

ISBE Newsletter

International Society for Behavioral Ecology
www.behavecol.com

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ISBE photo competition 2011

We have received over 20 entries for the inaugural ISBE photo competition. The winners for the three categories are:

Student Entry: Raoul Schwing

Behavioral Ecology in Action: Wolfgang Forstmeier

Behavior & Interaction: Alecia Carter



Kea (*Nestor notabilis*) will often play in the updrafts created by their montane habitat



Two individually colour-banded and radio-tagged male Pectoral Sandpipers engaging in a territorial



Two juvenile male chacma baboons *Papio ursinus* play-fight at sunrise

All entries will soon be displayed on the ISBE website.

New look newsletter

A change is as good as a Nature paper, and the ISBE newsletter certainly was in need of an update. This is now the second edition in the new format and I am eager to hear if you have any suggestions for further improvement.

In addition to an updated look, the society also started a photo competition with its first round of submissions in February 2011. Despite the rather short notice, we received over 20 entries for the three categories: Behavior and Interactions; Behavioral Ecology in Action and Student entry.

The photos were assessed blindly by the ISBE executive and councilors. Congratulations to Raoul Schwing, Wolfgang

Forstmeier and Alecia Carter for their winning entries. I look forward to continue this competition next year with even more entries. Thanks to everyone who submitted their excellent photos, which will be on display on the ISBE website soon. If you have any suggestions for future photo competitions, please let me know.

Finally, I am as always grateful to Richard Peters who manages the ISBE website!

Cheerio,

**Mariella Herberstein
Macquarie University**

G A G G L E O F I S B E P R E S I D E N T S



ISBE 2010 Poster Prize winners

Bibiana Rojas

Deakin University Australia

A potential role of colour patterns in intra-specific communication in the poison frog

Zoe Squires,

Mark Norman , Bob Wong, Devi Stuart Fox

University of Melbourne, Australia

What do female squid gain from mating multiply?

New address

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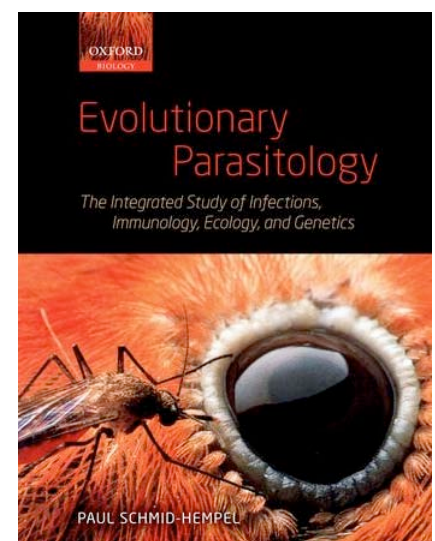
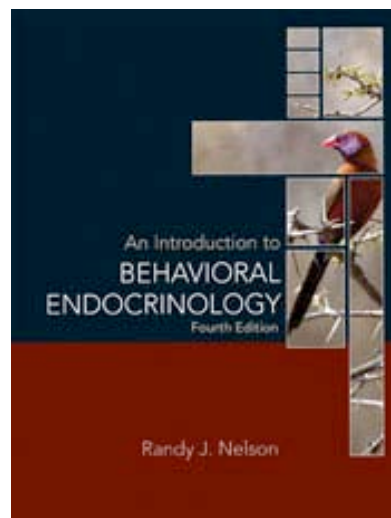
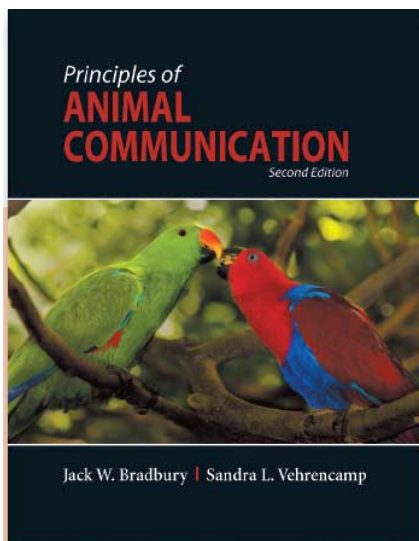
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When we found a bush cricket in King's Park



Thanks Lotta Kvarnemo for the exotic bush cricket search in King's Park. A female *Kawanaphila nartee* on a Kangaroo paw, is receiving our full attention and admiration (from the left Gerlind Lehmann, Lotta Kvarnemo, Malin Ah-King, Elisabet Forsgren & Trond Amundsen).

B O O K S F O R R E V I E W



If you are interested in receiving AND reviewing these books, please email me (marie.herberstein@mq.edu.au). The due date for the review is September 2011.

ISBE 2012 Lund, Sweden

The 14th International Behavioral Ecology Congress will be hosted by Lund University, Sweden, in 2012. The congress is scheduled for August 12-17. Lund University is Scandinavia's largest institution for higher education with around 6000 employees and 46000 students. The University was founded in 1666 although a college for higher education was founded here already in 1425. The city of Lund is even older, it was founded by the Danish king around 990 and the present cathedral (there was a previous one!) was founded 1085. The city of Lund has around 100,000 inhabitants and it is situated in the southernmost Swedish province Skåne (Scania).

