



## ANIMAL SCIENCE

# The evolution of the concept of sensory ecology and the influence of behavioral ecology

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**Abstract:** The science of sensory ecology formally emerged in the book of Ali (1978), when behavioral ecology was gaining popularity. Until 2020, three main books were written on the subject, in 1992 (Dusenbery 1992), 2001 (Barth & Schmid 2001) and 2013 (Stevens 2013). The definitions of sensory ecology provided by Ali emphasize adaptation, optimality and fitness. These are main concepts of behavioral ecology but the last two are not necessarily fundamentals of sensory ecology. Here I looked at the evolution of the concept of sensory ecology and tried to understand whether there is evidence that the definitions given in 1978 had been influenced by behavioral ecology. I have counted the appearances of these three words (adapt\*, optim\* and fitness) in these books, divided by the number of words in each book, and compared the numbers to the definitions of sensory ecology given. Authors in Ali's book often use adaptation but seldom deal with optimality or fitness. I suggest that the appearance of these keywords of behavioral ecology in the definitions of sensory ecology in Ali's book was maybe a necessity to fit in the paradigms of that time. Sensory ecology was actually mechanistic in 1978 and 1992. Sensory ecology is now both mechanistic and evolutionary.

**Key words:** historical context, behavioral ecology, ethology, mechanism, proximal.

## INTRODUCTION

Knowledge evolves, paradigms and definitions change, and science makes progress. Throughout history, however, historical context within and outside sciences clearly influences the way we act and think (Kalikow 1983). Scientific literature not always fits the standards of an epoch (Radick 2007, Lepistö 2015). After Edward Wilson dared to attribute genetic influence on human behavior in 1975 in "Sociobiology", students rioted in Harvard squares. After World War II and eugenics, people were not ready for it (Segerstrale 2000). As Robert Trivers puts it, researchers in social sciences had pre-Darwinian and pre-Mendelian views on the social and psychological world (Dawkins 1976) and would not accept genetics in this context. However, today we have no doubt of

the interaction between genes and environment in shaping human behavior.

As researchers gain more information on a subject, specifics within a branch of knowledge often change. Therefore, anachronic interpretations of older texts are misleading because historical context, including the knowledge on the subject at a specific decade, matters. I give two examples in the fields of evolutionary biology and animal behavior: the handicap principle proposed to explain the evolution of exaggerated characters in males such as the peacock tail, proposed by Zahavi in 1975, was said to be "hard to accept" (Dawkins 1976). Kirkpatrick, in 1986, stated in the title of his paper that "The handicap mechanism of sexual selection does not work". However, after Grafen (1990a, b) has shown in 1990 that it is

possible under some scenarios, the handicap mechanism is now widely accepted and cited in textbooks of evolution and animal behavior (e.g. Ridley 2004, Davies et al. 2012). A second example is that Geoffrey Parker mentions that around 1965 one's article would not get published unless group selection was invoked. But ten years later, it was hard to publish unless you were a kin selectionist (Segerstrale 2000).

These two examples show that scientific community have expectations based on the current knowledge on the subject and related areas. Again, historical context matters. Emerging scientific areas undergo the same issue, namely acceptance by the current scientific community. Below I will introduce the emergence of sensory ecology and the context at that time.

### **A short history of behavioral ecology**

To contextualize the emergence of sensory ecology, I will briefly give an introduction of the history of studies on animal behavior. Experimental studies on animal behavior can be traced back to the XIX century, but only in the XX century did ethology got its name (Danchin et al. 2008) and was treated as a discipline (Barnard 2004). Because ethologists started to establish correlations between the behavior and ecology when discussing feeding, predation and use of habitat, ecology came into play in behavioral studies. With the great theoretical input of economic models of behavior, evolutionary stable strategies, the development of selfish gene and inclusive fitness paradigms, behavioral ecology was born (Krebs & Davies 1997) and, again, the approach given to studies in animal behavior changed. Perhaps the historically most important book on Behavioral Ecology had its first edition published in 1978, edited by Krebs & Davies. This book has summarized the advances in the sixties and seventies with four subsequent editions (1978, 1984, 1991, 1997) (Simmons 2014).

