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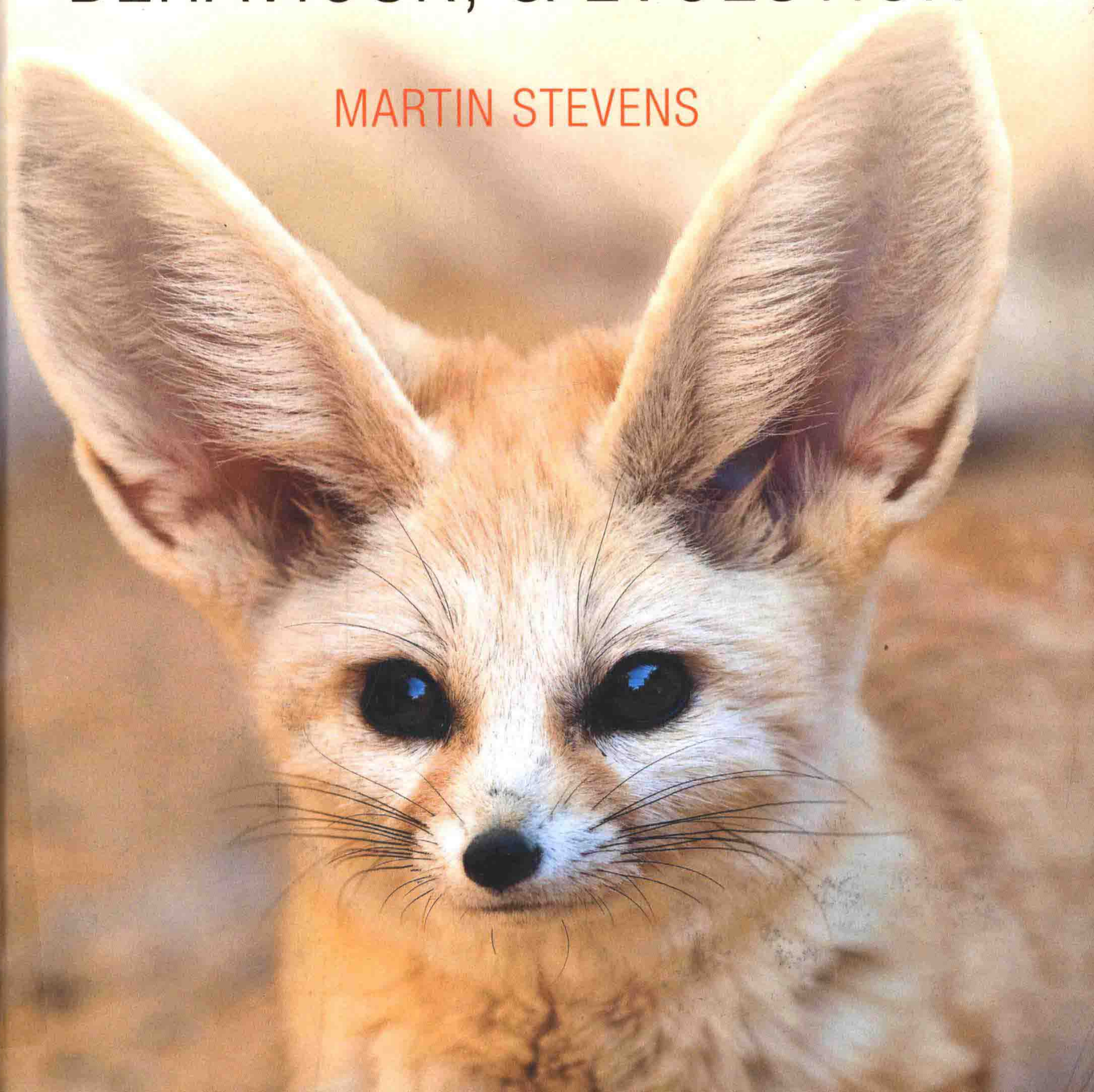
SENSORY ECOLOGY, BEHAVIOUR, & EVOLUTION

MARTIN STEVENS



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Preface

Writing this book has been an illuminating and rewarding journey. Before beginning the project I thought I had a reasonable idea of just how exciting and vibrant the subject of sensory ecology is. I was wrong! It was only as I really got stuck into working on the book that I truly realized just how much incredible and innovative work is being undertaken every year in this field, and the many remarkable examples of natural history that have formed the inspiration for much of this research. I hope I have done the subject at least some of the justice it deserves.