The conference venue will be in the picturesque old parts of the University in downtown Lund. Here the lecture halls and a poster exhibition hall are closely situated around the old University Square.

The large international Copenhagen Airport (in Denmark) is situated only 30 minutes away by train. These trains connect the airport to Lund every 20 minutes.

Welcome to Lund in 2012.

**Anders Brodin, Susanne Åkesson
Dennis Hasselquist, Erik Svensson
and Anders Hedenström.**

I



ISBE Lund
2012
14th international
BEHAVIORAL
ECOLOGY CONGRESS

Lund University
ISBE 2012 will be held 12-17 August in Lund, Sweden
Scandinavia's largest University, 46000 students
Info at: <http://www.isbe2012lund.org/>
See you in Lund 2012!

Photo: f

Animal Behaviour: Evolution and Mechanisms

Peter Kappeler (Ed.). Springer, 2010. 707Pp.
 ISBN 978-3-642-02623-2, e-ISBN
 -978-3-642-02624-9 1

Animal Behaviour: Evolution and Mechanisms is an edited volume divided into four major sections: communication and cognition, conflict and cooperation, sex and reproduction, and behavioral variation. I will summarize the contents and strengths of each section before giving an overall assessment of the book.

Part I: Communication and Cognition

The communication and cognition section is somewhat heterogeneous in subject matter: for example, Dustin J. Penn's and Joachim G. Frommen's chapter (Chapter 3) on kin recognition, while clearly an excellent contribution, seems a slightly odd fit with the other chapters in the section. The first chapters of the section, on visual communication by H. Martin Schaefer (Chapter 1), and vocal communication in the context of social groups by Claudia Fichtel and Marta Manser (Chapter 2), share some theoretical underpinnings; in fact, both of these chapters provide definitions of the terms *communication*, *signal*, and *cue*, leading to some repetitiveness when the chapters are read consecutively. However, this repetition also allows each chapter to stand alone if read independently. Fichtel and Manser present a convincing argument for the importance of considering the multiple senders and receivers within a communication network, rather than only dyadic interactions, making their chapter an excellent choice as a reading for an upper-level undergraduate course.

In the remaining two chapters in the section, Mario Pahl, Jürgen Tautz, and Shaowu Zhang convincingly make the case for the suitability of honeybees (*Apis mellifera*) as a model system for studying learning and memory (Chapter 4), while Kurt Kotrschal, Isabella B. R. Scheiber, and Katharina Hirschenhauser use the female-centered social structure of greylag geese (*Anser anser*) to examine questions about hormonal coordination and the role of social alliances in reducing social stress (Chapter 5). Because these questions have perhaps most often been investigated in studies of social mammals, the greylag goose example proves an interesting comparison.

Part II: Conflict and Cooperation

The conflict and cooperation section is very strong overall. Both Jürgen Heinze in Chapter 6 and Judith Korb in Chapter 7 emphasize the broad application of cooperation theory: Heinze shows how similar principles contribute to conflict between cells in a body and between workers in social insect colonies, while Korb discusses insights from the study of social insects that have potential applications to explaining cooperation at other levels and among different taxa. Chapter 6 is also an excellent primer on conflict and conflict resolution (including behaviors such as policing and punishment) in social insect societies. Chapter 8, in which Redouan Bshary incorporates game theoretic concepts as well as his own empirical research on the interactions

between cleaner wrasse and their clients, stands out as an important summary of the complex issues arising in the evolution of cooperation among unrelated individuals.

In his chapter on group decision-making in animal societies (Chapter 9), Gerald Kerth provides an interesting discussion of the role that fission-fusion dynamics can play in affecting the options available to group members, before outlining several open questions and possible experiments; this consistent attention to articulating specific questions for future study is a strength throughout the book. Fritz Trillmich examines parental care at both proximate and ultimate levels (Chapter 10), including discussions of parent-offspring conflict and cooperative brood care. The chapter could perhaps benefit from a more in-depth discussion of conflict between parents over investment in care, although Trillmich points out that this topic is the subject of a recently published review.

Part III: Sex and Reproduction

The chapters in the sex and reproduction section cohere as a group perhaps better than those in any other section, with Chapters 13, 14, and 15 particularly interesting when read together. In Chapter 13, on extra-pair behavior, Bart Kempenaers and Emmi Schlicht review a very active field, providing a comprehensive overview of current thinking on the evolution of extra-pair behavior in birds. This chapter would be an excellent starting point for any student interested in the field. Chapter 14, in which F. Bernhard Kraus and Robin F. A. Moritz examine the evolution of polyandry in the social Hymenoptera, provides an interesting contrast to Chapter 13, as the selection pressures affecting polyandry in birds and in social insects may overlap in some respects and differ in others. In Chapter 15, Jutta Schneider and Lutz Fromhage explore the evolution of monogynous mating strategies in spiders, investigating explanations for the limited mating frequency by males in a large number of spider species.

The remaining chapters of this section also contain important contributions: Wolf Blanckenhorn discusses the importance of quantifying natural and sexual selection, providing a useful guide for researchers who wish to calculate selection coefficients but lack the knowledge to do so (Chapter 11); Nils Anthes explores the interesting topic of mate choice and reproductive conflict in simultaneous hermaphrodites, revealing the sometimes surprising reproductive strategies that have evolved in these unique taxa (Chapter 12); and Wolfgang Goymann and Heribert Hofer discuss the effects of hormones on social behavior and mating systems, an important and complex topic that the authors explain skillfully (Chapter 16). Continuing the overall trend of the book, the section on sex and reproduction succeeds in providing succinct reviews of published research while also pointing out important directions for future research.