By the fifties onwards, classical ethology was criticized by researchers in several areas, with attacks peaking in 1973 (Danchin et al. 2008). By then, the adaptationist approach was already an explanatory system in studies of animal behavior, but adaptive significance meant the suitability of behavior considering the characteristics of the environment, with no specific relation to selfish genes. Although Lorenz has discussed the concepts of mutation, selection and adaptation during his career (Garcia 2005), he explicitly mentions a “good for the species” approach in his seminal book “Vergleichende Verhaltensforschung: Grundlagen der Ethologie”, published in 1978 (Lorenz 1978). The ideas by George Williams’ “Adaptation and Natural Selection” (Williams 1966) and Richard Dawkins’ “The Selfish Gene” changed the approach to adaptations: they emphasized that behavior is actually a phenotypic trait heavily influenced by genes. Bodies are only machines built by genes to replicate themselves (Dawkins 1976). With a few exceptions, animals should only invest in themselves and counterparts that have their genes (Davies et al. 2012, Simmons 2014), contradicting the “good for the species” idea. Therefore, the concept of fitness, namely “the contribution to the next generation of one phenotype relative to the contribution of other genotypes – Wilson 1975) was now crucial to interpret how animals behave. The renewed concept of adaptation in animal behavior and the concept of fitness were two of the cornerstones of behavioral ecology.

In the sixties and seventies, animal behavior was interpreted as decision making processes: questions such as how much time a foraging animal should spend in a patch or which food item it should choose mattered. Mathematical models collectively known as optimal foraging theory have been proposed (Dugatkin 2009). Because natural selection was

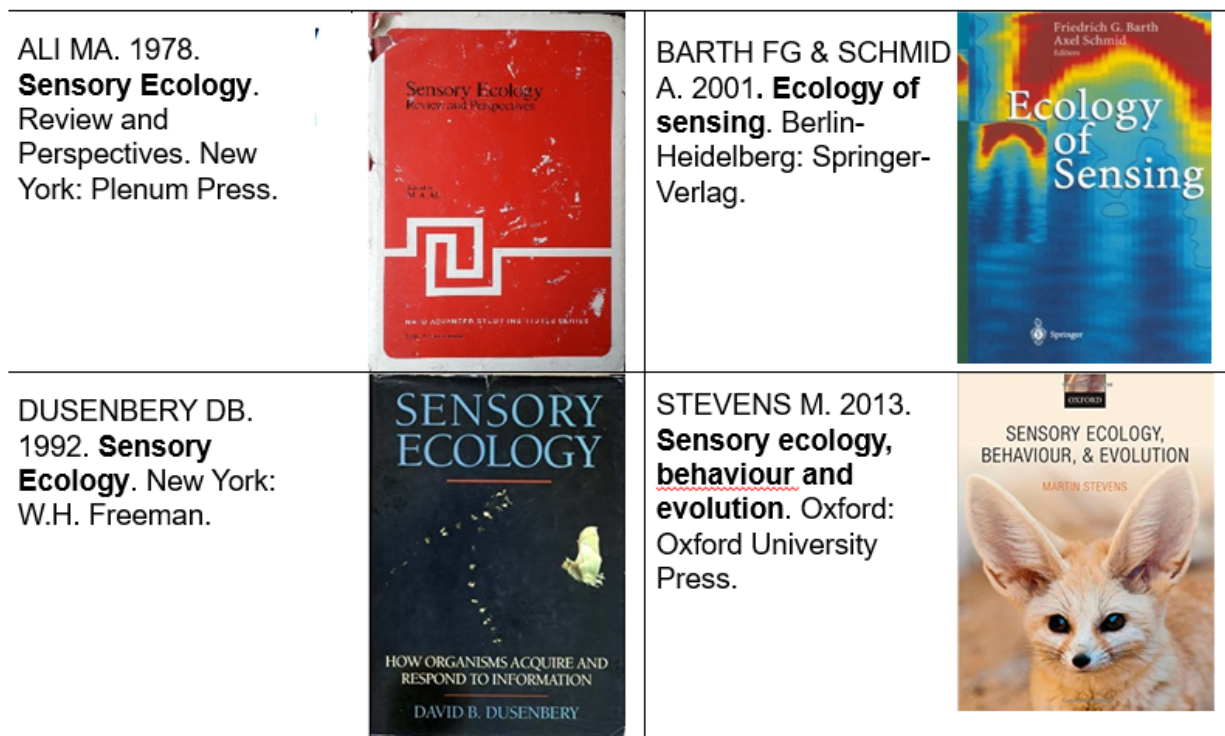
seen as an optimizing agent, choices made by animals were supposed to maximize their fitness. Optimization models were one of the cornerstones of the rising behavioral ecology and implied the concepts of fitness and selfish gene, which are other cornerstone concepts of behavioral ecology. Discussions on the validity of fitness and optimization are beyond the scope of this manuscript and can be found in Rapport (1991) and Birch (2018). Within this historical context and the rising of behavioral ecology, sensory ecology was born.

