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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

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Jay McCartney

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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gathered previously unpublished data and extracted data from the literature to make comparative analyses among 33 *Poecilimon* taxa.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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The Friedrich Alexander Universität (Institute für Zoology II) in Erlangen was an enjoyable place to do science. The blame for this can partly be given to the beer vending machine outside my office, but mostly this was due to the people that graced the department's halls (mainly near the beer vending machine). Special thanks goes to my colleagues and friends: Eric Petit (and his wife Eva), Sylvia Creamer, Sandra "Hootenbuegle", Wolfgang and Masha Edrich, Klaus-Reinhardt, Arne and Gerlind Lehmann, Gerald Heckle, Volker Runkel and Christian Voigt; not only were conversations always stimulating, but their constant friendship, hospitality and understanding made the long dark winters of data entry and lab work enjoyable. I am also indebted to Frieder Mayer and his technical staff, Melanie and Sandra, who allowed me to work in the DNA lab, and most certainly cleaned up my mess after I had been running tests all night. I also thank Nico Micheals from the Max-Plank Institute in Seewiesen, who proved to me that job interviews could be conducted in an ancient beer-producing monastery. He and his outstanding prodigies, Latetia, Martin, Jaco, and yes, even Tim, opened a new door to me on cuisine, culture and debate (although I still don't think manta rays could fly if they were pushed off a cliff). Erlangen (Nürnberg) was a lively place to live; working at Steinbach Braürei and the Baüstelle not only kept me sane but introduced me to the non-academic side of Germany – a completely different place. Special thanks go to my friends in Germany: Mark, Jörg, Kevin, Dea, Emily, Ena, Jennifer-Monique, Babette, and the entire Steinbach crew. Vielen Dank für alles, die guten Zeiten und die schönen Erinnerungen.

Back to Aotearoa. A few intermittent years were first spent in Palmerston North, teaching and acclimatizing, before Mary convinced me to transfer the thesis to New Zealand to complete. I owe much of the opportunity to stay in academia during

that time to Ian Stringer, Murray Potter, Doug Armstrong, Alastair Robertson and Darryl Gwynne. Working at Massey rekindled my passion for science and research. Officially transferring the thesis to New Zealand could not have occurred without Murray or Alastair (or the Massey University Doctoral Research Scholarships that supported my research); neither knew anything of my research area at that stage, but had enough faith in me (or was it my persistent badgering?) to see me through to the end of my PhD. The all-inspiring Darryl Gwynne also played a huge part: his stature, wisdom, experience and expertise in animal mating systems more than once helped clarify the goals of my research. On many occasions, Murray, Alastair and Darryl directed me through difficult times. On that note I also wish to thank Glenn Morris; Glenn undoubtedly spent many hours tapping away on the keyboard, supplying me with e-mails filled with wisdom, kindness and positivity. He not only supported my ideas through some of the more blurry parts of my thesis and manuscript production, but showed me how to be professional about getting the ideas on paper. Ian Stringer also deserves individual thanks; if he had not left Massey for the calmer waters of the Department of Conservation, I would never have landed his office and computer. Perhaps more importantly, however, once he was a part of the DoC family, Ian was generous and faithful in supplying me with a continuous 'String' of contracts that helped me fund my family and thesis.

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Chapter 8 (continued)

"[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)