Part IV: Behavioral Variation

Given the extensive recent interest in explaining individual differences in behavior, this section represents an important appraisal of the current state of a rapidly developing field. As throughout the volume, the authors in this section examine their topics from multiple levels of analysis. Focusing on mammals, Norbert Sachser and Sylvia Kaiser explore the

effects of maternal and early social environment on the development of individual differences in behavior (Chapter 17). Michael Taborsky and H. Jane Brockmann examine the evolution of alternative reproductive tactics, including an instructive discussion of differences in the occurrence of such tactics among taxa (Chapter 18). Ralph Bergmüller discusses animal personality and behavioral syndromes, providing a useful overview of current research in an emerging field (Chapter 19). Carel P. van Schaik explores the topic of social learning, including discussions of learning through information and through interaction, and an examination of the conditions under which social learning is adaptive (Chapter 20). The chapter closes with the topic of culture in non-human animals, emphasizing the need for a theory of culture. In the concluding chapter (Chapter 21), Peter M. Kappeler and Cornelia Kraus provide an extensive review of the evolution of variation in behavior at levels from the species to the individual, focusing on the possible influence of evolutionary history on behavioral variability.

Conclusions

This book is an excellent summary of several important research areas. The consistent attention to both proximate and ultimate approaches to studying behavior is a significant strength of the book, and the tone throughout is suitable for upper-level undergraduate courses or for introductory graduate courses. The glossary sections that appear at the ends of several chapters are a valuable addition, allowing students who may not be familiar with advanced terminology to access the material.

I think the book is strongest as a source for instructors of upper-level undergraduate courses, who could assign individual chapters or sections as valuable introductions to a research area, and especially to recent advances in the field. The book is less strong when considered for use as the sole

textbook for a course because, as the editor states in his introduction, the set of topics included is a reflection of the interests of researchers in central continental Europe. As the editor points out, other recent textbooks in the field have similarly had a regional focus (e.g., Danchin et al. 2008). However, the self-acknowledged regional bias of these books may be a weakness if instructors are looking for a textbook in which the topics included were selected based only upon their importance to the current incarnation of the field. Hence, an updated textbook in the model of the *Behavioural Ecology: An Evolutionary Approach* volumes edited by Krebs and Davies (e.g., Krebs and Davies 1984) is still needed and would serve a complementary purpose.

Overall, *Animal Behaviour: Evolution and Mechanisms* presents an array of interesting chapters on diverse topics, and I think this book will prove to be an important source for instructors looking for up-to-date, concise reviews of research areas, and for advanced students who wish to cement their understanding of important concepts in the field of animal behavior.

Caitlin Stern
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Danchin É, Giraldeau L-A, Cézilly F (eds). 2008. *Behavioural Ecology*. Oxford: Oxford University Press.

Krebs JR, Davies NB (eds). 1984. *Behavioural Ecology: An Evolutionary Approach*. Oxford: Blackwell Scientific Publications.

Evolutionary Behavioral Ecology

David F. Westneat and Charles W. Fox (eds). Oxford University Press, 2010. 641 pp.

ISBN 978-0-19-533193-6 (hardcover), ISBN 978-0-19-533192-9 (paperback)

The precedent for this edited collection is Krebs and Davies' *Behavioural Ecology: An Evolutionary Approach*. Because its objective is to provide an introduction for graduate students, however, the detail and eclecticism of the earlier series have been sacrificed in the interest of full coverage. Chapters are said to be 'aggressively edited' to ensure that they rigorously present core concepts, and are both consistent with and cross-referenced to other chapters. Each chapter has a conclusion and/or a section on future directions, as well as suggestions for further reading. Additional devices contributing to unity and flow are the use of boxes to separate technical primers, and the inclusion of chapter references in the bibliography. The decision not to include a glossary of terms may reflect subtle differences in usage among the various authors, or possibly the need to define an excessively long list of terms.

This review will adopt the standpoint of a graduate student, appropriate not only because this is the target audience, but also because your reviewer happens to be one himself. The primary focus of *Evolutionary Behavioral Ecology* is to provide theoretical explanations. Empirical findings are referred to only to illustrate the theory or to point to broad patterns that require explanation. Although chapters vary in the demands placed on the reader, the presentation is only occasionally impenetrable. Symbolic models are frequently used, but the mathematically-challenged need not be discouraged. In most cases, the mathematics is straightforward, and is used as a means of conceptual explication: what assumptions are made, how do the assumed factors interrelate, and what predictions follow?

