2006; Thomas *et al.* 2007; Alonzo 2010).). The social mating system depends largely on the relative net benefits each sex can gain by either investing in parental care or by deserting the current offspring and seek alternative breeding options, and by the opportunities present in the surrounding population in terms of sex ratio and mate availability. On the contrary, the benefits gained through engaging in extra-pair copulations are not fully understood, but extra-pair copulations may provide indirect genetic benefits for the offspring (reviewed by e.g. Birkhead and Møller 1992a; Birkhead and Møller 1995; Jennions and Petrie 2000; Westneat and Stewart 2003).

Social monogamy, the most common mating system among birds, is most often associated with biparental care, because mate desertion reduces the probability of successfully rearing young, especially when a single parent cannot raise the brood alone (Lack 1968; Owens and Bennett 1997; Bennett and Owens 2002). Consequently, the costs of desertion would exceed the benefits (Owens and Bennett 1997; Bennett and Owens 2002). On the contrary, social polyandry is most often associated with a reversal of the sex roles; male-only parental care and larger females (e.g. Jenni and Collier 1972; Reynolds 1987; Andersson 1994; Tarboton 1995; Andersson 2004, 2005). In such a mating system, females may gain from desertion and increase their reproductive success by breeding with additional males while the first male incubates the first clutch. Bird species may be predisposed to offspring desertion and therefore to certain mating systems due to their evolution in life history characteristics over a long time span (Owens and Bennett 1997; Arnold and Owens 1998; Bennett and Owens 2002; Owens 2002), but contemporary ecological factors and the behaviour of the entire population will determine whether a mating strategy will be adopted by individuals (Davies 1989, 1992; Owens and Bennett 1997; Bennett and Owens 2002).

The Brown Kiwi (*Apteryx mantelli*) with its unique characteristics of male-only parental care for precocial chicks, and the sexual size dimorphism with larger females, represents an interesting model species to investigate mating system theory, parental care and sexual selection (Bennett and Owens 2002). The only previously reported social system for this species is monogamy with long-term male-female pairs, and high territoriality (Colbourne and Kleinpaste 1983; McLennan *et al.* 1987; McLennan 1988; Taborsky and Taborsky 1991, 1992, 1999). However, speculations about the Brown Kiwi mating system have been ongoing, because of their high potential for polyandry, as well as the difficulties of studying this species. Therefore, the aims of this thesis were to provide a more detailed picture of the social and mating behaviour of the Brown Kiwi, and to address the overall question of Brown Kiwi mating system. In particular, my four main aims were to determine the social organisation, pairing and roosting behaviour (objective 1), the spacing behaviour in relation to the reproductive period of Brown Kiwi (objective 2), the nesting success and breeding behaviour (objective 3), and the underlying genetic mating system and kinship (objective 4). For this purpose the Ponui population of Brown Kiwi was chosen as this population is still of exceptional density and easily accessible, providing a perfect scenario to investigate the above stated objectives. I combined behavioural, spatial and genetic data to reveal some novel insights into the reproductive ecology of the Brown Kiwi. Below I discuss the key findings in relation to my four objectives (chapter 2-5), and how these findings fit into the broader context of avian mating system theory, and draw a conclusion on the mating system of the study population. I further acknowledge the limitations of the current study and recommend avenues for future research.

Roosting behaviour and social associations between individuals

The type, the temporal patterns and the quality of social relationships between individuals are the key components that shape the social organisation of a population (Hinde 1976; Lott 1984, 1991). Social interactions form the basis of investigating such relationships, but are particularly difficult to evaluate in nocturnal and cryptic species such as the Brown Kiwi. Investigating roosting behaviour by employing radio-telemetry was the most promising method to assess the type and duration of social associations between identified Brown Kiwi individuals.

Previous radio-telemetry studies suggest that Brown Kiwi live in long-term monogamous female-male pairs that are highly territorial (Colbourne and Kleinpaste 1983; McLennan *et al.* 1987; McLennan 1988; Taborsky and Taborsky 1991, 1992, 1999). In concordance, I determined, based on the frequency and duration of roost sharing, monogamous pair relationships that lasted for several years and that were maintained over several breeding and non-breeding seasons. Brown Kiwi switched roost sites often, but were loyal to a number of roost sites, indicating defined home ranges and/or territories. However, while previous studies describe social interactions as occurring almost exclusively between pair members and the majority of social interactions between neighbouring birds to consist almost solely of long-distance calls (Colbourne and Kleinpaste 1983; Taborsky and Taborsky 1992), social stable relationships were detected between more individuals than just the male and female pair members in the Ponui Brown Kiwi population. In fact, this is the first report of long-term socially polyandrous trios in this species. In addition, brief social encounters and roost sharing were detected between several birds, indicating spatial overlap between individual range owners.

Groupings of more than the pair members have only been observed in the Tokoeka (*A. australis*) on Stewart Island (Sturmer and Grant 1988; Colbourne 1991, 2002). However, Tokoeka groupings have been proposed to consist of family groups rather than unrelated adult birds (Colbourne 1991, 2002). Brown Kiwi groupings found on Ponui consisted of birds of breeding age and members were not genetically related (chapter 5). Thus, while the majority of tagged birds lived in socially monogamous pairs, a small number of Brown Kiwi individuals exhibited social polyandry with long-term arrangements. In a monogamous social system, it is expected that neither sex can gain at the expense of the opposite sex (Emlen and Oring 1977; Davies and Houston 1986; Davies 1989). However, female Brown Kiwi would be expected to gain at the expense of the male, because females may benefit by their freedom from parental care and their subsequent opportunities for additional breeding attempts, while the male is left to care for the brood (Taborsky and Taborsky 1999). Thus, polyandry is the type of mating system that would be expected for Brown Kiwi considering their reproductive characteristics typically found in species that are polyandrous. The rate of social polyandry was certainly low in the Ponui population and might have been facilitated by the high population density. In fact, one of the main limitations of polyandry has been suggested to be mate availability (Emlen and Oring 1977; Schamel and Tracy 1977; Reynolds 1987; Colwell and Oring 1988), but this can certainly be excluded in the Ponui population which is still at exceptional density. Both sexes are expected to adapt their behaviours according to environmental conditions such as increased population density to guarantee maximised individual reproductive success. In such environmental conditions, floater and/or unpaired males might join existing breeding pairs to increase their chances to reproduce, because of their inability to breed independently (Davies and Houston 1986; Carrete *et al.* 2006).For example, this scenario has been observed in the Bearded Vulture (*Gypaetus barbatus*) with an increase in the frequency of polyandrous trios due to habitat saturation (Carrete *et al.* 2006).

Long-term mate retention was evident in pairs as well as in trios within the Ponui population, and has been found to be positively related to the reproductive success of a species (Ens *et al.* 1996; Black 2001; Naves *et al.* 2007). In addition, it is often found in long-lived birds such as the Brown Kiwi (Ens *et al.* 1996; Black 2001). In fact, the acquisition of a new mating partner as well as a new territory is time consuming and imposes energetic costs and the risk of mate incompatibility (Danchin 1987; Sullivan 1994). On the other hand, remaining with the same partner may be advantageous by preventing the costs associated with mate searching, and by improving coordination and cooperation with the same mate. Long term mate retention should be advantageous for monogamous Brown Kiwi pairs, but also for polyandrous trios, to minimize the high energetic cost of mate searching, considering the immense energetic investment of Brown Kiwi females during egg production, and of Brown Kiwi males during the long incubation period. Despite the majority of Brown Kiwi on Ponui living in female-male relationships, the stability of trios may be indicative of a socially polyandrous mating system, at least for some individuals of the

Ponui population. Thus, the potential to exhibit variable social systems is certainly evident in the Ponui Brown Kiwi population.

Spacing systems and the implication on kiwi mating system

The spatial distribution of individuals within a population is strongly affected by a variety of social and ecological factors, such as mating system, metabolic requirements, population density, climate and the distribution of resources (e.g. McNab 1963; Fisher and Owens 2000; Lurz *et al.* 2000; McLoughlin *et al.* 2000; Dahle and Swenson 2003; Hingrat *et al.* 2004; Edelman and Koprowski 2006). Space use patterns of the sexes can often provide insights into the social organisation and mating system of a population because in most species the strategies that maximise reproductive success differ between the sexes due to conflicting interest over mating rates and parental care.

The spacing system of the Ponui Brown Kiwi population is characterised by variable but often insignificantly larger home ranges of females, large range overlap between socially associated birds (pairs and trios), and a small degree of overlap between ranges of neighbouring birds. Range overlap between socially associated birds in both the breeding and non-breeding seasons indicates strong long-term mate and site fidelity. Such space use characteristics are suggestive of a monogamous mating system, and are in concordance to previous radio-telemetry studies (McLennan *et al.* 1987; Taborsky and Taborsky 1991, 1992). However, range overlap was certainly underestimated, given the high degree of nightly interactions between tagged birds, the high number of individuals that were detected within focal bird ranges, the inability to account for any untagged birds, and because inferences on space use were only based on a small number of tracked birds.

The freedom of Brown Kiwi females from parental duties should be reflected in their space use patterns. For example, the spacing system of the highly polyandrous Wattled Jacana (*Jacana jacana*) is characterised by large female ranges that superimpose several male ranges (Emlen and Wrege 2004). Jacana females then sequentially produce clutches for each male who then care for the brood (Emlen and Wrege 2004). Indeed, female Brown Kiwi on Ponui enlarged their ranges during the breeding season compared to the non-breeding season, potentially to engage in remating opportunities. However, the high population density should provide females with additional mates for engaging in extra-pair paternity (EPP). In addition, the rate of EPP found in the study population was very low (chapter 5), and genetic polyandry was not detected (chapter 5). Thus the larger ranges of females during the breeding season compared to the non-breeding season are more likely to be explained by their larger body size and higher energetic demands during egg production, while males are bound to the nesting area and therefore inhabited smaller ranges. In contrast to the Jacana mating system, Brown Kiwi are unlikely to be sequentially polyandrous, but some individuals may instead be cooperatively polyandrous as implied by the structure and stability of trios of Brown Kiwi on Ponui (chapter 2), the cooperative breeding of two trio males (chapter 4), and that genetic polyandry was not evident (chapter 5). In a cooperative polyandrous mating system, members of a polyandrous group may share territories rather than female ranges superimposing several single male ranges. The home ranges of all members of polyandrous groups in the Ponui population overlapped to a great extent and all members have been found roosting together simultaneously (chapter 2). Although the spacing system of the Ponui population is indicative of monogamy, the differences between a spacing system suggestive of monogamy and one suggestive of cooperative polyandry might not be as clear. Nevertheless, space use patterns combined with information on the type and duration of social associations between birds revealed aspects of the Brown Kiwi social and mating system consistent with polyandry.

Nesting success and breeding ecology

A sound knowledge of a species' breeding behaviour and reproductive success is not only important for its conservation, but also for understanding the species social and mating system. Documented breeding behaviour and nesting success rates of the Brown Kiwi are scarce. In fact, only two previous studies provide crucial information about the reproductive success of Brown Kiwi

(McLennan 1988; Potter 1989). In these studies, the populations under investigation occurred at different densities and overall reproductive success was low (McLennan 1988; Potter 1989). In comparison, nesting success of the Ponui Brown Kiwi population was exceptionally higher. Nonetheless, in concordance to previous studies (McLennan 1988; Potter 1989), the highest mortality rate occurred during the incubation period. Once chick hatched, fledging success was very high, typical for precocial chicks.

Breeding in Brown Kiwi was previously only known from monogamous pairs (McLennan 1988; Potter 1989; Taborsky and Taborsky 1999). Similarly, most breeding males of the Ponui population appeared to be in a monogamous male-female pair-relationship (chapter 2). However, two males of a polyandrous trio (chapter 2) were found to attend the same nest, sequentially and simultaneously. The potentially shared incubation of one clutch by the two males is the first reported case of potential cooperative breeding in the Brown Kiwi. Furthermore, one intra-group offspring of a second polyandrous trio was genetically determined and those two males were potentially sharing incubation the season following the completion of this study (chapter 5).

High population density has been suggested to influence reproductive success; negative effects of population density on reproduction has been found in some bird species (e.g. Arcese and Smith 1988; Arcese *et al.* 1992; Both 1998; Nummi and Saari 2003; Armstrong *et al.* 2005; Brouwer *et al.* 2009), but not in others (e.g. Alatalo and Lundberg 1984; Nicolaus *et al.* 2009). However, density-dependent effects on reproduction are particularly difficult to detect and might only have a negative impact on populations that are at high densities already. The high population density of the Ponui population did not seem to have any negative effects on the nesting success of this population, especially when compared with the Brown Kiwi population studied by McLennan (1988), which was at very low-density with significantly lower nesting success than the Ponui population. Yet, the occurrence of breeding trios, and the case of nest usurpation, may be indicative of a shortage of suitable breeding habitat and/or territories, and mating partners. For example, in the polyandrous Wattled Jacana (*Jacana jacana*), acquiring a territory is the most important prerequisite for breeding (Emlen and Wrege 2004). Individual Jacanas that were unable to obtain and defend a territory were prevented from breeding (Emlen and Wrege 2004). The high degree of nest reuse in the Ponui population may also be a consequence of the high population density and the shortage of suitable nesting habitat. However, it has been proposed that long-term mate retention, as found in monogamous pairs and polyandrous trios of the Ponui Brown Kiwi (chapter 2), combined with high site fidelity for breeding, is positively related to a higher reproductive success (Cézilly *et al.* 2000; Black 2001). Mate and site fidelity reduces the energetic costs that would arise through searching for a new mate and territory. Also, it can be expected that in high density populations such territories once left, would quickly be filled by new occupants. Indeed, breeding males of the Ponui population that used the same nesting burrow consecutively, hatched significantly more chicks, compared to nesting attempts using novel nesting burrows.

