

Supplement to Behavioral Ecology

ISBE

International Society for Behavioral Ecology

Newsletter

Editor: Ken Otter
Ecosystem Science & Management Program
University of Northern BC
Prince George, BC, Canada V2N 4Z9
Phone - (250) 960 5019
Fax - (250) 960 5539
email - otterk@unbc.ca

web.unbc.ca/isbe/

Volume 15, Issue 2
Fall 2003

Editorial – ISBE Elections

This issue contains the ballot form and pertinent information on the candidates for the current ISBE elections.

Elections for executive positions within the ISBE are held prior to the biennial conferences. On pages 18-19 of this issue, you will find the histories of the candidates nominated for **President Elect** and two **Councillor** positions. A single candidate has been nominated for the position of society **Treasurer**; a vote for this candidate will affirm our support. **The ballot for voting is located on the final page of the newsletter.**

All members of the society are eligible to vote: please select among the candidates on the ballots and return these to the recording secretary, Paul Ward, within one month of receipt of this newsletter. Only original ballots will be counted; no photocopies, please.

Please take the time to register your vote. Results of the elections will be posted in the spring newsletter and announced at the conference.

Also in this edition, you will find an invitation to attend the 10th Jubilee Conference of the ISBE, to be held in Jyväskylä, Finland, 10-15 July 2004. We hope to see you at the conference.

Ken Otter
Newsletter

Contents of this Issue

Editorial	1
Executive	2
Society News	3
Conferences, Grants and Jobs	3
Invitation to ISBE 2004	3-4
Book Reviews	
Living in Groups (Krause & Ruxton 2002) Review by Scott Creel	4-5
Behavior and Its Neural Control in Gastropod Molluscs (Chase 2002) Review by Bruno Baur	5-6
Behavioural Diversity in Chimpanzees and Bonobos (Boesch et al. 2002) Review by Clara B. Jones	6-8
The Evolution of Begging . (Wright & Leonard 2002) Review by Douglas W. Mock	9-10
Acoustic Communication in Insects and Anurans (Gerhardt & Huber 2002) Review by Peter K. McGregor	10-11
Seasonal patterns of stress, immune function & disease . (Nelson et al. 2002) Review by Dennis Hasselquist	12-13
Lizard Social Behavior (Fox et al. 2003) Review by Ken Otter	13-14
Workshop & Conference Reviews	
Sperm Tales: Biology of Spermatozoa international conference W. Edwin Harris	14-18
ISBE ELECTION SLATE – Bios of Candidates	18-19
Contributing to the ISBE Newsletter	19
ISBE ELECTION BALLOT	20

Current Executive

President**Malte Andersson**

Animal Ecology
Department of Zoology
Göteborg University
Box 463, SE 405 30 Göteborg, Sweden
Tel: +46 31 773 3695
Fax: +46 31 416729
E-mail: malte.andersson@zool.gu.se

Past-President**Nick Davies**

Department of Zoology
Cambridge University
Downing Street
Cambridge CB2 3EJ U.K.
Tel.: +44 (0)1223 334405
Fax: +44 (0)1223 336676
E-mail: n.b.davies@zoo.cam.ac.uk

President-elect**Jack Bradbury**

Cornell University Lab of Ornithology
159 Sapsucker Woods Road
Ithaca NY 14850 USA
Tel: +1 607 254 2493
Fax: +1 607 254 2439
E-mail: jwb25@cornell.edu

Secretary**Paul Ward**

Zoologisches Museum der Universität Zürich
Winterthurerstrasse 190
CH 8057 Zürich, Switzerland
Tel: +41 1 635 4760
Fax: +41 1 635 4780
E-mail: pward@zoolmus.unizh.ch

Treasurer**Walt Koenig**

Hastings Reservation
38601 E. Carmel Valley Rd.
Carmel Valley, CA 93924 U.S.A.
Tel: +1 831 659 5981
Fax: +1 831 659 0150
Email: wicker@uclink4.berkeley.edu

Councillors**Marty Leonard**

Department of Biology
Dalhousie University
Halifax, Nova Scotia, Canada B3H 4J1
Tel: +1 902 494 2158
Fax: +1 902 494 3736
E-mail: mleonard@is.dal.ca

Linda A. Whittingham

Dept. of Biological Sciences
University of Wisconsin-Milwaukee
Lapham Hall, P.O. Box 413
Milwaukee, WI 53201 U.S.A.
Tel: +1 414 229 2252
Fax: +1 414 229 3926
e-mail: whitting@csd.uwm.edu

Hanna Kokko

Department of Ecology and Systematics
Biocenter 3 PO Box 65 (Viikinkaari 1)
00014 University of Helsinki
Finland
Tel: +358 9 1915 7702
Fax : +358 9 1915 7694
E-mail : hanna.kokko@helsinki.fi

Nina Wedell

The School of Biology,
University of Leeds, L. C. Miall Building
Clarendon Way, Leeds, LS2 9JT, U.K.
Tel: +44 (0) 1133 433051
Fax: +44 (0) 1133 432835
E-mail: N.Wedell@leeds.ac.uk

Society News

DONATED SUBSCRIPTION PROGRAMME

Please help colleagues in need. Every donation will help increase scientific contacts across the world. In a time when nationalism is again raising its ugly head, this is more important than ever. For details, see the advertisement on the inside back cover of *Behavioral Ecology* volume 12(4).

SPOUSAL MEMBERSHIP

For \$5 per year spouses of full members can become members of ISBE. Spousal members receive the newsletter and information concerning biannual meetings, but do not receive a subscription to the journal. Contact the Treasurer for more details.

ISBE 2004 CONFERENCE

The 10th Jubilee Congress of the ISBE will be held in Jyväskylä, Finland, 10-15 July 2004. Details can be found at www.isbe2004.com.

WORKSHOPS AND OTHER MEETINGS

XIXth (NEW) International Congress of Zoology will be held in 2004 in Beijing, China.

Basic information, such as correspondence, first announcement, online registration and how to organize a symposium, is available on the web page <http://www.icz.ioz.ac.cn/>.

The research papers presented in the congress will be published in *Acta Zoologica Sinica*.

The 24th International Ornithological Congress will be held in Hamburg, Germany, 13-19 August 2006.

The scientific program committee has been formed and a web page is in place:
<http://www.i-o-c.org/>

A second circular will follow in autumn of 2003 soliciting suggestions for symposium topics. Pertinent deadlines will be included in that circular.

We hope that you will circle this date on your calendar and plan to attend. We look forward to seeing you in Hamburg!

Susan Hannon (Chair, Scientific Program Committee)

Franz Bairlein (Secretary General)

GRANTS AND JOBS

Due to application deadlines often occurring between publications of the newsletter, faculty and postdoc and graduate student opportunities are posted on the webpage under "Ads & Positions".

web.unbc.ca/isbe/newsletter/index.htm

Members who have positions may send the text to the Newsletter editor for posting to the webpage. Please send this as text either in an email or as a Word file.

ISBE 2004 Conference, Jyväskylä, Finland

The organising committee would like to invite you to attend the 10th Jubilee Conference of the ISBE held in Jyväskylä, Finland between 10th and 15th of July 2004. Jyväskylä is a university town in the heart of the famous Lake District of Finland. Our Evolutionary Ecology unit has gained a strong status in behavioural ecology research, and has been appointed as the Centre of Excellence in Research by the Academy of Finland. However, within our section of Ecology and Environmental Management at the Department of Biological and Environmental Sciences, there are also many other research projects covering wide taxonomic array of study, including applied research, and we emphasize an integrative approach in our research.

ISBE was established in late 1980's, and today the need

for the interdisciplinary approach is expanding far beyond its initial integrative framework (e.g. to genetics, systematics, physiology and conservation). We will encourage the integrative approach during the Jubilee meeting of the society at Jyväskylä, and the wide variety of topics is illustrated by our choice of plenary and Hamilton lecture speakers. We are proud to announce that the Hamilton lecture 2004 will be delivered by Mary Jane West-Eberhard and that the list of plenary speakers consists of Manfred Milinski, Josephine Pemberton, Vladimir Pravosudov, Barry Sinervo, Liselotte Sundström, William Sutherland, Fritz Vollrath and Christer Wiklund.

In addition to the scientific program we are planning to organise a boat trip to the beautiful lake Päijänne, a possibility to try traditional Finnish smoke sauna and a midnight sun football tournament.

We invite you to Finland for the Jubilee Conference of the ISBE!

