

## Understanding Animal Behaviour

### What to Measure and Why

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All students and researchers of behaviour – from those observing animals behaving freely in the field to those conducting more controlled laboratory studies – face the problem of deciding what exactly to measure. Without a scientific framework on which to base them, however, such decisions are often unsystematic and inconsistent. Providing a clear and defined starting point for any behavioural study, this is the first book to make available a set of principles for how to study the organisation of behaviour and, in turn, how to use those insights to select what to measure. The authors provide enough theory to allow readers to understand the derivation of the principles, and draw on numerous examples to demonstrate clearly how the principles can be applied. By providing a systematic framework for selecting what behaviour to measure, the book lays the foundations for a more scientific approach for the study of behaviour.

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Between them, the authors have published more than 250 scientific journal articles and chapters, along with a book titled *The Playful Brain: Venturing to the Limits of Neuroscience* (Oneworld Publications, 2009).

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Sergio Pellis , Vivien Pellis  
Frontmatter  
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## Contents

|   |                 |
|---|-----------------|
| Preface   | <i>page</i> vii |
| Acknowledgements  | xi              |
| <b>1 What Is the Problem and What Is the Solution?</b>                | <b>1</b>        |
| <b>2 Behaviour as a Means, Not an End</b>                             | <b>23</b>       |
| <b>3 The Deep Structure of Behaviour</b>                              | <b>47</b>       |
| <b>4 The Brain Is Not Alone</b>                                       | <b>61</b>       |
| <b>5 Bringing It All Together: Steps in the Descriptive Process</b>   | <b>75</b>       |
| <b>6 What of the Future?</b>  | <b>98</b>       |
| <b>Epilogue</b>   | <b>113</b>      |
| Appendix A: Eshkol-Wachman Movement Notation and Descriptive Analysis | 116             |
| Appendix B: Practice, Practice, Practice                              | 126             |
| References  | 129             |
| Index   | 153             |

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## Preface

This is the book we would like to have had available in the 1970s when we first started studying the behaviour of animals. When conducting one of the first detailed studies of play behaviour in a bird, the Australian magpie, we found precious little guidance in the literature as to what aspects of behaviour to measure. For more global measurements – such as how much of the day is spent playing – the advice reflected in papers and books that were available at the time, and which still have validity (e.g., Altmann, 1974; Dawkins, 2007; Lehner, 1996; Martin & Bateson, 2007), proved very useful (Pellis, 1981a). More difficult was finding advice on what to measure at a micro level, when the birds were playfully wrestling with one another. We explored a variety of statistical approaches at the time – such as those that assessed the probability that one action followed another (e.g., Delius, 1969) or those that assessed how particular actions clustered together geometrically (e.g., Miller, 1975) – but in trying to apply them, we came up against the persistent problem of how to parse the stream of ongoing behaviour into heuristically meaningful units. We found help from methods that made the selection of such units the product of analysis rather than the starting points of analysis (Golani, 1976), and gained considerable insight into the organisation of complex, multi-component behaviour, such as the playful wrestling of magpies (Pellis, 1981b).

What started with Australian magpies expanded into a life-long journey of studying the behaviour of a variety of species, and in each case, it became clear that Ilan Golani was correct – that the most convincing units of behaviour suitable for measurement resulted from the analysis of how that behaviour was organised. With studying diverse species engaging in a variety of behaviours, enduring principles of how behaviour is organised became apparent. We do not take credit for those principles, as most were articulated before we entered the scene, but our own experiences revealed to us that some of those principles are widely applicable. In this book, we make those principles explicit and show how they can be used to gain insight into how behaviour is organised and, in turn, by gaining deeper

viii Preface

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insight into the organisation of behaviour, to characterise behavioural units or markers of value for quantitative scoring.

One of the most influential papers in the field of Animal Behaviour was by Niko Tinbergen<sup>1</sup> (1963). Tinbergen advocated that a behaviour performed by an animal can be explained in four different ways: by understanding how it promotes the animal's survival and reproduction (function); how the species to which that individual belongs came to acquire that behaviour (phylogeny); the psychological, physiological, and neural processes that make it possible for an individual to express that behaviour (mechanism); and how those mechanisms emerge over the individual's lifetime (ontogeny). In various forms, this 'four whys' approach has become de rigueur for the field (e.g., Alcock, 2013; Bolhuis & Giraldeau, 2005). Unfortunately, another key component of the argument made by Tinbergen in that landmark paper has fallen by the wayside. Tinbergen argued that description is a necessary precursor to answering any of the four whys (Hinde, 1982). Indeed, Konrad Lorenz,<sup>1</sup> another one of the founders of the discipline of animal behaviour, wrote a paper despairing about the demise of description (Lorenz, 1973). We agree with the view that description is instrumental to the study of the behaviour of animals. However, we have also learned that there are two important considerations to take into account when integrating description into current studies of behaviour.