Nonetheless, it remains to be investigated whether females in a cooperative polyandrous mating system have an increased reproductive success. For example, polyandrous trios of Dunnocks had a higher reproductive success compared with monogamous pairs, but this was mainly due to both males provisioning the young (Davies 1986). But Brown Kiwi chicks are not known to be fed by the parents (McLennan 1988; *pers. obs.*). Males, on the other hand are expected to have lower reproductive outcome in a cooperative polyandrous mating system compared to a monogamous one, because of shared paternity (Davies 1986).

Genetic mating system and kinship

The genetic assessment of parentage and kinship in the studies of avian mating systems has revealed that the social mating system, determined based on the number of social mates, can substantially differ from the genetic mating system, determined based on the number of actual sexual partners (Bennett and Owens 2002). Most of the socially monogamous Brown Kiwi pairs of the Ponui population and the WKS population were indeed genetically monogamous. Females in many socially monogamous species have been found to engage in extra-pair copulations as a strategy to seek better and more diverse genes for her offspring while exploiting the benefits of her social mate (e.g. Birkhead and Møller 1992a; Jennions and Petrie 2000), but EPP rates below 5% have been suggested to deserve explanations (Petrie and Kempenaers 1998; Griffith *et al.* 2002). Both of the study populations exist at exceptionally high densities; under such situations it would be expected that social interactions between birds are increased and re-mating opportunities are provided. Yet, the levels of EPP in the Ponui population and in the WKS population were at the lower range for socially monogamous species (Petrie and Kempenaers 1998; Griffith *et al.* 2002). The low rate of EPP might be explained by the potentially high costs of desertion of the clutch by the cuckolded male (Cezilly and Nager 1995; Møller and Cuervo 2000). Because, if the male deserts, then the clutch would fail, resulting in zero reproductive success for both sexes (Cezilly and Nager 1995; Møller and Cuervo 2000). Consequently, the rate of EPP should be relatively low in species with male-only parental care (Cezilly and Nager 1995; Møller 2000; Møller and Cuervo 2000; Sheldon 2002); there is strong selection pressure on males to guard paternity even though it is debated whether males can adjust their parental investment based on their certainty of paternity (commented by Kempenaers and Sheldon 1997). Scrutinizing Brown Kiwi populations of different densities may in the future provide a means of assessing whether population density affects the rate of EPP.

Genetic polyandry was not detected in both study populations. Instead some birds were cooperatively polyandrous (chapter 2, 4). Polyandrous trios were found to consist of unrelated adults in breeding age, except for one trio that consisted of two females and the son of one of them. Indeed, genetic assessment revealed that one of the polyandrous trios produced an intra-group offspring. Furthermore, those two males were potentially sharing incubation the season following the completion of this study. However, the frequency and stability of polyandrous trios remains to be investigated, as well as whether all males of trios gain paternity under this mating strategy, before a conclusion can be drawn that Brown Kiwi exhibit genetic cooperative polyandry.

Conclusion on the social organisation and mating system of the Brown Kiwi on Ponui Island

In conclusion, the social and the mating system of the Brown Kiwi population on Ponui Island can be described as predominantly monogamous, but with low rates of potential cooperative polyandry. Monogamy and cooperative polyandry is reflected in the formation and stability of pairs and trios, the space use patterns of monogamous pairs and polyandrous trios during the breeding and the non-breeding season, the breeding behaviour of monogamous males and the cooperative breeding of males of a trio, as well as the underlying genetic mating system. The predominance of monogamy in the study population of Brown Kiwi is in concordance with previous radio-telemetry studies (McLennan 1988; Taborsky and Taborsky 1992, 1999).

Nevertheless, male-only parental care of Brown Kiwi with the subsequent freedom of females from parental duties, lead to the expectation that females could increase their reproductive success by engaging in additional breeding (McLennan 1988; Potter 1989; Taborsky and Taborsky 1999). In addition, males could potentially become the limiting sex (the operational sex ratio OSR; Emlen and Oring 1977), causing females to compete more intensely over access to males (Bennett and Owens 2002; Andersson 2004). According to sexual selection theory, the more competing sex evolves secondary sexual characteristics, for example larger body size, as a competitive advantage over access to mating partners (Darwin 1871). Indeed, Brown Kiwi exhibit a sexual size dimorphism with females being about 20% larger than males (reviewed by Sales 2005), indicating that selection pressure acts more strongly on females compared with males. The evidence for Brown Kiwi leads to the intriguing possibility that this species should in fact be polyandrous rather than monogamous (McLennan 1988; Potter 1989; Taborsky and Taborsky 1999).

Andersson (2005) suggested three steps towards the evolution of polyandry; male-only parental care, increased female fecundity, and competing females. Males are the sole providers of parental care in the Brown Kiwi, while females produce exceptionally large and energy-rich eggs (Reid 1971a; Calder *et al.* 1978; Calder 1979). Egg production takes approximately 27-30 days (Cockrem *et al.* 1992; Jensen and Durrant 2006), and both functional ovaries are used alternately (Kinsky 1972). Theoretically, this would enable female Brown Kiwi to produce several eggs during the long period males are required to successfully incubate a single egg (c. 74-84 days; Calder *et al.* 1978). Given the large size of kiwi eggs it is difficult to imagine that males are physically able to successfully incubate more than two eggs. Thus Brown Kiwi fulfil all three steps suggested to lead to the evolution of polyandry (Andersson 2005).

And still, the rate of polyandry found in the Ponui population was low and the majority of birds were truly monogamous, socially and genetically. Male availability has been suggested as one of the main limitations of polyandry (Reynolds 1987), as this should increase the ratio of available males (due to male-only care) to competing females (OSR) and thereby increasing the rate polyandry. However, Schamel *et al* (2004) did not find a positive relationship between the proportion of males re-entering the breeding pool and the proportion of polyandrous females in the Red-necked Phalarope (*Phalaropus lobatus*), a sequentially polyandrous shorebird. Considering the high density of the Ponui population, mate availability is unlikely to constrain polyandry in this population. A number of birds, regardless of their sex remained unpaired in the Ponui population. Taborsky and Taborsky (1999) proposed that monogamy in kiwi combined with male-only parental care is due to the costs of parental investment rather than the OSR and whether mating opportunities exist. Taborsky and Taborsky (1999) suggested that the high energetic costs of egg production by female Kiwi and the subsequent physical exhaustion bear on Kiwi mating system. Indeed egg production is an extreme energetic demand for female Brown Kiwi, and this might constrain females from being sequentially polyandrous but rather facultative monogamous. Female Brown Kiwi have been found to loose on average 9% of their peak body weight for each egg they lay and weight loss was cumulative when females laid more eggs consecutively (Potter 1989). If females have low reserves after egg-production and males have high reserves than male-only care should prevail (Barta *et al.* 2002). Comparative studies show that egg size significantly decreased after the origin of polyandry in shorebirds (Liker *et al.* 2001). Andersson (2004) suggested that a change from monogamy to social polyandry leads to the evolution of smaller egg, because this makes it possible for females to sequentially produce clutches for several males. This might be especially important for some ground-nesting shorebirds with high predation rates. Male-only parental care and smaller eggs then enable females to quickly produce replacement clutches and save time and energy and other resources that would otherwise be spent on parental care (Andersson 2004).

The high energetic cost of reproduction of Brown Kiwi may indeed be the main factor that leads to a monogamous mating system. However, while Brown Kiwi males assume the majority of parental care (McLennan 1988; Taborsky and Taborsky 1999; Colbourne 2002), females of other kiwi species (Great Spotted Kiwi (McLennan 1990; Sales 2005), Rowi (Colbourne 2002; Sales 2005), and Tokoeka (Sturmer and Grant 1988; McLennan 1990; Colbourne 1991, 2002; Sales 2005)) share in incubation duties after egg-laying; egg production also bears immense energetic costs to females of such kiwi species. In addition, contemporary environmental factors such as high population density will certainly affect the outcome of a species mating system. After the translocation of Brown Kiwi to Ponui, the population was initially very low with as few as 13 founders (Miles and Castro 2000). Since then the population growth has been rapid and the population is now likely to be near carrying capacity. High population density will ultimately lead to a shortage of resources important for successful reproduction such as breeding habitat, food, and potential mating partners (Møller 1991; Westneat and Sherman 1997; Stewart *et al.* 2010). This could have led to some birds of the Ponui population being cooperatively polyandrous. Cooperative polyandry might be a plausible explanation for the Brown Kiwi interactions outlined in this study. In this type of mating system, two or more males form stable social relationships with a single female (Heinsohn *et al.* 2007), and remarkably non-aggressive behaviours between unrelated group members have been observed in cooperatively polyandrous species (e.g. Heredia and Donazar 1990; Bertran *et al.* 2009). An excess of unpaired males provide the material and the pressure for group formation in a high density condition with little or no opportunities for independent breeding (Faaborg *et al.* 1980; Carrete *et al.* 2006). Monogamy is a mating system in which neither sex is predicted to gain an advantage at the expense of the other. However, in cooperative polyandry females may gain while males often have lower reproductive success than in monogamy (e.g. Maynard Smith and Ridpath 1972; Davies and Houston 1986). Cooperative polyandry is likely to be an adaptive strategy to such conditions and given the long life span of kiwi, the number of reproductively active years should compensate polyandrous males for gaining paternity only sporadically (Faaborg *et al.* 1980; Heinsohn *et al.* 2007). I suggest that Brown Kiwi are more flexible in their mating system than previously documented, and that the slight variation in mating strategies found in the Ponui population represent the different outcomes of sexual conflict.

Limitations of this study

This study has addressed some important questions regarding the Brown Kiwi social and mating system, but I must stress that this study has a number of shortcomings, some of them being specific to the current study, and some being general to the study species investigated. The most important limitation to the overall study was that any inferences about Brown Kiwi social behaviour and mating system are based on a single population on a New Zealand offshore island. Comparisons of Brown Kiwi behaviour with other Brown Kiwi populations were made solely on documented material, with neither investigating a comparative population nor conducting any experimental studies. The exception was the genetic comparison of genetic diversity and parentage of the Ponui and the WKS population. In addition, my findings are based on a sample of radio-tagged birds which may or may not represent the behaviour and genetics of the entire Ponui population.

Therefore the results presented here have to be treated within the context of the study and generalizations about Brown Kiwi social and mating behaviour may not apply to other populations and other kiwi species, especially given that most remaining kiwi populations live under very different ecological conditions, with some mainland birds suffering immense predation pressure and/or are intensively managed. On the contrary, kiwi populations introduced to predator-free offshore islands exist as closed populations without predation-pressures. Population density, spacing behaviour and general demographic characteristics (e.g. higher survival of offspring; recruitment of young birds into the breeding population, dispersal) might be very different in closed populations compared to open mainland populations and to heavily managed populations, which will be reflected in kiwi social and mating behaviour.

The main limitations regarding the species, the Brown Kiwi itself, are that experimental studies are difficult in endangered, highly protected species, and that the nature of the Brown Kiwi makes any investigations on their behaviour extremely labour-intense, somewhat invasive, and costly. At the current stage radio-telemetry offers the best methods to reveal at least some aspects of kiwi behaviour, but this is extremely labour-intense, costly and may alter the behaviour of the birds. The combination of these factors resulted in fairly small sample sizes in the present study. Furthermore, due to the longevity and slow maturation period of Brown Kiwi, long-term and detailed studies are necessary in order to assess factors that influence Kiwi social and mating behaviour and whether such factors can lead to behavioural shifts in the species' social and mating system. This study over three years provides a snapshot of the reproductive life of Kiwi and the Ponui population.

Suggestions for future research

This study has addressed some fundamental questions about Brown Kiwi reproductive ecology, but has inevitable raised as many questions that provide some interesting avenues into future research. I will briefly outline areas for future research that I believe need to be addressed to contribute and understand the reproductive ecology of kiwi.