On behalf of the organising committee, Rauno Alatalo, Janne Kotiaho, Johanna Mappes and Hannu Ylönen.

Website: <http://www.isbe2004.com>

E-mail:
info@isbe2004.com



Book Reviews

Living in Groups

Jens Krause & Graeme D. Ruxton, Oxford University Press, 2002. 210 Pp.
ISBN 0 19 850818 2 (paperback)

Behavioral ecology has a long and deep history of studying the costs and benefits of living in groups, the evolutionary origins of sociality, and the behavioral consequences of group living. Jens Krause and Graeme Ruxton have done a great job of compiling this massive body of work into an astonishingly small book (158 pages of text). To achieve this brevity, Krause & Ruxton do not attempt a comprehensive review of all the empirical work. Rather, they focus on identifying major concepts and then providing concrete illustrations from particularly informative studies. These examples and case studies come from a broad range of taxa, with a nice mixture of observational and experimental studies. The focus of the chapters also shifts between mechanistic and evolutionary approaches in a balanced way.

This broad and well-rounded approach makes the book essential reading for graduate students or advanced

undergraduates trying to penetrate the enormous primary literature on group living. The book is very well written, with an average of 6-7 figures per chapter, and it could certainly be used in courses. For researchers active in the area, the book will be of value as a concise summary that has sifted and evaluated many papers.

About half of the book falls into three chapters that review the benefits of grouping, costs of grouping, and optimal group size. For a 72 page review of research at the core of group living, this material will be very hard to beat. The next five chapters are a little more idiosyncratic, jumping among topics such as heterogeneity among group members in the costs and benefits of grouping, mechanisms that affect aggregation, and environmental effects on grouping. These five chapters are not as fully developed as the first three, but still provide an excellent synthesis of both old and recent (through 2000) work. The final chapter is an eight page

summary of subjects for future work. The book has 29 pages of references and well-prepared author and subject indices.

If I had to make a complaint about the book, it would be that its brevity means that few subjects receive detailed discussion. For example, the role of dominance is discussed in three sections totaling six pages. This has been a central topic in decades of work on kin selection, cooperative breeding and eusociality, and 60 or 600 pages would no doubt have been possible. By sticking closely to their focus on

identifying key concepts and illustrating them briefly, Krause & Ruxton forego some of the more detailed synthesis that a bigger book could attempt.

That said, the book does an excellent job of meeting its stated goals, and I recommend it highly.

Scott Creel

*Department of Ecology
Montana State University
Bozeman, MT 59717*

Behavior and Its Neural Control in Gastropod Molluscs

Ronald Chase. Oxford University Press, 2002. 314 Pp.
ISBN 0-19-511314-4

Molluscs are numerically the second largest phylum in the animal kingdom with more than 120,000 living species. Gastropods (snails and slugs) constitute by far the largest and most diverse class of molluscs, with an estimated 105,000 species. Many people may think that the behavior of snails is sluggish and that they have no brain at all; Chase's book cures this prejudice. During the past quarter century our knowledge about the behavior and neurobiology of gastropods has substantially increased. This book focuses on recent discoveries that reveal the neural control of behavior in various groups of gastropods.

The introductory chapter presents general features of gastropods and ideas about their origins and diversification. This is followed by a detailed description of the central nervous system in different gastropod groups. One widely appreciated property of some gastropod neurons is their large size, which renders several species (e.g. *Aplysia*) as ideal model organism for neurobiological studies. Chase also explains how taxonomists began to construct phylogenies for the gastropods based on nervous characters. Chapter 3 is devoted to sensory systems. Gastropods have eyes, but in only a few species they allow object recognition. Distance perception of gastropods depends on olfaction, and the perception of near objects is dependent on a combination of chemoreception and mechanoreception. In this and the following chapters Chase's approach to the subject assumes that behavior is controlled by the cellular connections between specific neurons that operate within circuits.

Chapter 4 gives a description of various types of muscles and the peripheral nervous system. It explains that the renowned slow behavior of gastropods can be attributed to the lack of a hard skeleton, which limits the amount of amplification and antagonism that can be achieved from muscular action. Chapter 5 reviews the regulation of respiration, blood circulation and excretion. Chapter 6 considers locomotion. It explains how waves of pedal contractions propel gastropods, and shows interesting differences in crawling mechanisms. Of particular interest are the various mechanisms of orientation. Chase explains how snails and slugs respond to wind and water currents, chemical stimuli, gravity and light. Gastropods show an adaptive radiation in feeding behavior. In each of the diverse habitats in which gastropods reside, specializations of the feeding apparatus permit the animals to harvest whatever food may be available. The specialization led to grazers, rasps, suckers, collectors, cutters and hunters. Chapter 7 gives a review on the neural control of different types of feeding.

Chapter 8 is devoted to reproduction. There are two fundamental types of sexuality in gastropods: gonochorism and hermaphroditism. The hermaphrodites possess, at least during some part of their lives, both a functional female system and a functional male system. As the reproductive interests of males and females are typically different, this may result in a sexual conflict between gender within an individual. During the past two decades different hypotheses have been proposed to explain the outcome of sexual conflicts in hermaphroditic gastropods. Chase fairly reviews the facts that support or contradict the various hypotheses. However, a final answer to this hotly debated issue is not

yet available. This chapter gives an excellent overview on the variation in mating strategies in gastropods, their ways to find mates and the nervous control of courtship, copulation and egg laying. The reader might also be surprised by the diversity of extraordinary morphological structures and behaviors in gastropods (e.g. copulating slugs with a body length of 13-15 cm exchange their sperm externally at the tips of their 85-cm long everted penes). Chase shows that several gastropods species may be well-suited for studies on sexually selected behavior (e.g. sperm competition), but the potential as experimental organisms has only partly been exploited by behavioral and evolutionary biologists. Assessment of mate quality and sperm selection (either in the form of a selective storage or digestion) might occur in gastropods, and their elaborate mating behavior may rival the complexity of those of various vertebrates. Dart shooting is one of the illustrative examples presented in the book. Some terrestrial snails pierce their partners with "love" darts during courtship. The darts are made of calcium carbonate crystals and they are typically very sharp. The adaptive function of this bizarre behavior was discussed for many decades. Recent studies of Chase and coworkers showed that successful dart shooters sired more offspring than unsuccessful shooters. Thus, dart shooting might have evolved in the context of sperm competition as a way to increase the reproductive success of the shooter.

Chapter 9 considers defense mechanisms against predators. It explains behaviors that aim to prevent attacks and presents neurobiological aspects of

withdrawal reflexes. The final chapter is devoted to the temporal organization of behavior. There are times of the day and times of the year when a gastropod will not respond, or respond only poorly, to stimuli that usually elicit a certain behavior, simply because the time is not right. Chase reviews seasonal and daily cycles and endogenous circadian clocks in gastropods and explains the controlling neuronal processes.

I enjoyed this book very much and found all the chapters interesting and informative. The literature cited is well up-to-date with many 2000 references and also a few from 2001. The production quality of the book is high and the figures and tables are clearly set out. The book as a whole yields a comprehensive overview of the current state of neurobiology and behavior in gastropods, making it a suitable entry point into this integrative field and a useful reference book for graduate students and researchers. For persons not familiar with gastropods, and who want to learn more about the behavior and its neural control in these animals, this book is an eye-opener, and I can hardly imagine a more attractive introduction to them.

Bruno Baur

*Section of Conservation Biology,
Department of Integrative Biology,
Basel University,
St. Johannis-Vorstadt 10,
CH-4056 Basel, Switzerland*

Behavioral Flexibility and Evolution in *Pan* (Primates: Hominidae)

Behavioural Diversity in Chimpanzees and Bonobos.

Christophe Boesch, Gottfried Hohmann & Linda Marchant (Eds). Cambridge University Press, 2002. 296 Pp. ISBN: 0521006139

One of the first lessons learned in introductory statistics is that events in the world vary. As Christophe Boesch points out in his introductory chapter to the volume under review, however, some species exhibit a greater range of variability, in particular, behavioral diversity, than others. The editors of *Behavioural Diversity in Chimpanzees and Bonobos* aimed to document "species-typical behavioral patterns" and to explore "geographic variation in behavior across populations of the same species" (p. ix). West-Eberhard (2003) has recently pointed out that the study of phenotypic

diversity is the study of polymorphisms (genotypically regulated alternative responses) and polyphenisms (environmentally switched alternatives), stressing that the study of behavioral diversity actually involves broad questions related to development and to evolution in general. The purpose of this review is to evaluate Boesch et al.'s volume within the program advanced by West-Eberhard (2003) and other recent projects in evolutionary biology.

