Human Facial Expression: An Evolutionary View.

Do facial expressions reflect our emotional states, or are they signals that we use to serve specific social motives and often to manipulate and deceive others? Fridlund decidedly rejects the 'emotion' view of facial displays in favour of the evolutionary view. He argues that facial expressions have social meanings specifiable only in their context of occurrence and evolve in response to specific selection pressures.

Based on just the title of this book, I enthusiastically endorsed its main message, that a functional analysis of non-verbal communication is much needed and that evolutionary theory can provide a solid theoretical framework for research in this area. The book, however, turns out to be a critique of the emotion view of facial expressions and of emotion research in general, rather than a clear outline of an evolutionary research program to study non-verbal communication. This is unfortunate because the emotion and evolutionary views of facial expressions need not be incompatible. In fact, the emotion view mostly provides an account of causation of displays, whereas the research approach favoured by Fridlund places strong emphasis on function. Fridlund recognizes that emotions may be or include the expression of social motives, but dismisses this 'diplomatic' solution (page 182) because of the lack of adequate criteria to assess emotions.

In addition to contrasting emotion and evolutionary views of displays, Human Facial Expression is intended to provide a comprehensive overview of research on facial expressions, with historical and interdisciplinary perspectives. In this respect, the book is quite successful. Chapter 1 briefly reviews the historical views on facial expression prior to the publication of Darwin's (1872) The Expression of the Emotions in Man and Animals. Chapter 2 argues that Darwin invoked non-adaptiveness of facial expression to attack the natural theology of Charles Bell and its arguments from design about expressions. Chapter 3 reviews early post-Darwinian research on facial expression and outlines some methods of contemporary evolutionary research. Chapter 4 discusses some mechanisms for the evolution of facial displays including use-inheritance and ritualization of intention movements. Chapter 5 is a technical chapter on muscular structure and neural control of the facial mask, and chapter 6 deals with the facial reflexes and the ontogeny of facial expressions. The next two chapters contrast the emotion versus evolutionary views of facial expression, and chapters 9–11 criticize cross-cultural studies of facial expressions. The bulk of this critique, however, does not come from Fridlund himself but from a reprinted article by Russell (1994), which takes up about one quarter of the book. Ekman (1994) and Izard (1994) have accused Russell of faulty logic and misinterpretation of their research, but their rebuttals are not mentioned in the book, perhaps because they were published after Russell's article and the book was already in press. The last chapter before the epilogue is a discussion of facial paralanguage and gesture.

Fridlund is to be commended for exploring the animal behaviour literature, but some of his interpretations of the evidence from animals are questionable. For example, according to Fridlund, the emotion view of facial displays predicts that deception should be displayed only by animals with high encephalization quotients, but the evolutionary view predicts that deception should be present throughout the phylogenetic tree. Fridlund's conclusion that 'the evidence here decidedly favors the Behavioral Ecology View' (page 143) is undermined by his interpretation of intentional deception and mimicry as though they were the same phenomenon.

Fridlund also contends that any approach aimed at establishing behavioural homologies between species or cultures is doomed to failure, because commonalities may reflect not genetic control but cultural transmission. For example, he argues that the fact that many non-human primates, as well as humans, grimace when under threat or in pain might be explained by social shaping of a reflex or by cultural transmission via imitation rather than by behavioural homology. In view of the lack of solid evidence for social shaping, imitation and cultural transmission of social signals in non-human primates, however, I fail to see why we should favour this explanation over one of homology.

The book's best parts are the historical accounts of pre-Darwinian, Darwinian and early post-Darwinian research on facial expressions, the original discussion of some mechanisms for the ontogeny and phylogeny of displays, and the chapter on paralanguage. Overall, Human Facial Expression: An Evolutionary View is a valuable contribution to the study of non-verbal communication.
Expression is a very enjoyable book that anyone interested in animal or human communication should have on their shelf.

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References


Feeding and foraging behaviour have been topics of significant interest for many decades. In this volume, the result of a symposium held in 1992 in Erice, Sicily, Italy, the editors have put together a series of papers that deals with several key aspects of factors affecting feeding behaviour in mammals. In my reading, I found four major themes: (1) events that occur prenatally or soon after birth can affect food selection later in life; (2) social influences, including mother's milk, can influence food selection; (3) a variety of behavioural factors can affect diet selection; and (4) these various influences on diet selection may have critical importance with respect to control of pest mammals, particularly rodents.