1. *Investigation into the social organisation and mating system of other kiwi species*

   All five kiwi species show some interspecific differences in their pairing and/or grouping behaviour, and modes of parental care (McLennan 1988; Sturmer and Grant 1988; Jolly 1989, 1990; McLennan 1990; Colbourne 1991; Taborsky and Taborsky 1999; Colbourne 2002; Sales 2005). Yet, they have all been suggested to be monogamous. Although detailed information on aspects of their reproductive success, space use patterns in relation to the reproductive period, group formation and stability, and the genetic assessment of their mating system and kinship is very scarce. I suggest that more detailed research on the social organisation and mating system as well as the factors that drive group formation and biparental care in some kiwi species are required. And what are the benefits and costs for males and females from group living (e.g. family groups in Tokoeka, unrelated polyandrous groups in Brown Kiwi), pair living, biparental or uniparental care? The overall question of why monogamy should prevail in kiwi should be addressed. I do acknowledge that certain information on social behaviour is difficult to obtain for kiwi species that have suffered extreme population declines with the remaining populations being of low density and being intensively managed, such as the Rowi. Nevertheless, using historical information in combination with results that arise out of new research on kiwi reproductive ecology may enable us to find some common correlates of monogamy and factors that can explain the differences in parental care and social organisation.

2. *Assessment of environmental factors that influences social organisation and mating system of kiwi*

   While species are predisposed to a certain mating system due to the evolution of life history traits over a long time span (Arnold and Owens 1998), ecological factors will certainly influence the strength and direction of a certain mating system (see intro of this chapter). Such factors can be the populations' sex ratio and demography, population density, food availability, climatic changes and predation pressure. I suggest the investigating into environmental factors that are likely to affect kiwi social behaviour and mating system.

   For example, sex ratio biases have been shown to alter the mating system of the generally monogamous Lesser Spotted Woodpecker (*Picoides minor*); in a population with a male-biased sex ratio the mating system changed from monogamy to polyandry (Wiktander *et al.* 2000).

The knowledge about a populations' sex ratio is important to understand and explain variations in mating strategies (e.g. Kvarnemo and Ahnesjo 1996). A biased sex ratio can increase the intensity of competition for the limiting sex (Emlen and Oring 1977). Despite an apparently equal operational sex ratio of males to females within the Ponui study site (as indicated by the proportion of males and females captured, chapter 4) the need exists to explore sex ratio and the demography of the population further at all stages (primary, chicks, juveniles, breeders and non-breeders). Although sex ratios change over time, in Brown Kiwi it will only gradually change due to their high adult survivorship, longevity and slow maturation (usually 3-5 years; McLennan et al. 2004).

Likewise, population density will ultimately lead to an increase in competition over resources important for reproduction such as food availability, nesting habitat and mates. To assess the impacts of population density on kiwi reproduction and sociality, comparative studies with low density populations would be needed. Alternatively, long-term monitoring of the behaviour of e.g. a newly established introduced kiwi population that increase over time, could reveal direct indications on whether kiwi alter their behaviour due to increased population density.

Further, temporal environmental variability such as highly seasonal, variable rainfall patterns have been found to be positively associated with cooperative breeding (Rubenstein and Lovette 2007). Rainfall mediates food availability which influences individual fitness, timing of reproduction and the ability to maintain high-quality long-term territories (Komdeur 1992; Rubenstein and Lovette 2007). Also the distribution and availability of food in space and time influences the ability of individuals to monopolise mates (Emlen and Oring 1977). For example, a shift to a habitat with rich food resources enabled female Black Coucals to form additional clutches in short succession for several males (Andersson 1995). In combination with male-only parental care this led to the evolution of polyandry (Andersson 1995). Additionally, in areas where food is scarce, food stressed females may not engage in incubation because of the need to spend significant time feeding (Graul *et al.* 1977; Andersson 2005).

3. *Investigation on the energetic demands of females in reproduction*
   Taborsky and Taborsky (1999) suggested that the energetic investment of female Brown Kiwi in egg production is the main constraint for polyandry and the reason for exhibiting monogamy with male-only parental care. Indeed, the costs of egg production are immense given their production of such huge and energy-rich eggs, but why do females of e.g. the Great Spotted Kiwi and the Rowi share in incubation after the costly egg production? In addition, female Brown Kiwi have been observed to produce up to seven eggs within one breeding season (Colbourne 2002). Despite that the consecutive egg production may be in replacement of lost clutches, the investment in egg production remains the same. I suggest engaging in further research on investigating the energetic demands imposed on females during egg production and how quickly females regain pre-egg laying condition, and whether this factor can be used as an explanation for facultative monogamy as suggested by Taborsky and Taborsky (1999).

In conclusion, detailed monitoring over several decades is needed in order to answer questions of life histories of identified individuals within a population and to gain comprehensive information on kiwi reproductive ecology (Clutton-Brock and Sheldon 2010), especially given the long life span and slow maturation rate of kiwi. The Ponui Island population is of great importance as a study population, because the birds are so abundant, show high nesting success and, due to their rapid population growth after their introduction, Ponui kiwi have similar levels of genetic diversity to mainland populations (e.g. Whangarei Kiwi Sanctuary population). The Ponui population is ideally suited for studies aimed at understanding kiwi behaviour and ecology; i.e., it is a stable high-density and accessible kiwi population. Long term investigation of kiwi populations will eventually address questions about age structure and demography, quantification of the social structure, linkage between life history stages, linkage between generations, and the assessment of lifetime reproductive success and the impacts of sexual selection on a population (Clutton-Brock and Sheldon 2010). A complete picture of kiwi ecology and life history characteristics will ultimately contribute to the conservation of existing populations in relation to the understanding of genetic contributions in a population. These factors influence productivity, population dynamics and the demographic trends of a population.

REFERENCES

Aitken, K. E. H., K. L. Wiebe and K. Martin (2002). Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. *Auk* **119**(2): 391-402.

Alatalo, R. V. and A. Lundberg (1984). Density-dependence in breeding success of the Pied Flycatcher (*Ficedula hypoleuca*). *Journal of Animal Ecology* **53**(3): 969-977.

Alonzo, S. H. (2010). Social and coevolutionary feedbacks between mating and parental investment. *Trends in Ecology & Evolution* **25**(2): 99-108.

Alonzo, S. H. and K. L. Heckman (2010). The unexpected but understandable dynamics of mating, paternity and paternal care in the ocellated wrasse. *Proceedings of the Royal Society B-Biological Sciences* **277**: 115-122.

Amos, W., J. I. Hoffman, A. Frodsham, L. Zhang, S. Best and A. V. S. Hill (2007). Automated binning of microsatellite alleles: problems and solutions. *Molecular Ecology Notes* **7**: 10-14.

Andersson, M. (1994). Sexual selection. Princeton University Press, Princeton, NJ.

Andersson, M. (1995). Evolution of reversed sex roles, sexual size dimorphism, and mating system in coucals (*Centropodidae*, Aves). *Biological Journal of the Linnean Society* **54**: 173-181.

Andersson, M. (2004). Social polyandry, parental investment, sexual selection, and evolution of reduced female gamete size. *Evolution* **58**(1): 24-34.

Andersson, M. (2005). Evolution of classical polyandry: Three steps to female emancipation. *Ethology* **111**(1): 1-23.

Andersson, M. and Y. Iwasa (1996). Sexual selection. *Trends in Ecology & Evolution* **11**(2): 53-58.

Andersson, M. and L. W. Simmons (2006). Sexual selection and mate choice. *Trends in Ecology & Evolution* **21**(6): 296-302.

Arcese, P. and J. N. M. Smith (1988). Effects of population-density and supplemental food on reproduction in song sparrows. *Journal of Animal Ecology* **57**(1): 119-136.

Arcese, P., J. N. M. Smith, W. M. Hochachka, C. M. Rogers and D. Ludwig (1992). Stability, regulation, and the determination of abundance in an insular song sparrow population. *Ecology* **73**(3): 805-822.

Armstrong, D. P. (1991). Aggressiveness of breeding territorial honeyeaters corresponds to seasonal changes in nectar availability. *Behavioral Ecology and Sociobiology* **29**(2): 103-111.

Armstrong, D. P., R. S. Davidson, J. K. Perrott, J. Roygard and L. Buchanan (2005). Density-dependent population growth in a reintroduced population of North Island saddlebacks. *Journal of Animal Ecology* **74**(1): 160-170.

Armstrong, D. P., E. H. Raeburn, R. G. Powlesland, M. Howard, B. Christensen and J. G. Ewen (2002). Obtaining meaningful comparisons of nest success: data from New Zealand robin (*Petroica australis*) populations. *New Zealand Journal of Ecology* **26**(1): 1-13.

Arnold, K. E. and I. P. F. Owens (1998). Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**(1398): 739-745.

Arnold, S. J. (1994). Bateman's principles and the measurement of sexual selection in plants and animals. *American Naturalist* **144**(1): 126-149.

Arnqvist, G. and L. Rowe (2002). Antagonistic coevolution between the sexes in a group of insects *Nature* **415**: 787–789.

Baker, A. J., C. H. Daugherty, R. Colbourne and J. L. McLennan (1995). Flightless Brown Kiwis of New Zealand possess extremely pubdivided population structure and cryptic species like small mammals. *Proceedings of the National Academy of Sciences of the United States of America* **92**(18): 8254-8258.

Barclay, R. M. R. (1988). Variation in the costs, benefits, and frequency of nest reuse by Barn Swallows (*Hirundo rustica*). *Auk* **105**(1): 53-60.

Barri, F. R., M. B. Martella and J. L. Navarro (2009). Reproductive success of wild Lesser Rheas (*Pterocnemia -Rhea- pennata pennata*) in north-western Patagonia, Argentina. *Journal of Ornithology* **150**(1): 127-132.

Barta, Z., A. I. Houston, J. M. McNamara and T. Székely (2002). Sexual conflict about parental care: The role of reserves. *The American Naturalist* **159**(6): 687-705.

Basse, B., J. A. McLennan and G. C. Wake (1999). Analysis of the impact of stoats, Mustela erminea, on northern brown kiwi, *Apteryx mantelli*, in New Zealand. *Wildlife Research* **26**(2): 227-237.

Bassett, S. (2006). BNZ Operation Nest Egg Kiwi Egg Candling Workshop Study Guide. Bank of New Zealand Save the Kiwi Trust, Auckland, New Zealand.

Bates, D. and M. Maelcher (2010). Lme4: linear mixed-effects models using S4 classes, URL: http://lme4.r-forge.r-project.org.

Bateman, A. J. (1948). Intra-sexual selection in *Drosophila*. *Heredity* **2**: 349-368.

Bennett, P. B. and I. P. F. Owens (2002). Evolutionary ecology of birds. Life histories, mating systems and extinction. Oxford University Press, Oxford.

Berglund, A., G. Rosenqvist and I. Svensson (1988). Multiple matings and paternal brood care in the pipefish *Syngnathus typhle*. *Oikos* **51**: 184-188.

Bertram, B. C. R. (1980). Vigilance and group size in ostriches. *Animal Behaviour* **28**: 278-286.

Bertram, B. C. R. (1992). The ostrich communal nesting system. Princeton University Press, Princeton, N.J.

Bertran, J., A. Margalida and B. E. Arroyo (2009). Agonistic behaviour and sexual conflict in atypical reproductive groups: The case of Bearded Vulture *Gypaetus barbatus* polyandrous trios. *Ethology* **115**(5): 429-438.

Birkhead, T. (1998). Cryptic female choice: criteria for establishing female sperm choice. *Evolution* **52**: 1212-1218.

Birkhead, T. and J. D. Biggins (1987). Reproductive synchrony and extra-pair copulation in birds. *Ethology* **74**: 320-334.

Birkhead, T. and A. Møller (1992a). Faithless female seeks better genes. *New Scientist* **135**(1828): 34-38.

Birkhead, T. and A. P. Møller (1992b). Sperm competition in birds. Evolutionary causes and consequences. Academic Press, San Diego, CA.

Birkhead, T. R., L. Atkin and A. P. Møller (1987). Copulation behaviour of birds. *Behaviour* **101**: 101-138.

Birkhead, T. R. and A. P. Møller (1992c). Sperm competition in birds: evolutionary causes and consequences. Academic Press, San Diego.

Birkhead, T. R. and A. P. Møller (1995). Extra-pair copulation and extra-pair paternity in birds. *Animal Behaviour* **49**(3): 843-848.

Black, J. M. (2001). Fitness consequences of long-term pair bonds in barnacle geese: monogamy in the extreme. *Behavioral Ecology* **12**(5): 640-645.

Blondel, D. V., J. Pino and S. M. Phelps (2009). Space use and social structure of long-tailed singing mice (*Scotinomys xerampelinus*). *Journal of Mammalogy* **90**(3): 715-723.

Blundell, G. M., J. A. K. Maier and E. M. Debevec (2001). Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecological Monographs* **71**(3): 469-489.

Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari and T. Coulson (2006). Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology* **75**: 1393-1405.

Both, C. (1998). Experimental evidence for density dependence of reproduction in great tits. *Journal of Animal Ecology* **67**: 667-674.

Boutin, S. and S. Schweiger (1988). Manipulation of intruder pressure in red squirrels (*Tamiasciurus hudsonicus*): effects on territory size and acquisition. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **66**: 2270-2274.

Brigham, R. M. (1991). Flexibility in foraging and roosting behaviour by the big brown bat (*Eptesicus fuscus*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **69**: 117-121.