The best starting-point for this review is not at the beginning, but in chapter 2, contributed by the editors themselves, as this reveals the editors' own style. Their subject is adaptation. Two approaches are contrasted: *current utility*, which asks how behavior currently contributes to fitness in a specified environment, and the much more demanding *historical* approach, which employs the term *adaptation* only where three conditions are met: behavior has changed over evolutionary time, this change was due to natural selection, and selection was tied to performance of a particular task with fitness consequences. Although current utility is implicitly accepted by most behavioral ecologists, it does not on its own allow inferences about history, including the inference that current utility explains maintenance of the behavior (unless we know that current behavior has persisted for some time). On the other hand, phylogenetic

analyses yield little information for the historical approach to work with if the behavior has persisted, for example because selection has always been stabilizing. Westneat and Fox recommend supplementing the current utility approach with multiple competing hypotheses, including non-adaptive ones, to reduce the risk of 'just-so' stories. Their treatment is clear, persuasive and gives due weight to rival viewpoints. The only unconvincing suggestion is that, although the term *adaptation* should be reserved for use within the historical approach, it is nevertheless valid to use *adaptive* within the current utility approach. Although this appears to reflect current usage, it seems a flimsy support on which to hang such a critical distinction. Would it not be clearer if adherents of the current utility approach used the term *function*, and avoided *adaptation* in all its grammatical forms? In Tinbergen's four-part scheme, function (or 'survival value') is clearly distinct from evolution and hence history (Tinbergen, 1963).

Section I deals with conceptual foundations, and commences with a history of the discipline. Behavioral ecology, argue Birkhead and Monaghan, represents an advance over ethology because it recognizes the importance of individual selection in 'a more explicitly evolutionary approach'. By this, they do not appear to mean 'explicitly historical' (although phylogeny is clearly important), but rather that the best explanatory models are dynamic because they include not only selection but also the genetic response to selection. Unfortunately, this chapter does not explain why the new discipline adopted the label *behavioral ecology*, which emphasizes current environmental context, rather than the evolutionary perspective said to be distinctive. It is probably because of the shortcomings of this label that both this collection and the Krebs and Davies collections include explicit reference to evolution in their titles.

Chapter 3 on selection by Sinervo and Calsbeek casts a broad net, but concentrates on forms of selection most relevant to the evolution of behavior. For example, opposing sources of selection on single traits or on correlated traits form the basis of frequently-used optimality models, while social signaling is strongly influenced by frequency-dependent selection. In chapter 4, Hunt and Hodgson suggest that fitness is one of the most difficult to understand concepts in evolution. In the opinion of your reviewer, however, the difficulty arises because too much is expected. The concept started life as a lock-and-key analogy, and hence as the name of a relationship (degree of fit to an environment), but has now morphed into an attribute of organisms, traits or alleles. In this usage, it represents a measure of reproductive success, which is invoked to explain relative abundances of organisms, traits or alleles from one generation to the next. The authors worry that competing measures are context-dependent and usually difficult to implement, while proxies for these measures often turn out

to be unreliable, especially when used alone, but these are critical problems only if one assumes that fitness is a single, measurable attribute which uniquely accounts for relative abundances (Ariew and Lewontin, 2004). Just as it was always understood that organisms might 'fit' their environment in multiple ways, should we not expect that organisms, traits or alleles will have context-dependent measures of reproductive success?

Optimality models can be used as though the underlying genetics are unimportant, thereby implying that the genetics are simple. In chapter 5 on the genetic basis of behavioral variation, Shaw and Wiley argue that explicit consideration of the underlying genetic architecture can improve understanding, even when the genes are unknown. For example, as compared with traits under the control of a single gene, traits under the control of multiple genes will move more slowly toward an optimum if that optimum lies within standing variation (because favorable alleles may be concealed by variation at other loci), but will move more quickly if the optimum lies outside standing variation (because there are more sources of new variation).

In chapter 6, Ghalambor, Angeloni and Carroll review phenotypic plasticity (the capacity for a given genotype to generate different phenotypes in different environments), arguing that behavioral ecologists have been slow to adopt this perspective, even though behavior is an obvious candidate for its adoption. For example, although female guppies prefer males with more carotenoid pigments, their preference is stronger in a carotenoid-impoverished environment. Lack of a similar plasticity among males suggests that female plasticity is explained by mate choice rather than sensory bias. Ord and Martins (chapter 7) review three methods for actively using phylogenetic information to infer evolutionary history: reconstructing ancestral traits, estimating the degree of phylogenetic signal in traits, and incorporating phylogeny explicitly in statistical tests rather than, as in the independent contrasts method, attempting to remove it from the data beforehand.

In Section II on decision-making, a decision is assumed to occur when an animal behaves in a particular way when there was at least one other alternative available, with no implication about the behavior being conscious or even cognitive. Ydenberg's discussion of decision theory (chapter 8) is refreshingly frank, for example some modeling assumptions are characterized as 'productive lies'. Mappes and Stevens (chapter 9) review the ways in which sensory and information processing are linked to decisions, and cite some interesting findings, for example that color patterns in coral-reef fish often perform a camouflage function when viewed from a distance, but are nevertheless conspicuous when in close proximity. In chapter 10, Healy and Rowe review the ecology and evolution of cognitive abilities

including the role that learning about a signal can play in signal design. For example, chickens rewarded for pecking at any blue-green object and avoiding a blue object, preferentially pecked at the blue-green object that was furthest away from blue. This preference for the strongest contrast suggests an explanation for exaggerated signals.