### A brief history of sensory ecology

Sensory ecology did not exist as a science field prior to 1977. Before that, sensory physiologists would study the responses of an organ to a stimulus with no ecological implication, ethologists would study behavioral responses with no ecological implication and ecologists would study ecological interactions without

referring to sensory modalities (Ali 1978). That year, an Advanced Study Institute on Perspectives in Sensory Ecology was held at Bishop's University, Quebec, Canada. The purpose was to interface sensory physiology with ecology. From that meeting resulted the book by MA Ali: *Sensory Ecology, review and perspectives*, 1978. This book has been launched when classic ethology was already declining and behavioral ecology was the main stream behavioral science. Three other important books were later published on sensory ecology, until 2020: Dusenbery (1992), Barth & Schmid (2001), Stevens (2013) (Figure 1). I have chosen these books because these are widely accepted classics that do not deal with specific taxa and because they were published within a large time range (35 years).

There has been no specific attempt in the literature to trace the origins or the evolution of the concept of sensory ecology. In this paper I aimed at analyzing a part of the history of



**Figure 1.** The four books analyzed in this paper.

the field, specifically looking at definitions, approaches and historical context. Ali's definitions of sensory ecology emphatically mention adaptation, optimization and fitness. At least the last two are not usually mentioned in the literature of sensory ecology, but these three concepts were, as mentioned, very important for behavioral ecology. Because Ali's book was launched at the heydays of behavioral ecology, I looked for evidences of the influence of behavioral ecology in Ali's book. I have attempted to discriminate between an actual incorporation of some of the main concepts of behavioral ecology throughout the book from a mere use when defining sensory ecology. From the definitions of sensory ecology in Ali's book "Sensory Ecology: review and perspectives" and the other three aforementioned books, I will show that the original understanding of sensory ecology changed throughout the years, as did the approach given by researchers. I will also argue that the context in which sensory ecology emerged possibly influenced the way Ali defined this term back in 1978.

## MATERIALS AND METHODS

In addition to a qualitative comparison of the approach given by each book to the subject, I also wanted to compare the putative influence of behavioral ecology in definitions and approach given by Ali's, since his book appeared in the heyday of behavioral ecology. If there was an influence of the historical context and the paradigms of behavioral ecology in sensory ecology, we could expect the cornerstone concepts of behavioral ecology to be widely used in Ali's book. Alternatively, these concepts could be only "must use" keywords in the first pages of a book (in the definition of sensory ecology), maybe to fit in the mainstream science of the epoch, but not actually used as relevant concepts

throughout the book. If such concepts were really relevant to the understanding of sensory ecology, I would expect them to be widespread and often used in the book. But if these concepts were used in definitions of sensory ecology only as a necessity to include sensory ecology in the valid paradigm of behavioral ecology, I would *not* expect such concepts to be widespread and often used in the book.

