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October 30, 2018

I am writing in support of Jason Bertram's application for a tenure-track position in Ecological/Evolutionary Theory at Florida State University, in the strongest possible terms. He is expert in both ecological and evolutionary theory.

Jason was a postdoc in my lab from February 2015 to August 2018. In that time, he acquired an extraordinary degree of mastery in multiple fields that were entirely new to him, wrote three first-author manuscripts with a fourth in progress and ideas and preliminary results for several more (excluding finishing up manuscripts from his Ph.D.), wrote an NSF grant proposal, was primary advisor for three undergraduates and co-advisor for one ongoing Ph.D. student and one rotation student, co-taught a semester-long class, and ran the primary NSF Broader Impacts activity (an annual Wikipedia Edit-a-thon) for the grant I funded him on. In other words, Jason has what it takes to succeed in the competitive world of science.

I rank Jason as the very strongest, bar none, of the eleven postdocs I have advised, two of whom have previously secured tenure-track faculty positions, plus a third who undoubtedly could have if he had not chosen instead a highly desirable private-sector job. Jason is very independent, and almost from the outset has been more my colleague than my advisee, a valued sounding board whose input I seek out. In fact, it makes more sense to compare Jason to me than to compare him to other postdocs: quite simply, Jason is better than me, both smarter and more careful, and I have been extraordinarily lucky to have him as my lieutenant these past three years. Only my extra years of experience have allowed me to keep up to the point of being a (I hope) useful advisor to a postdoc who is more talented than I am. Jason's true peers do not just secure tenure-track faculty positions, but do so in the most elite institutions in the world, and go on to have spectacular careers that influence the course of science.

Jason began this postdoc in theoretical population genetics with a strong background in mathematics and physics, and with experience in macroecology, but with no prior knowledge of population genetics or indeed evolutionary biology in general. Population genetics is a notoriously difficult field to master; the mathematics aren't easy, both evolution and stochastic processes can be highly unintuitive, and there is no remotely satisfactory textbook to guide newcomers. Jason got on top of the basics in a mere matter of months, putting my own postdoctoral learning curve of the same material to shame. Beyond the basics, mastery relies on reading widely to make connections among a disconnected literature. Jason is a voracious reader who isn't satisfied until he understands something deeply, and who also loves to read something new. Through both reading and extensive attendance at seminars and journal clubs, he now has a remarkable knowledge covering a broad range of topics, i.e. he has both breadth and depth, and the curiosity to ensure his knowledge gets ever broader. He also interacts well with others from diverse backgrounds, e.g. at conferences, motivated both to expand his own knowledge and also to better understand specific experimental systems and explore future collaborations.

The primary thrust of Jason's research has been to model evolution such that every birth and every death simultaneously affects both population size and allele frequencies. The last major attempt to achieve this was r/K selection theory, which had a number of weaknesses, and never displaced standard population genetic theory in the way it was originally intended to.

Two of Jason's manuscripts use simple alternatives designed for custom purposes. The first combined density-dependent birth with density-independent death. It is remarkable as the only paper, to my knowledge, to

mathematically derive macroevolutionary patterns from population genetics principles, applying the results to the interpretation of paleontological data. Specifically, he found that relatively sudden population collapse and extinction need not be caused by dramatic environmental catastrophe, but is the null expectation of a stochastic process of adaptation to a thousand randomly distributed cuts, once you condition on extinction.

The second constructed a relatively simple model that is nevertheless able to simultaneously describe four different theories, two of them genetic and two ecological, about coexistence/maintenance of genetic variation driven by an environment that varies over time, and thus to compare them. Only one of the four ("reversal of dominance") is able to stabilize alleles of small effect, but ironically this crowds out any possible large-effect loci, which are thus more plausibly driven by the other three mechanisms. The paper is also a model of clarity on the often-confusing "storage effect" of ecology, bringing it into relatively simple population genetic models.

The third manuscript developed a more ambitious mathematical framework that distinguishes between three different kinds of selection: selection for rapid growth, selection to avoid mortality, and zero-sum interference contests with conspecifics. This framework is a generalization of the lottery model of ecology (itself a generalization of the Wright-Fisher model of population genetics to the case of generations that only partly overlap) to treat arbitrary population and genotype densities properly. This work is mathematically sophisticated, with non-obvious conditional probabilities and consistency criteria that arise from the discrete nature of individuals having a surprising ability to affect the overall properties of the system. It replaces the current shaky foundations of the relative fitness term w of population genetics as set out in seminal texts such as Crow & Kimura with something much more rigorous, making explicit the conditions under which w can be used. It also sets the foundation for a promising research program that could transform population genetics once it is integrated into an inferential framework – something Jason is well set up to do during his tenure-track years.

