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Review of Luděk Berec's habilitation thesis

Dear Professor Horová,

The habilitation thesis by Luděk Berec is entitled 'Mathematical modeling in ecology and epidemiology'. The scholarship demonstrated in this thesis, both in quality and quantity, is excellent and a great contribution to the field of mathematical biology.

Research in mathematical biology can be very much on the mathematical side (e.g., referring to a biological motivation but lastly doing mathematics for the sake of mathematics) or on the biological side (e.g., using models to fit them to available data). The work presented in the current thesis is right in the middle between these two extremes. Mathematical models are carefully and wisely built to address meaningful biological problems. Their analysis is based on rigorous maths and systematic simulation techniques. Most importantly, the results provide new knowledge and novel insights —which are carefully interpreted biologically to recommend solutions to pressing biological problems.

Structure and content of the thesis—Relevance and quality of the research

The thesis is divided into three parts. A preceding introduction summarises the underlying background (both mathematically and biologically), gives some historical notes and describes the field of mathematical biology. It's a succinct and highly fitting introduction that synthesises the state of the art and open questions—a great motivation for the following chapters.

Optimal foraging The first part of the thesis is concerned with optimal foraging theory. This is based on maximising the net energy intake rate of predators (or, more generally, consumers). Classical models predict that predators either always attack only the more profitable prey or abruptly change to attack both prey species (depending on the prey availability). Empirical evidence, however, suggests that the transition between these foraging strategies is not abrupt but rather gradual. A number of mechanisms have been suggested that can produce such patterns; the work presented here describes another mechanism. Particular attention is also paid to 'partial preferences' of predators (opposing the almost artificially looking all–or–nothing predictions); emerging functional responses; and the stability of species communities. The models presented take into account (i) encounter

patterns between predators and prey and (ii) perceptual constraints of predators to assess the availability of prey species.
This part is based on some of the author's earlier work, but he has been continually publishing in and contributing to this active research area up to recent years.

Allee effects This is the most extensive part of the thesis. It covers a lot of the author's main work over the past decade and represents, in my opinion, the most successful contributions of his to mathematical ecology.
The Allee effect describes a positive effect on fitness when populations increase at small densities. In turn, this means that smaller populations lose fitness—something that can tremendously impact the viability of endangered species, in particular. While the Allee effect originates from the 1920's and 30's, its importance has been recognised only in the past dozen years.
The work presented in this thesis demonstrates that the author has been at the forefront of developing the theory of Allee effects. He has played a major and leading role in the mathematical modelling, especially when it comes to (i) emerging Allee effects in structured populations; (ii) the occurrence, interaction and synergy of multiple Allee effects; and (iii) the dynamically complex interplay of Allee effects and predator–prey systems.
This part of the thesis is actually sub-divided into two different sections. The first one focuses on Allee thresholds that are key in determining population extinction or persistence. While ecologists often perceive Allee thresholds as a single number, the author works out beautifully how various forms of population structure (e.g. in sex, age and developmental status) transform this threshold into stable manifolds or hypersurfaces in state space.
The existence of multiple Allee effects in a population has been completely ignored until a highly influential publication under the lead of Luděk Berec. This is a prime example of interdisciplinary collaboration and mathematical biology, where mathematical modelling is used to (a) develop novel ecological theory and (b) inspire the collection and synthesis of empirical evidence.
The second section in this part incorporates Allee effects into either prey or predator population dynamics when these two species interact. The analysis of these models is challenging, because the complex dynamics of predator–prey is further complicated by the Allee effect. Luděk Berec is one of the key figures in driving forward the research in this area.