Brouwer, L., J. M. Tinbergen, C. Both, R. Bristol, D. S. Richardson and J. Komdeur (2009). Experimental evidence for density-dependent reproduction in a cooperatively breeding passerine. *Ecology* **90**(3): 729-741.

Brown, C. R., M. Bomberger Brown and B. Rannala (1995). Ectoparasites reduce long-term survival of their avian host. *Proceedings of the Royal Society B-Biological Sciences* **262**(1365): 313-319.

Brown, J. L. (1964). The evolution of diversity in avian territorial systems. *The Wilson Bulletin* **76**(2): 160-169.

Brunton, D. H. (1988). Sexual differences in reproductive effort: time activity budgets of monogamous killdeer, *Charadrius vociferus*. *Animal Behaviour* **36**: 705–717.

Brunton, D. H. (1990). The effects of nesting stage, sex, and type of predator on parental defense by killdeer (*Charadrius vociferous*): testing models of avian prental defense. *Behavioral Ecology and Sociobiology* **26**(3): 181-190.

Buller, W. L. (1888). A history of the birds of New Zealand. The Author, London, UK.

Burbidge, M. L., R. M. Colbourne, H. A. Robertson and A. J. Baker (2003). Molecular and other biological evidence supports the recognition of at least three species of brown kiwi. *Conservation Genetics* **4**(2): 167-177.

Burnham, K. P. and D. R. Anderson (2002). Model selection and multimodel inference. A practical information-theoretical approach. Springer, Berlin.

Burnham, K. P., D. R. Anderson, G. C. White and C. Brownie (1987). Design and analysis methods for fish survival experiments based on release-recapture *American Fisheries Society Monograph* **5**, American Fisheries Society, Bethesda, MD.

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* **24**(3): 346-352.

Butchart, S. H. M. (2000). Population structure and breeding system of the sex-role reversed, polyandrous Bronze-winged Jacana *Metopidius indicus*. *Ibis* **142**(1): 93-102.

Butchart, S. H. M., N. Seddon and J. M. M. Ekstrom (1999). Polyandry and competition for territories in bronze-winged jacanas. *Journal of Animal Ecology* **68**(5): 928-939.

Butler, D. and J. A. McLennan (1991). Kiwi recovery plan. Threatened species recovery plan 2. Department of Conservation, Wellington, New Zealand.

Butler, J. M. and T. J. Roper (1996). Ectoparasites and sett use in European badgers. *Animal Behaviour* **52**: 621-629.

Calder, W. A. (1979). Kiwi and egg design - evolution as a package deal. *Bioscience* **29**(8): 461-467.

Calder, W. A., C. R. Parr and D. P. Karl (1978). Energy content of eggs of brown kiwi *Apteryx australis* - extreme in avian evolution. *Comparative Biochemistry and Physiology a-Physiology* **60**(2): 177-179.

Carpenter, F. L. and R. E. MacMillen (1976). Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. *Science* **194**(4265): 639-642.

Carrete, M., J. A. Donazar, A. Margalida and J. Bertran (2006). Linking ecology, behaviour and conservation: does habitat saturation change the mating system of bearded vultures? *Biology Letters* **2**(4): 624-627.

Castro, I., K. M. Mason, D. P. Armstrong and D. M. Lambert (2004). Effect of extra-pair paternity on effective population size in a reintroduced population of the endangered hihi, and potential for behavioural management. *Conservation Genetics* **5**(3): 381-393.

Castro, I. C. (2006). North Island brown kiwi, *Apteryx mantelli*, on Ponui Island, Hauraki Gulf: Preliminary reports from two studies. *Kokako* **13**(2): 27-30.

Cézilly, F. and R. G. Nager (1995). Comparative evidence for a positive association between divorce and extra-pair paternity in birds. *Proceedings of the Royal Society B-Biological Sciences* **262**: 7-12.

Cézilly, F., M. Préault, F. Dubois, B. Faivre and B. Patris (2000). Pair-bonding in birds and the active role of females: a critical review of the empirical evidence. *Behavioural Processes* **51**: 83-92.

Chapman, T. (2006). Evolutionary conflicts of interest between males and females. *Current Biology* **16**: 744-754.

Chapman, T., G. Arnqvist, J. Bangham and L. Rowe (2003). Sexual conflict. *Trends in Ecology & Evolution* **18**(1): 41-47.

Chaverri, G., M. Gamba-Rios and T. H. Kunz (2007). Range overlap and association patterns in the tent-making bat *Artibeus watsoni*. *Animal Behaviour* **73**: 157-164.

Chaverri, G. and T. H. Kunz (2006). Reproductive biology and postnatal development in the tent-making bat *Artibeus watsoni* (Chiroptera: Phyllostomidae). *Journal of Zoology* **270**(4): 650-656.

Choudhury, S. (1995). Divorce in birds: a review of the hypotheses. *Animal Behaviour* **50**: 413-429.

Clutton-Brock, T. (1989a). Mammalian mating systems. *Proceedings of the Royal Society B-Biological Sciences* **236**: 339-372.

Clutton-Brock, T. (1989b). Review lecture: Mammalian mating systems. *Proceedings of the Royal Society B-Biological Sciences* **236**(1285): 339-372.

Clutton-Brock, T. (2007). Sexual selection in males and females. *Science* **318**(1882): 1882-1885.

Clutton-Brock, T. and B. C. Sheldon (2010). Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution* **25**(10): 562–573.

Clutton-Brock, T. H. (1991). The evolution of parental care. Princeton University Press, Princeton, NJ.

Cockburn, A. (2006). Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B-Biological Sciences* **273**(1592): 1375-1383.

Cockrem, J. F., R. Goudswaard, M. D. Sibley, E. K. Fox, T. M. Johnson and M. J. Bell (1992). The breeding season of three species of kiwi (*Apteryx*) in captivity as determined from egg-laying dates. *Journal of Zoology* **226**: 95-107.

Coddington, C. L. and A. Cockburn (1995). The mating system of free-living emus. *Australian Journal of Zoology* **43**(4): 365-372.

Colbourne, R. (1991). Further evidence of female incubation and family grouping in Brown Kiwis *Notornis* **38**.

Colbourne, R. (2002). Incubation behaviour and egg physiology of kiwi (*Apteryx* spp.) in natural habitats. *New Zealand Journal of Ecology* **26**(2): 129-138.

Colbourne, R. and R. Kleinpaste (1983). A banding study of North Island brown kiwis in an exotic forest. *Notornis* **30**: 109-124.

Colwell, M. A. (1986). The first documented case of polyandry for Wilson's phalarope (*Phalaropus tricolor*). *Auk* **103**: 611-612.

Colwell, M. A. and L. W. Oring (1988). Variable female mating tactics in a sex-role-reversed shorebird, Wilson's phalarope (*Phalaropus tricolor*). *National Geographic Research* **4**: 408-415.

Conrad, K. F., P. V. Johnston, C. Crossman, B. Kempenaers, R. J. Robertson, N. T. Wheelwright and T. Boag (2001). High levels of extra-pair paternity in an isolated, low-density, island population of tree swallows (*Tachycineta bicolor*). *Molecular Ecology* **10**(5): 1301-1308.

Coulson, J. C. (1966). The influence of the pair-bond and age on the breeding biology of the kittiwake gull *Rissa tridactyla*. *Journal of Animal Ecology* **35**(2): 269-279.

Crome, F. and L. A. Moore (1990). Cassowaries in northeast Queensland: a report of a survey and a review and assessment of their status and conservation and management needs. *Australian Wildlife Research* **17**: 369-385.

Csillery, K., T. Johnson, D. Beraldi, T. Clutton-Brock, D. Coltman, B. Hansson, G. Spong and J. M. Pemberton (2006). Performance of marker-based relatedness estimators in natural populations of outbred vertebrates. *Genetics* **173**(4): 2091-2101.

Cunningham, E. J. A. and T. Birkhead (1998). Sex roles and sexual selection. *Animal Behaviour* **56**: 1311-1321.

Cunningham, S., I. Castro and M. Alley (2007). A new prey-detection mechanism for kiwi (*Apteryx* spp.) suggests convergent evolution between paleognathous and neognathous birds. *Journal of Anatomy* **211**(4): 493-502.

Currie, D. R., T. Burke, R. L. Whitney and D. B. A. Thompson (1998). Male and female behaviour and extra-pair paternity in the wheatear Animal Behaviour. *Animal Behaviour* **55**: 689-703.

Dahle, B. and J. E. Swenson (2003). Home ranges in adult Scandinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology* **260**: 329-335.

Danchin, E. (1987). The behaviour associated with the occupation of breeding site in the kittiwake gull *Rissa tridactyla* The social status of landing birds. *Animal Behaviour* **35**: 81-93.

Darwin, C. (1871). The descent of man, and selection in relation to sex. John Murray, London.

Davies, N. B. (1986). Reproductive success of Dunnocks, *Prunella modularis*, in a variable mating system. 1. Factors influencing provisioning rate, nestling weight and fledging success. *Journal of Animal Ecology* **55**(1): 123-138.

Davies, N. B. (1989). Sexual conflict and the polygamy threshold. *Animal Behaviour* **38**: 226-234.

Davies, N. B. (1992). Dunnock behaviour and social evolution. Oxford University Press, New York.

Davies, N. B. and A. I. Houston (1986). Reproductive success of Dunnocks, *Prunella modularis*, in a variable mating system. 2. Conflicts-of-interest among breeding adults. *Journal of Animal Ecology* **55**(1): 139-154.

Davies, N. B. and A. Lundberg (1984). Food distribution and a variable mating system in the dunnock *Prunella modularis*. *Journal of Animal Ecology* **53**: 895-912.

De Solla, S. R., R. Bonduriansky and R. J. Brooks (1999). Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology* **68**: 221-234.

Dixon, A., D. Ross, S. L. C. O'Malley and T. Burke (1994). Paternal investment inversely related to degree of extra-pair paternity in the reed bunting. *Nature* **371**: 698-700.

Dunn, P. O., L. A. Whittingham, J. T. Lifjeld, R. J. Robertson and P. T. Boag (1994). Effects of breeding density, synchrony, and experience on extrapair paternity in tree swallows. *Behavioral Ecology* **5**: 123-129.

Eccard, J. A., J. Meyer and J. Sundell (2004). Space use, circadian activity pattern, and mating system of the nocturnal tree rat *Thallomys nigricauda*. *Journal of Mammalogy* **85**(3): 440-445.

Edelman, A. J. and J. L. Koprowski (2006). Seasonal changes in home ranges of Abert’s squirrels: impact of mating season. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **84**: 404-411.

Emlen, S. T. and L. W. Oring (1977). Ecology, sexual selection, and evolution of mating systems. *Science* **197**(4300): 215-223.

Emlen, S. T. and P. H. Wrege (2004). Size dimorphism, intrasexual competition, and sexual selection in Wattled Jacana (*Jacana jacana*), a sex-role-reversed shorebird in Panama. *Auk* **121**(2): 391-403.

Ens, B. J., S. Choudhury and J. M. Black (1996). Mate fidelity and divorce in birds. In: Partnerships in birds. The study of monogamy. J. M. Black (ed.). Oxford University Press, Oxford: 344-401.

Ens, B. J., U. N. Safriel and M. P. Harris (1993). Divorce in the long-lived and monogamous oystercatcher *Haematopus ostralegus*: incompatibility or choosing the better option? *Animal Behaviour* **45**: 1199-1217.

Erckmann, W. J. (1983). The evolution of polyandry in shorebirds: an evaluation of hypotheses. In: Social behavior of female vertebrates. S. K. Wasser (ed.). Academic Press, New York, NY: 114-168.

Ewen, J. G., D. P. Armstrong, B. Ebert and L. H. Hansen (2004). Extra-pair copulation and paternity defense in the hihi (or stitchbird) *Notiomystis cincta*. *New Zealand Journal of Ecology* **28**(2): 233-240.

Excoffier, L., G. Laval and S. Schneider (2005). Arlequin (version 3.0): An integrated software package for population genetics data analysis. *Evolutionary Bioinformatics* **1**: 47-50.

Faaborg, J., T. Devries, C. B. Patterson and C. R. Griffin (1980). Preliminary observations on the occurrence and evolution of polyandry in the Galapagos Hawk (*Buteo galapagoensis*). *Auk* **97**(3): 581-590.

Faaborg, J. and C. B. Patterson (1981). The characteristics and occurrence of cooperative polyandry. *Ibis* **123**(4): 477-484.

Fairbairn, D. J., W. U. Blanckenhorn and T. Székely (2007). Sex, size and gender roles: Evolutionary studies of sexual size dimorphism. Oxford University Press, Oxford.

Fernandez, G. J. and J. C. Reboreda (1998). Effects of clutch size and timing of breeding on reproductive success of Greater Rheas. *Auk* **115**(2): 340-348.

Fisher, D. O. and I. P. F. Owens (2000). Female home range size and the evolution of social organization in macropod marsupials. *Journal of Animal Ecology* **69**: 1083-1098.

