17 Afterword

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17.1 Introduction

As the chapters in this volume have shown, the field of escape behavior is both active and diverse. What has particularly excited us while editing this book is how a simple economic framework, pioneered by Ydenberg and Dill (1986) that (as they wrote in the forward) had problems getting published, has stimulated so much work about so many different aspects of escape. Theoretical advances have been coupled with empirical study. Indeed, we suggest that the study of escape provides a textbook example of the reciprocally illuminating interplay between theoretical models, observational and experimental empirical studies, and comparative studies, including meta-analyses. Many, but not all, escape decisions can be studied without specialized equipment. This simplicity and elegance puts the emphasis on clear thinking and focused hypothesis testing. We have taught classes and short courses on quantifying escape behavior. Students learn the methods quickly and are able to produce high-quality data soon. Thus we believe that the study of escape will continue to be a highly productive field. This is good because while we have learned a lot, as our authors have noted, there's much room for future discovery! In this afterword, we will briefly highlight five themes or questions that have emerged from this book, and touch on a sixth theme that we did not have sufficient room to properly discuss.

17.2 The importance of studying individuals

The field of behavioral ecology has fully embraced the importance of understanding individual variation (Carere & Maestripieri 2013). Indeed, the publication of papers showing that individuals behave in consistently different ways – they have personalities – has exploded over the past decade. However, many of the studies of escape behavior, especially those of FID and hiding time conducted in the field, do not follow individually identified animals. There are some notable exceptions (Carrete & Tella 2010; Ibáñez *et al*. 2014; Williams *et al*. 2014).

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The study of unmarked individuals has permitted remarkably large comparative data sets to be produced. This is a particularly notable characteristic of the escape literature. However, by not following individually identified animals, we are prevented from asking some sorts of questions. Individually marked animals are required to properly study the processes of habituation or sensitization to repeated exposure to predators (Runyan & Blumstein 2004). Individually marked animals are required to study the maintenance of personality variation (FID is a metric of boldness – Petelle *et al*. 2013). Without individually marked animals we cannot understand the importance of individual variation for escape decisions. Without studies of marked individuals we cannot study the quantitative genetics of escape behavior and understand selection and evolutionary dynamics.

We encourage others to continue to study unmarked animals when such data permit answers to salient questions, and when such studies also help expand large comparative data sets. However, we strongly encourage future researchers to study escape decisions of marked animals. By doing so, we will be able to address unanswered, but addressable, questions, that will reveal a level of complexity and nuance heretofore just hinted at.

17.3 The interplay between interspecific studies and intraspecific studies

This brings us to a second emergent question – the interplay between comparative results and results from single species. Meta-analyses and comparative analyses have shown that body size is an important determinant of escape decisions (Stankowich & Blumstein 2005; Blumstein 2006; Chapter 3). However, the range of body size across species is much greater than the range of body size within a species. Intraspecific studies often yield much smaller effect sizes than meta-analyses or do not find significant effects of body size on escape decisions (Petelle *et al.* 2013).

It is therefore relevant to ask: what can we learn from interspecific studies with respect to understanding decisions that individuals of a single species make? We encourage future researchers to test specific hypotheses about trade-offs and constraints identified from comparative studies using data from focused, single-species studies to conduct comparisons of multiple species. By doing so, we will better understand the limits of interspecific conclusions for understanding individual decisions. Furthermore, comparative studies permit detection of phylogenetic trends and important effects of ecology, life history, morphology, and physiology that may not be detectable using studies limited to single species.

17.4 Using physiology to define decision-making mechanisms

The third theme emerged from a careful reading of Chapter 13. In that chapter Litvin *et al.* highlighted the huge disconnect between field studies of escape and the detailed, and nuanced, insights that emerge from studies of escape behavior in laboratory rodents.