Section III is problematic, not because of the individual chapters, but because the unifying theme is unclear and the title (Ecology of Behavior) is too broad to be informative. While two of the chapters (12 and 13) are principally about risk, this is true to only a limited degree of the remaining chapter. Hamilton's discussion of foraging theory (chapter 11) draws some important parallels with rationality in economics. In his discussion of methods used to manage risk (chapter 12), Dall gives considerable emphasis to niche construction, a process which occurs when organisms engineer their own environment, thereby modifying the selection pressures on themselves (Laland and Sterelny, 2006). In this reviewer's opinion, niche construction is unduly neglected in evolutionary studies. Nonacs and Blumstein (chapter 13) investigate ways in which predation risk operates as a selective force on anti-predator defense, their central prediction being that anti-predator defense is highest when individuals are likely to encounter an intermediate number of predators.

Section IV deals with social behavior, and commences with Wolf and Moore's treatment of interacting phenotypes and indirect genetic effects (chapter 14). This chapter contains some of the most challenging models in the book, made more difficult by proofreading errors in the text. The argument is most clear in the case of maternal effects, and seems to be as follows: individuals inherit environments as well as genes from their mothers; because those environments are expressions of their mother's genes, maternal genes have an indirect as well as a direct effect on offspring phenotypes, the indirect effect taking the form of selection pressure on the focal individual. When applied more generally, this approach treats social behavior as both a source and a target of selection, and might be regarded as an alternative to niche construction. Briffa and Sneddon's review of contest behavior in chapter 15 is a clear summary of game-theory models, in particular hawk-dove, sequential assessment, war of attrition, cumulative assessment, and variations thereof.

Arguing that animal signals are not necessarily about the transfer of information, Enquist, Hurd and Ghirlanda (chapter 16) distinguish between performance signals and strategic signals, and within the latter between handicap and conventional signals. There is an interesting discussion of what makes a signal effective, including how mating signals often have their origin in feeding behavior. Earley and Dugatkin (chapter 17) consider the possible costs and

benefits of group living, social structure being conceived as the differential allocation of costs and benefits within the group. In chapter 18, Gardner, Griffin and West provide a clear exposition of inclusive fitness theory, and distinguish the various possible mechanisms for the evolution of cooperation. Queller and Strassmann (chapter 19) are also interested in the evolution of cooperation, but with specific reference to eusociality in the social insects. They argue that, while it is not necessary for helpers to be more closely related to beneficiaries than to their own offspring, relatedness is nevertheless critical for the evolution of eusociality because kinship is the only kind of allele-sharing that allows for agreement across the genome. Recent advances, however, have focused less attention on relatedness, and more on costs, benefits and power relationships tied to the biology of individual species.

Section V is on reproductive behavior, the first chapter (chapter 20) being a broad review of sexual selection by Jennions and Kokko. Sexual selection is usually directional rather than stabilizing, and favors traits that are often exaggerated and otherwise wasteful because the competition involved is zero-sum. There is considerable focus on attempting to explain greater investment by females than by males in parental care. Greater initial investment by females in gametes is often identified as a key influence, but such an approach commits the 'Concorde fallacy' of focusing on past costs when only future costs matter. It is suggested instead that males have more to lose by caring, not because males in general have more to lose, but because the only males who count in this regard, being males faced with the decision to care or desert, are those who have successfully mated, and it is these males who perceive themselves as having more to lose, having just received feedback that they are competitively successful. In his review of sexual selection in external fertilizers, Levitan (chapter 21) measures the strength of sexual selection by plotting Bateman gradients, which show how much individuals gain in offspring production by increasing their mating rate. In common with findings in many internal fertilizers, male gradients are positive, while female gradients vary from positive to zero to negative. In chapter 22 on postcopulatory sexual selection, Pitnick and Hosken emphasize that cryptic female choice and sperm competition are not independent phenomena, but are opposite ends of a continuum.

Fricke, Bretman and Chapman (chapter 23) point out the strong overlap between sexual selection and sexual conflict, in that both focus on selection for reproductive success, but distinguish the two as follows: whenever the fitness impact of a given trait is positive for one sex but negative for the other, then sexual conflict is the appropriate model. In their review of mate choice, Brooks and Griffith (chapter 24) have some interesting observations about indirect choice, where the effect of selection is on offspring fitness rather than that

of the chooser. Paradoxically, once pairing has occurred in a socially-monogamous system, and hence direct benefits have been determined, female choice is often less constrained, and it is possible for females to use extra-pair copulations to obtain indirect benefits, which they apparently do using a different preference function. They suggest that 'Fisherian runaway processes' and 'good genes' are a false dichotomy in the understanding of indirect selection, and that non-additive genetic variation is more important than previously recognized (in the form of female choice for genetic compatibility). Shuster (chapter 25) reviews alternative mating strategies, concentrating on the role of frequency dependent selection. Kvarnemo (chapter 26) assesses various attempts to explain why females predominantly provide parental care, and finds all of them wanting, not least because they do a poor job of explaining why predominantly male care evolves in some cases. She argues that, contrary to these approaches, male care should not be treated as exceptional, and mating effort does not need to be fastidiously separated from parental effort.