The 18 chapters are arranged into five sections on (1) individual development of flavour preferences, (2) social learning of food preferences, (3) social learning of feeding skills, (4) studies in semi-natural enclosures and (5) rodent control. There are 10 chapters that I would classify as review papers, six that contain primarily new data and that are written more as journal articles, and two chapters that are a mix of review material and new data. Almost all of the review articles deal with individual species, including house mice, Mus domesticus, vervet monkeys, Cercopithecus aethiops, Norway rats, Rattus norvegicus, and humans, Homo sapiens, or groups of mammals (e.g. primates, ungulates, rodents). Of the data chapters, those by Terkel on pine-cone feeding in black rats, R. rattus, and Hudson & Altbäcker on food preferences in European rabbits, Oryctolagus cuniculus, provide some exciting new insights on feeding phenomena in mammals.

Together, these chapters constitute a rich resource, summarizing a considerable body of information in a subfield of animal behaviour that, while not explosive in its development, has seen a steady increase in interest. There are some interesting contrasts in terms of the manner in which mammals learn their food habits. Rats appear to be able to learn about which foods to eat and which to avoid from conspecifics (demonstrators in experimental test situations), but primates operate in terms of individual trial-and-error and do not learn about the noxious aspects of certain foods from conspecifics. There are also some strong similarities among the mammals that have been studied. In particular, the bond between a mother and her offspring prenatally, during early ontogeny while lactation is predominant, and as the progeny develop towards independence leads to considerable influence on subsequent dietary habits. The volume may also be important for explaining a variety of methods for exploring factors that influence the early development of food habits, pitfalls that may be encountered when using these methods and how to interpret data obtained from them. Such information will be most useful for those studying mammals, but it may also be worthwhile for investigators exploring the development of feeding habits in other vertebrates.

The volume is generally well edited; there are very few technical problems. My only significant general complaint is that there is no author index, which is necessary in a reference volume of this sort for it to be truly useful. I suggest that the volume might have started with the applied presentations, setting the stage for the knowledge that has come from more basic studies. Given that our knowledge about applied aspects is presently rather limited, however, the chosen arrangement is satisfactory.

From the authors of the various papers in this volume and the thinking that is engendered by reading through the material, there seem to be several important areas for future exploration. Additional studies involving field populations, both natural and in enclosures, will enhance our knowledge about both the translation of what has been learned about basic, underlying processes under laboratory conditions to field settings and the application of that knowledge to rodent control and other applied problems. Bridging the
gap between laboratory and field will also enhance our ability to use that information in appropriate applied, animal control contexts. Several chapters (e.g. Galaverna & Nicolaidis; Booth) provide small insights into the underlying brain and possible hormone mechanisms involved in the development and functioning of dietary selection processes in mammals. With new techniques available from neuroscience and endocrinology, considerable additional progress should now be possible with respect to integrating function and mechanism. As a review volume this book is well above average; if it was not priced so highly, I suspect that the important messages that it contains would reach a wider audience.

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Dennis Power has ended his 12-year tenure as editor of this successful annual with the publication of this volume. It occurred to me while reading several of the earlier volumes that these each might have been sub-titled and this one reasonably could have been called Current Ornithology: Current Animal Behavior. There are six chapters, half the number that were in some of the earlier volumes, so Volume 12 is probably a bit pricey for the numbers of papers one gets. This ranking does not matter, however, because the quality of the individual papers struck me as decidedly above average. Nevertheless, as much as I enjoyed the individual chapters, I am not convinced that this is a book that belongs on everyone’s shelf. I have told my students to save their meagre fortunes and read it in the library, and indeed I do suggest that all of you recommend that university libraries buy this useful series.

The chapters in Volume 12 are ‘Testosterone and polygyny in birds’ by Les Beletsky, David Gori, Scott Freeman & John Wingfield; ‘Using migration counts to monitor landbird populations: review and evaluation of current status’ by Ricki Dunn & David Hussell; ‘Ptilochronology: a review and prospectus’ by Tom Grubb; ‘Individual voice discrimination in birds’ by Marcel Lanbrechts & André Dhondt; ‘The evolution of bird coloration and plumage elaboration: a review of hypotheses’ by Uno Savalli; and ‘Hatching asynchrony and the onset of incubation in birds, revisited: when is the critical period?’ by Scott Stoleson & Steve Beissinger. I enjoyed reading each of these chapters.

