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# **Influences of environmental and biological factors on song complexity in songbirds**

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## Frontispiece



A small group of tui (*Prosthemadera novaeseelandiae*) at a feeding station (photo: Anna Arrol, with permission).

*“The Parish I live in is a very abrupt, uneven country, full of hills and woods, and therefore full of birds”.*

*(Gilbert White)*

# Abstract

In songbirds, song is important for mate attraction and territory defence. Females of some species preferentially select males that have more complex songs, an honest signal for male fitness. Examining variation in song complexity provides important insights into the evolution of sexually-selected vocal characteristics. In this thesis, hypotheses examining song complexity variation and a series of biological and environmental factors were tested. A socially monogamous songbird with highly complex songs and high extra-pair paternity (tui, *Prosthemadera novaeseelandiae*) was selected as the main study model. Firstly, the hypothesis that song complexity in songbird broadcast songs would be higher than in interactive songs was tested. In addition, it was predicted that there would be a positive association between song complexity and extra-pair paternity frequency. This was conducted across 78 songbird species, the most comprehensive analysis in this study area to date. Concordant with the predictions, tui broadcast songs were found to have higher complexity than interactive songs. Furthermore, after controlling for phylogenetic relatedness, a significant positive association between extra-pair paternity frequency and within-song complexity was found across multiple species. Secondly, I tested the hypothesis that tui song complexity would be higher at dawn than at solar noon and dusk. It has previously been established that dawn is a critical period for intensified songbird vocal displays, such as increased song rate. However, little research has been conducted on diurnal variations in song complexity, which was predicted to be higher at dawn. As predicted, both tui song complexity and intrusion rates were significantly greater at dawn than at dusk. In addition, two song

complexity variables were inversely correlated with intrusion rate. Thirdly, the hypothesis that male tui would respond more aggressively to more complex songs was tested, to assess whether song complexity plays a role in male-male interactions. Male responses to rival male songs of different degrees of complexity were subsequently examined using playback experiments. Male tui songs with higher complexity evoked stronger and more aggressive intrasexual responses than simple song as predicted. Fourthly, I tested the hypothesis that habitat complexity would correlate positively with tui song complexity. The association between habitat structure and tui song complexity was investigated by comparing male song complexity in two types of habitat: forest remnants with high complexity, and open habitats with lower complexity. As predicted, habitat complexity correlated positively with tui song complexity. Overall, the findings in this thesis provide evidence that several biological and environmental factors are associated with the evolution of song complexity; a socially-selected vocal trait. This study suggests that complex songs in vocally complex songbirds may have evolved under extra-pair paternity, territorial and environmental pressures. It therefore has implications for furthering our understanding of song complexity evolution in songbirds.

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## Permits and ethics

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