Functional and Evolutionary Ecology of Fleas

Fleas are one of the most interesting and fascinating taxa of ectoparasites. All species in this relatively small order are obligatory haematophagous (blood-feeding) parasites of higher vertebrates. This book examines how functional, ecological and evolutionary patterns and processes of host–parasite relationships are realized in this particular system. As such it provides an in-depth case study of a host–parasite system, demonstrating how fleas can be used as a model taxon for testing ecological and evolutionary hypotheses. The book moves from basic descriptive aspects, to functional issues and finally to evolutionary explanations. It extracts several general principles that apply equally well to other host–parasite systems, so will appeal not only to flea biologists but also to mainstream parasitologists and ecologists.

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A Model for Ecological Parasitology

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CAMBRIDGE
UNIVERSITY PRESS

CAMBRIDGE UNIVERSITY PRESS
Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo, Delhi

Cambridge University Press
The Edinburgh Building, Cambridge CB2 8RU, UK

Published in the United States of America by Cambridge University Press, New York

www.cambridge.org
Information on this title: www.cambridge.org/9780521882774

First published 2008

Printed in the United Kingdom at the University Press, Cambridge

A catalogue record for this publication is available from the British Library

Library of Congress Cataloguing in Publication data

Krasnov, Boris R., 1955–
Functional and evolutionary ecology of fleas : a model for ecological parasitology / Boris R. Krasnov.
p. cm.
Includes bibliographical references and index.
ISBN 978-0-521-88277-4 (hardback)
1. Fleas–Ecology. 2. Fleas–Evolution. 3. Host-parasite relationships.
I. Title.
QL599.5.K73 2008
595.77′517857 – dc22 2007053048

ISBN 978-0-521-88277-4 hardback

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Preface

I was privileged to be introduced to the study of zoology in the Department of Zoology and Comparative Anatomy of Terrestrial Vertebrates at the Moscow State University in Russia. I began my scientific career studying behavioural mechanisms that influence the spatial structure of rodent populations in different landscapes, from the tundra and the Arctic shore of the Chukchi Peninsula to the rainforests of southern Vietnam. At the time, academic staff members and students of the department under the leadership of Professor Nikolai Naumov were working intensively on rodent ecology, aiming to understand their role in infectious zoonoses, mainly the plague. Consequently, every student who studied rodent ecology was introduced to fleas, as they are the principal vectors of the plague.

In the beginning of the 1990s, I started to work at Ben-Gurion University of the Negev and continued to study rodents and other desert-dwelling animals (tenebrionid beetles and lizards) in the Negev Desert. These studies resulted in a book, *Spatial Ecology of Desert Rodent Communities*, written together with my colleagues Georgy Shenbrot and Konstantin Rogovin, and published by Springer-Verlag in 1999 (Shenbrot *et al*., 1999a). However, I also subliminally continued to collect fleas from every captured rodent, not being sure at that time why exactly I was doing this. In the mid 1990s, I read several papers by Robert Poulin, Serge Morand and Jean-François Guégan, which opened my eyes to an enthralling new world of parasites. I was so fascinated with the ideas and findings of ecological and evolutionary parasitology that, in the middle of my scientific career, I abruptly switched from studying behaviour and spatial ecology to studying the ecology of host–parasite relationships. Naturally, fleas and rodents were a familiar and very convenient model association that allowed me to combine the ecology of free-living organisms and parasitology, two parallel worlds, wherein scientists too often are not aware of each others' achievements.

Parasites are becoming increasingly important in studies of ecology and evolution. This is mainly due to the numerous advantages of using parasites to examine patterns and processes in animal communities because of, for example, the relative ease of obtaining replicated samples (e.g. host individuals or host species) and the fact that parasites of the same taxon share a trophic level. Another advantage of studying parasite communities is that most hosts are usually parasitized by several closely and/or distantly related parasite species that use the same resource. Thus, the study of the community organization of parasites allows a better understanding of the processes of competition and facilitation in biological communities. Ecological and evolutionary studies of parasites, in turn, are powerful tools for understanding the spread of dangerous zoonotic diseases and provide a theoretical basis for their control and prevention. All these issues have led to a sharp increase in empirical, comparative and theoretical studies of host–parasite relationships. Patterns and processes in host–parasite systems have been documented and studied at a variety of levels, across various habitats, in different biogeographical regions and for various parasite taxa. The goal of this book is to examine how functional, ecological and evolutionary patterns and processes of host–parasite relationships are realized in one particular host–parasite system. I attempt to demonstrate how Siphonaptera can be used as a model for testing ecological and evolutionary hypotheses.