The studies they discussed have begun to identify specific neurophysiological pathways underlying specific escape behaviors. In some cases they have shown us that what a field-oriented biologist may assume is one type of escape behavior is actually controlled in a very proximate sense by different mechanisms and thus is a more complex behavior than initially realized. Clearly, detailed neurophysiological studies will shed light on different decision-making mechanisms and, by doing so, will enable us to better understand the drivers of escape decisions. Much work remains to be done in this exciting field and future field investigators who draw insights from laboratory studies have the potential to make fundamental advances in understanding decision-making in natural situations.

Much of this book is focused on FID, but effects of physiology on FID have only rarely been studied in the field. One study cited in Chapter 13 detected a relationship between corticosterone level and FID in a lizard (Thaker *et al*. 2009). We know of only two other studies of the physiology of FID, both of which confirm the importance of corticosterone in lizards (Berger *et al.* 2007; Rödl *et al*. 2007). Although these studies cover only a single aspect of the diverse neuroendocrine mechanisms that modulate escape behavior, the findings of the few field studies are as predicted from our knowledge of the physiological underpinnings of other aspects of escape behavior gained from laboratory studies. This suggests that other previously identified neuroendocrine mechanisms of escape behaviors may similarly affect FID and perhaps other aspects of escape in the field. An almost entirely unexplored avenue of research, that promises to be extremely fruitful, awaits future investigation.

17.5 The importance of sensory physiology

As Chapter 12 so clearly demonstrated, a fundamental understanding of sensory physiology is important to create realistic assumptions when modeling escape decisions. Tyrrell and Fernández-Juricic clearly showed us in Chapter 12 how it is essential to understand, at a fundamental level, what animals can see, hear, and smell, if we are to understand how they make escape decisions. For instance, it is essential to know about an animal's visual field to properly understand if individuals engaged in searching for food pay a cost in terms of reduced vigilance. This reminds us that models of decision-making may be flawed if assumptions do not properly capture sensory constraints on acquisition of information. These warnings should stimulate considerable work, and it will be exciting to see its outcomes.

17.6 Utility, range, and testability of theory

The escape theory described extensively in Chapter 2 provides the basis for predicting effects of many factors discussed in later chapters. The economic models of FID and hiding time, including optimality models and other models in which escape and hiding decisions are based on costs and benefits of fleeing, have been very successful in the sense that their predictions have been broadly supported for many factors affecting escape by diverse prey taxa. Despite their successes, current models are limited in scope, and critical tests to distinguish between predictions of alternative models have not been forthcoming.

Current escape models describe decisions about escape behavior for only limited aspects of the range of predator–prey interactions that are the most amenable to empirical study. They apply primarily to decisions to flee by an immobile prey monitoring a predator as it approaches and to emerge from refuge after some interval spent hiding. Recently, the latency to flee from an immobile predator by an immobile prey has been modeled successfully. In Chapter 2 these models are extended to another scenario in which the prey approaches the predator and the more complex scenario in which both predator and prey are moving is discussed, but models of these scenarios remain to be tested. Indeed, the latter scenario will be more difficult to study than the others, and will likely require video and computer equipment to measure movements of predator and prey simultaneously. Current economic models also do not predict escape strategies or changes in strategy discussed in the chapter on escape strategy (Chapter 8) and some of the taxonomically oriented chapters. These will be important topics for future theoretical exploration.

Two types of models, some with extensions, have been used to predict decisions involving distance and time. Ydenberg and Dill's (1986) original graphical escape model predicted that prey flee when the cost of not fleeing equals the cost of fleeing. This model was later adapted by Martín and López (1999) to predict hiding time in a refuge. Cooper and Frederick (2007a,b) developed optimality models for both FID and hiding time. In the optimality models, prey make decisions that afford them greater fitness at the end of the encounter than do the other models.

Although the quantitative predictions of the two types of models differ, we are currently unable to perform the critical tests needed to choose the better sort of model because we have not measured the effects of relevant variables on fitness, which is the currency of all of these models. In studies of escape behavior, behavioral ecologists are confronted by the same inability to measure fitness, and therefore the same inability to adequately test quantitative predictions, that has plagued fitness-based models in studies of foraging and other behaviors. A second general problem that applies to all current escape models is that animals may not be capable of making decisions that are exactly optimal or of determining the exact distance between predator and prey. It is to be expected that they reach approximations of such decisions by using rules of thumb to gauge predation risk (Bouskila & Blumstein 1992), cost of fleeing, and their own initial fitness.