Section VI (Extensions) opens with a review by Rundle and Boughman (chapter 27) of the possible role of behavior in reproductive isolation and hence speciation within a 'biological species' approach. For example, regardless of lake of origin, limnetic and benthic sticklebacks have been shown to be reproductively isolated from each other, while limnetic-limnetic and benthic-benthic mating occurs readily, suggesting that different light environments can drive divergent male nuptial colors and female preferences. Grozinger (chapter 28) argues that, as compared with classical genetic approaches, genomics allows organisms to be studied with less manipulation in their natural environments, and supports the simultaneous study of multiple genes. In chapter 29, Schlaepfer, Sherman and Runge use the term 'evolutionary trap' when, as a result of anthropogenic changes, animals make a suboptimal decision among multiple available alternatives. The responses open to animals and the management implications are discussed. Sih, Bell and Johnson (chapter 30) use the term 'behavioral syndrome' when animals exhibit consistent behaviors across multiple contexts, for example they are consistently bold in both mating and foraging contexts. An interesting implication is that behaviors that may be maladaptive when viewed in isolation may nevertheless be adaptive when viewed as part of a syndrome. Behavioral syndromes have been explained as a product of inflexible proximate mechanisms such as hormonal control or as an adaptation, the possible benefits being specialization, predictability, and continuing to do what you are experienced in doing. In chapter 31, Lieberman and Gangestad review human behavioral ecology and evolutionary psychology, treating the former as equivalent to behavioral ecology and the latter as primarily focused on proximate mechanisms.

Graduate students will find in this collection a multiplicity of theoretical concepts, models and techniques, for the most part clearly and persuasively presented. I have only two general suggestions for improvement. Many of the chapters are written in the style of a paper for journal publication, with large amounts of densely-packed information presented impersonally, when a more relaxed, conversational style would communicate more successfully. In a similar vein, there is a tendency to soften the disagreement between rival approaches by burying them in a thicket of caveats. Better to highlight the disagreement frankly.

David Wells

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- Tinbergen N, 1963. On aims and methods of ethology. *Zeitschrift für Tierpsychologie* 20:410-433.



LION KING: DELETED SCENES

ATER

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Research Interests: Behavioural ecology, the evolution of brain size and cognition, the use and function of social support, play behaviour.

Selected Papers:

Logan CJ. 7 July 2010. Settling arguments, the corvid way: Kiss and make up or snuggle with your partner? Why it matters what you do after a fight. *New Scientist*.

O'Donnell S, Kumar A, Logan C. 2010. Species differences in army ant raid attendance and bivouac checking behavior among Neotropical montane forest birds. *Wilson Journal of Ornithology* 122(3):503-512.

Logan CJ, Pepper JW. 2007. Social learning is central to innovation, in primates and beyond. *Behavioral and Brain Sciences* 30:416-417.

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Selected Papers:

Rittschof CC 2001 Mortality risk affects mating decisions in the spider *Nephila clavipes*. *Behavioral Ecology*, DOI: 10.1093/beheco/arq222

Michalik P, Rittschof CC 2011 A comparative analysis of the morphology and evolution of permanent sperm depletion in spiders. *PLoS ONE* 6:e16014.

Rittschof CC 2010. Male density affects large-male competitive advantage in the golden silk spider *Nephila clavipes*. *Behavioral Ecology*, 21:979-985.

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Research Interests: evolution of cooperation and social behavior, dispersal, social networks, biological markets, maternal effects, behavioral endocrinology

Selected Papers:

Smith JE, Powning KS, Dawes SE, Estrada JR, Hopper AL, Piotrowski SL, Holekamp KE 2011. Greetings promote cooperation and reinforce social bonds among spotted hyenas. *Animal Behaviour* 81:401-415.

Smith JE, Van Horn RC, Powning KS, Cole AR, Graham KE, Memenis SK, Holekamp KE. 2010. Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behavioral Ecology*, 21:284-303.

Smith JE, Kolowski JM, Graham KE, Dawes SE, Holekamp KE. 2008. Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. *Animal Behaviour* 76:619-636.

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Research Interests: Trade-offs between immune function and sexually selected traits, insect mating systems, male mating strategies and their effect on female mating frequency and fitness.

Selected Papers:

McNamara, KB., Elgar, MA. & Jones, TM. 2008. No cost to males of sperm competition in the hide beetle, *Dermestes maculatus*, *Behavioral Ecology*, 19: 433-40.

McNamara, KB., Elgar, MA & Jones, TM. 2008. Seminal compounds, female receptivity and female fitness in the almond moth, *Cadra cautella*. *Animal Behaviour*, 76: 771-7.

McNamara, KB., Jones, TM. & Elgar, MA. 2007. No cost of male mating experience on female reproductive success in the almond moth, *Cadra cautella* (Lepidoptera; Pyralidae). *Behavioral Ecology and Sociobiology* 61: 1177-84.

Ecology of sex roles Symposium, ISBE 2010, Perth Australia

Summary

Animal sex roles, in a wide sense, were the focus of a stimulating post-symposium of the International Society of Behavioral Ecology (ISBE) meeting in Perth 2010. The sex roles symposium consisted of short presentations and an hour of role-play designed to promote refreshed thinking and discussion of "the ecology of sex roles". In a strict sense, sex roles are defined according to which sex that competes most for matings (Vincent et al. 1992). Here, several contributors discussed empirical findings of flexibility in sex role behaviour, also including mate choice, in relation to ecological, social and demographic factors. We discussed the usefulness of the term "sex roles" and the assumptions often associated with the terminology. The notion that variation within and between individuals - irrespective of their sex - may paradoxically account for sex roles was a theme of the discussions. We discussed empirical findings showing that mate choice and mating competition are flexible in response to ecology, social circumstances, and internal factors in both males and females of a taxonomically wide array of animals. Theory development is accompanying the empirical trend and is emphasizing the adaptive benefits of individually flexible mating decisions. We concluded that variation in mating competition and mate choice seems ubiquitous, and pointed out future directions for the investigation of ecological effects on individual reproductive decisions and competition