Most behavioral diversity in primates probably arises (via associative or cognitive processes) as novel

responses to heterogeneity in the physical and/or biotic, including social, environment. If responses with underlying genetic variation are exposed to the environment and acted upon by selection, they may lead to genetically programmed mechanisms switching the phenotype from one alternative to another (see Gross, 1996; Schlichting & Pigliucci, 1998; West-Eberhard, 2003; also see Jones & Agoramoorthy, 2003). As behavioral psychologists have long understood, novel responses may be exhibited initially through a process of “trial and error.” In these cases, it is thought, the environment’s response to the alternative phenotype’s expression will determine, on average, how likely the response is to be repeated (one type of learning).

Boesch’s (pp. 2-3) assertion that dependence upon learning should be positively correlated with environmental unpredictability is not strictly correct since the particular phenotypic strategy adopted will be a function of the relationship between generation time (T) and the rate of environmental change (see Roughgarden, 1979; Jones, 1997 a). Thus, it would be a mistake for primatologists to assume that increased behavioral flexibility by the mechanisms of learning necessarily explains behavioral diversity. It is also important for primatologists to keep in mind that learning mechanisms will themselves be “hard-wired” and that they are likely to be related genetically and physiologically to switch mechanisms governing the expression of alternative behavioral phenotypes.

Genetic and/or phenotypic conflicts of interest are likely to be ubiquitous in primates who may employ force, coercion, persuasion, persistence, manipulation, exploitation, deception, cooperation, alliances, coalitions, altruism, scrambles, social parasitism, dispersal, and/or spite to resolve or manage them (Jones & Agoramoorthy, 2003). Where one individual or group imposes severe costs to inclusive fitness upon another individual or group, the latter may adopt a counterstrategy (conscious or otherwise) to minimize its costs (see Matsumoto-Oda, Chapter 12, this volume). A counterstrategy may, in turn, impose costs upon the original actor(s), and so on, possibly yielding an evolutionary “chase” (“interlocus contest evolution”: Rice, 2000; see Nunn, 2003). Most of the papers in *Behavioural Diversity in Chimpanzees and Bonobos* suggest that (genetic and phenotypic) conflicts of interest, and attempts to mitigate them, may explain many of the fascinating and well-documented findings for these species. For females (“energy-maximizers”), theory (Schoener, 1971) predicts that conflict will

pertain primarily to competition for food (see Wallis, Chapter 13; Williams et al., Chapter 14) while, for males (“time minimizers”), conflict will pertain primarily to competition for mates.

Doran et al. (Chapter 1) use comparative statistical methods to analyze similarities and differences within and between the two *Pan* species. Among these authors’ findings interpretable with conflict theory are bonobos’ greater tendency to demonstrate associations among females, female dominance in *Pan paniscus*, and the expression of “homosexual” behavior (G-G rubbing) by bonobo females, responses which might represent “antagonistic” reactions to costs (e.g., mating rates) imposed by bonobo males (Rice, 2000; Gavrillets et al., 2001; also see Wrangham, Chapter 15). Furuichi & Hashimoto’s results (Chapter 11) strongly suggest that characteristics of female bonobo behavior are a function of mating costs, and, contrary to the popular image of bonobos as non-competitive, female-female competition apparently plays a very significant role in bonobo society (Vervaecke et al., 2003). That males of the genus *Pan* are also sensitive to potential genetic and/or phenotypic conflict is Newton-Fisher’s report (Chapter 9) documenting constraints in time allocation for this sex.

Differences between populations of *Pan troglodytes* versus in western Tanzania compared to chimpanzees at eastern sites is especially evident in tool use and the incidence of infanticide. Tool use, a behavioral novelty, is well developed at western sites where populations are characterized by greater genetic heterogeneity than in eastern populations of chimpanzees. Further, infanticide is rare or absent in the western study populations of this species. Both of these findings may reflect greater genetic and/or phenotypic conflict among eastern chimpanzees whose phenotypes (niches) are more likely to overlap due to lower genetic variability. Several other chapters in Boesch et al.’s volume document related within and between species differences that may have resulted from genetic and/or phenotypic conflict (e.g., Anderson et al., Chapter 6; Mitani et al., Chapter 7; Hohmann & Fruth, Chapter 10).

Hunt & McGrew (Chapter 2), for example, found that hunting by chimpanzees is more common in moister and, presumably less stressful, forests than in drier, and presumably more stressful, ones. When the two drier sites were compared, however, significant differences were found in hunting behavior and rates of aggression (also see Muller, Chapter 8). These within species and within and between habitat findings highlight the need

for genetic analyses of these populations (see Bradley & Vigilant, Chapter 19) and for the evaluation of interindividual competitive regimes, including coefficients of competition, in order to test the idea that genetic and/or phenotypic conflict drives patterns of behavioral diversity. Other studies of hunting and additional behavioral novelties (see Thompson, Chapter 4; Nakamura, Chapter 5, Part IV) provide examples of behavioral phenotypes varying within and between species that may have derived from genetic and/or phenotypic conflict between groups or populations. In this perspective, a cultural trait may be viewed as a type of “self-referent phenotype matching” or a “green beard” employed to identify phenotypes similar to or different from oneself. Finally, hunting by males may sometimes represent a form of “restraint” by this sex to minimize costs for females (Jones, 1996), possibly an example of involuntary altruism (see Jones, 1997 b). Such a response by males might evolve as a counterstrategy to costs imposed by females.

West-Eberhard (2003) points out that the study of development in evolutionary biology requires a broad definition including “the ontogeny of all aspects of the phenotype, at all levels of organization, and in all organisms” (p. vii). For primatologists, this approach means that the study of intraindividual and interindividual variation, including within and between species diversity, will integrate development with the study of inclusive fitness maximizing and of proximate causation. In primatology, our current knowledge of the cooperatively breeding marmosets and tamarins comes closest to the attainment of West-Eberhard’s program (e.g., Abbott et al., 1998). The chapters on *Pan* presented in Boesch et al.’s volume, in combination with literature reflecting current thinking in behavioral and population ecology and evolutionary biology (e.g., Gross, 1996; West et al., 2002), might form the reading list of a very stimulating graduate-level seminar in anthropology, psychology, or sociology or provide supplementary reading in a course on vertebrate behavioral ecology. The book will also be a valuable reference work for all students of mammals interested in solid empirical studies of primates.

Clara B. Jones

Department of Psychology, Livingstone College
Salisbury, NC 28144, U.S.A.
Community Conservation, Inc.
Gays Mills, WI 54631, U.S.A.

References

- Abbott DH, Saltzman W, Schultz-Darken NJ, Tannenbaum PL. 1998. Adaptations to subordinate status in female marmoset monkeys. *Comp Biochem Physiol Part C* 119:261-274.
- Gavrilets S, Arnqvist G, Friberg U. 2001. The evolution of female mate choice by sexual conflict. *Proc R Soc Lond B* 268:531-539.
- Gross MR. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trend Ecol Evol* 11:92-97.
- Jones CB. 1996. The selective advantage of patriarchal restraint. *Human Nat* 7:97-102.
- Jones CB. 1997 a. Life history patterns of howler monkeys in a time-varying environment. *Boletin Primatologico Latinoamericano* 6:1-8.
- Jones CB. 1997 b. Social parasitism in the mantled howler monkey, *Alouatta palliata* Gray (Primates: Cebidae): Involuntary altruism in a mammal? *Sociobiol* 30:51-61.
- Jones CB, Agoramoorthy G. 2003. Alternative reproductive behaviors in primates: towards general principles. In: *Sexual selection and reproductive competition in primates: New perspectives and directions* (Jones CB, ed). Norman, OK: American Society of Primatologists. pp. 103-139.
- Nunn CL. 2003. Comparative and theoretical approaches to studying sexual selection in primates. In: *Sexual selection and reproductive competition in primates: New perspectives and directions* (Jones CB, ed). Norman, OK: American Society of Primatologists. pp. 593-613.
- Rice WR. 2000. Dangerous liaisons. *PNAS USA* 97:12953-12955.
- Roughgarden J. 1979. *Theory of population genetics and evolutionary ecology: An introduction*. New York: Macmillan Publishing Co., Inc.
- Schlichting CD, Pigliucci M. 1998. *Phenotypic evolution: A reaction norm perspective*. Sunderland, MA: Sinauer Associates.
- Schoener TW. 1971. Theory of feeding strategies. *Ann Rev Ecol Syst* 2:369-404.
- Vervaecke H, Stevens J, Van Elsacker L. 2003. Interfering with others: Female-female reproductive competition in *Pan paniscus*. In: *Sexual selection and reproductive competition in primates: New perspectives and directions* (Jones CB, ed). Norman, OK: American Society of Primatologists. pp. 231-253.
- West SA, Pen I, Griffin AS. 2002. Cooperation and competition between relatives. *Science* 296:72-75.
- West-Eberhard M-J. 2003. *Developmental plasticity and evolution*. New York: Oxford University Press.