Sensory ecology as a scientific discipline has boundaries that are hard to define. It is perhaps for this reason that few books specifically on sensory ecology actually exist, despite the subject's substantial importance in modern day biology and its rapid growth in the last decade or so. Historically, sensory ecology emerged as discipline that linked conventional ecology with studies of animal behaviour, grounded in the idea that animals need to obtain and use information to behave appropriately in a given environment. This was the approach that Dusenbery's (1992) seminal book, *Sensory Ecology* took, and the idea of information is still central to sensory ecology today. Dusenbery focused on the physics of how different modalities work (for example, sound, light, chemicals), and related this to various ethological examples, such as navigation, searching, and so on. Undoubtedly, this approach is important and the content of that book remains valuable. However, partly thanks to the rise and continued popularity of subjects like behavioural and evolutionary ecology, sensory ecology today deals with all that Dusenbery discussed, but spans across into behavioural ecology and evolutionary processes. For that reason, a modern book on sensory ecology should cover the way that sensory system work, the principles and areas of animal behaviour, through to evolutionary processes. Clearly, to cover all of this in depth would require a massive book, therefore this text should be seen as a broad introduction. The principal aim is not to present an updated version of Dusenbery (1992), but to introduce the subject of sensory ecology, including how sensory systems work and sensory processing, from a more behavioural and evolutionary framework (reflecting how the field has evolved in the last two decades).

I also did not wish to write a book that dealt with each sensory modality one by one in isolation. There are various excellent books devoted to specific sensory modalities and that go into far more detail than I do here. On the contrary, I wanted to produce a book that dealt with the role of sensory systems in a modern behavioural framework, including what sensory systems are used for and how they guide the many behavioural tasks animals must complete during their lives. I also wanted to give the book an evolutionary context, showing how important sensory systems are in processes like diversification and speciation. The various sensory modalities in the book are discussed together, and the aim is to highlight common principles (and differences) across sensory modalities, and what they mean in terms of the way that animals behave and process information. There is much that I have omitted regarding sensory physiology and processing, but my aim was not to present a book focusing only on how sensory systems work. Instead, I have sought to present enough information for the reader to understand important concepts so that the more behavioural and evolutionary issues and discussions could be understood from this basis. Some sensory modalities are presented and covered in more detail, whereas others arise less often or with respect to only some subject areas. This partly reflects the state of play in the subject, with some modalities being worked on from a more behavioural/evolutionary perspective, but also no doubt limitations in my expertise. It is not a suggestion that some sensory systems are more or less important than others, because, as we shall see, the value of any sensory modality depends on the species, environment, and specific behaviour. That said, I acknowledge that this book necessarily reflects some bias in the literature towards studying sensory modalities that are particularly important to humans (especially vision) and consequent relative understudy of some ecologically important modalities (e.g. electroreception and magnetoreception) that we lack.

Generally, this book is more focused on recent work and discoveries, rather than presenting an historical overview of the various topics introduced. The intention here is certainly not to do disservice to older work, which is of course fundamental for new work to build upon. Rather, any bias towards more recent studies is to help illustrate where the field currently stands, to show the diverse and exciting work that is being done today, and to hint at where the important next steps might be. As stated above, this book is intended to be an introduction to sensory ecology. There were various studies that I could not include, and some subjects that are discussed only briefly. For those studies that have been left out, it is not a reflection on their quality, but rather an inevitable outcome when trying to summarize such an diverse and vibrant field. Sometimes I have used well-studied systems or species in several chapters. This is partly intended to help with continuity across the chapters and to highlight the depth of understanding to which researchers have gained from some species and systems. Finally, this book does not explicitly discuss cognition and 'higher' level processes. Clearly these are important in decision making too, yet this goes beyond the sensory scope of this text.

The book is intended to present stand-alone chapters, while also providing a progression from one chapter to the next. It begins with key concepts such as information, and then moves onto the various sensory systems, sensory physiology, and nerve cells, through to important areas in behaviour and communication, and finally to fundamental issues in evolution, such as arms races and divergence. The first chapter discusses how the sensory information available to animals varies greatly across species owing to the sensory systems they have. It introduces the idea that sensory ecology deals with how animals gather and use information from their environment, and that the ecology of a species shapes the form and function of its sensory systems to best acquire and process information and to use it in behaviour.