Empirical and theoretical development

Appropriately the symposium took place in Perth, where studies of katydids (*Kawanaphila nartee*) showed some of the first examples of individual flexibility in sex roles, in this specific case, solely due to the availability of food resources (Gwynne & Simmons 1990). Ecological influences on animal behaviour have been the focus of much research on e.g. optimal foraging and mating systems. Traditionally, investigators have often supposed that sex roles are static within individuals and species so that sexual selection research still focuses primarily on male-male competition and female choice, though there may often also be aspects of female-female competition and male choice as well as other sexual selection mechanisms.

Yet, a relatively large number of studies have demonstrated that mate choice change under ecological circumstances, suggesting that sex roles may be highly dynamic in many species, and if this is so, new dynamic and integrated theory is needed (Cornwallis and Uller 2010; Safran et al 2010). We agreed that new theory is needed for (1) understanding unexplained variability in already-conducted studies of mate choice and mating competition and (2) organizing new directions for studies of sexual selection in an evolutionary ecological perspective. Some of the questions that emerged in the sex role symposium included: What is it about ecology

that favors sex role dynamism? What really is the definition of "sex-roles"?

Highlighting flexibility in sex roles

The presentations spanned a broad variety of questions and organisms, stimulating many perspectives. Patty Gowaty began with the switch point theorem (Gowaty & Hubbell 2009) that predicts that individuals (not sexes) adjust their acceptance or rejection of potential mates flexibly and adaptively when ecological circumstances change. She argued that sex differences in accept/reject behaviour is influenced as much by what Darwin called 'habits of life' as by genes for choosy or indiscriminate behaviour (Gowaty & Hubbell 2009). The switch point theorem simplifies ecology into effects on five parameters, each of which may affect an individual's time available for mating. These parameters are: survival probability s , encounter probability e , the handling time after a mating before an individual is receptive again l , the number of potential mates in the population n , and the w -distribution, which is based on the matrix of fitness that would be conferred if each individual of one sex in the population mated with all potential mates. The model says that e , s , l , n , and the fitness that would be conferred induce individual decisions to accept or reject this or that potential mate. The model thus says that sex differences in ecological constraints on e , s , l , n and the w -distribution produce systematic differences in reproductive decisions.

Several contributors presented empirical studies showing flexibility in mating competition and mate choice. Elisabet Forsgren showed examples of within species variation (in space and over time) regarding which sex faces the strongest mating competition (*i.e.*, sex roles). She and co-workers also put forward the question of how mating competition should be measured in practice, and discussed the discrepancy of results from laboratory and field studies when it comes to predicting competitive behaviour in relation to operational sex ratio.

Nathan Bailey discussed how variation in social environments and experience during development, not just genes for sex-specific behaviour, affected the behaviour of male *Drosophila*. Comparing males raised with conspecific males and those raised in isolation, he found that rearing conditions affected same-sex sexual behaviour. Thus, Bailey emphasized the importance of learning as a source of variation and apparent flexibility in adult sexual behaviour.

Gerlind Lehmann discussed her studies which show that female bushcrickets (*Xederra charactus*) change their propensity to mate in relation to population density: they reject fewer males when there is less time available for mating and also with lower mate density. The weight of the glandular mass in males, a sexually selected character, was positively correlated with the number of matings obtained only in high but not in low densities (Lehmann 2007). In

reviewing empirical studies of flexible mate choice, Malin Ah-King and Patricia Gowaty, discussed accumulating evidence of the existence of flexibility in a taxonomically wide variety of taxa and among males as well as females. All of these accumulated empirical findings are consistent with the theoretical prediction that all individuals should be able to adaptively adjust their mating decisions as ecological circumstances change.

Ally Harari discussed factors influencing male mate choice. Her work on moths (*Agrotis segetum* and *Lobesia botrana*) showed that there is between-female variation in pheromone emission, that the males invest resources in costly spermatophores and are sperm limited, thus resulting in male mate choice.

The role of ecology for the evolution of mating behaviour was another interesting topic. David McDonald described the behavioural ecology of the peculiar mating system of long-tailed manakins (*Chiroxiphia linearis*), in which two unrelated males dance on leks in duets. He argued that a number of specific ecological factors may have been prerequisites for the evolution of females visiting lekking males performing collaborative dancing duets – the feeding habits, the harsher habitat in comparison to other manakins leading to larger home ranges. He also discussed how differences in increased memory capacity as shown by larger home ranges can be related to hippocampus size and the ecology of this species which in turn enables females to memorize the difference in dance performance at different sites for many consecutive years.

To explore the tensions produced when empirical observations come in conflict with classic theory, the symposium organizers, Ah-King and Ahnesjö invited the symposium participants to a role play. The stage was set as the first meeting of a student's graduate advisory committee. The protagonists were the student, who was seeking a thesis on sex roles, and her three advisors. The advisors included a passionate natural historian, a "conservative" one with a classical view of female choice and male-male competition and one "questioner", opposing to categorizing into traditional sex-roles. An enjoyable and fun discussion emerged: "Everybody knows what a sex-role is" but actually there was no consensus on what are sex roles. There was, however, consensus on the importance of ecology on what individuals do. We also agreed that it is important to attend, not just to the variation in what animals do, but in variation in our approaches to the study of what animals do. Consequently, it was highlighting and mind-opening to spend a day on the Ecology of sex-roles!