Sex, lies, and *extensive* videotaping: a review.

The Evolution of Begging. Competition, Cooperation, and Communication.

J. Wright and M.L. Leonard (eds.) Kluwer Academic Publ., Dordrecht. 2002

ISBN: 1-4020-0571-7

"Billion here, a billion there; pretty soon you're talking about real money!"

U.S. Senator Everett Dirksen

This book contains two-dozen invited chapters filling just over 500 pages on the subject of begging by nestling birds to their parents. Based on a symposium held in Wales (summer 2000), it stands immediately as tangible issue of a tremendous recent surge in research interest on parent-offspring interactions. Before going any further, I salute the contribution that Jon Wright and Marty Leonard have made by organizing the conference and producing a book that will anchor many dissertations and other forays into the mysteries of these ubiquitous but little-understood signals. Great quantities of excellent research is summarized in these pages, coming at the phenomena from six identified angles under which the book is organized, namely signal theory, signal costs, nestling physiology, sibling competition, brood parasitism, and statistics. Still, one retains the overall impression that we are only starting to grasp what these signals might mean. That is, the key issues remain to be defined in a lucid and balanced way. I do not mean this to be any sort of put-down to the organizers and contributors, but merely that the bulk of the literature is remarkably young and, as such, remains a hodgepodge of issues from which the main themes are only beginning to emerge.

It seems almost misleading to tack a single label like "begging" on the mélange of vocal screeches and peeps -- accompanied by the stretches, gapes, and jostles -- that young birds perform in the nest. These motor patterns appear most reliably when a parent arrives, which gives us the impression of importuning for some kind of investment (proverbially a worm). But these same behaviors have the worrying habit of occurring also when nestlings have no adults to target. What's that all about, rehearsal? Error? Intimidation? We don't know. (Alexandre Roulin's chapter has the provocative suggestion that the siblings are negotiating among themselves.)

I would like to suggest that there are non-salacious parallels between offspring begging and sex, or at least how we study both subjects. Begging is just now becoming a hot research area, so perhaps we can learn from that more mature literature. Unlike sex, begging has been largely ignored as familiar but uninteresting for centuries. Provocative scientific questions about

begging simply were not recognized until the mid-70s, when Trivers's concept of parent-offspring conflict began the sea change by exposing that these two kin-roles have incongruent fitness interests. (Note that he'd made basically the same point about sexual partners facing evolutionary conflict two years earlier.) This time, Trivers contended that offspring selfishness could depress parental fitness, but the anemic physical prowess of babies forces them to rely on 'psychological weaponry' to extract lavish investment from parents. In short, babies should prevaricate about being in dire straits; and parents may be unable to call the bluff because of imperfect information on offspring needs. That sank in slowly, but in 1991, Charles Godfray published an elegant model (borrowing heavily from Zahavi's handicap principle for sexual selection) that showed how a particular constellation of assumptions *could* constrain offspring signals so that they were honest signals of need. This paper set off the research avalanche that followed.

This is not the place to review and critique the whole field, but I think the book itself has an unhealthy bias toward the Godfray view, despite offering several chapters that quietly expose serious problems with it. For one thing, Godfray's Honesty logic explicitly required begging to be costly. The empirical evidence, on both the physiological (= energetics) and ecological (= predation-risk) fronts, suggests it is not. No problem...some new models now hold that cost probably should never have been listed as essential. Whatever. But if costs really are important, we must think hard about magnitude: *how* costly must signals be for selection to curb their escalation? Clearly it is insufficient to demonstrate merely that some kind of cost is statistically detectable. If begging takes a few calories away from growth is that enough? The original handicap argument was cast in terms of phenotypic costs actually reducing fitness (e.g., the price an Irish elk stag paid for brandishing huge antlers). How many calories, then, should count as "costly" for a baby bird? From the wisdom of Senator Dirksen we sense considerable latitude in scale.

For another thing, the Honesty approach assumes that the only thing nestlings can do to affect food distribution

is to provide parents with information on their needs: the parent alone has hegemonic power over who actually gets fed. Perhaps I have spent too many years in blinds watching egret bullies usurp that decision brutally, but it just seems way too early in our exploration of nonviolent birds to assume that offspring have no say whatever in the allocation process. After all, one of Trivers's primary points was to purge the view that offspring are mere passive vessels into which parental investment is poured.

A third concern of mine, shared by a few chapter authors (e.g., Anne Clark) but summarily ignored by others, is a general discomfort with assuming that an offspring's 'needs' are fairly represented by its short-term desires (i.e., 'hunger'). The existence of a worldwide heroin market suggests that what one *wants* is not always what one *needs* for maximizing lifetime reproductive success! As usual, theory promises castles built with perfect bricks of Darwinian fitness; sadly, we empiricists tend to use mud-based substitutes we can measure (like hunger).

Overall, the skew toward one fascinating theoretical approach while eschewing equally fascinating alternatives has narrowed this book's scope more than seems optimal for such a young field of study. The most obvious alternative theoretical framework is the one that preceded the Honesty bandwagon, namely the view that offspring themselves actively influence/control who gets fed by the parents. This might be done nonviolently through scramble competitions of relative position or signal strength. Scrambles may be less exciting than the notion that the signaler presents its case to a judge (parent) who then evaluates intrinsic quality (in this case neediness) and makes the key decisions. Once again, a close parallel can be found with the sexual selection literature, where most interest focuses on inter-sexual rather than intra-sexual modes. We're back to Darwin vs. Wallace. Even on the mate

choice side of that ledger the *active choice* models, where courtship features that are imagined to inspire comparisons, are much more popular than the scramble view that signal effectiveness hinges simply on which are more easily perceived (*passive choice*). Similarly, sperm competition (intra-sexual) may now have less cachet than the inter-sexual alternative of cryptic female choice.

My quibbles notwithstanding, this book is a very important coming-of-age event in the emergence of family social dynamics as a general research area. The chapters are well written, organized, and presented. The amount of material is staggering. One can already perceive major sub-topics, such as a lovely quartet of chapters addressing how brood parasitism casts special light on begging dynamics (because cuckoos and their ilk have no fitness stake in hosts). A lively interaction between proximate mechanisms and ultimate/strategic issues permeates many chapters (e.g., Schwabl and Lipar on hormones; Ricklefs on growth rates; Saino and Møller on immunology). The book's final two chapters, which deal with statistical matters (Daniela Monk on logistical regression tools and Scott Forbes on deadly sins like pseudoreplication and low power), call attention to some basic problems of measurement that need to be confronted if the field is going to become numerically robust. Clearly, bricks need not only to be of the right variety for the job, but also to be mortared properly into place.

Douglas W. Mock

*Department of Zoology
University of Oklahoma
Norman, OK 73019 USA*

References

Godfray, H.C.J. 1991. Signalling of need by offspring to their parents. *Nature* 352: 328-330

Acoustic Communication in Insects and Anurans: Common Problems and Diverse Solutions

H. Carl Gerhardt & Franz Huber, The University of Chicago Press, 2002. 531 Pp.
ISBN 0-226-28833-1

There is a wealth of knowledge about acoustic communication in the animal groups covered by this book – insects (particularly orthopterans and cicadas) and anuran amphibians (frogs and toads). Much of this knowledge concerns aspects of mechanisms of acoustic

communication that many behavioral ecologists would consider peripheral to their interests – even if their interests lay in communication. However, most behavioral ecologists will also be aware of chorusing behavior and experiments on mate choice in insects and

anurans, topics much closer to the current core interests of the field. This book covers both mechanism and function, with rather more mechanism than function, if measured by the pages devoted to each. But that's not really the point; does this combination of animal groups and levels of question work?

It works in terms of coherence. The text reads clearly, with potentially distracting detail dealt with in boxes or in one of the four appendices. Well-drawn, well-captioned figures are common (at a ratio of about one figure per two or three pages of text) and support the text well. Each chapter concludes with a summary and suggestions for future studies. It is an excellent guide to the almost overwhelming amount of information on communication in these animals.

