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

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degree

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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, *Prothemadera 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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# Table of contents

|  |            |
|--|------------|
| Frontispiece.....  | II         |
| <b>Abstract.....</b>   | <b>III</b> |
| Acknowledgements.....  | V          |
| Permits and ethics .....   | VIII       |
| Table of contents.....   | IX         |
| List of figures.....   | XIII       |
| List of tables.....  | XVII       |
| <b>1. General introduction .....</b>   | <b>1</b>   |
| 1.1 Songbird vocal behaviour .....   | 2          |
| 1.1.1 Song complexity .....  | 4          |
| 1.1.2 Song complexity variation .....  | 6          |
| 1.1.3 General methods and summary of song complexity measures .....  | 13         |
| 1.2 Main study species.....  | 17         |
| 1.3 Thesis structure and objectives .....  | 21         |
| <b>2. It's complicated: the association between songbird extra-pair paternity<br/>and within-song complexity .....</b> | <b>27</b>  |
| Abstract.....  | 28         |
| 2.1 Introduction.....  | 29         |
| 2.2 Methods .....  | 34         |
| 2.2.1 Data collection: testing association between EPP and song complexity in<br>multiple species.....                 | 34         |

|   |           |
|---|-----------|
| 2.2.2 Data collection: testing song complexity variation between tui song classes...            | 36        |
| 2.2.3 Song variables and data analysis for EPP and song complexity in multiple species .....    | 42        |
| 2.2.4 Phylogenetic correction.....  | 45        |
| 2.2.5 Mating system .....   | 46        |
| 2.2.6 Sexual dichromatism.....  | 47        |
| 2.2.7 Parental care .....   | 48        |
| 2.2.8 Song variables and data analysis for tui song classes .....                               | 49        |
| 2.2.9 Within-group multivariate analysis.....   | 49        |
| 2.2.10 Between-group multivariate analysis.....   | 50        |
| 2.2.11 Song variables .....   | 52        |
| 2.3 Results.....  | 53        |
| 2.3.1 Testing association between EPP and song complexity in multiple species ....              | 53        |
| 2.3.2 Phylogenetic correction.....  | 55        |
| 2.3.3 Mating system, sexual dichromatism and parental care.....                                 | 57        |
| 2.3.4 Tui song classes: within-group (tui IS) comparison .....                                  | 58        |
| 2.3.5 Comparison between tui BS and IS .....  | 58        |
| 2.4 Discussion.....   | 61        |
| <b>3. Higher song complexity and intrusion rate at dawn in a vocally complex songbird .....</b> | <b>66</b> |
| Abstract .....  | 67        |
| 3.1 Introduction.....   | 68        |
| 3.2 Methods .....   | 72        |
| 3.2.1 Study site.....   | 72        |
| 3.2.2 Song recording .....  | 73        |

|   |            |
|---|------------|
| 3.2.3 Intrusion rate (intruder pressure).....   | 75         |
| 3.2.4 Song variables.....   | 77         |
| 3.2.5 Statistical and graphical methods.....  | 79         |
| 3.3 Results.....  | 81         |
| 3.3.1 Relationship between song complexity and intrusion rate.....  | 86         |
| 3.4 Discussion.....   | 88         |
| <b>4. Fighting talk: complex song elicits more aggressive responses in a<br/>vocally complex songbird .....</b> | <b>94</b>  |
| Abstract.....   | 95         |
| 4.1 Introduction.....   | 96         |
| 4.2 Methods .....   | 100        |
| 4.2.1 Locations.....  | 100        |
| 4.2.2 Stimuli.....  | 102        |
| 4.2.3 Playback experiment.....  | 106        |
| 4.2.4 Statistical analysis .....  | 110        |
| 4.2.5 Complexity measures of vocal responses .....  | 112        |
| 4.3 Results.....  | 114        |
| 4.3.1 Complexity of vocal responses .....   | 118        |
| 4.4 Discussion.....   | 121        |
| <b>5. Local habitat complexity correlates with song complexity in a vocally<br/>elaborate honeyeater.....</b>   | <b>125</b> |
| Abstract.....   | 126        |
| 5.1 Introduction.....   | 127        |
| 5.2 Methods .....   | 129        |