Gaulin, S. J. C. and R. W. FitzGerald (1988). Home-range size as a predictor of mating systems in Microtus. *Journal of Mammalogy* **69**(2): 311-319.

Gauthier, M. and D. W. Thomas (1993). Nest-site selection and cost of nest-building by Cliff Swallows (*Hirundo pyrrhonota*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **71**(6): 1120-1123.

Gowaty, P. A. (1996). Battles of the sexes and origins of monogamy. In: Parterships in birds: the study of monogamy. J. M. Black (ed.). Oxford University Press, Oxford: 21-52.

Goymann, W., A. Wittenzellner and J. C. Wingfield (2004). Competing females and caring males. I. Polyandry and sex-role reversal in African black coucals, *Centropus grillii*. *Ethology* **110**: 807-823.

Graul, W. D., S. R. Derrickson and D. W. Mock (1977). Evolution of Avian Polyandry. *American Naturalist* **111**(980): 812-816.

Griffith, S. C. and S. Immler (2009). Female infidelity and genetic compatibility in birds: the role of the genetically loaded raffle in understanding the function of extrapair paternity. *Journal of Avian Biology* **40**(2): 97-101.

Griffith, S. C., I. P. F. Owens and K. A. Thuman (2002). Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology* **11**(11): 2195-2212.

Guo, S. W. and E. A. Thompson (1992). Performing the exact test of Hardy-Weinberg proportion for multiple alleles. *Biometrics* **48**(2): 361-372.

Handford, P. and M. A. Mares (1985). The mating systems of ratites and tinamous - an evolutionary perspective. *Biological Journal of the Linnean Society* **25**(1): 77-104.

Harestad, A. S. and F. L. Bunnel (1979). Home range and body weight - a reevaluation. *Ecology* **60**(2): 389-402.

Harris, S., W. J. Cresswell, P. G. Forde, W. J. Trewhella, T. Woollard and S. Wray (1990). Home-range analysis using radio-tracking data - review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* **20**(2/3): 97-123.

Hasselquist, D., S. Bensch and T. von Schantz (1996). Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature* **381**: 229-232.

Heather, B. D. and H. A. Robertson (2005). The field guide to the birds of New Zealand. Penguin, Auckland, New Zealand.

Heinsohn, R., D. Ebert, S. Legge and R. Peakall (2007). Genetic evidence for cooperative polyandry in reverse dichromatic Eclectus parrots. *Animal Behaviour* **74**: 1047-1054.

Heredia, R. and J. A. Donazar (1990). High-frequency of polyandrous trios in an endangered population of Lammergeiers *Gypaetus barbatus* in Northern Spain. *Biological Conservation* **53**(3): 163-171.

Hinde, R. A. (1976). Interactions, relationships and social structure. *Man* **11**(1): 1-17.

Hingrat, Y., M. Saint Jalme, F. Ysnel, F. Lacroix, J. Seabury and P. Rautureau (2004). Relationships between home-range size, sex and season with reference to the mating system of the Houbara Bustard *Chlamydotis undulata undulata*. *Ibis* **146**(2): 314-322.

Hitchmough, R. (2002). New Zealand Threat Classification list-2002. Threatened species occasional publication 23, Department of Conservation, Wellington, New Zealand.

Hoffman, J. I. and W. Amos (2005). Microsatellite genotyping errors: detection approaches, common sources and consequences for paternal exclusion. *Molecular Ecology* **14**: 599-612.

Hoi, H. and M. Hoi-Leitner (1997a). An alternative route to coloniality in the Bearded Tit: Females pursue extra-pair fertilizations. *Behavioral Ecology* **8**: 113-119.

Hoi, H. and M. Hoi-Leitner (1997b). An alternative route to coloniality in the bearded tit: Females pursue extra-pair fertilizations. *Behavioral Ecology* **8**: 113–119.

Holzapfel, S., H. A. Robertson, J. A. McLennan, W. Sporle, K. Hackwell and M. Impey (2008). Kiwi (*Apteryx* spp.) recovery plan, 2008–2018. Threatened Species Recovery Plan 60, Department of Conservation, Wellington, New Zealand.

Hoset, K. S., J.-F. Le Galliard, G. Gundersen and H. Steen (2008). Home range size and overlap in female root voles: effects of season and density. *Behavioral Ecology* **19**: 139-145.

Hosken, D. J., P. Stockley, T. Tregenza and N. Wedell (2009). Monogamy and the battle of the sexes. *The Annual Review of Entomology* **54**: 361-378.

Hough, D., B. Wong, G. Bennett, K. Brettschneider, M. Spinocchia, N. Manion and R. Heinsohn (1998). Vigilance and group size in Emus. *Emu* **98**(324-327).

Houston, A. I., T. Székely and J. M. McNamara (2005). Conflict between parents over care. *Trends in Ecology & Evolution* **20**(1): 33-38.

Huynen, L., C. D. Millar and D. M. Lambert (2002). A DNA test to sex ratite birds. *Molecular Ecology* **11**(4): 851-856.

Jacobs, J. (1974). Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. *Oecologia* **14**(4): 413-417.

Jamieson, A. and S. S. Taylor (1997). Comparisons of three probability formulae for parentage exclusion. *Animal Genetics* **28**(6): 397-400.

Jehle, G., A. A. Y. Adams, J. A. Savidge and S. K. Skagen (2004). Nest survival estimation: A review of alternatives to the Mayfield estimator. *Condor* **106**(3): 472-484.

Jenni, D. A. (1974). Evolution of polyandry in birds. *American Zoologist* **14**(1): 129-144.

Jenni, D. A. and G. Collier (1972). Polyandry in American Jacana (*Jacana spinosa*). *Auk* **89**(4): 743-765.

Jennions, M. D. and M. Petrie (2000). Why do females mate multiply? A review of the genetic benefits. *Biological Reviews* **75**(1): 21-64.

Jensen, T. and B. Durrant (2006). Assessment of reproductive status and ovulation in female brown kiwi (Apteryx mantelli) using fecal steroids and ovarian follicle size. *Zoo Biology* **25**(1): 25-34.

Jensen, T., K. J. Nutt, B. S. Seal, L. B. Fernandes and B. Durrant (2008). Isolation and characterization of microsatellite loci in the North Island brown kiwi, *Apteryx mantelli*. *Molecular Ecology Resources* **8**(2): 399-401.

Jolly, J. N. (1989). A field-study of the breeding biology of the Little Spotted Kiwi (*Apteryx owenii*) with emphasis on the causes of nest failures. *Journal of the Royal Society of New Zealand* **19**(4): 433-448.

Jolly, J. N. (1990). The Little Spotted Kiwi, *Apteryx owenii*. In: Kiwis. E. Fuller (ed.). SeTo Publishing, Auckland: 86-96.

Jones, A. G., C. M. Small, K. A. Paczolt and N. L. Ratterman (2010). A practical guide to methods of parentage analysis. *Molecular Ecology Resources* **10**(1): 6-30.

Jones, A. G., D. Walker and J. C. Avise (2001). Genetic evidence for extreme polyandry and extraordinary sex-role reversal in a pipefish. *Proceedings of the Royal Society B-Biological Sciences* **268**: 2531-2535.

Kalinowski, S. T., M. L. Taper and T. C. Marshall (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* **16**(5): 1099-1106.

Kempenaers, B. (1997). Does reproductive synchrony limit male opportunities or enhance female choice for extra-pair paternity? *Behaviour* **134**(7/8): 551-562.

Kempenaers, B. and B. C. Sheldon (1997). Studying paternity and paternal care: Pitfalls and problems. *Animal Behaviour* **53**: 423-427.

Kempenaers, B., G. R. Verheyen, M. Van den Broeck, T. Burke, C. Van Broeckhoven and A. A. Dhondt (1992). Extra-pair paternity results from female preference for high-quality males in the blue tit. *Nature* **357**: 494-496

Kenward, R. E., R. T. Clarke, K. H. Hodder and S. S. Walls (2001). Density and linkage estimators of home range: nearest-neighbor clustering defines multinuclear cores. *Ecology* **82**(7): 1905-1920.

Kenward, R. E., S. S. Walls, A. B. South and N. M. Casey (2008). Ranges8: For the analysis of tracking and location data. Online manual. Wareham, UK, Anatrack Ltd.

Kernohan, B. J., R. A. Gitzen and J. J. Millspaugh (2001). Analysis of animal space use and movements. In: Radio tracking and animal populations. J. J. Millspaugh and J. M. Marzluff (eds.). Academic Press, San Diego, California: 126-168.

Kimwele, C. N. and J. A. Graves (2003). A molecular genetic analysis of the communal nesting of the ostrich (*Struthio camelus*). *Molecular Ecology* **12**(1): 229-236.

Kinsky, F. C. (1972). Paired Ovaries Consistently Present in Kiwis (Aves, Apterygiformes). *Journal of Ornithology* **112**(3): 334.

Kokko, H. and M. D. Jennions (2008). Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology* **21**: 919-948.

Kokko, H. and W. J. Sutherland (1998). Optimal floating and queuing strategies: Consequences for density dependence and habitat loss. *American Naturalist* **152**(3): 354-366.

Komdeur, J. (1992). Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles Warbler. *Nature* **360**(6406): 768-768.

Konovalov, D. A., C. Manning and M. T. Henshaw (2004). KINGROUP: a program for pedigree relationship reconstruction and kin group assignments using genetic markers. *Molecular Ecology Notes* **4**(4): 779-782.

Kvarnemo, C. and I. Ahnesjo (1996). The dynamics of operational sex ratios and competition for mates. *Trends in Ecology & Evolution* **11**(10): 404-408.

Lack, D. (1968). Ecological adaptations for breeding in birds. Methuen Ltd., London.

Lehmann, T. (1993). Ectoparasites: direct impact on host fitness. *Parasitology Today* **9**(1): 8-13.

Lessells, C. M. (2006). The evolutionary outcome of sexual conflict. *Philosophical Transactions of the Royal Society B-Biological Sciences* **361**: 301-318.

Lewis, S. E. (1995). Roost fidelity of bats: a review. *Journal of Mammalogy* **76**(2): 481-496.

Ligon, J. D. (1999). The evolution of avian breeding systems. Oxford University Press, Oxford.

Liker, A., J. D. Reynolds and T. Székely (2001). The evolution of egg size in socially polyandrous shorebirds. *Oikos* **95**: 3-14.

Lokemoen, J. T. and R. R. Koford (1996). Using candlers to determine the incubation stage of passerine eggs. *Journal of Field Ornithology* **67**(4): 660-668.

Lott, D. F. (1984). Intraspecific variation in the social systems of wild vertebrates. *Behaviour* **88**(3/4): 266-325.

Lott, D. F. (1991). Intraspecific variation in the social systems of wild vertebrates. Cambridge University Press, New York.

Lovallo, M. J. and E. M. Anderson (1995). Range shift by a female bobcat (*Lynx rufus*) after removal of neighboring female. *American Midland Naturalist* **134**: 409-412.

Lurz, P. W. W., P. J. Garson and L. A. Wauters (2000). Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels (*Sciurus vulgaris* L.). *Journal of Zoology* **251**: 167-178.

Macdonald, D. W., F. G. Ball and N. G. Hough (1980). The evaluation of home range size and configuration using radiotracking data. In: A handbook on biotelemetry and radiotracking. C. J. Amlaner and D. W. Macdonald (eds.). Pergamon Press, Oxford, United Kingdom: 405-425.

Mace, T. R. (2000). Time budget and pair-bond dynamics in the Comb-crested Jacana, *Irediparra gallinacea*: A test of hypotheses. *Emu* **100**: 31-41.

Maher, C. R. and D. F. Lott (1995). Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Animal Behaviour* **49**: 1581-1597.

Maher, C. R. and D. F. Lott (2000). A review of ecological determinants of territoriality within vertebrate species. *American Midland Naturalist* **143**(1): 1-29.

Maniatis, T., E. F. Fritsch and J. Sambrook (1989). Molecular Cloning: A Laboratory Manual, Cold Spring Harbor Laboratory Press, New York.

Manly, B. F. J. (1997). RT, a program for randomization testing, version 2.1. Cheyenne, WY, Western EcoSystems Technology Inc.

Manly, B. J. (2007). Randomization, bootstrap and Monte Carlo methods in biology. Chapman & Hall, Boca Raton, FL.

Marshall, T. C., J. Slate, L. E. B. Kruuk and J. M. Pemberton (1998). Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology* **7**(5): 639-655.

Maynard Smith, J. and M. G. Ridpath (1972). Wife sharing in the Tasmanian native hen, *Tribonyx mortierii*: a case of kin selection? *American Naturalist* **106**: 447-452.

McGraw, K. J. and G. E. Hill (2004). Mate attentiveness, seasonal timing of breeding and long-term pair bonding in the House Finch (*Carpodacus mexicanus*). *Behaviour* **141**(1): 1-13.

McLennan, J. A. (1988). Breeding of North Island Brown Kiwi, *Apteryx australis mantelli*, in Hawkes Bay, New Zealand. *New Zealand Journal of Ecology* **11**: 89-97.