Does it work in terms of the insights gained from considering the similar communication problems faced by these two animal groups that are hinted at by the subtitle? Before answering this question it's necessary to look at the common problems that the authors consider link the two groups. They subdivide these problems into physical / physiological traits (small size and ectothermy) and natural history (chorusing and the presence of acoustically-orienting predators and parasites). But perhaps the most important shared aspect of natural history is their short lives and/or short breeding periods, meaning that learning plays no part in the development of signals. The mantra is that these animals don't learn. I share the authors' scepticism that learning does not play a role in communication at any level. There seem to have been few studies that have looked for such a role. One recent study that did, found bullfrogs to be capable of territorial songbird-like neighbour-stranger discrimination (Bee and Gerhardt, 2001). As the authors point out in their suggestions for future research, there is clearly scope for much more work in this area, perhaps (my suggestion) by behavioral ecologists.

I found that the "common problems" approach worked best when considering chorusing (because of the similarities of the underlying mechanisms), quite well in the treatment of peripheral and central processing of signals and sound location (for the same reason), and least well in the chapters on mate choice and acoustic competition (perhaps because of the "no learning" mantra). For these reasons the approach will have less relevance to a behavioral ecologist than, say, a

neuroethologist. It will also have less relevance to communication in birds and mammals where the role of learning in signal diversity and use is well established.

At a more specific level this book has two features to recommend it to behavioral ecologists. First, it integrates mechanism and functional approaches to acoustic communication, often in a way that those working on birds and mammals can only dream of. These are emphasized and developed by the suggestions for further research that round off each chapter. If there is still anyone out there who thinks that constraints imposed by mechanism are unimportant when considering function, they must read this book. Second, the authors gently, but firmly, indicate questions that they consider require a higher standard of investigation. Anyone interested in mate choice, regardless of the taxon being studied and whether the information is encoded acoustically, would do well to heed their comments on the weakness of many current experimental mate choice paradigms.

The presence of a particular book on a bookshelf often defines the research interests of the person – an example in bird song is Kroodsma and Miller (1996). Gerhardt & Huber is one such marker book; anyone doing research on insect or anuran acoustic communication will have it on their shelves already. It also deserves to be found on the bookshelves of those interested in communication more broadly and anyone looking for a good example of an integrative approach to a topic.

Peter K. McGregor
Centre for Applied Zoology
Cornwall College
Newquay
Cornwall, UK
 &
Dept. of Animal Behaviour,
Zoological Institute,
University of Copenhagen, Denmark

References

- Bee MA, Gerhardt HC. 2001. Neighbor stranger discrimination by territorial male bullfrogs (*Rana catesbeiana*). I. Acoustic basis. II. Perceptual basis. *Anim Behav* 62: 1129-50
- Kroodsma DE, Miller EH. 1996. *Ecology and Evolution of Acoustic Communication in Birds*. Ithaca, New York: Cornell University Press.

Seasonal patterns of stress, immune function & disease.

R. J. Nelson, G. E. Demas, S. L. Klein & L. J. Krieglfield. Cambridge University Press, 2002. 291Pp. ISBN 0-521-59068-X (hb).

Over the last two decades there has been a growing interest among researchers of many disciplines to study interactions between the neuronal, immune and endocrine systems. This research area merging several disciplines was first endeavoured by researchers in medicine and often by experts in e.g. immunology or endocrinology. The level of analysis was often mechanistic to answer proximate questions (e.g. is a certain cytokine able to bind to receptors located at the pituitary gland, or are there receptors for a certain hormone on cells of the immune system). However, during the 1990's this research area was approached also by other groups of researchers, such as ecologists and endocrinologists, that applied more of a "whole animal" approach because they were mainly interested in ultimate (evolutionary) questions (i.e. why do we have interactions between neuro-, immune and endocrine systems, which are the underlying trade-offs for these interactions, what are the fitness consequences, etc). A seminal paper inspiring this latter development was the article by Folstad & Karter (1992) that proposed that a negative trade-off between levels of androgen hormones and immune function could be a mechanism ensuring that secondary sexual ornaments remained honest signals of male quality. Since this paper in 1992, we have seen an explosion of studies in immunoecology and neuro-immune-endocrine interactions conducted by researchers applying an evolutionary perspective.

The book by Nelson, Demas, Klein & Krieglfield is devoted to one such sub-area of research in which these authors have been seminal; the seasonal effects on stress, immune system and disease. However, this book actually presents a very broad overview of research conducted in many different disciplines that are important for central questions in immunoecology. Besides seasonality of disease and immune function also energetics of immune function, hormonal modulation of immune function, and immune function in relation to gender.

In the first two chapters of the book, basics of seasonality and immune function are described to provide the non-specialist readers with a general overview of processes and systems. In chapter 3 and 4, seasonal changes in disease prevalence and immune function are reviewed, and the authors conclude that

such affects occur and that, in general, both peak in autumn/winter (to me, however, the wealth of data they provide in the book on these aspects do not show such a clear-cut pattern). Chapter 5 provides an extensive review of the effects of melatonin (and photoperiod) on immune function. It provides compelling evidence that melatonin generally enhances immune function and counteract stress. In chapter 6, energetics of immune function is in focus. Here the authors' main message is that immune responses are very demanding in terms of energy consumption. I find it surprising that Nelson et al. are so "locked" into favoring the "energetic trade-off" hypothesis because, as is also pointed out by the authors, there are very few studies that have investigated the energetic cost of immune responses and the results of such studies are equivocal. Nelson et al. do not even mention the alternative hypotheses (e.g. "avoidance of immunopathology" or "avoidance of oxidative stress"). Chapter 7 is devoted to the effects of hormones and immune function. A wealth of information mainly from mechanistic studies are provided in this chapter, which makes it a useful tool to find references but a bit hard to read. In the final chapter, the authors' aim at putting their ideas into a "human clinical" perspective, which I think was an interesting twist at the end of the book.

The book by Nelson et al. is clearly rooted in an evolutionary framework, but it also provides a wealth of mechanistic information, in particular from research on mammals (including humans). In that respect it can be recommended to a broad audience of researchers as a source for finding relevant references of the topics covered by the book. I do not, however, recommend this book as a means of quickly getting an overview of these research areas – it is just too thick with information not the least in terms of rather monotonous extensive presentations of cited studies. For those that are more interested to get a general overview of stress and immune function in vertebrates, I would instead recommend the book by Sapolsky (1998). A thing that I found irritating with the book by Nelson et al. is the bias in the interpretation of studies in favor of their own hypotheses at the expense of alternatives (often without even mentioning such alternative hypotheses). As the book is now written one often gets the impression that the case is closed, even in cases where the evidence is weak.

Despite these shortcomings, I think this is a very useful book that introduce the evolutionary framework of seasonality, stress and immune function not the least to researchers in human and veterinary medicine. Moreover it provides an exhaustive source of references on these subjects that is very useful for immunoecologists.

Dennis Hasselquist

*Department of Animal Ecology,
Lund University,
Ecology Building,
223 62 Lund, Sweden*

Lizard Social Behavior

Stanley F. Fox, J. Kelly McCoy & Toy A. Baird. John Hopkins Press. 2003. 438Pp
ISBN: 0-8018-6893-9

I have a confession; I have always wanted to work on lizards. However, working at a University in northern Canada where no species of lizards exists has put a bit of a damper on this ambition. Lizards have always provided a wonderful species for demonstrating behavior and conducting student projects, but as yet I have not turned this into anything more than a general fascination. My interest in lizards stems from a belief that lizards are among the most ideal species to study both mating and signaling systems, and the new text *Lizard Social Behavior* suggests that I am not alone in my thinking.