My hope is that, on the one hand, this book will be of specific interest for biologists studying fleas, providing them with an up-to-date review of the biology of their study animals. On the other hand, I hope that the book will serve a much greater audience and be relevant to both parasitologists and ecologists. The book provides an in-depth case study of a model host–parasite system, looking at it from many angles, and extracting from it several general principles that apply equally well to other host–parasite systems. Often, a book with detailed information on one taxon inspires research on other taxa, and this book could become a guideline for further research into both parasitism and animal population and community organization.

Fleas represent one of the most fascinating taxa of ectoparasites. All species in this relatively small monophyletic order are obligatory haematophagous parasites of mammals and birds. From the ecological and evolutionary perspectives, fleas represent an interesting model. In particular, this is related to the characteristic *modus vivendi* of these insects. On the one hand, in contrast to endoparasites and permanent ectoparasites such as lice, they spend much time off their hosts and are therefore affected, not only by factors linked to the host per se, but also by the off-host abiotic environment. On the other hand, in contrast to temporary ectoparasites such as mosquitoes and ticks, they spend more time on their hosts than is required merely to obtain a blood meal. This creates a causal chain of

flea–host–environment interactions, which in itself is an important and interesting subject for investigation. Another advantage of using fleas as a model taxon is the opportunity to manipulate flea infestation on living hosts both in the field and in the laboratory and to monitor changes in an individual host over time. Indeed, fleas, in contrast to many other parasites, can be counted on a live animal that itself than can be marked, released, recaptured and examined again.

Fleas serve as the vectors of many diseases dangerous to humans. Apart from this, the veterinary aspect of flea parasitism is also very important, with flea-bite allergies and hypersensitivity being serious problems for both livestock and pets. However, in spite of the importance of fleas and their convenience as models for ecological and evolutionary studies, there is a lack of literature dealing with flea bionomics from modern ecological and evolutionary perspectives. Although there have been several brilliant reviews dealing with flea life history (e.g. Marshall, 1981a; Traub, 1985; Vashchenok, 1988), most ecological and evolutionary approaches that have been developed during the last two decades have not been applied to these animals. This book is aimed at filling the gap between the descriptive biology of fleas and current ecological and evolutionary theory.

An additional issue of note is that fleas have been, and are being, extensively studied in countries of the former USSR; thus much flea literature is in Russian. Moreover, these papers were published in exotic journals, periodicals and collective volumes, making them difficult to obtain and to understand for the Western scientific community. Two reviews of Russian flea literature (Bibikova, 1977; Bibikova & Zhovty, 1980) were published in English, but both are outdated. Given that Western flea-related sources, at least, up to the late 1970s, were carefully reviewed by Adrian Marshall (1981a) and Robert Traub (1980, 1985), I tried to include as many examples as possible from studies done in the former USSR and post-USSR countries as well as in Eastern Europe. Many studies of fleas were done in China. I regret that the Chinese literature has not been as thoroughly reviewed as it should have been. Nevertheless, I did my best to use Chinese sources as well. In this endeavour I obtained help from one of my colleagues and collaborators, Dr Liang Lu, from the Chinese Centre for Disease Control and Prevention in Beijing.

