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

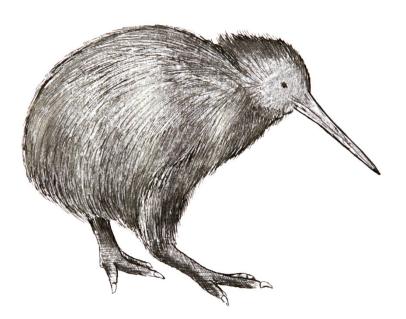
A thesis presented in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Ecology at Massey University, Albany, New Zealand

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'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

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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.

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