The depth and care of Jason's thinking is extraordinary. He is not easily satisfied, either with the rigor of a result, or with the significance of a line of enquiry. He aspires to ask the deepest and most general questions possible, and to obtain satisfactory answers. His relatively frequent switching between fields acts to his advantage here. He doesn't leave a field until he has absorbed its essence, and he takes that essence with him to enrich his understanding of future fields. He is setting the groundwork for being able to answer truly profound questions whose impact will be high.

Jason is also easy to work with, very outgoing and well-liked within the group. He has been primary supervisor of three undergraduates, and co-advisor of one EEB Ph.D. student rotation and one ongoing Applied Math Ph.D. thesis. The latter Ph.D. student and one of the undergraduates are Hispanic and the first generation in their families to attend college. Jason has been patient and encouraging and helped them build confidence; both have flourished and are doing exceptionally well, in no small part due to Jason's help. Jason's fourth manuscript (still in prep) results from the work of this undergraduate, and documents saltationist evolutionary dynamics in the case of non-obligate sexual reproduction. The undergraduate, at the end of her sophomore year, came runner-up at the poster competition for *graduate students* at the annual Evolution meeting – this spectacular achievement, and the resulting paper, owes a lot to Jason's mentorship skills. Jason is currently adding analytical insights to her simulation-based results, which will further strengthen the work. Jason will also be a co-author on the Ph.D. student's paper using 2-dimensional travelling wave models to analyze the (in)stability of the G-matrix under strong linkage disequilibrium in asexuals. Jason has a few other projects in the works too, including one on protein evolution.

Jason volunteered to do some classroom teaching as a way to gain experience. Under my supervision and coaching, he co-taught (together with me and Anna Dornhaus) a mostly graduate class on mathematical modeling that aims to get non-theoretical biologists to critically read a theory paper even while they skip math that goes beyond their knowledge. I have given up the lecture format in favor of more active learning approaches – Jason was initially skeptical about this shift, but was open to the data showing their impact on the achievement

gap and willing to give it a try. This was only the second time the course was offered, and based on past feedback we were in any case giving it a near-complete overhaul, so Jason designed all of his teaching materials from scratch, and I have continued to use them since then. The bulk of the course consisted of students reading seminal theory papers and being led through ways of analyzing them. Jason was definitely the expert in the room on ecological neutral theory and on climate models, and we would have been happy to have him if only for his key insights on these and other topics. Leading class for a third of semester was enough for Jason to get the hang of preparing for and running an active learning classroom, and he was quite skilled at it by the end of semester. Having been through the experience of discovering where students actually are compared to naïve expectations, and seeing that transformation take place in Jason, I cannot imagine that he will return to sage-on-the-stage instruction. His teaching skills are now strong, and on a trajectory to soon become a boasting point for any department that houses him. Jason has a profound commitment to social justice and remedying educational inequities, which shapes both his mentorship and his teaching.

You have an incredible opportunity offered to you in the form of hiring Jason. You should snap him up.

Yours sincerely,

Joanna Masel
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Dpt. Ecology & Evolutionary Biology
Graduate Interdisciplinary Program in Applied Math
Graduate Interdisciplinary Program in Genetics
Graduate Interdisciplinary Program in Statistics
Ethology and Evolutionary Psychology Program
Biochemistry and Molecular & Cellular Biology Graduate Program
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ANU COLLEGE OF SCIENCE

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31 October 2018

Assistant Professor, 9 Month Salaried (Ecological/Evolutionary Theory) position at Florida State University

Letter of recommendation for Jason Bertram

Dear Selection Panel,

I was Jason Bertram's PhD supervisor at the Australian National University in Canberra. He started his PhD in September 2011 and submitted his thesis exactly 3 years and 1 week later, in September 2014.

Jason came to me with a background in physics and mathematics, and a strong desire to apply his quantitative skills to problems in biology, even though he had had no formal training in biology.

During his PhD he worked on several problems in ecology as well as fluid turbulence, all brought together under the common theme of using optimisation principles to understand complex systems. In addition to the impressive quality and breadth of his work, Jason demonstrated a strong capacity for adaptability and independent thinking. He is by far the best PhD student I have supervised in my 27 years' experience.

His thesis generated 4 articles published in peer-reviewed journals (*Ecology*, *AIP MaxEnt Proceedings*, *Theoretical Ecology*, *Journal of Fluid Mechanics*). It is impressive that he achieved this output in only 3 years with no biological background. Another chapter is currently in the advanced stages of preparation for submission (Bertram, Newman and Dewar, to *Global Ecology and Biogeography*).

Two stand-out pieces of work during his PhD are (i) his application of the statistical principle of Maximum Entropy (MaxEnt) to gain new insights into the relationship between diversity and stability in ecological communities (*Theoretical Ecology*), and (ii) his work on maximum kinetic energy dissipation in fluid turbulence, which applies optimisation principles to predict turbulent flow patterns without recourse to large-scale numerical simulations (*Journal of Fluid Mechanics*). Both are first-class contributions to theoretical biology and physics that bring new insights and much-needed rigour to both fields.

