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**Spermatophore size variation  
in the bush-cricket genus *Poecilimon***

A thesis presented in partial fulfilment

of

the requirements for the degree

of

Doctor of Philosophy

in

Ecology

at

Massey University,

Palmerston North – New Zealand

**Jay McCartney**

**2010**



*I dedicate this thesis to the light and strength in my life,*

*Mary,*

*and the beauty in my world,*

*Milla and Nikau*



# **Spermatophore size variation across the bush-cricket genus *Poecilimon***

## *Abstract*

During mating, male bush-crickets transfer a costly nuptial gift to the female to consume while the ejaculate is transferred into her. The nuptial gift functions primarily as ejaculate protection, although in some larger spermatophore-producing species the gift functions additionally as paternal investment. While costly, production of large spermatophores may increase male fitness by providing a way in which males outcompete conspecific male sperm competition and female control over mating. For females, the nuptial gift may provide nutrients that increase her fecundity or allow greater fitness; however, larger gifts may also reduce a female's mating optima. A large variation in spermatophore size exists among bush-crickets; traditionally this is attributed to environmental and physiological differences. However, interspecific size variation may also be due to behaviour or common ancestry. Few studies have documented the evolutionary ecology of spermatophore size variation while accounting for environmental variation and relatedness.

Controlling for body mass, common ancestry, and diet, my thesis is a study of the variations in spermatophore size of the genus *Poecilimon*. I investigate aspects of operational sex ratio, reproductive effort, mating effort, paternal investment, ejaculate protection, sperm competition, mate choice, sexual conflict and reproductive fitness. I

gathered previously unpublished data and extracted data from the literature to make comparative analyses among 33 *Poecilimon* taxa. For specific focal comparisons, I further intensively studied five taxa in the field that vary markedly in spermatophore size.

First, I observed that variation in *Poecilimon* spermatophore size is as wide as that of the entire bush-cricket family (Tettigoniidae), and thus can be viewed as the ideal model system for investigating gift size variations across tettigoniids. Furthermore, using a phylogenetically independent contrast analysis I showed that evolutionary history has been of little importance in preventing changes in spermatophore size. I present evidence that both ejaculate protection and paternal investment are behind the evolution of larger spermatophore investments within *Poecilimon*. However, potential increases in spermatophore size are predicted to be selected against by female opportunities to increase fitness through multiple mating. In contrast, in a small spermatophore-producing species I found female mate choice for young, virgin males that are likely to transfer greater sperm volumes than previously mated males. In this small spermatophore-producing species I found selection for larger spermatophores. Theory predicts further restrictions to nuptial gift production, as a trade-off between alternative reproductive efforts. However, I found increases in paternal assurance enhanced by transferring larger spermatophores may allow for increased selection to advertise expensive gifts; because spermatophore size and investment in mate attraction are coupled, it appears there is no trade-off between these expensive mating efforts. Moreover, I found that spermatophore size within *Poecilimon* is correlated with a risk-shift in pair-formation protocol between taxa

whereby stationary males that call and wait for females to approach are able to produce larger spermatophores than males that approach calling females. Sexual conflict has been predicted to influence spermatophore size variation because dose-dependent manipulations of gift size on female polyandry occur in most insects, yet I found large spermatophore-producing *Poecilimon* taxa to have a larger per mating fitness increase than small spermatophore-producing taxa. Furthermore, I observed no direct cost of spermatophore size on female fitness. In fact, independent of the spermatophore size received per mating, females of different taxa typically receive similar volumes of spermatophore over their lifetime. Spermatophore size variation across *Poecilimon* reflects predictable within-species adjustments that males make to each spermatophore component in response to environmental constraints, ejaculate protection, paternal investment, and female selection as conditional strategies to maximize reproductive fitness.



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This thesis, in no unsure terms, has occupied a large portion of my life. Many factors have played a crucial part over its duration, yet none more so than the people I have inflicted my thesis upon; most have supported, aided and even cajoled me along the way towards its eventual completion.