Beletsky et al. review what is known about testosterone and breeding in male birds. Their review is comprehensive and should be of interest to anyone seeking to know the hormone and behaviour literature. Reading this paper should disabuse anyone of the archaic notion that hormones determine behaviour. Rather, it seems, based on naturalistic observation and experimental evaluation of circulating testosterone levels after exposure to environmental or social stimuli, that behaviour may determine hormone levels. Among the authors’ conclusions is that males in socially polygynous species have longer periods of high testosterone levels than males in socially monogamous species, but mean and peak seasonal circulating testosterone levels do not vary much between socially polygynous and socially monogamous species. Males with territories have higher testosterone levels than males without. Surprisingly perhaps, territorial males do not have necessarily higher testosterone levels than floater males. Peak seasonal testosterone levels do not change as a function of male age (again, suggesting that it is not intrinsic variation in males alone that affects testosterone levels). A guarded, but highly likely conclusion from the above is that aggressive interactions stimulate testosterone secretion and it is the high levels of aggressive social interactions that determine high circulating testosterone. Interestingly, high circulating testosterone in male birds may be incompatible with the expression of male provisioning of offspring. Most interesting perhaps is the conclusion that high testosterone levels are costly to individuals, in that males implanted with exogenous testosterone suffered more injuries (presumably from fights) than control males.

Dunn & Hussell’s chapter is a review and evaluation of the current understandings of what migration counts contribute to monitoring of landbird populations. Meticulous operational descriptions and careful evaluation of the difficulties of each kind of usual sampling make this a paper useful to anyone teaching field ecology or field ornithology courses. In fact, I will particularly alert students in Forestry and Wildlife Departments about the existence and utility of this paper. It goes to the heart of one of our most important conservation problems: what are population sizes, and how are they changing?”

Grubb’s paper is a review of ptilochronology, a relatively non-invasive method for evaluating the nutritional status of individuals in wild-living populations. The method involves collecting a
feather grown during known conditions, say after a moult, or a feather induced to grow during a specified and controlled time period (induced growth), and measuring the width of dark and adjacent light bands that occur on almost all feathers in almost all species. Controlled studies indicate that a combination of one dark band and an adjacent light band, which together are called ‘a growth bar’, constitutes a 24-h growth of a feather. The relative size of growth bars is a measure of the relative nutritional status of individuals. Grubb’s review contains descriptions of the causes of growth bars, their ubiquity, the significance of individual voice recognition and discrimination. They discuss the potential significance of individual voice recognition and signature traits.

Savalli’s chapter seems to be a truly comprehensive review of the hypotheses to explain colour variation, pattern and ornamentation in birds. He describes 30 hypotheses, and their sometimes competing predictions, that potentially explain colour variation, pattern and ornaments. His conclusions are interesting and should increase the overall quality of studies of colour and ornaments, in birds and other organisms. He points out that most of the hypotheses have not been tested and that studies at most examine only two hypotheses at a time (and these are rare studies). He also points out that some of the most exciting and interesting hypotheses have received much less attention from ornithologists than they probably deserve; e.g. warning signals of unpalatability to predators, a rather marvellous idea, perhaps too novel when it was first articulated for birds by Robin Baker and Geoff Parker in 1979! I think this is a must-read chapter for students of behavioural ecology.

Similarly, Stoleson & Beissinger’s chapter on hatching asynchrony hypotheses is fascinating in its description of ‘a stagnant backwater of population biology’ (quoted from a review of their NSF proposal!). What some short-sighted reviewers consider a stagnant backwater appears vital to me primarily because of Stoleson & Beissinger’s articulation of the ‘Paradox of hatching asynchrony’, that notes that avian parents in comparison to parents in other taxa have the almost unique ability to control birthing intervals; that control, paradoxically, can and does facilitate siblicide and apparent waste of parental effort and resources. They review 17 hypotheses for hatching asynchrony; the only one that has been tested is the Brood Reduction hypothesis, yet this hypothesis remains without strong support. Their review urges avian researchers to refocus their attention away from adaptive hatching patterns and towards the ‘events surrounding the onset of incubation during egg laying’. Their phylogenetic analysis of hatching patterns indicates that synchronous hatching is the primitive condition among birds, most common in precocial taxa, while in altricial taxa asynchronous hatching is most common. They also demonstrated the use of a stochastic model using empirical data. This is an exceptionally strong paper. Anyone interested in issues of parental care should read it, whether ornithologist or not.