The concepts chosen were adaptation, optimization and fitness. Because these were main concepts in behavioral ecology as explained above, I used them as proxies of the influence of that science in the books I have analyzed. I have counted the number of times that "adapt\*", "optim\*" and "fitness" appear in the book. The symbol "\*" as in "adapt\*", for example, allows the inclusion of words such as adaptation, adapted, adapting, etc. I then divided such number of appearances by the number of words in the entire book. This procedure gave a value that could be compared among books. As a reference, I used the same procedure with three other books previously mentioned, which have been published in 1992, 2001 and 2013 (Dusenbery, Barth and Schmid and Stevens, respectively) (Figure 1). I have removed from the counting all the words (not only the three keywords) in: affiliations, cataloguing data, contents, headers, index, mathematical equations, names of authors in each chapter, references and titles. I have also deleted large tables with raw data (3 tables in Ali), since the other 3 books do not have tables with raw data. Specific words that would have been included following the methods but had other meanings were excluded (eg. "optimistic", "figure adapted from", "If exploration is in fact a major element in migration, it is easy to understand how migrations can adapt rapidly to changing climatic conditions"). The term "sensory adaptation",

when used in the physiological sense, was also excluded from the counts.

## RESULTS AND DISCUSSION

### Overview of each book

Ali (1978) edited the first book on sensory ecology. It has 597 pages in 20 chapters, some of which Ali also co-authored with the other 18 contributors. Ali's book begins by giving a general introduction, written by himself and then follows with a "survey of ecosensory functions". In this second part of the book, Ali and colleagues first provide a taxonomic survey of sensory modalities in Protozoa and Metazoans. After a chapter on taxes (phototaxis, chemotaxis etc) in unicellular organisms, other chapters cover sensory biology of invertebrates and vertebrates. The third part of the book has 9 chapters, each about a specific sensory modality. The book contains some parts with an evolutionary approach, but it is mostly mechanistic/descriptive.

Dusenbery (1992) is the sole author of the book with 558 pages in 19 chapters. He first provides an introduction and then divides the book in two parts: "Information basics", where he discusses the function of information, how to measure it and how different stimuli are transmitted. The author closes this first part with a fourth chapter on signal detection. Part 2 is on the stimulus properties, part 3 on stimulus generation and part 4 on "Exploiting spatial goals" (e.g. navigation, migration, etc). The approach is mechanistic throughout.

The book edited by Barth & Schmid (2001) was an outcome of a symposium organized by the two editors in Austria. They have edited and are part of a team of 25 contributors in a book with 341 pages divided in 16 chapters. After two introductory chapters, the book is divided in sensory modalities ("Sound and hearing", "Light and Vision", "Hygro- and Thermoreception", etc),

with a mechanistic approach. An exception is the chapter by Chittka and Briscoe, "Why sensory ecology needs to become more evolutionary – insect color vision as a case in point" (see discussion below).

Finally, Stevens (2013) is the single author of its book with 247 pages in 12 chapters. His approach is very distinct from the other 3 books: he dedicates only 19 pages for all the 6 sensory modalities he discusses and the book is organized by subjects in a way that it resembles to a book on behavioral ecology (chapters on "Signalling and communication"; "Arms races, coevolution and diversification", etc). The approach is both mechanistic and evolutionary and very conceptual.

### The definitions of sensory ecology

I give below the definitions of sensory ecology in each book. The reader can notice that Ali (1978) gives emphasis to adaptation, optimization and fitness. Dusenbery (1992) is clearly mechanistic, Barth & Schmid (2001) are mainly mechanistic and Stevens (2013) is both mechanistic and evolutionary.

#### **Ali (1978)**

In the introductory chapter, authored by Ali, he gives four definitions of sensory ecology. "1. Sensory Ecology deals with the means by which the fitness of organisms of a species is optimized through adapting to the constraints of information input of both the physical and biotic environments. 2. Sensory Ecology deals with the sensory means by which the survival of organisms is rendered optimal in response to the constraints of the environment. 3. Sensory Ecology is the study of means by which the fitness of organisms is rendered optimal to cope with environmental pressures through adaptive radiation of sensory mechanisms. 4. Sensory

Ecology deals with sensory strategies to cope with the environmental constraints.”