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While sometimes hard to believe (although there are photos to prove it), I did have a life before my PhD. A handful of people, during that time, had such an influence on me that I was driven to seek something beyond the paper route. I am deeply indebted to my parents, Joe and Deborah McCartney, who supported my fascination with all things living, through exploding fish tanks, insomnia-inducing tree frogs, axolotls in the swimming pool, man-eating spiders, hairy eels in the toilet at 3.00am, and spluttering geckos in the vacuum cleaner. Without their enduring belief in me I'd still be working with pot-heads - chipping foam and laminating kitchen panels. I am also deeply grateful to my sister Cher; for many years I was the horse in our cowboys and Indians routine (I still don't know why I couldn't be an Indian). Without staring so closely at the ground for interminable hours, I would never have been introduced, or become fascinated by, the billions of creatures living beneath my feet. Seriously, Cher was an inspiration. She taught me the value of determination, hard work, self-belief, and a good hair-cut, all traits that helped me make it through the long-haul thesis flight. So, "thank-you Big Sis", from the bottom of my heart. I am also indebted to Kim Teltscher for her support from the early days of my Honours thesis, through to encouraging me to apply for the PhD position in Germany, and beyond, to her massive contribution to field-work in Greece over two years. I will always be grateful to her for this.

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At the risk of sounding like I have spent much of my time watching the All Blacks, this dissertation can be grossly classified as a thesis of two halves; the temporal point connecting these halves was not only when I returned to New Zealand from Germany, but when my objectives changed from the primary goal of data collection and entry and analysis, to the secondary goal of getting it all down in an intelligible form on paper.

The German thesis. I owe great thanks to Dr Klaus-Gerhard Heller who had the most difficult task of mentoring a naïve Kiwi lad in international research. He played a major role in my induction to a foreign land and obtained the original funding from the D.F.G. (many thanks to the Deutsche Forschungsgemeinschaft which supported my PhD). I must also thank him for introducing me to the most interesting research I could have hoped to discover. I also thank Roland and Dagmar Achmann, who taught

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# Table of Contents

	Page
<b>Abstract</b> .....	<b>i</b>
<b>Acknowledgements</b> .....	<b>v</b>
<b>Table of Contents</b> .....	<b>xi</b>
<b>Chapter 1: Introduction</b> .....	<b>1</b>
NUPTIAL GIFT FEEDING IN INSECTS .....	3
OPERATIONAL SEX RATIO .....	4
MATING EFFORT AND PARENTAL INVESTMENT .....	5
EJACULATE PROTECTION AND SPERM COMPLETION .....	7
SEXUAL CONFLICT AND REPRODUCTIVE FITNESS .....	8
NUPTIAL FEEDING IN BUSH-CRICKETS .....	10
NUPTIAL GIFT FUNCTION IN BUSH-CRICKETS .....	11
NUPTIAL GIFT SIZE VARIATION IN BUSH-CRICKETS .....	13
NUPTIAL FEEDING IN <i>POECILIMON</i> .....	17
SUMMARY.....	19
A NOTE ON THESIS STRUCTURE AND CO-AUTHOR CONTRIBUTIONS .....	20
CHAPTERS .....	23
REFERENCES .....	32
<b>Chapter 2: Understanding nuptial gift size in bush-crickets: an analysis of the genus <i>Poecilimon</i> (Tettigoniidae: Orthoptera)</b> .....	<b>45</b>
ABSTRACT .....	47
INTRODUCTION.....	48
METHODS .....	52
Collection.....	53
Determination of male body mass, spermatophore size, and sperm number.....	53
Analysis.....	55
RESULTS .....	57
Comparisons between <i>Poecilimon</i> and other Tettigoniidae .....	57
Variation within <i>Poecilimon</i> .....	63
Intraspecific variation .....	64
Spermatophore components.....	65
DISCUSSION .....	69
Spermatophore variation, ejaculate protection and paternal investment .....	69
Spermatophore size variation within <i>Poecilimon</i> .....	72
Spermatophore differences between field and laboratory-raised individuals.....	74
CONCLUSIONS .....	75
REFERENCES .....	77
APPENDIX 1 .....	85