|  |            |
|--|------------|
| 5.2.1 Study sites .....  | 129        |
| 5.2.2 Data analysis .....  | 131        |
| 5.2.3 Sound recordings.....  | 134        |
| 5.2.4 Comparison of song complexity between habitats .....                                   | 139        |
| 5.3 Results.....   | 143        |
| 5.3.1 Habitat complexity.....  | 143        |
| 5.3.2 Song complexity.....   | 145        |
| 5.4 Discussion.....  | 148        |
| <b>6. Conclusions and future directions.....</b>   | <b>151</b> |
| 6.1 Song complexity and extra-pair mate attraction.....                                      | 153        |
| 6.2 Song complexity and territoriality.....  | 155        |
| 6.3 Song complexity, temporal song variables and habitat type .....                          | 157        |
| <b>References.....</b>   | <b>160</b> |
| <b>Appendices.....</b>   | <b>203</b> |
| <b>Appendix 1: Reprints of published chapters and chapters in press .....</b>                | <b>204</b> |
| <b>Appendix 2: Extra-pair paternity frequencies.....</b>                                     | <b>265</b> |
| <b>Appendix 3: Reprints of other papers published or in press during PhD<br/>study .....</b> | <b>285</b> |
| <b>Appendix 4: Statement of contribution forms .....</b>                                     | <b>333</b> |

# List of figures

Figure 1.1: A spectrogram of a male tui song highlighting total number of syllables, song duration and syllable diversity. This example has eight syllables in total and seven different syllables (syllable five is repeated). The syllable rate of this song is  $8 \div 2 \text{ sec} = 4$  syllables per second..... 14

Figure 1.2: Ten-second song spectrographic examples of tui and three other vocally complex songbird species ..... 20

Figure 2.1: The location of the eight study sites around the Auckland region including a) the five offshore islands (map from NIWA, with permission) and b) the location of the three mainland study sites in relation to Auckland’s central business district..... 39

Figure 2.2: The phylogenetic tree of the 78 songbird species within this study, including the scale. The units of branch length are nucleotide substitutions per site i.e. the number of changes or 'substitutions' divided by the length of the sequence..... 46

Figure 2.3: Spectrographic representation of the variables employed to measure song complexity in this study. Spectrograms show the a) male tui BS, including trills, which were only used in the analysis of tui song classes as it is a consistent feature of tui songs, and b) a tui BS showing how the number of syllable transitions (ST) were calculated for each song across all species..... 51

Figure 2.4: The relationship (non-phylogenetic linear regression with mean +/- 95% confidence intervals) between EPP frequency and overall song complexity (log-transformed) ..... 54

Figure 2.5: The NMDS ordination plot based on Euclidean distance of BS (red crosses) and IS (blue squares) in tui ..... 59

Figure 3.1: Map of Tawharanui Regional Park showing the three study locations where tui were recorded and observed within the park (1. Jones Bay, 2. Lagoon area, 3. Ecology Bush)..... 73

Figure 3.2: A spectrogram of a male tui song highlighting total number of syllables, song duration and syllable diversity. This example has eight syllables in total and seven different syllables (syllable five is repeated). The syllable rate of this song is  $8 \div 2 \text{ sec} = 4$  syllables per second ..... 79

Figure 3.3: NMDS plot of the tui song complexity data showing differences in the centroids of the three different times of day (dawn, solar noon, and dusk). The plot suggests dawn complexity parameters correlate with higher number of syllables, song duration and syllable diversity as the dawn datapoints were situated generally towards the right of the plot. Dusk on the other hand had lower complexity in terms of these variables as the dusk datapoints were situated more towards the left of the plot. The inset shows a unit circle (radius = 1) with vector length describing the Spearman rank correlation of the song variables ..... 85

Figure 4.1: Map showing the location of Tawharanui Regional Park and the 12 playback locations within the park. Playback locations 6, 8, 9, 10 had banded focal males ..... 100

Figure 4.2: Spectrographic representation of total number of syllables, song duration, syllable diversity (total number of different syllables) and syllable transitions (ST) calculation. This two second tui song example has eight syllables in total, seven different syllables (as syllable five is repeated), and six syllable transitions..... 103

Figure 4.3: Sixty-second exemplars of the song stimuli with different levels of complexity (the stimuli): complex song, simple song and control heterospecific song (grey warbler) used in these playback experiments. Each period of signal represents a single song bout and each song stimulus had a concordant signal-to-silence ratio ..... 105

Figure 4.4: PCA scatterplot with Eigenvalue scales along the axes (crosses: complex song, unshaded squares: simple song, shaded squares: control heterospecific song) ..... 117

Figure 4.5: An exemplar of tui song responses to complex song and simple song playback ..... 120