First, while we agree that knowing what needs to be explained must precede attempts to explain the phenomenon, we have also come to understand that description is an iterative process. Experimentation and further comparative analyses can yield novel insights into the organisation of the behaviour that add to or alter the original description. In this way, descriptions – although necessary starting points – are not immutable, but rather, are works in progress. Second, to begin the descriptive process, organisational principles that have proven helpful in other behavioural analyses may be useful. From such a description, behavioural markers can be abstracted that can then be scored quantitatively. Importantly, this

<sup>1</sup> In 1973, the Nobel Prize in Physiology or Medicine was awarded to Nikolaas Tinbergen, Konrad Lorenz and Karl von Frisch. The award was given for their work in elucidating the organisation of individual and social behaviour patterns. Basically, they were instrumental in laying the foundations for the biological study of behaviour (Burkhart, 2005).



principled approach provides an objective framework with which to test the usefulness of the abstracted behavioural markers, not only by the researchers proposing those markers, but also by others.

Most particularly, we aim to show that behavioural markers that are a close reflection of the underlying organisation of the behaviour being investigated are more likely to be useful for experiments and comparisons that require numerical assessments. Consequently, this book is intended not only for novices making their first attempts to describe and measure behaviour, but also for experienced researchers who are switching from studying one type of behaviour to another. To make the process of description and the selection of behavioural markers as explicit as possible, we provide a detailed presentation of the principles that we have found most useful in this endeavour.

There are many researchers who have conducted their studies, whether explicitly or implicitly, with some or all of these principles as their guide (for many fine examples, see *Behavioural Brain Research*, Volume 231, Issue 2, 2012), and wherever possible, we use such examples to illustrate the points we are making in the book. However, we give readers fair warning that the majority of the examples we use are from our own studies. This is simply because we know these examples the best and so can use them to the greatest effect to ensure that we convey the underlying methodological issue to the reader. Also, since this is a book intended to provide a methodological guide for abstracting behavioural markers that can then be quantified, we feel no compunction to provide an exhaustive bibliography. What we do provide are sufficient citations so that readers have a starting point from which to explore the primary literature for themselves.

There is one last point we wish to make clear. In articulating the principles and their uses, we only provide sufficient theoretical detail to make them understandable to readers. To develop each of these principles fully, both with regard to the historical conceptualisations that were involved in their development and the biological underpinnings for their evolution and usage by animals, a different book would be needed. For readers interested in exploring the historical origins of some of these principles and how they are used, we recommend the books by Gallistel (1980), Glimcher (2003) and Mook (1996). Although these sources are dated and the principles discussed need to be integrated with the knowledge gained in the intervening years (e.g., Gomez-Marín & Ghazanfar,

**x Preface**

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2019), they are still a very good starting point to get the feel for those conceptualisations. However, for our current purposes, it is sufficient that readers be able to understand the basic principles and then judge their value themselves by looking at the behaviour of animals. Does the behaviour make more sense now than it did before? Whether the answer is yes or no, by going through the exercise, the observer will have gained a deeper insight into the behaviour in question. What we provide as a guide is intended as an opening gambit for making explicit some of the principles that underlie the organisation of behaviour. As we show in Chapter 6, there may be additional principles that in the future need to be integrated with the ones that we present in the pages that follow. By making behavioural description and the extraction of behavioural markers as explicit as possible, the framework outlined in this book can be built on as new insights and methods arise in the future.

## Acknowledgements

This book has been percolating in the back of our minds for many years as we have come to understand the complexities of how to extract useful behaviour heuristically to measure quantitatively, and how to teach our students to appreciate the difficulties. It was Megan Keirnan from Cambridge University Press who saw the value in pursuing such a project and encouraged us to prepare a proposal. Interestingly, the proposal we submitted was theory heavy and the reviewers suggested that we would likely reach a broader audience by making the text more practical with real-life examples of animal behaviour to illustrate the conceptual issues we want to convey. They were right, and this volume attempts to follow the spirit of that advice. Certainly, this approach makes the book more readily accessible to senior undergraduate and graduate students. We thank Megan, the reviewers and our students for their valuable feedback and advice.

Many skilled observers of animal behaviour have influenced our thinking and approach to studying behaviour. Some have been mentors and collaborators, such as Philip Teitelbaum and Ian Wishaw; some have been instrumental in training us, most particularly, Ilan Golani; and some have influenced us via their research papers and other writings, such as Robert and Caroline Blanchard, Valerius Geist and Bill Powers, who we were lucky enough to get to know in person; and others who preceded our active research careers, such as Jakob von Uexküll and Niko Tinbergen. There are many others who have been important influences, but we simply cannot name them all for fear of leaving someone out, but as you read the book, the references cited will reveal these folks. We thank them all.

Once we wrote a draft that we were happy to have others read, some colleagues volunteered to read and critique the tome. The valuable corrections, comments, insights and references provided by Heather Bell, Gordon Burghardt, Evelyn Field and J.-B. Leca have been invaluable in improving the final version of the book. In addition, as the book was written with people at the beginning of a career in studying animal behaviour in mind, we tested its readability and comprehensibility on our current graduate students Candace Burke, Jackson Ham, and Rachel Stark, and in a fourth year

**xii      Acknowledgements**

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seminar course comprising undergraduates majoring in animal behaviour or neuroscience. The feedback was favourable; the key message got through and they enjoyed the read. Candace and Rachel were also instrumental in either adapting and modifying existing figures or creating new ones. We thank them all for helping make this book possible. Finally, we want to thank Megan Keirnan, Aleksandra Serocka, Niranjana Harikrishnan and the other members of Cambridge University Press team who have helped in the completion of the book.