	Page
<b>Chapter 3: A preliminary analysis of mate choice in a bush-cricket (<i>Poecilimon laevissimus</i>: Tettigoniidae) suggests virginity is more important than body size .....</b>	<b>87</b>
ABSTRACT .....	89
INTRODUCTION .....	90
METHODS .....	92
RESULTS AND DISCUSSION .....	94
REFERENCES .....	98
<b>Chapter 4: Evidence of natural and sexual selection shaping the size of nuptial gifts among a bush-cricket genus (<i>Poecilimon</i>, Tettigoniidae): an analysis of sperm transfer patterns .....</b>	<b>103</b>
ABSTRACT .....	105
INTRODUCTION .....	106
MATERIALS AND METHODS.....	110
Species and sites .....	110
Spermatophore consumption time, male body mass and spermatophore mass .....	112
Sperm transfer .....	113
ANALYSIS .....	115
Sperm transfer and spermatophore consumption.....	115
Relative spermatophore mass and proportion of sperm transferred.....	116
Phylogenetic independent comparisons .....	116
RESULTS .....	117
Spermatophore consumption and sperm transfer.....	117
Relative spermatophore mass and proportion of sperm transferred.....	120
DISCUSSION .....	121
REFERENCES .....	129
<b>Chapter 5: Lifetime spermatophore investment in natural populations of two closely related bush-cricket species (Orthoptera: Tettigoniidae: <i>Poecilimon</i>).....</b>	<b>135</b>
SUMMARY.....	139
INTRODUCTION.....	140
METHODS .....	144
Spermatophore size .....	144
RESULTS .....	145
Investment pattern.....	145
Seasonality.....	147
DISCUSSION .....	150
Seasonality of investment .....	150
Spermatophore scaling .....	151
REFERENCES .....	155

	Page
<b>Chapter 6: Sex roles in mate attraction and searching: a comparative test using bush-crickets (<i>Poecilimon</i>: Tettigoniidae) .....</b>	<b>161</b>
ABSTRACT .....	163
INTRODUCTION.....	164
METHODS .....	169
Our study taxon: <i>Poecilimon</i> .....	169
Male body mass, spermatophore size, and sperm number .....	169
Analysis.....	174
RESULTS .....	175
DISCUSSION .....	176
REFERENCES .....	181
<b>Chapter 7: Is there evidence of a macro-evolutionary trade-off between reproductive investments in mate attraction and nuptial gift size in bush-crickets?.....</b>	<b>189</b>
ABSTRACT .....	191
INTRODUCTION.....	192
METHODS .....	196
Male body mass, spermatophore size, and sperm number .....	196
Syllable and impact number per day and PCF.....	200
Phylogenetic construction.....	200
Comparative analyses.....	201
RESULTS .....	204
DISCUSSION .....	206
REFERENCES .....	212
<b>Chapter 8: Larger nuptial gifts increase male per-mating fitness across a bush-cricket genus (<i>Poecilimon</i>), but do they “manipulate” females?.....</b>	<b>221</b>
ABSTRACT .....	223
INTRODUCTION.....	224
METHODS .....	229
<i>Poecilimon</i> .....	229
Data collection, body mass and spermatophore mass.....	229
Population mating frequency.....	232
Mature female longevity .....	233
Daily egg batch laying frequency.....	234
Egg mass and hatching success .....	235
Male per-mating reproductive fitness.....	235
Female lifetime reproductive fitness and total lifetime spermatophore material received.....	236
Analysis.....	236
Phylogenetic independent comparisons.....	237

	<b>Page</b>
 <b>Chapter 8 (continued)</b>	
RESULTS .....	238
Body mass and spermatophore mass .....	238
Population mating frequency .....	238
Mature female longevity .....	242
Daily egg batch laying frequency .....	243
Egg mass and hatching success .....	244
Male per-mating reproductive fitness (eggs laid, egg mass and number of eggs hatched per mating) .....	246
Differences between species in female lifetime reproductive fitness .....	248
Male per-mating reproductive fitness .....	249
Female lifetime reproductive fitness and total lifetime spermatophore material received .....	251
DISCUSSION .....	251
REFERENCES .....	260
 <b>Chapter 9: Discussion and conclusions .....</b>	
<b>Discussion and conclusions .....</b>	<b>267</b>
<i>POECILIMON</i> AS A MODEL TAXON .....	269
CONTROLLING FOR NATURAL VARIATIONS IN A CLOSELY RELATED TAXON .....	271
MATING EFFORT, PATERNAL INVESTMENT, EJACULATE PROTECTION AND SPERM COMPETITION .....	274
REPRODUCTIVE EFFORT .....	278
MATE CHOICE .....	282
OPERATIONAL SEX RATIO, SEXUAL CONFLICT AND REPRODUCTIVE FITNESS .....	285
FUTURE RESEARCH .....	288
CONCLUSIONS .....	289
REFERENCES .....	291

*"[Sexual selection] depends, not on a struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitors, but few or no offspring."*

Darwin (1859), *On the Origin of Species* (p. 103)

