ESSENTIAL ANIMAL BEHAVIOR

For Lisa, William, and Adam

Essential Animal Behavior

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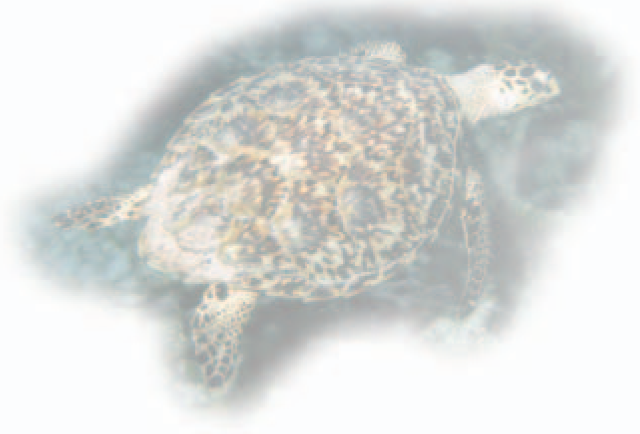

My aim in writing this book has been to provide a concise but thorough introduction to the study of animal behavior. I want to convey the idea that animal behavior is a multidisciplinary field which draws into it many aspects of the broader field of biology.

In an introductory level textbook, it is impossible to cover all of the classic works of earlier times, but I have incorporated a sufficient number of them to provide the reader with some sense of the development of the field. I have also provided information on very recent and current work, and indicated that some questions remain unanswered.

My primary goals have been to produce a book that will be readable, be useful to both students and tutors, and will encourage readers to pursue their interest further.

The book puts the study of animal behavior in an applied context, emphasizing the implications for animal welfare and animal conservation. Social behavior is covered throughout and new, exciting examples from both the terrestrial and marine environments highlight current research alongside the classic examples.

Aimed at undergraduate students taking introductory and non-majors courses in animal behavior and related areas, the book is essential reading for degree-level students in biology, zoology, marine biology, and psychology departments.

Various pedagogical features have been incorporated into the book, and it has been carefully designed to meet the needs of students studying the subject for the first time. The features included are explained below:

- **"Focus on" boxes:** cover selected points, examples, and concepts in more depth.
- **"Concept" boxes:** highlight key terms and concepts, allowing students to see at a glance the important themes and ideas covered in each chapter.
- **"Application" boxes:** describe how theory can be applied to real-world examples, bringing the subject to life.
- **"Case study" boxes:** take examples a step further, providing extra information and allowing more in-depth discussion.

Other features include:

- **Chapter summaries:** aid understanding, provide a quick reference to each chapter, and can help to guide revision.
- **"Questions for discussion" boxes:** encourage students to think in more depth about key topics and provide discussion points for tutorials.
- **"Key reference" boxes and Further reading:** allow the student to take each topic further, highlighting key papers and good sources of information, and helping to guide revision.
- **"Link" boxes:** color-coded links to other chapters in the book provide cross-referencing between related areas. These help students navigate around the book and also serve to demonstrate the interrelationships between the topics.

Additional resources for lecturers are available either as a CD ROM or for download from www.blackwellpublishing.com/scott. These include all the figures and artwork in Powerpoint and in JPEG format.

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Although the book has a single author, it is not the result of the efforts of a single person. Without the dedication of those persons actively engaged in animal behavior research I would have nothing to write about! They further our understanding of the world and deserve our thanks for it. I would like to thank my family for putting up with me during the writing of the book, and especially Lisa for all the help that she gave me. The editorial and publishing team that have produced the book have given me gratefully received support. Ian Sherman, Sue Hull, Michelle Tobin, Chris Saunders, Magnus Johnson, and Ian McFarland all patiently read and commented on various bits of the text, and I am indebted to them all.

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Fig. 1.2: Tinbergen, N. (1963) The shell menace. *Natural History*, **72**, 28–35.

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Fig. 2.7(b): Camhi, J.M. (1984) *Neuroethology: Nerve Cells and the Natural Behaviour of Animals*, p. 231, Sinauer Associates, Sunderland, MA; from Ewart, J.P. (1980) Concepts in vertebrate neuroethology. *Animal Behaviour*, **33**, 1–29.

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Fig. 4.3: Hall, M. & Halliday, T., eds (1998) *Behaviour and Evolution*. The Open University/Springer Verlag, Berlin; from Bentley, D. & Hoy, R.R. (1972) Genetic control of the neuronal networks generating cricket song patterns. *Animal Behaviour*, **20**, 478–92.

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Fig. 4.5: Carew, T.J. (2000) *Behavioral Neurobiology*. Sinauer Associates, Sunderland, MA; from Wine, J. (1975) Habituation and inhibition of the crayfish lateral giant fibre escape response. *Journal of Experimental Biology*, **62**, 771–82.