The following three chapters deal with how sensory systems work. Chapter 2 introduces the different types of sensory system that have evolved to capture information from sound, light, electric, magnetic, mechanical, and chemical stimuli. It describes the overall features of these different sensory modalities, including the sensory receptors involved and what tasks the sensory system is used for. The chapter also describes how some animals have evolved an active sense with an ability to emit signals or calls into the environment and measure changes in the properties of returning reflections to assess the world around them. Chapter 3 focuses on some specific examples in more detail, mainly from vision, hearing, and olfaction to demonstrate the neural mechanisms that exist in sensory processing to encode important information. It covers key principles demonstrating how sensory systems remove redundant information and encode change in the environment, including filtering, feature detectors, receptive fields, adaptation, and parallel processing, and how these processes are made possible by the flexibility of connections between nerve cells and circuits. Chapter 4 discusses how sensory systems face energetic costs, as well as trade-offs in the way that they work to encode different types or features of stimuli. The chapter deals with if and when sensory systems are optimized for one task, as opposed to having features that have evolved to work in many. The second half of the chapter describes how sensory systems do not work in isolation, but rather that animals often integrate information from several modalities and that this can decrease uncertainty about a stimulus or environment.

Chapters 5–8 cover important areas regarding communication in animals. Chapter 5 introduces fundamental concepts relating to signals, cues, and communication in general. It defines what signals and communication are (and the controversy that still surrounds this), and how signals differ from cues. The chapter also argues that to understand the diversity of signals and communication systems in nature fully, we need to carefully consider how signals have evolved in response to the sensory system of the receiver. Chapter 6 introduces the idea of multimodal signals, which involve the use of signal components across two or more sensory modalities. The chapter discusses a framework for understanding multimodal signals and what constitutes one. It covers explanations for the existence and benefits of multimodal signals, including facilitating effective signalling under noisy or variable environments, and allowing receivers to extract different information ('messages') from a signal. Chapter 7 begins by discussing how signalling and communication carry significant costs, not just in terms of energetics, but also through how signals are exploited by eavesdroppers, such as predators, prey, and competitors. The chapter then describes how animals might reduce risks of eavesdropping, including evolving less conspicuous or localizable signals, changes in behaviour, or signalling in a modality that the eavesdropper cannot detect or to which it is insensitive. Finally, the chapter discusses when and how organisms combine multiple functions with the same signal form to perform multiple tasks. The final chapter in this section, Chapter 8, discusses how many signals in nature are dishonest, including various forms of mimicry. This can involve organisms exploiting the communication systems of other species in order to deceive an animal into mistaking it for something else, or exploiting pre-existing biases in the sensory systems of animals to manipulate the receiver's response. The chapter discusses how sensory exploration and mimicry is widely found in mating signals and communication systems, and how exploitation and sensory biases can lead to exaggeration in signal form.

The final three chapters discuss the role of sensory systems in key evolutionary processes, and how the environment shapes sensory systems and communication. Interactions between species or groups of organisms, both cooperative and antagonistic can be powerful generators of biological diversity. Chapter 9 focuses on two such driving forces: arms races and coevolution. It discusses how predator–prey relationships provide clear examples of arms races, but also how there is little evidence for genuine coevolutionary responses in the sensory systems of the predators to overcome prey defences. In contrast, coevolution seems widespread and diverse in brood and social parasites in birds and insects, and this has lead to extraordinary defences and counter-adaptations in both parasite and host across a range of modalities. Chapter 10 deals with how the environment affects the way that sensory systems work and how organisms interact and communicate. It outlines how organisms use different signal forms in different environments, switch between sensory modalities, or tune their sensory systems to cope best with features of their habitat. The chapter then discusses how different habitats and environments influence the way that information is acquired, how signals are transmitted, and how environmental noise (including those from anthropogenic sources) can interfere with obtaining relevant information. The final chapter (Chapter 11) discusses how sensory and communication systems are involved and are crucial in leading to divergence between populations and speciation. The chapter outlines how we are starting to understand more fully both the molecular mechanisms underlying some of these changes, as well as the selective advantage incurred, and how certain mechanisms can lead to divergence and speciation, including reproductive character displacement, disruptive selection, so-called magic traits, predation pressure, and mate selection, and how these factors operate in different groups and sensory modalities. Finally, the chapter discusses how the environment may cause divergence and speciation in some groups through the process of sensory drive.

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Contents

PART 1

Introduction

CHAPTER 1

Sensory Ecology, Information, and Decision-Making

Box 1.1 Key Terms and Definitions

Information: Acquired by organisms from the general environment or from other individuals and reduces uncertainty about a feature or state of the environment, individual, or future events.

Personal Information: Information that individuals gather themselves by directly interacting with the environment.

Proximate Explanation: This is the causal explanation or underlying mechanism explaining *how* something happens.

Socially Acquired Information: Information gathered from other organisms of the same or a different species.

Ultimate Explanation: This is the function or evolutionary advantage explaining *why* something happens.