Future directions

How ecology influences sex roles and sexual selection is a promising and vivid field of study that has just begun to be explored. Our conclusions, like our discussions were wide-ranging: (1) Sex roles are flexible and variable in relation to

ecological circumstances. (2) We need to continue investigating the role of ecology for individual reproductive decision-making and (3) when exploring the ecology of sex-roles it should be without being biased or constrained by either traditional expectations of how the sexes behave or ought to behave. (4) There exist diverse meanings to "sex roles". (5) The intuitive notions connected to the term often imply much more than the definition which sex competes most for matings (Vincent et al. 1992). (6) It is important to distinguish between definitions and explanations or processes influencing sex roles. (7) We urge each other and other investigators to be operational in future studies and in discussions.

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How to contribute to the newsletter

The ISBE Newsletter publishes Book Reviews, Conference and Workshop Reviews and Commentary Articles of interest to the International Society for Behavioral Ecology. The ISBE Newsletter will only consider work that is not already published or intended to be submitted for publication elsewhere.

Book Reviews: Reviews are generally solicited by the Editor as new books arrive at the office, and are deemed to be of interest to the society. Persons involved in the publishing of books who would like these to be considered for review in the Newsletter should contact the Editor and arrange for their publisher to forward a review copy to this office. Authors may submit a list of possible reviewers. Alternately, members who wish to review a particular text should contact the Editor. The Editor will provide reviewers with instructions and a style sheet. Reviews are typically 1500-2000 Words.

Workshop/Conference Reviews: Workshop and/or Conference reviews should be prepared in one of the following two formats. **Brief synopses** (max 1500 words) and **Longer reports** (max 3000 words) Graduate students and postdocs are strongly encouraged to consider contributing to writing these reports.

Cartoons: Cartoonists and other artists are encouraged to submit artwork, either in hardcopy, or as TIFF or high resolution (300 dpi) GIF files. All cartoons published in the newsletter will be credited to the illustrator, and will appear on the Newsletter's website (www.behavecol.com).

7th Ecology & Behaviour Meeting

May 2-6 2011, Rennes, France
serl2011.univ-rennes1.fr

The Society for the Study of Evolution, Annual Meeting

June 17-21, 2011, Norman, Oklahoma, USA
<http://www.evolutionsociety.org/meetings.asp>

Gordon Research Conference: Ecological and Evolutionary Genomics

July 10-15, 2011, University of New England Biddeford, USA
<http://www.grc.org>

The 16th International Symposium on Carotenoids

July 17-22 July 2011, Krakow, Poland
www.carotenoid.pl

International Ethological Conference

July 25-30 2011. Bloomington IN, USA
www.indiana.edu/~behav11

13th European Society for Evolutionary Biology Congress

August 20-25 2011, Tübingen in Germany
<http://www.eseb2011.de/>

European Ornithologists' Union (EOU) 8th Conference

August 27-30 2011, Riga, Latvia
<http://eou.biology.lv/>

XXIII meeting of the International BioAcoustic Council (IBAC)

September 12th - 16th 2011, La Rochelle, France
<http://www.cb.u-psud.fr/ibac2011/>

Australasian Ornithological Conference

September 28-30 2011, Cairns Australia
<http://www.birdsaustralia.com.au>

2nd World Conference on Biological Invasions and Ecosystem Functioning

November 21-24, 2011, Mar del Plata, Argentina
<http://www.grieta.org.ar/biolief/>

Association for the Study of Animal Behaviour Summer Meeting 2011: Understanding Animal Intelligence

August 18- 19 2011, University of St Andrews, UK
<http://asab.nottingham.ac.uk/meetings/index.php>

7th Biennial Meeting of the Australasian Evolution Society

25th - 27th September 2011, Townsville, QLD.
<http://aes.eriophora.com.au/>

25th International Congress for Conservation Biology

5 - 9 December 2011, Auckland, New Zealand
www.conbio.org/2011

VIII Göttinger Freilandtage: Behavioral Constraints and Flexibility

December 06-09 2011, Göttingen, Germany
<http://www.soziobio.uni-goettingen.de/congresses.php>

.....and beyond 2011

7th Symposium of the European Association of Acarologists

July 9-13, 2012, Vienna, Austria
<http://euraac.boku.ac.at/SympVienna>

International Congress of Entomology

August 19-25 2012, Korea
www.ice2012.org/

14th Congress of the International Society for Behavioral Ecology

August 11-17 2012, Lund, Sweden

Society for Integrative and Comparative Biology

January 3-7, 2013, San Francisco, USA
<http://sicb.org/meetings/2013/callsymp.php3>

IEC/ASAB Summer meeting

4th-8th August 2013, Newcastle Gateshead, UK
<http://iec2013.com/>

XVII IUSSI International Congress

July 2014, Cairns, Australia
<http://www.iussi.org/>



LACKING A "PRETTY" VOICE, CROWS ARE OFTEN RELEGATED TO PLAYING THE TRIANGLE DURING THE DAWN CHORUS