McLennan, J. A. (1990). The Great Spotted Kiwi, *Apteryx haastii*. In: Kiwis. E. Fuller (ed.). SeTo Publishing, Auckland: 72-85.

McLennan, J. A., L. Dew, J. Miles, N. Gillingham and R. Waiwai (2004). Size matters: predation risk and juvenile growth in North Island brown kiwi (*Apteryx mantelli*). *New Zealand Journal of Ecology* **28**(2): 241-250.

McLennan, J. A. and M. A. Potter (1992). Distribution, population changes and management of Brown Kiwi in Hawkes Bay. *New Zealand Journal of Ecology* **16**(2): 91-102.

McLennan, J. A., M. A. Potter, H. A. Robertson, G. C. Wake, R. Colbourne, L. Dew, L. Joyce, A. J. McCann, J. Miles, P. J. Miller and J. Reid (1996). Role of predation in the decline of kiwi, *Apteryx* spp, in New Zealand. *New Zealand Journal of Ecology* **20**(1): 27-35.

McLennan, J. A., M. R. Rudge and M. A. Potter (1987). Range size and denning behaviour of brown kiwi, *Apteryx australis mantelli,* in Hawke's Bay, New Zealand. *New Zealand Journal of Ecology* **10**: 97-107.

McLoughlin, P. D., S. H. Ferguson and F. Messier (2000). Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. *Evolutionary Ecology* **14**: 39-60.

McNab, B. K. (1963). Bioenergetics and the determination of home range size. *American Naturalist* **97**: 133-140.

McNay, R. S., J. A. Morgan and F. L. Bunnell (1994). Characterizing independence of observations in movements of Columbian black-tailed deer. *Journal of Wildlife Management* **58**: 422-429.

Miles, J. and I. Castro (2000). Survey of Northern Brown Kiwi (*Apteryx mantelli*) on Ponui Island, Hauraki Gulf, 1999. Department of Conservation, Wellington, New Zealand.

Mock, D. W. and M. Fujioka (1990). Monogamy and long-term pair bonding in vertebrates. *Trends in Ecology & Evolution* **5**(2): 39-43.

Mohr, C. O. (1947). Table of equivalent populations of North American small mammals. *American Midland Naturalist* **37**(1): 223-249.

Møller, A. P. (1986). Mating systems among European passerines: a review. *Ibis* **128**(2): 234-250.

Møller, A. P. (1990). Effects of parasitism by a hematophagous mite on reproduction in the Barn Swallow. *Ecology* **71**(6): 2345-2357.

Møller, A. P. (1991). Density-dependent extra-pair copulations in the swallow *Hirundo rustica. Ethology* **87**(3-4): 316-329.

Møller, A. P. (1994). Sexual selection and the barn swallow. Oxford University Press, Oxford.

Møller, A. P. (2000). Male parental care, female reproductive success, and extrapair paternity. *Behavioral Ecology* **11**: 161-168.

Møller, A. P. (2003). The evolution of monogamy: mating relationships, parental care and sexual selection. In: Monogamy: mating strategies and partnerships in birds, humans and other mammals. U. Reichard and C. Boesche (eds.). Cambridge University Press, Cambridge.

Møller, A. P. and T. R. Birkhead (1993a). Certainty of paternity covaries with paternal care in birds. *Behavioral Ecology and Sociobiology* **33**: 261-268.

Møller, A. P. and T. R. Birkhead (1993b). Cuckoldry and sociality - a comparative study of birds. *American Naturalist* **142**(1): 118-140.

Møller, A. P. and J. J. Cuervo (2000). The evolution of paternity and paternal care in birds. *Behavioral Ecology* **11**(5): 472-485.

Moore, L. A. (2007). Population ecology of the southern cassowary *Casuarius casuarius johnsonii*, Mission Beach north Queensland. *Journal of Ornithology* **148**(3): 357-366.

Morton, E. S., L. Forman and M. Braun (1990). Extrapair fertilizations and the evolution of colonial breeding in Purple Martins. *Auk* **107**: 275-283.

Muck, C., B. Kempenaers, S. Kuhn, M. Valcu and W. Goymann (2009). Paternity in the classical polyandrous black coucal (*Centropus grillii*)-a cuckoo accepting cuckoldry? *Behavioral Ecology* **20**(6): 1185-1193.

Mulder, R. A., P. O. Dunn, A. Cockburn, K. A. Lazenby-Cohen and M. J. Howell (1994). Helpers liberate female Fairy Wrens from constraints on extra-pair mate choice. *Proceedings of the Royal Society B-Biological Sciences* **255**(1344): 223-229.

Naves, L. C., E. Cam and J. Y. Monnat (2007). Pair duration, breeding success and divorce in a long-lived seabird: benefits of mate familiarity? *Animal Behaviour* **73**: 433-444.

Newton, I. (1994). The role of nest sites in limiting the numbers of hole nesting birds - a review. *Biological Conservation* **70**(3): 265-276.

Nicolaus, M., C. Both, R. Ubels, P. Edelaar and J. M. Tinbergen (2009). No experimental evidence for local competition in the nestling phase as a driving force for density-dependent avian clutch size. *Journal of Animal Ecology* **78**(4): 828-838.

Noble, G. K. (1939). The role of dominance in the social life of birds. *The Auk* **56**(3): 263-273.

Norman, M. D. and G. P. Jones (1984). Determinants of territory size in the pomacentrid reef fish, *Parma victoriae*. *Oecologia* **61**: 60-69.

Nummi, P. and L. Saari (2003). Density-dependent decline of breeding success in an introduced, increasing mute swan *Cygnus olor* population. *Journal of Avian Biology* **34**(1): 105-111.

Orians, G. H. (1969). On the evolution of mating systems in birds and mammals. *American Naturalist* **103**(934): 589-&.

Oring, L. W. (1986). Avian polyandry. *Current Ornithology* **3**: 309-351.

Oring, L. W. and D. B. Lank (1982). Sexual selection, arrival times, philopatry and site fidelity in the polyandrous Spotted Sandpiper. *Behavioral Ecology and Sociobiology* **10**(3): 185-191.

Owens, I. P. F. (2002). Male-only care and classical polyandry in birds: phylogeny, ecology and sex differences in remating opportunities. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **357**(1419): 283-293.

Owens, I. P. F. and P. M. Bennett (1997). Variation in mating system among birds: ecological basis revealed by hierarchical comparative analysis of mate desertion. *Proceedings of the Royal Society B-Biological Sciences* **264**(1385): 1103-1110.

Owens, I. P. F. and I. R. Hartley (1998). Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proceedings of the Royal Society B-Biological Sciences* **265**(1394): 397-407.

Parker, G. A. (1979). Sexual selection and sexual conflict. In: Sexual selection and reproductive competition in insects. M. S. Blum and N. A. Blum (eds.). Academic Press, London: 123-166.

Parker, G. A. (1984). Sperm competition and the evolution of animal mating systems. In: Sperm competition and the evolution of animal mating systems. R. L. Smith (ed.). Academic Press, New York: 1-60.

Parker, G. A. (2006). Sexual conflict over mating and fertilization: an overview. *Philosophical Transactions of the Royal Society B-Biological Sciences* **361**: 235-259.

Petrie, M. and B. Kempenaers (1998). Extra-pair paternity in birds: explaining variation between species and populations. *Trends in Ecology & Evolution* **13**(2): 52-58.

Petrie, M. and A. P. Møller (1991). Laying eggs in others nests - intraspecific brood parasitism in birds. *Trends in Ecology & Evolution* **6**: 315-320.

Pogány, A., I. Szentirmai, J. Komdeur and T. Székely (2008). Sexual conflict and consistency of offspring desertion in Eurasian penduline tit *Remiz pendulinus*. *BMC Evolutionary Biology* **8**: 242-248.

Potter, M. A. (1989). Ecology and reproductive biology of the North Island brown kiwi (*Apteryx australis mantelli*). *PhD thesis*. Massey University, Palmerston North

Potter, M. A. and J. F. Cockrem (1992). Plasma-levels of sex steroids in the North Island Brown Kiwi (*Apteryx australis mantelli*) in relation to time of year and stages of breeding. *General and Comparative Endocrinology* **87**(3): 416-424.

Powell, R. A. (2000). Animal home range and territories and home-range estimators. In: Research techniques in animal ecology: Controversies and consequences. L. Boitani and T. K. Fuller (eds.). Columbia University Press, New York, New York, USA: 65-110.

Queller, D. C. and K. F. Goodnight (1989). Estimating relatedness using genetic markers. *Evolution* **43**(2): 258-275.

Reboreda, J. C. and C. J. Fernandez (1997). Sexual, seasonal and group size differences in the allocation of time between vigilance and feeding in the Greater Rhea (*Rhea americana*). *Ethology* **103**: 198-207.

Reckardt, K. and G. Kerth (2007). Roost selection and roost switching of female Bechstein's bats (*Myotis bechsteinii*) as a strategy of parasite avoidance. *Oecologia* **154**: 581-588.

Reichard, M., C. Smith and W. C. Jordan (2004). Genetic evidence reveals density-dependent mediated success of alternative mating behaviours in the European bitterling (*Rhodeus sericeus*). *Molecular Ecology* **13**: 1569-1578.

Reid, B. (1971a). Composition of a kiwi egg. *Notornis* **18**: 250-252.

Reid, B. (1971b). The weight of the kiwi and its egg. *Notornis* **18**: 245-249.

Reid, B. and G. R. Williams (1975). The kiwi. In: Biogeography and ecology in New Zealand. G. Kuschel (ed.). Junk, The Hague, the Netherlands: 301-330.

Reynolds, J. D. (1987). Mating system and nesting biology of the rednecked phalarope *Phalaropus lobatus*: what constrains polyandry? *Ibis* **129**: 225-242.

Reynolds, J. D. (1996). Animal breeding systems. *Trends in Ecology & Evolution* **11**(2): A68-A72.

Reynolds, T. D. and J. W. Laundre (1990). Time intervals for estimating proghorn and coyote home ranges and daily movements. *Journal of Wildlife Management* **54**(2): 316-322.

Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution* **43**(1): 223-225.

Rice, W. R. (1998). Intergenomic conflict, interlocus antagonistic coevolution and the evolution of reproductive isolation. In: Endless forms: species and speciation. D. J. Howard and S. H. Berlocher (eds.). Oxford University Press, Oxford: 261–270.

Robertson, B. C., S. M. Degnan, J. Kikkawa and C. C. Moritz (2001). Genetic monogamy in the absence of paternity guards: the Capricorn silvereye, *Zosterops lateralis* chlorocephalus, on Heron Island. *Behavioral Ecology* **12**(6): 666-673.

Robertson, H. A. and R. M. Colbourne (2003). Kiwi (*Apteryx* spp.) Best Practice Manual. I. Castro, C. Miller and M. Cresswell (eds.). Department of Conservation/Kiwi Recovery Trust, Wellington, New Zealand.

Robertson, H. A. and J. R. Fraser (2009). Use of trained dogs to determine the age structure and conservation status of kiwi *Apteryx* spp. populations. *Bird Conservation International* **19**(2): 121-129.

Roper, T. J., T. P. Jackson, L. Conradt and N. C. Bennett (2002). Burrow use and the influence of ectoparasites in Brants' Whistling rat *Parotomys brantsii*. *Ethology* **108**: 557-564.

Rubenstein, D. R. and I. J. Lovette (2007). Temporal environmental variability drives the evolution of cooperative breeding in birds. *Current Biology* **17**: 1414-1419.

Rutberg, A. T. (1983). The evolution of monogamy in primates. *Journal of Theoretical Biology* **104**: 93-112.

Sales, J. (2005). The endangered kiwi: a review. *Folia Zoologica* **54**(1-2): 1-20.

Schamel, D. and D. M. Tracy (1977). Polyandry, replacement clutches, and site tenacity in the red phalarope (*Phalaropus fulicarius*) at Barrow, Alaska. *Bird Banding* **48**: 314-324.

Schamel, D., D. M. Tracy and D. B. Lank (2004). Male mate choice, male availability and egg production as limitations on polyandry in the red-necked phalarope. *Animal Behaviour* **67**: 847-853.

Schradin, C. and N. Pillay (2005). Intraspecific variation in the spatial and social organization of the African striped mouse. *Journal of Mammalogy* **86**(1): 99-107.

Schradin, C., G. Schmohl, H. G. Rödel, I. Schoepf, S. M. Treffler, J. Brenner, M. Bleeker, M. Schubert, B. König and N. Pillay (2010). Female home range size is regulated by resource distribution and intraspecific competition: a long-term field study. *Animal Behaviour* **79**: 195-203.

Schwagmeyer, P. L., R. C. St Clair, J. D. Moodie, T. C. Lamey, G. D. Schnell and M. N. Moodie (1999). Species differences in male parental care in birds: a reexamination of correlates with paternity. *Auk* **116**: 487–503.

Seber, G. A. F. (1982). The estimation of animal abundance and related parameters. Charles Grifin & Company, London.

Seutin, G., B. N. White and P. T. Boag (1991). Preservation of avian blood and tissue samples for DNA analyses. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **69**(1): 82-90.

