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Escaping from Predators: an Integrative View of Escape Decisions

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978-1-107-06054-8 - Escaping From Predators: An Integrative View of Escape Decisions

Edited by William E. Cooper and Daniel T. Blumstein

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Escaping From Predators

An Integrative View of Escape Decisions

When a predator attacks, prey are faced with a series of “if,” “when,” and “how” escape decisions – these critical questions are the foci of this book.

Cooper and Blumstein bring together a balance of theory and empirical research to summarize over 50 years of scattered research and benchmark current thinking in the rapidly expanding literature on the behavioral ecology of escaping. The book consolidates current and new behavior models with taxonomically divided empirical chapters that demonstrate the application of escape theory to different groups. The chapters integrate behavior with physiology, genetics, and evolution to lead the reader through the complex decisions faced by prey during a predator attack, examining how these decisions interact with life history and individual variation. The chapter on best practice field methodology and the ideas for future research presented throughout ensure this volume is practical as well as informative.

Electronic supplementary material is available for download at www.cambridge.org/9781107060548.

William E. Cooper, Jr. is Professor Emeritus of Biology at Indiana University-Purdue University Fort Wayne, and a Research Associate in the Department of Ecology and Evolution at University of Arizona. A behavioral ecologist by background, he has over 35 years of teaching and research experience in behavior, ecology, and evolution. He has specialized in escape behavior for the past 20 years, with particular interest in reptilian behavior.

Daniel T. Blumstein is Professor and Chair of the Department of Ecology and Evolutionary Biology at UCLA, and a Professor in UCLA’s Institute of Environment and Sustainability. He has studied animal behavior throughout the world, with research focusing on the evolution of social and antipredator behavior and the effects that mechanisms of behavior have on higher-level ecological processes and for wildlife conservation.

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“Should I stay or should I go now?

If I go there will be trouble

An’ if I stay it will be double”

The Clash, “Should I Stay Or Should I Go”

(Lyrics reproduced with permission)*

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Foreword

Our 1986 paper “The economics of fleeing from predators” had a difficult birth. It was originally written for an edited volume on behavior, stillborn when the publisher reneged on the contract. Subsequently it was negatively reviewed for the *American Naturalist*. The reviewer’s comments on the manuscript consisted of seven question marks, two marginal notes (“I disagree” and “too simplistic”), and the remark “The predictions are more extensions of the model’s definitions than deductions” – which we still do not understand. Fortunately, others gave our model a more sympathetic hearing. Jay Rosenblatt and Colin Beer, who ran the annual publication *Advances in the Study of Behavior*, invited us to submit a manuscript after hearing LMD speak at the 1984 Animal Behavior Society meeting in Cheney, Washington. We accepted, and are still grateful to them.

In contrast to the frustration of pushing it out into the world, the gestation of the model was fun and exciting. The model’s working title was “The economics of the third F,” referring to the position of “fleeing” among the 4 Fs of behavior (feeding, fighting, fleeing, and reproduction). It was conceived at a time when behavioral ecology was just coming into its own at our university and at many others. As we noted in the introduction to the paper, “economic” (that is, costs and benefits in a fitness framework) ideas were being applied to feeding, fighting, reproductive and social behavior: the application to antipredator behavior seemed to us a natural step.

It was a happy and busy time. The Behavioral Ecology Research Group (BERG) at SFU was coalescing, and we were engaged with plans to host in Vancouver the 1988 meeting of the brand new International Society for Behavioral Ecology. We would like to thank the many colleagues who gave us useful input on our model, and we submitted a manuscript to “*Advances*” in April 1985, which was duly published the following year.

Thereafter, things went quiet – for a decade. The paper was not cited at all for a few years, then sporadically, and did not receive more than ten annual citations until 1997. Thereafter it has been cited more often in each subsequent year, as in the mid-90s the number of papers on escape began to climb. This increase was just one part of the swelling interest in antipredator behavior.

In spite of having been cited many hundreds of times, the basic model in “The economics of fleeing from predators” has not received much rigorous scrutiny. It does so in this volume, and we are a little embarrassed to agree that, strictly speaking, it is wanting. Perhaps the referee whose comments we castigated above had a point after all! But if the criticisms were justified, they also missed the bigger picture, something that

Professors Rosenblatt and Beer saw more clearly. Our model expressed the predator–prey interaction in a simple way that captured the essence of an idea that was in the air. In spite of its shortcomings, it provided a conceptual framework and suggested an empirical approach in a way that inspired many investigators to undertake their own studies.