Fig. 4.6: Kandel, E.R. (1979) Small systems of neurons. *Scientific American*, **241**(3), 67–76.

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Fig. 4.9: Pearce, J.M. (1997) *Animal Learning and Cognition: An Introduction*. Psychology Press, Hove.

Fig. 4.10: Pearce, J.M. (1997) *Animal Learning and Cognition: An Introduction*. Psychology Press, Hove; from Macphail, E.M. (1993) *The Neuroscience of Animal Intelligence*. Colombia University Press, New York.

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by Healy, S., pp. 1–17. Oxford University Press, Oxford.

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Fig. 5.3: Rosenthal, G.G. & Evans, C.S. (1998) Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. *Proceedings of the National Acdaemy of Science, USA*, **95**, 4431–6.

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Fig. 5.6: de la Torre, S. & Snowdon, C.T. (2000) Environmental correlates of vocal communication of wild pygmy marmosets, *Cebulla pygmaea*. *Animal Behaviour*, **63**, 847–56.

Fig. 5.7: Marler, P. (1959) Developments in the study of animal communication. In *Darwin's Biological Work*, ed. by Bell, P.R., pp. 150–202. Cambridge University Press, Cambridge.

Fig. 5.8: Zuberbühler, K. (2002) A syntactic rule in forest monkey communication. *Animal Behaviour*, **63**, 293–9.

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Fig. 6.4: Major, P.F. (1978) Predator–prey interactions in two schooling fishes, *Carex ignoblis* and *Stolephorus purpureus*. *Animal Behaviour*, **26**, 760–77.

Fig. 6.5: Göttmark, F., Winkler, D., Andersson, M. (1986) Flock-feeding on fish schools increases success in gulls. *Nature*, **319**, 589–91.

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Fig. 6.8: Walton, P., Ruxton, G.D. & Pitelka, F.A. (1998) Avian diving, respiratory physiology and the marginal value theorem. *Animal Behaviour*, **56**, 165–74.

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Fig. 7.1: Götmark, F. & Olsson, J. (1997) Artificial colour mutation: do red-painted great tits experience increased or decreased predation? *Animal Behaviour*, **53**, 83–91.

Fig. 7.2: Cresswell, W. (1994) Flocking is an effective anti-predator strategy in redshanks, *Tringia totanus*. *Animal Behaviour*, **47**, 433–42.

Fig. 7.3: Myers, J.P, Connors, P.G. & Pitelka, F.A. (1979) Territory size in wintering sanderlings: the effects of prey abundance and intruder density. *Auk*, **96**, 551–61.

Fig. 7.4: Krebs, J.R. & Davies, N.B. (1993) *An Introduction to Behavioral Ecology*. Blackwell Science, Oxford.

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Fig. 7.6: Brown, C. & Hoogland, J.L. (1986) Risk in mobbing for solitary and colonial swallows. *Animal Behaviour*, **34**, 1319–23.

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Fig. 7.8: Caro, T.M. (1986) The functions of stotting in Thompson's gazelles: some tests of predictions. *Animal Behaviour*, **34**, 663–84.

Fig. 7.9: Caro, T.M. (1986) The functions of stotting in Thompson's gazelles: some tests of predictions. *Animal Behaviour*, **34**, 663–84.

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Fig. 8.3: Davies, N.B. (1992) *Dunnock Behaviour and Social Evolution*. Oxford University Press, Oxford.

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Fig. 8.5: Davies, N.B. (1992) *Dunnock Behaviour and Social Evolution*. Oxford University Press, Oxford.

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Fig. 8.9: Krebs, J.R. & Davies, N.B. (1993) *An Introduction to Behavioural Ecology*. Blackwell Science, Oxford; from Orions, G.H. (1969) On the evolution of mating systems in birds and mammals. *American Naturalist*, **104**, 589–603.

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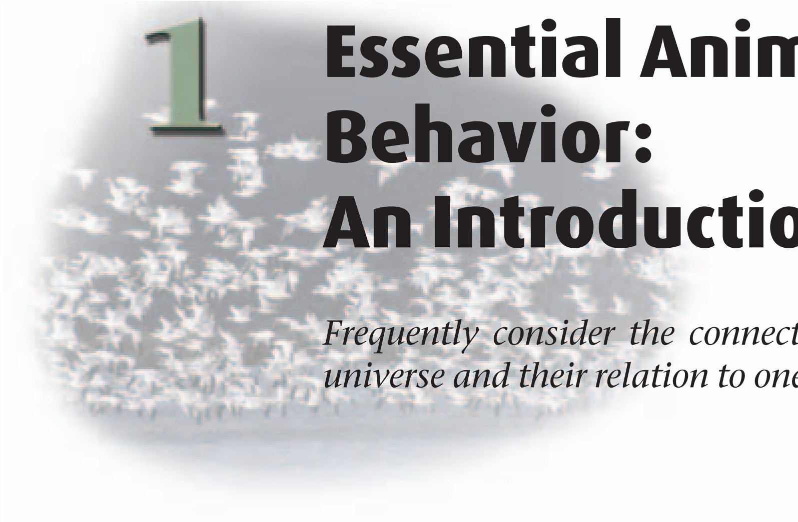