As an ethologist interested in animal welfare issues, I had hoped that this book would do great things. It carries an endorsement by Jane Goodall describing it as ‘important’ and ‘scholarly’, and the dust jacket claims that it is ‘the first book since Darwin’s time to explore the full range of emotions throughout the animal kingdom’. My enthusiasm, however, dropped through the floor on the first page of the Prologue, and it never struggled back into view despite some interesting accounts of animal behaviour that the book contains.

In the Prologue, Masson states that Donald Griffin’s (1976) The Question of Animal Awareness made him want to read a book that would treat animal emotions as Griffin had treated cognition and consciousness. Finding that such a book had yet to be written, he and co-author
Susan McCarthy began searching for evidence that would help to illustrate the emotional lives of animals. The resulting book consists of several general chapters, plus nine others filled mainly with anecdotal and other reports of animal behaviour drawn from researchers, animal trainers, pet owners, and others.

The anecdotal material, grouped roughly according to the emotion that the authors believe to be demonstrated, provides an interesting and well referenced assortment, but with little critical attempt to distinguish solid reports by experienced observers from the most dubious material. The authors relate Thelma Rowell’s account of mother–infant attachment in baboons, and they retell Jane Goodall’s description of the chimpanzee Flint grieving after the death of his mother. At the other extreme are a popular writer’s claim that when a puma was ‘seen to lie down and softly pat a bighorn sheep he had just killed’, the animal was showing gratitude to the mother. In his single-author Prologue and Conclusion, Masson goes further by attaching moral significance to ‘finding that animals lead emotional lives’ (page 226). He expresses outrage ‘at the thought of any kind of animal experimentation. Can we justify these experiments when we know what animals feel as they undergo these tortures?’ (page xxiii). He suggests, further, that scientists’ ‘professional and financial interests in continuing animal experimentation’ help to explain their resistance to the idea that animals experience emotions (page xx). The reader is thus left with the trite and superficial view of scientists as villains, wilfully denying that animals have emotions so as to be able to carry on torturing them for personal gain.

How many animal behaviourists really believe that non-human animals are unfeeling automata? I suspect very few indeed, although I think that a close reading of Kenedy (1992) shows that the author, after a life of studying insect behaviour, was probably of that persuasion. Masson & McCarthy’s own evidence for this belief among animal behaviour scientists is rather thin. They give various quotations such as an unnamed zoo director who said, ‘When people start saying that animals have emotions, they cross the bridge of reality’ (page 87). They rightly quote Kenedy (1992) on what he condemned as pervasive anthropomorphism in behavioural research, and they note that in The Oxford Companion to Animal Behaviour (McFarland 1981), animal behaviourists are advised ‘to study the behaviour, rather than attempting to get at any underlying emotion’ (page 9). On the other hand, they quote many animal behaviour researchers who cheerfully make inferences or hypotheses about the subjective experiences of the animals they study.

A central claim of the book is that most modern scientists (‘especially those who study the behavior of animals’; page xiii) have been blinded by their training into believing that animals do not have feelings and emotions. Since Darwin, the authors state, ‘So persistent are the forces that militate against even admitting the possibility of emotions in the lives of animals that the topic seems disreputable, almost taboo’ (pages 1–2). They contrast this ‘willful blindness of science to the world of animal emotions’ (page xx) with the commonsense view of animal trainers, pet owners and other non-scientists. Thus, the authors try to align themselves with the common sense of the reader, in contrast to ‘scientists who refuse to acknowledge what will probably seem obvious to you’ (page xxiii).