Sheldon, B. C. (2002). Relating paternity to paternal care. *Philosophical Transactions of the Royal Society B-Biological Sciences* **357**: 341-350.

Shepherd, L. D. and D. M. Lambert (2006). Nuclear microsatellite DNA markers for New Zealand kiwi (*Apteryx* spp.). *Molecular Ecology Notes* **6**(1): 227-229.

Shepherd, L. D. and D. M. Lambert (2008). Ancient DNA and conservation: lessons from the endangered kiwi of New Zealand. *Molecular Ecology* **17**(9): 2174-2184.

Shields, W. M. (1984). Affecting nest and site fidelity in Adirondack Barn Swallows (*Hirundo rustica*). *The Auk* **101**(4): 780-789.

Shier, D. M. and J. A. Randall (2004). Spacing as a predictor of social organization in Kangaroo Rats (Dipodomys heermanni arenae). *Journal of Mammalogy* **85**(5): 1002-1008.

Slatkin, M. (1994). Linkage disequilibrium in growing and stable populations. *Genetics* **137**(1): 331-336.

Slatkin, M. and L. Excoffier (1996). Testing for linkage disequilibrium in genotypic data using the expectation-maximization algorithm. *Heredity* **76**: 377-383.

Smolker, R. A., A. F. Richards, R. C. Connor and J. W. Pepper (1992). Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour* **123**: 38-69.

Spottiswoode, C. and A. P. Møller (2004). Genetic similarity and hatching success in birds. *Proceedings of the Royal Society of London Series B-Biological Sciences* **271**(1536): 267-272.

Stanley, T. R. (2000). Modeling and estimation of stage-specific daily survival probabilities of nests. *Ecology* **81**(7): 2048-2053.

Stewart, S. L. M., D. F. Westneat and G. Ritchison (2010). Extra-pair paternity in eastern bluebirds: effects of manipulated density and natural patterns of breeding synchrony. *Behavioral Ecology and Sociobiology* **64**: 463-473.

Stradiotto, A., F. Cagnacci, R. Delahay, S. Tioli, L. Nieder and A. Rizzoli (2009). Spatial organization of the yellow-necked mouse: effects of density and resource availability. *Journal of Mammalogy* **90**(3): 704-714.

Sturmer, A. T. and A. D. Grant (1988). Female kiwis incubating. *Notornis* **35**: 193-195.

Stutchbury, B. J. and E. S. Morton (1995). The effect of breeding synchrony on extra-pair mating systems in songbirds. *Behaviour* **132**: 675-690.

Stutchbury, B. J. M. (1998). Extra-pair mating effort of male hooded warblers *Wilsonia citrina*. *Animal Behaviour* **55**: 553-561.

Stutchbury, B. J. M., E. S. Morton and W. H. Piper (1998). Extra-pair mating system of a synchronously breeding tropical songbird. *Journal of Avian Biology* **29**: 72-78.

Stutchbury, B. J. M. and R. J. Robertson (1985). Floating populations of female Tree Swallows. *Auk* **102**: 651-654.

Sullivan, M. S. (1994). Mate choice as an information gathering process under time constraint: implications for behaviour and signal design. *Animal Behaviour* **47**: 141-151.

Swihart, R. K. and N. A. Slade (1985a). Influence of sampling interval on estimates of home range size. *Journal of Wildlife Management* **49**: 1019-1025.

Swihart, R. K. and N. A. Slade (1985b). Testing for independence of observations in animal movements. *Ecology* **66**: 1176-1184.

Swihart, R. K. and N. A. Slade (1997). On testing for independence of animal movements. *Journal of Agricultural, Biological, and Environmental Statistics* **2**: 48-63.

Székely, T., A. Kosztolanyi, C. Kupper and G. H. Thomas (2007). Sexual conflict over parental care: a case study of shorebirds. *Journal of Ornithology* **148**: S211-S217.

Székely, T., J. N. Webb, A. I. Houston and J. M. McNamara (1996). An evolutionary approach to offspring desertion in birds. In: Current Ornithology. V. J. Nolan and E. D. Ketterson (eds.). Plenum Press, New York. **13**: 271-330.

Taborsky, B. and M. Taborsky (1991). Social organization of North Island Brown Kiwi - long-term pairs and 3 types of male spacing behavior. *Ethology* **89**(1): 47-62.

Taborsky, B. and M. Taborsky (1992). Spatial organization of the North Island Brown Kiwi *Apteryx australis mantelli* - sex, pairing status and territoriality. *Ibis* **134**(1): 1-10.

Taborsky, B. and M. Taborsky (1995). Habitat use and selectivity by the brown kiwi (*Apteryx australis mantelli*) in a patchy environment. *Auk* **112**(3): 680-689.

Taborsky, B. and M. Taborsky (1999). The mating system and stability of pairs in kiwi *Apteryx* spp. *Journal of Avian Biology* **30**(2): 143-151.

Taborsky, M. (1988). Kiwis and dog predation: observations in Waitangi state forest. *Notornis* **35**(3): 197-202.

Tarboton, W. R. (1995). Polyandry in the African Jacana: The roles of male dominance and rate of clutch loss. *Ostrich* **66**(2-3): 49-60.

Taylor, E. L., D. Blache, D. Groth, J. D. Wetherall and G. B. Martin (2000). Genetic evidence for mixed parentage in nests of the emu (*Dromaius novaehollandiae*). *Behavioral Ecology and Sociobiology* **47**(5): 359-364.

Thomas, G. H., T. Székely and J. D. Reynolds (2007). Sexual conflict and the evolution of breeding systems in shorebirds. *Advances in the Study of Behavior* **37**: 279–342.

Travis, S. E., C. N. Slobodchikoff and P. Keim (1995). Ecological and demographic effects on intraspecific variation in the social system of prairie dogs. *Ecology* **76**(6): 1794-1803.

Trivers, R. (1972). Parental investment and sexual selection. In: Sexual selection and the descent of man 1871-1971. B. Campbell (ed.). Aldine Press, Chicago: 139-179.

Van Dijk, R. E., A. Pogány, J. Komdeur, P. Lloyd and T. Székely (2010). Sexual conflict predicts morphology and behavior in two species of penduline tits. *BMC Evolutionary Biology* **10**: 107-115.

Van Dongen, W. F. D. and R. A. Mulder (2009). Multiple ornamentation, female breeding synchrony, and extra-pair mating success of golden whistlers (*Pachycephala pectoralis*). *Journal of Ornithology* **150**: 607-620.

Van Horn, R. C., J. Altmann and S. C. Alberts (2008). Can't get there from here: inferring kinship from pairwise genetic relatedness. *Animal Behaviour* **75**: 1173-1180.

Van Oosterhout, C., W. F. Hutchinson, D. P. M. Wills and P. Shipley (2004). MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes* **4**(3): 535-538.

Verner, J. and M. F. Willson (1966). The influence of habitats on mating systems of North American passerine birds. *Ecology* **47**(1): 143-147.

Wallander, J., D. Blomqvist and J. T. Lifjeld (2001). Genetic and social monogamy - does it occur without mate guarding in the Ringed Plover? *Ethology* **107**: 561-572.

Walsh, P. S., D. A. Metzger and R. Higuchi (1991). Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. *Biotechniques* **10**: 506-513.

Wauters, L. A., S. Bertolino, M. Adamo, S. Van Dongen and G. Tosi (2005). Food shortage disrupts social organization: the case of red squirrels in conifer forests. *Evolutionary Ecology* **19**: 375-404.

Weatherhead, P. J. and R. J. Robertson (1979). Offspring quality and the polygyny threshold: "The sexy son hypothesis". *The American Naturalist* **113**(2): 201-208.

Webster, M. S., K. A. Tarvin, E. M. Tuttle and S. Pruett-Jones (2007). Promiscuity drives sexual selection in a socially monogamous bird. *Evolution* **61**(9): 2205-2211.

Weller, T. J. and C. J. Zabel (2001). Characteristics of Fringed *Myotis* day roosts in Northern California. *The Journal of Wildlife Management* **65**(3): 489-498.

Westneat, D. F. and P. W. Sherman (1997). Density and extra-pair fertilizations in birds: a comparative analysis. *Behavioral Ecology and Sociobiology* **41**(4): 205-215.

Westneat, D. F., P. W. Sherman and M. L. Morton (1990). The ecology and evolution of extra-pair copulations in birds. Plenum Publishing Corporation, New York.

Westneat, D. F. and I. R. K. Stewart (2003). Extra-pair paternity in birds: Causes, correlates, and conflict. *Annual Review of Ecology Evolution and Systematics* **34**: 365-396.

White, G. C. and R. A. Garrott (1990). Analysis of wildlife radio-tracking data. Academic Press, New York, USA.

Whitehead, H. (1995). Investigating structure and temporal scale in social organizations using identified animals. *Behavioral Ecology* **6**: 199-208.

Whitehead, H. (1997). Analysing animal social structure. *Animal Behaviour* **53**: 1053-1067.

Wiebe, K. L. (2009). Nest excavation does not reduce harmful effects of ectoparasitism: an experiment with a woodpecker, the northern flicker *Colaptes auratus*. *Journal of Avian Biology* **40**(2): 166-172.

Wiebe, K. L., W. D. Koenig and K. Martin (2007). Costs and benefits of nest reuse versus excavation in cavity-nesting birds. *Annales Zoologici Fennici* **44**(3): 209-217.

Wiktander, U., O. Olsson and S. G. Nilsson (2000). Parental care and social mating system in the Lesser Spotted Woodpecker *Dendrocopos minor*. *Journal of Avian Biology* **31**: 447-456.

Willis, C. K. R. and R. M. Brigham (2004). Roost switching, roost sharing and social cohesion: forest-dwelling big brown bats, *Eptesicus fuscus*, conform to the fission-fusion model. *Animal Behaviour* **68**: 495-505.

Willis, C. K. R. and R. M. Brigham (2005). Erratum. *Animal Behaviour* **69**: 755.

Wilson, A. B., I. Ahnesjo, A. C. J. Vincent and A. Meyer (2003). The dynamics of male brooding, mating patterns, and sex roles in pipefishes and seahorses (family *Syngnathidae*). *Evolution* **57**: 1374-1386.

Winkler, D. W. (2001). Nests, eggs, and young: Breeding biology of birds. In: Handbook of Bird Biology. S. Podulka, J. R. Rohrbaugh and R. Bonney (eds.). The Cornell Lab of Ornithology, Ithaca, NY.

Withey, J. C., T. D. Bloxton and J. M. Marzluff (2001). Effects of tagging and location error in wildlife radiotelemetry studies. In: Radio tracking and animal populations. J. J. Millspaugh and J. M. Marzluff (eds.). Academic Press, San Diego: 45-69.

Wittenberger, J. F. and R. L. Tilson (1980). The evolution of monogamy: hypotheses and evidence. *Annual Review of Ecology and Systematics* **11**: 197-232.

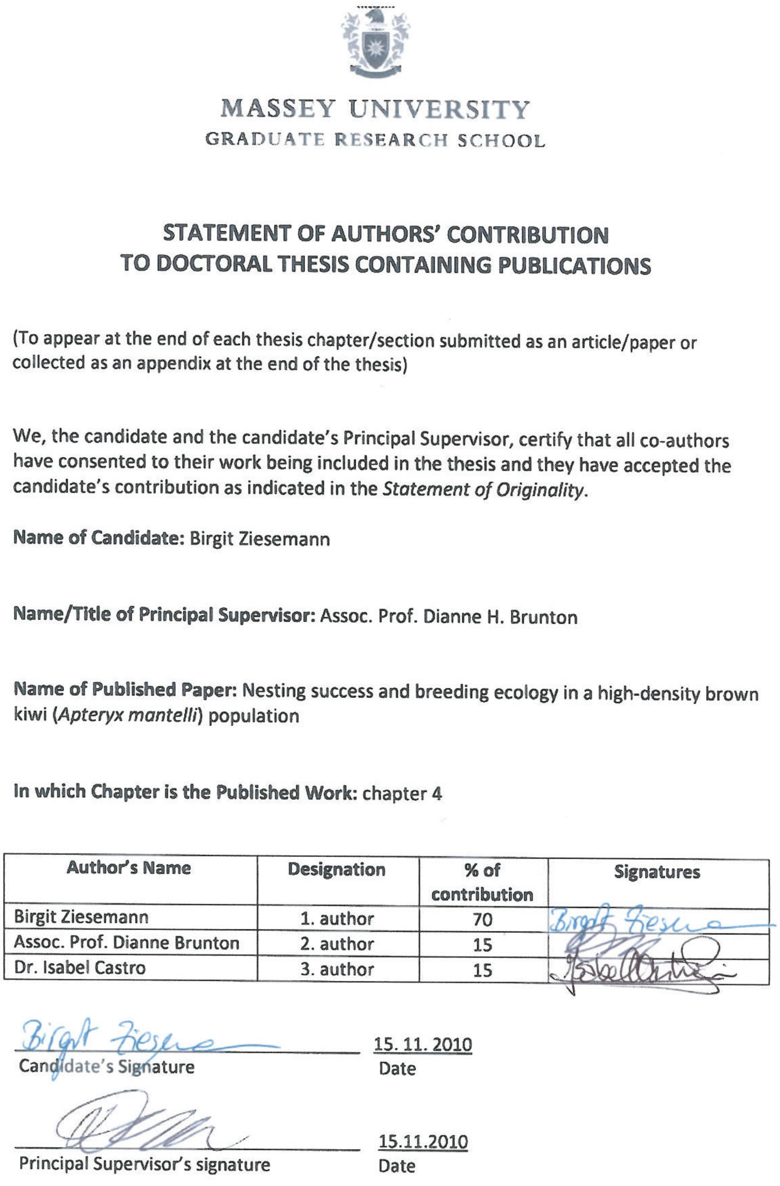
Wodzicki, K. A. (1950). Introduced mammals of New Zealand. Department of Scientific and Industrial Research Bulletin No.98. Department of Scientific and Industrial Research, Wellington, New Zealand.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**(1): 164-168.

