Trait Integration as a Constraint on Phenotypic Evolution

Submitted by William Ronald Pitchers, to the University of Exeter as a thesis for the Degree of Doctor of Philosophy in Biological Sciences, June 2010.

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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signed: W. R. Pitchers

..........................................................
ABSTRACT

One of the most compelling features of biology is the apparent complexity of phenotypes. The morphology and behaviour of organisms are wonderfully varied, and as evolutionary biologists we attempt to understand the patterns and mechanisms that underlie this diversity. Though evolution leads to changes in gene frequency over time, it is upon the phenotype that selection acts. The integration that allows phenotypes to function as coherent systems, by exposing only certain trait combinations to selection, may therefore act to divert or constrain phenotypic evolution.

I begin this thesis with a quantitative review, where I uncover a pattern of stronger potential integrative constraint on sexual signals than morphology. I then present empirical work using the black field cricket, *Teleogryllus commodus*, as a model system. Specifically, I employ estimates of the phenotypic variance-covariance matrix (\( P \)) to summarise integration within a five-dimensional characterization of the structure of the males’ sexual advertisement call. In Chapters 3 and 4, I show that despite changes in trait means, the structure of \( P \) for the advertisement call is stable among genetically divergent populations, over time and between diets. In Chapter 5, I reveal a novel link between the size and shape of the male forewing, which is used in the production of calls, and call structure. Finally, I use artificial calls to test for divergence in female call preference across populations and whether this varies with diet, and show that female choosiness is condition-dependent.

Collectively, my results highlight the utility of \( P \) as a tool for studying the integration of complex traits. The extreme stability of \( P \) in *T. commodus* suggests that it is likely to act as a constraint on the evolution of call structure in this species. This insight, together with the link between call structure and wing morphology, illustrates the value of treating evolution as a multivariate process.
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Since joining the CEC I've always found someone willing to discuss ideas (whether over coffee or something stronger) or to critique my writing and analyses; all my colleagues in the postgrad office deserve thanks in this regard, but particularly Sahran Higgins, Damo Smith, Xav Harrison, MD Sharma, MattLab Witt, Emma Barrett and Princess Stott. Most of all, thanks to Fiona Ingleby for believing in me and being right all the time.

Before I could undertake any empirical work, I had to establish captive populations of crickets for study. John Hunt and I made a collection trip to Australia, and we thank all the landowners who allowed us to collect crickets from their properties. During this trip we were assisted by Rob Brooks and Erik Postma, and thanks are particularly due to Michael Jennions for his generosity with both time and resources at ANU, without which our collections might not have been possible.

My time in the Hunt Lab was made immeasurably more enjoyable by the friendship and teamwork of my colleagues: thanks to Ruth Archer, Chris Mitchell and Probie. Also, it should be said that the Lab itself would be a far less pleasant place to work without the indefatigable efforts of Corrina Lowry.

I would not be here without the encouragement of Jason Wolf and Paula Kover, who gave me new direction and reminded me why I wanted to be a scientist in the first place. The only people to have encouraged me more would my parents; I couldn't have asked for more stalwart support, and ought to tell them so more often.

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# TABLE OF CONTENTS

**ABSTRACT** .................................................................................................................................................. 2

**ACKNOWLEDGEMENTS** ................................................................................................................................. 3

**TABLE OF CONTENTS** .................................................................................................................................. 4

**TABLES AND FIGURES** ................................................................................................................................. 6

**AUTHOR'S DECLARATIONS** .......................................................................................................................... 9

**CHAPTER 1: An Introduction to Integration** ................................................................................................. 10

1.1. **INTEGRATION** ..................................................................................................................................... 10

1.2. **VIEWING INTEGRATION FROM A MATRIX PERSPECTIVE** ................................................................. 12

1.3. **THE EVOLUTION OF INTEGRATED PHENOTYPES** ........................................................................... 15

1.4. **ADVERTISEMENT CALLS AS A COMPLEX SEXUAL TRAIT** ............................................................... 18

1.5. **TELOGRYLLUS COMMODUS AS A MODEL SYSTEM** ........................................................................ 20

1.6. **THESIS OUTLINE** ............................................................................................................................... 21

**CHAPTER 2: The Prevalence of ‘Evolutionary Lines of Least Resistance’ in Morphology, Life-History and Sexual Signals** ......................................................................................................................... 25

2.1 **ABSTRACT** ........................................................................................................................................... 25

2.2 **INTRODUCTION** .................................................................................................................................. 26

2.3 **METHODS** ......................................................................................................................................... 28

2.4 **RESULTS** ............................................................................................................................................. 32