This is made apparent in the introduction to the text by the editors (Fox, McCoy and Baird), in which they suggest that lizards are models subjects for behavioral research: in some aspects, their simplified behavioral repertoire, such as a lack of parental care in reproduction in most species, make them somewhat simpler for studying sexual selection and mate choice than other taxa, yet other aspects of behaviors, such as signaling, can be quite complex. This is coupled with the fact that many species are easy to catch, mark and manipulate, as well as fairly limited spatial dispersal between individuals (with some authors boasting entire study sites smaller than the average territory of one of my birds), do entice the reader. Perhaps, though, the biggest affirmation of their “model-species” assertions comes from introductions to each section of the book being written by a top researchers known for their work on behavioral ecology in other taxa (Peter Marler, Gordon Orions and George Barlow), all of whom seem to share an enthusiasm for the contributions lizards can

References

- Folstad I, Karter, AJ. 1992. Parasites, bright males and immunocompetence handicap. *Am Nat* 139: 603–622.
Sapolsky RM. 1998. Why zebra’s don’t get ulcers: an updated guide to stress, stress-related diseases, and coping. San Francisco: W. H. Freeman & Sons.

make to behavioral research

The book itself is comprised of 11 contributed chapters nicely divided into 3 sections: Variation among Individuals; Variation among Populations; and Variation among Species. The first of these sections is work done on behavioral ecology within a single species, and chapters focus on a number of common themes: intersexual differences in territoriality; conditional strategies, such as sneaking, across age categories (Baird et al.); status signaling and badge display variation (Whiting et al.); a particularly fascinating chapter on ecological context of alternate mating strategies (Zamudio & Sinervo); and the competitive interaction between predator flight and mating/territorial behavior (Cooper). Many of these themes are common in other literature, but these chapters provide a nice insight into how these processes are studied and interpreted in a particular taxonomic group. Similarly, cross-species comparative approaches (some multispecies, some comparing only a limited number of species) were used effectively in the final section of the book to look at variation in behavior, morphology and sexual dimorphism of species associated with endocrinology (Hew & Quinn), habitat type (Gier), elevation (Fox & Shipman) or ecological niches (Losos et al.).

It was the middle section of the book, however, that I found the most intriguing. In this section, variation in behavior among populations of the same species is correlated with changes in environmental circumstances, such as differences in predation and/or parasite threat (chapters by Hasegawa and Stone et al.) or patchiness and defensibility of resources and display sites (McCoy

et al.). Some of these same themes were reiterated in the final section of the book in cross-species comparisons at explaining the evolution of behavioral variation, but it was this cross-population approach that suggested a particularly strong method of approaching the topic.

While this book makes a strong case that behavioral ecologists could advance our understanding of fundamental questions by looking across taxa at parallel examples in the lizard world, it is this very concept that created my only criticism with the book. While a number of chapters have been obviously influenced by recent developments and theories being advocated in other taxonomic groups, some other chapters are still grounded on theories that have tended to lose favor in the literature over the last decade. One example that occurred repeatedly between chapters was the assumption that sexual selection was driven by Fisherian processes. Little mention of honest advertisement models - favored in the signaling literature since Grafen's (1990) work (e.g. Espmark et al. 2000) - are

made despite various chapters providing data that variation in male quality may be correlated with signal production. However, this is a minor criticism in an otherwise excellent book that would be useful on the shelf of any behavioral ecologist, regardless of the taxa on which you primarily work.

Ken Otter

*Ecosystem Science and Management
University of Northern BC
Prince George, BC, Canada*

References

- Grafen A. 1990 Biological signals as handicaps. *J Theor Biol*, 144: 517-546
- Espmark Y, Amundsen T, Rosenqvist G. 2000. Animal Signals. Adaptive Significance of Signalling and Signal Design in Animal Communication, Proc. Fifth Int. Kongsvoll Symp., Trondheim, Norway: Tapir Publishers.

Workshop & Conference Reviews

Sperm Tales

Biology of Spermatozoa international conference, Derbyshire, UK, 26-30 September 2003

Over thirty years ago, Geoff Parker (Parker, 1970) outlined a simple thesis: Females commonly mate multiply and store sperm that remain viable until fertilization, resulting in competition among males both before and after mating for obtaining offspring. Thus, the term sperm competition was defined and since then an extraordinarily active research field in evolutionary biology has examined how this process has resulted in anatomical, physiological and behavioral adaptations not only in males, but indeed in both sexes (Birkhead and Moller, 1992; Birkhead and Moller, 1998; Simmons, 2001). Understanding the enormous diversity of spermatozoan structure and function, ejaculate production, male and female reproductive tract variation and mating systems is consequently a goal stimulating research in seemingly disparate areas such as behavioral ecology, physiology, cell biology, bioinformatics and human fertility.

Researchers recently convened to share and compare ideas at the Biology of Spermatozoa, an international conference held biennially at Losehill Hall, Derbyshire, UK, and funded by the Wellcome Trust and the University of Sheffield. The meeting has been organized for the past decade by Professors Tim Birkhead and

Harry Moore (University of Sheffield). The high level of excitement among attendees reflected stimulating academic exchange and people were enthusiastic about the style of the meeting. The conference is held in an intimate setting, promoting a cross-fertilization of ideas from different academic perspectives and encouraging interdisciplinary thinking, and structured with a schedule that allows maximum discussion and presentation. Participants hailed from universities across Europe, Asia, Australia and North and Central Americas, and ranged from graduate students to senior level researchers.

Relatively recently, as reflected by the past several conferences (Hosken and Stockley, 1998; Pitnick and Karr, 1996), researchers have been developing the idea that the female reproductive tract plays an important role in fertilization and sperm competition during the movement of sperm within females to the site of fertilization, but there is clearly more to learn. Plenary speaker Michael Eisenbach (Weizmann Institute of Science, Israel) presented evidence for a "sperm guidance system" within the female reproductive tract in mammals. Eisenbach argued that such a guidance system would act to synchronize sperm capacitation and

ovulation and showed that sperm move along a chemical gradient towards factors released by the egg-cumulus complex. These results may suggest coevolution between egg and sperm for coordination of fertilization.

Matt Anderson (San Diego Zoo, USA) showed that across mammal species oviduct length is positively correlated with the degree females have multiple mating partners, suggesting a functional role for the female reproductive tract as an arena for sperm competition. The idea that females can choose among sperm of mates to allow only preferred males to fertilize their eggs is a compelling one. However observing this phenomenon inside females is almost impossible, hence it is referred to as cryptic female choice (Eberhard, 1996). Tom Pizzari (University of Leeds, UK) mated males with sisters or unrelated females and showed that relatively fewer sperm are present on the surface of eggs when females are mated to brothers. This suggests that females manipulate sperm usage to effect cryptic mate choice, possibly as a way to avoid costs associated with inbreeding. Andrea Pilastro (University of Padova, Italy) presented similar findings in guppies, where females tended to retain relatively more sperm when mating with preferred males in simultaneous mate choice tests. Studies such as these begin to shed light on the complex role of females in post-copulatory sexual selection.

Biologists have begun to adopt genetic tools to examine adaptation in novel ways. One approach is to attempt to explain the amount of phenotypic variation that is due to underlying genetic architecture (Boake et al., 2002). Talks by Trish Moore (University of Manchester, UK) and Tim Birkhead (University of Sheffield) described studies focusing on the contribution and constraint of genetics on sperm production. Moore described how many ejaculate characteristics in a cockroach are heritable, including a measure of sperm viability, spermatophore size and sperm numbers. However, there is a negative genetic correlation between sperm number and all other ejaculate characteristics, implying that complex evolutionary pressures have acted on ejaculates that are not detectable using phenotypic measures alone.

Birkhead presented an experiment investigating the adaptive significance of variation in sperm morphology, which has been of interest in the field but for which controversy remains (Gage and Freckleton, 2002; Pitnick et al., 2003). He found heritable variation in total sperm length and components thereof. Interestingly, he found a negative genetic correlation between sperm size and male condition, perhaps suggesting an evolutionary constraint on characteristics

important to male survival and sperm competition or sexual selection.

Genetic markers were first used over a decade ago by researchers interested in sperm competition to discover mixed paternity in clutches of birds previously thought to be monogamous (Birkhead and Moller, 1992). These tools continue to allow researchers to assess sperm utilization patterns. Bart Kempenaers (Research Center for Ornithology of the Max Planck Society, Germany) and Marie-Jose Naud (Flinders University, Australia) both addressed the enduring question of where in the female reproductive tract sperm competition may be most intense. Kempenaers used a competitive DNA amplification technique to estimate the relative amount of sperm contributed by different males that are actually found on the surface of the egg in birds. He found that sperm from different males were present when females multiply mated, suggesting that sperm competition is intense at the site of fertilization. Naud presented results of an ongoing study of sperm competition in cuttlefish. Both sexes mate multiply and males place bundles of sperm inside the female buccal cavity. The sperm bundles can be identified using microsatellite markers, mapped spatially for positioning around the site of fertilization and then used to compare to patterns of paternity in female clutches. This approach shows promise to be able to examine male sperm allocation and sperm competition at the site of fertilization.

Females may mate multiply to obtain some direct or indirect benefit from males (Kokko et al., 2002), however males may evolve mechanisms to avoid sperm competition, especially by increasing the cost of mating.