For the most part, however, Masson & McCarthy’s views about behavioural research and researchers seem to stem from a muddled reading of the scientific literature. In places they misinterpret cautious wording as a denial of animal emotions. Thus, when Honoré & Klopf (1990) note that a dog’s behaviour may allow us to say that it acts ‘as if embarrassed’ but not that it ‘is embarrassed’, Masson & McCarthy think that the wording ‘evades acknowledging animal emotion’ (page 184). When scientists write about behaviour rather than emotion (e.g. flight instead of fear, aggression instead of anger), Masson & McCarthy conclude that ‘this kind of language employs distance and the refusal to identify with another creature’s pain’ (page 34). In other places, the authors misinterpret functional and evolutionary
accounts of behaviour as alternatives to emotion-based causal explanations. Where sociobiologists have noted that a young wolf helping its parents raise another litter may thus increase its indirect fitness, the authors propose, ‘Or perhaps it is just a caring wolf, helping out the family’ (page 164). Where sociobiologists see indirect fitness benefits in much altruistic behaviour, Masson & McCarthy misconstrue this as ‘a widespread denial of the possibility of compassion in animals’ (page 11).

With such elementary faults as these, it is surprising to find parts of the text that are distinctly better. Some passages recognize that our beliefs about animal emotions must remain as inferences rather than observational knowledge. One passage notes that ideas about animal emotions will be ‘more difficult for the scientific method to verify in the usual ways’ (page 13). In places the authors seem clearly aware that causal explanations involving animals’ emotions are compatible with, not alternative to, function-based evolutionary ones (page 200). Even on their basic thesis that animal behaviourists deny feelings to animals, the authors sometimes convey contradictory messages. Thus, one passage proposes, ‘Although many scientists have believed that the animals they observed had emotions, few have written about it’ (page xxii). Here the text is realistic and reasonable, but far removed from the message conveyed in other parts of the book.

Why such inconsistencies? Perhaps the dual authorship stood in the way of a more coherent message. Masson, a psychoanalyst with a Ph.D. in Sanskrit, is sole author of the Prologue and the Conclusion, where the distortions and superficiality are most pronounced. McCarthy, who has a degree in biology, is probably more knowledgeable about scientific explanation and better informed about animal behaviour research. Whatever the cause, the result is a book that is hard to pin down, sometimes making blunders typical of beginning undergraduates, at other times showing some awareness of the difficulty of using science to understand the subjective lives of other beings; sometimes claiming that scientists deny that animals have emotions, at other times merely lamenting that scientists do not focus more on animal emotions in their writing.

The book’s greatest surprise is that it completely ignores the work of those scientists who do study animal behaviour specifically to understand the subjective experiences of animals. I searched in vain through the 45 pages of bibliography and notes for Marian Dawkins’ two books (1980, 1993) on this topic, or for any mention of Dawkins, Ian Duncan and others who, since the 1970s, have done exactly what Masson & McCarthy claim scientists should begin doing now. This 20-year body of research punches large holes in Masson & McCarthy’s thesis that animal behaviour scientists deny that animals have feelings. Masson & McCarthy must have encountered this work in their extensive reading, and their failure to acknowledge it pushes the book outside the limits of honest reporting.

None the less, When Elephants Weep does draw attention to a valid point. Non-scientists who want to ‘understand’ animals see the emotions and cognitions of animals as a significant part of the picture, especially if we are to make appropriate ethical decisions about animal use. Hence, the public wants science to address what Burghardt (1995) calls the fifth aim of animal behaviour research: understanding the private experiences of animals. If animal behaviourists do not use their skills and knowledge to address this issue, then non-scientists will fill the void. Many contemporary animal behaviour scientists have indeed been taught that the subjective lives of animals fall outside the scope of scientific enquiry, and that emotions and feelings are not acceptable as explanatory constructs in animal behaviour. This empiricist ideology does not mean that scientists believe animals to be ‘unfeeling brutes’ (the title of Chapter 2) as Masson & McCarthy seem to think, but it does mean that scientists have focused little attention on animal emotions, thus making their work less relevant to the interests and moral concerns of society.

Who should read this book? If there really are animal behaviourists who believe non-human animals to be unfeeling automata, some of the anecdotal material in this book would certainly challenge them, but Dawkins (1980, 1993) does this job far better. For intelligent discussion of how Positivism deflected animal behaviour research away from the use of cognition and emotion as explanatory concepts, Rollin (1989) is far more insightful. For philosophical arguments showing how our beliefs about the subjective lives of animals influence our moral decisions, Midgley (1983) and Rollin (1992) are much better choices. None the less, When Elephants Weep should not be ignored, because it signals an area where behavioural research is missing an opportunity to contribute to society, and because it conveys a misrepresentation of behavioural research that scientists would do well to correct.