### ***Dusenbery (1992)***

The author does not spell out a straightforward definition, but cites a table (Table 1-2, page 7) to mention that “sensory ecology concentrates on third and fourth levels from the top of the behavioral pyramid, addressing questions such as what strategies are used to locate resources, what information is used, and how it is obtained”. The topics “reproductive fitness, survival and reproduction” are on the first and second levels of the table, suggesting that Dusenbery does not consider these to be within the realm of sensory ecology.

### ***Barth & Schmid (2001)***

“Sensory Ecology in its widest sense deals with the acquisition of information and the ways in which an organism responds to sensory information to organize its interaction with its environment”. This mechanistic definition is in the preface, written by both the editors. However, the same David Dusenbery of the 1992 book now mentions in his chapter in Barth & Schmid’s book that “Understanding why an organism responds to a particular sensation with a particular behavioral response (i.e. the function of the sensory system and the behavior) requires knowing the causal input later in the chain; and understanding how the sensory input is amplified and how it controls behavior (i.e. its mechanism) requires knowledge of physiology. Thus sensory ecology must be intimately involved with ecology, behavior, and physiology, as well as evolution.”

### ***Stevens (2013)***

“Sensory ecology deals with how animals acquire, process and use information in their lives, and more recently the role of sensory systems in

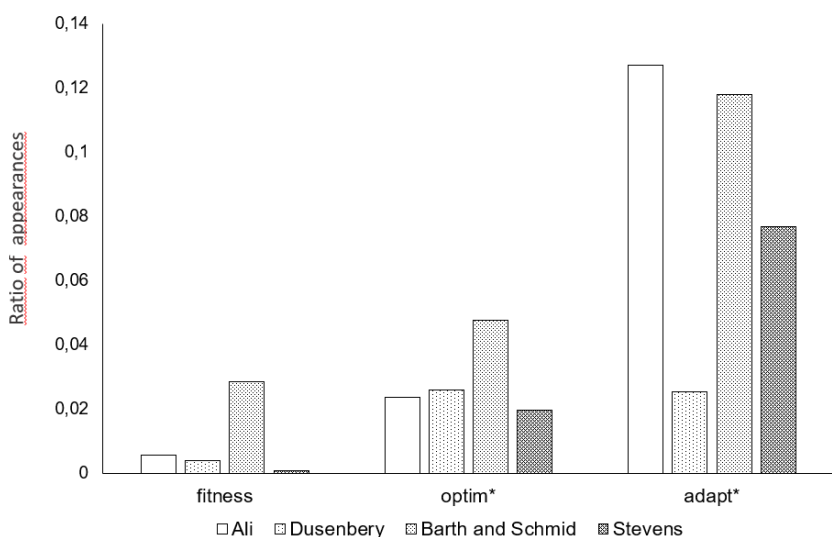
evolutionary change...it covers everything from the way the sensory systems work (physiology and neurobiology), to the way sensory systems are used (e.g. in behavior) to the role of sensory systems in evolutionary processes (for example, reproductive isolation)”. Later in the same chapter Stevens writes that “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?”

### **Comparing keywords of behavioral ecology between the definitions and the actual texts in each book**

Here I will first describe quantitatively the appearances of “fitness”, “optim\*” and “adapt\*” in each book, and then discuss all at once.

#### ***Fitness***

As the reader could notice above, Ali mentions the word “fitness” to define what sensory ecology is in definitions 1 and 3. In contrast, 14 years later, Dusenbery suggests that sensory ecology does not focus on fitness. Barth & Schmid (2001) and Stevens (2013) do not mention the term in their definitions. Throughout the text, authors in Ali’s book use the word fitness only 8 times within the 597 pages (Figure 2), seven of which in the same chapter, on the ecological niche dimensions and sensory functions in amphibians. In 1992, Dusenbery uses the concept in 6 out of the 7 occasions in the same chapter, on communication. In 2001, although “fitness” is not mentioned in the definition of sensory ecology, the authors in the book edited by Barth and Schmid use it more often than in Ali, even if we do not consider the single chapter that contains 60% (18/30) of the appearances



**Figure 2.** Ratio between the number of appearances of the words *fitness*, *optim\** and *adapt\** (see Materials and Methods) and the number of words in the four books analyzed in the paper.

of “fitness” of the book: Chittka and Briscoe, “Why sensory ecology needs to become more evolutionary – insect color vision as a case in point.” Finally, Stevens do not use it at all (Figure 2).