1 Essential Animal Behavior: An Introduction

Frequently consider the connection of all things in the universe and their relation to one another.

Marcus Aurelius AD 121–80

People have probably always been fascinated by the behavior of animals. Indeed an understanding of the behavior of prey animals must have been essential to our early ancestors; their paintings on the walls of caves suggest that they could have been fairly familiar with behavioral concepts such as herd size and migration. The earliest stock-farmers would have needed to understand the behavior of the charges in their care just as their modern counterparts do today.

Some members of society (and even some biology students) may wrongly think of the study of animal behavior in an academic context as being a soft science or even an easy option.

Key points

- The field of animal behavior is diverse and may be studied from a variety of perspectives.
- It is useful to consider behaviors as adaptations.
- A single behavior will not serve, or serve the same purpose in all situations, and behaviors are adapted to be effective in the environment of the animal performing them.
- It is wrong to think of animal behavior as a general interest or a purely academic subject. The study of animal behavior is an important science which has a clear applied context.

Contents

However, I hope to show you in this introduction to the subject that it is an important and rigorous science and that it has a clear application to some of the problems that we face in the modern world.

Cephalopod inking behavior

Many species of octopus and squid are known to exhibit a particularly effective behavior that enables them to escape from predators. In the region of their intestines the animals have a special sac-like organ. In the wall of this sac there is a gland which secretes a brown or black liquid rich in the pigment melanin, this is ink. When threatened the animal has the ability to compress the ink sac and squirt a jet of the liquid from its anus. It is thought that the cloud of ink hanging in the water forms a dummy squid termed a pseudomorph, which attracts and holds the attention of the predator allowing the animal to dart away to safety. The deception is made all the more effective because long thin species produce long thin pseudomorphs and more round species produce rounder clouds of ink (Plate 1.1).

Squid and octopus are molluscs, taxonomic relatives of the garden slug and snail. Can you imagine a slug squirting out ink to leave a pseudomorph hanging in the air to decoy a bird predator while the slug made its escape? Of course you can't, for the simple reason that this behavioral strategy can only work when the animal is surrounded by a medium that will support the ink cloud for a sufficient period to allow the escape. In water this works, but in the less dense medium of air it would not.

Plate 1.1 An animal this shape should produce a long, thin pseudomorph. © C. Waller.

Some species of octopus and squid are inhabitants of the ocean depths. Here light penetration from the surface is minimal or zero and the seawater is a constant inky black. Obviously the ink-dummy strategy would be no more effective here than it would be in air. The pseudomorph would hang in the water column, but it is unlikely that an ink-black shape would be seen against the inky-black backdrop. In this situation species such as the deep-water squid *Heteroteuthis* secrete a luminescent ink, creating a brief flash of light which is thought to confuse a potential predator just long enough for an escape to be affected.

From this example I hope that I have made a few key points about behavior. Firstly, that behaviors are adaptations which serve specific functions, and we will consider this point further later in this chapter. Secondly, that a single behavior may not serve, or serve the same function, in all situations (a point to be borne in mind throughout this book). Finally, behaviors are adapted to be effective in the environment of the animal performing them.

What is behavior?

Before investigating the amazing diversity of behaviors that animals exhibit, it is necessary for us to gain some insight into the concept of behavior itself. We need to decide what the word **behavior** means to us in the current context and to examine the various avenues open to us for the study of animal behavior.

So what is behavior? Dictionary definitions of the word typically include phrases such as "acting or functioning in a specified or usual way." This suggests to us that behavior is a predictable thing. Another common phrase is "the response of an organism to a stimulus." This suggests that behaviors are **made** to happen by something. In the case of this definition the "something" concerned is not specified, and may be internal or external to the animal involved. Each of these ideas is in its own way an adequate response to the question. Behaviors are in many cases predictable given sufficient information concerning their context (although many appear initially to be highly unpredictable). Similarly behaviors are often linked to a stimulus in an immediate sense at some level. The shortcoming of such definitions, however, is that they attempt to narrowly confine behavior in an easily described and highly specific way. Given the diversity of behavior such an