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The field of endocrine physiology flourished through much of the 20th century. However, in recent years the study of endocrinology, at least in its purest form, i.e. isolating hormones, characterizing them and discovering what they do, has neared completion. A few new hormones are still being discovered (especially growth factors), but by and large the ‘classical era’ of endocrinology is over. The field has now turned to other exciting directions, particularly molecular endocrinology and its clinical implications. There are other important and rich research directions, however, where endocrinology interfaces with behaviour and the organism in its environment. These two books provide a broad overview of the current state of knowledge at the interfaces of hormones and behaviour. They are integrative in the sense that the word behaviour immediately conjures up visions of the organism (at least to readers of Animal Behaviour), whereas the word endocrinology infers biochemical, cell and molecular mechanisms. It is very difficult to strike a balance that will satisfy behavioural biologists and endocrinologists alike, but nevertheless these books have in many ways set the standard.

These books take very different approaches. The Becker et al. volume is edited, and thus is a collection of articles written by specialists in their particular field. The result is that some papers are highly focused on a specific process whereas others are very broad (e.g. ‘Insights from invertebrate systems’). In contrast, the Nelson book is more uniform in style, although it does not cover as wide a range of subjects as the Becker volume.

I must say quickly that these points do not detract from the value of these books. In fact, they complement one another in many ways. Both have introductory sections that outline the inter-relationships of hormones, behaviour and nervous systems. This introduction is very extensive in Nelson’s book; indeed, it is an excellent overview of the vertebrate endocrine system with simple, clear illustrations and an easy-to-read text that puts across the fundamentals without overwhelming the reader with details. This book will be particularly useful to those who have little background knowledge in endocrinology. In fact, I would also recommend it as a useful text for introductory endocrinology classes as well! Having said this, I would be remiss if I also did not point out that both books focus primarily on mammals, with other tetrapod vertebrates coming in a distant second. This is understandable, since the books are aimed at a market that is primarily biomedical in its outlook. However, the endocrinology of fishes is a highly developed field (even more so than non-mammalian tetrapods), and of course behavioural endocrinology of invertebrates has made a major contribution to neurosciences in general. Jim Truman’s chapter in the Becker et al. volume stands alone as an introduction to the vast literature on invertebrates. On the other hand, it is difficult to see how much more information could have been crammed into these books (both run to about 600 pages). It will be a challenge indeed for the next generation of texts on this topic to cover all the bases.

Following the introductory section, Nelson’s book goes on to cover the development of hormone–behaviour interactions and then explores behavioural endocrinology mostly in a reproductive context. Later chapters cover memory and learning, mood, biological rhythms and homeostasis. The Becker et al. volume also begins with developmental aspects and goes on to discuss the hormonal control of reproductive and associated behaviour. However, there follow several chapters that cover neural mechanisms,
stress, cognitive functions, biological rhythms and others more extensively than in the Nelson volume. These approaches separate the books and together they cover a vast literature. I feel that Nelson’s book is ideal for an introduction to behavioural endocrinology at the upper division undergraduate and graduate level. Having put across the basics so clearly delineated in his book, the articles in the Becker et al. volume then become ideal for discussion groups or as a base for the second half of a course. This is how I intend to use these volumes. They will provide an exceptionally sound and broad introduction to an exciting and rapidly growing field, even though the focus is primarily biomedical.

I can recommend these books highly. Endocrinology is now branching in many directions and becoming part of what were previously regarded as separate fields. As mentioned above, it is never easy to write a text that satisfies specialists in either behaviour or endocrinology, but in my view these two books have done an exceptional job. The future looks exciting indeed, but I do hope that the next generation of texts in hormones and behaviour will attempt to incorporate the rapidly growing literature on fish as well as integrate invertebrate endocrinology into the story. Perhaps the scope of such books to date has been moulded by the ‘tyranny’ of biomedical research, which is a worthy cause of course, but as basic biologists we know that our world faces other challenges such as loss of biological diversity and conservation biology. Behavioural endocrinology has a major role to play here too, although this field has barely begun to be studied. Whatever the future brings, however, and whether it will ever be possible to incorporate all aspects of behavioural endocrinology, it is clear that Randy Nelson and the authors of the Becker et al. volume have set the standard for all of us to follow.

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