### **Optim\***

Ali uses it in 3 out of his 4 definitions of sensory ecology: “fitness of organisms of a species is optimized”, “survival of organisms is rendered optimal” and “fitness of organisms is rendered optimal”. The other 3 authors/editors of the books analyzed do not mention “optim\*” in the definitions. Throughout the text, the authors in Barth and Schmid use it 2x more than the authors of the other three books, which share a similar number (Figure 2).

### **Adapt\***

Ali uses it twice in his definitions: “adapting to the constraints of information” and “adaptive radiation of sensory mechanisms”. Again, the other 3 authors do not mention “adapt\*” in the definitions of sensory ecology. The term appears 6x more in Ali’s book than in Dusenbery’s, the one with fewer mentions of it. Interestingly, authors in Barth and Schmid also use “adapt\*”

more often than Stevens, the book with the most evolutionary approach (Figure 2).

### **Considerations on the use of “fitness”, “optim\*” and “adapt\*” by each author**

There seems to be a contrast between what the editor Ali and what the authors of the book chapters understand about the relevance of fitness and optimality when discussing sensory ecology. The number of cites of these two words is very low and comparable to that of Dusenbery, with its very mechanistic approach. It should be mentioned that a careful reading of the book shows that the authors in Ali’s book did not use the concepts of optimal and fitness using other words. The low number of appearances of these words actually reflects the rare use of the concepts. Stevens, which explicitly and really deals with evolutionary questions, does not use “fitness” anywhere in the book. These data suggest, contrasting to Ali’s several mentions in the definitions, that it is not necessary. Possibly, Stevens acknowledges the difficulties of measuring what fitness really is (see Davies et al. 2012) and chose not to use it. The relative high number of mentions of “fitness” in Barth and Schmid is mainly because of the single

chapter that discusses that sensory ecology has to become more evolutionary. This chapter actually contrasts with the rest of the mainly mechanistic book.

Despite the fact that Dusenbery is indeed a mechanistic book, it uses “optim\*” more often than Stevens. Indeed, Dusenbery mentions that “The advantages and limitations of various sensory modalities are described herein and optimal strategies are considered”. Stevens, in turn, discusses that “because it is now clear that often animals do not behave as would be expected by optimality models, optimality models are either wrong or animals do not behave optimally.” Therefore, it is obviously expected that he seldom uses the concept in his book. Stevens often uses optimality in a context in which trade-offs are considered, or for specific functions (e.g. preface: “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.”; page 173 “spacing of the cone types across the bird visual spectrum may be optimal to capture the range of different colours that birds may encounter in nature”). In Barth and Schmid, 38% of the 50 appearances of “optim\*” of the book are in a single chapter on the metabolic cost of information. Another 28% are in a chapter the authors tested for optimal color receptors. Throughout the book, the word is often used in a physiological context (page 51: “ideally a 60-fold transformation of pressure is required for optimal impedance matching”; page 175: “The optimization of neural coding”). These justify the relatively high number of uses of optim\* in the book.

Ali’s introduction creates an expectation that the book will be very adaptation-fitness focused. One can discuss if adaptation was used loosely in the book (see Gould & Lewontin 1979), but it is indeed the one that mostly used the concept. Although Barth and Schmid’s is