Biological control of pest species This is the shortest part of the thesis, but one that contains another exciting avenue of timely research. Invasive species and other pests represent some of the most pressing threats to biodiversity and ecosystem functioning in our globalised world. Hence, there is keen interest to develop effective control methods. One promising candidate is virus-vectored immunocontraception (VVIC), the idea of which is to release sterilising pathogens. As a biological control method, it is self-disseminating and likely to be efficient. Moreover, as sterilising rather than killing biocontrol agent it accommodates ethical concerns over alternative methods.
The work presented here draws upon a simple biological fact that, however, has never been taken into account yet. Namely, roughly speaking, individuals that don't reproduce live longer. In a mathematically rigorous analysis, the author is able to demonstrate that

sterilising pathogens can be expected to be more effective than previously thought. To the best of my knowledge, this argument has never been made before, so the insights gained by this research might substantially influence the ongoing discussion on biological control methods—and the future prospect of VVIC.
The author also details some vibrant ideas how this recent research can be extended. Sexually transmitted infectious diseases operate the same mechanism as the mating system, but these two processes have never been combined in a mathematical model. This idea suggested by the author can be expected to provide further intriguing insights.

General comments on the research

The research presented in this thesis is highly interdisciplinary. Based on rigorous mathematical modelling and analysis as well as simulation techniques, important biological problems are thoroughly studied. Techniques used include dynamical systems methods such as equilibrium and attractor as well as stability analysis; bifurcation theory; numerical continuation; and extensive simulations. Model types range from systems of nonlinear differential and difference equations to spatially explicit individual-based models. The author thus demonstrates masterly knowledge and application of a wide range of mathematical and modelling techniques. The use of individual-based models and their mean-field approximations when appropriate is skilful and has been innovative.

What strikes me most, and what I am most impressed of, is the author's extreme rigour in developing ecological theory. Its foundation on biological mechanisms, embedding in existing literature and meaningful discussion is exemplary and to an outstandingly high standard.

International perception

The thesis is based on a large number of peer-reviewed publications in international journals. Part I is based on two papers; part II on eight papers; and part III on one paper. The author has additionally published respectively four, seven and one further paper(s) in these areas. One paper that was in review has been accepted and is available online by now.

With the exception of two publication outlets (one being conference proceedings and the other one being a *Comments* journal), all papers have appeared in highly respected and leading journals of the field. As a matter of fact, a considerable number of papers appeared in the ecological literature (e.g. *Conservation Biology*, *Population Ecology*, *Evolutionary Ecology Research*), where it is intrinsically challenging to publish theory—especially based on mathematical models. The author's achievements therefore underline the importance of his results and his ability to gain impact across boundaries of disciplines. Particularly noteworthy are his publications in *Trends in Ecology & Evolution* and *American Naturalist* (both as first author) as well as in *Ecology Letters* (as co-author), which are top-notch journals in ecology. All other journals are excellent venues for mathematical biology research.

Luděk Berec's research is very well cited in both the mathematical biology and the ecological

community. In my perception, he is internationally recognised as a world-leader in modelling Allee effects. According to *ISI Web of Knowledge*, his work received well over 80 citations per year since 2009. Some publications are highly cited: three papers on Allee effects (with 76, 73 and 55 citations) and one on individual-based models (70 citations).

What might gain the most influential impact, however, is the 2008 book on Allee effects (published by Oxford University Press), where Luděk Berec is the second author and (I suppose) he mainly contributed to the modelling sections (actually a rare but welcome phenomenon in ecology books). This is the first and only book on Allee effects (despite the original contribution by Allee himself in the early 20th century), and I dare say that it has been applauded and enthusiastically received by all researchers I have to talked to. Considering the long-lasting impact of such a book, I may speculate that it may shift some extra attention to those papers that have not been cited that frequently yet, but would certainly deserve so.

Summary

With the research presented in this thesis, Luděk Berec has demonstrated a high and internationally leading level of scholarship in the field of mathematical modelling in ecology and epidemiology. His sustained contributions to the theory of Allee effects are particularly noteworthy and outstanding.

In my opinion, due to his scholarly achievements, Luděk Berec fully qualifies as a professor. In international terms that I am familiar with, I would rank him as Associate Professor (US and Canada), Reader (UK) and W2-Professor (Germany), or higher.

I recommend the habilitation of Luděk Berec in the strongest possible terms. If I am to grade his thesis, I choose the highest mark possible.

Yours sincerely,

Frank Hilker

(Dr. Frank M. Hilker)