I intentionally avoided the purely applied aspects such as, for example, the control of fleas on domestic animals, as this book is not meant to be either a medical or a veterinary text. Instead, the book moves from basic descriptive aspects, to functional issues and finally to evolutionary explanations. Part I provides a brief description of flea taxonomy, life cycles, and flea–host associations, addressing the question: *what* do fleas do? Part II addresses the functional

ecology of fleas. It deals with proximate causes of flea responses to their hosts and environment and, thus, addresses the question: *how* do fleas do what they do? Finally, Part III deals with the evolutionary ecology of fleas and the ultimate explanations of observed patterns, addressing the question: *why* do fleas do what they do? In addition, (a) in contrast to many earlier texts on parasitology and (b) following Claude Combes's (2001) idea of a parasite and a host being involved in a durable and intimate interaction, I consider both fleas and their hosts together as two partners in the same game.

During my studies on fleas, and while writing this book, I was helped by many people. Robert Poulin, Allan Degen and Berry Pinshow (in chronological order) were the very first persons with whom I shared the idea of writing this book. It would not have been written without their encouragement. I would like to thank my collaborators and co-authors in publications (in alphabetical order): Zvika Abramsky, Allan Degen, Laura Fielden, Kevin Gaston, Michael Hastriter, Michael Kam, Irina Khokhlova, Tatiana Knyazeva, Natalia Korallo, Carmi Korine, Liang Lu, Sergei Medvedev, Dana Miklisova, Serge Morand, Ladislav Mošanský, David Mouillot, Berry Pinshow, Robert Poulin, David Saltz, Georgy Shenbrot, Marina Spinu, Michal Stanko, Valentin Vashchenok, Diego Vázquez and Maxim Vinarski. These people represent countries from Russia to New Zealand and from China to Canada. Members of my team in the Mitrani Department of Desert Ecology (Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev), Sergei Burdelov and Nadezhda Burdelova, have worked with me during the past 12 years, in the field and in the laboratory, and I am very grateful for their help. I thank my research students and postdoctorate fellows (in alphabetical order): Marine Arakelyan, Dikla Bashary, Tatiana Demidova, Lusine Ghazaryan, Joëlle Goüy de Bellocq, Hadas Hawlena, Ana Hovhanyan, Mariela Leiderman, Maria Lizurume, Natella Mirzoyan, Isik Oguzoglu, Luis Rios, Michal Sarfati, Pirchia Sinai and Kelly Still. They represent not only Israel, but also (in alphabetical order) Argentina, Armenia, Guatemala, France, Russia, Turkey and the USA. I hope they learned not only to study fleas, but also to view them as interesting and charming animals rather than repulsive and aggravating pests. The ideas in this book were discussed over the years with colleagues who helped with their suggestions. They are (in alphabetical order): Vladimir Ageyev, Michael Begon, Frank Clark, Claude Combes, Natalia Darskaya, Katharina Dittmar de la Cruz, Lance Durden, Kenneth Gage, Terry Galloway, Heikki Henttonen, Matthias Kiefer, Michael Kosoy, Marcela Lareschi, Kim Larsen, Herwig Leirs, Douglas Morris, Kosta Mumcuoglu, Robert Pilgrim, Yigal Rechav, Michael Rosenzweig, Lajos Rózsa, Uriel Safriel, Arkady Savinetsky, Svetlana Shilova, Albert Survillo, Viktor Suntsov, Andrey Tchabovsky, David Ward and Michael Whiting. Omar Amin, Daniel Frynta, Ryszard Haitlinger, Liang Lu, Elena Naumova, Michal

Stanko and Elena Zharikova provided me with some rare literature. My colleagues (in alphabetical order): Allan Degen, Kirill Eskov, Megan Griffiths, Michael Hastriter, Irina Khokhlova, Burt Kotler, Serge Morand, Berry Pinshow, Robert Poulin and David Ward read earlier versions of chapters of this book and made helpful comments. Zoe Grabinar and Marcia Chertok improved the English prose. I thank Cambridge University Press and, in particular, Jacqueline Garget for the opportunity to publish this book with a leading scientific publisher. Finally, I thank Irina Khokhlova, who is not only my collaborator of many years, but also my spouse, and our children Helena and Alexander for their continuous support and patience.

For taxonomy and names, I followed Medvedev *et al*. (2005) for fleas, Clements (2007) for birds and Wilson & Reeder (2005) for mammals. Consequently, some species names differ from those in the original sources.