Evolutionary consequences and fitness correlates of extra-pair mating in the tūī, *Prosthemadera novaeseelandiae*

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Frontispiece

"Me he korokoro tūī"

"How eloquent he is; he has the throat of a Tūī"

Maori proverb

Abstract

Animals of many different taxa exhibit sexual dimorphism in phenotypic traits that have evolved through male-male competition and/or female mate choice. Many bird species also engage in extra-pair mating that can exert significant selection pressures on male secondary sexual characters. Studies examining the evolution of sexual dimorphism in birds have demonstrated that the degree of plumage dimorphism is positively related to rates of extra-pair paternity (EPP) among species. In contrast, it is generally argued that sexual size dimorphism (SSD) is not related to EPP but instead is associated with social polygamy. Thus understanding the adaptive function of extra-pair mating may shed light on the evolution of male sexually selected traits. It is argued that females increase offspring fitness by maximising the benefits they receive from males through extra-pair mating. Females are hypothesised to gain direct benefits such as parental care or territory quality through social mate choice, as well as indirect benefits such as compatible genes or good genes benefits through extra-pair mate choice. However, despite much research, the exact adaptive function of female genetic polyandry is still debated.

This thesis investigates the influence of sexual selection on the evolution of reproductive behaviours and male secondary sexual characters. We examine correlates and fitness consequences of female within-pair and extra-pair mate choice in the New Zealand tūī, *Prosthemadera novaeseelandiae*. Tūī are unusual for a socially monogamous passerine in that they exhibit extreme SSD. They also

possess unique ornamental white throat feather plumes which are larger in males, but of which the functional significance is unknown. We discover that tūī possess one of the highest rates of EPP of any socially monogamous bird: EPP occurred in 72% of all broods and 57% of all offspring were extra-pair. Our results show that tūī exhibit a level of SSD normally associated with strong polygamy, with males being 50% heavier than females. In addition, male body size and ornament size are strong predictors of paternity success. Thus, contrary to current opinion, these findings demonstrate that EPP can be causal in the evolution of SSD. Furthermore, this study provides needed evidence that selective pressures, acting via EPP, can lead to the evolution of male ornaments.

Females paired with large social males gained direct benefits that increased offspring survival. Parental ability was not related to male size suggesting that large males may instead provide higher quality territories. Two traits correlating with male extra-pair mating success also predicted offspring fitness: extra-pair young and the offspring of genetically dissimilar sires possessed faster growth rates, and females mated to highly ornamented males overproduced sons to gain offspring with greater reproductive potential. These findings suggest that females gain indirect benefits from extra-pair mate choice, and support both the Fisher-Zahavi good genes and compatible genes hypotheses as functional benefits of female genetic polyandry.

Examination of tūī parental provisioning rates revealed that males provided significantly less parental care than females. Male ornament size was inversely related to paternal effort, providing further support that ornamentation indicates indirect rather than direct benefits in tūī. In addition, males with lower paternity of

their broods provided more care than males gaining full paternity. When considered together with female choice for highly ornamented extra-pair males, these findings suggest the existence of alternative male reproductive strategies in which males trade-off investment in offspring with mating effort in response to their residual reproductive potential.

Tūī are unusual in that they possess several attributes commonly associated with social polygyny, such as extreme SSD, multiple male traits, and reduced paternal care. Although the selection pressures leading to the evolution of ornamentation and SSD in tūī remain to be clearly resolved, the relationship between these two traits is likely complex. We argue that these traits may have evolved through male-male competition but are reinforced by female choice for dominant males. This study substantially furthers our knowledge of tūī mating behaviours and makes a significant contribution towards understanding the functional significance of male traits and EPP. Finally, our findings have implications for sexual selection theory pertaining to the evolution of SSD.

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