Figure 5.1: Map showing the location of the two study sites: Tawharanui and Wenderholm Regional Parks ..... 129

Figure 5.2: Maps showing the location of the habitat complexity survey sites plus the transect lines (T) and bird recording transect lines (B) at Tawharanui (a) and Wenderholm Regional Park (b)..... 133



Figure 5.3: A spectrographic representation of the variables employed in this study to measure song complexity in tui ..... 140

Figure 5.4: A CAP analysis plot showing the forest and open habitats at both Tawharanui, and Wenderholm versus the first canonical axis. The CAP plot chooses an axis that best discriminates the song complexity data and plots the data on that axis. The CAP analysis correctly classified 93.3% of the songs, strongly indicating that a high degree of variation in song complexity between the forest and open habitats existed in both nature reserves..... 147

# List of tables

|   |    |
|---|----|
| Table 1.1: An overview of reproductive and vocal behaviour that varies across a sample of vocally complex songbird species. Also shown are the song complexity measures used in previous research for the various songbird species.....   | 19 |
| Table 1.2: A summary of the knowledge gaps, and the research questions designed to help fill these knowledge gaps within the four data chapters of this thesis .....  | 26 |
| Table 2.1: Tui song recording sites and number of tui recorded.....   | 41 |
| Table 2.2: Song variables employed in this study to compare song complexity in 78 different songbird species with varying EPP frequencies, and between BS and IS in tui.....  | 44 |
| Table 2.3: A summary of the linear regression scores for the relationship between EPP frequency and each of the song complexity parameters.....   | 55 |
| Table 2.4: The relationship between EPP and song complexity, tested using PGLS analysis. The <i>P</i> -values here signify that the $\lambda$ values for all variables were not significantly different from zero. This suggests that these traits showed greater divergence between taxa than would be expected under a Brownian motion model of trait evolution ..... | 57 |
| Table 2.5: Differences in song complexity parameters between BS and IS of male tui .....  | 60 |

|  |     |
|--|-----|
| Table 3.1: The descriptive statistics showing the average song complexity parameters and intrusion rate at dawn, solar noon, and dusk from 401 long-range songs at dawn, 203 songs at solar noon, and 316 songs at dusk in a tui population (N = 15, 11, 16) .....   | 82  |
| Table 3.2: A matrix showing the test statistic/P values of pairwise PERMANOVA tests that compared song complexity levels between the 3 times of day (999 permutations) .....   | 83  |
| Table 3.3: The number of males that either decreased (↓), increased (↑), or remained the same (→) for each song complexity variable and IR at dusk compared to dawn. Note that three individuals did not sing during both dawn <i>and</i> dusk recording sessions so were omitted from the tally .....             | 84  |
| Table 3.4: The eigenvalues, variance explained and factor loadings of the variables following exploratory factor analysis for the song complexity variables that were to be used to test for associations with intrusion rate. Those variables with factor loading values greater than 0.8 are shown in bold ..... | 87  |
| Table 4.1: The mean complexity values ± standard error per song of the tui playback stimuli used in this study .....   | 104 |
| Table 4.2 Variables recorded as measures of the levels of aggressiveness of territorial male tui in response to the playback stimuli (Beecher & Campbell 2005, Parker et al. 2010):.....   | 109 |

|  |     |
|--|-----|
| Table 4.3: Eigenvalues, variance explained and factor loadings of the response variables following principal component analysis (PCA) for the response of focal males to complex, simple or control stimuli. *Variables with factor loading values greater than 0.7 .....  | 116 |
| Table 4.4: The descriptive statistics including the means $\pm$ standard error values and <i>P</i> values from the Wilcoxon matched-pairs signed ranks test of the eight variables employed in this study for all three stimuli types. Note that only the <i>P</i> values for complex vs simple song are shown ..... | 118 |
| Table 4.5: The means $\pm$ standard error of male song complexity variables in response to playback of complex and simple songs .....  | 119 |
| Table 5.1: The number of recorded birds, the number of songs recorded (625 songs in total), mean songs recorded per individual and the sampling effort in each habitat .....   | 137 |
| Table 5.2: Variables employed in this study to measure song complexity ..  | 141 |
| Table 5.3: The habitat complexity descriptive statistics of two habitats at Tawharanui and Wenderholm. The number of trees and shrubs in each habitat relative to each PCQ is also presented .....   | 144 |
| Table 5.4: The descriptive statistics of the five variables measuring song complexity in two tui subpopulations at Tawharanui Regional Park and Wenderholm Regional Park .....   | 146 |