While his PhD work mainly involved theoretical modelling, from the start Jason was very keen to connect his predictions to observational data (e.g. remote-sensing data on savanna tree cover; empirical stability-diversity patterns). To do this he talked with many people at ANU and elsewhere who were close to the data, and also sourced data from the literature and online. Jason is a very sociable person who enjoys interacting with others, physicists and biologists alike. He is no ivory tower theorist. Equally, though, during his PhD Jason showed great independence and tenacity in his approach to new tackling problems. He rapidly gained ownership of his PhD project.

Jason is also an excellent communicator with a special ability to convey ideas from physics to a biology audience. A case in point is his PhD exit seminar given before a largely non-mathematical audience of biologists at ANU, which was highly praised by many who attended.

Jason participated in 4 international workshops on complex systems science: *Maximum Entropy Production* (ANU, Canberra, Sept 2011), *Frontiers in Macroecology* (UC, Berkeley, Jan 2013), *Mathematics for Fluid Earth* (Isaac Newton Institute for Mathematical Sciences, Cambridge, Nov 2013) and *MaxEnt 2013* (Canberra, Dec 2013); he gave oral presentations at the latter 3 workshops.

During his PhD project he single-handedly developed and demonstrated impressive skills in computational biology and systems biology, including mining and analysis of remote-sensing data on global vegetation cover, and mathematical modelling of ecological communities. The main mathematical technique he used – maximum entropy – is a very general and powerful theoretical tool for analysing and predicting the behaviour of complex systems, with many applications throughout quantitative ecology.

Jason has that rare combination of big-picture vision and formidable attention to detail. At the start of his PhD his quest for perfection held back his writing, but on the papers we co-authored I found that a regular to-and-fro writing process worked well, and by the end of his project his writing skills had matured considerably.

It is a pleasure to recommend Jason Betram for this position at Florida State University.

Kind regards,

Prof. Roderick C Dewar

Department of Mathematics

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Ecol./Evol. Theory Search Committee
Department of Biological Sciences
Florida State University
Tallahassee

Reference letter Dr. Jason Bertram

Vienna, November 3rd, 2018

Dear Members of the Selection Committee:

It is my pleasure to recommend Jason Bertram for the position as Assistant Professor of Ecological and Evolutionary Theory at Florida State University.

I got to know Jason Bertram around three years ago when we communicated by email over a preprint that he and his postdoc adviser Joanna Masel had been working on and which they had sent me for comments. We stayed in contact and I met Jason in person several times (e.g. in August at the Evolution conference in Montpellier). On these occasions, we talked in detail about several of his current projects.

Jason Bertram is a physicist by training who got into theoretical biology during his PhD (completed 2014). Later, he fully switched his research to theoretical ecology and evolution. This transition from physics to theoretical biology is of course a route that others have taken before. Former physicists in biology are often technically strong and Jason Bertram is no exception. However, Jason goes beyond technical excellence in important ways. He has a keen interest in the biological assumptions, from both genetics and ecology, which underlie his models. In contrast to the (stereo-) typical former physicist, he embraces biological complexity. Jason is a truly deep thinker and his combination of technical excellence, biological diligence, and a fresh look from the outside lead to valuable new insights. I rarely have met people with whom discussing science is more rewarding. Jason Bertram's work regularly results in manuscripts somewhat off the beaten track that take a little longer to get published, but that are already in their raw shape more interesting to read than many published studies.

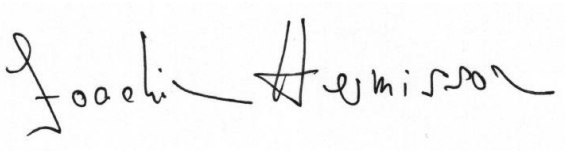
Jason Bertram's research interests and the methods that he uses are broad. They range from models for the role of recombination in microbial adaptation (building on models of clonal

competition as introduced by Desai, Fisher *et al*) to models of frequency-dependent selection in evolutionary ecology. An example for the latter is the recent preprint on Grime's triangle (available on bioRxiv) that introduces a very interesting and natural extension of the so-called "lottery model" of species coexistence in temporally variable environments. I have already used some lucid ideas from this preprint in my own work in progress on related issues. His future research plan combines these two approaches, with the aim to account for both genetic and ecological complexity in a model. There is clearly a need for such models and Jason's results so far hold promise that progress is indeed possible.

Summarizing, I think that Jason Bertram is an upcoming high potential in the field of theoretical ecology and evolution. He has only recently fully switched to evolutionary research but has already contributed fresh ideas to more than a single topic. He is a sincere scientist and most pleasant to interact with. For a faculty hire, he is definitely a candidate who is worth a close look – in particular, since his expertise and research topics are an excellent fit for the advertised position.

I fully support his application.

Sincerely yours,



Joachim Hermisson.