This results in an evolutionary conflict of interest between the sexes (Parker, 1979). One approach to detecting sexual conflict and its consequences are population crosses where it is predicted that traits in males and females that have coevolved in an "evolutionary arms race" have diverged (Chapman et al., 2003). Tristan Long (Queen's University, Canada) showed the results of cross-breeding among 6 different *Drosophila* lines that had been maintained as separate populations in the lab for almost 600 generations. Males produce seminal proteins that increase the cost of mating for females and perhaps reducing the risk of sperm competition for males (Chapman et al., 2003). Female resistance is expected to coevolve with these ejaculate proteins within populations, however Long's results indicate a very heterogeneous pattern of fitness across lines relative to within-line pairings. These results underscore how traits important for sexual conflict may

vary between allopatric populations in complex ways (Chapman et al., 2003). Confounding factors in this type of study are controlling degree of genetic differentiation and accumulation of genetic incompatibility leading to speciation. Willie Swanson (University of Washington, USA) investigated patterns of positive selection on sperm and egg proteins important in fertilization in different species of broadcast-spawning abalone. He showed evidence that the sperm protein Lysine has undergone rapid, adaptive change across species with complimentary changes in the 3-D structure of an egg surface receptor protein. Using these molecular tools can provide insight to the evolution of species isolation barriers as well as a mechanistic understanding of sperm-egg interactions. Tim Karr (University of Bath, UK) presented work that expands what we know about sperm structure and function using a bioinformatics approach. He is identifying the complete complement of proteins expressed in *Drosophila* sperm, or, the sperm "proteome", which has the advantage of having a manageable small number of proteins. Using a gene database it is then possible to cross reference a catalogue of information then about proteins found in sperm, for example to resolve proteins types and their functions.

In general, sperm have two interactions within the female: with the female reproductive tract where they travel to the site of fertilization, and with the egg at the moment of fertilization. Understanding diversity in sperm structure and function is important to begin to understand such post-copulatory male-female interactions. Peter Sutovsky (University of Missouri-Columbia, USA) gave a plenary lecture about the multiple functions of ubiquitin in sperm biology. Using biochemical techniques, Sutovsky suggested that defective sperm are differentially tagged with poly-ubiquitin chains inside the epididymus for identification and active removal. Further, patterns of ubiquitin staining to identify defective sperm are sometimes independent of morphological defects. These findings have possible implications for both understanding the mechanistic basis of sperm quality control within males, but also for the practical issue of measuring fertility in males. Jim Cummins (Murdoch University, Australia) talked about the evolution of sperm and significance of mitochondria in the sperm mid-piece. These mitochondria typically degenerate after entering the egg in mammals, but Cummins offered an explanation for very rare observations of paternal mitochondrial transmission to offspring. Sperm mid-piece mitochondria often fuse before degrading and in rare

cases may fuse with a maternal mitochondrion and thus persist. His talk concluded by pointing out a paradox of mammalian fertilization biology that is yet to be understood: it is female rather than male factors that determine the success of sperm, with genes from matrilineal mitochondria and those from the X chromosome being primarily responsible for sperm functions. Revealing the evolutionary significance of this may be a fruitful avenue for research in the future.

Sperm vary not only in quality within males, but also morphologically. Sperm heteromorphism is known in a few taxa (Swallow and Wilkinson, 2002), for example Lepidoptera that exhibit small (apyrene) and large (eupyrene) morphotypes only the latter of which are capable of fertilizing ova. Nina Wedell (University of Leeds, UK) and Helen Crudgington (University of Sheffield, UK) gave talks about the adaptive hypothesis that sperm polymorphism allow males to reduce the costs of large ejaculate production in response to sperm competition. Wedell used selection lines in a butterfly with imposed monandry and found that males produce fewer non-fertile sperm relative to multiply-mating lines.

Increasing apyrene sperm numbers may be a relatively efficient way for males to increase their ejaculate size and inhibit female remating, thereby avoiding sperm competition. Crudgington used a similar approach in *Drosophila* and showed rapid divergence in sperm polymorphisms between selection lines subjected to differing degrees of polyandry.

Variation in ejaculate size has long interested researchers in sperm competition. Theory predicts that males should increase their ejaculate size as the risk of sperm competition increases (Parker, 1998), which has empirical support both across and within species (Wedell et al., 2002). Geoff Parker (University of Liverpool, England), presented a new sperm allocation model for species encountering a range of sperm competition risk. Males are predicted to increase their average ejaculate size with the risk of encountering sperm competition, however when fertilization is inefficient (i.e., the amount of sperm required to fertilize ova is large), or when the perceived risk of sperm competition is low, it will sometimes be best to allocate more sperm to virgin females. Considerable research has been stimulated by Parker's previous models, some of which comes from the general empirical observation that in a number of taxa relative testes size increases with the risk of sperm competition (Wedell et al., 2002).

Plenary speaker Scott Pitnick (Syracuse University,

USA) described a study examining sperm competition as a possible explanation of variation in brain size in bats due to a direct tradeoff with testes investment. Although the idea that sperm production can be costly for males is not new (Dewsbury, 1982), Pitnick pointed out that studies have rarely demonstrated such a cost. Some of the variation in the sensory center of the brain in bats can be explained by mating system: bats with fewer mates tend to have larger brains for their body size compared to bats with many mates. However due to the sometimes extreme increase in relative testes size across the same mating system range, Pitnick suggests an evolutionary tradeoff between investment in energetically costly cognitive machinery and testes depending on sperm competition. Aside from variation in ejaculate size, many taxa exhibit large variation in their range of mating behavior. Such variation is obvious across rodent species and Paula Stockley (University of Liverpool, UK) spoke about sperm competition and mating behavior in this group. While sperm competition can explain variation in testes size across species in some taxa, the situation is more complex in rodents due to a relationship between mating activity in males and ovulation and sexual receptivity in females. Stockley examined the relationship between mating systems and mating behaviors such as increase in intromission number, a pace of copulation and copulation duration. Some of the variation in these traits can be explained by the degree to which males are likely to experience sperm competition. It seems clear that comparative approaches are leading to a better understanding of the evolution of reproductive characteristics as a result of sperm competition.

Bob Montgomerie (Queens University, Canada) provided a history of sperm research in the introductory plenary talk of the conference. He indicated that the etymology of the word sperm can be traced to its first usage in the English language in the Chaucer's Canterbury Tales, and that historically the investigation of fertilization has proceeded like finding disconnected pieces of a puzzle. However, a phase of rapid advancement of our knowledge in this field has proceeded over the past three decades since Parker's revolutionary paper (Parker, 1970). Montgomerie showed evidence of an exponential increase of the number of papers investigating sperm competition, which has driven advancement in the field of fertilization biology. This is due to both progress in exploring the evolution of reproductive behavior and a more profound mechanistic understanding male and female reproductive tracts and the process of

fertilization. Thus it is in the collegiate spirit that travelers to the Biology of Spermatozoa international conference continue to make use of this forum for advancement in this field.

W. Edwin Harris

*School of Biological Sciences
University of Manchester
Manchester, UK, M13 9PT*

Acknowledgments

Thanks go to Tim Birkhead and Harry Moore for organizing the meeting, as well as to the participants who helped make it a great success. Thanks also to Patricia J. Moore and Allen J. Moore for providing helpful comments on this article.