The world around us is full of sights, sounds, smells, and textures that stimulate our various sensory systems and enable us to interact appropriately with the environment. Our sensory systems are crucial to survival, and this was even more the case when we lived in the wild without modern aids and comforts. We needed them to find food, communicate, navigate, detect predators, and much more. In the modern world, the information our sensory systems provide is every bit as important. To other animals, sensory systems also make the difference between life and death on a daily basis. Sensory systems are the products of hundreds of millions of years of evolution and, given their importance, are breathtakingly diverse across and sometimes even within species. They are often closely linked to the ecology of a species, and have been shaped by an array of selection pressures to enable an animal to perform numerous behaviours. In short, sensory systems are fundamental to survival and reproduction and shape much of evolution and behaviour.

1.1 What is Sensory Ecology?

In the conclusion of *The Origin of Species*, Darwin (1859) presented the description of an entangled bank, with plants of many kinds, birds singing in the trees, insects going about their business, and worms moving through the ground below. In doing so, he illustrated the importance of the environment in the evolution of different types of species, the niches they live in, and the complex interactions between organisms. It is often helpful to think about species in terms of the niches they inhabit, based on a physical separation in space or time. Yet, even organisms living in the same place, at the same time, inhabit different worlds: they live in different sensory environments, bounded by the properties of their sensory organs. For example, a bee using colour vision to search for flowers may be right next to a snake waiting to detect the infrared cues of its prey or an ant following chemical pheromone trails to food. Animals should, and do, only pay attention

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to features of the habitat that are important to them. What they can detect and respond to is dictated by their sensory systems and how they are constructed over evolution. Animals can be almost touching each other in space, but be worlds apart in perceptual terms.

Unsurprisingly, animals have evolved a staggering array of sensory organs that are fundamental to survival and reproduction, and shape a great deal of evolution and behaviour. Sensory ecology deals with how animals acquire, process, and use information in their lives, and more recently the role of sensory systems in evolutionary change. Defining almost any subject in biology is difficult because the boundaries between disciplines are frequently blurred. This is certainly the case for sensory ecology, which spans a broad range of ideas and subject areas. On a basic level, it covers everything from the way that sensory systems work (physiology and neurobiology), to the way sensory systems are used (e.g. in behaviour), to the role of sensory systems in evolutionary processes (for example, reproductive isolation).

In many respects, sensory ecology is not a new subject; the classic works on visual ecology by Hailman (1977) and Lythgoe (1979) constitute sensory ecology in the modern sense. However, the subject was perhaps first formally presented as a whole by Dusenbery (1992). At that time, sensory ecology essentially comprised the integration of more 'conventional' ecology with sensory neurophysiology (Bowdan and Wyse 1996). Dusenbery's book focused on the idea that information existed in the environment and that animals needed to obtain and use this information. The book, although a landmark, largely focused on the physics of such potential information, the physiology of the sensory systems, and a few selected ethological examples, such as navigation. Dusenbery (1992) dealt only briefly with many of the evolutionary and ecological implications of these ideas. In the last decade, sensory ecology has come of age. Partly thanks to the rise and continued popularity of subjects like behavioural and evolutionary ecology, sensory ecology now deals with all that Dusenbery discussed, but also spans into behavioural ecology and evolutionary mechanisms. The central issues in sensory ecology are: *i*) how do animals gather and use information from their environment and from other organisms, *ii*) what role does the ecology of a species have in shaping the form and function of sensory systems to best acquire and process information, and *iii*) how does this influence behaviour and evolution? We will return to the idea of information shortly, because it is an essential (albeit sometimes controversial) concept central to much of sensory ecology. First, however, we discuss some examples of how the information that is available to animals depends on their sensory systems.

1.2 Many Animals Detect and Use Sensory Information Humans Cannot Perceive

Animals often do not perceive the world in the same way that humans do, and we need to be aware of this in studying sensory and behavioural ecology. First, there are entire sensory modalities that humans lack. For example, various animals have a magnetic sense, which they use to navigate over both relatively shorter and longer distances. Likewise, many fish (and some mammals and amphibians) have an electric sense. This can be both passive, involving detecting electric information from the environment (e.g. prey) or active, where the fish emits electricity to the environment and detects the changes in the returning signal. Electric senses are used in many ways, including detecting food, navigation, object detection, and aggressive and courtship interactions. We will discuss how the different senses work and their uses in Chapters 2 and 3.

Equally importantly, even in sensory modalities that humans have, we can only detect certain proportions of the information available to other animals. Here, we focus on examples from two important senses in humans, hearing and vision.