2.5 **DISCUSSION** ....................................................................................................................................... 34

**CHAPTER 3: Stability of the Phenotypic Variance-Covariance Matrix (P) over Evolutionary Time and Geographic Space** ......................................................................................................................... 38

3.1 **ABSTRACT** ........................................................................................................................................... 38

3.2 **INTRODUCTION** .................................................................................................................................. 39

3.3 **METHODS** ......................................................................................................................................... 42

3.4 **RESULTS** ............................................................................................................................................. 47

3.5 **DISCUSSION** ....................................................................................................................................... 53
<table>
<thead>
<tr>
<th>CHAPTER 4: The Stability of the Phenotypic Variance-Covariance Matrix under Nutritional Stress</th>
<th>56</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.1 ABSTRACT</td>
<td>56</td>
</tr>
<tr>
<td>4.2 INTRODUCTION</td>
<td>57</td>
</tr>
<tr>
<td>4.3 METHODS</td>
<td>60</td>
</tr>
<tr>
<td>4.4 RESULTS</td>
<td>63</td>
</tr>
<tr>
<td>4.5 DISCUSSION</td>
<td>73</td>
</tr>
<tr>
<td>CHAPTER 5: Secondary Sexual Morphology and the Evolution of an Acoustic Signal</td>
<td>78</td>
</tr>
<tr>
<td>5.1 ABSTRACT</td>
<td>78</td>
</tr>
<tr>
<td>5.2 INTRODUCTION</td>
<td>79</td>
</tr>
<tr>
<td>5.3 METHODS</td>
<td>83</td>
</tr>
<tr>
<td>5.4 RESULTS</td>
<td>86</td>
</tr>
<tr>
<td>5.5 DISCUSSION</td>
<td>97</td>
</tr>
<tr>
<td>CHAPTER 6: Inter-Population Variation in Mate Choice Behaviour under Nutritional Stress in <em>Teleogryllus commodus</em></td>
<td>103</td>
</tr>
<tr>
<td>6.1 ABSTRACT</td>
<td>103</td>
</tr>
<tr>
<td>6.2 INTRODUCTION</td>
<td>104</td>
</tr>
<tr>
<td>6.3 METHODS</td>
<td>108</td>
</tr>
<tr>
<td>6.4 RESULTS</td>
<td>112</td>
</tr>
<tr>
<td>6.5 DISCUSSION</td>
<td>117</td>
</tr>
<tr>
<td>CHAPTER 7: General Discussion</td>
<td>122</td>
</tr>
<tr>
<td>APPENDICES</td>
<td>137</td>
</tr>
<tr>
<td>APPENDIX I</td>
<td>137</td>
</tr>
<tr>
<td>APPENDIX II</td>
<td>146</td>
</tr>
<tr>
<td>APPENDIX III</td>
<td>147</td>
</tr>
<tr>
<td>REFERENCES</td>
<td>148</td>
</tr>
</tbody>
</table>
TABLES AND FIGURES

Chapter 1

Figure 1.1: The components of a 5-dimensional covariance matrix .......................................................... 13
Figure 1.2: The plane described by a singular matrix ................................................................................. 15
Figure 1.3: The biasing effect of \( g_{\text{max}} \) on response to selection when traits co-vary ............. 17

Chapter 2

Table 2.1: Summary table for all animal traits assigned as sexually selected ................................. 30
Table 2.2: Results of a randomised full-factorial general linear model ........................................... 33
Figure 2.1: Boxplot to show differences in \( E_{hi} \) between trait types ................................................. 34

Chapter 3

Table 3.1: Results of a MANOVA on the structure of the advertisement call of \( T. \) commodus among populations and between generations .............................................................................. 48
Table 3.2: Pairwise comparisons between populations using Mantel test ........................................ 49
Table 3.3: Matrix comparison by MANOVA of Jackknife pseudovalues matrix elements ............... 50
Table 3.4: The results of matrix comparison by CPC analysis using Flury’s hierarchy .............. 51
Table 3.5: The results of geometric matrix comparisons ...................................................................... 51
Figure 3.1: Means and 95% confidence ellipses for each population and each generation for the first 2 principal components of call structure .............................................................. 52