References

- Birkhead TR, Moller AP, 1992. Sperm Competition in Birds. London: Academic Press.
- Birkhead TR, Moller AP, 1998. Sperm Competition and Sexual Selection. London: Academic Press.
- Boake CRB, Arnold SJ, Breden F, Meffert LM, Ritchie MG, Taylor BJ, Wolf JB, Moore AJ, 2002. Genetic tools for studying adaptation and the evolution of behavior. *Am Nat* 160:S143-S159.
- Chapman T, Arnqvist G, Bangham J, Rowe L, 2003. Sexual conflict. *Trends Ecol Evol* 18:41-47.
- Dewsbury DA, 1982. Ejaculate cost and male choice. *Am Nat* 119:601-610.
- Eberhard WG, 1996. Female Control: Sexual Selection by Cryptic Female Choice. Princeton NJ: Princeton University Press.
- Gage MJG, Freckleton RP, 2002. Relative testis size and sperm morphometry across mammals: no evidence for an association between sperm competition and sperm length. *Proc R Soc Lond B* 270:625-632.
- Hosken DJ, Stockley P, 1998. Sperm counts. *Trends Ecol Evol* 13:91-92.
- Kokko H, Brooks R, Jennions MD, Morely J, 2002. The evolution of mate choice and mating biases. *Proc R Soc Lond B* 270:653-664.
- Parker GA, 1970. Sperm competition and its evolutionary consequences in the insects. *Biol Rev* 45:525-567.
- Parker GA, 1979. Sexual selection and sexual conflict. In: Sexual selection and reproductive competition in insects (Blum MS, Blum NA, eds): Academic Press; 123-166.
- Parker GA, 1998. Sperm competition and the evolution of ejaculates: towards a theory base. In: Sperm competition and sexual selection (Birkhead TR, Moller AP, eds). Cambridge: Cambridge University Press; 3-54.
- Pitnick S, Karr TL, 1996. Sperm caucuses. *Trends Ecol Evol* 11:148-151.
- Pitnick S, Miller GT, Schneider K, Markow TA, 2003. Ejaculate-female coevolution in *Drosophila mojavensis*. *Proc R Soc Lond B* 270:1507-1512.
- Simmons LW, 2001. Sperm competition and its evolutionary consequences in the insects. Princeton:

Princeton University Press.
 Swallow JG, Wilkinson GS, 2002. The long and short of
 sperm polymorphisms in insects. *Biol Rev* 77:153-182.
 Wedell N, Gage MJG, Parker GA, 2002. Sperm

competition, male prudence and sperm-limited females.
Trends Ecol Evol 17:313-320.

ISBE Elections

Every two years, the ISBE elects new officers whose term begins at the next Society meeting. Below, we provide brief biographical summaries for all candidates. **The ballot and voting instructions are on the last page of this newsletter.** Everyone receiving this newsletter is eligible to vote.

(1) Candidates for PRESIDENT-ELECT (to become PRESIDENT at the 2006 meeting, and to serve in that capacity for two years).

Marlene Zuk

My research interests include sexual selection and mate choice as well as the evolution of host-parasite interactions. I have used both birds and insects as study subjects, and try to combine field and laboratory approaches. More recently, I wrote a book, *Sexual Selection*, about the ways people use (and misuse) animal behavior to understand gender issues in humans, and through this I have made connections with non-scientists from a variety of fields. I received my Ph.D. from the University of Michigan and am a Professor of Biology at the University of California, Riverside. I am currently an editor of *Behavioral Ecology* and helped with the National Science Foundation grant to bring junior scientists to the 2004 ISBE meeting.

Andrew Cockburn

Currently Professor of Evolutionary Ecology at the Australian National University. My PhD is from Monash, and I did postdocs at UC Berkeley, Monash and CSIRO. I am a field biologist and have worked with rodents, marsupials and birds. My current theoretical research involves comparative analysis of parental care and social systems in birds, and my field research uses the superb fairy-wren as a model for understanding the evolution of social complexity and the benefits of female choice. Previous service to ISBE includes convening the Sixth Congress (1996) and membership of the Editorial Board of *Behavioral Ecology* (1997-2002).

(2) Candidate for TREASURER (to take office in 2004 and server a 4-year term). Only a single candidate has been nominated for this office.

Walt Koenig

I received my Ph.D. from UC Berkeley in 1978 and have pretty much remained there ever since, primarily as a Research Zoologist stationed at Hastings Reservation in central coastal California. My interests include social behavior, the evolution of mating, and patterns of spatial synchrony in ecological phenomena. I've been involved in the ISBE since the beginning, serving as a councillor (1992-1994), treasurer (2000-), and attending 7 of 9 meetings, including the 1998 meeting at Asilomar which I organized along with Janis Dickinson.

(3) Candidates for COUNCILOR (2 positions vacant, each to serve for 4 year terms from 2004).

Ben Hatchwell

I received my PhD from University of Sheffield (1988) and after post-docs in Cambridge and Oxford, I returned to Sheffield in 1993. My principal research interests concern reproductive strategies and social evolution and my general approach is to use long-term behavioural and ecological studies of birds, combined with field and lab experiments to address evolutionary questions. I am also involved in long-term studies of avian population ecology. Current work includes studies of the ecological basis of sociality, the role of kin selection in the evolution of cooperation, and the decision rules of individuals in cooperative groups and their fitness consequences.

Ben Sheldon

I took my PhD (avian sperm competition) at Sheffield University with Tim Birkhead. Following that I held a number of postdoctoral research fellowships at Uppsala, Edinburgh, and then Uppsala again. I moved to Oxford in 2000 on a Royal Society Research Fellowship. My research addresses different facets of the ecology and

evolution of reproductive decisions, mostly using wild birds as a model system. I have worked on questions ranging from the evolution of mate choice, sex allocation, parental investment, clutch size and reproductive timing. I particularly enjoy work that combines experimental approaches with insights drawn from analyses of long-term studies of populations of marked individuals.

Naomi Langmore

I received my PhD from the University of Cambridge in 1995 and continued post-doctoral work there on bird song, and in particular the functions of female song, until 1999. In 1999 I took up an Australian Research Council Fellowship at the Australian National University to study coevolution between Australian cuckoos and their hosts. This study is continuing (now funded by the Leverhulme Trust, UK), and I and collaborators are investigating whether coevolution between cuckoos and hosts is driving speciation of the Australian cuckoos.

Mats Olsson

Mats did his undergraduate years in biology, geology and statistics at the University of Gothenburg, where he also did his PhD on sexual selection and the evolution of life histories in lizards. He then moved to Sydney, Australia for a five-year post-doctoral fellowship, working on evolutionary ecology in several lizard species. The last five years, Mats has been back in Sweden, working on evolutionary ecology and genetics in lizards, with a focus on molecular immunobiology mechanisms in mate choice, post-copulatory sperm choice, and sperm competition. Recently, Mats accepted a position in Australia, to work on related questions in agamid lizards.

Contributions to the ISBE Newsletter

The ISBE Newsletter publishes Book, Conference and Workshop Reviews of interest to the *International Society for Behavioral Ecology*.

Book Reviews: Persons involved in the publishing of books who would like these to be considered for review in the Newsletter may contact the Editor and arrange for their publisher to forward a review copy to be forwarded to this office. Authors may submit a list of possible reviewers. Alternately, members who wish to review a particular text should contact the Editor.

Workshop/Conference Reviews: Workshop/ Conference reviews should be prepared in one of the following two formats. Brief synopses (max 1000 words) may be submitted by either participants or conference organizers at the regular newsletter deadlines. These can include synopses of workshops that will be published in more detailed accounts (book or special journals), and should include information as to where the information will be published. Longer reports (max 2500 words) will be considered from large workshops/conferences for which other publications are not stemming. The purpose of the latter format is to provide a venue to disseminate information and discussions that would otherwise not be available to non-conference participants. Anyone attending such a workshop and wishing to publish in the Newsletter should contact the Editor at least **one month** prior to submission deadlines. Reports should aim at a critical assessment of the conference, as well as a synthesis of the convergent ideas presented. A

synopsis of future directions of research that were reached at the end of the conference should also be included. Anyone attending the workshops may submit reports, but preference will be given to submissions not be authored by conference organizers. A single application for a workshop will be considered, so it may be appropriate to agree upon a reporter at the conference. Graduate students and postdocs are strongly encouraged to consider contributing to writing these reports.

Commentaries: Responses to commentary articles published in the newsletter or articles eliciting discussion or topics relevant to the society will be considered for publication in the newsletter. Authors of such articles should contact the Editor at least **one month** prior to regular submission deadlines to outline the content of the article. The Editor may request submission of the article earlier than regular deadline should need for outside reviewing be deemed necessary.

Cartoons: Cartoonists 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

(web.unbc.ca/isbe/newsletter).

Deadlines for submission to the spring newsletter will be March 15, 2004.

Ken Otter
Newsletter Editor

ELECTION OF ISBE OFFICERS

Please mark your chosen candidates with a cross
(see pages 18 & 19 for information on each candidate)

(1) PRESIDENT ELECT

Marlene Zuk ☐

Andrew Cockburn ☐

(2) TREASURER

Walt Koenig ☐

(3) COUNCILLOR (vote for two candidates)

Ben Hatchwell ☐

Ben Sheldon ☐

Naomi Langmore ☐

Mats Olsson ☐

Return ballot slips to:

Paul Ward
Zoologisches Museum der Universität Zürich
Winterthurerstrasse 190
CH 8057 Zürich
Switzerland

(Closing date: one month after arrival of this newsletter. Only original ballots will be counted – no photocopies please)