1.2.1 Ultrasonic and Infrasonic Communication

Humans can hear sounds approximately in the region of 15–20,000 Hz (although the ability to hear high frequencies often declines with age). In contrast, many animals can hear sounds at higher frequencies than we can (ultrasonic sounds), and some animals can hear lower frequencies (infrasonic).

Wild house mice (*Mus musculus musculus*) have complex ultrasonic vocalizations (USVs) with frequencies around 30 kHz. These are used by pups to solicit maternal care, but also by males towards females during courtship. Structurally, these vocalizations are similar to songs, such as used by birds, with repeated phrases. Using specialist sound detection equipment, Musolf *et al.* (2010) found that male mice would produce USVs when presented with females or olfactory cues of females, but not towards other males. They then played back sounds of male calls to females and looked at the time females spent associating with different speakers. Females preferred the USVs of males compared to noise, and also preferred the calls of unfamiliar (non-kin) males to those of related males. As yet, it is not clear what aspects of the signal females are choosing and exactly what benefits they may get from this (e.g. male quality or genetic compatibility). Recent work in rats indicates that there are several types of USVs produced, which may play different roles in communication, including in aggressive, feeding, and courtship encounters (Takahashi *et al.* 2010). Beyond rats and mice, ultrasonic communication has also been shown in the calls of some frogs (Feng *et al.* 2006), ground squirrels (Wilson and Hare 2004), and a range of insects, bats, and cetaceans.

Some mammals, such as elephants and certain species of whale, produce infrasonic sounds. African elephants (*Loxodonta africana*) produce low frequency calls with a considerable component below the human hearing range. Playback experiments in the field by Longbauer *et al.* (1991) indicate that elephants respond to these calls even over a distance of several kilometres. Although there is some debate, because low frequency sounds travel further more effectively than higher frequencies, which attenuate quickly, infrasonic calls may allow elephants to communicate and maintain contact between individuals over long distances and for individuals to re-establish contact with a herd. The low frequency vocalizations also have seismic components that are transmitted through the substrate. Field experiments with playbacks of alarm calls to wild elephants indicates that they respond behaviourally to seismic components, including by clumping together more in herds and orientating perpendicular to the playback source (O'Connell-Rodwell *et al.* 2006).

1.2.2 Ultraviolet and Fluorescent Signals in Mate Choice

In humans, colour vision is based upon the relative stimulation of and interactions between three cone types, each tuned to relatively shorter (SW), medium (MW), and longer (LW) wavelengths of light. Although we are highly visual animals, many other species have different, and potentially better, colour vision than us. Birds, for example, have colour vision involving the use of four cone types, including types of SW, MW, and LW cones, but also a class sensitive to ultraviolet light (UV cones). Birds can therefore probably see and discriminate between colours unavailable to us. In fact, the ability to detect UV light is widespread in animals, in both invertebrates and vertebrates.

Some animals, like parrots, have signals that absorb UV light and re-emit it at longer wavelengths (fluorescence). These colour patches are often found adjacent to plumage that reflects UV light strongly. In an experiment with budgerigars (*Melopsittacus undulatus*), Pearn *et al.* (2001) used coloured filters to selectively remove certain wavelengths of light from the ambient spectrum, allowing them to abolish either the UV reflectance of the feathers, and/or the fluorescence of the adjacent patches. They found that fluorescence was used in mate choice, but only when accompanied by the UV reflecting patches. A later experiment by Arnold *et al.* (2002), also with budgies, applied sunblock only to the fluorescent

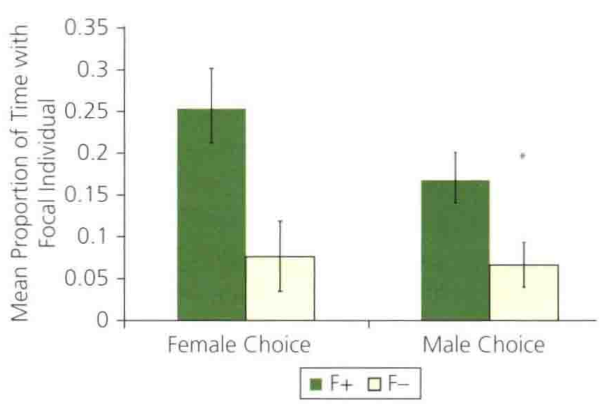

Figure 1.1 When presented with potential mates lacking fluorescence (F–) both male and female budgies spent less time associating with those individuals than individuals with fluorescence (F+). Data from Arnold *et al.* (2002). Error bars are standard errors.