the second book that most use adapt\*, they cite Chittka and Briscoe’s chapter in the book they have edited to emphasize that adaptation should be used more carefully: “This issue is the widespread habit of sensory ecologists (and many others) to rely on adaptive explanations without demonstrating the impact of an “adaptive” trait on fitness and without considering alternative explanations offered by evolutionary biology. In short, a good match between the functional properties of a sense organ or a sensory system and behaviorally relevant natural stimulus patterns should not be called “adaptation” without proper analysis.” Or, as Chittka and Briscoe themselves put it (page 33): “We are also emphasizing that if we want to demonstrate adaptiveness, it is not sufficient to show that sensory traits appear well (or even optimally) matched to the environment. Instead, we must show that animals carrying the sensory characteristics in question are fitter than those that do not”. Stevens is also careful: “Although dealing relatively little with concepts of adaptive behaviour and evolutionary processes, the book covers the physics and physiology of sensory ecology, and the framework of information in great detail.” Dusenbery contrasts behavioral ecology with sensory ecology: whereas the former is more interested in “determining the adaptive advantages and evolution of behavior... this book emphasizes mechanisms.” It is therefore not surprising that, coherently, Dusenbery seldom uses the concept of adaptation.

### **The evolution of the concept of sensory ecology and the relevance of historical context**

If we follow the definitions of sensory ecology from 1978 to 2013, we would conclude that this field started up as evolutionarily focused (Ali 1978), then became very mechanistic (Dusenbery 1992), continued with a mechanistic



approach but now slightly concerned about evolutionary questions (Barth & Schmid 2001), and is now both mechanistic and evolutionary (Stevens 2013). However, I argue that sensory ecology was not evolutionary focused in 1978. It seems that, maybe facing the pressure of the mainstream behavioral science at that time (behavioral ecology), Ali maybe decided to use keywords that belonged to that science. Data I have shown here suggests that the essence of the book is not evolutionary. The concepts used in the definitions are not really used within the book, and a careful analysis of the book by readers would reveal the same. It should also be mentioned that not only did Ali's book appeared in the flourishing days of behavioral ecology, but that it also preceded the famous critique to adaptationism by Gould & Lewontin (1979). We can only speculate whether the definitions of sensory ecology would have been different following the repercussion of the Spandrel's paper. Anyway, Barth & Schmid (2001) was the first, among these four books, to question the necessity of "becoming more evolutionary", which actually happened in 2013.

Although Ali's book (1978) is the first one on the subject, Dusenbery (1992) does not specifically mention previous works on sensory ecology and is cited by both Barth & Schmid (2001) and Stevens (2013) as having written the seminal book that has first formally presented the discipline. Ali's is not cited in any of the other 3 books. Stevens (2013) actually only cites two previous books on visual ecology (Hailman 1977, Lythgoe 1979) that "constituted sensory ecology in the modern sense". Barth & Schmid (2001) mention that, in *Umwelt und Innenwelt der Tiere*, Jakob von Uexküll (Von Uexküll 1909) emphasized the importance of studying the sensory worlds of animals to understand which features of the environment are relevant for them. It is unclear why Ali has not been cited.

I highlight, however, the great importance of the book. It followed what was maybe the first symposium on sensory ecology, which came as a conceptual necessity well explained in the book and briefly treated in the introduction of this paper. It gathered information on a great variety of organisms, from protozoa to both invertebrate and vertebrates. It covered 7 sensory modalities. A 600 pages first compilation of information that has inaugurated a research field certainly has its place in history.

I have shown that the concept of sensory ecology has changed in 35 years. Ali's book is of great historical importance and the author seems to have been influenced by the historical context, namely the rising of behavioral ecology, when defining sensory ecology. This research area has been mainly proximal until it became multidisciplinary and also evolutionary in later years. This tendency should probably remain in future decades.

### Acknowledgments

I thank Gabriel Murayama, Guilherme Pagoti, Julio Segovia and Nathalia Fernandes for reading and commenting on a draft of the manuscript. Two reviewers also provided great suggestions. This work was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo, Brazil (Grant number 2020/05158-5) and Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil (Grant number 302879/2016-1).

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#### How to cite

WILLEMART RH. 2023. The evolution of the concept of sensory ecology and the influence of behavioral ecology. *An Acad Bras Cienc* 95: e20220302. DOI 10.1590/0001-3765202320220302.

*Manuscript received on April 8, 2021;  
accepted for publication on September 4, 2022*

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