Yezerinac, S. M. and P. J. Weatherhead (1997). Reproductive synchrony and extra-pair mating strategy in a socially monogamous bird, *Dendroica petechia*. *Animal Behaviour* **54**: 1393-1403.

APPENDIX 1

Statement of author contribution for manuscript accepted for publications: “Nesting success and breeding ecology in a high-density population of Brown Kiwi (*Apteryx mantelli*)” (chapter 4):



MASSEY UNIVERSITY
GRADUATE RESEARCH SCHOOL

STATEMENT OF AUTHORS’ CONTRIBUTION TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate’s Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate’s contribution as indicated in the *Statement of Originality*.

Name of Candidate: Birgit Ziesemann

Name/Title of Principal Supervisor: Assoc. Prof. Dianne H. Brunton

Name of Published Paper: Nesting success and breeding ecology in a high-density brown kiwi (*Apteryx mantelli*) population

In which Chapter is the Published Work: chapter 4

Author’s Name	Designation	% of contribution	Signatures
Birgit Ziesemann	1. author	70	Birgit Ziese
Assoc. Prof. Dianne Brunton	2. author	15	
Dr. Isabel Castro	3. author	15	

Birgit Ziese
Candidate’s Signature

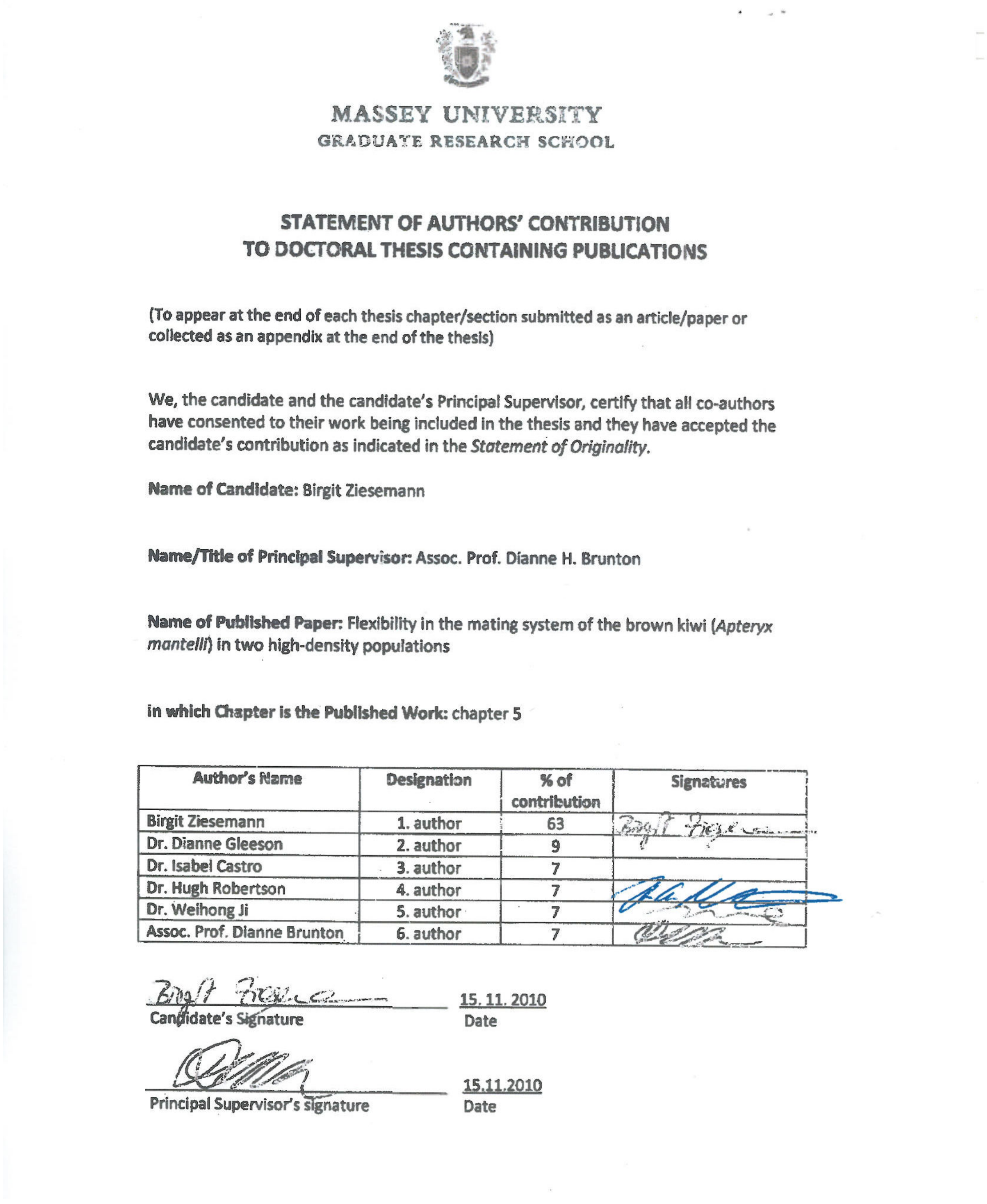
15. 11. 2010
Date

Principal Supervisor’s signature

15.11.2010
Date

APPENDIX 2

Statement of author contribution for manuscript submitted for publication: “Flexibility in the mating system of the Brown Kiwi (*Apteryx mantelli*) in two high-density populations” (chapter 5):



MASSEY UNIVERSITY
GRADUATE RESEARCH SCHOOL

STATEMENT OF AUTHORS’ CONTRIBUTION TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate’s Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate’s contribution as indicated in the *Statement of Originality*.

Name of Candidate: Birgit Ziesemann

Name/Title of Principal Supervisor: Assoc. Prof. Dianne H. Brunton

Name of Published Paper: Flexibility in the mating system of the brown kiwi (*Apteryx mantelli*) in two high-density populations

In which Chapter is the Published Work: chapter 5

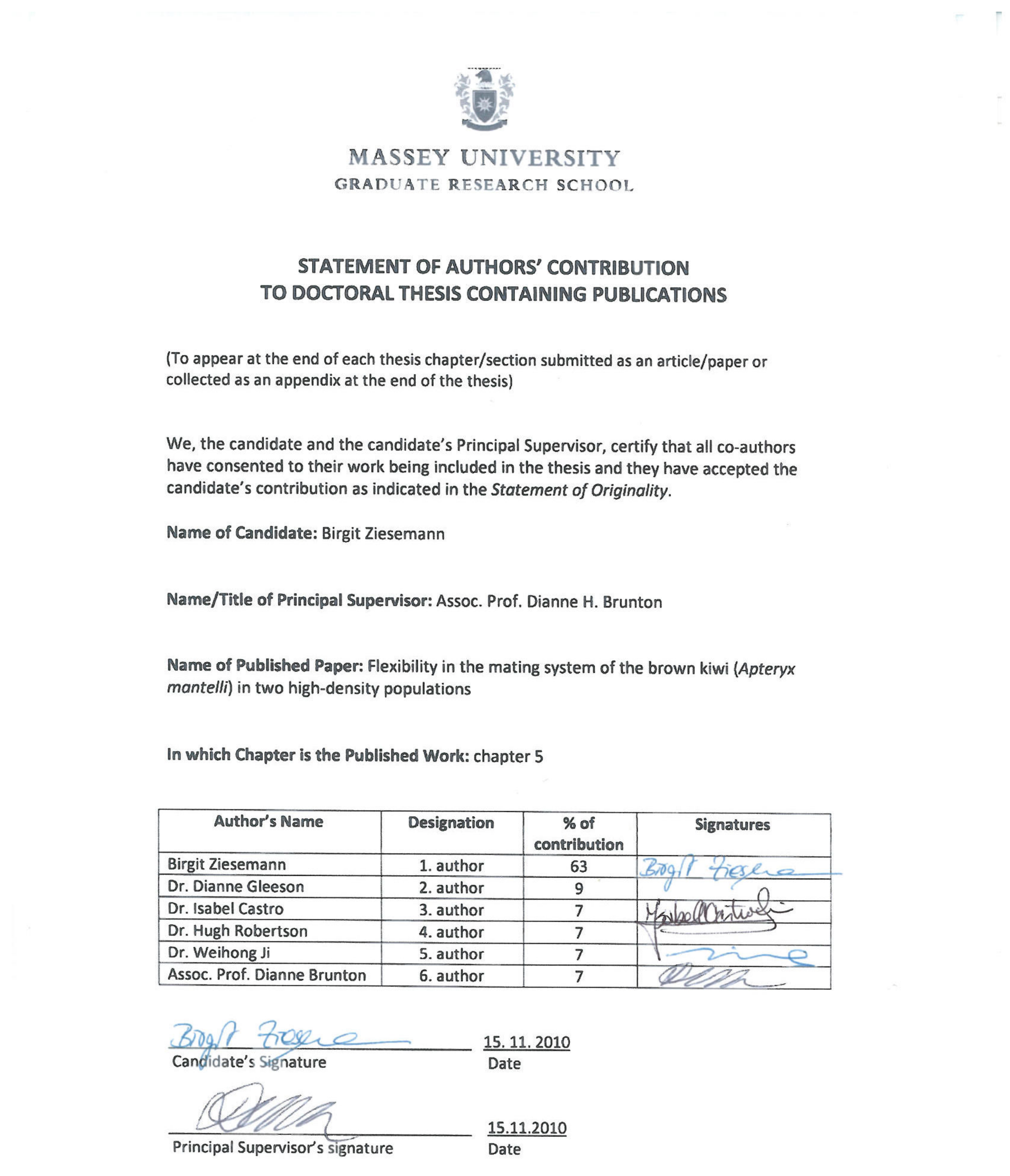
Author’s Name	Designation	% of contribution	Signatures
Birgit Ziesemann	1. author	63	
Dr. Dianne Gleeson	2. author	9	
Dr. Isabel Castro	3. author	7	
Dr. Hugh Robertson	4. author	7	
Dr. Weihong Ji	5. author	7	
Assoc. Prof. Dianne Brunton	6. author	7	

Candidate’s Signature

15. 11. 2010
Date

Principal Supervisor’s signature

15.11.2010
Date



MASSEY UNIVERSITY
GRADUATE RESEARCH SCHOOL

STATEMENT OF AUTHORS' CONTRIBUTION TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

Name of Candidate: Birgit Ziesemann

Name/Title of Principal Supervisor: Assoc. Prof. Dianne H. Brunton

Name of Published Paper: Flexibility in the mating system of the brown kiwi (*Apteryx mantelli*) in two high-density populations

In which Chapter is the Published Work: chapter 5

Author's Name	Designation	% of contribution	Signatures
Birgit Ziesemann	1. author	63	
Dr. Dianne Gleeson	2. author	9	
Dr. Isabel Castro	3. author	7	
Dr. Hugh Robertson	4. author	7	
Dr. Weihong Ji	5. author	7	
Assoc. Prof. Dianne Brunton	6. author	7	

Candidate's Signature — 15. 11. 2010 Date

Principal Supervisor's signature — 15.11.2010 Date

MASSEY UNIVERSITY
GRADUATE RESEARCH SCHOOL

STATEMENT OF AUTHORS' CONTRIBUTION TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

Name of Candidate: Birgit Ziesemann

Name/Title of Principal Supervisor: Assoc. Prof. Dianne H. Brunton

Name of Published Paper: Flexibility in the mating system of the brown kiwi (*Apteryx mantelli*) in two high-density populations

In which Chapter is the Published Work: chapter 5

Author's Name	Designation	% of contribution	Signatures
Birgit Ziesemann	1. author	63	
Dr. Dianne Gleeson	2. author	9	
Dr. Isabel Castro	3. author	7	
Dr. Hugh Robertson	4. author	7	
Dr. Weihong Ji	5. author	7	
Assoc. Prof. Dianne Brunton	6. author	7	

Candidate's Signature — 15. 11. 2010
Date

Principal Supervisor's signature — 15.11.2010
Date

Jules 2006

Jules 2008

‘In the darkness they shine’