Chapter 4

Table 4.1: Results of a MANOVA showing the effects of population and diet treatment on male life-history .......................................................................................................................... 64
Table 4.2: Results of a MANOVA showing the effects of population and diet treatment on advertisement call structure .............................................................................................................. 68
Table 4.3: 2-tailed \( p \)-values from matrix comparisons by Mantel test .................................................. 69
Table 4.4: Results of a MANOVA on Jackknife pseudovalues for call trait P matrix elements. .. 70
Table 4.5: Results of common principal components analysis comparing P matrices using the Flury's hierarchy .......................................................... 71
Table 4.6: Results of a geometric comparison of P matrix eigenvectors ................. 71
Figure 4.1: Reaction norms for the three life-history traits measured .................. 65
Figure 4.2: Reaction norms for the five call traits measured .......................... 67
Figure 4.3: Ellipses representing the first two eigenvectors and associated eigenvalues of P for all 6 populations and for both diets ........................................... 72

Chapter 5

Table 5.1: Results of a MANOVA of Procrustes coordinates after model reduction .......... 87
Table 5.2: Results of a MANOVA of standardised call parameters ......................... 86
Table 5.3: Results of a full factorial ANOVA of centroid size values after model reduction ... 90
Table 5.4: Coefficients for call traits from analyses of the covariance of wing centroid size and call traits .............................................................. 91
Table 5.5: Coefficients for call traits from analyses of the covariance of wing shape and regression residuals for standardised call traits ........................ 92
Table 5.6: The matrix of Pearson correlation coefficients for call structure measures and pronotum width ......................................................................... 94
Table 5.7: A summary of previous studies that have examined the relationships between forewing morphology and some aspect(s) of advertisement call in Gryllid crickets. .... 96
Figure 5.1: A simplified outline drawing of the venation of male forewings, with landmark points indicated ................................................................. 85
Figure 5.2: Mean wing shapes for our six populations and two generations ................ 89
Figure 5.3: Plot to show the relationships between call parameters and body size .......... 94
Figure 5.4: Shape variance associated with the 1st PLS axis from a partial least squares regression with Procrustes coordinates against standardised call traits .......... 93
Figure 5.5: Shape variance associated with the 1st PLS axis from a partial least squares regression of Procrustes coordinates against standardised call traits, with variance pooled within generations ........................................ 93
Chapter 6

Table 6.1: Numbers phonotaxis trials conducted by diet treatment and population. ............111
Table 6.2: The effect of diet on female life-history traits; means and ANOVA statistics .........113
Table 6.3: Results of a GLM on female preference....................................................114
Table 6.4: Results of an ANOVA to test for differences in latency to choose ..................115
Figure 6.1: Reaction Norm plots for the three life-history traits we measured ....................112
Figure 6.2: Preference functions for females reared on both diet treatments ....................113
Figure 6.3: Plots to illustrate the significant interaction of population x diet x test for
responsiveness........................................................................................................116

Chapter 7

Table 7.1: The results of a MANOVA on Jackknife pseudovalues for the phenotypic variances
and covariances calculated for the common-garden reared cohort from Chapter 3 and
the control (high-nutrient) group from Chapter 4.....................................................126
Table 7.2: (a) The results of my geometric matrix comparisons of P within each population
for the two different collection dates and (b) comparison of mean divergence values
from this analysis with those from Chapter 3 and Chapter 4......................................127
Table 7.3: The results from between-collections comparisons of P for each population using
Common Principal Components analysis......................................................................128
Table 7.4: The results of comparisons between the all-populations P from my 2007
collection and the G estimated for the Smith’s Lake population.................................135
Figure 7.1: Characterizing multivariate phenotypic change.........................................124
Figure 7.2: (a) Scree plot of the distribution of variance among the eigenvectors of the
advertisement call P matrix, and (b) Preference function for inter-call duration............132
Figure 7.3: Trait covariance as a potential constraint on call evolution ............................133
AUTHOR’S DECLARATIONS

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Chapter 2: As a quantitative review, this chapter necessitated the use of matrices estimated by a large number of researchers at enormous cumulative effort. See the search strategy in Section 2.3 for details of what was included and Appendix I for a reference list for the dataset that was generated.

Chapter 3: The cricket calls analysed for this chapter were originally recorded by J. Hunt as part of a previous experiment, conducted at the University of New South Wales.

Chapter 4: I made the call recordings for this chapter using a semi-automated call recording setup that was developed by T. Tregenza and J. Hunt, with advice from M. Jennions, and built by J. Wood of Ruthern Instruments, J. Hunt and me.

Chapter 5: For this chapter I combined the call data from Chapter 3 with morphometrics data gathered from preserved crickets provided by J. Hunt, and analysed using software donated by C. P. Klingenberg (University of Manchester).

Chapter 6: M. Cupper and C. Mitchell helped set up this experiment, and the phonotaxis trials were carried out in an arena that J. Hunt and I constructed for the purpose.