Despite these handicaps, both types of models are useful. The mathematical functions implied by their graphs, or stated explicitly by their equations, were selected to meet some criteria for the escape and hiding scenarios. However, they are merely illustrative because the shapes of the fitness functions are unknown. Therefore empirical determinations of the distance and time functions cannot distinguish between the models. New methods are needed to measure fitness directly or to equate fitness units among variables such as cost of fleeing, cost of not fleeing, and initial fitness. One of the most difficult challenges for empiricists using escape theory will be to untangle the effects of factors such as body size, autotomy, and female reproductive status on multiple variables in the models.

Fortunately, the models are very useful despite these limitations. The qualitative predictions of both models are similar with slight alterations of the original graphical models to incorporate the effect of the prey's fitness at the start of a predator–prey encounter. Tests of the qualitative predictions support the models equally well. They continue to provide useful frameworks for future advances in understanding effects of numerous factors on escape behavior and seem well suited for extensions predicting simultaneous effects of multiple variables and modification to make predictions for other escape variables and changes in escape strategy.

17.7 Application to wildlife conservation and management

The application of escape behavior to improve wildlife conservation and management, the last major theme of this chapter, is an important field that has already begun to yield insights and can be expected to produce more useful aids to conservation and wildlife management. The chapters in this volume have shown, in exquisite detail, how the rules dictating when and how to escape are the outcome of natural selection and sexual selection that have traded off costs and benefits of escape. Such rules have evolved to be "optimal" in the environment in which they were selected. Sadly, humans have had a remarkably huge impact on the natural world. Animals may now find themselves in situations where old decision rules are no longer adaptive (Candolin & Wong 2012; Gill & Brumm 2014). Such evolutionary mismatches have consequences for fitness.

Thus, there is a need to properly understand the environmental drivers of decisions about escape. Doing so may permit us to understand and identify which key environmental drivers (such as habitat type, predator density or diversity, patch size, food type, etc.) have a disproportionate impact on escape behavior. Much of the field of conservation behavior is focused on managing decisions individuals make. Thus armed with this knowledge we may identify what to conserve or manage.

However, knowledge of escape behavior can be used more directly. As has been discussed elsewhere (Blumstein & Fernández-Juricic 2010), by quantifying AD and FID, we can develop set-back zones that aim to reduce the impact of humans on sensitive wildlife. Physiological effects of being approached and of escaping on prey may become important considerations in the establishment of set-back distances. By understanding the costs and benefits of hiding, we can begin to quantify disturbance in ways that may be particularly useful to managers tasked with reducing human impacts on sensitive wildlife.

17.8 Conclusions

The questions we ask about escape are not without controversy. As our chapter on best practice (Chapter 16) illustrates, there are unresolved methodological questions. And there are unresolved mechanistic hypotheses. For instance, what is the magnitude of attentional costs? Is the flush early and avoid the rush (FEAR) hypothesis supported? Which theoretical models best describe prey behavior? We hope that the rapid rate that new results are generated will, in another decade, allow us to look back and not only have answers to some of these and more questions, but also have developed new and unforeseen questions.

We have written much about escape behavior in the hope that it will be interesting to you, our readers, and to provide enough information to stimulate new research. We know that the book will have some heuristic value because writing and editing it has given us many new ideas, some of which we have already begun to explore. Our overarching goal has been to present the information, but we have neglected to convey a major motivation that drives our work. The sheer joy of developing new ideas, designing experiments and observational studies, analyzing data statistically to test predictions, writing to share our findings, are our rewards, as well as working with colleagues at all of these stages of the scientific process. New ideas flow when writing about the findings. For many of us, the most exciting times are spent in the field in beautiful natural habitats. Enough writing: it's clearly time to get back into the field, scare some animals, and reveal the wonderful complexity by which animals escape their predators!

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