The benefit of escape from predators has always seemed obvious – in fact, blindingly so. Few thought of fleeing as a “decision,” or saw that there were costs, most notably lost opportunity, i.e., a fleeing animal cannot perform other fitness-enhancing activities. Many prey escape to a refuge, and it seemed natural to us to use the same approach to ask how long animals should remain before re-emerging. This interesting question requires a game theoretic approach, of which we anticipate much more in future work.

These two prey decisions – flight initiation distance and hiding time – have been the subject of most work and represent the majority of the research summarized in the present volume. But the field has expanded to consider other sorts of escape decisions, such as how far and in what direction to flee, prey strategies while being pursued by predators, and alternative tactics when fleeing is not feasible. The range of species in which these issues has been addressed is impressive, as Part II amply demonstrates. Particularly interesting is the recent work on genetics of escape, and the role of individual personality differences (the shy–bold continuum). Research described in Part III, on the physiology of escape, holds the promise of a more quantitative predictive theory than has existed to date. This will benefit the application of this work to animal welfare and conservation, as discussed in Chapter 16.

We are gratified that our work led to such an explosion of empirical and theoretical studies and contributed to the growth and maturation of an important subdiscipline of behavioral ecology. As the editors say in their introductory chapter, “The story is still unfolding, and many aspects of our topic have not yet been addressed theoretically and many generalizations and exceptions remain to be discovered through empirical studies.” This book should go a long way to furthering the development of this exciting field.

We had always intended that “escape” be interpreted more broadly, as a general metaphor for decisions about antipredator behavior, with costs and benefits. The importance of antipredator behavior was first grasped in foraging, and is now beginning to be appreciated in the evolution of a broad range of phenomena including migration, metamorphosis, hibernation, clutch size, and others – classical topics that have rarely or never in their historical development considered that the risk of predation might be vital. Basic ecological topics such as population dynamics and community structure are being reshaped by the realization that facultative adjustments to danger have profound impacts that can be enormous in extent (kilometers and years) relative to the small (minutes and meters) behavioral changes that individuals make.

In closing we’d like to draw attention to an important point that continues to be misunderstood. How should “predation risk” be assessed? Many ecologists evidently think that risk can be assessed by the level of mortality. Accordingly, situations with low mortality are considered “safe.” But, is this so? In previous commentaries we have made analogies with pedestrians (as prey) and cars (as predators), and noted that one could observe a busy downtown street for a long time and never observe a “predation event”

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(i.e., pedestrian struck by car). The situation is obviously dangerous for pedestrians, but they are struck infrequently because they are cautious. The analogy is imperfect (unlike real predators, drivers are generally careful of pedestrians) but it makes the point that mortality *per se* is a poor measure of risk. The “true” level of risk is the mortality that would occur if pedestrians were completely heedless. It must be assessed by techniques such as “flight initiation distance” or “giving-up density” (or, to pursue our analogy, how far a pedestrian would go to use a crosswalk rather than to jaywalk). This insight has turned the meaning of risk upside down. Rather than mortality setting the level of antipredator behavior, we see now that antipredator behavior sets the mortality rate. And because danger management also influences reproduction, an animal population, through the behavioral decisions of its members, in effect sets its own life table! It would be too much to claim that this startling conclusion could be deduced solely from our model’s simple premises. As in all science, the cross-fertilization of ideas and data, such as those presented in this volume, is essential. However, we feel it is not too much to claim that this simple model, with all its shortcomings, opened a window that gave a different perspective on an everyday phenomenon. Read this volume and enjoy the view.

Ronald C. Ydenberg**Lawrence M. Dill**

Acknowledgments

It has been extremely fun and educational to work with our contributors; we've learned a lot and we thank them for their contributions to what we believe is an exciting volume that summarizes past research and sets the stage for future discoveries! We're extremely grateful to Ron Ydenberg and Larry Dill for writing their historical preface that so nicely frames the book. Book chapters were thoughtfully reviewed by a mix of contributors and external reviewers (Peter Bednekoff, Don Kramer, Michael Jennions, Simon Lailvaux, Julien Martin, Sandrine Meylan, Mats Olsson, Terry Ord, and Matt Petelle). We are grateful for their incisive comments that helped us all improve individual contributions.

We were saddened by the passing of Robert J. Blanchard during the writing of this book. Bob was a pioneer in the field of defensive behavior and his loss is notable.

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